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REVIEW

Uses and abuses of fractal methodology in ecology

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Abstract

Fractals have found widespread application in a range of scientific fields, including ecology. This rapid growth has produced substantial new insights, but has also spawned confusion and a host of methodological problems. In this paper, we review the value of fractal methods, in particular for applications to spatial ecology, and outline potential pitfalls. Methods for measuring fractals in nature and generating fractal patterns for use in modelling are surveyed. We stress the limitations and the strengths of fractal models. Strictly speaking, no ecological pattern can be truly fractal, but fractal methods may nonetheless provide the most efficient tool available for describing and predicting ecological patterns at multiple scales.

Keywords

Scale, scaling, spatial pattern, multifractals, species distribution.

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USES OF FRACTALS IN ECOLOGY AND OTHER SCIENCES

Introduction

Until recently, ecologists thought about spatial and temporal patterns in terms of the analytical tools available to them – classical Euclidean geometry. Although these tools were recognized as inadequate to understand or even describe spatial and temporal patterns observed in nature (Erickson 1945), there was little consensus as to where the problem lay. This changed with Mandelbrot's famous synthesis and popularization of fractals (Mandelbrot 1983) and the rapid percolation of his ideas through all fields of science. Since then, there has been an explosion of interest in applying fractal methods to various natural phenomena, including: spatial patterns in geomorphology, clouds, surface roughness and other properties of materials, galactic structure, protein structure, climatic variation, earthquakes, fires, blood and lymph networks, cortical area and DNA sequences (reviewed by Feder 1988; Falconer 1990 and Turcotte 1997). Fractal ideas have been applied to virtually every field of science, including ecology.

Although a formal definition tends to be resisted by theorists (Falconer 1990; Cutler 1993), the key property of a fractal is a degree of self-similarity across a range of spatial scales (or resolutions) of observation: simply put, a small piece of the object looks rather like a larger piece or the object as a whole (Feder 1988). Another key feature of fractals is that they usually have non-integer dimensions, as opposed to Euclidean objects which can only have integer dimensions (e.g. 1 for a line, 2 for a plane, 3 for a solid). Indeed, we can describe a fractal object in terms of a fractal dimension D, which measures the object's ability to fill the Euclidean space E in which it is embedded (Mandelbrot 1983). Thus, a set of points distributed on a line has a scale-specific dimension between 0 and 1, whereas a set of points on a plane would have dimensions between 0 and 2. If these dimensions are the same across many (in the limit, all) scales, then we can refer to a single fractal dimension for the set. In a sense, classical Euclidean geometry is based on a set of platonic ideal shapes, to which nature provides at best imperfect representations; whereas fractal geometry attempts to summarize the messy complexity of shapes we see around us (Mandelbrot 1983).

What processes might produce natural fractals?

Many possible processes could produce a given pattern (a familiar concept for ecologists). Nevertheless, we can identify a few ways in which natural fractals might be produced.

(1) Inheritance: a fractal pattern may simply be a reflection of another underlying fractal e.g. a fractal species

distribution pattern may just reflect the fractal distribution of suitable habitat.

(2) Multi-scaled randomness: certain combinations of random processes, operating at different resolutions, generate statistical fractal output patterns (Halley 1996; Halley & Kunin 1999).

(3) Iterated mappings or successive branching rules e.g. plant morphology (Turcotte 1997).

(4) Diffusion-limited aggregation, in which an object grows by accretion of randomly-moving building blocks (Feder 1988).

(5) Power-law dispersal: with colonies established by relatively rare but sometimes long-distance migration e.g. Levy Dust processes (Cole 1995; Harnos *et al.* 2000)

(6) Birth–death processes, in which the birth process is random but the death process spatially aggregated, or vice versa (Shapir *et al.* 2000).

(7) Self-organized criticality produces fractals in a variety of ways (Bak *et al.* 1988).

Many of these processes can be mimicked and used in developing random fractal patterns for use in ecological modelling (see Appendix 3).

Fractals in ecology

The swift acceptance of fractal ideas in ecology came about for several reasons. First, it was realized that many natural objects of interest to ecologists have (as fractals do) relevant features on a variety of different scales. Furthermore, fractals often emerge naturally in ecological models. A third reason for the interest in fractals is that power laws, which are so closely connected with fractals, had already been a major descriptive tool in ecology. Finally, the ecological notion that the variance is more informative than the mean, finds a natural explanation in fractal geometry.

Natural objects are not ideal fractals, but their properties are often sufficiently similar across a wide range of feasible scales that the tools of fractal geometry can be used, providing novel insights where Euclidean tools were found to be insufficient for describing such objects (Hastings & Sugihara 1993; Azovsky 2000; Gisiger 2001). For example, a cone is the appropriate Euclidean model for the canopy of a fir tree, but it is easy to understand that the actual occupied volume of the canopy is much lower than it is for the corresponding Euclidean cone, while the total surface area is much higher. Fractal geometry provides better tools for describing such a complex natural form. Motivated by fractal ideas, there are various models that can mimic natural branching (Chen *et al.* 1994; West 1995; Turcotte 1997; Zamir 2001). Complex forms resembling natural structures, can also be produced by relatively simple Lindenmeyer systems or 'grammars' (Enquist *et al.* 1998). With such fractal generating processes, only a small amount of information is needed to construct very complex forms, and conversely rather small changes of a rule may result in huge changes of the resulting form. Hence, variations in symmetry and other instabilities of the branching architecture during development caused from various stress factors can be measured using fractal tools (Escos *et al.* 1997). West *et al.* (1997) argue that fractal branching networks are almost bound to evolve as a solution to the joint selective pressures to maximize surface areas while minimizing transport distances and infrastructure costs, as seen in the mammalian circulatory or respiratory systems or in water transport in plants. When considering the different foraging strategies of plants or fungi, increasing preference for exploration vs. the utilization of local resources, can be expressed as a decrease in the fractal dimension of the root or mycelial structure (Bolton & Boddy 1993).

Even before the advent of fractal geometry, power laws such as Taylor's (Taylor 1961) and allometric relationships (Peters 1989) were playing an important role in ecological thinking. The arrival of fractal geometry provided a deeper and more satisfying rationale for these relations. For example, the surface-to-volume ratio of Euclidean objects scales with the two-thirds power of radius (fractals, although typically associated with power laws, are nonetheless not strictly necessary to produce them). If we were to observe a slightly greater scaling factor, under a purely Euclidean interpretation, we would be obliged to attribute this to sampling error. In the age of fractal geometry, the case needs more consideration (see West *et al.* 1997): it may indicate a wrinkled, fractal-like, surface, as is the case with many natural surfaces.

At a coarser scale, fractal dimensions have been used extensively as landscape metrics for describing the spatial distribution of species and habitats (Krummel *et al.* 1987; Palmer 1988; Mladenoff *et al.* 1993; Kunin 1998). With fractals, scaling-up and scaling-down becomes 'natural', so provided again that properties are similar or identical at a wide range of feasible scales, self-similarity can be used to infer properties at larger or smaller scales. For example, Kunin (1998) and Kunin *et al.* (2000) attempted to estimate fine scale abundance from coarser scale distributions with some success, although distributions were not strictly fractal over the range of scales considered. Even with departures from power law scaling, extrapolations can be made if the departures are systematic and predictable. Care should be taken, however, to identify any discontinuities in the scaling properties of plant spatial distributions, such as those recorded in field studies (Mladenoff *et al.* 1993; Hartley *et al.* 2004).

If many habitat or species distributions are approximately fractal, then it is reasonable to suppose that many ecological processes are acted out upon a fractal stage. Many recent spatially-explicit studies use fractal landscape models as the arena for ecological processes (Keitt 2000) in order to obtain a more realistic understanding of species distributions and diversity extinction thresholds (Hill & Caswell 1999; With & King 1999b), dispersal (With & Crist 1995), competition (Palmer 1992; Lavorel & Chesson 1995) and foraging (Ritchie 1998). Even if natural landscapes are not precisely fractal (as we will discuss below), such models provide the simplest available means of simulating spatially complex landscapes, and thus serve as the null or 'neutral' habitat model (With & King 1997; Gardner 1999) against which real patterns of environmental heterogeneity may be compared.

Body size is a focal issue in ecology that, in contrast to fractals, introduces a single preferred scale of reference for any organism (Azovsky 2000). However, the interaction of body size with a fractal environment may have major consequences for community structure. This realization has been highly productive in explaining the observed distribution of body sizes in a community (Shorrocks *et al.* 1991) and the relation of species richness with habitat properties (Haslett 1994). For example, in fractal habitats there is disproportionately more usable space for smaller animals (Shorrocks *et al.* 1991). Experimental testing of the relation between fractal properties of the habitat and community structure (Gunnarsson 1992, McIntyre & Wiens 1999) can provide new insights in the understanding of species–habitat interactions.

