Lacunarity indices as measures of landscape texture

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Abstract

Lacunarity analysis is a multi-scaled method of determining the texture associated with patterns of spatial dispersion (i.e., habitat types or species locations) for one-, two-, and three-dimensional data. Lacunarity provides a parsimonious analysis of the overall fraction of a map or transect covered by the attribute of interest, the degree of contagion, the presence of self-similarity, the presence and scale of randomness, and the existence of hierarchical structure. For self-similar patterns, it can be used to determine the fractal dimension. The method is easily implemented on the computer and provides readily interpretable graphic results. Differences in pattern can be detected even among very sparsely occupied maps.

Introduction

The effects of spatial pattern on ecological processes is a key problem area in landscape ecology (Forman and Godron 1986, Turner and Gardner, 1991). Pattern determines how consumers move on the landscape (Wiens and Milne 1989) and utilize resources (O'Neill *et al.* 1988b). Dispersal processes interact with pattern to separate competitors in space (Comins and Noble 1985, Geritz *et al.* 1987) and permit coexistence. Coexistence through spatial heterogeneity has been shown for both animals (Kareiva 1986) and plants (Pacala 1987) and has been modeled by Palmer (1992).

The importance of spatial effects on ecological processes has motivated the development of a number of indices for quantifying landscape pattern. Useful indices have been developed from statistical measures of dispersion (Elliot 1977), information theory (O'Neill *et al.* 1988a), fractal geometry (Krummel *et al.* 1987, Milne 1992), and percolation theory (Gardner *et al.* 1987, Gardner and O'Neill 1991). A problem with all these indices is that different spatial patterns can be realized for any single value of the respective index. For example, Mandelbrot (1983) recognized that objects with identical fractal dimensions can have greatly different appearances.

The fact that deterministic fractals with identical dimensions can have greatly different appearances can be illustrated by Fig. 1 which shows a 1-dimensional fractal sequence of points and gaps (Cantor dusts; see Feder 1988) with a fractal dimension of 0.5. The difference between the two sequences is in the distribution of the size of the gaps. In Fig. 1a the ratio between successively smaller gaps is 4:1, while the object in Fig. 1b has a ratio of 9:1. The distribution of gap sizes has been termed *lacunarity* by Mandelbrot (1983), with geometric objects being more *lacunar* if gap sizes are distributed over a greater range; *e.g.* the sequence in Fig. 1b is more *lacunar* than the one in Fig. 1a.
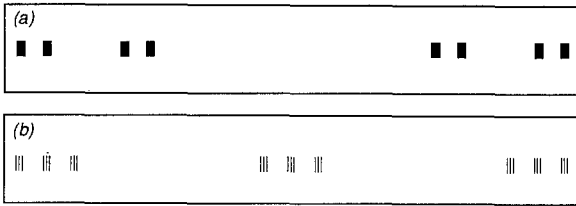
Fig. 1. Cantor dusts. The fractal dimension D of the dusts equals $\ln N / \ln (1/r)$, where N is the number of smaller pieces generated and r is the size reduction at each iteration (Mandelbrot 1983; Feder 1988). Each dust is shown after 3 iterations. A: $N = 2$ and $r = 1/4$. B: $N = 3$ and $r = 1/9$. Both dusts have a D of 0.5. The differences in appearance or texture are measured by their lacunarity.

Table 1. Lacunarity calculation for 12 × 12 random may (Fig. 2a). The size of the gliding box is $r \times r$, with $r = 2$. S is the number of occupied sites or mass of the gliding box; $n(S,r)$ is the frequency of boxes of size r with mass S; $Q(S,r)$ are the corresponding probabilities; $Z^{(1)} = \Sigma\, SQ(S,r)$ and $Z^{(2)} = \Sigma\, S^2 Q(S,r)$ are the first and second moments, respectively. The lacunarity, $\Lambda(r) = Z^{(2)}/(Z^{(1)})^2$.

	S	n(S,r)	Q(S,r)	SQ(S,r)	S²Q(S,r)
r = 2	0	3	0.024	0	0
	1	35	0.289	0.289	0.289
	2	46	0.380	0.760	1.520
	3	29	0.239	0.719	2.157
	4	4	0.066	0.264	1.057

$Z^{(1)} = 2.033$ $Z^{(2)} = 5.024$

$\Lambda(2) = 1.215$

Lacunarity can thus be thought of as a measure of the 'gappiness' or 'hole-iness' of a geometric structure (Kaye 1989).

