

Diversity pattern and spatial scale: a study of a tropical rain forest of Malaysia

FANGLIANG HE, PIERRE LEGENDRE and CLAUDE BELLEHUMEUR

Département de sciences biologiques, Université de Montréal, C. P. 6128 Succursale Centre-ville, Montréal, Québec, Canada H3C 3J7

JAMES V. LaFRANKIE

Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Panama

Received October 1994; revised January 1995

Scale is emerging as one of the critical problems in ecology because our perception of most ecological variables and processes depends upon the scale at which the variables are measured. A conclusion obtained at one scale may not be valid at another scale without sufficient knowledge of the scaling effect, which is also a source of misinterpretation for many ecological problems, such as the design of reserves in conservation biology.

This paper attempts to study empirically how scaling may affect the spatial patterns of diversity (tree density, richness and Shannon diversity) that we may perceive in tropical forests, using as a test-case a 50 ha forest plot in Malaysia. The effect of scale on measurements of diversity patterns, the occurrence of rare species, the fractal dimension of diversity patterns, the spatial structure and the nearest-neighbour autocorrelation of diversity are addressed. The response of a variable to scale depends on the way it is measured and the way it is distributed in space.

We conclude that, in general, the effect of scaling on measures of biological diversity is non-linear; heterogeneity increases with the size of the sampling units, and fine-scale information is lost at a broad scale. Our results should lead to a better understanding of how ecological variables and processes change over scale.

Keywords: fractal dimension, richness, scale, Shannon diversity, spatial structure, tree density, variogram

1. Introduction

Ecology must deal with scale, because the objects it focuses on, the organisms and types of environment, are rarely found to be homogeneously distributed through space or time. Environmental forcing, population and community dynamics, and chance events, are all sources of heterogeneity (Dutilleul and Legendre, 1993) and contribute to create spatial structures of various kinds, the most common of which are gradients and patches (Borcard and Legendre, 1994; Legendre and Fortin, 1989). Thus heterogeneity makes ecological variables and processes scale-dependent. An exploration of how diversity patterns change over scale is needed for extrapolation of fine-scale results to broader-scale phenomena, or the reverse. The concept of spatial scale refers to three main components of the sampling design:

- (i) Grain size, or size of the sampling unit, which is the surface or volume support of any particular measurement.
- (ii) Extent of the total area being sampled, or field size.

- (iii) Sampling interval (called 'lag' in time series), which is the average distance between neighbouring samples.

Grain and extent define the upper and lower limits of resolution of a study. Inference in any study is limited by its grain and extent. No generalization exceeding grain or extent could be derived without an assumption that the variables and processes are scale-independent. Comprehension of how grain and extent affect our perception of ecological phenomena is fundamental to an understanding of scaling effects. Furthermore, in ecology the sampling interval is considered as another aspect of the spatial scale of a study (Fortin and Legendre, 1989; Palmer, 1988). However, the aspect of scale defined by sampling interval is not our concern here. The present paper studies scale only in terms of the range of resolution of a study, characterized by grain and extent.

Many ecological variables and processes such as plant succession (Dale and Blundon, 1990), foraging behaviour (Kareiva, 1982), competition (Shorrocks *et al.*, 1979), predator–prey interactions (Huffaker, 1958; Chesson, 1978), dispersal (Southwood, 1962; Wiens and Milne, 1989), nutrient cycling (Allen and Hoekstra, 1991), and the spread of disturbances (Minnich, 1983; Knight, 1987) are scale-dependent. Variables estimated and processes identified at one scale may not be important at another. Studies of large-scale ecological processes often require the extrapolation of fine-scale results to a broader-scale phenomenon (Steele, 1991); such an extrapolation is not possible if the effect of scaling on these ecological processes is unknown. For example, in a tropical rain forest in Malaysia, He, Legendre and LaFrankie (unpublished) found that some populations that are abundant and highly clumped at larger scale may demonstrate regular distributions at smaller scale, which implies that competition may not have been detected by a broad-scale study although it is present at finer scale. On the other hand, in a global comparison of biome maps predicted by two different models, the value of the kappa (κ) statistic (which is a measure of agreement of two spatial distributions) was found to be scale-dependent (Prentice *et al.*, 1992).

Early work in plant ecology has recognized that sampling scale is a key in describing the spatial patterns of a community (Greig-Smith, 1952). Nevertheless, the importance of scale in ecology has been widely ignored, until the past decade or so, for lack of proper methods to study it (Dayton and Tegner, 1984; Wiens *et al.*, 1986; Giller and Gee, 1987; Meentemeyer and Box, 1987; Wiens, 1989; Kolasa and Pickett, 1991). Most theories in ecology ignore the scale effect, which is one of the major reasons for ecological controversies such as the role of density-dependent factors in population regulation (Antonovics and Levin, 1980); the importance of herbivores in structuring a plant community (Brown and Allen, 1989); equilibrium theories in tropical communities (Janzen, 1970; Connell, 1978; Hubbell, 1979); and so on. Because they neglect scale dependence, many ecological theories poorly predict field observations. For example, two species which are predicted to be competition-exclusive by the Lotka–Volterra model may actually coexist in reality because of the existence of spatial structures which are not taken into account by this model (den Boer, 1968, 1971; Dewdney, 1984; Moloney, 1988). Fortunately, recent developments, especially in landscape ecology (Forman and Godron, 1986), in ecological hierarchical theory (Allen and Starr, 1982) and in the awareness of spatial problems in ecology (Legendre and Fortin, 1989; Dutilleul, 1993; Legendre, 1993), have emphasized the importance of spatial structures for ecological phenomena and of greatly expanding the spatial and temporal ranges of our studies.

In conservation biology and tropical rain forest studies, arguments have been developed that are closely related to the scale problem, raising interesting questions. For instance: what are the optimal spatial size and shape of areas that should be set aside for conservation of species (Shaffer, 1981; Gilpin, 1989)? How does the fragmentation of a forest affect the extinction of a species locally or globally (Harris, 1984; Hubbell, 1984)? How can we tell that a community is in equilibrium

(Connell, 1978; Hubbell, 1979)? It is not clear how these questions are related to scale, although some of them, such as those related to equilibrium theory, have been extensively studied.

The present study deals with how spatial scale affects the diversity patterns that can be measured in a tropical forest; we use a rain forest plot in Malaysia as a test case. In this study, diversity is measured by three community parameters: tree density, richness, and Shannon diversity. Specifically, the following four aspects will be tackled: (i) How does sampling scale affect the means and variances of measurements of tree density, richness and Shannon diversity? (ii) How are the occurrences of rare species affected by spatial scale? (iii) What is the relation between the fractal dimension of diversity patterns and grain size? (iv) How does scale affect the spatial structures and nearest-neighbour autocorrelations of diversity patterns? The results should be helpful to better understand how ecological variables and processes change with respect to scale.

2. Study site and methods

2.1 Study site

A tract of mapped forest, located at 102°18' W and 2°55' N, was established in the Pasoh Reserve, Negeri Sembilan, Malaysia, to monitor long-term changes in a primary forest (hereafter called the Pasoh forest). The vegetation is primary rain forest and falls within the south-central subtype of the red meranti-keruing forest type of Wyatt-Smith (1987). The upper canopy is dominated by red meranti, *Shorea* section Muticae, especially *S. leprosula* Miq., *S. acuminata* Dyer, and *S. macroptera* Dyer. Other important canopy emergents are keruing, *Dipterocarpus cornutus* Dyer, balau, *Shorea maxwelliana* King, and chengal, *Neobalanocarpus heimii* (King) Ashton. Mean annual rainfall at Pasoh is about 2000 mm, which puts it among the driest stations in Peninsular Malaysia.

The forest tract under study is a rectangle 1 km long and 0.5 km wide (50 ha). The survey enumerated all free-standing trees and shrubs at least 1 cm in diameter at breast height (dbh), positioning each one by geographic coordinates on a reference map, and identifying the species. The diversity of the plot is quite high: there are 334 077 trees, belonging to 825 species. There are no obvious dominant species. The most abundant one, *Xerospermum noronhianum* (Sapindaceae), accounts for only 2.5% of the total number of trees (Kochummen *et al.*, 1991).

This data set is almost unique in that all individual trees and shrubs at least 1 cm dbh are identified, sized, and geographically located. So we can artificially 'sample' this forest in whichever way we like, using a computer. We will actually reorganize the study area in quadrat units, changing the quadrat size (grain) from 5 × 5, 10 × 5, 10 × 10, 20 × 10, 20 × 20, 40 × 20, 50 × 50, 100 × 50 to 100 × 100 m (Fig. 1A). In each quadrat of a given sampling design (= size), tree density, richness and Shannon diversity were measured, which makes a scaling study possible. Besides changing the grain size, the extent (= the area included in the study) was also changed from 10 × 10, 20 × 20, 40 × 40, 80 × 80, 160 × 160, 320 × 320, 620 × 500 to 1000 × 500 m, starting from the center of the Pasoh forest plot, with a fixed grain size of 5 × 5 m (Fig. 1B).