It is sometimes said that in ecology the variance is more informative than the mean (Benedetti-Cecchi 2003). This seems to contradict the almost commonsense prerequisite that for any kind of dynamic understanding, we must have 'stationarity' (that is, a well-defined mean and variance, independent of the scale of observation). Thus, the analyses of Pimm and others (Pimm & Redfearn 1988; Inchausti & Halley 2002) showing that the variance of population time series increases with observation time, apparently without limit, might seem pathological. However, as with the tendency for the length of a coastline to grow with the resolution of the measurement (Mandelbrot 1983), fractal geometry elegantly frames such behaviour in the context of multi-scale variability. Stochastic processes defined in terms of fractal geometry, $1/f$ noise models (Halley 1996) or Lévy flight models (Cole 1995) can thus describe much ecological variability. The $1/f$ noise process has also been used in simulation models of extinction rates (Halley & Kunin 1999) and in laboratory experiments for testing population-dynamic hypotheses (Cohen *et al.* 1998).

Fractal objects or behaviour often emerge in ecological models even if the models are not explicitly designed as such (Pascual *et al.* 2002). For example, fractal geometry has proved essential to an understanding of the dynamics of chaotic population models (Schroeder 1991; Gisiger 2001); for random walk models (Cole 1995; Harnos *et al.* 2000) and for a number of spatial epidemic models involving self-organized criticality (Rhodes & Anderson 1996). Fractals also appear naturally in simulations of the macroevolutionary patterns of species originations and extinctions in the fossil record (Newman & Palmer 1999; Plotnick & Sepkoski 2001), and in models of multi-resource competition (Huisman & Weissing 2001). Finally, a fractal perspective has rekindled fresh interest and insights into some familiar ecological concepts, such as species–area relationships (Harte *et al.* 1999; Azovsky 2000; Lennon *et al.* 2002) and species diversity indices (Borda-de-Água *et al.* 2002).

DIFFICULTIES IN APPLYING FRACTAL METHODS

Too few scales

Because of the highly productive infusion of fractal ideas into ecology, and also because it has become fashionable, there has been a natural tendency to see 'fractals, fractals, everywhere', even in situations where the evidence is not strong. For example, before fractality can be affirmed, a power-law relationship between scale and occupancy should hold over a reasonable number of scales (see 'scale' in Glossary, Appendix 1). Many of the power laws 'observed' in the literature span less than two orders of magnitude of scale (i.e. ratio of maximum scale to minimum scale is less than 100), often without good correlation. This is clearly problematic if the aim is to show the existence of self-similar mechanisms. Figure 1 illustrates some of the many observations of fractal dimension. As can be seen, in some cases the domain of 'scaling' is very short indeed.

The problem of observing too few scales is not unique to ecology; Hamburger *et al.* (1996) pointed out, in the physical sciences, that the largest numbers of observations of 'fractality' are for small ranges. This raises problems of incorrect estimation of dimension or even 'apparent fractality' (see below). Many recent papers (e.g. Berntson & Stoll 1997) emphasize the fact that fractal dimensions of real-world objects can only apply over a finite range of scales. It is worth noting that actual observations of fractal relationships spanning more than three orders of magnitude are very rare, in any branch of science. Indeed, two of the largest-ranged power-laws: the frequency of meteor collisions (Schroeder 1991) and Sayles and Thomas' power spectrum of generalized surface texture (Sayles & Thomas 1978; Feder 1988), both exhibit exponents close to 2.0, a value which often arises in *non-fractal* systems. Lovejoy's observation of $D = 1.35$, for the area–perimeter relationship of clouds and rain patches, is sustained over three and a half orders of

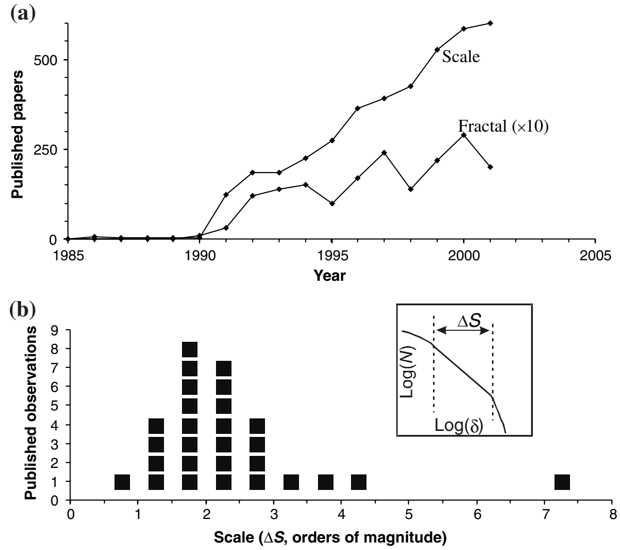

Figure 1 (a) Papers on fractals published in ecological journals. The number of papers that contain the words 'fractal* and ecolog*', or 'scale* and ecolog*', per year from the Web of Science, 1983–2001. (b) Range of scales (i.e. range of powers of 10 of diameter; see 'scale' in Glossary) used in ecological publications. Note that the large number of scales observed in Kunin (1998) used successive sampling and only applies for a single species. Inset figure: The range of scales, ΔS, should be the range of values of log(δ) for which the relationship between log[N(δ)] and log(δ) is linear.

magnitude and remains one of the best cases documented (Lovejoy 1982; Schroeder 1991).

Small as the total range often is, the *usable* range of scales is usually even smaller, as the end-points must often be excluded from the analysis (see below). Thus, if we are to test the true value of fractal methods in ecology, we need to start collecting more data over a wider range of scales. One of the most promising avenues of progress is remote sensing, which will provide ecologists with increasingly fine-scale data over vast areas, greatly increasing the range of scales available for analysis. For field-collected data, however, there is clearly a limit to how much we can do this, given that every order of magnitude scale increase (in finer resolution or broader extent) requires a 10-fold to a 1000-fold increase in the data array and thus in effort and expense. Obviously, some kind of sampling approach is needed. Cluster sampling (Thompson 1992), using successively smaller subsets of the grid as we measure on successively finer scales, has been used to look at plant species distributions over six to seven orders of magnitude in scale (Kunin 1998; Hartley *et al.* 2004). A number of alternative sampling approaches, for example, using transects and Cantor grids, have been used explicitly for the purpose of detecting fractal distributions (Kallimanis *et al.* 2002). Another promising statistical method, originating in geostatistics, is kriging (Cressie 1991). Although well-established techniques like cluster sampling and kriging have yet to be fully integrated with the theory of fractal objects, they have rich potential to allow us to increase the number of scales of observation at acceptable cost (for recent synthesis see Cheng 1999a,b and Keitt 2000).

Effects of abundance or occupancy on *D*

Some fractal analyses (in particular, the most widely used method: box counting, see Appendix 2) are very sensitive to the amount of area occupied in a grid (at the finest scale) and the pattern of its distribution. In the limit, of course, this is inevitable: a fully occupied grid becomes a solid rectangle with $D = 2$, whereas a single record will behave as a point with $D = 0$. Indeed, sometimes knowing the number of grid cells occupied at a given scale is sufficient to calculate the box-counting dimension (see Fig. 2a).

In analysing real data, however, the relationship between occupancy and D is somewhat less constrained, at least over a range of scales. Such 'quasi-fractals' (see Glossary) can behave in a fractal fashion with any D until reaching one of two outer constraints: either saturating the entire grid (Fig. 3b) or being reduced to a single point (Fig 3c; see also Appendix 2 in Lennon *et al.* 2002). Analyses of such patterns should ignore all coarser scales after approaching either of these limits (see below); failure to do so will result in estimates of D that are greatly influenced by the density of occupancy, but almost completely insensitive to the actual spatial pattern it displays.

One rough-and-ready way to derive a useful measure of pattern from box-counting analyses is to attempt to factor out the effects of abundance; to test whether the case in question is more or less space-filling than would be *expected for its level of occupancy*. This might be performed by comparing the observed D to those of other cases (e.g. species) of similar abundance, or to a D measured from a random pattern with the same level of coverage. Perhaps the best solution, however, is to estimate higher-order fractal dimensions (e.g. information or correlation dimensions, Appendix 2) that examine the *relative density* of points and are thus less sensitive to saturation than presence–absence box-counting (Cutler 1993, pp 51, 59–60).

