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FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

On definition and quantification of heterogeneity

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General guidelines on the quantitative representation of heterogeneity in ecology are still lacking. Without a precise definition and sound quantification of heterogeneity, statements involving the concept will continue to be confusing, and comparative studies and hypothesis testing will be ineffective. To solve this problem we propose an operational definition of ecological heterogeneity that facilitates quantification based on the data types of concern. We use two examples to demonstrate how our definition and quantification of spatial heterogeneity can be applied in practice.

Dutilleul and Legendre's (1993) discussion of the definition and quantification of spatial heterogeneity is timely. Heterogeneity has become a buzzword in the ecological literature in recent years – a result of a broad recognition by the ecological community that heterogeneity is an important characteristic of ecological systems and affects a wide range of theoretical and practical issues (Kolasa and Rollo 1991, Dutilleul and Legendre 1993). While major progress toward an ecological theory of heterogeneity is being made (Risser et al. 1984, Addicott et al. 1987, Turner 1987, 1989, Kotliar and Wiens 1990, Shorrocks and Swingland 1990, Grace 1991, Kolasa and Pickett 1991, Turner and Gardner 1991, Allen and Hoekstra 1992, Milne 1992, Dutilleul and Legendre 1993, Wiens et al. 1993), the concept is frequently misused because heterogeneity presently means different things to different ecologists (Kolasa and Rollo 1991, Dutilleul and Legendre 1993). There is also the danger that quantification of heterogeneity is done without a clear notion of what is exactly being quantified (Li and Reynolds 1994). Given the many aspects of heterogeneity that have been identified (Kolasa and Rollo 1991, Dutilleul and Legendre 1993), a researcher must explicitly answer the question: heterogeneity of what? This has not been the common practice.

To overcome these serious problems, we need a quantitative, operational definition of heterogeneity (e.g., Loehle 1988, Palmer and White 1994). In this paper we extend the discussion of the definition and quantification of ecological heterogeneity advocated by Dutilleul and Legendre (1993) and Kolasa and Rollo (1991). We propose an operational definition of ecological heterogeneity, suggest an approach for quantifying heterogeneity that is consistent with this definition, and provide two examples that illustrate how our scheme can be applied in practice.

Operational definition

We define heterogeneity based on two components: the system property of interest and its complexity or variability (Fig. 1). A *system property* can be anything that is of ecological interest, e.g., plant biomass, soil nutrients, temperature, and so on. *Complexity* refers to qualitative or categorical descriptors of this property, while *variability* refers to quantitative or numerical descriptors of the property. Heterogeneity is thus defined as the complexity and/or variability of a system property in space and/or time.

Two related issues merit discussion. First, our operational definition emphasizes the structural characteristics that can be observed and analyzed. This is termed *structural heterogeneity*, that is, the complexity or variability of a system property measured without reference to any functional effects (e.g., Kolasa and Rollo 1991). Hence, *functional heterogeneity* is the complexity or variability of a system property that can be shown to affect ecological processes, e.g., population density, nesting or foraging behavior, growth rate, etc.

Second, heterogeneity is a function of scale (e.g., Kolasa and Rollo 1991, Allen and Hoekstra 1992, Dutilleul and Legendre 1993) (Fig. 1). From an observational viewpoint, *grain* and *extent* are the primary scaling factors that affect complexity or variability and, hence, heterogeneity. Grain is the finest resolution of data (e.g., pixel size for lattice data, minimum time step for time