Tree density is the number of trees per square metre in a quadrat. Richness is the number of species in a quadrat. The Shannon diversity index is computed as:

$$H = -\sum_i p_i \log p_i$$

where p_i is the proportion of the abundance of the i th species to the total abundance in a quadrat (natural logarithms were used). The units of H are bits per sample if base 2 logs are used, and nats (or nits) with natural logs. Margalef (1958) proposed using this measure of entropy as an index of diversity.

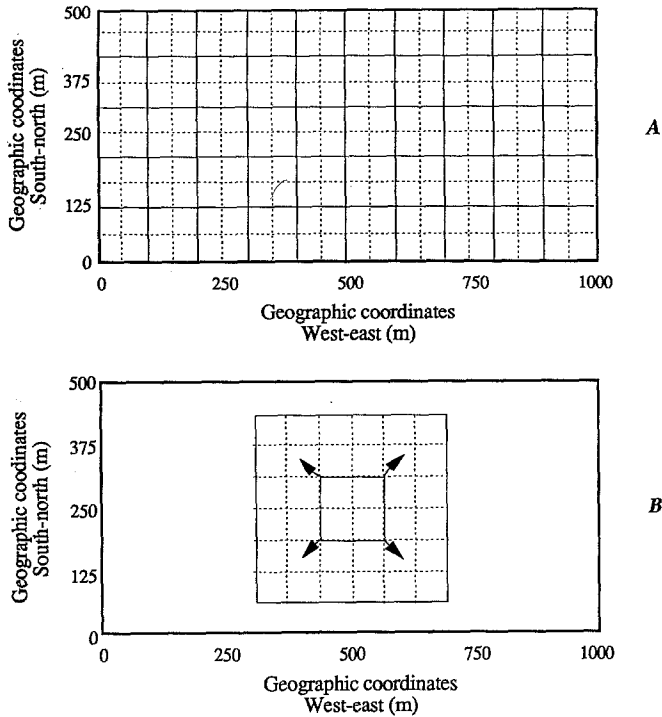


Figure 1. Schematic sampling design used on the data of the 50 ha Pasoh forest. In each sampling quadrat, tree density, richness and Shannon diversity are counted or calculated. *A.* The dashed lines are an example of fine-scale grain sampling quadrats, while the solid lines delimit the broad-scale sampling units. Nine grain sizes were actually used to study the effect of grain size on diversity patterns: 5×5 , 10×5 , 10×10 , 20×10 , 20×20 , 40×20 , 50×50 , 100×50 and 100×100 m. *B.* The sampling design was used to study the effect of sampling extent on diversity patterns. Holding the grain size constant (5×5 m, dashed grid), the extent (solid frame) is changed from 10×10 , 20×20 , 40×40 , 80×80 , 160×160 , 320×320 , 620×500 to 1000×500 m.

2.2 Data analyses

2.2.1 Spatial variance and predictability

Each grain size and extent produces a mean and spatial variance computed among quadrats, for each observed ecological variable (diversity, etc.). The mean and variance, which will be used for descriptive purposes only, are calculated using the standard formulas, without special allowance for spatial autocorrelation:

$$\text{mean of a spatial variable } x: \quad m_x = \frac{1}{n} \sum_{i=1}^n x_i \quad (1)$$

$$\text{variance of a spatial variable } x: \quad s_x^2 = \frac{1}{n-1} \sum_{i=1}^n (x_i - m_x)^2 \quad (2)$$

where x_i is the observation at location i and n is the total number of observations. All these

quantities vary as functions of the parameters of the sampling scale: grain and extent. Tree density, richness and Shannon diversity of the Pasoh forest will be analysed in the present paper.

Our perception of the occurrence of rare species changes over sampling scales. We will attempt to determine how important rare species may be on diversity measures, for various sampling scales. The influence of rare species can be measured by correlating the diversity variables with all species included, to their counterparts when rare species are excluded. The question can be asked in another way: To what extent can the real information be estimated if rare species are absent from the data? That is, how important are the rare species in this estimation? It is obvious that this estimation varies with scale. So the correlation (the coefficient of determination R^2 will actually be used) between the two data series is a function of grain size. For the purpose of this study, the species whose density is equal to or less than 1 tree per hectare are defined as rare species; this sets the limit to at most 50 individuals in the 50 ha plot (Hubbell and Foster, 1986).

2.2.2 Variogram and fractal dimension

The variogram is the theoretical basis and methodology of geostatisticians for the estimation and mapping of regionalized variables. Recently it has been widely used to describe the spatial structure of ecological variables (Phillips, 1985; Palmer, 1988; Legendre and Fortin, 1989; Rossi *et al.*, 1992). Variograms measure spatial variability, giving the relative degree of dissimilarity between values separated by a vector $\mathbf{h}$, which is characterized by an intensity (distance) and a direction. The experimental variogram is given by:

$$\gamma^*(\mathbf{h}) = \frac{1}{2N(\mathbf{h})} \sum_{i=1}^{N(\mathbf{h})} (x_i - y_i)^2 \quad (3)$$

where $N(\mathbf{h})$ is the number of pairs, x_i is the value at one end of vector $\mathbf{h}$, and y_i is the value at the other end. The locations of the two values x_i and y_i are separated by vector $\mathbf{h}$.

Journal and Huijbregt (1978, pp. 161–95) proposed a series of variogram models describing the spatial continuity of a random function modelling the dispersion of a variable through space. This function is chosen after examination of the experimental variogram. They proposed two main types of models characterized by the presence or absence of a sill.

The presence of a sill implies stationarity of the covariance, i.e. the covariance exists and depends only on the vector $\mathbf{h}$:

$$C^*(\mathbf{h}) = \left[\frac{1}{N(\mathbf{h})} \sum_{i=1}^{N(\mathbf{h})} x_i \cdot y_i \right] - m^2 \quad (4)$$

where m is the mean. Stationarity of the covariance implies stationarity of the variance and of the variogram. Models without a sill correspond to random functions that are said to be only intrinsic. Their *a priori* variance and covariance are not defined. The increment $(x_i - y_i)$ has a finite variance which does not depend on their locations but only on $\mathbf{h}$.

All experimental variograms for tree density, richness and diversity index reported in the results show a well-defined sill and indicate isotropic phenomena, i.e. $\gamma(\mathbf{h})$ does not depend on the direction of $\mathbf{h}$. They were fitted using an exponential model plus a nugget effect:

$$\begin{aligned} \gamma(\mathbf{h}) &= C_0 + C_1(1 - \exp(-\mathbf{h}/a)) & \text{if } \mathbf{h} > 0 \\ \gamma(\mathbf{h}) &= 0 & \text{if } \mathbf{h} = 0 \end{aligned} \quad (5)$$

where C_0 is the *nugget effect*, which represents the discontinuity at distance zero. Several factors

such as sampling error or fine-scale spatial variability may result in a nugget effect. The ratio of the nugget effect to the sill, called the relative nugget effect, can be used to evaluate sampling error and fine-scale spatial effects. C_1 is the variability due to the structure in the exponential model and a is a parameter. The exponential model reaches its sill ($C_0 + C_1$) asymptotically. The *range* of a model with a sill is the distance where the spatial influence disappears, i.e. $\gamma(h)$ ceases to increase. The practical range of an exponential model is defined as $3a$, the distance at which the variogram is 95% of C_1 .

In the present study, the nugget effect, the relative nugget effect, the sill and the range are used to describe the spatial features of a variable and to demonstrate how these parameters change with sampling scales; this will allow us to evaluate the effect of scale on the estimation of spatial structures.

The fractal dimension D is a measure commonly used to study the features of surfaces and the effect of scaling (Burrough, 1981; Phillips, 1985; Culling, 1986; Frontier, 1987; Krummel *et al.*, 1987; Palmer, 1988; Milne, 1991). Several methods allow us to calculate the fractal dimension of surfaces (Carr and Benzer, 1991; Bolviken *et al.*, 1992). For a fractal surface, the variogram follows the equation (Mandelbrot, 1983, p. 353):

$$\gamma(h) = Kh^{2H} \quad (6)$$

corresponding to a power model. The fractal dimension of the surface is given by

$$D = 3 - H. \quad (7)$$

This result allows one to calculate the fractal dimension D for a real data set from the log-log plot of the variogram:

$$\log(\gamma(h)) = \alpha + \beta * \log(h) \quad (8)$$

The slope $\beta (= 2H)$ of the equation is then equal to $6 - 2D$.

We have mentioned previously that the variograms of the variables of interest follow exponential models which have a sill and a defined and finite *a priori* variance. The power model, which describes a self-similar fractal, corresponds to a phenomenon with an unlimited capacity for spatial dispersion and with an undefined *a priori* variance (Journel and Huijbregts, 1978). So the fractal nature or the self-similarity of the phenomenon is only defined locally, near the origin where the variogram is linear in the log-log plot. It is bounded by a lower and an upper scale of self-similarity. If a variable is strongly autocorrelated both in the short and long distances, i.e. $\gamma(h)$ is approximately a parabolic function of the distance h , D is close to 2; conversely, if a variable has its values randomly distributed in space (no autocorrelation), D equals 3. The fractal dimension is a measure of the degree of spatial dependence of a variable. So the relation of D to the sampling scale indicates the trend of the spatial structure of a variable.