A more precise definition of lacunarity was given by Gefen et al. (1983); lacunarity measures the deviation of a geometric object, such as a fractal, from translational invariance. That is, at a given scale, how similar are parts from different regions of a geometric object to each other? Low lacunarity geometric objects are homogeneous and translationally invariant because all gap sizes are the same. In contrast, objects with a wide range of gap sizes are heterogeneous and not translationally invariant; they have high lacunarity. Note that translational invariance is highly scale dependent; objects which are heterogeneous at small scales can be quite homogeneous when examined at larger scales or vice versa. Lacunarity can thus be considered a scale dependent measure of heterogeneity or texture.

Note that translational invariance is *not* the same as self-similar. The Cantor dusts in Fig. 1 were generated by a process that guarantees that they are self-similar; *i.e.*, the units at successively finer scales appear identical to the units at the broader scales. However, because the entire sequence has a wide range of gap sizes, it is not translationally invariant.

Method of calculating lacunarity

Methods for calculating lacunarity were given in general terms by Mandelbrot (1983) and more spe-

cifically by Gefen et al. (1984) and Lin and Yang (1986). More recently, Allain and Cloitre (1991) described a straightforward algorithm for the calculation of the lacunarity of both deterministic and random fractals; it is Allain and Cloitre's algorithm that we have utilized and will now describe.

The gliding box algorithm

We will use some simple examples to demonstrate the use of Allain and Cloitre's (1991) 'gliding box' algorithm. Fig. 2a represents a 12 × 12 random map; each square has a probability of 0.5 of belonging to a particular habitat type (indicated by 1's). An $r \times r$ box ($r = 2$) is placed over the upper left corner of the map. Of the four sites covered, 2 are occupied by the habitat of interest. The number of occupied sites is referred to as the box mass. The box is now moved one column to the right and the box mass is again counted. This process is repeated over all rows and columns producing a frequency distribution of the box masses (Table 1). The number of boxes of size r containing S occupied sites is designated by $n(S,r)$ and the total number of boxes of size r by $N(r)$. If the map is of size M, then

$$N(r) = (M - r + 1)^2.$$

This frequency distribution is converted into a probability distribution $Q(S,r)$ by dividing by the

(a)

```
1 1 0 1 1 1 0 1 0 1 1 0
0 0 0 0 0 1 0 0 0 1 1 1
0 1 0 1 1 1 1 1 0 1 1 0
1 0 1 1 1 0 0 0 0 0 0 0
1 1 0 1 0 1 0 0 1 1 0 0
0 1 0 1 1 0 0 1 0 0 1 0
0 0 0 0 0 1 1 1 1 1 1 1
0 1 1 0 0 0 1 1 1 1 0 0
0 1 1 0 1 1 0 1 0 0 1
0 1 0 0 0 0 0 0 0 1 1 1
0 1 0 1 1 1 0 1 1 0 1 0
0 1 0 0 0 1 0 1 1 1 0 1
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(b)

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1 1 1 1 1 1 1 1 1 1 1 1
1 1 0 0 0 0 0 0 0 0 1 1
1 1 0 0 0 0 0 0 0 0 1 1
1 1 0 0 0 0 0 0 0 0 1 1
1 1 0 0 0 0 0 0 0 0 1 1
1 1 0 0 0 0 0 0 0 0 1 1
1 1 0 0 0 0 0 0 0 0 1 1
1 1 0 0 0 0 0 0 0 0 1 1
1 1 0 0 0 0 0 0 0 0 1 1
1 1 0 0 0 0 0 0 0 0 1 1
1 1 1 1 1 1 1 1 1 1 1 1
1 1 1 1 1 1 1 1 1 1 1 1
```

