

Fractal analysis of dispersal

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Abstract: We develop a fractal method, based on dispersal data, for quantifying the 'degree of clustering' of spatial point patterns. Clustered spatial patterns are commonly encountered in biology, from local to landscape spatial scales. We begin by outlining Mandelbrot's 'Lévy dust' fractal model for generating spatial point patterns. In this model, a high fractal dimension ($D = 2$) results in a relatively even distribution of points in the plane. Lowering the fractal dimension ($D < 2$) generates point patterns with increasing levels of clustering at all spatial scales. The Palm intensity method for determining the fractal dimension of point patterns is briefly discussed. Next, we note that the distribution function of dispersal distances ('Lévy flights') for the Lévy dust model is an inverse power function. Since diaspore dispersal curves for higher plants also take the form of an inverse power function, the fractal point pattern dimension D for a given species can be estimated from a log-log dispersal plot. We apply this method to published dispersal curves. Our results suggest that species with limited diaspore dispersability have $D > 2.0$, indicating that they occur in the landscape as a colonizing front (a 'phalanx' colonization strategy). Species with special adaptations for potential long-distance dispersal, by contrast, generally have $D < 1.0$. Such species tend to disperse through the landscape as isolated colonists, forming new colonies far from the parent plant (a 'guerilla' colonization strategy).

Introduction

Clustered (under-dispersed) spatial patterns are commonly encountered in vegetation. At local scales, a regular (over-dispersed) pattern may result from intra- or interspecific interactions (e.g., Kenkel 1988, 1993). However, at broader scales under-dispersed spatial patterns are almost invariably encountered. This is generally attributed to environmental heterogeneity and habitat patchiness, though stochastic factors such as the nature of diaspore dispersal and historical disturbance are undoubtedly also important. Thus, the specific spatial pattern encountered in the field is determined by a complex of factors. Despite this complexity, dispersal information can be used to predict general spatial patterns encountered in nature. Such a strategy was first used by van der Plank (1960) to predict the dispersal of pathogens through field crops. He found that pathogens having limited dispersability tend to advance as a wave front or 'horizon', while those with higher dispersability often expand from isolated local infection spots. Harper (1977: 54-56) has generalized van der Plank's ideas in a discussion of

seed dispersal in higher plants. He speculated that "isolated plants are unlikely to form horizons of colonization but that dense stands will colonize as an advancing front". He goes on to say that "there are far too few studies of dispersal for valid generalizations to be made at this stage but van der Plank's approach to the problem of epidemic spread provides a stimulating model against which new observations can be compared and new studies designed". We expand on these ideas in this paper.

Mandelbrot (1983: § 32) outlined a method for the generation of clustered spatial point patterns having fractal properties (refer to Kenkel & Walker (1993) for an introduction to fractal geometry, and examples of fractal applications in ecology). Fractal point patterns, known as Lévy dusts, show statistical self-similarity. For our purposes, self-similarity in this context refers to consistency in the intensity of clustering at different spatial scales. The intensity of clustering increases with decreasing fractal dimension D (see Mandelbrot 1983: 298, for examples). The Lévy dusts model generates patterns that reflect the distribution of

galaxies, and has been used successfully to model the spatial distribution of earthquake epicenters (Ogata & Katsura 1991) and myocardial blood vessels in heart tissue (King et al. 1990).

In this paper, we examine potential applications of fractal analysis to the quantification of vegetation pattern. Our emphasis is on spatial point patterns and their fractal analysis, particularly as they relate to dispersability. Specific objectives are: (i) to outline the Lévy dust clustered point pattern model, and to produce illustrative examples at various fractal dimensions; (ii) to outline the Palm intensity method for determining the fractal dimension of empirical spatial point patterns; and (iii) to develop a strategy for determining the fractal dimension D from dispersal data. We also briefly speculate on the application of fractal concepts to the analysis of pattern and scale in vegetation.

Methods

(a) Simulated Lévy dust of various dimensions

Mandelbrot (1983, § 32) describes the generation of clustered point patterns using the Lévy dust model. These spatial point patterns are simply the set of 'landing points' between 'Lévy flights'. Each Lévy flight is determined by a vector, with a random direction chosen uniformly from $[0, 2\pi)$ and a flight length r chosen from the conditional probability

$$P(R > r_0 | R > r_0) = \begin{cases} 1 & r \leq r_0, \\ (r_0/r)^D & r > r_0, \end{cases} \quad (1)$$

where r_0 is the minimum flight length. A random simulation of such a pattern can thus be obtained by generating a series of r values according to:

$$r = r_0 (1 - x)^{-1/D} \quad (2)$$

where x is a random uniform value from $[0, 1)$, and D is the fractal dimension. Ogata & Katsura (1991) used this method to generate approximate Lévy dusts (2-dimensional unit square torus, $N = 1000$ points) with $D = 1.0$ and $r_0 = 0.001$. We use a similar algorithm, but without toroidal boundary conditions.

