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Roughness of soil pore surface and its effect on available habitat space of microarthropods

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ABSTRACT

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Like the majority of natural objects, soil pores can be described by means of fractal geometry. Since the area of a fractal surface depends on the scale of measurement, the amount of available pore area for different size classes of non-burrowing soil animals should depend on the fractal dimension of the soil pore surface following the relationship $A(\delta)\approx\delta^{2-D_s}$, were A is the area measured on scale δ, and D_s is the fractal dimension of the surface. We estimated D_s by photographing and digitizing thin sections of various Austrian soils. Images were analyzed using the area-perimeter method following the relationship $P\sim A^{D_p/2}$, where P is the perimeter of an intersected soil pore measured at any convenient scale, A is its sectional area, and D_p is the fractal dimension of the boundary line. $D_p/2$ can be recovered by a linear regression in a plot of $\ln P$ against $\ln A$. Under the assumption of isotropy adding 1 to D_p yields the estimate of the fractal dimension of soil pore surface. Our estimates of $D_s\approx 2.3$ suggest that a decrease in an order-of-magnitude of body length will increase available habitat-space approximately 4 times. We discuss the usefulness of the measurement of pore-wall roughness for predicting a size-class abundance/body size relationship in soil micro-arthropod communities.

INTRODUCTION

In the past two decades much emphasis in ecological research has been laid on the analysis of the relationships between the number, abundance and size of species in natural communities. Numerous papers have been published on relations between two of these community variables (e.g. May, 1975; Griffiths, 1986; Brown and Maurer, 1986; Lawton, 1989). Only until recently has the shape of a three-dimensional surface been investigated, i.e., one defined by the three variables as given above (Harvey and Lawton, 1986; Morse et

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al., 1988; Blackburn et al., 1990). Little information exists on the species number/abundance distribution in soil animal communities (Usher, 1985; Vegter et al., 1988; Kampichler, 1992), and even less on the other relationships (e.g. Haarløv, 1960). This paper concentrates on the importance of certain physical properties of the soil environment for predicting a size-class abundance/body size distribution in soil microarthropods.

Several studies have dealt with fractal concepts in order to describe or to explain a variety of pedological features (e.g. Ahl and Niemeyer, 1989; Tyler and Wheatcraft, 1989; Toledo et al., 1990; Bartoli et al., 1991; Young and Crawford, 1991). Since we aim at an analysis of available habitat space for a group of non-burrowing animals which are restricted to the surfaces of existing air-filled crevices in soil, we confine our investigation to the estimation of the fractal dimension of the pore walls *.

In general, the mass M of a fractal object (length, surface, volume) depends on the scale of measurement δ, following the relationship:

$$M(\delta) \approx \delta^{d-D} \tag{1}$$

where d denotes the Euclidian dimension, and D is the fractal dimension. Area A of a fractal surface is measured as follows:

$$A(\delta) \approx \delta^{2-D} \tag{2}$$

Consequently, the amount of available pore area for individuals of non-burrowing species of different sizes depends on the fractal dimension of the pore walls (cf. Sugihara and May, 1990). As A increases with decreasing δ, usable area increases for smaller individuals. Hence small-sized individuals should be more abundant than large-sized individuals. Apart from other influencing factors we may expect that the rougher the pore walls in a given soil are — i.e., the higher their value of D — the steeper will be the size/abundance distribution of micro-arthropods. Morse et al. (1985) have shown that real data on the distribution of arthropod body lengths are broadly consistent with predictions based on the fractal dimension of the vegetation surface. From this point of view we must consider the estimation of the roughness of the soil pore surface necessary for developing a model on the relationships between number, body size and abundance of species of soil microarthropods.