(c)

```
1 0 1 0 1 0 1 0 1 0 1 0
0 1 0 1 0 1 0 1 0 1 0 1
1 0 1 0 1 0 1 0 1 0 1 0
0 1 0 1 0 1 0 1 0 1 0 1
1 0 1 0 1 0 1 0 1 0 1 0
0 1 0 1 0 1 0 1 0 1 0 1
1 0 1 0 1 0 1 0 1 0 1 0
0 1 0 1 0 1 0 1 0 1 0 1
1 0 1 0 1 0 1 0 1 0 1 0
0 1 0 1 0 1 0 1 0 1 0 1
1 0 1 0 1 0 1 0 1 0 1 0
0 1 0 1 0 1 0 1 0 1 0 1
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Fig. 2. Three 12 × 12 maps, with 1's representing occupied habitat. The percentage of occupied **P**, equals 0.5 for all 3 maps. A: Random map. $\Lambda(4) = 1.04$. B: Map with a single large gap. $\Lambda(4) = 1.810$. B: Perfectly regular (checkerboard) map. $\Lambda(4) = 1.00$.

total number of boxes:

$$Q(S,r) = n(S,r)/N(r)$$

(Table 1). The first and second moments of this distribution are now determined:

$$Z^{(1)} = \Sigma\, S\, Q(S,r)$$
$$Z^{(2)} = \Sigma\, S^2\, Q(S,r)$$

The lacunarity for this box size is now defined as:

$$\Lambda(r) = Z^{(2)}/(Z^{(1)})^2.$$

For the example given, $\Lambda(2) = 1.215$ (Table 1).

The statistical behavior of $\Lambda(r)$ can best be understood by recognizing that:

$$Z^{(1)} = \bar{S}(r),$$
$$Z^{(2)} = s_s^2(r) + \bar{S}^2(r)$$

where $\bar{S}(r)$ is the mean and $s_s^2(r)$ the variance of the number of sites per box. As a result,

$$\Lambda(r) = s_s^2(r)/\bar{S}^2(r) + 1.$$

From this relationship, we can determine that lacunarity is a function of:

1. the size of the gliding box. As box size increases, the average box mass also increases and the probability that box masses will greatly differ from the average decreases; *i.e.*, the relative variance decreases. The same map will thus have lower lacunarities as the size of the box increases. For the example above, $\Lambda(4) = 1.037$;

2. The fraction, *P*, of the map occupied by the habitat of interest. As the mean number of occupied sites goes to zero, $s_s^2(r)/\bar{S}(r)^2$ goes to ∞. Sparse maps will thus have higher lacunarities than dense maps, for the same gliding box sizes;

3. the geometry of the map. Fig. 2b shows a map with the same *P* as Fig. 2a, but with a single large gap in the middle. For this map, $\Lambda(2) = 2.053$ and $\Lambda(4) = 1.810$. This increase in lacunarity is due to the increase in both fully occupied ($S=4$) and totally empty ($S=0$) boxes produced by the clumping of the occupied sites. For a given *P*, therefore, higher

Table 2. Properties of random and hierarchically structured maps. Maps are 216 × 216, with three (L = 3) 6 × 6 levels. **P** is the total proportion of the map covered by the habitat of interest; p_i is the fraction of units at the ith level that contain the suitable habitat type; total edges are total number of non-habitat sites adjacent to habitat sites.

Map Type	p_1	p_2	$p3$	P	Total Edges
Top91	0.917	1	1	0.917	1080
Middle91	1	0.917	1	0.917	3072
Bottom91	1	1	0.917	0.917	15324
Same91	0.972	0.972	0.972	0.919	6556
Random91				0.917	14866
Top50	0.500	1	1	0.500	1656
Middle50	1	0.500	1	0.500	7956
Bottom50	1	1	0.500	0.500	48172
Same50	0.805	0.806	0.806	0.528	22540
Random50				0.500	46812
Top02	0.028	1	1	0.028	144
Middle02	1	0.028	1	0.028	864
Bottom02	1	1	0.028	0.028	5166
Same02	0.306	0.306	0.306	0.028	3998
Random02				0.028	5118
Dn02	1	0.167	0.167	0.028	4538
Up02	0.167	0.167	1	0.028	744

lacunarity represents higher contagion (fewer, but larger gaps).

In contrast, Fig. 2c is a totally regular (*i.e.*, translationally invariant) map, again with $P = 0.5$. The number of occupied squares within a gliding box would be constant at any location of the map (the variance is zero). The lacunarity of a totally regular array is thus 1 for any gliding box size larger than the unit size of the repeating pattern.