Minimum and maximum scales

The occupancy problems discussed above constrain the maximum scale for which fractal analyses are appropriate, given the box-counting framework. The fraction of cells occupied tends to increase as cells are grouped together at coarser scales, and the whole arena may become filled;

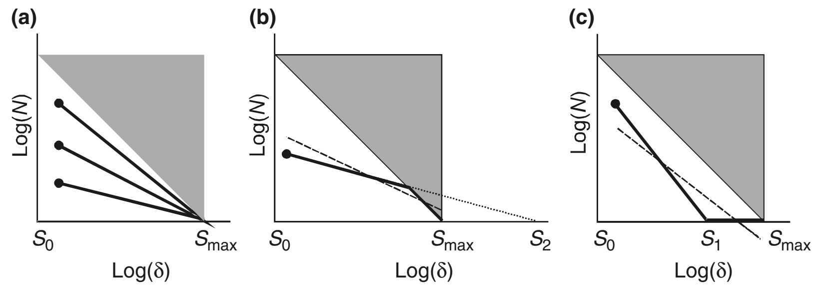

Figure 2 Effects of grid occupancy on box-counting fractals. Patterns occupying a given area at fine scale may display a range of fractal dimensions (dashed lines). (a) For an ideal fractal object in a well-chosen arena, the scale–area curve must pass directly through the lower right-hand corner of the graph (0,0), filling the grid just as the analysis reaches its coarsest scale (Smax = 0). For such a fractal, the number of cells occupied at the finest scale, S_0, determines the slope of the line, and thus the fractal dimension. Real ecological data, for which the object or distribution has not affected the choice of arena, do not necessarily behave this way. (b) For example, log N may fall slowly with cell size δ (a low D) until the entire grid is saturated (cross-hatched area) and continuation of this trajectory (dotted line) is not possible, after which point they must exhibit $D = 2$. (c) Alternatively log N may fall steeply with δ (high D) until it hits the lower constraint (occupying a single grid point), after which point $D = 0$; here the arena is 'too big'. If one analysed these patterns over the full range of scales (up to S_{max}) the two patterns shown would produce identical slopes (dashed lines); to capture the differences, analyses need to be restricted to the range of scales displaying meaningful pattern (>1 occupied cell, but less than complete saturation). Note that even such 'quasi-fractals' could be considered true fractals had a different maximum scale (S_1 or S_2) been chosen for the analysis.

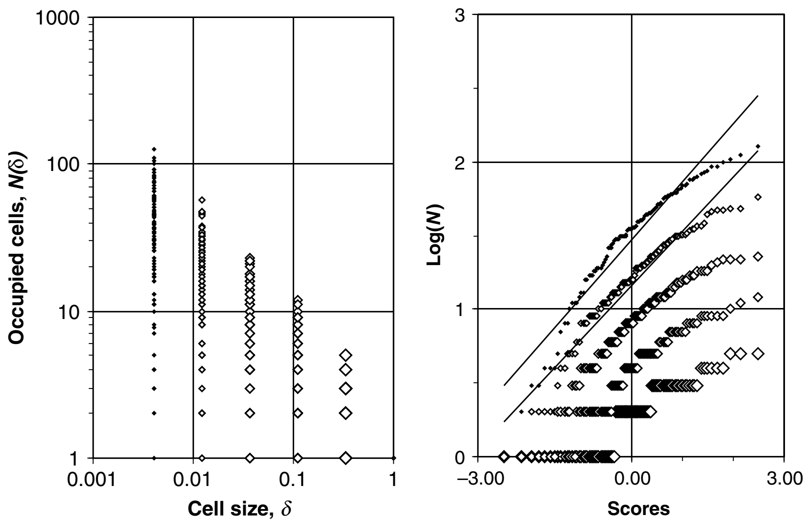

Figure 3 (a) Regression procedure for estimating fractal dimension. We carried out 100 realizations of a random fractal and in each case carried out box-counting (following Kallimanis *et al.* 2002). (a) Distribution of counts as a function of cell size (width of box), for five cell sizes. As is evident from the diagram, this procedure does not preserve the assumptions required to use regression in a statistical way. Notice how the scatter is non-uniform, and will break the constant–variance requirement. (b) Normal-scores plots for the distribution at each of the values of cell size. Curvature in this plot implies a departure from normality.

beyond that scale, the measured D will be 2 of necessity (Fig 2b). Even before complete grid saturation, progressively larger sections of the area will tend to be filled in, resulting in a gradual rise in the estimated D value. Conversely, if the occupied portion of the arena is relatively small, then at coarse scales of analysis, the entire occupied area may fit into a single grid square, so that the pattern will behave as a single point ($D = 0$) at all still coarser scales (Fig 2c). Taken together, these two processes can produce a characteristic 'wiggle' at coarse scales, with D estimates at first rising steeply and then dropping precipitously. Whilst this might be considered a realistic description of the pattern's scaling properties, if the object in question is a sample from a wider universe of points (i.e. when data is limited in spatial extent because of sampling constraints) then this behaviour should be considered an artefact of the particular subsample being examined. In short, it is always difficult to infer information about patterns at scales that approach the extent of the study area.

Different methodological issues arise at very fine scales of analysis and impose a minimum scale. At the extreme, a very fine-scale grid will be found such that no box contains more than one data point – an effect known as depletion. At all scales finer than this, a point data set will scale with a dimension of zero. Once again, whether this is considered to be an artefact or not will depend on whether the investigator believes that a single point is a reasonable description of the object of study at that scale. For example, if the object under study is the spatial distribution of a tree species, at a 1-km scale, it is reasonable to represent a tree as a point, but at a 1-m scale it is best considered as a space-filling object (Kunin *et al.* 2000). In this latter case, it is perfectly appropriate to analyse patterns at resolutions much finer than the size of an individual, as it is now the distribution of biomass, rather than of individuals *per se*, which is of interest.

To avoid artefacts of this nature, it is often recommended that analysis should be restricted within a maximum and a minimum scale. For a given set of points there is a minimum and a maximum inter-point distance. The maximum inter-point distance is usually referred to as the diameter of the set. The recommendation is that the maximum scale (coarsest resolution) should be (much) less than half the set's diameter, and the minimum scale (finest resolution) grid should be (much) greater than the minimum inter-point separation.

Problems with linear regression

Many of the methods used to estimate the fractal dimensions of objects rely on linear regression (Fig 3; also see Appendix 2). It would be very nice to be able to assign some confidence limits to such estimates. Unfortunately, when analysing the results of box-counting, or most other grid-based schemes, the linear regression may produce a decent estimate of the slope of the relationship (but see below), and thus of the fractal dimension, but the associated statistics (*p*-values and confidence intervals) do not apply (Fig. 3). This is because points are not independent – the *same* object is being analysed at multiple scales. Moreover, deviations are typically neither constant in variance nor Gaussian in distribution.

A second problem is that the slope (and thus the D value) provided by a linear regression analysis may be excessively low, when the scatter is large. The standard 'model I' linear regression supported by most statistics packages makes a sometimes inappropriate distinction between 'independent' and 'dependent' variables, and generally fits lines rather 'flatter' than the cloud of data; in many cases a model II regression would provide a better estimate. Further problems with the approach of box-counting and regression have been discussed by Cutler (1991, 1993) and Peitgen *et al.* (1992).

Even with an unbiased slope estimate and a confidence interval around it, we are left with one thorny unresolved problem: how is one to decide whether the observed pattern is fractal at all? Any pattern, fractal or not, will give a gratifyingly high R^2 value (to an ecologist) if analysed by box-counting and subsequent linear regression. Logarithmic axes tend to disguise irregularities that might seem discouragingly large on linear scales ('Baker's lemma': even an elephant appears linear if plotted on log–log axes!). Moreover, the fact that the regression fits a line to the data does not make the trend linear. In a fractal, the value of D should be the same at all scales (or at least, at all scales within some finite range for real-world objects). If we measure the attributes of some object at multiple scales, we can plot those values as a function of scale, and the slopes of the line segments they form will provide multiple, scale-specific, measures of D (e.g. Hartley *et al.* 2004). Those D values are bound to differ somewhat, but how do we distinguish a bit of estimation noise from systematic departure from fractality? Surprisingly little work has been performed on this potentially important issue.