(b) Estimating the fractal dimension D of clustered point patterns

A crude empirical method for estimating D of clustered point patterns was described by King et al. (1990). They used successive grids ('pixels') of different size to quantify variation in point counts at various spatial scales. In their method, $D = 1.5$ for random point patterns while $D < 1.5$ for clustered patterns. According to King et al. (1990), their D approaches 1

as "uniformity of the property over all length scales" is reached.

Ogata & Katsura (1991) describe mathematically more rigorous methods for the estimation of D . They outline non-parametric and maximum likelihood estimates based on two methods: (a) estimation through Palm intensity; (b) estimation through spectrum analysis (periodograms). Of these, the non-parametric Palm intensity method is the most straightforward and is described here. The Palm intensity, $\hat{\lambda}_0(u)$, is defined as the ratio of the number of vectors, Δ , inside an annulus $A(u_1, u_2)$. The vectors Δ are taken from the set of all vectors joining one point to another point in the pattern (thus, if there are n points in the pattern, there are by definition n^2 vectors). Note that the annulus, A , is defined as a ring of outer radius u_1 and inner radius u_2 . We implemented the algorithm as follows:

(consider each point in the pattern in turn).

- for a point Q , loop over all points in the pattern, including Q .
- determine the distance between point Q and the other point.
- decide which annulus this distance falls in.
- compute the area of the annulus, allowing for edge effects.
- add this contribution to the Palm intensity function.

Ogata & Katsura (1991) demonstrate that the slope of the log-log plot of Palm intensity vs. annular radius has a slope of $H = D - 2$.

It should be noted that this algorithm is suitable only for patterns containing a large number of points (say, $N > 1000$). Ogata & Katsura (1991) used this and other methods to determine the fractal dimension of epicenters of shallow earthquakes ($N = 1867$) in the Honshu region of Japan. Unfortunately, in biology data sets of this type and size are difficult and expensive to obtain. In the following section, we derive an alternative strategy involving estimation of the fractal dimension from dispersal data.

(c) Estimating the fractal dimension D from dispersal data

We develop a straightforward alternative method for estimating the fractal dimension D . The method uses dispersal data, which are widely available in the biological literature. Although this paper deals exclusively with higher plant diaspores, the method is equally applicable to the spores of lower plants, plant

pollen, fungal spores, and with some modification could be applied to animal dispersion.

The most widely used 'dispersal curve' model is the simple inverse power law. It has been widely used in the phytopathology literature (e.g., van der Plank 1960, Gregory 1968) and as a simple model of seed dispersal in plants (see Harper 1977, Okubo & Levin 1989). The model takes the general form:

$$y = \alpha s^{-\beta} \quad (3)$$

where y = probability density, s = distance from source, and α and β are constants. The log-log plot linearizes the inverse power law:

$$\log y = \alpha - \beta \log s. \quad (4)$$

The log-log form of the inverse power law was used by van der Plank (1960) to analyze the spread of plant pathogens. He concluded that pathogen species having limited dispersability (log-log slope > 3) tend to advance as a wave front, while those with higher disper-

