Fractals and ecology

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Abstract: The increasing number of applications of fractal theory in the environmental sciences reflects the recognized importance of spatial and temporal scale to the study of ecological systems and processes. In this paper, we summarize the various algorithms that have been developed for estimating the fractal dimension of such natural phenomena as landscapes, soils, plant root systems, paths of foraging animals, and so forth. We also discuss the potential utility and limitations of a fractal approach, and outline how fractals have been used in ecology.

Introduction

In recent years, biologists have come to recognize that spatio-temporal scaling must be considered when studying ecosystem patterns and processes (Wiens 1989; Juhász-Nagy 1992). The importance of scaling in biology was succinctly stated by Juhász-Nagy (1993):

> "... the most important biological processes (like evolution, succession etc.) are clearly spatio-temporal processes, where both space and time should be taken into account, even if the methodology involved is frequently troublesome."

The basic tenet of our contribution is that concepts derived from fractal theory are fundamental to the understanding of scale-related phenomena in ecology and the environmental sciences.

The term 'fractal' (from the latin *fractus*, meaning broken) was introduced by Mandelbrot (1975) to define spatial or temporal phenomena that are continuous by not differentiable; that is, every attempt to split a fractal into smaller pieces results in the resolution of still more structure. This contrasts with the more familiar differentiable continuous series, such as polynomials and other Euclidean constructs. Mathematical fractals are said to display 'self-similar' properties, since the same basic structure is repeated at all spatial scales. A detailed outline of mathematical fractal

geometry is beyond the scope of this paper, but excellent summaries of basic concepts can be found in numerous texts (e.g. Mandelbrot 1982; Frontier 1987; Schroeder 1991).

Fractal theory has been used by ecologists in a number of ways: to estimate the fractal dimension of natural objects, such as landscapes and habitats, plant root systems, and the path trajectories of beetles; to develop models and test theories of landscape complexity as it relates to the spread of disturbance, abundance relationships in organisms, the movement of organisms and so forth (e.g. Milne 1992); and to study the 'chaos' of ecological systems (e.g. Schaffer and Kot 1986; Sugihara et al. 1990). It is beyond the scope of this paper to discuss applications of chaos theory to ecology (see Frontier 1987: 355 for an introduction to the topic).

In this contribution we collect and summarize currently-available algorithms for estimating the fractal dimension of natural objects. We also discuss some problems with these estimation procedures, and outline current and potential applications of fractal theory to ecology and the environmental sciences.

Fractals and the fractal dimension

A formal or 'strict' definition of a mathematical fractal is a series for which the Hausdorff dimen-

sion (a continuous function) exceeds the topological dimension (a discrete function). Topological dimension refers to the familiar Euclidean spaces, i.e. a line is one-dimensional, a plane two-dimensional, and a cube three-dimensional. The dimension D of a fractal trace or path, however, is a continuous function with range $1 \leq D \leq 2$. A completely differentiable series has a fractal dimension $D = 1$ (the same as the topological dimension), while a Brownian path (which occupies the entire two-dimensional topological space) has a fractal dimension $D = 2$. Fractal dimensions between these extremes quantify the degree to which the trace 'fills' the plane. In the same way, fractal surfaces have dimensions $2 \leq D \leq 3$, with $D = 2$ for an absolutely 'smooth' surface and $D = 3$ for an infinitely crumpled one.

To illustrate how the fractal dimension can be estimated, consider the problem of determining the length of a 'coastline' Γ. For a given spatial scale δ, we can estimate the length $L(\delta)$ as a set of N straight-line segments each of length δ. Small 'peninsulas' and other features not recognized at coarser scales will become apparent at finer scales, so that the measured length increases as δ decreases (Mandelbrot 1967). We can express this relationship using the simple power law:

$$L(\delta) = K \delta^{1-D} \ (\ 1 < D < 2)$$

where the exponent D (the fractal dimension) is a fractional number quantifying the degree of 'complexity' of the coastline. A fundamental feature of a fractal is this dependence of the measured 'length' on measurement scale. The power law for the fractal dimension $\Delta(\Gamma)$ can also be expressed as a limiting function:

$$\Delta(\Gamma) = \lim_{\delta \to 0} \frac{1 + \log L(\delta)}{|\log \delta|}$$

In practice, D is estimated by taking the log of both sides of the above power law equation:

$\log L(\delta) = \log K + (1-D) \log \delta$ or
$\log (N\delta) = \log K + (1-D) \log \delta$

and plotting $\log (N\delta)$ versus $\log (\delta)$. The Y-intercept of the plot is $\log K$, and the slope of the line provides an estimate of D (to be pedantic, $D = 1$ - slope). Note that for a Euclidean object, the measured length is independent of the measuring scale used ($L(\delta) = K, D = 1$).

True or mathematical fractals are said to exhibit exact self-similarity at all spatial scales, since successive magnifications reveal the same structure.

This implies that fractals exhibit partial correlation over all scales (Burrough 1981). An example of a mathematical fractal is the so-called Koch 'curve' or 'snowflake' (Sugihara and May 1990; Schroeder 1991: 8). For this fractal, a reduction in the measuring scale by one-third ($\delta_{n+1}/\delta_n = 1/3$) always increases the measured length of the object by four-thirds (L_{n+1}/L_n) = 4/3. Substituting into the power law relationship we obtain:

$$(L_{n+1}/L_n) = (\delta_{n+1}/\delta_n)^{1-D}$$

$$(4/3) = (1/3)^{1-D}$$

$$4 = 3^D$$

$$D = \log 4/\log 3 = 1.26.$$

For natural objects, the elegant self-similar property of mathematical fractals does not apply, just as we do not expect to find true Euclidean objects (circles, squares). However, many natural objects (e.g. coastlines, ecological habitats and landscapes) do display some degree of 'statistical' self-similarity, at least over certain spatial scales (statistical self-similarity implies a scale-related repetition of overall complexity, but not of the pattern itself). However, it is not necessary that an object display statistical self-similar properties when applying fractal models (notwithstanding comments of Simberloff et al. 1987). Normant and Tricot (1993) emphasize this point:

"... a geographical line is seen as a fairly non-homogeneous curve, that is, with both straight lines (almost recifiable) and chaotic parts, whose local dimension is not the same everywhere. Such curves are not self-similar, not even statistically ... it is necessary to stress the fact that fractal does not imply self- similar, and thus coastlines are not self-similar, but fractal ... we assert that self-similarity is a restrictive point of view".

Could the same not be said of ecological habitats and landscapes? We feel that ecologists are drawn to fractal theory as a unifying concept relating pattern, process and scale, and as a methodology for characterizing the recognized complexity of natural systems.

The relevance of fractal theory to ecological problems is of course scale-dependent. For a forester interested in estimating stand board-feet, a Euclidean representation of tree trunks (as cylinders or elongate cones) is quite adequate. However, for an ecologist interested in modelling habitat availability on tree trunks (say, for

epiphytes or invertebrates), a fractal approach is more appropriate. The geometrically complex surface of a tree trunk can be a source of simplicity when fractal theory is applied. A diameter (DBH) tape ignores the surface roughness of the bark, giving but a crude estimate of the circumference of a tree. For an insect of length 10 mm, the 'distance' that it must travel to circumnavigate the tree trunk is much greater than the measured DBH value. For an insect of length 1 mm, this distance is greater still. This has consequences on the way that tree trunk 'habitats' are perceived by organisms of different sizes. If the bark has a fractal dimension D = 1.5, an insect an order of magnitude smaller than another perceives a length increase of $10^{1-D} = 10^{0.5} \approx 3.16$, or a habitat surface area increase of $\approx 3.16^2 \approx 10$. By contrast, for a smooth Euclidean surface, D = 1 and both insects perceive the same 'amount' of habitat. The higher the habitat fractal dimension, the greater the perceived rate of increase in length (surface) with decreasing measuring scale.