2.2.3 Nearest-neighbour autocorrelation

The method used here to study nearest-neighbour autocorrelation was proposed by Legendre and Borcard (1994). For n locations in space, the value at each location could be estimated at least partly from its neighbours if autocorrelation is present in the data. Assume that the i th location has p_i nearest-neighbours and that each neighbour contributes equally, i.e. with weight $1/p_i$, to the estimation of that location. A nearest-neighbour matrix $NM_{n \times n}$ is formed with $1/p_i$ as its entities if they are nearest neighbours, and 0 otherwise. The estimated value $X'_{n \times 1}$ from nearest-neighbour autocorrelation could be calculated by postmultiplying NM with the observed values $X_{n \times 1}$ (Fig. 2):

$$NM * X = X' \quad (9)$$

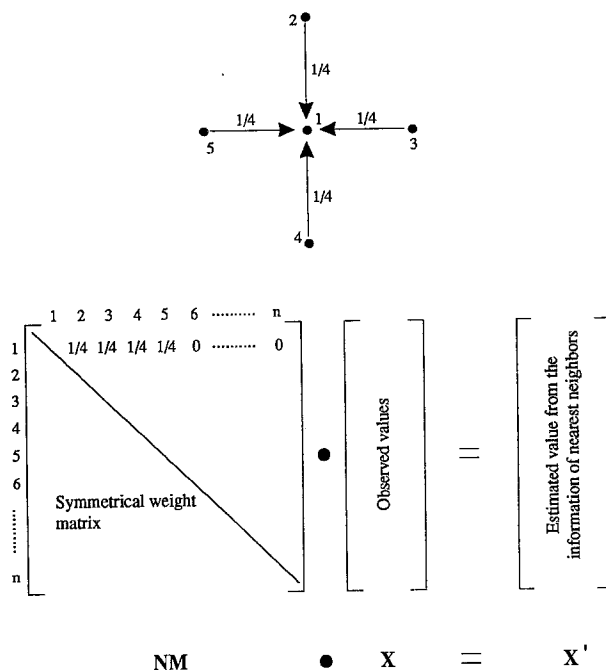


Figure 2. Illustration of the computation of the estimated value at any one point i based on the information of its nearest neighbours. This example assumes that each value has four nearest neighbours. The row of weights for point no. 1 is shown, assuming the nearest-neighbour structure displayed at the top.

The correlation between X' and X indicates the degree of nearest-neighbour influence. Our interest is to study how nearest-neighbour autocorrelation changes over sampling scales; of course, second or third, etc. nearest-neighbourhood effects could also be studied in the same way.

3. Results and discussion

3.1 Spatial mean and variance

Mean tree density (always measured per m^2 in this study) is a constant in the Pasoh forest, regardless of grain size, while mean richness and Shannon diversity are convex increasing functions of grain size if we hold the extent of the sampling zone constant (Fig. 3). Density is constant across scales. This variable is said to be additive, meaning that its values can be added or averaged to create larger quadrats, while retaining the same meaning as the original variable; values for tree density, which form an intensive variable (its values represent an 'intensity' defined independently of the size of the actual sampling units) can actually be averaged only if they are referred to the same unit of surface (here, the number of trees per m^2). Species richness and Shannon diversity are not additive; for example, the sum of the numbers of species in two adjacent quadrats is usually larger than the number of species in the combined quadrat. The relation of these variables to scale depends on the distribution patterns of the species and the grain size of the measurements.

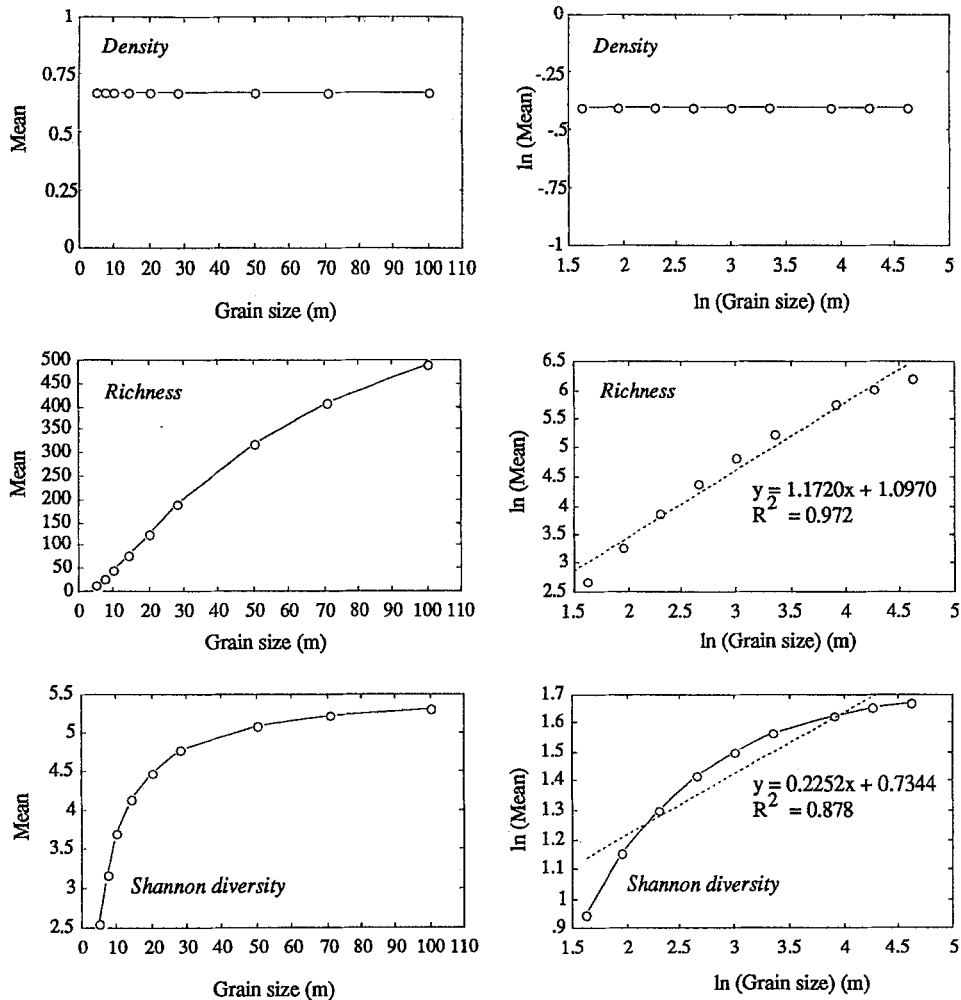


Figure 3. Relationships between mean tree density, richness and Shannon diversity on the one hand, and grain size on the other, showing how grain size affects the measurements. Right-hand plots are log-log transformations of left-hand plots. Mean tree density is scale-independent, while the other two measures are in inverse exponential relation with grain size. In the two lower right-hand plots, linear regression lines are shown as references against which the curvature of the displayed relationships can be appreciated.

The spatial variances of tree density and Shannon diversity in the Pasoh forest illustrated in Fig. 4 display concave decreasing relations with grain size, while richness shows a convex increasing relation.

The mean and variance of a variable are also a function of the spatial extent of the investigation. Holding grain size constant (5×5 m), the effect of sampling extent on tree density, richness and Shannon diversity were computed (Fig. 5). Compared to grain, the effect of extent is more complicated to explain. The heterogeneity of a variable generally increases with spatial extent, because more patches are included as the study area expands. Including a new type of patch may cause an abrupt change in variance. Or, new patches may be included which make the variance