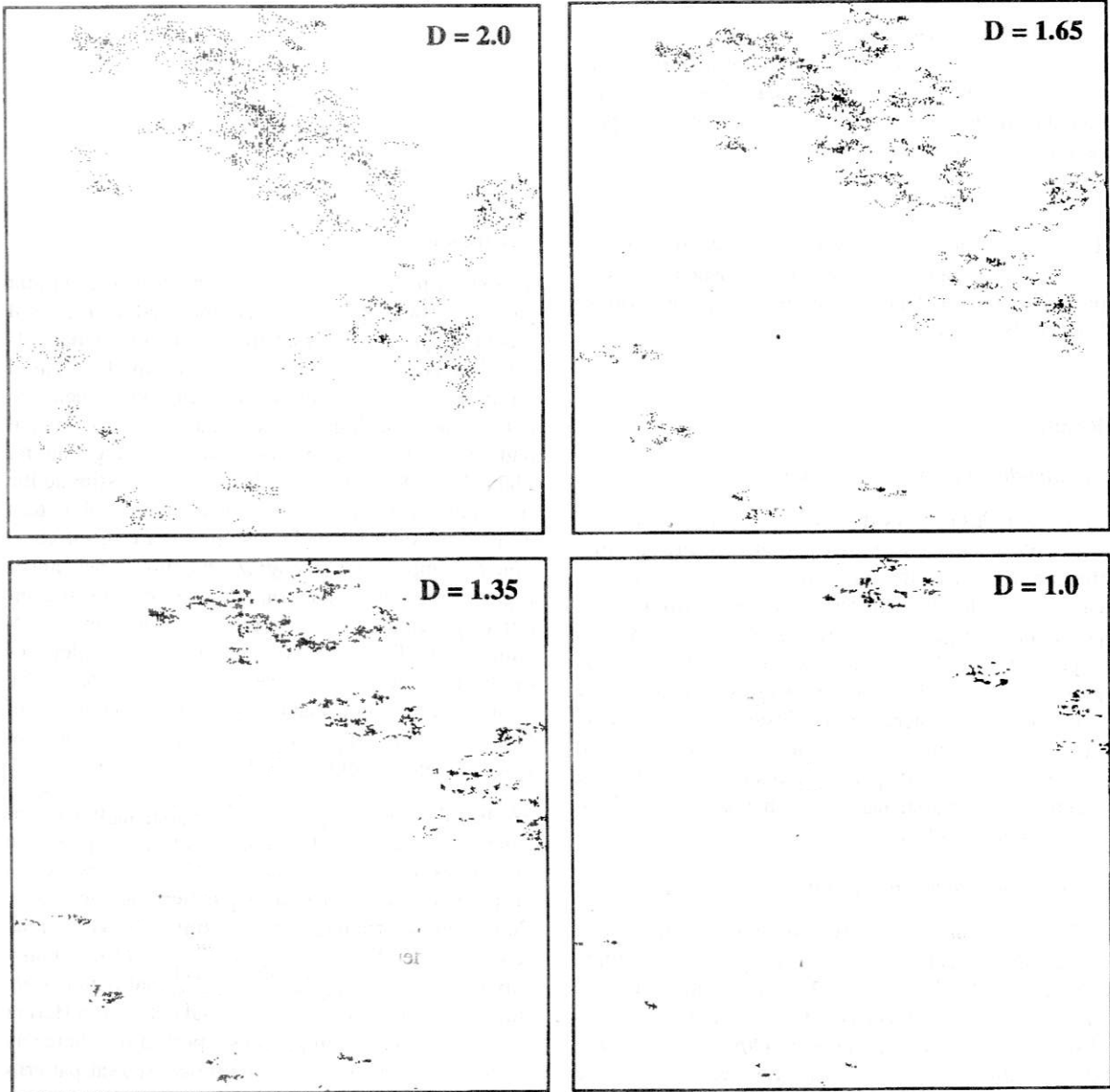


Figure 1. Random simulations of Lévy dust fractal point patterns ($N = 2500$, $r_0 = 0.001$). The quantity D is the fractal dimension. Note that the same random number initiator was used in each case.

sability (log-log slope < 2) expand as isolated local infection spots (see also Gregory 1968).

Returning to the conditional probability of Lévy dusts (equation [1]), the frequency distribution of Lévy flight distances can be derived as:

$$f(r) = D/r_0(r_0/r)^{-(D+1)} \quad (5)$$

Note that this has the form of the inverse power law. This can be linearized (log-log plot) to give:

$$\log f(r) = \log D/r_0 - (D+1) \log (r/r_0) \quad (6)$$

which has the form of the log-log plots of van der Plank (1960). An estimate of the point pattern fractal dimension D for a given species can therefore be obtained from the slope of the log-log plot of the dispersal curve ($D = -(\text{slope} + 1)$).

(c) Dispersal data

The fractal dimension D was computed for various vascular plant species, based on published dispersal data. We used the data summarized in log-log form by Harper (1977: 55).

Results

(a) Simulated Lévy dust fractal point patterns

Four examples of Lévy dust fractal point patterns ($D = 2.0, 1.65, 1.35$ and 1.0) are illustrated in Fig. 1. Note that we used the same initial random number in each case, to emphasize differences in the distribution of point clustering at various fractal dimensions. At $D = 2$, points tend to fill the plane, since almost all the dispersal distances (Lévy flight lengths) are relatively small. Points are increasingly clustered with decreasing fractal dimension, reflecting an increased probability of large dispersal distances. At $D = 1.0$, for example, the spatial pattern is characterized by isolated patches or clusters.

(b) Fractal dimension of plant species

Table 1 summarizes the results of slope and fractal dimension D calculations for eight vascular plant species. Fractal dimensions $D > 2$ are characteristic of species having no special adaptations for long-distance dispersal (e.g., *Papaver dubium*, *Dipsacus sylvestris*, *Dactylis glomerata*). Seeds of these species fall close to their parent, resulting in a 'phalanx' type of colonization (c.f. Fig. 1, $D = 2$). Species with wind-dispersed seeds (e.g. *Senecio jacobaea*, *Picea engelmannii*, *Verbascum thapsus*) have $D < 2$, resulting in a 'guerilla' type of colonization (c.f. Fig. 1, $D = 1$).