METHOD

Image analysis and fractal geometry

When an isotropic three-dimensional soil sample is intersected by a plane,

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*For an introduction to fractal geometry and its application in ecology see Fortin (1987) and Sugihara and May (1990).

then the intersected soil pores can be identified as two-dimensional patches (see qualifying comments below). A simple relationship exists between the fractal dimension of a patch perimeter D_p and the corresponding pore surface dimension D_s (cf. Mandelbrot, 1987, pp. 227–228):

$$D_p = D_s - 1 \tag{3}$$

Hence the analysis of D_s can be performed on the basis of image analysis of thin sections of soil (Protz et al., 1987; Ringrose-Voase, 1987; Moran et al., 1989; Bartoli et al., 1991).

To estimate the boundary dimension of patches, the relation between area and perimeter (the so-called area–perimeter or A–P relation) served as a convenient method (Lovejoy, 1982; Krummel et al., 1987; Mandelbrot, 1987).

TABLE 1

Locations, pedological features and depth of soil samples used for the thin sections[a] and results of the regression $\ln P = D_p/2 \times \ln A + \ln K$

Sections	$D_p/2$	S.E.	R^2	D_s
Hermannsdorf (Upper Austria) Arable land Stagnogley (≈Stagno-Gleyic Luvisol) Loamy silt Soil horizon Ag, 0–2 mm	0.70	0.02	0.96	2.39
Hermannsdorf (Upper Austria) Arable land Stagnogley (≈Stagno-Gleyic Luvisol) Loamy silt Soil horizon Ag, 2–9 mm	0.63	0.03	0.93	2.26
Kaltenleutgeben (Lower Austria) Deciduous forest Terra fusca (≈Chromic Cambisol) Soil horizon Ah, 0–5 cm	0.67	0.01	0.96	2.33
Kaltenleutgeben (Lower Austria) Deciduous forest Terra fusca (≈Chromic Cambisol) Soil horizon Bv, 12–16 cm	0.66	0.01	0.96	2.32
Trautenfels (Styria) Arable land Pararendzina (≈Calcaric Regosol) Loamy sand Soil horizon Ah, 10–20 cm	0.65	0.01	0.93	2.30

[a] Austrian soil taxonomy after Fink (1969) with corresponding units of the FAO system according to ISSS (1986) and Scheffer and Schachtschabel (1989), symbols of the soil horizons after Fink (1969).

The A–P relation is a measure of the contortion of the perimeter. A fixed length of smooth or rounded perimeter can enclose a larger area than a complicated one. The degree of roughness can be qualified by the dimension D_p of the perimeter, which is given by the solution of:

$$P \sim A^{D_p/2} \tag{4}$$

For smooth shapes $D_p = 1$, and $P \approx A^{1/2}$, whereas for highly contorted shapes, where the perimeter attends to fold back on itself thus filling the plane, and D_p approaches 2.

After calculating the perimeter P and the area A of each patch at some fixed δ at a pixel basis, the values of P against A are plotted on a double logarithmic scale. The slope of the regression line resulting from eq. (4) in the logarithmic form equals $D_p/2$.

Production and processing of images

The thin sections studied were derived from various localities in Austria (Table 1), and produced by the method described by Altemüller (1962). Photographic images of three to five sectors of each section were made with an ILFORD PAN-F film, developed with maximum contrast and magnified (Fig.