Based on these considerations, the use of a single-valued lacunarity estimate based on a single gliding box size for a given map is of limited value at best, and is probably meaningless as a basis for comparison of different maps. The useful feature of lacunarity measurements is the great deal of information which can be gained by calculating lacunarity over a wide range of gliding box sizes.

Note that the gliding boxes overlap; *i.e.*, they are not independent. This is a key difference from the typical ecological practice of non-overlapping spatial samples.
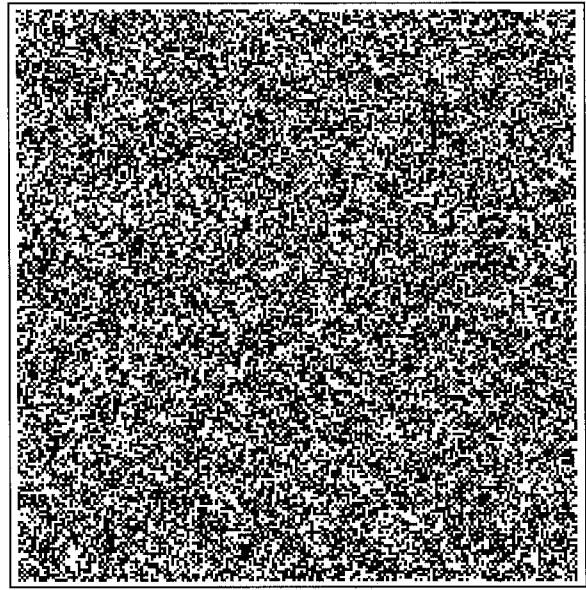

Fig. 3. 'Random' map. 216 × 216 random map with $\mathbf{P} = 0.5$.

Lacunarity analysis of simulated maps

Generation of random and hierarchical random maps

To examine the properties of the lacunarity statistic, we have calculated the lacunarity of a range of simulated landscape maps, which differ in the fraction, *P*, and the distribution of occupied habitat (Table 2, Figs 3–7) Two-dimensional random maps (hereafter referred to as 'Random') were formed by creating arrays with *M* columns and *M* rows and randomly setting the M^2 elements to 1 with a probability *P*. Array elements set to 1 represent suitable habitat, while elements left at 0 represent unsuitable sites. 'Random' maps were generated with *M* fixed at 216 (46,656 total sites) and *P* values of 0.028, 0.500, and 0.917 (Table 2; Fig. 3).

Hierarchically structured random maps were generated by a recursive algorithm derived from the methods of fractal geometry known as curdling and random trema generation (Mandelbrot, 1983; Gardner *et al.*, in press; O'Neill *et al.*, in press). These processes transform an initially uniform distribution into many small clumps of high density (Feder 1988), separated by gaps whose size and po-
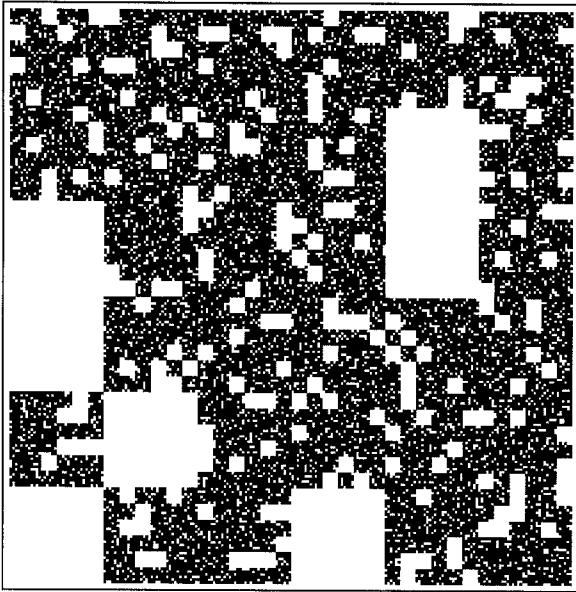
Fig. 4. 'Same' map. This map and those in figures 5–7 are 216 × 216 hierarchical maps (Table 2). For this map P equals 0.522 and $p_1 = p_2 = p_3 = 0.806$.

Fig. 5. 'Bottom' map, $p_1 = p_2 = 1$ and $p_3 = P = 0.5$.

sition are, to some extent, random. Our implementation of this algorithm specifies the number of levels L of successively finer scales within the map; the number of units m_i within the ith level; and the fraction p_i of units at the ith level that contain suitable habitat type.

A three level hierarchical map ($L = 3$) is illustrated in Fig. 4. A matrix of 6 × 6 ($m_i = 6$) elements was created with 29 of the elements randomly set to 1 ($p_1 = 0.806$). Each element that is set to 1 is then subdivided into a 6 × 6 matrix ($m_2 = 6$) and 29 of these elements are now randomly set to 1, with the remainder being set to 0 ($p_2 = 0.806$). The process is repeated at third time, with $m_3 = 6$ and $p_3 = 0.806$. The result is a random hierarchical map with a total number of sites M^2, equal to 46,656 $(m_1 \times m_2 \times m_3)^2$ and a total fraction of suitable sites P equal to 0.522 $(p_1 \times p_2 \times p_3)$. Note that this map is self-similar across the three hierarchical levels because the same number of units are set to 1 at each level.

A series of maps were generated with $L = 3$, all $m_i = 6$, and P's of 0.028, 0.500, and 0.917 (Table 2). In maps labeled 'Same' (Fig. 4), the values of p_i
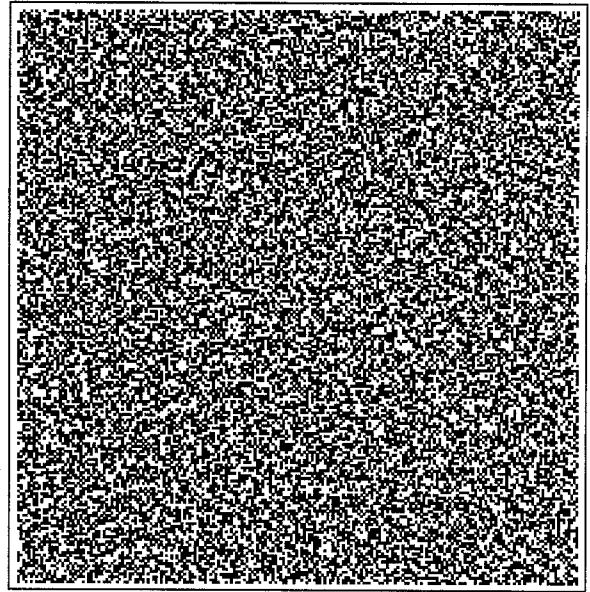