The simplest remedy, if the problem is simply the absence of an error estimate because of correlation between points on the regression slope, is to estimate the scale-specific slopes of the curve (and thus fractal dimension) directly, e.g. by examining the number of occupied subcells within a sample of occupied cells at each scale, as these slope values *are* statistically independent between scales. A regression on these scale-specific slope values could then be used to test whether the fractal dimension shifts systematically across scales. Another straightforward approach is to use Monte-Carlo simulation to find confidence bounds on dimension estimations (e.g. Kallimanis *et al.* 2002). Also a Monte Carlo approach may be applied to test how well the assumption of a scale-independent fractal dimension fits an observed data set (Green *et al.* 2003). A number of more technical solutions have also been proposed, which arrive at schemes radically different to box counting. These include nearest neighbour approaches (Guckenheimer 1984; Cutler 1991) – which estimate higher-order Rényi dimensions, Hill estimators (Mikosch & Wang 1995) and various maximum-likelihood schemes (e.g. Takens 1985). These elegant methods often make use of the knowledge of the process generating the pattern. Such features, and the fairly technical nature of the methods themselves, means that they should not be used in an 'off the shelf' way as box-counting can. Whether an apparent straight line on logarithmic axes really suggests a fractal or not is obviously a difficult and fundamental question. However, the fractal model, like the straight line in linear regression, may be seen as a simplifying frame that helps us understand certain features of reality, without necessarily having to be strictly 'true' itself.

Is the fractal an 'area' or a border?

In our experience, one of the most common misunderstandings of fractal methods in ecology is confusion between the fractal properties of an object *per se* and those of its edge (referred to here as 'bulk' and 'boundary' fractals). Many objects that might seem 'fractal' are not really so. For example, the land *area* of an island or the *area* covered by a particular vegetation type is, at the fine-scale limit, strictly two-dimensional, but the *boundaries* of the pattern may well be fractal. These boundaries may be of considerable ecological interest if one is modelling rates of expansion or contraction or the flow of materials between adjoining areas, but for other issues (e.g. total area) one may treat the patch as essentially Euclidean. Indeed, mathematically speaking, *any object on a map in which we can clearly draw a disc, however small, must be two-dimensional*, however 'fractal' other bits of it may appear.

This distinction, clear in theory, becomes confused in practice. Although we *should* find a box-dimension of two because of the area enclosed by a coastline, this is only exact in the limit. Convergence may be slow, especially for areas with heavily convoluted coastlines where the behaviour of the coastline may dominate fractal dimension estimation until the grid size is very fine indeed. Figure 4 shows how the box-counting procedure is affected by the boundary for the cases of maps of Ireland and Greece. One would expect that for coarse scales, the observed dimension of the bulk areas will be much less than 2.0, because of the effect of the boundary. However, as the scale of measurement becomes finer, the bulk dimension should converge to 2.0. This behaviour is observed as expected for Ireland, and for mainland Greece, which have reasonably fractal coastlines and well-defined interiors, although for Greece, the convergence is somewhat slower because of the more convoluted coastline. However, this behaviour for bulk dimension is shattered entirely for the latter when Greece's island archipelago is included.

In ecology, there remains considerable work to be performed before we can sort out the confusion between boundary and bulk fractals. This is not simply an issue of erroneous usage. For example, the same object may show different kinds of fractal properties when considered in different ways. This raises interesting questions of interpretation. For example, a forest may be defined by the area covered by the canopy of its leaves or by the set of the (point) positions of trees in space. Which one is chosen should depend on the question of interest (in the forest example: total photosynthetic area or tree density patterns), and will impose different constraints on the sort of dimensions that can be measured and on the value recorded (see Appendix 2). Meanwhile, it is important for researchers to be conscious of the distinctions between different types of fractals, and whether the region in which they are interested is a bulk fractal or an area with a fractal boundary, so that they can use the right tool for the job. When dealing with 'fractal' objects in practice, great care should be taken regarding the boundary and how it affects the bulk object: we may be very distant from the mathematical limit. Just how far depends on the specifics of the situation. As pointed out by Mandelbrot

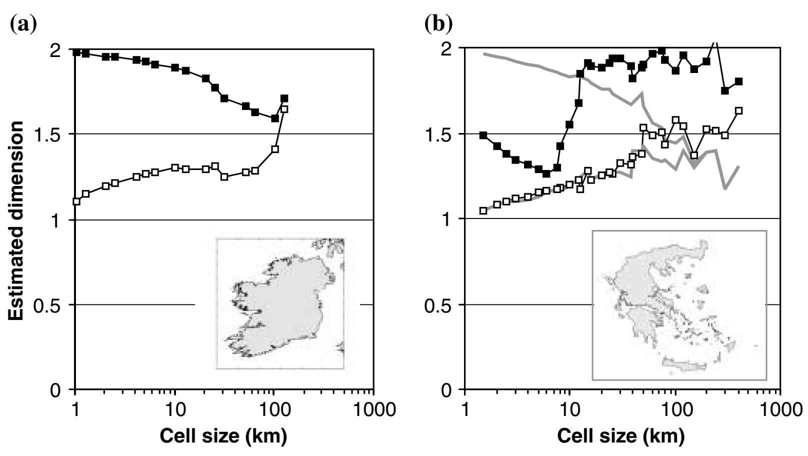

Figure 4 Boundary (open squares) and bulk (closed squares) box-counting on maps of Ireland and (b) the corresponding measurements for Greece. The upper and lower thick grey lines correspond respectively to bulk and boundary dimensions for mainland Greece (i.e. excluding all islands). Numbers of boxes were calculated for scales (cell sizes) from 260 m to 511 km for Ireland and 500 m to 1200 km for Greece, successive scales increased in ratios between 1.2 and 2.0. The dimension was estimated by finding the regression slope (See Appendix 2) over five consecutive scales and was associated with the median scale of five.

(1997) (pp. 17–22), fractal geometry cannot be 'automated' like ANOVA or regression: one must always 'look at the picture'.

Apparent fractality (measuring fractal dimensions of non-fractal objects)

Sometimes there is *no* correct fractal model. Apparent fractality is the term given to the erroneous detection of scaling; here 'fractal' behaviour is entirely an artefact and not caused by self-similarity at all (Hamburger *et al.* 1996). Consider, for example, a large number of small discs scattered randomly about a (two-dimensional) landscape (Fig. 5a). The discs themselves, of course, are 2-dimensional, and the fractal dimension of a random point pattern on a plane is also 2, so there is nothing intrinsically fractal in the picture. Hamburger *et al.* (1996), however, calculated explicitly the number of occupied cells in a covering grid as a function of the grid's mesh size, illustrated in Fig. 5b. Notice that if the cell size is very large (greater than the typical distance between nearest discs) then almost every cell is occupied, so the dimension is effectively two. Conversely, if the cell size is very small (much smaller than the diameter of discs) every disc contains many cells, so the relative positioning of the discs becomes irrelevant; once again the dimension is two. However, between these two scales, there is an inflexion so that scaling may appear uniform in this region, suggesting a fractal object. A dimension ($D < 2$) may appear to emerge from a 'good' regression over two orders of magnitude or more in scale (Hamburger *et al.* 1996). This fallacious detection illustrates the dangers of inferring a fundamental self-similarity on the basis of sets spanning only two orders of magnitude.

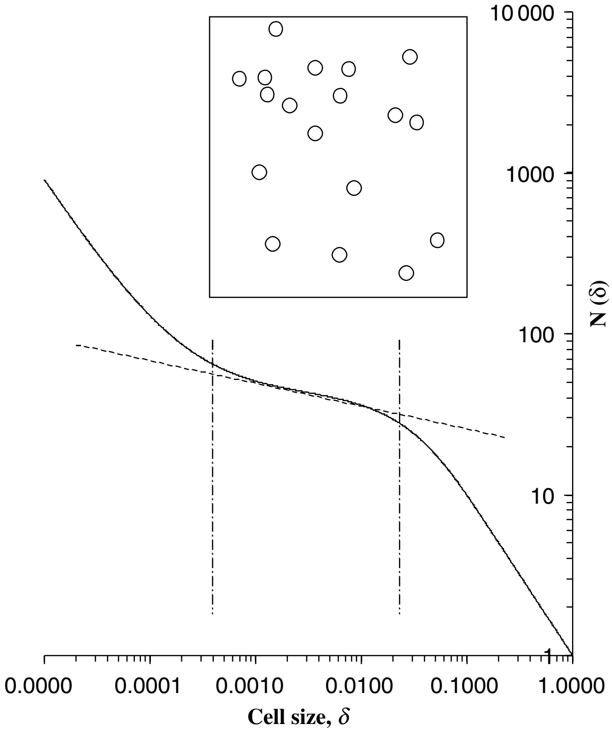

Figure 5 Apparent fractality. An object which consists of a random sprinkling of discs on a plane (inset) may exhibit apparently fractal behaviour over up to two orders of magnitude. In this case, the box dimension of an object consisting of size of 100 discs of radius 10^{-4} randomly placed within the unit square exhibits an almost linear scaling between cell size $\delta = 0.0004$ and $\delta = 0.026$. This, however, is only an artefact of the counting procedure, not a result of self-similarity.

In one sense there is no solution to this problem, as mentioned earlier ('Is it fractal? How can I be sure?'). However as before, if the phenomenon on significantly larger or smaller scales shows a very different dimension value, then this raises questions about the possibility of apparent fractality. One of the most important lessons is that a scaling relationship sustained over two orders of magnitude or less is not a strong evidence of genuine fractality.