Table 1. Estimated slope and fractal dimension D of various plant species. Based on the log-log dispersal plots in Harper (1977:55).

Species	Slope	Fractal dimension (D)
<i>Dactylis glomerata</i>	-5.24	> 2
<i>Papaver dubium</i>	-3.91	> 2
<i>Dipsacus sylvestris</i>	-3.83	> 2
<i>Picea engelmannii</i>	-2.55	1.55
<i>Verbascum thapsus</i>	-2.42	1.42
<i>Eucalyptus regnans</i>	-2.00	1.00
<i>Senecio jacobaea</i>	-1.64	0.64
<i>Tussilago farfara</i>	-1.02	0.02

Discussion

This study has shown that the 'Lévy dust' fractal point patterns (Mandelbrot 1983) can be used as a general model of species dispersal and vegetation spatial pattern. We have shown that the Lévy dust model is based on an inverse power law relationship. Published dispersal data for higher plant diaspores and fungal pathogens also fit the inverse power law (e.g. van der Plank 1960, Harper 1977). Thus one can estimate the fractal dimension D from dispersal data, which in turn allows one to visualize the resulting spatial configuration. It is important to recognize that this model cannot reproduce a specific pattern, but rather its essential underlying features (e.g. degree of clustering, self-similarity). This is analogous to the problem of describing coastline complexity (Mandelbrot 1967): while a fractal model cannot reproduce the coastline of Britain (say) exactly, it does summarize a number of essential features of the coastline.

We feel that the fractal 'Lévy dust' approach has considerable potential in modelling fungal pathogen epidemics, colonization and distribution of weeds in crop fields, and vegetation patterning generally. Published information on epidemic disease spread (e.g., van der Plank 1960, Gregory 1968) certainly supports our view that biological spatial patterns are fractal, and our analysis of dispersal data (from Harper 1977) offers further empirical support. But is there any evidence of fractal-like (self-similar) spatial patterns in vegetation? Unfortunately, very few maps of the spatial pattern of organisms over a number of spatial scales have been published. Perhaps the best example is the distribution of *Clematis fremontii* (Erickson 1945), which we have reproduced in Fig. 2 (at three



Figure 2. The spatial pattern of *Clematis fremontii* var. *riehlii* at three spatial scales (adapted from Erickson 1945).

scales; Silvertown & Lovett-Doust [1993: 108] illustrate the pattern over all five spatial scales mapped by Erickson). What is remarkable about this set of maps is the clear display of empirical self-similarity. Of course we recognize that this (or any other) spatial pattern is determined by a number of factors other than dispersal. For a species to occur at a given location, it must first of all arrive there. However, it may not succeed at a given site for a number of reasons. Abiotic conditions (e.g., edaphic factors) may not be favourable for germination and/or establishment, or the species may be outcompeted by other species. Historical factors (e.g. the occurrence and frequency of fire) will also play a role in determining species success at a site.

It is apparent that a complex of factors determine the actual pattern observed. Given this fact, is there any hope of modelling the actual spatial pattern of a species? As already mentioned, the fractal model is of limited use if one wishes to obtain an exact map. However, if our objective is to model and duplicate the 'overall look' of the pattern, the fractal model is particularly useful. As an example, consider the distribution of earthquake epicenters modelled by Ogata & Katsura (1991). Just as the determinants of biological patterns are complex, locations of earthquake epicenters are controlled by a complex of geomorphological and geophysical factors, which precludes development of an exact model of their spatial distribution. Nonetheless, Ogata and Katsura demonstrated that the empirical pattern of epicenters in Japan displayed fractal properties ($D = 1.26$). Thus the Lévy dust fractal point pattern model is applicable even if the processes generating the spatial pattern are complex and synergistic.

Our study suggests that plant species can be ordered along a 'dispersability gradient', with the position of a species along the gradient determined by its fractal dimension. Species with low dispersability have a higher fractal dimension ($D = 2$). As such, they are expected to move through the landscape as a slowly advancing front, and to be relatively evenly distributed across the landscape (see Fig. 1, $D = 2$). By contrast, species of low fractal dimension ($D < 1$) show higher dispersability (e.g. ruderal plant species). Such species are expected to move through the landscape in jumps, forming isolated colonies. As a result, they show a highly clustered pattern at all spatial scales (see Fig. 1, $D = 1$).

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