Algorithms for measuring the fractal dimension of natural objects

A number of reviews discussing the potential use of fractal theory in ecology have been published (Loehle 1983; Frontier 1987; Milne 1988, 1991; Sugihara and May 1990; Williamson and Lawton 1991). However, a number of new methods for estimating the fractal dimension have been developed since these reviews were published. While our summary is biased towards applications in landscape ecology, we have tried to include most if not all of the algorithms that have been used by environmental biologists. For the sake of brevity, mathematical derivations have purposefully been omitted from our descriptions. However, it should be recognized that many methods for estimating the fractal dimension D are empirically derived, based on the power law relationship. Mandelbrot (1982) and Voss (1988) should be consulted for general theory, as well as additional algorithms that may prove useful to biologists.

1. Dividers Method

This method is used to measure the fractal dimension of a simple plane curve (e.g. leaf edge, coastline, habitat or landscape edge). The procedure is analogous to that of moving a compass of fixed opening δ along the curve (Fig. 1a). The estimated length of the coastline is the product of N (number of compass dividers required to 'cover' the object) and the scale factor δ.

The relationship between the measuring scale δ and the length L = Nδ is:

$$L = K \delta^{1-D}$$

$$\log (N\delta) = \log K + (1-D) \log \delta$$

The fractal dimension is estimated by measuring the length of the object of interest at various scale values δ (the log-log plot has slope 1-D). Normant and Tricot (1991) note that this method is not well-founded theoretically, and that it is exact only for statistically self-similar curves. It should be noted that the value L = Nδ (for a given δ) may vary depending on starting position along the curve. It is therefore recommended that the procedure be repeated at different starting positions to account for this variation (Sugihara and May 1990). It is also possible that D will differ over a range of δ values (i.e. the log-log plot will vary in slope). The point at which the fractal dimension changes may be indicative of the scale at which the generative processes determining D change (Kent and Wong 1982).

In a geographical context, Longley and Batty (1989) refer to the above procedure as the 'structured walk' method. They outline a number of variants of this basic procedure. Normant and Tricot (1991, 1993) have recently described an alternative estimation algorithm, termed the 'constant deviation variable step' (CDVS) method, that emphasizes the local behaviour of the curve (thus curve self-similarity is not assumed). It involves dividing the curve into a series of subarcs (local convex hulls) of a given breadth ε. By varying ε, an estimate of fractal dimension is obtained using a simple modification of the above equation.

2. Grid or box-counting method

Like the dividers method, this procedure can be used to measure the fractal dimension of a simple plane curve (Longley and Batty 1989). However, in addition it can be applied to more 'complex' (e.g. overlapping) curves and other structures lacking self-similar properties (e.g. Peitgen et al. 1992: 240). It has proved particularly useful in determining the fractal dimension of vegetation when describing habitat complexity (Morse et al. 1985). In theory, the method involves obtaining a 'δ-cover' of the object, which is defined as the number of pixels of length δ required to cover the object (Voss 1988: 60). A practical alternative is to superimpose a regular grid of pixels of length δ on the object, and to count the number of pixels
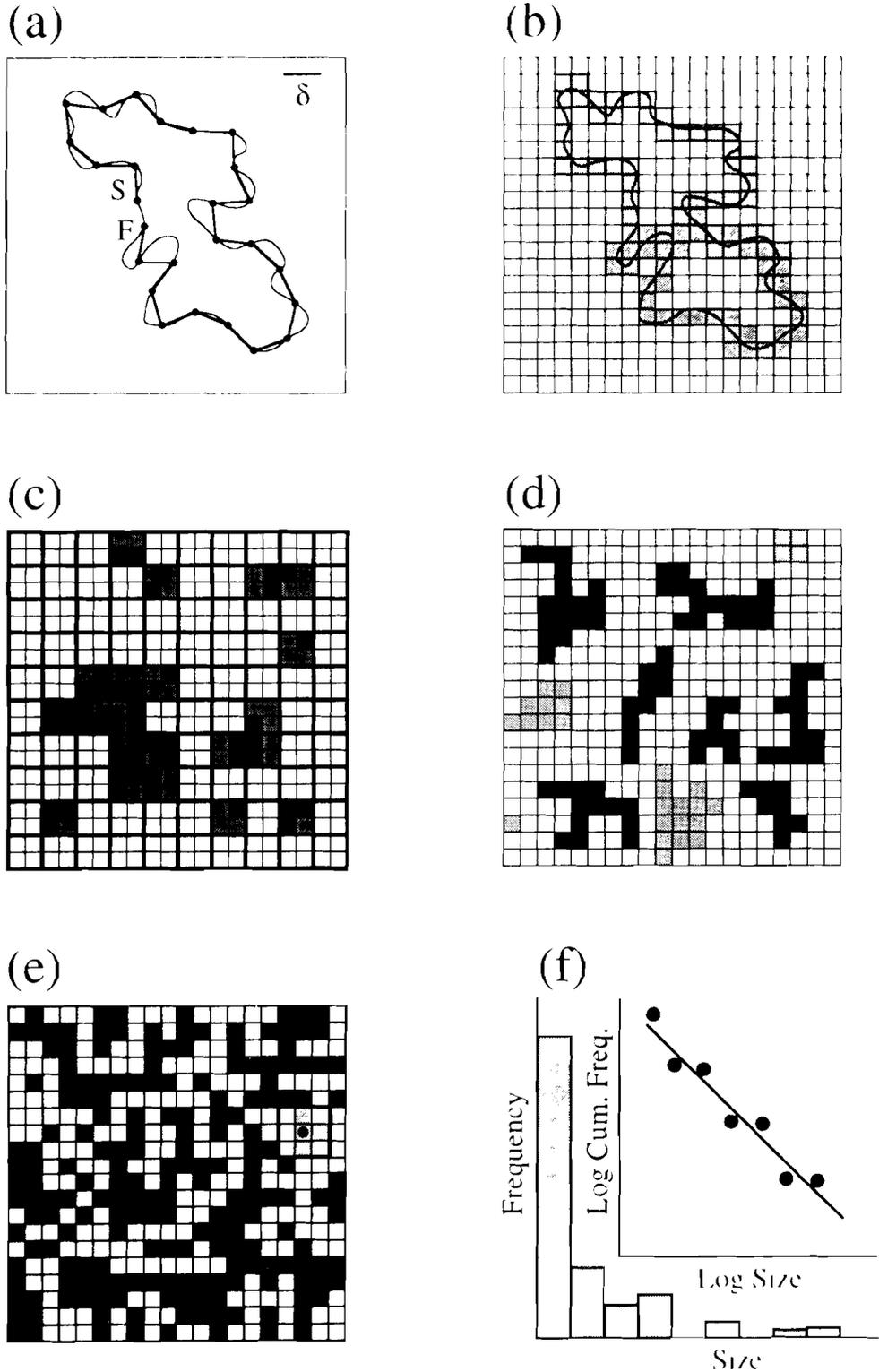
Figure 1. Some alternative approaches to estimating the fractal dimension of natural objects. (a) *Dividers method* - δ = measuring length, S = starting position and F = finishing position. In this case, N = 25; (b) *Grid method* - grey pixels cover the image; (c) *Grid method for pixel images* - The finest grid scale is the original pixel image (black pixels represent 'presence'). Heavy grid scale (grey pixels represent 'presence') corresponds to 2 x 2 window size; (d) *Area-perimeter relationships* - pixel islands are shown. Grey islands touch on the edges and should be excluded from consideration; (e) *Probability-density function* - a representative 3 x 3 window is shown (centered on dot), for which the count is 4; (f) *Frequency distribution* - original hypergeometric distribution, and cumulative log-log plot, are shown;

(g)

Value

Interval

Log γh

Sill

Semivariogram   Log h

Log P(ω)

Power Spectrum   Log ω

(h)