The union, sum and intersection of fractal objects

In strict mathematical terms, if two objects (fractal or otherwise) are combined to produce a single composite object (in math-speak: the union of the two), the composite object takes the dimension of whichever has the greater dimension (Falconer 1990). For example, the set composed of a disc ($D = 2$) and a Sierpinski triangle ($D = 1.585$) has an overall dimension of two. However, as with many aspects of fractal geometry, this principle, while true in the limit, may not be fully apparent if the object is analysed over a finite range of scales (as it is bound to be in practice).

Likewise, if there is an uncorrelated measurement error in the observations, then this is equivalent to an addition or intersection of the target object with another object of dimension 2 (as Poisson noise has $D = 2$). Figure 6 shows how this can distort the calculation of dimension. In this figure, we show the presence–absence box-counting fractal dimension calculated over 100 realizations for grids of sizes 2048×2048 and 256×256, given a steady level of error at the level of each pixel.

It is worth noting two points. First, contrary to intuition, here the grid with the *smaller* extent is the better estimator of dimension. This is because the higher accuracy of a larger grid is not worth the greater danger of box-counting a few 'dud' pixels. Second, a dangerous mirage is observed at fractal dimensions less than 1.2. Here, an apparent dimension of 1.35 is observed with a remarkable degree of consistency. This problem is another case of apparent

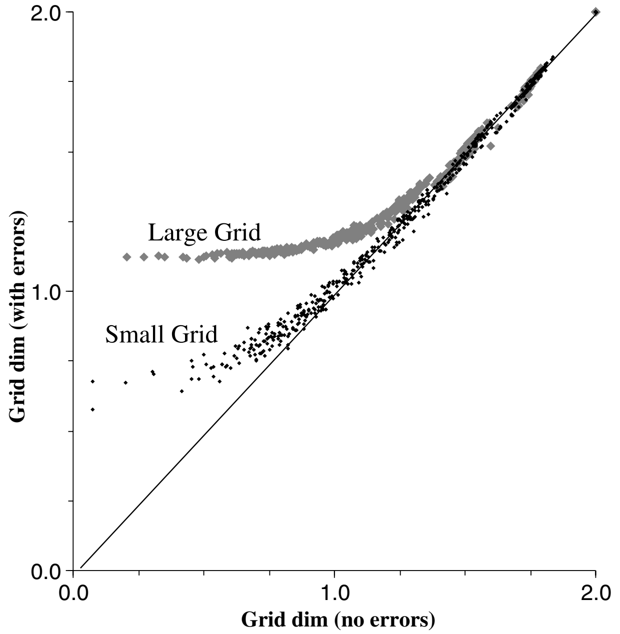

Figure 6 The effect of Poisson errors on dimension estimation can be very serious in least-squares based schemes. This figure shows the box-counting dimension, with errors, plotted as a function of that without errors. The error-free values are the results calculating the box-counting dimension of a percolation fractal. In the presence of errors, the dimension of the same is calculated, but first each cell of the grid is allowed to flip state, with a probability 0.00032. This is repeated for a range of theoretical values between 0 and 2 (see Appendix 3), with 100 replicates for each value. The grey symbols refer to the large 2048 × 2048 grid while the black refers to the smaller 256 × 256 grid. When the fractal has a lower dimension, error dominates the box-counting and estimates of dimension are pulled towards $D = 2$, especially for the larger grid.

fractality, also observed for information and correlation dimensions.

Another potential confusion occurs when different fractal objects are summed (note the distinction: the union of two binary patterns, discussed above, is another binary pattern of zeros and ones, but their sum, discussed here, can include higher positive integers as well – cells with values of two or more). Thus, for example, one might be interested in combining multiple (fractal) species distributions into a species–area curve. The naïve intuition might be that the sum of a pile of fractal patterns ought to be fractal, but it turns out that if fractal distributions with different D values are summed, the resulting species–area relationship does not follow a power law at all (Lennon *et al.* 2002). Indeed, if species–area curves do follow power laws (as they often do), and if species differ in their scaling properties (which they almost invariably do), it implies that at least one of the species distributions *must* not be fractal.

Just as the union and the sum of fractals may be of interest, so the intersection of fractal (or other) patterns may be of interest and potential benefit in some cases, in particular when designing sampling programmes to estimate the fractal properties of large objects (e.g. species distributions, Kallimanis *et al.* 2002). Here one examines presences and absences of a species in sampled cells – effectively the intersection of the pattern of interest and the sampling pattern employed (e.g. a linear transect with $D = 1$). In general, the dimension of the intersection of two fractal objects on a plane is the $D_1 + D_2 - 2$ (where D_1 and D_2 are the dimensions of the two objects, and 2 is the dimension of the plane). Although this relationship is exactly true only in the limit, in practice we can use it to establish the range of possible values that can be measured using any such sample, and to convert a measured fractal dimension within the sample into an estimate of the dimension of the whole pattern (Kallimanis *et al.* 2002).

Too many definitions

Another problem is widespread confusion over fractal definitions and terms. The founder of fractals, Benoit Mandelbrot, advised his colleagues not to define the term 'fractal' (or some of its related terms) too precisely (Mandelbrot 1983). Perhaps it is because of this that certain concepts such as multi-fractality and lacunarity have suffered from large numbers of potentially conflicting and generally confusing definitions. Sometimes these variant definitions are exactly or nearly equivalent, but sometimes they appear completely unrelated. The situation is not helped by the lack of consistent authoritative usage; Mandelbrot himself recognized that there are many ways for describing and quantifying the 'lacunarity' of fractals (Mandelbrot 1983). We have made a modest attempt to clear up some of the confusion (or at least to make it explicit) in our glossary (Appendix 1).

Lacunarity

The fractal dimension describes only one aspect of the complex geometry of an object across scales; for example, both a solid object and Poisson point pattern have $D = 2$, despite the extreme differences between them in the 'clumpiness' of the pattern. There is a widely felt need for some other index to reflect other aspects of pattern, and many have latched on to the concept of *lacunarity* to fill this perceived gap.

In general terms, however, lacunarity is an index of texture or heterogeneity. Highly lacunar objects possess large gaps or low-density holes, while low-lacunarity objects appear homogeneous. Thus, for example, in observations of

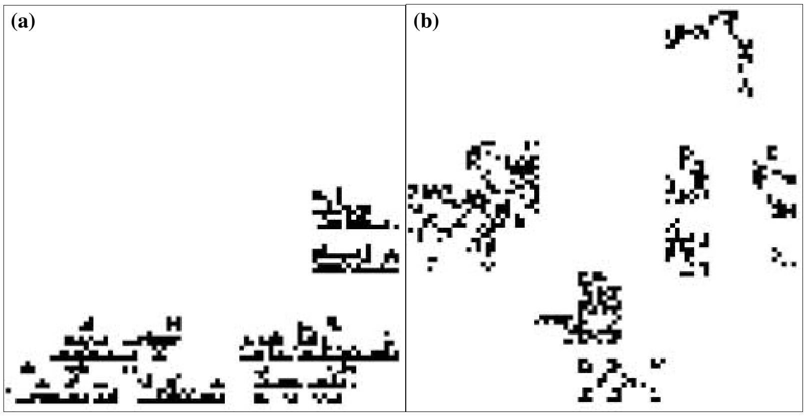

Figure 7 Lacunarity is a measure of the texture of a fractal object. Both objects shown here are stochastic fractals with the same fractal dimension. However, their texture differs. In object (a) the cells in the lower part have a higher probability to be occupied in each iteration, while in object (b) all cells have equal probability to be occupied.

vegetation cover using quadrats, lacunarity is low if we find very similar levels of cover in every quadrat (Plotnick *et al.* 1993). More precise definition of lacunarity has been problematic. Mandelbrot, for example, provides several vague, yet different, 'definitions' of lacunarity (Mandelbrot 1983). In addition to the many verbal definitions, at least six different algorithms have been proposed for measuring lacunarity (Allain & Cloitre 1991; Obert 1993). Four of these methods have been compared by Obert (1993), who finds surprisingly little agreement between them. Currently, the most widely accepted method is the gliding box algorithm of Allain & Cloitre (1991); for further description and applications relevant to ecology see Plotnick *et al.* (1993) and Cheng (1999a). In this method, boxes of size s are moved systematically across the pattern, and lacunarity (Λ) is measured by examining the number of points captured within the box as it 'glides' along: $\Lambda = \text{variance}/\text{mean}^2 + 1 = CV^2 + 1$ (Allain & Cloitre 1991). Objects will generally have different lacunarities depending on the size of the observation window; i.e. lacunarity is scale specific. Interestingly, two objects can have the same box-counting fractal dimension, but at any particular scale their appearance and lacunarity may differ (Fig. 7). This is because lacunarity is primarily a function of the first three Rényii dimensions (see Appendix 1 & 2): the box-counting, information and correlation dimensions (Cheng 1999b). If the object is a homogeneous fractal (i.e. all Rényii dimensions are equal) then a plot of log (lacunarity) vs. log(scale) will produce a straight line with slope equal to $D - E$ (Allain & Cloitre 1991).