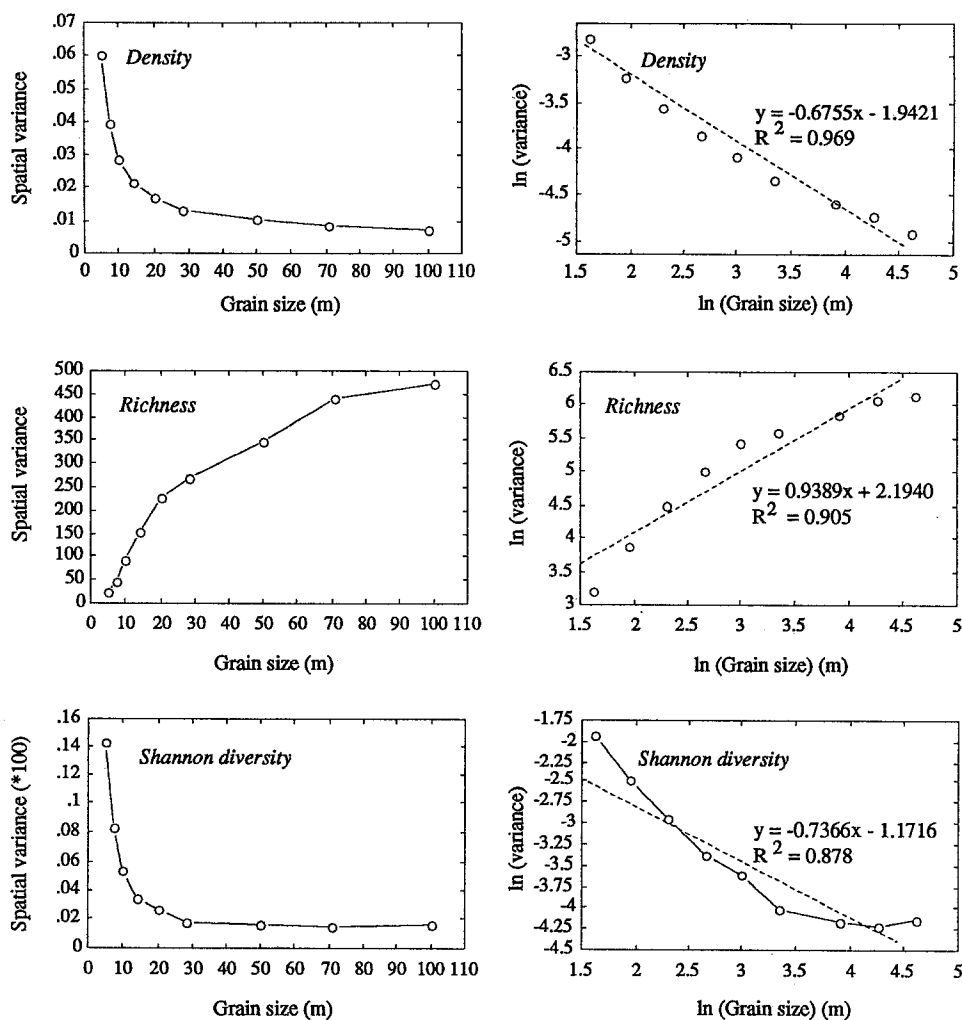


Figure 4. Relationships between the variance of tree density, richness, and Shannon diversity on the one hand, and grain size on the other (expressed as the square root of the grain surface area), showing how the variance of a measurement is a negative exponential function of grain size. Right-hand plots are log-log transformations of left-hand plots. In the right-hand plots, linear regression lines are shown as references against which the curvature of the displayed relationships can be appreciated.

display a periodic variation along the extent axis; Turner *et al.* (1989) have obtained this pattern in a landscape ecology study. Figure 5 also shows that at small extent values, the means and variances of variables are more variable (among extent values) than for larger extents. The reason is probably that for small extents, the spatial heterogeneity among sampling quadrats (for constant grain size) is higher; one is then more likely to find sample quadrats belonging to different patch types. As extent increases, the rate at which new types of patches are found slows down, and heterogeneity is gradually averaged out until the sample grows enough to incorporate another type of community.

It is obvious from Figs 3, 4 and 5 that scaling effects are important in the estimation of ecological parameters. How ecological phenomena respond to scale depends on the properties of the measurement, the sampling scheme and the spatial distribution. A population parameter measured, or a

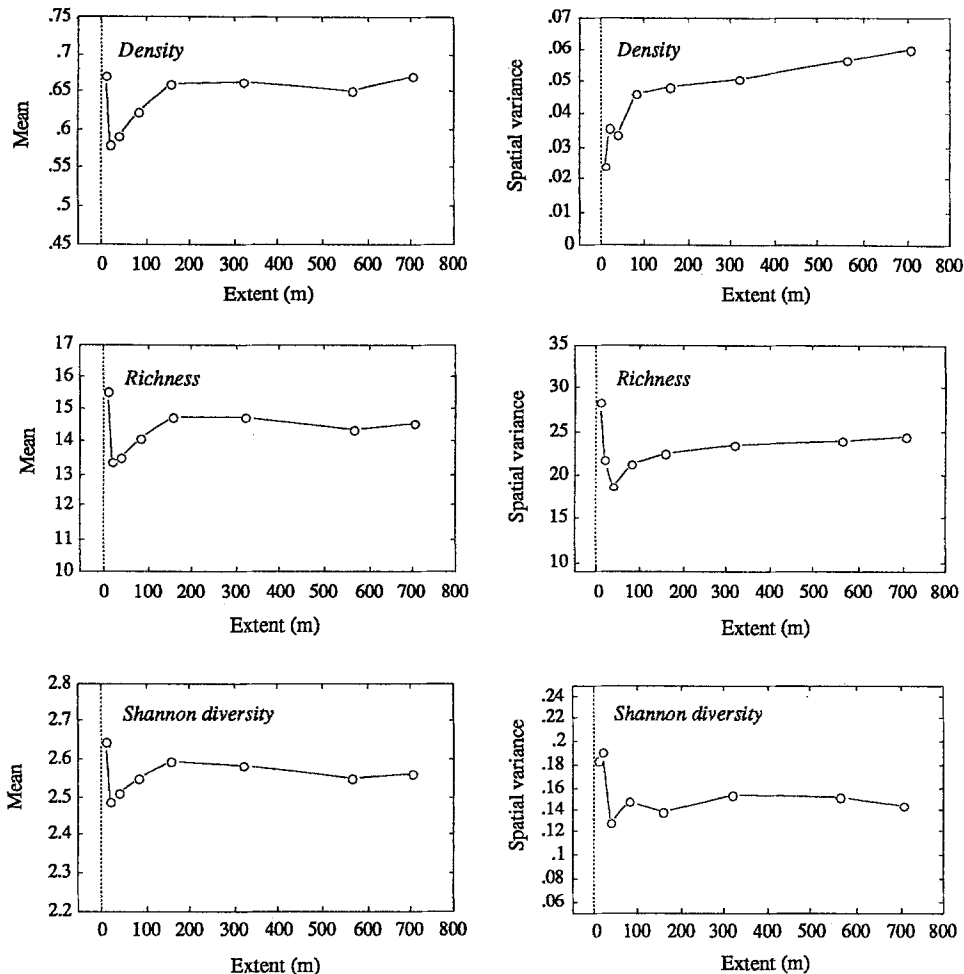


Figure 5. Relationships between extent size and the mean (left) and spatial variance (right) of tree density, richness and Shannon diversity, showing how extent affects the measurements. At small extent, the measurements are variable; they become stable for larger values of extent. This implies that a study area (extent) should be large enough to include sufficient information for an accurate estimation of these parameters.

conclusion obtained, at one scale may not hold at another scale. For example, Shannon diversity over the whole plot is 5.64 (nits) for the Pasoh forest, while at 50×50 and 10×10 grain scales its mean values are 5.10 and 3.68 respectively. As grain size increases, variances of tree density and Shannon diversity decrease, while the variance of richness increases. On the other hand, when increasing the spatial extent, the variance becomes more stable because proportionally fewer new patches become included in the analysis.

Classical statistical and geostatistical theories give analytical solutions to predict the change in variance due to different sampling unit sizes, for intensive additive variables such as tree density. For such variables, whose mean value in principle does not change with grain size if they have been sampled over a completely homogeneous area and there is no autocorrelation among samples,

statistical theory suggests that the dispersion variance of the quadrats should decrease linearly with the number of sampling units in a quadrat or a composite sample:

$$\text{Var}(V_c/A) = \text{Var}(V/A)/N \quad (10)$$

where $\text{Var}(V_c/A)$ is the variance of the composite samples in area A , $\text{Var}(V/A)$ is the original variance of the sampling units in the same area, and N is the number of sampling units in a composite. This relationship shows that the variance of the composite sample decreases linearly with the increase in size of the support (grain size). This conclusion is valid only for homogeneous systems where sampling units are independent. When the process is complicated by patterns of spatial heterogeneity, the above relationship is no longer valid. Levin (1989) and Wiens (1989) present some empirical results showing the complexity of such heterogeneous processes. In our results (Fig. 4), the relationship between $\ln(\text{variance})$ and $\ln(\text{grain size})$ for the density, with a slope of -0.675 , shows a departure from classical theory, which would have allowed us to expect a slope of -2 if the area had been homogeneous. The expected value is -2 because we used the square root of the surface area as a measure of grain size, and Fig. 4 is in log-log scale. This departure from classical theory results from performing a change of support in a heterogeneous, spatially autocorrelated area.

Problems of change of support (grain size) have received attention in the geostatistical literature dealing with ore reserve estimation (Journel and Huijbregts, 1978, pp. 61–94; Isaaks and Srivastava, 1989, Chapter 19). Geostatisticians want to perform estimations about the grades of large blocks from data obtained from small drill cores. Equation (10) cannot be used because the data are usually autocorrelated (underlying heterogeneous process). For a homogeneous area, reduction in variance associated with a given change of support is more important than for a heterogeneous area where spatial autocorrelation is present.