(i)
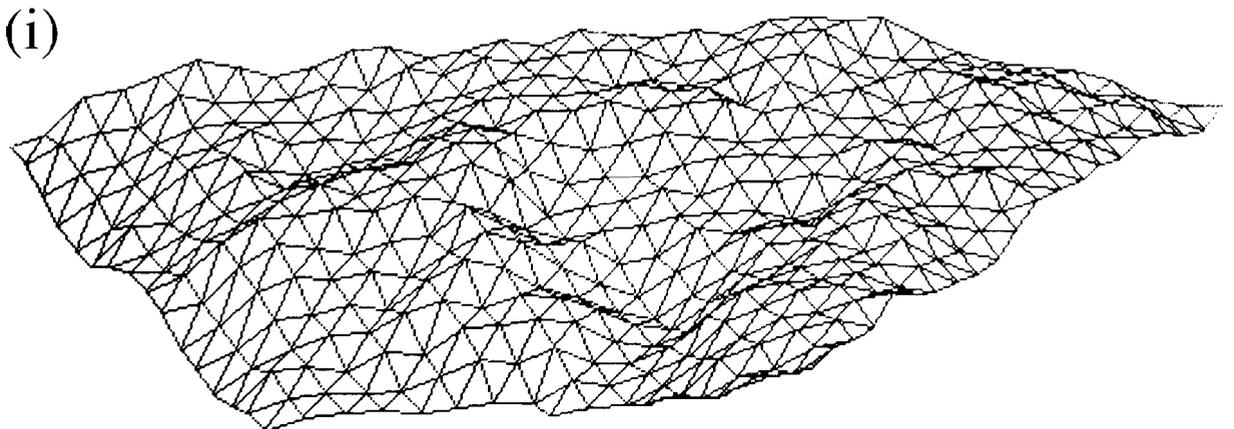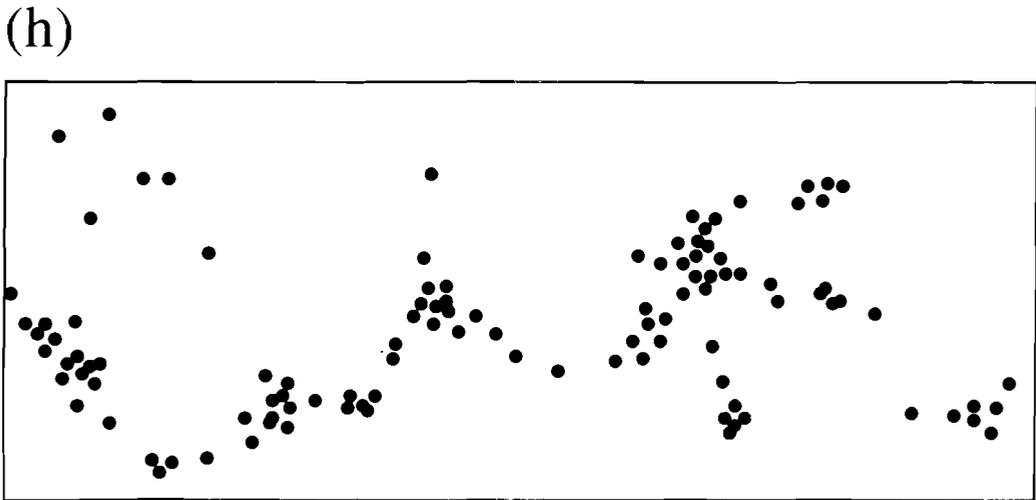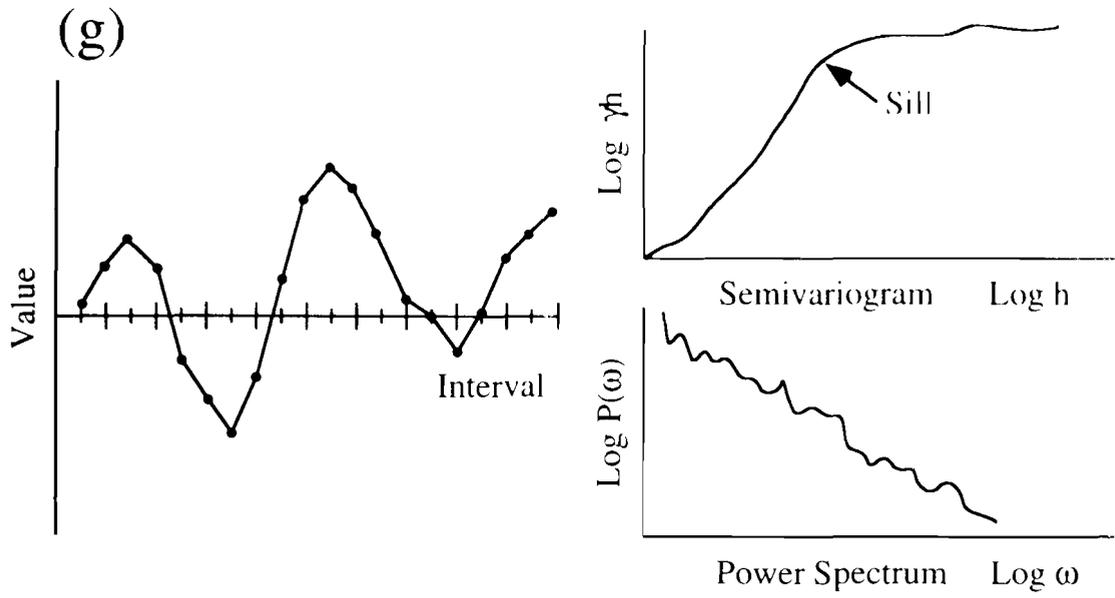
(g) *Spatial-temporal series* - example data set on the left, examples of semivariogram and power spectrum on the right;
(h) *Point pattern* - a representative clustered point pattern is shown; (i) *Surface models* - a representative surface is
shown.

(C) that are 'occupied' by the object (Fig. 1b). This procedure is then repeated using different values of δ (see Milne 1991: 207). The defining relationship is:

$$C = K \delta^{-D}$$

$$\log C = \log K - D \log \delta$$

For a plot of log C versus log δ, the fractal dimension D = - slope. Because slight re-orientations of the grid can produce different values of C for a given δ, different placements of grids should be used to obtain a distribution of D-values for the object. Tatsumi et al. (1989: 501) demonstrate an alternative method of implementing this procedure using an image processing system.

Longley and Batty (1989) state that "it is recognized that this method may be less suited to the task of hugging the more intricate details of the base curve but, because of its low computer processing requirements, it is recommended as a method suitable for yielding a first approximation to the fractal dimension". Normant and Tricot (1991) are more critical, stating that the box-counting method is "often unusable and, in any case, yields very imprecise results".

Morse et al. (1985) describe an algorithm, based on the box-counting method, for estimating the fractal dimension of ecological habitats (2 < D < 3). Consider the problem of estimating the fractal dimension of a spruce tree branch. In principal, the box-counting method could be generalized to the higher dimension by superimposing a three-dimensional grid on the branch and varying the size of 'counting-cubes'. In fact, Milne (1988: 73) recommends such a procedure for estimating the fractal dimension of a coded surface (e.g. surface describing an ordination configuration; see Section 8 for alternative methods). The 'counting cube' procedure is difficult if not impossible to implement in the field, however, at least given present technical limitations (Zeide and Gresham 1991: 1209). Morse et al. (1985) simplified the problem by photographing the habitat (in their case, plant branches) to obtain an image in two dimensions. They then used the box-counting method to determine the fractal dimension (1 < D < 2) of the image. Following Mandelbrot (1983: 365), they then determined the respective upper (2D) and lower (D+1) heuristic limits of the habitat fractal dimension, under the assumption that the photograph represents a randomly placed orthogonal plane through the habitat. This results in rather broad limits (e.g. for an observed

value D = 1.4, the expected limits are 2.4 and 2.8). Despite this limitation, the procedure has since been used by others to estimate habitat fractal dimension (e.g. Shorrocks et al. 1991; Gunnarsson 1993).

The box-counting method has also been used to determine the fractal dimension of pixel images (Milne 1992: 44; Virkkala 1993). Consider a raster map (e.g. 160 x 160 pixels) in which forested areas are coded black, and non-forested areas white. To determine the fractal dimension of the forest-image (black pixels), divide the image into coarser scales of pixel resolution ('windows') and count the number of windows occupied by a least one black pixel (Fig. 1c). The log-log plot (resolution scale vs. number of windows occupied) is used to determine the fractal dimension (D = -slope).