were equal at all three levels. Again, these maps are essentially self-similar, with gaps being generated over a range of sizes. In the remaining maps, gaps were generated at only one level; *i.e.*, the maps are random at one spatial scale. In 'Bottom' maps, $p_1 = p_2 = 1$ and $p_3 = P$ (Fig. 5), so gaps and contiguous blocks of habitat are small. Conversely, 'Top' maps (Fig. 6), $p_1 = P$ and $p_2 = p_3 = 1$, have very large gaps and large blocks of solid habitat. 'Middle' maps (Fig. 7) have gaps and habitat blocks at an intermediate scale $(p_1 = p_3 = 1$ and $p_2 = P)$.

Lacunarity analysis

For each map, the lacunarity was calculated for box sizes ranging from $r = 1$ to 128, by multiples of 2. A log-log plot was then made of lacunarity versus box size (Figs. 8 to 10).

The highest value of lacunarity is found for $r = 1$; *i.e.*, a gliding box equal in size to the grain of the map. At $r = 1$, $\Lambda(1) = 1/P$ (since $Q(1,1) = P$, $Z^{(2)}/(Z^{(1)})^2 = P/P^2$). This value is solely a function of the percentage of occupied sites and is independent of the overall size of the map and of the details of the distribution. As a result, all curves for a given
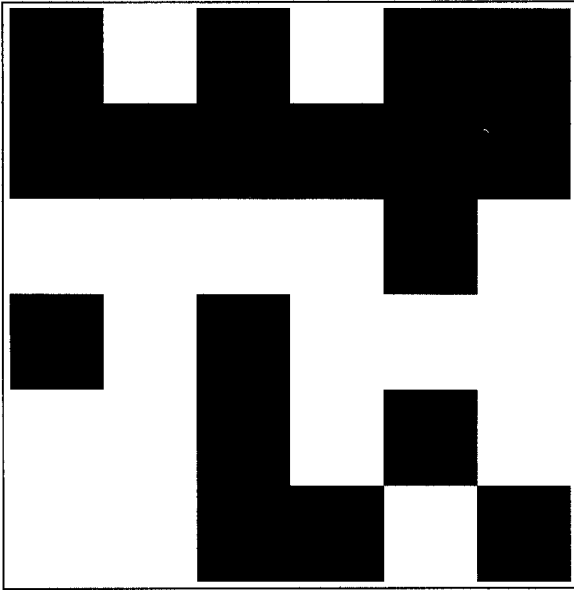
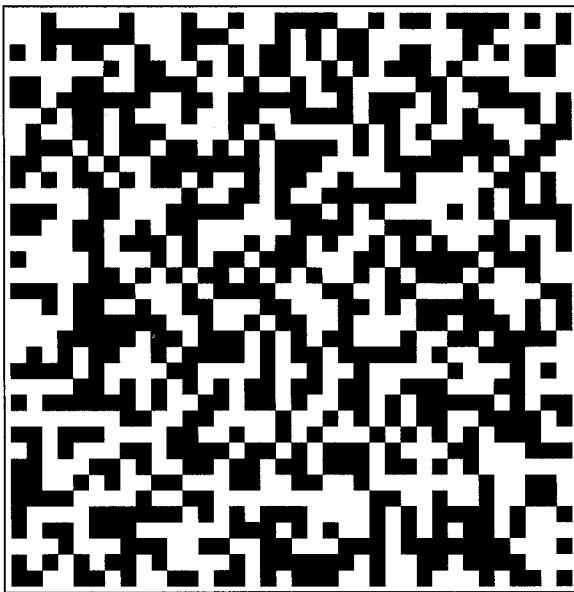Fig. 6. 'Top' map, $p_1 = P = 0.5$ and $p_2 = p_3 = 1$.

Fig. 7. 'Middle' map. $p_1 = p_3 = 1$ and $p_2 = P = 0.5$.

P have the same y-intercept. As P increases, this value increases (Figs. 8–10). At large r values, the curves are similarly constrained. If the box is the size of the entire M × M map, then the variance of box masses is 0 and $\Lambda(M)$ must equal 1.
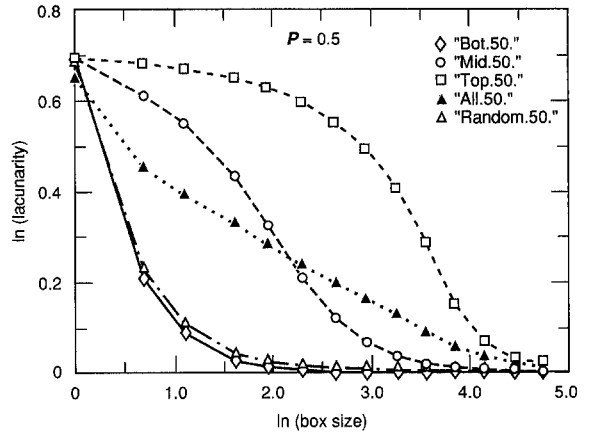
Away from the endpoints, the shapes of the

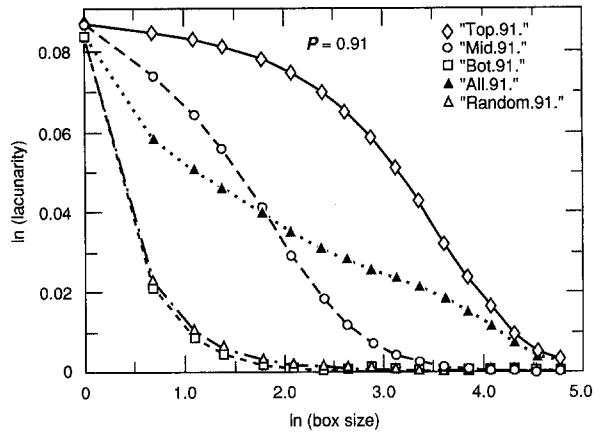Fig. 8. Log-log plot of lacunarity versus gliding box size for maps with $P = 0.5$ (Figs. 3–7; Table 2).

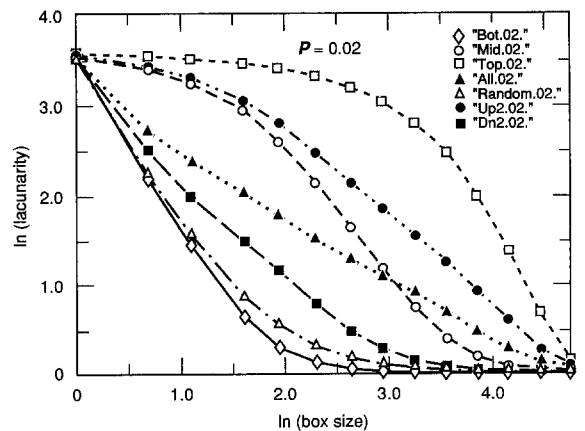Fig. 9. Same as Fig. 8, for maps with $P = 0.917$ (Table 2).

Fig. 10. Same as Fig. 8, for maps with $P = 0.028$ (Table 2.). 'Up' and 'Dn' maps respectively have top and middle or middle and bottom levels identical.

curves differ for the same *P*. For a particular box size, the lacunarity is now a measure of contagion. Higher lacunarity values represent greater relative clumping of a habitat type or, alternatively, a wider range of gap sizes in the distribution of the habitat.

If a map has a random structure at some scale, lacunarity depends upon the size of the gliding box relative to the characteristic scale of randomness. If the random pattern is smaller than *r*, then the variance of the mass distribution within the gliding boxes will approach zero and lacunarity will approach 1. If the gliding boxes are smaller than the scale of the randomness, then the map will appear heterogeneous at that scale and the lacunarity estimate will be higher.

The differences in the curves for the 'Bottom', 'Middle', and 'Top' maps for all three values of *P* demonstrate the scale dependent effects of randomness on lacunarity estimates. In 'Top' maps (Fig. 6), only solid 36 × 36 blocks are turned on or off, so the map is random only at scales greater than this. Lacunarity values are high for these maps until *r* approaches the block size; they then begin to decline and above the block size the lacunarity rapidly approaches zero. Similarly, 'Middle' maps have block sizes of 6 × 6 and 'Bottom' maps of 1 × 1. In both cases, as the size of the gliding box exceeds the block size, the lacunarity rapidly decreases towards zero.