In line with the growing popularity of fractal analyses, lacunarity is increasingly being used in ecology as an alternative measure of spatial pattern, where it has been shown to correlate with changes in a variety of ecological processes (e.g. With & King 1999a). However, there is presently little theory to link this pattern index mechanistically with generating processes. Further work in this direction may be rewarding.

Multifractals

A second term that suffers from multiple definitions is 'multifractal' (see glossary). While several different definitions have been bandied about the literature, it turns out that they are more similar in practice than they appear on paper. Whereas fractal analysis looks at the geometry of a *pattern* (e.g. presence/absence), multifractal analysis (MFA) looks at the arrangement of *quantities* (e.g. population density, proportions etc.). Hence, a pattern may be subjected to MFA if we consider, for example, the *density* of its points. MFA describes an object as the sum of many fractal subsets; the sets of points with each particular value of density forms its own fractal pattern. Thus, any given object may have an entire spectrum of fractal dimensions. This spectrum can be calculated from the Rényi dimensions (see glossary) and vice versa. An interesting ecological example is by Borda-de-Água *et al.* (2002) who examined the multifractal dimensions of how the abundances (of individuals) are partitioned across species and across space. Other applications have been in the description of plankton distributions (Pascual *et al.* 1995) and the analysis of extinction and speciation rates (Plotnick & Sepkoski 2001). A full description of multifractals is beyond the scope of this paper, but put simply, there exists a family of fractal dimensions (the Rényi dimensions) which differ in the relative weighting they place on high vs. low density areas of the object. (Box-counting treats all non-zero densities as equivalent). The interested reader is referred to the discussion of information and correlation dimensions (see Appendix 1 & 2) and a fuller discussion in Pascual *et al.* (1995); Cheng (1999a,b); Harte (2001) and Borda-de-Água *et al.* (2002). Multifractals should not be confused with 'mixed fractals' (*sensu* Russ 1994) in which the slope of a log–log plot changes abruptly at some particular scale.

There is reason to think that multifractal analysis may prove increasingly useful to ecologists in time, although relatively few applications have appeared to date in the ecological literature. However, most of the properties of multifractal analysis have only been demonstrated 'at the limit', at infinitesimal scales (as indeed is true with fractals), and little is known about their robustness for use in analysing real-world objects over limited ranges of scales. Just as the application of fractal methods to ecological and other data have thrown up quite a few unexpected wrinkles along with the new opportunities, so it is likely that a similar number of pitfalls await those venturing into this new realm.

The road behind us, and the road ahead

There has been a gradual shift through time in the way ecologists have dealt with spatial and temporal scale. For a long time, the dominant approach (still common) was to ignore scale completely. Patterns in nature were analysed at a single, arbitrary scale, chosen for the convenience of the researcher. Almost all studies of spatial aggregation that rely on mean/variance ratios, or negative binomial *k*'s, fall into this category. The problem, of course, is that the scale chosen for the study may be convenient for the researcher, but may not be ideal for measuring the pattern being considered, or the process generating it. As a consequence, a more sophisticated approach was developed, in which researchers would attempt to identify the 'correct' scale for studying the focal system. Various methods have been developed to choose optimal scales (reviewed in Dale 1998), and have been applied with varying degrees of success. Nature, however, is difficult to pin down to a particular scale, however well chosen. Some researchers began appreciating that processes of more than one scale may impinge on a population. The response was to develop hierarchical approaches, which modelled nature at two or more nested scales of analysis (e.g. Allen & Starr 1982; O'Neill *et al.* 1992). Later still, many of the fractal methods reviewed above have become increasingly popular. These methods search for constant properties, which can be used to describe a pattern or process across a wide range of (or indeed, all) scales.

Both hierarchical and fractal approaches take scale seriously, but adopt almost opposite approaches. Hierarchical approaches assume each process to act on a single scale (or narrow range of scales), and thus allow the properties of an object to be independent at different scales; whereas fractal models assume the properties of the object to be similar or identical across the full range of ecologically relevant scales. Between these two poles there is a wide spectrum of possibilities, the properties either shifting gradually across scale space (cross-scale negative binomial, He & Gaston 2000) or changing abruptly at specific scales (hierarchical fractals) systematically or otherwise (Russ 1994; Hartley *et al.* 2004).

The subject of scale in ecology is inescapable. Nature shows pattern at all scales: species ranges are subdivided, habitats are patchy, populations occupy only parts of the available habitat, and individuals are clumped within local populations. Most processes of interest to ecologists act across ranges of scales, but are also scale-specific (that is, their strength varies across scales). Indeed, many quantities of interest to ecologists, including species diversity and population density cannot even be defined without reference to a specific scale or range of scales (Wiens 1989). We need to develop methods to deal with scale explicitly, if we are to progress. Fractal models are certainly attractive as potential tools in that effort.

But just as it is clear that scale cannot be ignored, it is equally clear that few if any ecological phenomena are truly fractal. Mathematical fractals have identical properties at all scales. If, for example, the distributions of plants (treated here as space-filling objects) were truly fractal, we should expect the global distribution patterns of each species population to resemble the species' leaf shape or growth form; species with entire leaves or rosette growth would form dense clusters, whilst creepers or plants with finely cut foliage would form spidery populations and geographical distributions as well. Clearly this is absurd: different processes are responsible for the growth of leaves and the growth of populations or biogeographic ranges. Any attempt to apply fractal analyses to ecological data must be limited to a finite range of scales. Even within that range, scaling patterns may shift gradually or abruptly (that has certainly been our experience in our own data: Kunin 1998; Kunin & Lennon 2003; Hartley *et al.* 2004).

Why then use fractals at all, if ecological phenomena are not truly fractal? The reason is that fractals may still be as close as simple models can get to the messy multi-scale nature of natural phenomena. If real distributions are not exactly fractal, they are certainly not Euclidean and so it may be much better to use fractal assumptions than to assume continuous expanses of uniform space. Fractals thus have an important role to play in ecological research, both as a first step towards dealing with scale-dependence and as the null model against which to compare more complex natural patterns.

There are a number of difficulties involved in the application of fractals to ecological data; most of this paper is devoted to reviewing them. Because this is a relatively young science, and because of their very nature, fractal models should not be fitted mindlessly. In fitting fractal models, users should think about what property of their data they are interested in, what sort of fractal dimension to measure (Appendix 1), and which method of estimation to use (Appendix 2). Potential users should also be wary of drawing conclusions from too narrow a range of scales, for fear of being fooled by apparent fractality. If we are to test the true value of fractal methods in ecology, there is no getting away from the fact that we need to collect larger sets of data, on a wider scale. Perhaps, as fine-scale remote sensing data become more widely available and as various fractal sampling techniques and statistics are developed, we will have a real opportunity to see how these tools work on the 'open road'. In the meantime, most of our data sets are hardly big enough to get us out of the driveway.

Fractals are arguably the simplest method we have for describing an object across a range of scales. As such they provide the best null model against which to judge the real behaviour of multi-scale natural patterns, just as spatial randomness is the null model against which we compare spatial patterns at a single scale. The null model of fractality may prove most valuable by allowing us to measure departures from it (for example, by finding the points where the scaling changes or breaks down altogether). Just as we have developed an effective arsenal of statistical methods to test for significant non-randomness, so too we need to develop techniques to test for significant departures from fractal structure. Only by doing so, we can begin to identify and quantify the scaling properties of nature. The ecological world may not be truly fractal, but fractals may nonetheless play a pivotal role in helping us understand it.

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APPENDIX 1: GLOSSARY

In this glossary, we concentrate on the terms commonly encountered in the environmental sciences, highlighting areas of particular confusion.

Dimension, ***D***: there are a large number of types of dimension (Falconer 1990; Cutler 1993). Of those listed below, only the Euclidean and Hausdorff are true dimensions in a strict mathematical sense, but the others represent measurable properties of an object's scaling behaviour.