3. Area-perimeter relationships

These methods are normally used to estimate the fractal dimension from raster-based digitized maps. It is assumed that the image consists of a set of discrete pixel 'islands' or patches (that is, discrete objects with measurable areas and perimeters, Fig. 1d). Depending on objectives, two approaches are possible: (a) perimeter-based, to determine the extent that an island perimeter fills the plane; (b) area-based, to determine the extent that the island itself fills the plane. Both methods are normally applied to an 'archipelago' of islands, though they can also be used to determine the fractal dimension of individual 'islands'.

(a) *Perimeter dimension.* This method measures the extent that the patch perimeters 'fill' the two-dimensional plane. The perimeter-area relationship for pixel islands is given by:

$$A = K P^{2/D}$$

$$\log A = \log K + 2/D \log P$$

where the area A is simply the number of pixels making up a given 'island', and the perimeter P is a count of the number of pixel edges. For a log-log plot of area-perimeter relationships of a set of islands, D = 2/slope (Burrough 1986:127) is the average fractal dimension of the landscape islands. Using this method, perfectly square islands (perimeter: area ratio low) have a fractal dimension D = 1, while highly complex convoluted islands (perimeter:area ratio high) have fractal dimensions approaching 2. The method is useful

in determining the relative 'edginess' of a landscape.

(b) *Area dimension.* Pixel islands are again examined, but we now ask: "what proportion of the two-dimensional space is occupied by the island?". Voss (1988: 61) suggests that the 'box' dimension of an island can be measured as $D = \log A/\log L$, where L is the maximum of the row and column lengths of the pixel-island. Square islands ($A = n^2$, $L = n$) completely fill the two-dimensional space and therefore have a fractal dimension $D = \log (n^2)/\log (n) = 2$, while rectangular islands of length n and width 1 ($A = n \times 1$, $L = n$) have a fractal dimension $D = (\log n)/(\log n) = 1$. Milne (1991: 225) suggests as an alternative the 'area' dimension $D = \log (A)/\log (P/4)$. The relationship between these area-perimeter measures of fractal dimension (and their relationship to the perimeter dimension) is poorly understood and deserving of study.

If an archipelago of islands is to be characterized using this method, the length-area relationship is described as:

$$A = L^D$$

$$\log (A) = D \log (L)$$

Thus the fractal dimension D is simply the slope of the log-log plot.

4. Probability-density function

This method can be used to estimate the fractal dimension of a pixel image (digital map in raster form). However, unlike the area-perimeter methods, discrete habitat islands are not required (Fig. 1e). The probability-density function ρ_L is obtained from square (L x L) sampling 'windows' successively placed on each pixel representing a given cover type (e.g. forest cover). Within each window, a count is made of the number of pixels (n) of the cover type of interest. The frequencies of counts are then expressed as probabilities:

$$\sum_{n=1}^{N(L)} \rho_L = 1$$

where $N(L) \leq L^2$. For a given value of L, the first moment of the probability distribution is given by:

$$M(L) = \sum_{n=1}^{N(L)} n \rho_L$$

These computations are repeated for various values of L (because each window is centred on a single pixel, L must be an odd number). Voss (1988: 66-67) shows that the following power law holds for fractal images:

$$M(L) = k L^D$$

$$\log M(L) = \log K + D \log L$$

Thus the fractal dimension D can be estimated from the slope of the log-log plot of the first moment as a function of L (see Milne 1992: 47). This method can also be applied using higher moments of the probability distribution: see Voss (1988) for a complete discussion.

The behaviour of this method for different landscape patterns is poorly understood, though Milne (1992: 41-45) did perform a preliminary comparison of three artificial landscapes (each half-covered with 'filled' pixels).

5. Frequency distributions

(a) *Distribution of areas (Korcak empirical relation).* For an archipelago of 'self-similar' islands, the relationship between island size (area) and frequency is given by the cumulative hypergeometric size-frequency distribution (Hastings et al. 1982; Kent and Wong 1982; Burrough 1986:127):

$$N = k \, a^{(-D/2)}$$

$$\log N = \log k + (-D/2) \log a$$

where N is the number of islands larger than area a. The slope of the log-log plot is -D/2 (Fig. 1f). This function implies that an archipelago of irregularly-shaped islands (i.e. D large) should be dominated by many small islands. For a set of 100 islands:

Island Size	D = 2	D = 1
smallest	77	57
intermediate	15	25
large	8	18

Note that only the distribution of island areas is required to determine the fractal dimension. Kent and Wong (1982) used this method to estimate the fractal dimension of lake boundaries (littoral zone) in the Precambrian Shield of Ontario, Canada.

Hastings et al. (1982), following Mandelbrot (1982), suggested that there is a relationship between persistence (H = parameter of a Brownian diffusion model) and landscape fragmentation (D = fractal dimension of patches as determined from the hypergeometric distribution). While the exact relationship between D and H depends on the model chosen, Sugihara and May (1990) state that "increased persistence (more memory in the process) should correspond to smoother boundaries and patches with larger and more uniform areas; whereas reduced persistence will correspond to more complex and highly fragmented landscapes dominated by many small areas". Under certain limiting assumptions (Sugihara and May 1990: 83), the relationship between H and D is:

$$H = 2 - D$$

This implies that landscapes with many small patches with complex boundaries (high D) are less persistent (low H). Sugihara and May (1990: 83) summarize the relationship as:

H	D	Nature of Process
> 0.5	< 1.5	'persistent'
= 0.5	= 1.5	Brownian or random
< 0.5	> 1.5	'anti-persistent'

Hastings et al. (1982) used this method of examining persistence-patchiness relationships to compare cypress (early successional) and broadleaf evergreen (late successional) patches in Okefenokee Swamp. They found that cypress patches had a higher fractal dimension (D = 1.25, H = 0.75) than broadleaf evergreen patches (D = 1.0, H = 1.0), implying that the earlier successional vegetation is less persistent ('stable' in their terminology). A later study (Meltzer and Hastings 1992) points out a number of methodological problems associated with this approach. While the method may prove useful in remote sensing studies (Sugihara and May 1990), objective tests are required to determine whether persistence-patchiness relationships developed under limiting theoretical assumptions are valid for ecological systems. Note also that Meltzer and Hastings' (1992) definitions of 'persistence' and 'stability' differ from the usual ecological meanings.

(b) Distribution of volumes (Rosin's law). Turcotte (1986) derived a hypergeometric frequency dis-

tribution relation for particle size in soils and other geological material:

$$N = kR_i^{-D}$$

$$\log N = \log k - D \log R_i$$

where N is the number of particles whose radius is greater than R_i, and D is the fractal dimension. The fractal dimension is indicative of the nature of the soil (Tyler and Wheatcraft 1989):

Fractal Dimension	Nature of Soil
D = 0	all particles are of equal diameter.
D = 3	number of particles greater than a given radius R_i doubles with each corresponding decrease (by half) of particle mass.
0 < D < 3	greater proportion of larger particles than D = 3 (sand).
D > 3	greater proportion of smaller particles than D = 3 (silt, clay).

Tyler and Wheatcraft (1989) show that silt-clay soils have fractal dimensions in the range 3.0 - 3.5. They computed one-dimensional 'pore trace' D values for their soils using a method suggested by Mandelbrot et al. (1984). For a soil of fractal dimension D = 3.2, the fractal increment D_i = D - 3 = 0.2 measures the degree to which the soil 'exceeds' the Euclidean three-dimensional space. The one-dimensional pore trace is simply 1 + D_i = 1.2 (a trace of D = 2 would completely fill the space, as expected for a soil containing a high proportion of very small particles).

This inverse power law has been used to examine frequency distributions of objects as disparate as taxonomic systems (Burlando 1990) and seed sizes (Hegde et al. 1991). Hegde et al. (1991) found for seeds that frequency is inversely proportional to the square root of seed size, and suggested that this reflects the fractal nature of ecological habitats.