The additivity property of variances in nested designs allows us to write

$$\text{Var}(v/A) = \text{Var}(v/V) + \text{Var}(V/A) \quad (11)$$

where $\text{Var}(v/A)$ is the dispersion variance associated with a small volume v in area A ; $\text{Var}(V/A)$ is the dispersion variance associated with a large volume V in area A ; and $\text{Var}(v/V)$ is the dispersion variance associated with a small volume v in the large volume V . Journel and Huijbregts (1978, pp. 66–7) show that the dispersion variance $\text{Var}(v/V)$ is related to the variogram as follows:

$$\text{Var}(v/V) = \bar{\gamma}(V, V) - \bar{\gamma}(v, v) \quad (12)$$

where $\bar{\gamma}(V/V)$ is the average variogram value calculated over all possible distance vectors $\mathbf{h}$ contained in V . It represents the within-surface variance. The mean values $\bar{\gamma}(V, V)$ can be calculated numerically from function $\gamma(\mathbf{h})$ by discretizing the support V into a finite number of small volumes. Journel and Huijbregts (1978, pp. 108–23) developed a series of auxiliary functions giving a pre-calculated mean value of $\bar{\gamma}(V, V)$ corresponding to simple geometries of V that are frequently found in practice. Tables and graphs allowing to calculate $\bar{\gamma}(V, V)$ from these auxiliary functions are given in Journel and Huijbregts (1978, pp. 125–47) for some variogram models.

When a support v is used to compute experimental variograms, a regularized form of variogram is estimated. We must deduce a point-support model $\gamma(\mathbf{h})$ (i.e. $v = 0$) from a regularized model $\gamma_v(\mathbf{h})$. Using the approximate formula of Journel and Huijbregts (1978, p. 89):

$$\gamma_v(\mathbf{h}) = \gamma(\mathbf{h}) - \bar{\gamma}(v, v) \quad \text{for } \mathbf{h} > v \quad (13)$$

where $\gamma_v(\mathbf{h})$ is the variogram defined for a support of size v . If $\gamma_v(\infty) = C_1$, which is the sill value, or the variance component of the spatial structure for the non-point support, then

$$C_1 = C'_1 - \bar{\gamma}(V, V) \quad (14)$$

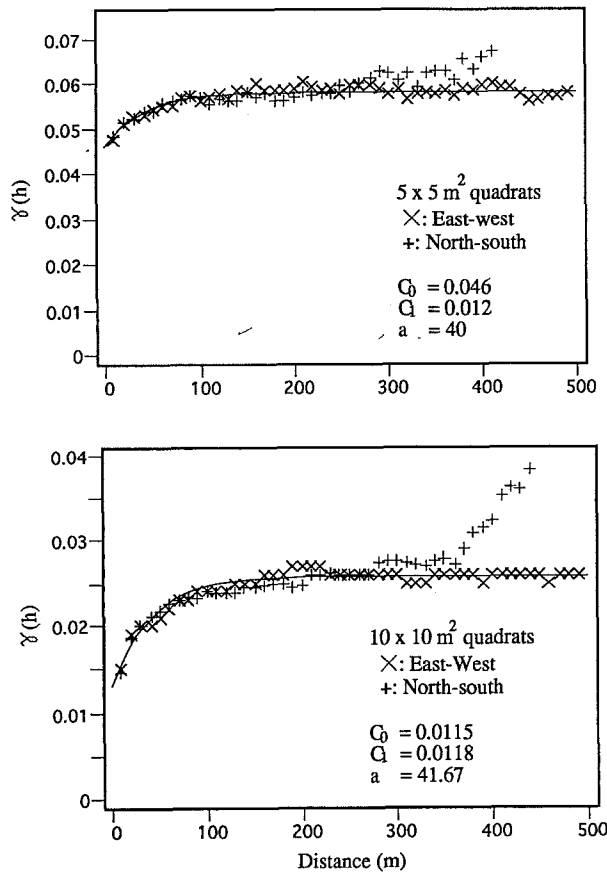


Figure 6. Directional variograms of the tree density variable, and parameters of exponential variogram models (curves) for 5×5 and $10 \times 10 \text{ m}^2$ quadrats. C_0 is the nugget effect; C_1 is the variability due to the structure in the exponential model ($C_0 + C_1$ is the sill); a is a parameter of the exponential model.

where C'_1 is the sill value of the point support. This correction only transforms the spatially structured part of the variance. The variance component ascribed to random variations and modelled by a nugget effect follows the classical relationship (Equation 10).

The range of the spatial structure is also affected by the size of the sampling units. Journel and Huijbregts (1978, p. 84) show that the range of a spatial structure estimated from a support of size L , is $a + L$, where a is the practical range that would be measured if the support was a point. Therefore, changing the size of the support produces changes in the overall dispersion variance and in the parameters characterizing the variogram (nugget effect, relative nugget effect, structured variance component and range).

Figure 6 gives experimental variograms and model parameters for the tree density corresponding to 5×5 , and $10 \times 10 \text{ m}^2$ quadrat sizes, for the north–south and east–west directions. These experimental variograms show well-defined sills and are isotropic, i.e. $\gamma^*(h)$ does not depend on the direction of h . Exponential models with nugget effect (curves in the figure) were fitted to these experimental variograms.

All variogram values up to $h = 250$ m in the north–south direction and to $h = 500$ m in the east–west direction, were estimated with at least 2500 pairs for 5×5 quadrats, and 1250 pairs for 10×10 quadrats. The limit of reliability of these variograms is 250 m in the north–south direction. This limit is generally set to one half the length of the area to ensure that vector h and increments $(x_i - y_i)$ characterize the whole study area, and not only the edge points. Beyond 250 m in the north–south direction, there is an increase in variogram values, indicating the presence of another structure with a range that cannot be evaluated from the available data.

For the 5×5 m² quadrat size, the practical range is 120 m (3×40) and the parameter a' of a point model is equal to $a' = (3a - l)/3 = 38.3$. The point sill value is given by formula (14) as:

$$\begin{aligned} C_1 &= C'_1 - \bar{\gamma}(V, V) \\ 0.012 &= C'_1 - C'_1 \cdot F(5; 5) \\ C'_1 &= 0.0128 \end{aligned}$$

where $F(5; 5)$ is an auxiliary function ($F(L, l)$) defined as the proportion of C'_1 corresponding to the mean value of $\gamma(h)$ when the extremities of h describe a rectangle of sides L and l (Journel and Huijbregts, 1978, p. 138).

The theoretical point-support variogram is an exponential model:

$$\gamma(h) = 0.0128(1 - \exp(-h/38.3)). \quad (15)$$

From this theoretical model, it is possible to calculate the dispersion variance of any given support in the whole area and to find an appropriate variogram model describing the spatial structure features for various quadrat sizes. For example, for 10×10 m² quadrats:

$$\begin{aligned} \bar{\gamma}(V, V) &= C'_1 \cdot F(10; 10) \\ \bar{\gamma}(V, V) &= 0.0016. \end{aligned}$$

From Equation (14), the structured variance component for the 10×10 m² quadrat size is:

$$\begin{aligned} C_{1(10 \times 10)} &= C'_1 - \bar{\gamma}(10, 10) \\ C_{1(10 \times 10)} &= 0.0128 - 0.0016 \\ C_{1(10 \times 10)} &= 0.0112. \end{aligned}$$

The classical relationship (Equation 10) allows to calculate the expected nugget effect (random component) for 10×10 m² quadrats from the knowledge of the nugget effect of the 5×5 m² quadrats ($C_{0(10 \times 10)} = 0.046/4 = 0.0115$). This random component plus the spatially structured component ($C_{1(10 \times 10)}$) represent an analytical solution giving an estimation of the overall variance for 10×10 m² quadrats ($C_{0(10 \times 10)} + C_{1(10 \times 10)} = 0.0227$). The experimental variance value for 10×10 m² quadrats is 0.028, while the classical approach would have given $0.0615/4 = 0.015$. The analytical solution is closer to the experimental values than the classical relationship. The slight underestimation may be due to a long-range spatial structure in the north–south direction which is not modelled, considering the size of this scale compared with the size of the study area.

3.2 Rare species occurrence and predictability

Rare species are of special interest in tropical rain forests, not only because of their contribution to diversity, but also for purposes of conservation (Hubbell, 1984; Hubbell and Foster, 1986). Forest

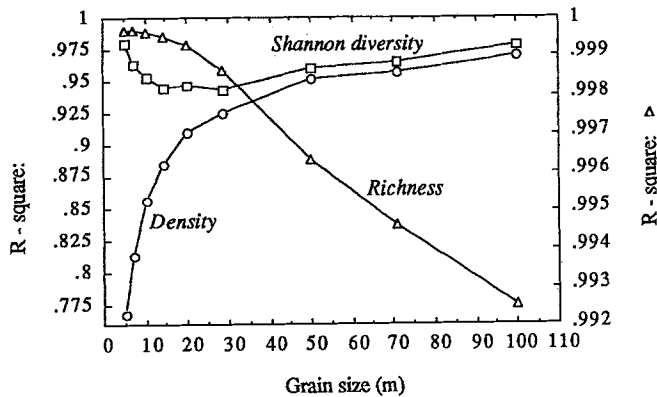


Figure 7. Effect of scaling on the occurrence of rare species. R^2 measures the relation between the values of the variables with all species included, and their counterparts with rare species excluded. So it is a measure of the importance of rare species for these diversity measures. High R^2 means that rare species play a lesser role in a measurement, and vice versa. The graph shows that scale differently affects the effect of rare species on diversity variables.

reserves should be created large enough to allow rare species to maintain a viable population. How much space a rare species requires is a source of controversy among conservation biologists; we believe this to be essentially a problem of scale. This problem is obviously too complex to be completely addressed here. This section has the more limited objective of contributing to understand the effect of scale on our perception of the occurrence of rare species.