Box-counting dimension (D_B) – the dimension that is observed using the box-counting technique (see Appendix 2), and the one most often referred to as *the* fractal dimension in the ecological literature. It measures the number of 'boxes' (e.g. grid cells) required to cover an object as a function of scale (the size of the box). At the limit it provides an estimate of the Kolmogorov dimension, which for most objects is equal to (or slightly greater than) the more abstract **Hausdorff dimension.**

Correlation dimension (D_{Mass}) – a dimension relating the rate at which 'mass' accumulates as one searches larger and larger 'volumes' around points belonging to the object in question. ('Mass' may be the cumulative number of points, individuals or the probability of occupancy). Also called the **cluster dimension** or the **mass dimension**.

Euclidean dimension (E) – an integer dimension describing the number of independent axes of space required to fully contain an object. This is the classical notion of dimension people refer to when talking about, e.g. a '2-dimensional' or '3-dimensional' object. For a single point $E = 0$, for a line $E = 1$, for a plane surface $E = 2$, and for a solid volume $E = 3$.

Hausdorff dimension (D_H) – a (fractional) dimension that describes how much of the available Euclidean space is 'occupied' by the object in question. It is the preferred mathematical version of fractal dimension, but is difficult to calculate in most cases of interest.

Information dimension (D_I) – a dimension that describes how the information content (entropy) of an object's spatial distribution changes with the scale of observation. The measure is related to the Shannon index, commonly used in ecology as a measure of diversity.

Rényi dimensions (D_q) – a family of dimensions of order q (where q is any real number) based upon the Rényi information content of an object. When $q = 0$, D_0 equals the **box-counting dimension**; when $q = 1$, D_1 equals the **information dimension** and when $q = 2$, D_2 equals the mass dimension. By necessity, $D_0 \geq D_1 \geq D_2$ (see also **multifractals**). In general, as q increases, the relative weight given to the densest bits of the pattern increases; in box counting, a single occurrence within a box counts as heavily as a dense patch, but this ceases to be the case in information or mass dimensions.

Fractal – used to describe objects that possess self-similarity and scale-independent properties; small parts of the object resemble the whole object. They typically have non-integer values for one or more of the dimensions described above. True fractals exist only as abstract idealized mathematical objects, as they require identical properties across an infinite range of scales.

Homogeneous fractal – an object in which the same scaling law applies at all positions on the object. If different scaling laws apply at different positions, it is instead termed an **inhomogeneous fractal**.

Lacunarity (Λ) – a scale-specific measure of texture or departure from translational invariance (Mandelbrot 1983; Allain & Cloitre 1991; Plotnick *et al.* 1993). See text for further details.

Multifractal – In the applied-science literature, at least three definitions of a multifractal are found: i) An object whose Rényi dimensions decrease with increasing parameter q; ii) An **inhomogeneous fractal** (as defined above); iii) An object with two or more scaling regions of different fractal dimension. For idealized (mathematical) multifractals, the first two of these are essentially equivalent.

Noise spectrum (or 'power spectrum') – any pattern in time (or space) can be split into a 'spectrum' of basic waves each associated with a characteristic wave frequency or 'colour'. In 'white' noise, all frequencies occur with equal power, while for 'reddened' spectra, power increases with decreasing frequency. A spectrum in which this decrease obeys a **power law** is called $1/f$ noise ('or $1/f^{a}$-noise') and is a signature of fractal behaviour.

Power Law: a relationship of the form $y = ax^b$. It can be made linear by taking logarithms: $\log(y) = \log(a) + b^*\log(x)$. Here a is termed the 'prefactor' and b is the 'exponent' and (in a fractal object) is closely related to the fractal dimension.

Quasi-fractal – an object that shows power law scaling over a finite range of scales. All real-world objects are at best quasi-fractals. Even simulated fractal patterns must have a finite extent and a minimum cell size ('grain'), making them quasi-fractals as well.

Scale (δ) – In this paper, we define the scale of an object as its maximum diameter, or in the case of square-grid based measurements, it is the cell-, box- or pixel-width. If the range of scales of a series of measurements ranges from the coarsest at L_{max} to the finest at L_{min} then we say that this range of scales spans $\log_{10}[L_{max}/L_{min}]$ **orders of magnitude.** Thus, for example, if finest cell-size is 10 m and we have information recorded over a square region of 1 km each side, then the range of scales spans $\log_{10}(1000/10) = 2$ orders of magnitude.

Self-similar – an object exhibits strict geometrical self-similarity if it appears invariant under expansion or contraction, i.e. a small part looks like the whole and vice versa. An object exhibits *statistical* self-similarity if its statistical properties remain scale-invariant.

Self-affine – an object exhibits self-affinity if expanding a small part looks like the whole, but stretched or compressed in one direction. This kind of fractal behaviour is characteristic of mountain surfaces, for which the vertical axis scales differently from the two horizontal axes.

Self-organized criticality (SOC) – A system which maintains itself in a 'critical' state through a 'balance' between a steady accumulation of 'pressure' and its release through a series of discrete events. The classic paradigm is the sandpile with a steady trickle of grains to the top. The pile maintains approximately the same steepness through regular avalanches. Though the exact timing is random, 'pressure' accumulates continuously between events so the expected magnitude of an event increases, the longer it is delayed. Other models of SOC are forest fires (with fuel accumulating) and earthquakes (shear pressure accumulation). A key signature of SOC is that the magnitudes of events and the intervals between them follow **power laws.**

APPENDIX 2 – COMMON METHODS FOR MEASURING FRACTAL DIMENSION

The most appropriate method for measuring a given type of fractal dimension will depend on the nature of the object, the purpose of the analysis and on practical considerations such as ease of computation. Those methods based upon a regular grid of boxes are usually the simplest. Alternatively, when locations are recorded in continuous space, sets of irregularly placed boxes or circles may be more appropriate.

In all of the methods below, apart from spectral methods, the relevant fractal dimension is usually found by estimating the slope of $\log N(s)$ plotted against $\log(1/s)$, where s is the scale of analysis and $N(s)$ is the number of objects observed at that scale. It may be preferable to use a model II regression rather than the more widely used model I analysis (see text). This is not supported by most statistics packages, but is easily calculated by dividing the model I slope estimate by the Pearson's correlation coefficient between the two variables.

Many of the measures below are based on superimposing a grid over the dataset. The precise location of the grid can sometimes matter – especially at coarser scales of analysis where there are relatively few grid cells, so the law of large numbers doesn't apply. It may be prudent to repeat an analysis several times, using shifting grids, and to use the mean or median results.

I. Point data sets (e.g. the locations of individuals)

These data will consist of a set of N_0 points, with a minimum and maximum inter-point separation of d_{min} and d_{max} respectively.

A. Box-counting dimension: D_B *or* D_0

1) Using a regular grid of boxes of side-length, s.
   i) Overlay the grid onto the set of point data.
   ii) Count the number of occupied boxes, $N(s)$.
   iii) Repeat steps i) and ii), incrementing the size of the boxes from s_{min} to s_{max}, typically by multiplicative steps (e.g. 2, 4, 8, 16…).
   iv) Plot the log of these $N(s)$ values as a function $\log(1/s)$
   v) The slope of this log–log graph is an estimate of the box dimension.
2) Using a set of irregularly placed boxes (or circles) of side-length (or diameter), s, the procedure is the same as A.(1) above, except for step (i), where we cover the object with boxes or circles, placing them so that we use a minimum number to cover the object.

B. Information dimension, D_I

1) This is calculated exactly the same way as Box-counting dimension A.(1) above, except that in step (ii) we calculate the Shannon index,

$$I_1(S) = -\sum_k P_k \log P_k$$

(where p_k is the proportion of the points that fall in the k^{th} box, and the summation is across all occupied boxes) instead of $N(s)$.

2) Using circles of diameter, s. Proceedure is the same as (B1) above except for step (i) where we centre a circle over each point, and calculate the mean number of points, $N(s)$, enclosed by each circle. Use this to calculate p and $I_1(s)$, as above.

C. Mass, correlation and other Rényi dimensions, D_q

The entire series of Rényi dimensions (with the exception of the information dimension) can be calculated by following the recipe A.(1) or A.(2) above, but using in step (ii) calculating the proportion of the points falling in each box and raising it to power of the Rényi-number q, then summing this quantity across all boxes. The logarithm of this result, divided by 1-q then replaces $N(s)$ in the box-counting procedure.

More precisely, $I_q(s)$, which replaces $N(s)$, is given by the general equation

$$I_q(s) = \frac{1}{1-q}\log\sum_k P_k^q$$

(where p_k is the proportion of the points that fall in the k^{th} box, the summation is across all occupied boxes and q is the order of the desired Rényi dimension). For box-dimension, $q = 0$, and for correlation dimension $q = 2$.