6. Spatial and temporal series

These methods are suited to the analysis of a unidimensional sequence of equally-spaced temporal or spatial values X (Fig. 1g), with the fractal dimension D measuring the spatial (temporal) dependence of the sequence. An uncorrelated or spatially independent sequence of values

(equivalent to 'white noise') will have a fractal dimension D = 2. Increasing spatial dependence results in a lowering of the fractal dimension; for complete dependence, D = 1.

(a) Semivariance. The semivariance γ_h (Curran 1988) describes the relationship between variance and lag distance (sampling interval) h for an observed series. It is defined as:

$$\gamma_h = 1/(2N_h) \sum_{i=1}^{N_h} (X_i - X_{i+h})^2$$

The semivariogram (a plot of γ_h as a function of h) summarizes the relationship between semivariance and lag distance. At a certain lag distance L, semivariance reaches a maximum (the so-called 'sill'; Fig. 1g). This sill value is approximately equal to the variance of the entire data set. The distance L, termed the range, specifies the average distance over which the values of the sequence are spatially dependent (Phillips 1985). It can be shown (Burrough 1983) that the fractal dimension of the series is described by:

$$2 \gamma_h = h^{4-2D}$$

$$\log \gamma_h = (4-2D) \log h$$

The log-log semivariogram can therefore be used to determine the fractal dimension D = (4 - slope)/2 (Burrough 1986:127), where the slope is determined for the linear portion of the semivariogram (that is, over the lag range 1 to L). For white noise (i.e. successive values of the sequence are completely independent), the slope of the log-log semivariogram is zero and the fractal dimension is, as expected, D = (4-0)/2 = 2. At the opposite extreme, the log-log semivariogram for a simple linear trend (complete spatial dependence at all scales) has a slope of 2 (the maximum possible value), giving D = (4-2)/2 = 1. For a statistically self-similar series, D ≈ 1.5 (Palmer 1988: 94).

In practice, a log-log semivariogram often does not have a constant (linear) slope even for values below the sill; there may be a single linear slope (fractal dimension) for one range of lag distances, and another slope for a second set of lag distances. The lag distance at which this change in slope occurs may indicate the scale at which different processes become operational.

Palmer (1988) used the semivariance method to examine spatial dependence of vegetation along a transect of quadrats. Hauser (1991) modified this

method to examine a two-dimensional grid of quadrats, defining:

$$\gamma_{RhCh} = 1/(2N_{RhCh}) \sum_{i=1}^{N_{RhCh}} (X_{RiCi} - X_{Ri+Rh,Ci+Ch})^2$$

where X_{RiCi} is the value of the variable at point i, Rh is the row offset and Ch the column offset, and $X_{Ri+Rh,Ci+Ch}$ is the value of the variable at a point separated from point i by Rh,Ch.

(b) Spectral analysis. Spectral analysis can also be used to obtain the fractal dimension of a sequence (Burrough 1981). Details of the method are beyond the scope of this review; see Huang and Turcotte (1989:7492) for a lucid account of the method. Briefly, the spectral power $P(\omega)$ is defined for various frequency values ω, and their relationship summarized as a log-log spectral power plot (Fig. 1g). The fractal dimension for this spectral plot is approximated by the relation:

$$P(\omega) \cong \omega^{-(5-2D)}$$

Thus the log-log spectral plot can be used to determine D = (5 + slope)/2 (Burrough 1986:127). The spectral method has been used mainly in the earth sciences.

(c) Katz method. Katz (1988) has taken a completely different approach to the analysis of waveforms. He defines a waveform as "a collection of (x,y) point pairs, where the values of x increase monotonically". He empirically derives a crude measure of waveform fractal dimension:

$$D = \frac{\log n}{\log n + \log (d/L)}$$

where n = the number of 'steps' in the sequence (i.e. number of x-values), d = maximum Euclidean distance between any point pair in the sequence, and L = total linear (Euclidean) length of the waveform. It should be noted that inclusion of L makes this method sensitive to the absolute amplitude of the waveform (that is, one or more 'spikes' in the waveform will increase D). The method should therefore only be used to compare waveforms standardized to the same scale on the Y-axis. Because the method assumes that x increases monotonically, D has a maximum value of 1.5. A value of D = 1 occurs when d = L (i.e. for a straight line).

7. Point patterns

Ogata and Katsura (1991) and King et al. (1989) have developed methods for determining the fractal dimension of spatial point patterns (Fig. 1h). Although these methods have not been extensively used, they may have some potential for the analysis of ecological pattern. They were developed to examine the degree of clustering: highly clustered points will have a fractal dimension approaching 1 (simulated fractal 'dust', Ogata and Katsura 1991:469), whereas a statistically random pattern will have D = 1.5. For regular point patterns, other methods such as the Gibbs likelihood should be used.

(a) Palm intensity. For a set of coordinates of points on the plane $\{\rho_1, \rho_2, ..., \rho_n\}$, compute all pairwise vector 'distances':

$$\Delta_{i,j} = |\rho_i - \rho_j| \ (i = 1 \ \text{to} \ n; j = 1 \ \text{to} \ n; i \neq j)$$

A nonparametric estimation of the Palm intensity is found by counting the number of vectors within an annular region of area A (with radii of u_1 and u_2). Dividing this value by the area of A gives an estimate of the Palm intensity $\lambda(\Delta)$ at $\Delta = u$ (where $u_1 \leq u < u_2$). The log-log plot of $\lambda(\Delta)$ vs. u has a slope of H = 2 - D under certain limiting conditions. A parametric maximum likelihood estimation method for D is derived by Ogata and Katsura (1991: 465-466). Frontier (1987: 350) describes a similar estimation procedure for clouds of points with self-similar properties.

(b) Spectral intensity. This method is related to the power spectrum procedure outlined in Section 6. The averaged 'marginal periodogram' with respect to wave number (ω_r) is estimated as:

$$\emptyset(\omega_r) = j^{-1} \sum_{j=1}^{J} I(\omega_r \cos \omega_\theta^j, \omega_r \sin \omega_\theta^j)$$

The linear portion of the log-log plot of $\emptyset(\omega_r)$ vs. ω_r has slope = -D. However, Ogata and Katsura (1991: 467) recommend a parametric maximum likelihood estimation of the fractal dimension.

(c) Grid or box-counting method. A point pattern within a rectangular area is assumed. The area is divided into n square grid units (pixels) of size δ, the number of points within each grid unit is counted, and the relative dispersion (RD) = (standard deviation)/(mean) of counts is determined. This is repeated for various values of δ. The power law describing the relationship between number of pixels and relative dispersion is:

$$RD = K \, n^{D-1}$$

$$\log RD = \log K + (D-1) \log n$$

The log-log plot has slope = D - 1. King et al. (1989) demonstrate that random uncorrelated noise (i.e. statistically random spatial pattern) has a fractal dimension D = 1.5. A value of D = 1.0 reflects "uniformity of the property over all length scales"; the slope is zero, meaning that there is no change in relative dispersion with changing scale (grid size). Simulation studies are required to determine what sort of point pattern would have this characteristic.

The spatial correlation between regions of defined size or separation distance is given by:

$$r = 2^{3-2D} - 1$$

For D = 1.5 (random pattern), the correlation r = 0, while for D = 1.0 the correlation is maximal (r = 1.0). King et al. (1989) show that, at least for some simulated point patterns, the slope of the log-log plot may not be constant.

8. Surface Models

Polidori et al. (1991) derive a straightforward algorithm for direct estimation of the fractal dimension of topographic surfaces (Fig. 1i). Their method is derived from the fractional Brownian motion model described in Section 5 (see also Goodchild 1980; Sugihara and May 1990: 83). An estimate of the fractal dimension (2 < D < 3) is obtained from the relation:

$$\log |e| = \log k + H \log d$$

where $|e|$ is the mean elevation (height) difference between points that are horizontal Euclidean distance d apart. A measure of fractal dimension is given by D = 3 - H. Polidori et al. (1991) interpret the Brownian parameter H as follows:

H	D	Interpretation
> 0.5	< 2.5	height variations likely have the same sign.
= 0.5	= 2.5	height variations are independent.
< 0.5	> 2.5	height variations likely have opposite signs.