The curve for the 'Random' maps closely follows that for the 'Bottom' maps. This is due to the similar spatial scales of the randomness for the two map types. Note, however, that the curve for 'Bottom' always plots slightly below that for 'Random'. This is certainly due to the greater regularity of the 'Bottom' map produced by the curdling algorithm; each 6 × 6 unit at the lowest level is constrained to have exactly the same number of occupied elements. In contrast, the number of occupied elements in similar sized block on a 'Random' map can vary.

The three 'Same' maps (labeled as "All" in Figs. 8–10) have equal curdling probabilities at all three levels. The lacunarity curves for these maps are very nearly linear and, therefore, the closest to being truly self-similar. As described by Allain and Cloitre (1991), the lacunarity curve for self-similar fractals should be a straight line with a slope equal to D−E,
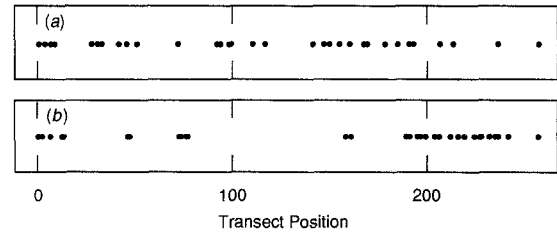

Fig. 11. Two simulated 258 point transects, with 33 occurences of habitat or organism of interest. A: Randomly distributed points. B. A random fractal series of points. This series is a Lévy dust, which is a randomized version of the Cantor dusts in Fig. 1 and has a fractal dimension of 0.8 (Mandelbrot 19983, Voss 1988). Notice the clumping of points.

where D and E are the fractal and Euclidean dimensions, respectively.

To confirm that a linear lacunarity plot indicates self-similarity, two hierarchically structured maps, 'Up02' and 'Dn02', were produced with identical upper $(p_1 = p_2)$ or lower $(p_2 = p_3)$ two levels, respectively (Table 2). The lacunarity curve for 'Up02' (Fig. 11) is straight over the range of box sizes corresponding to the two identical levels and then curves over the range of smaller box sizes. Similarly, the curve for 'Dn02' curves over the largest size range and is then straight over the middle and small range.

Finally, of especial interest is that the differences among the spatial patterns on the maps can be detected even when the map is sparsely occupied. The properties and relationships among the curves are essentially the same whether the map is 91% occupied (Fig. 9) or 2% occupied (Fig. 10)

Use with transect data

The 2-dimensional techniques for estimating lacunarity can be easily adapted for the analysis of transect data. To do so, the gliding box is simply replaced with a set of one-dimensional boxes or bins.

Figure 11 illustrates two 258 point transects, in which dots represent habitat sites of interest. In Fig. 11A, the probability of any site being occupied is 0.128. Notice that although there is some clumping, as would be expected from a random process, the
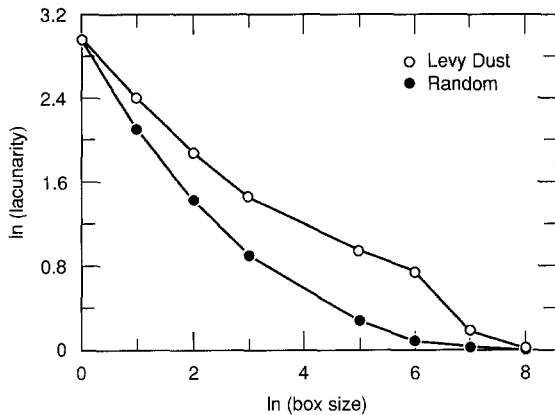
Fig. 12. Lacunarity anaylsis of the two transects in Fig. 11.

points are more or less evenly distributed over the line. In Fig. 11B, the same number of sites are occupied (33), but the points are very distinctly clumped. This sequence is a randomized version of the Cantor dusts shown in Fig. 1, with $D = 0.8$ and is statistically self-similar (Mandelbrot 1983, Voss 1988).

The lacunarity plots for these two sets are shown in Fig. 12. Two important features to note are: 1) as expected, the lacunarity of the clumped sequence is much higher than that of the random sequence; 2) the lacunarity curve of the self-similar sequence is straighter than that of the random dust, which is continuously curved. The results for the one-dimensional distributions are thus identical to those for the two-dimensional cases.