II. Line data sets

The above methods for point data may also be used to estimate the fractal dimensions of line data (e.g. time series, pathways of movement, habitat boundaries, surface contours with dimension at least one). However, in practice for many of these objects it makes more sense to use the dividers method to estimate the dimension:

A. Divider Dimension.

Using dividers of step-length, s.

i) 'Walk' the dividers along the line.
ii) Count the number of steps, $N(s)$, required to travel the line.

Steps (iii)–(v) as for box-counting dimension, above.

B. The perimeter–area method

Another approach used for estimating the fractal dimension, especially in GIS applications, is the perimeter–area method. In this approach, the perimeter P of a patch is related to the area A of the same patch by $P = A^{D/2}$. For all patches, regress log(P) against log(A), and estimate the fractal dimension as twice the regression slope.

III. Lattices of non-negative numbers (e.g. presence–absence grid maps, gridded surfaces of abundance, remote-sensing data)

A. Adaptations of point methods

These may be analysed with one of the grid-based measures discussed in section I for point data (e.g. the box dimension, IA1; information dimension, IB1; or the mass dimension, IC1). The occupied (or non-zero) cells of the lattice may be treated as a set of weighted points (with weights equal to the value of the variable being analysed). For presence/absence data (or for box-counting analyses of other data), this then becomes a matrix of 0's and 1's, and requires no further changes in the recipe. To calculate the information or mass dimensions (or any other Rényi dimension), the values of p are calculated as the proportion of the total 'weight' that falls in each box.

B. Gliding box method

Another frequently applied method for dealing with grid-based data involves using 'gliding box' algorithms. Indeed, this approach can be used in any of the grid based point pattern analyses, described above, as an alternative to examining multiple grid overlays. In these methods an 'analysis window' of side length, s, is located in all possible positions on the lattice, and the quantity of interest (i.e. $N(s)$ or $I(s)$) is calculated from this sample set. A disadvantage of these methods is that the spatial pattern towards the centre of the lattice contributes much more to the sample set than the pattern near the edge (especially at coarse scales).

IV. Lattices or time-series of data values (may include negative and positive values)

A. Spectral methods

Where one has a continuous run or matrix (in time or space) of data-points that form a jagged line or surface, spectral methods can be a powerful tool for analysing spatial pattern, including fractals such as fractal Brownian motion or $1/f$ noise (see Appendix 3). If the pattern analysed has fractal properties (if it is self-similar or self-affine) the power-spectrum will appear linear on logarithmic axes. In general, spectral methods should be used with caution when series have fewer than about 200 points (or 100^2 points for a two-dimensional pattern).

1) DFT (Discrete Fourier Transform) The most commonly used spectral method is based on the DFT. It is computationally quick and widely available in commercial mathematics computer packages. One serious disadvantage, however, is that it is very sensitive to missing values.

i) Convert data to a series of density-values upon a regular grid.
ii) Carry out the DFT on these data, to get $F(f)$.
iii) Find the power spectrum $S(f)$, that is $S(f) = |F(f)|^2$
iv) Fractal dimension is determined by the slope, v, of $S(f)$ against f on a log-log scale.
v) Fractal dimension is $D \approx \min\{E,(2N + 1 - v)/2\}$, N is the Euclidean dimension of the embedding space and $E = 1$, 2 or 3 depending on whether the data are supported on a line, plane or surface. This relation holds only approximately because the surface is self-affine, not self-similar.
vi) The autocorrelation, if needed, is the DFT of $S(f)$.

2) Other spectral methods include the Lomb periodogram, which can be used for irregularly-spaced points, and wavelet analysis (Keitt 2000).

B. Semivariogram method

Semivariograms are amongst the best known methods borrowed from geostatistics, and represent the degree to which values of some variable differ as a function of the distance between sampled points. They are particularly appropriate where one has data points scattered irregularly across a landscape, or where some points are missing from an otherwise regular grid or series of data-points.

i) Compute the distance between every pair of points in your data-set (a to b, a to c, b to c, etc). This is easily performed using Pythagoras' theorem: distance $= \sqrt{((x_1 - x_2)^2 + (y_1 - y_2)^2)}$
ii) Compute the difference in the value of interest between each pair of points, and square it
iii) Plot the log of this squared difference against the log distance between the points
iv) For a fractal pattern on a two-dimensional landscape, the relationship should be linear, with $D = 2 - m/2$, where m is the slope of the regression.

APPENDIX 3: RECIPES FOR RANDOM FRACTALS

A great many different recipes have been developed for deterministic and random fractals (e.g. Peitgen *et al.* 1992, Schroeder 1991, Russ 1994; Keitt 2000); those of interest and potential use for ecology are outlined here.

Midpoint displacement

Used as a model of fractional Brownian motion (fBm, Mandelbrot 1983; Feder 1988). For the simplest case (time-series), starts with two endpoints, and displaces the midpoint between them. At each iteration, the midpoint between pairs of existing points is displaced randomly. The magnitude of the displacement decreases by interpoint distance times $1/2^H$ to produce a graph of dimension $D = 2 - H$. The same process, starting to the midpoint of a square rather than that of a line-segment, can be used to generate a surface of dimension $D = 3 - H$. Uses: commonly applied to generating surfaces ('neutral landscapes') and time-series. Advantages: rapid computations; relatively easy to understand and describe. Disadvantages: produces imperfect fBm with subtle artefacts ('folds' in surface).

Spectral synthesis

Fractal surfaces or time-series can also be created using the DFT. The fractal is assembled from a series of sinewave components of different frequencies, the amplitudes of which satisfy a power law relationship: $S(f) \propto f^{-(2N+1-2D)}$, where f is frequency, N is the Euclidean dimension of the embedding space and D is the required fractal dimension. To produce the fractal, this 'power spectrum' is then transformed using the DFT from the frequency domain to the spatial (or temporal) domain. Randomness is introduced by choosing the phases (the starting points) of the component sine waves at random (Russ 1994; Keitt 2000). Uses: same as midpoint displacement, spatio-temporal modelling. Advantages: framework is very general and adaptable, spatio-temporal modelling easy. Disadvantages: intuitively less obvious and harder to describe than midpoint displacement.

'Slices' of fractal surfaces

A random fractal 'surface' generated by midpoint displacement or spectral synthesis (with dimension D_{surf}) can be used to create another object with boundary dimension $D_{surf} - 1$ by taking a horizontal slice through the surface. Uses: in ecology to generate random archipelagos with constant fractal boundary properties but different amounts of 'land.' Advantages: simple to use, can 'grow' a particular random pattern from low to high cover. Disadvantages: *often used without the realization that only the boundary is fractal.*

'Percolation' fractals (Falconer 1990) or 'Random curdling' (Mandelbrot 1983; Keitt 2000)

Iteratively subdivides an 'occupied' area into equally-sized sub-areas and defines each sub-area as occupied or empty according to a fixed probability p. The choice of this probability and the degree of subdivision determines the fractal dimension. Variations on the way the subcells are chosen lead to subtly different fractals with the same

D – e.g. *exactly* the same number of subcells can be chosen each time, or this can vary randomly around a mean (moreover, the distribution around this mean can be varied, too). For a fractal in the plane, and a subdivision of each cell into b^2 subcells, pb^2 of which are on average occupied, $D = \log(b^2p)/\log b$ Uses: presence/absence patterns. Advantages: simple to understand and implement. Disadvantages: produces patterns that are 'boxy' and so look different from ecological patterns.

Cookie-cutter sets (Mandelbrot 1983; Peitgen *et al.* 1992)

'Holes' are repeatedly cut from a continuous sheet or block; the sizes of the holes are chosen at random from a power-law frequency distribution. The remaining material has a fractal dimension determined by the exponent in the power-law distribution of hole sizes. Uses: no known ecological application, but may be potentially useful for models of disturbance, land-use change and local extinction.

Self-avoiding random walks in the plane (e.g. Gautestad & Mysterud 1994)

There are several construction methods e.g. fractional Brownian motion in the plane is generated and only those parts that enclose area ('islands') are retained. Uses: presence/absence patterns, boundary fractals, habitat patch networks.

Levy Dusts

A point is allowed to execute a 'Lévy flight'. From an initial point, another is chosen in a random direction at a distance r away, r being a random variable taken from a Pareto or other long-tailed (power-law decay) probability distribution. This new point becomes the current location, and the jumping process is repeated as many times as desired. Uses: modelling point-patterns in a plane or in 3-space. Advantages: conceptually simple, possibly analogous to some forms of dispersal. Disadvantages: our experience is that dimension estimation on these objects using box-counting can be problematic.

Other processes

Various other processes produces fractals such as diffusion limited aggregation (DLA), diffusion percolation (DP) and branching processes (Schroeder 1991). These processes are rarely used in ecology because of various limitations. DLA and DP are limited by the fact that only one dimension is produced. Branching processes have found widespread use in studies of morphology.