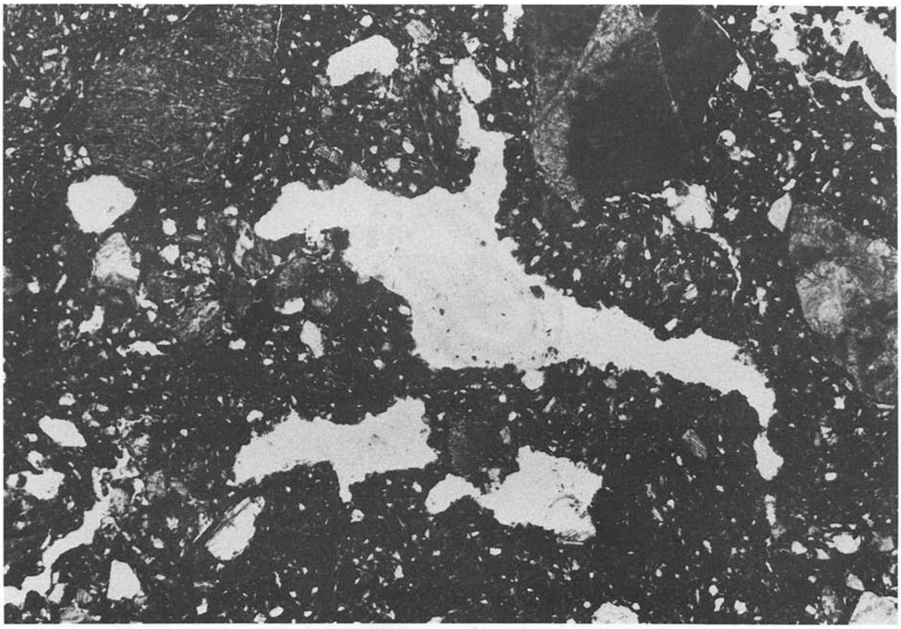

Fig. 1. Photograph of a sector of a soil thin section from arable land (Trautenfels, cf. Table 1). Size of the sector: 4 mm × 6.4 mm.

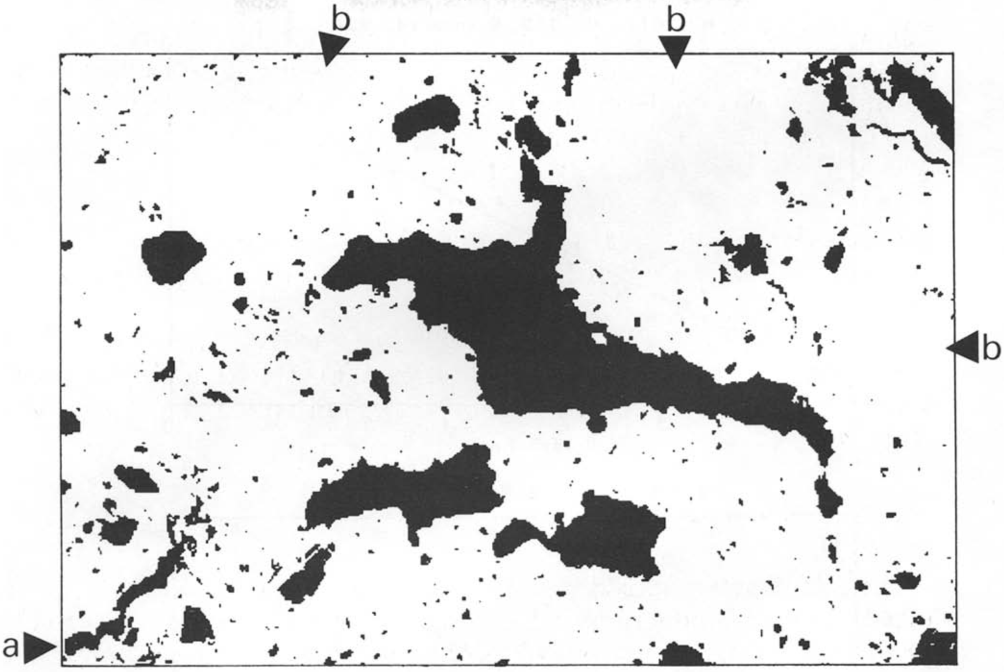

Fig. 2. Digitized image of Fig. 1 (see text for explanation).

1). Then the images were scanned with a MICROTEK MSF-400G scanner into a MACINTOSH cxII computer with a band width of 1 bit (in order to obtain only either black or white areas) at a resolution of 72 dpi (dots per inch). The smallest discernible unit (pixel) of the digitized images corresponded to 6 or 12 μm, depending on the sector size. The pores were now represented as contiguous areas of white color, whereas the soil was black. Using a painting program the images were inverted, so that the pores were now black and the soil white (Fig. 2).