In sum, examination of the graphs produced by an analysis of lacunarity reveals the overall fraction of the map occupied by the habitat type of interest, the level of contagion between occupied sites at a particular scale, the scale at which the map approximates a random pattern, and the range of scales over which a map exhibits self-similarity. The method can thus detect the presence of a hierarchical structure. The technique is apparently robust against differences in P.

Discussion

Numerous methods exist to measure the degree of spatial clumping or aggregation of biological popu-

lations (Pielou, 1969; Elliot 1977). Many of these are based on quadrat sampling and are designed to determine whether, or to what extent, the variance-to-mean ratio of samples/quadrat differs from random (Poisson) expectation. Lacunarity is clearly related to these measures.

As pointed out by Pielou (1969), populations will usually differ in both mean density and degree of aggregation; various measures of aggregation are more-or-less sensitive to differences in mean density. This is certainly the case for any individual lacunarity value. However, as can be seen by comparing Figs. 8–10, the shapes of the lacunarity curves depend on the pattern of aggregation and are *independent* of the density. Changes in P are reflected in the positions of the curves, not their shapes.

The use of lacunarity plots, rather than a single value, also confirms the suggestion of Pielou (1969:104) that 'much can indeed be learned by examining the way some measure of aggregation varies with quadrat size.' The usefulness of graphing changes in an index over different scales was recognized long-ago by Morisita (1959) and Grieg-Smith (1964). We suggest that any single-valued index will be inadequate for characterizing heterogeneous landscapes. Instead, it is the change of the value of lacunarity over different gliding box sizes that yields the most information.

Various alternative measures of aggregation are based on determing the distribution of distances among individuals (distance or neighborhood analysis methods; Pielou 1969). For example, a technique referred to as second-order neighborhood analysis was used by Getis and Franklin (1987) to quantify clustering. This extension of neighborhood analysis examines the proportion of points on a map within a given distance of a chosen point and determines whether the pattern of dispersion differs from random (Poisson) expectation. A major drawback of all neighborhood analysis methods is that they are sensitive to the edge of the map. The boundary correction given by Getis and Franklin (1987) assumes that the pattern seen within the map boundary continues outside the edge. This assumption is often questionable, especially when large areas or gradients are included in the study area.

Multi-scaled lacunarity measurements are not affected by the boundary of the map, although the size of the map will impose an upper limit on the scale of the pattern which can be analyzed.

O'Neill *et al.* (1988a) developed an index for contagion, D_2, derived from information theory. This index is based on the probability that grid points belonging to two different landscape types are adjacent to each other. O'Neill *et al.* (1988) indicated that D_2 captures fine grained texture, but not broad scale patterns. Lacunarity analysis, in contrast, captures pattern over the entire range of scales from the individual grid point to that of the entire map.

Several other indices of landscape pattern have been described by Gardner *et al.* (1987; in press). Of these, the one most similar in purpose to lacunarity is total amount of edge, E, which is the total number of non-habitat sites adjacent to habitat sites. As shown in Table 2, the number of edges peaks at 0.5 occupancy; it is therefore *not* rank correlated with lacunarity.