As expected, the fractal dimension of 'rough' topographic surfaces (negative correlation of height variation) is high, while smooth surfaces

(positive correlation of height variation with distance) have a low fractal dimension.

The semivariance and spectral methods outlined in Section 6 are easily modified to determine the fractal dimension of landscape surfaces (Huang and Turcotte 1989). For the semivariance:

$$\gamma_h = 1 \; (4N_h) \sum_{i=1}^{N_h} \sum_{j=1}^{N_h} |(X_{ij} - X_{i+h,j})^2 + (X_{ij} - X_{i,j+h})^2|$$

From the log-log semivariogram, $D = 3$ - slope/2 (Bian and Walsh 1993).

Surface fractal dimension can also be estimated indirectly by examining 'profiles' (one-dimensional transects) extracted from the surface. Lam (1990; see also Goodchild 1980) used a cell-counting algorithm based on the fractional Brownian motion model. At various step sizes, counts are made along 'transects' extracted from the surface. The fractal dimension is estimated separately for each transect from the log-log plot of cell count vs. step size ($D = 2$ - slope, where $1 < D < 2$). The average of these values plus one provides an estimate of the surface fractal dimension.

Another method involves 'converting' the surface plot to a contour map, and using the 'dividers' method (Section 1) to determine the fractal dimension of the contours (the surface fractal dimension is equal to the mean of these D-values plus one). Roy et al. (1987) compared some of these methods and found that they can give quite different results (e.g. range in D of 2.01 - 2.33 for the same image). Their study also determined that the fractal dimension of an image is often not a constant, but instead varies spatially.

9. Two-surface method

Zeide and Pfeifer (1991; also Zeide and Gresham 1991) developed an empirical procedure for estimating the fractal dimension of tree crowns. They point out that it is currently not possible to estimate tree crown D using the 'cube-counting' method. As an alternative, they suggest relating two easily obtained measures (total leaf area, and the surface area of a convex hull that envelops the crown) using a power law. If leaf area and crown surface area are equal, it can be inferred that leaves are largely restricted to the surface of the tree crown (as in shade-tolerant tree species growing in the understory). The tree crown therefore has a 'planar' form of fractal dimension $D = 2$. An increase in leaf area implies that more leaves

occur inside the crown, which increases the fractal dimension of the canopy. The defining relation is:

$$A = k\,E^{D/2}$$

$$\log A = \log K + D/2 \log E$$

where A is the total leaf area and E is an estimate of the surface area of a convex hull that envelops the crown. As this is a measure of crown surface, the fractal dimension range is $2 < D < 3$. Zeide and Gresham (1991) suggest that crown fractal dimension may vary with site quality and thinning intensity and therefore may be a useful indicator of site conditions.

10. Information theory

Milne (1988: 71-75) considered scaling problems in the computation of the familiar Shannon diversity:

$$H = -\sum_{i=1}^{m} p_i \ln p_i$$

Scale relationships in the determination of H can be examined using the relation:

$$H_r = H_o - \sigma \ln r$$

where r is the 'size' of the sampling unit (e.g. quadrat), H_o is a constant (H as r approaches 0) and σ is the lower bound of the Hausdorff dimension (i.e. a scale-independent parameter). This method could be used to characterize changes in various measures of diversity with changing scale (c.f. Juhász-Nagy 1993).

Frontier (1987: 358-364) demonstrates that the familiar evenness measure $J = H/H_{max}$ can be thought of as a measure of the fractal dimension of the distribution of individuals among species.

Ecological applications of fractal theory

Fractal theory has been used by ecologists and environmental scientists in a number of ways. The following is a summary of some of these applications. In Table 1 we have listed, by methodological algorithm, a selection of articles in which fractal dimensions of natural objects have been estimated.

1. Organism size and number of individuals

Morse et al. (1985) argued that since habitat has a fractal structure, there will be more 'useable' space for smaller animals than for larger ones. Working with invertebrates, they found that predictions of the number of individuals (by size class) based on body mass and metabolic rate

Table 1. Summary of selected applications of fractal analysis in ecology and related disciplines.

Method	Application	Reference
Dividers	fractal dimension (D) of root systems.	Fitter and Strickland (1992)
	littoral zone complexity of Pre-cambrian shield lakes, Canada.	Kent and Wong (1982)
	territory size in bald eagles, measured D of Alaska shorelines.	Pennycuick and Kline (1986)
	D for leaf outlines of tree species.	Vlcek and Cheung (1986)
	Australian coral reefs, variation in D with spatial scale.	Bradbury et al. (1983, 1984)
Grid (Box-Count)	size-abundance relations in spider populations.	Gunnarsson (1992)
	aquatic invertebrate colonization, artificial substrates of differing D.	Jeffries (1993)
	size-abundance relations in arthropods, based on habitat D	Morse et al. (1985)
	size-abundance relations in arthropods on lichen thalli.	Shorrocks et al. (1991)
	fractal dimension of roots systems of crop plants.	Tatsmui et al. (1989)
	ranges of bird species in Finland.	Virkkala (1993)
	'landscape' complexity of grassland at the scale of beetle species.	Wiens and Milne (1989)
Area Perimeter	landscape scale, deciduous forest patches in Louisiana, Mississippi.	Krummel et al. (1987)
	D of rain and cloud areas, from radar and satellite data.	Lovejoy (1982)
	D of large landscape units, eastern seaboard and mid-west USA.	O'Neill et al. (1988)
	landscape patches, aerial photos (1930- 1980) of Georgia.	Turner and Ruscher (1988)
Probability Density	D of bare soil areas in grasslands, to model habitat fragmentation.	Milne (1988, 1991, 1992)
Frequency Distributions	taxonomic systems.	Burlando (1990)
	D and H (hypergeometric) of forest patches.	Hastings et al. (1982)
	distribution of seed sizes across species.	Hegde et al. (1991)
	D and H (hypergeometric) of grazed areas over time, Zimbabwe.	Meltzer and Hastings (1992)
	particle-size distribution, various soils.	Tyler and Wheatcraft (1989)
Space Time Series	D of landscapes and other environmental data.	Burrough (1981)
	semivariogram D, soil data along transects.	Burrough (1983)
	semivariogram D, transects in plant communities.	Palmer (1988)
	semivariogram D, environmental gradient of shoreline erosion.	Phillips (1985)
Point Pattern	counts of microspheres in baboon hearts; simulations.	King et al. (1990)
	epicentres of shallow earthquakes in Japan; simulations.	Ogata and Katsura (1991)
Surface Models	scale dependence of topography and vegetation, Montana.	Bian and Walsh (1993)
	surface topography, Arizona.	Huang and Turcotte (1989)
	surface topography, digital elevation model, Columbia.	Polidori et al. (1991)

alone underestimated field values for smaller size classes. Predictions were considerably improved when the fractal dimension of the habitat was incorporated into the model: smaller organisms 'perceive' more space and are therefore comparatively more abundant. Shorrocks et al. (1991) confirmed this general result, as did Gunnarsson (1992) and Jeffries (1993) using artificial substrates of differing fractal dimension.

2. Landscapes

Krummel et al. (1987) examined the fractal dimension of forest patches ('islands') using the perimeter-area method. They found that smaller forest patches had lower mean D than larger patches. The transition zone from low to high fractal dimension occurred at ≈ 60-73 ha. They concluded that small forest patches are the result of anthropogenic activities (woodlots in agricultural areas). Natural woodlots have more convoluted edges. This decrease in landscape complexity with increasing anthropogenic activity has also be reported by O'Neill et al. (1988) and Turner and Ruscher (1988). A recent study by Bian and Walsh (1993) used two-dimensional semivariance and fractal analysis to examine scale dependency in the relationship between topography (elevation, slope angle and slope aspect) and reflectance/absorbance of vegetation at Glacier National Park, Montana. A number of studies concerned with the estimation of the fractal dimension of geomorphological features are

summarized in Goodchild and Mark (1987), Lam (1990) and Lam and Quattrochi (1992).