The following corrections were done on the digitized images:

(1) All patches of pores that crossed any of the edges of the picture were excluded from the analysis, as then a part of the perimeter of those pores is a straight line and distorts the overall calculation. Exceptions were made when the length of the section line was negligibly short in comparison to the total perimeter of the pore. In that case the straight section line was replaced by a piece of original pore perimeter of the same length (see arrow *a* in Fig. 2).

(2) Large pores with narrow interconnections of one or two pixels width were separated.

(3) After scanning mineral grains in the soil sections appeared as spotted areas. They were removed completely (see arrows *b* in Fig. 2).

(4) A change in dimension with size scale may indicate a shift in generating

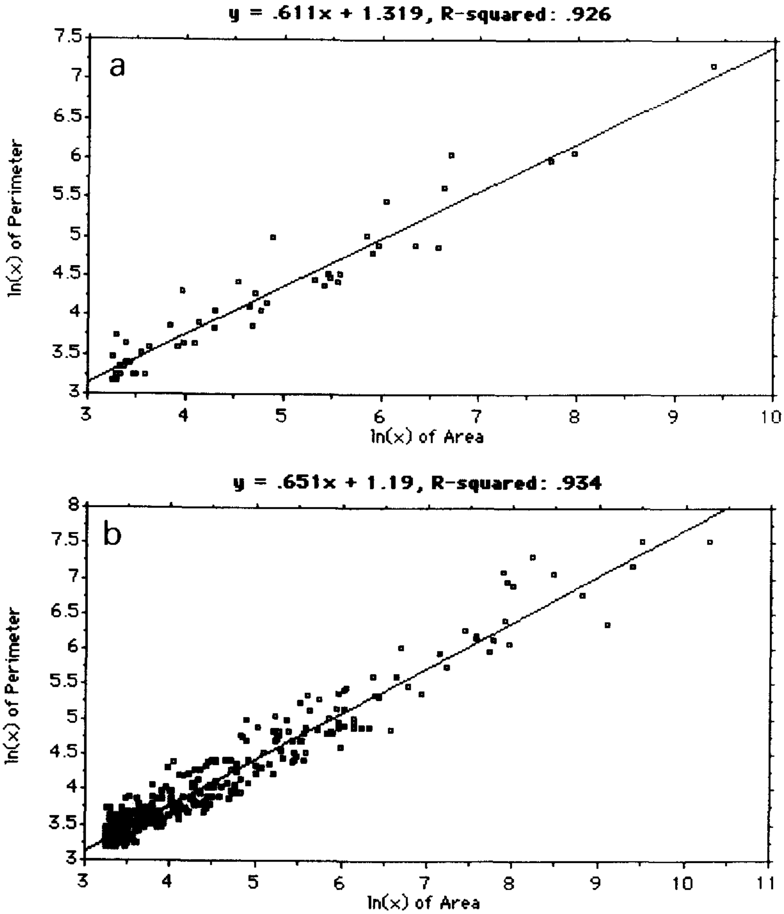

Fig. 3. Regression of ln $P = D_p/2 \times \ln A + \ln K$. (a) Regression based on the digitized image of Fig. 2. (b) Regression based on pooled data from Fig. 2 and three additional photographs from the same thin section. Both axes in pixel units; length of 1 pixel = 12 μm.

process and is indicated by a kink in the regression line (Sugihara and May, 1990). In contrast to Bartoli et al. (1991), this study restricts itself to soil pores that actually are habitable to micro-arthropods, in order not to mix together pore wall dimensions originating from different soil forming processes. Therefore, a lower threshold was established at a patch area of approximately 0.003 mm^2. Thus, only pores having an area of at least 0.003 mm^2 and larger were analyzed.