Discussion

When Mandelbrot (1983:310) introduced the concept of lacunarity he stated that 'texture is an elusive notion which mathematicians and scientists tend to avoid because they cannot grasp it.' The use of lacunarity to characterize landscape texture allows us to begin to quantify the effect of texture (and change in texture) on broad-scale ecological processes.

Lacunarity has several practical advantages over other indices of landscape pattern: (1) the algorithm is simple to implement and is not computationally expensive compared to calculations that require habitat clusters to be identified (Gardner *et al.*, in press); (2) the gliding box algorithm exhaustively samples the map to quantify changes in contagion and self-similarity with scale; 3) unlike many nearest-neighbor indices, the results are not sensitive to the boundary of the map; and 4) the technique can be reliably used for the analysis of very sparsely occupied maps.

The methods described here allow us to quantify landscape texture; it is interesting, therefore, to speculate on the effect that texture might have on patterns of species abundance. A variety of theoretical studies (Kareiva, 1990) have shown that variation in species composition and abundance at landscape scales depends on the degree of habitat heterogeneity and species specific patterns of dispersal and resource use. However, the relationships between landscape texture and abundance may be obscured when landscapes are infrequently disturbed because biotic effects (*e.g.*, competition, predation, and mutualistic interactions) may be the local determinates of abundance of species. When disturbances alter landscape texture (*i.e.*, the creation of large gaps by storms, fire, etc.) then patterns of species abundance should be altered in a manner that reflects the textural changes. In other words, disturbances that destroy identical proportions of habitat should have different impacts on species composition and abundance if the landscape's original texture has been significantly altered.

The relationship between landscape texture and species abundance should also be clear for species reinvading after a disturbance, since they will often be free of confounding effects of biotic interactions (*i.e.*, competition and predation). Patterns of resource use by these species should be closely related to the texture of the landscape.

Habitats that occur as linear structures on the landscape (*i.e.*, riparian zones or shoreline areas) are particularly vulnerable to disturbances that increase lacunarity by the removal of segments of habitat. The process or recolonization of these systems should be related to the change in landscape texture and the dispersal characteristics of species reinvading these habitats.

Habitat fragmentation is probably the most prevalent and important impact that humans have on landscapes (Forman and Godron 1986). Humans can change the distribution of land use types very quickly and at a variety of spatial scales (Krummel *et al.* 1987). The sensitivity of lacunarity analysis will make these effects easily detectable. Because the effect of pattern on landscape processes is scale specific (Gosz 1992), the quantification of these changes by a lacunarity analysis will allow appropriate scales for empirical studies to be quantitatively defined.

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