3. Environmental transects

Burrough (1981) used the semivariogram method to estimate D for various environmental transects (e.g. soil factors, vegetation cover, iron ore content in rocks, rainfall levels, crop yields). He found high fractal dimensions in all cases, from D = 1.4 (iron ore content at 3 m intervals) to D = 2.0 (soil pH at 10 m intervals). Very high fractal dimensions indicate spatial independence of successive values. While some of the series displayed self-similarity over many scales (i.e. a linear log-log plot slope), other trends suggested a change in D with changing scale. Palmer (1988) used the same method to examine spatial dependence of vegetation along transects. Values were generally high but not scale-invariant. Based on a fractal analysis, Phillips (1985) concluded that erosion along a portion of the Delaware coast could not be easily predicted.

4. Plant structure

Vlcek and Cheung (1986) measured the fractal dimension of leaf edges in a number of species. They found that the fractal dimension was highly variable in some species (e.g. oaks), and concluded that D could be a useful taxonomic character. The fractal dimension of root systems was examined by Tatsumi et al. (1989) using the box-counting method. They found fractal dimensions in the range of 1.46 and 1.6 for mature crop plants. Fitter and Strictland (1992) used the dividers method to demonstrate an increase in D over time (to a maximum of D ≈ 1.35). They found some differences between species. Zeide and Gresham (1991) estimated the fractal dimension of the crown surface of loblolly pine trees in North Carolina and found evidence of variation in D with site quality and thinning intensity.

5. Size-frequency distributions

The hyperbolic distribution, because it lacks a characteristic scale, describes the sizes of self-similar phenomena and has an associated Brownian parameter H (Goodchild and Mark 1987). Meltzer and Hastings (1992) examined the size distribution of grazed areas in Zimbabwe over time, and related H to the relative stability of vegetation patches. Overall, they found that increases in cattle decreased patch stability. Using similar methods, Hastings et al. (1982) found lower stability in earlier successional patches. The

hyperbolic distribution has also been fit to taxonomic systems (Burlando 1990) and the size-distribution of seeds (Hegde et al. 1991). Frontier (1987:359-367) discusses applications of fractal theory to rank-frequency diagrams of the distribution of individuals among species.

6. Soil physics

Tyler and Wheatcraft (1989) used particle-size distributions to determine the fractal dimension of various soils, and to relate D to such soil properties as percolation and surface water retention. Perfect and Kay (1991) used a similar method to examine soil fragmentation, while Bartoli et al. (1991) used various methods to estimate the mass, pore and surface fractal dimensions of silty and sandy soils. Tyler and Wheatcraft (1990) offer a useful overview of fractal scaling as applied to soil physics (their Fig. 8.6 is a useful illustration of fractal scaling in natural objects). Frontier (1987: 340) suggests that it would be interesting to examine the relationship between the soil microflora-fauna and soil fractal geometry.

7. Movements of organisms

Fractional Brownian motion models (Frontier 1987: 351-353) have been used to characterize the movement of organisms. Dicke and Burrough (1988) used fractal analysis to examine spider mite movements on smooth surfaces, in the presence and absence of a dispersing pheromone. Wiens and Milne (1989) took a different approach, examining beetle (genus *Eleodes*) movements in natural fractal landscapes. They found that observed beetle movements deviated from modelled (fractional Brownian) ones. A follow-up study by Johnson et al. (1992) found that beetle movements reflect a combination of ordinary (random) and anomalous diffusions. The latter may simply reflect intrinsic departures from randomness, or be the result of barrier avoidance and utilization of corridors in natural landscapes.

8. Ecotone and interfaces

Frontier (1987: 337-343) discusses the ecological significance of contact zones (ecotonal boundaries) between ecosystems, and outlines how fractal theory can be used to examine boundary phenomena. Consider for example contact surfaces in aquatic ecosystems created by turbulence (the geometry of which is fractal, Mandelbrot 1982; Milne 1988: 72). Turbulent regions (e.g. interfaces between warm and cold water) have high phytoplankton productivity due to increased con-

tact with resources (nutrients and light), which in turn 'feeds' higher trophic levels. It follows that spatial patterns determined at fine spatial scales determine patterns at broader scales. Kent and Wong (1982) used fractal analysis to determine the extent of the littoral zone in Precambrian Shield lakes, while Pennycuick and Kline (1986) estimated D to determine territory size in bald eagles along rocky coastlines in Alaska. Forest-grassland ecotones could also be examined in this way to determine habitat available to foraging animals, or to plant species restricted to ecotonal environments.

9. Habitat complexity and fragmentation

A simplifying assumption of many classical ecological models is that habitats are uniform, or that they vary linearly with distance. Some recent studies have examined these assumptions and/or modified the classical models in light of the recognized fractal nature of habitats. Scheuring (1991) modified the classical species-area relationship model to include the fractal nature of vegetation. Palmer (1992) modified the 'competition along an environmental gradient' model of Czárán (1989) to include fractal habitat complexity. He found that species coexistence increased with increasing landscape fractal dimension. Milne et al. (1992) examined mammalian herbivore foraging in artificial fractal landscapes. They concluded that the fractal nature of landscapes is an important determinant of resource utilization rate. Milne (1992) examined the fractal geometry of landscapes from the viewpoint of habitat fragmentation. He concluded that habitat fragmentation affects ecosystem processes, and that this must be recognized in developing a view of landscapes and habitats that is ecologically meaningful.

What can the fractal dimension tell us?

The fractal dimension is a summary statistic measuring overall 'complexity' of a system. Like any summary statistic (e.g. mean, species diversity measure), it is obtained by 'averaging' the variation in the data structure (Normant and Tricot 1993). In doing so, information is necessarily lost. Thus the estimated fractal dimension of a lakeshore tells us nothing about the actual size and overall shape of the lake, nor can we reproduce a map of the lake from D alone. This of course does not mean that the fractal dimension of the lake is a meaningless measure, for it tells us a great deal about the relative complexity of the lakeshore. Used in conjunction with other measures, it is an important descriptor of the lake.

During the mid-1970's, much was written about the utility (and limitations) of species diversity measures in ecology. Many of the points raised by these authors now seem relevant to applications of fractal theory in ecology. For example, Green (1979:97) states that "diversity indices have been extensively and often uncritically applied, without regard to the assumptions implicit in the various diversity formulae and the biases in their estimation and despite many published critiques and premature funerals". We feel that a similar statement applies to fractal theory, the major difference being the relative lack of published critiques on the subject. However, this is to be expected given the range of applications of fractal theory, and the fact that applications in ecology have only recently begun to appear in the literature. As another example, Poole (1974) states that diversity measures are "... answers to which questions have not yet been found". While somewhat cynical, we feel that this statement applies equally well to the current state of fractal theory as used in ecology. While ecologists recognize that habitats and landscapes have fractal properties, many studies have simply reported the fractal dimension as a summary statistic. Further progress is to be expected as fractal analysis is used more and more to generate and test hypotheses about the relationship between pattern and process at various spatial scales (c.f. Loehle 1983; Lam 1990).

The diversity of approaches for determining the fractal dimension of natural objects reflects both: (a) differences in the type of data analyzed; and (b) differences in the objectives of the study, that is in the questions being asked. It follows that the method chosen should reflect the objectives of the study, since the various methods measure quite different things. As an example, consider a landscape consisting of pixel 'islands' (Fig. 1d). A study focussing on ecotonal boundaries (edges) would use the perimeter dimension method. With this method, convoluted islands have a high D, as do long and thin islands. A study focussing on acquisition and retention of space, however, would use the area dimension. This method computes a high fractal dimension for objects that best 'fill up' two-dimensional space (i.e. isodiametric islands). Here, the argument can be made that an isodiametric patch of vegetation (area to edge ratio high) is more likely to retain that space than a thin, convoluted patch (area to edge ratio low). Both methods measure a fractal dimension, but application and interpretation are quite different.