In the Pasoh forest, the percentage of rare species is astonishingly high (301 rare species, represented by 4985 individual trees); our criterion for rarity is defined in 2.2.1. The occurrence of rare species in different grain sizes has different effects on tree density, richness and Shannon diversity. The R^2 between the values of the three diversity variables (measured in the various quadrats) with all species included, and their counterparts with rare species excluded, shows the importance of rare species to diversity measures (Fig. 7). A higher R^2 implies that rare species have less influence on the diversity measures, and vice versa. The most distinguishing feature is that different measurements respond differently to the effect of scaling. Figure 7 shows that at small grain size (≤ 20 m), tree density is greatly affected by rare species; that is, the samples without rare species cannot provide adequate information, and depart substantially from the samples with all species included. The R^2 of richness decreases roughly linearly with grain size, because rare species are better represented in samples with large grain size. The Shannon diversity curve is a little more complicated; at both small and large grains, it is less influenced by rare species, compared to grain sizes between 10 and 30 m.

This effect of the occurrence of rare species on diversity estimates may be exacerbated or alleviated, largely depending on the sampling scale and the nature of the diversity measures, for instance the spatial distribution of a measurement used in the calculation of the diversity measure (Turner *et al.* in Wiens, 1989). Census data based on sampling are usually not error-free, contrary to the Pasoh data base used in the present study. Our results show that with such data, which usually underestimate rare species, more precise estimates of density are obtained using a large grain size, while more precise estimates of richness require small grain size. Shannon diversity provides relatively stable estimates over the whole scale of grain sizes, although it does slightly worse at intermediate grain size values. No grain size is optimal for all diversity variables.

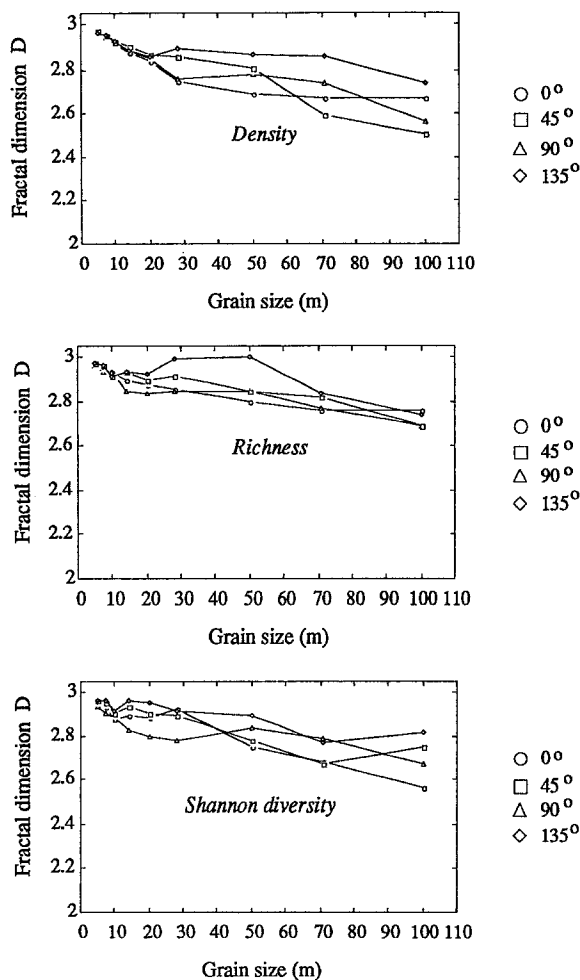


Figure 8. The effect of grain size on the fractal dimensions (D) of tree density, richness and Shannon diversity in the Pasoh forest. D generally decreases with larger grain size, which means that heterogeneity increases.

3.3 Fractal dimension

Fractal dimension is a useful measure of the complexity of a surface pattern. For a surface, the fractal dimension D takes values between 2 and 3. A low D value means that the heterogeneity of the variable is high (strong autocorrelation) and there may be dominant long-range effects, while high D indicates that the variable is randomly distributed in space (weak or no autocorrelation) and that only weak short-range effects exist. It has been shown that the fractal dimension is not a constant over varying sampling intervals (Palmer, 1988, but his method of calculating D is doubtful, since it gives rise to D values exceeding 2 in the case of transects). How the fractal dimension changes with grain size has not been investigated yet, however. In the Pasoh forest, we found that the fractal dimensions of tree density, richness and Shannon diversity are generally high (close

to 3). The fractal dimension of diversity patterns decreases with increasing grain size, although it may increase locally (Fig. 8). This trend implies that at small sampling scales, diversity patterns display more homogeneous distributions, i.e. weaker autocorrelation; on the contrary, at broad sampling scale they show relatively high spatial heterogeneity, i.e. significant autocorrelation.

The reason for the high fractal dimensions and homogeneity in the Pasoh forest lies in the fact that most species are present at low density (He, Legendre and LaFrankie, unpublished). With reduction of grain size (increasing resolution), the similarity (autocorrelation) in species composition between adjacent sampling quadrats becomes very low or nil. In contrast, similarity increases with larger grain size. Interpolation or mapping may prove difficult, especially at small scale in tropical rain forests, because of the high fractal dimension. Using different sampling scales, opposite conclusions may be reached; for instance, a given scale may indicate that a distribution is isotropic, while it may look anisotropic at another scale (Fig. 8). It is obvious here that scale is a source of ecological controversies. Scale of studies is probably the first thing to look at in cases of controversies.

3.4 Analysis of variograms

Many ecological processes are spatially structured, as argued in the introduction. This is the underlying reason why ecological processes are scale-dependent. It is interesting to explore how scale (grain size) affects the spatial structure of a variable. The variogram is one of the most common methods used to describe the spatial structure of a variable in ecology (Burrough, 1987; Legendre and Fortin, 1989). The scaling effect on the spatial structure is quantified by the range and relative nugget effect of the corresponding variogram. Figures 9 and 10 show how the ranges and nugget effects of the variograms of tree density, richness and Shannon diversity change with grain size.

The range of a variogram is considered to be a measure of the size of a patch, i.e. the region inside of which there is autocorrelation among locations. The range is not always defined (for example in the case of gradients), or may be difficult to determine. Figure 9 presents the mean range estimated from exponential variogram models of tree density, richness and Shannon diversity in the north–south and east–west directions of the Pasoh forest plot (Figure 1). We find that the range increases

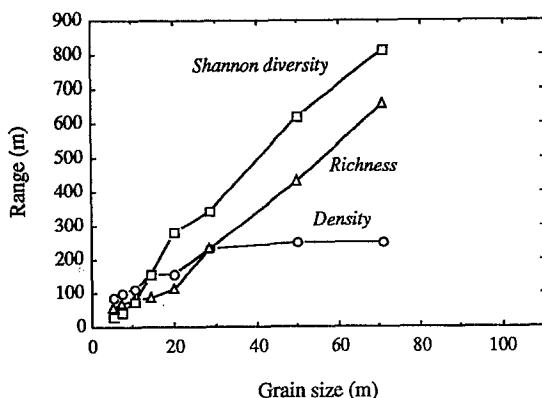


Figure 9. The effect of grain size on the ranges of the variograms (in the east–west direction) of tree density, richness and Shannon diversity in the Pasoh forest. The ranges of the diversity indices increase about linearly with grain size.

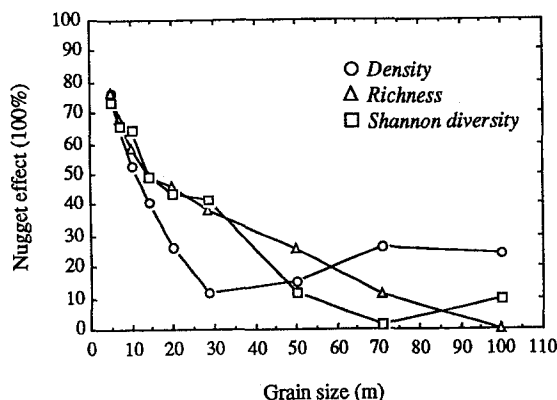


Figure 10. The effect of grain size on the relative nugget effects of the variograms of tree density, richness and Shannon diversity in the Pasoh forest in the east–west direction. Nugget effects of the diversity indices are not linear functions of grain size. For small grain sizes (≤ 30 m), nugget effects decrease approximately linearly with increasing grain size.

with grain size, which is consistent with the solution given in Section 3.1 and with the expectation of the fractal dimensions shown in Fig. 8, in which autocorrelation expands (decreasing D) with increasing grain. So, patch size estimations may differ with scales. This is not an artefact but a problem of scale. What sampling grain size is appropriate for a study depends on its objectives. For example, if the interest is in the spatial structure of a community, a fairly small-scale sampling scheme (small grain) may be appropriate, while if the interest is in the structure of a landscape system which usually embodies several communities, a relatively broad-scale scheme may be used.