The so retouched images were then processed by a specially designed computer program that measures P and A of every distinguishable patch. Using a statistics program the linear regression was carried out (Fig. 3).

The application of the P–A relation method is restricted to specific soil conditions. For example in a two-dimensional section the identification of pores as discrete patches should be possible. Sections that show an interwoven network of soil matter and crevices cannot be analyzed by the computer program used here.

RESULTS

Table 1 presents the results of the regression of ln P on ln A. As stated in eq. (3), adding 1 to D_p yields the fractal dimension of the pore surface D_s. Although originating from different soils, D_s varies only slightly around 2.32.

We inserted this result into eq. (2) to estimate the available area for microarthropods of different size. After a reduction in linear body size by the factor 0.1 the reduction in individual "cover" (=area of the vertical projection of a specimen upon the substratum, introduced by Haarløv, 1960) can be estimated by squaring (cf. Morse et al., 1985). Thus, we assume a $(0.1\times0.1)^{-0.32} \approx 4$-fold increase in available habitat space. Accordingly an order-of-magnitude decrease in body length should result in a 4-fold increase in density of individuals on a given pore area.

DISCUSSION AND CONCLUSIONS

Usefulness of the method

As stated above the A–P relation can only be used when specific presuppositions are satisfied. The strict criteria on the selection of soil sections might by all means be responsible for the narrow range of D_s ascertained in this study. In particular the need for fractal analysis of organic layers — where the most diverse soil microarthopod communities can be found — will set a limit to the applicability of this method. Further analysis of the boundary dimensions of soil pores should be based on a grid method or the "flexible yard stick" method (Vlcek and Cheung, 1986; Tatsumi et al., 1989; Sugihara and May, 1990).

Implications for size class distribution

The fractal dimension as a measure for the roughness of soil pore walls constitutes the first step in the development of a theoretical account of the abundance/body size distribution. It predicts available habitat space not for species but for individuals of a certain size and may therefore help to predict the size-class abundance/body size distribution (cf. Morse et al., 1988, for the differences and connections between these types of relationships). Inserting D_s into eq. (2), calculating available habitat space and drawing inferences from the result about abundance of microarthropods of different size supposes that all soil crevices are accessible to all soil micro-arthropods, from the smallest to the largest. This obviously cannot be the case. Techniques of image analysis should bring about a correction by investigation of the share of pore diameter classes on total pore area, which could yield a factor of pore accessability for any size class of microarthropods.

Further investigations will have to concentrate on the variability of fractal dimension of habitable pore surface in time and space. Particularly in organic layers we expect seasonal changes and high spatial variability due to comminution and decomposition of plant debris. Collemboles with their high reproductive rate and their ability of synchronized reproduction (Joosse, 1983) may adjust to changing habitat features rather rapidly. Compared with this oribatid mites have a lower reproductive rate, need several months for development and show only moderate changes in population size (Butcher et al., 1971; Petersen, 1982). Data on velocity and extent of changes of D_s may enable us to answer if microarthropod communities or at least certain taxa actually equilibrate with the geometric features of their habitats.

It also must be remembered that a specific relation exists between abundance of animals and their metabolic rates that influences the size-class abundance:body size distribution. Metabolic rates of meso- and macrofauna in soil and litter scale to the power of 0.813 with respect to body weight (Ryszkowski, 1975). Hence, if animal abundance is reciprocal to metabolic rate (Morse et al., 1985; Damuth 1987), a decrease in body size at an order-of-magnitude will result in an increase of density by a factor of $0.1^{3\times(-0.813)}\approx 275$.

The multiple effects of soil pore roughness, accessability of pores per size class and body-size:metabolic-rate relationship yield a simple model for a theoretical consideration of the size-class abundance:body size distribution, which can be verified in a subsequent check of the data. The next step will be to produce a comprehensive account on body size, abundance and number of species in microarthropod communities from the organic layers of a spruce forest and from arable land.

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