Some unresolved problems

1. Regression analysis to estimate D

Most fractal dimension estimation methods are based on a power law and therefore use the regression slope of a log-log plot to estimate D. The estimated slope (and D) will thus depend on which measure is defined as the 'dependent' variable. The choice is not always straightforward. In computing the perimeter dimension, for example, Burrough (1986) uses the power law relationship $A = k P^{2/D}$ (log A vs. Log P, D = slope/2) whereas Lovejoy (1982) plotted log P vs. log A (D = twice the slope). Both methods are valid, but they do not have the same slope. In such situations, Zeide and Gresham (1991) suggest that bivariate methods (such as those developed by Leduc 1987 and Ricker 1984) be used to estimate slope. Alternatively, the principal component can be used.

2. Edge effects and maps

This problem, which has not been discussed in the literature, is particular to the area-perimeter and probability-density function methods. For the area-perimeter method, inclusion of 'islands' abutting the edge of the study area (grey islands in Fig. 1d) will result in a biased estimate of fractal dimension. The simplest solution is to ignore these islands, but this will very likely lead to the exclusion of a greater proportion of large islands (which may also bias the estimate of D). For the probability-density method, increases in the window size (L) result in exclusion of a greater proportion of pixels along the periphery of the map (Fig. 1e). This will result in some bias unless it can be demonstrated that the mapped pattern is isotropic and homogeneous, in which case an edge correction can be implemented (c.f. Ripley 1977).

3. Orientation

In raster-based (pixel) digitizing systems, a line drawn at 45° to the horizontal is approximated as a 'staircase'. This results in an increase in the 'perimeter' of an object relative to its area, resulting in a biased estimate of D when area-perimeter methods are used. Walker and Kenkel (unpublished data) found that estimates of D depended on the orientation of the image during scanning. We recommend that the image be digitized in a number of orientations to quantify this variation. The same will be true for the dividers and cell count methods, and for this reason it is recommended that different orientations (or in the case of the dividers method, dif-

ferent starting positions) be used to determine the distribution of D-values (Sugihara and May 1990).

4. Island size

This problem (which is specific to the area-perimeter method) is discussed by Milne (1991: 224-226). He points out that, while the theoretical range is $1 \leq D \leq 2$, these limits are not reached when small islands (< 30 or so pixels) are used. For very small islands, this bias is considerable. Milne (1991) suggests an empirical correction based on actual limits for a given island size, but further studies are required. A preponderance of small islands indicates that a more detailed map is required.

5. Resolution

The measurement of fractal dimension requires that a fractal structure be 'approximated' in Euclidean space using Euclidean geometry (e.g. map, digitized photograph, spatial series, etc.). Thus the *paradox of fractal dimension measurement:* the estimate of D for a fractal object is based on a Euclidean approximation of that object. This can create problems, since the fine-scale structure of an object is lost during this translation. Map resolution is limited by cartographic approximations, while digital scanner and software limitations determine the resolution of digitized images. The consequences of this paradox are not always appreciated. For the dividers method and related techniques, smaller measuring lengths will tend to underestimate the fractal dimension, for the simple reason that the resolution of the analyzed image is limited. Kent and Wong (1982; see also Goodchild and Mark 1987: 267) found that the fractal dimension of lakeshores was lower at finer spatial scales. They interpreted this as indicating that different processes operate at different scales. However, preliminary studies (Walker and Kenkel, unpublished) have indicated that this change in fractal dimension with scale may be an artifact of the limited resolution of the image (the result is a curvilinear log-log plot). While Kent and Wong (1982) fitted separate linear regression to their data (for small and large scales), careful examination of their log-log plots reveals that the trend is actually curvilinear. Could it be that reported changes in fractal dimension with scale (e.g. Krummel et al. 1987; Metzler and Hastings 1991) are artifactual? Cartensen (1989) examined the problem of estimating landscape fractal dimension from maps (though in a slightly different con-

text), concluding that "... extrapolations from measurements of map data to natural environments is unwise". Given that many workers assume that scale-related changes in fractal dimension are indicative of different operational processes in ecosystems (e.g. Wiens 1989:393), it is imperative that a detailed examination of this problem be undertaken.

6. Extrapolation to different dimensions

Sampling and technological limitations, and a lack of robust methodologies, make the direct measurement of fractal dimension of vegetation and other higher- dimensional images difficult if not impossible. The alternative is to measure D at a lower dimension and extrapolate to higher dimensions. Morse et al. (1985) quantified vegetation complexity by estimating 'edge' D from photographs of branches ($1 \leq D \leq 2$) and extrapolating this to the next highest ('surface') dimension. Quite apart from the fact that this results in rather broad limits, there is some evidence that extrapolation to (or from) higher dimensions is invalid (Roy et al. 1987; Huang and Turcotte 1989). Oldeman (1992) suggests that forests show some similarities to such fractal constructions as the Menzer sponge (Schroeder 1991: 180) and should be modelled as such. Another possibility is to view forest canopies as existing in the range $3 \leq D \leq 4$. Such a 'volume dimension' would be appropriate in examining habitat available to 'flying' organisms (e.g. butterflies and birds, but also pollen). However, models of this type are numerically and conceptually difficult (Voss 1988: 33).

7. Extrapolation to different scales

For natural systems, it is known that fractal dimension may vary with both location and scale (e.g. Roy et al. 1987; Normant and Tricot 1993), implying that extrapolation from one scale to another is unjustified. For example, the semi-variance method determines fractal dimension based on equally-spaced samples (say, pH of soil cores at 5 m intervals). The resulting estimate of D is strictly relevant only for this 5 m scale, unless it is assumed (or can be demonstrated) that soil pH is self- similar over all scales. Similarly, an estimate of lakeshore D based on aerial photographs may not be relevant when determining habitat available to fish fry. The scale range of the measurement device used in determining D should ideally include the scale relevant to the organism being studied.

8. Limits of the sampling unit

Landscape images (e.g. individual Landsat pixels, aerial photographs, etc.) can be thought of as sampling units or 'quadrats'. It is well known that pattern detection and parameter estimation are dependent on the scaling of sampling units (Kenkel et al. 1989). Unfortunately, the landscape ecologist has no control over the scaling (size and shape) or the relative position of landscape images. This is somewhat related to the resolution problem discussed earlier, and leads to another paradox: in estimating the scale-invariant measure D, ecologists are restricted to limited measuring scales. The arbitrary positioning of landscape units (landscape dissection) is also problematic. Consider two adjacent aerial photographs with estimates of $D_1 = 2.02$ and $D_2 = 2.32$ respectively. If a third photo is taken covering one-half of each of photos 1 and 2, we might compute $D_3 = 2.13$. The fractal dimension varies continuously, but the results reflect arbitrary discontinuities.

Concluding remarks

Concepts of scale and scaling are central to the geographical sciences (Lam and Quattrochi 1992), and their importance to ecology is being increasingly recognized (e.g. Wiens 1989; Milne 1992; Juhász-Nagy 1992). To the ecologist, fractal theory is a unifying concept integrating ecosystem concepts of spatial scale, scale-dependence and complexity. Zeide and Gresham (1991) describe as "self-evident" the fractal nature of biological structures and systems. We feel that the greatest challenge facing ecologists lies in translating this "self-evident" concept into experimentally testable ecological hypotheses. This is not to say that estimation of the fractal dimension of natural systems and structures is not important. To give a few examples, estimation is useful for comparative purposes (e.g. landscape complexity of natural vs. anthropogenically-manipulated areas), in generating hypotheses about scaling in nature, and in quantifying the relationship between organism size and perceived niche availability.

Given that fractal theory is such a new science, it is hardly surprising that ecologists are still grappling with the concept and its potential applications to natural systems. We feel that recognition of the fractal geometry of nature has important implications for many ecological processes, including organism dispersal and foraging, the spread of disease, species, habitat and niche diversity, the complexity and heterogeneity of habitats,

species competition and coexistence, evolutionary rates, and ecosystem stability.

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