Figure 10 shows how the relative nugget effects of the variograms of tree density, richness and Shannon diversity change with grain size in the east–west direction. These variables have high nugget effect, as high as 80%. The nugget effect is not a linear function of sampling scale. For example, the nugget effect of tree density at small scale and broad scale is higher than at intermediate grain sizes.

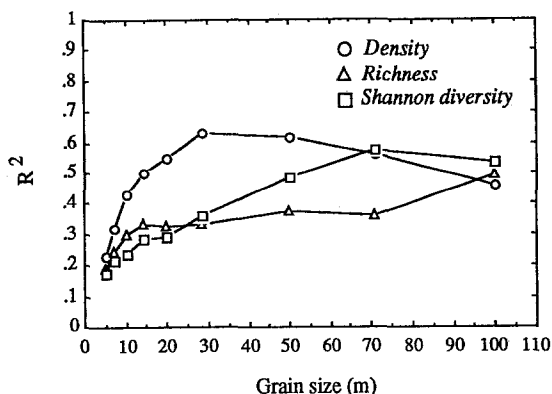


Figure 11. The scaling effect of the nearest-neighbour autocorrelation of tree density, richness and Shannon diversity in the Pasoh forest. The nearest-neighbour effect is a non-linear function of sampling scale. At small grain size (≤ 15 m), the nearest-neighbour effect linearly increases with grain size. Beyond that scale, it may increase or decrease.

3.5 Spatial structure and nearest-neighbour autocorrelation

Small-scale autocorrelation can also be looked at from the point of view of nearest-neighbour autocorrelation. Figure 11 shows the coefficients of determination (R^2) obtained when comparing the actual values at the various locations, to the estimates of these same values by their nearest-neighbour influence, for each grain size. High values of R^2 indicate strong nearest-neighbour influence. The R^2 values are small to intermediate in size, between 0.174 and 0.633; this means that on average, 17.4% to 63.3% of the variation in observed values of tree density, richness and Shannon diversity could be explained by nearest-neighbour values, depending on the variable and grain size. In all three panels of Fig. 11, R^2 increases steadily for grain sizes between 5×5 m and 15×15 m. For tree density, R^2 slightly decreases after 30×30 m, while for richness and diversity it keeps increasing in a stepwise manner. These pictures are almost perfect mirror images of Fig. 10 depicting the evolution of the nugget effect with grain size. Spearman rank correlation coefficients computed between nugget effects and nearest-neighbour autocorrelation curves for tree density, richness and Shannon diversity are -0.883 ($p = 0.0125$), -0.967 ($p = 0.0063$) and -1.000 ($p = 0.0047$), respectively; low nearest-neighbour autocorrelation corresponds to high nugget effect, while high nearest-neighbour autocorrelation is associated with low nugget effect. Sampling error and the presence of microstructures were considered above to be responsible for high nugget effects for small grain sizes. So, low nearest-neighbour autocorrelation should be the main explanation for high nugget effect. For example, a homogeneous Poisson pattern has 100% nugget effect and zero nearest-neighbour autocorrelation, no matter the value of grain size, or how much one can reduce sampling error. Avoiding sampling error or choosing an appropriate sampling scale can reduce the nugget effect, as shown in Fig. 10, but it will never be reduced to zero. When nearest-neighbour autocorrelation rises, the corresponding first-distance-class variogram value should drop; and since the first-distance-class variogram value is closely related to the 0-distance-class variogram value (= nugget effect), then the result is as expected. Nugget effect is a common feature of phenomena in nature; it is caused jointly by sampling errors and microstructures occurring if the distance between sampling units, or the size of sampling units, are greater than the ranges of microstructures.

4. Conclusion

The way we perceive ecological patterns in nature depends to a large extent on the scale at which we look at them. Ecological variables and processes are rarely scale-free. How they are affected by scaling is heavily dependent upon the way they are measured and distributed through space.

The current study on the diversity patterns of the Pasoh forest, Malaysia, showed that the effect of scale on these measurements is complex. In our forest plot, mean tree density, which is simply the count of individual trees in quadrats, is a constant over scales, while the means of richness and Shannon diversity are scale-dependent. Procedures or criteria are needed to establish the proper relation between scaling mechanisms underlying the spatial patterns of tree density, richness and Shannon diversity, and other ecological variables. Our study leads to the three following important conclusions: (i) scaling (i.e. grain size) usually has a non-linear effect on non-additive measurements. (ii) heterogeneity generally increases with the increase of sampling scales, as shown by fractal dimensions. (iii) detailed information on a spatial structure is often lost at broad scale because samples then average out the fine-scale differences.

As a matter of fact, each of the diversity variables we studied responds differently to scale. A scale appropriate for one variable may not be appropriate for another. More precise estimates of density are obtained using a large grain size, while more precise estimates of richness require small grain

size. Shannon diversity provides relatively stable estimates over the whole scale of grain sizes, although it does slightly worse at intermediate grain size values. No grain size is optimal for all diversity variables. This finding should be properly taken into account when planning ecological surveys of plants or animals.

If one's interest is, for example, to reduce the nugget effect of variograms for the Pasoh forest data to a proportion of 11% of the total spatial variability of the signal, then our study shows that a grain size of 30 m may be appropriate for tree density, 70 m for Shannon diversity, and 50 m for richness. At small grain size, the measurements of tree density (≤ 20 m), richness (≤ 10 m) and Shannon diversity (≤ 10 m) are either relatively constant, or linear functions of scale. They are the 'domains of scale' of these variables. Outside these domains, extrapolation of information from scale to scale is difficult. Although our current 50 ha forest plot is very small compared to the extent of the world tropical rain forest, and the vegetation is by and large of a uniform type, the current study demonstrates that extrapolation of information among scales (possible up-scale only) may be possible but very difficult. More studies of this kind in other ecosystems are needed before theories and generalizations about scaling effects can be formulated. In large-scale ecological studies, extreme caution should be exerted with respect to scale.

Acknowledgements

The large-scale forest plot at the Pasoh Forest Reserve is an ongoing project of the Malaysian Government, directed by the Forest Research Institute of Malaysia through its Director-General, Datuk Dr Salleh Nor, under the leadership of N. Manokaran, Peter S. Ashton, and Stephen P. Hubbell. Mr K. Kochummen supervised the initial identification of trees while a Senior Fellow at the Smithsonian Tropical Research Institute. Supplemental funds from the following sources are gratefully acknowledged: National Science Foundation (USA) BSR Grant No. INT-84-12201 to Harvard University through Peter S. Ashton and Stephen P. Hubbell; Conservation, Food and Health Foundation, Inc. (USA); United Nations, through the Man and the Biosphere programme, UNESCO-MAB grants nos. 217.651.5, 217.652.5, 243.027.6, 213.164.4, and also UNESCO-ROSTSEA grant no. 243.170.6; NSERC grant No. OGP0007738 to P. Legendre.

References

- Allen, T.F.H. and Hoekstra, T.W. (1991) Role of heterogeneity in scaling of ecological systems under analysis. In *Ecological Heterogeneity* (J. Kolasa and S.T.A. Pickett, eds), pp. 47–68. Springer-Verlag, New York.
- Allen, T.F.H. and Starr, T.B. (1982) *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press.
- Antonovics, J. and Levin, D.A. (1980) The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics* **11**, 411–52.
- Bolviken, B., Stokke, P.R., Feder, J. and Jossang, T. (1992) The fractal nature of geochemical landscapes. *Journal of Geochemical Exploration* **43**, 91–109.
- Borcard, D. and Legendre, P. (1994) Environmental control and spatial structure in ecological communities: an example using Oribatid mites (Acari, Oribatei). *Environmental and Ecological Statistics* **1**, 37–53.
- Brown, B.J. and Allen, T.F.H. (1989) The importance of scale in evaluating herbivory impacts. *Oikos* **54**, 189–94.
- Burrough, P.A. (1981) Fractal dimensions of landscapes and other environmental data. *Nature* **294**, 240–2.
- Burrough, P.A. (1987) Spatial aspects of ecological data. In: *Data Analysis in Community and Landscape Ecology* (R.H.G. Jongman, C.J.F. ter Braak, and O.F.R. van Tongeren, eds), pp. 213–51. PUDOC, Wageningen.

- Carr, J.R. and Benzer, W.B. (1991) On the practice of estimating fractal dimension. *Mathematical Geology* **23**, 945–58.
- Chesson, P.L. (1978) Predator-prey theory and variability. *Annual Review of Ecology and Systematics* **9**, 323–47.
- Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–10.
- Culling, W.E.H. (1986) Highly erratic spatial variability of soil-pH on Iping common, West Sussex. *CATENA* **13**, 81–98.
- Dale, M.R.T. and Blundon, D.J. (1990) Quadrat variance analysis and pattern development during primary succession. *Journal of Vegetation Science* **1**, 153–64.
- Dayton, P.K. and Tegner, M.J. (1984) The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In *A New Ecology, Novel Approaches to Interactive Systems* (P.W. Price, C.N. Slobodchikoff and W.S. Gaud, eds), pp. 457–81. John Wiley & Sons, New York.
- den Boer, P.J. (1968) Spreading of the risk and the stabilization of animal numbers. *Acta Biotheoretica* **18**, 165–94.
- den Boer, P.J. (1971) Stabilization of animal numbers and the heterogeneity of the environment: The problem of the persistence of sparse populations. In *Dynamics of Populations* (P.J. den Boer and G.R. Gradwell, eds), pp. 77–97. Proceedings of the Advanced Studies Institute, The Netherlands.
- Dewdney, A.K. (1984) Sharks and fish wage an ecological war on the toroidal planet Wa-Tor. *Scientific American* **251**, 14–22.
- Dutilleul, P. (1993) Spatial heterogeneity and the design of ecological field experiments. *Ecology* **74**, 1646–58.
- Dutilleul, P. and Legendre, P. (1993) Spatial heterogeneity against heteroscedasticity: an ecological paradigm versus a statistical concept. *Oikos* **66**, 152–71.
- Forman, R.T.T. and Godron, M. (1986) *Landscape Ecology*. John Wiley & Sons, New York.
- Fortin, M.-J. and Legendre, P. (1989) Spatial autocorrelation and sampling design in plant ecology. *Vegetatio* **83**, 209–22.
- Frontier, S. (1987) Applications of fractal theory to ecology. In *Developments in Numerical Ecology*. NATO ASI Series, Vol. G 14 (P. Legendre and L. Legendre, eds), pp. 335–78. Springer-Verlag, Berlin.
- Giller, P.S. and Gee, J.H.R. (1987) The analysis of community organization: the influence of equilibrium, scale and terminology. In *Organization of Communities, Past and Present* (J.H.R. Gee and P.S. Giller, eds), pp. 519–42. Blackwell Scientific Publications, Oxford.
- Gilpin, M.E. (1989) Spatial structure and population vulnerability. In *Viable Populations for Conservation* (M.E. Soulé, ed.), pp. 125–39. Cambridge University Press.
- Greig-Smith, P. (1952) The use of random and contiguous quadrats in the study of the structure of plant communities. *Annals of Botany*, New series **16**, 293–316.
- Harris, L.D. (1984) *The Fragmentated Forest: Island Biogeography Theory and the Preservation of Biotic Diversity*. University of Chicago Press.
- He, F., Legendre, P. and LaFrankie, J.V. Point pattern and intraspecific competition in a tropical rain forest of Malaysia. Submitted.
- Hubbell, S.P. (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* **203**, 1299–1309.
- Hubbell, S.P. (1984) Methodologies for the study of the origin and maintenance of tree diversity in tropical rainforest. In *Biology International* (G. Maury-Lechon, M. Hadley and T. Younes, eds) IUBS, Special Issue No. 6, pp. 8–13.
- Hubbell, S.P. and Foster, R.B. (1986) Commonness and rarity in a neotropical rain forest: implications for the tropical tree conservation. In *Conservation Biology, the Science of Scarcity and Diversity* (M.E. Soulé, ed.) pp. 205–31. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Huffaker, C.B. (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* **27**, 343–83.
- Isaaks, E. and Srivastava, R.M. (1989) *An Introduction to Applied Geostatistics*. Oxford University Press, New York.
- Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**, 501–28.
- Journal, A.G. and Huijbregts, C.J. (1978) *Mining Geostatistics*. Academic Press, London.
- Kareiva, P. (1982) Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* **52**, 261–82.

- Knight, D.H. (1987) Parasites, lightning, and the vegetation mosaic in wilderness landscapes. In *Landscape Heterogeneity and Disturbance* (M.G. Turner, ed.), pp. 59–83. Springer-Verlag, New York.
- Kochummen, K.M., LaFrankie, J.V. and Manokaran, N. (1991) Floristic composition of Pasoh forest Reserve, a lowland rain forest in Peninsular Malaysia. *Journal of Tropical Forest Science* **3**, 1–13.
- Kolasa, J. and Pickett, S.T.A. (eds) (1991) *Ecological Heterogeneity*, vol. 86. Springer-Verlag, New York.
- Krummel, J.P., Gardner, R.H., Sugihara, G., O'Neill, R.V. and Coleman, P.R. (1987) Landscape patterns in a disturbed environment. *Oikos* **48**, 321–4.
- Legendre, P. (1993) Spatial autocorrelation: Trouble or new paradigm? *Ecology* **74**, 1659–73.
- Legendre, P. and Borcard, D. (1994) Rejoinder. *Environmental and Ecological Statistics* **1**, 57–61.
- Legendre, P. and Fortin, M.-J. (1989) Spatial pattern and ecological analysis. *Vegetatio* **80**, 107–38.
- Levin, S.A. (1989) Challenges in the development of a theory of ecosystem structure and function. In *Perspectives in Ecological Theory* (J. Roughgarden, R.M. May and S.A. Levin, eds) pp. 242–55. Princeton University Press.
- Mandelbrot, B.B. (1983) *The Fractal Geometry of Nature*. Freeman, San Francisco.
- Margalef, R. (1958) Information theory in ecology. *General Systems* **3**, 36–71.
- Meentemeyer, V. and Box, E.O. (1987) Scale effect in landscape studies. In *Landscape Heterogeneity and Disturbance* (M.G. Turner, ed.), pp. 15–34. Springer-Verlag, New York.
- Milne, B.T. (1991) Heterogeneity as a multiscale characteristic of landscapes. In *Ecological Heterogeneity* (J. Kolasa and S.T.A. Pickett, eds), pp. 69–84. Springer-Verlag, New York.
- Minnich, R.A. (1983) Fire mosaic in southern California and northern Baja California. *Science* **219**, 1287–94.
- Moloney, K.A. (1988). Fine-scale spatial and temporal variation in the demography of a perennial bunchgrass. *Ecology* **69**, 1588–98.
- Palmer, M.W. (1988) Fractal geometry: a tool for describing spatial patterns of plant communities. *Vegetatio* **75**, 91–102.
- Phillips, J.D. (1985) Measuring complexity of environmental gradients. *Vegetatio* **64**, 95–102.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. and Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography* **19**, 117–34.
- Rossi, R.E., Mulla, D.J., Journel, A.G. and Franz, E.H. (1992) Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs* **62**, 277–314.
- Shaffer M.L. (1981) Minimum population sizes for species conservation. *BioScience* **31**, 131–4.
- Shorrocks, B., Atkinson, W.D. and Charlesworth, P. (1979) Competition on a divided and ephemeral resource. *Journal of Animal Ecology* **48**, 899–908.
- Southwood, T.R.E. (1962) Migration of terrestrial arthropods in relation to habitat. *Biological Reviews* **37**, 171–214.
- Steele, J.H. (1991) Can ecological theory cross the land-sea boundary? *Journal of Theoretical Biology* **153**, 425–36.
- Turner, M.G., O'Neill, R.V., Gardner, R.H. and Milne, B.T. (1989) Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology* **3**, 153–62.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology* **3**, 385–97.
- Wiens, J.A. and Milne, B.T. (1989) Scaling of 'landscapes' in landscape ecology, or, landscape ecology from beetle's perspective. *Landscape Ecology* **3**, 87–96.
- Wiens, J.A., Addicott, J.F., Case, T.J. and Diamond, J. (1986) Overview: The importance of spatial and temporal scale in ecological investigations. In *Community Ecology* (J. Diamond and T.J. Case, eds), pp. 145–53. Harper and Row, New York.
- Wyatt-Smith, J. (1987) Manual of Malayan silviculture for inland forest: red meranti-keruing forest. Research Pamphlet Number 101. Forest Research Institute Malaysia, Kepong, Malaysia.

Biographies

Fangliang He is a vegetation scientist, community ecologist, and modeller. After a Master's in plant population dynamics at the Institute of Applied Ecology, Academia Sinica, China, he obtained his Ph.D. from

Université de Montréal, Canada, where he worked on the spatial organization of the Malaysian rain forest studied in the present paper. He is currently an NSERC post-doctoral research fellow in the Canadian Forest Service, involved in a wetland ecology project (Ontario laboratory in Sault Ste. Marie) and a pest management project (Pacific laboratory in Victoria, B.C.).

Pierre Legendre is professor of quantitative biology at Université de Montréal. Fellow of the Royal Society of Canada and former Killam Research Fellow (1989–91), he received in 1994 the Distinguished Statistical Ecologist Award of the International Congress of Ecology (INTECOL) and in 1995 the Romanowski Medal (environmental science) of the Royal Society of Canada. He is the author of over 100 refereed articles, and over 250 papers presented at scientific meetings and research seminars, dealing with numerical ecology, community ecology, environmental assessment, spatial analysis and phylogenetics, as well as textbooks (in French and English) on numerical ecology.

Claude Bellehumeur is a geostatistician and earth scientist. After a Ph.D. in exploratory geochemistry and geostatistics at Université du Québec à Montréal, he joined P. Legendre's lab in 1993 where he worked on ecological assessment, spatial structures and ecological sampling theory. He is now a research associate in the Department of Chemical Engineering of Université de Sherbrooke, Canada.

James V. LaFrankie is a field ecologist and taxonomist with the Smithsonian Tropical Research Institute. He is in charge of the ongoing long-term monitoring program of the Pasoh Reserve in Negeri Sembilan, Malaysia.