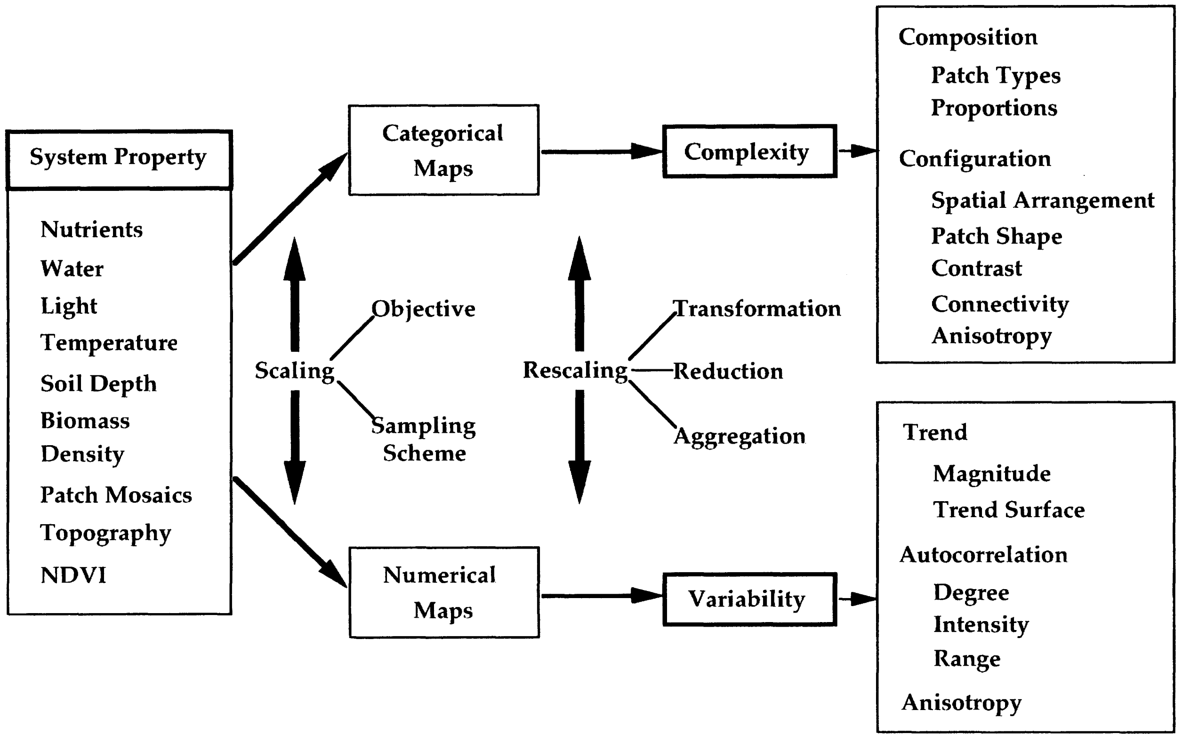


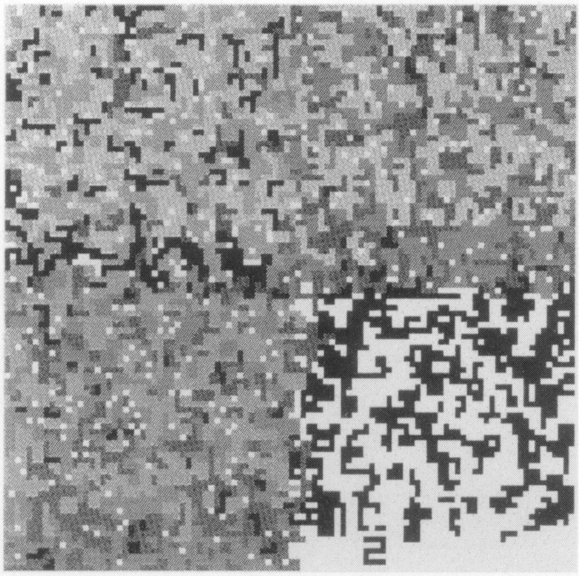
Fig. 1. A landscape example of quantification of spatial heterogeneity. See the text for discussions.

series data), and extent is the area or duration encompassed by a study. The observational scale (i.e., grain or extent) is dependent on the sampling scheme used, which in turn is determined by the nature of the phenomenon (i.e., the "organism's grain and extent" as suggested by Kotliar and Wiens 1990) and the research objective. The observed data determine what kind of heterogeneity may be measured. From a data analysis viewpoint, *rescaling* of data, including data transformations, data reduction, data aggregation, and resampling (e.g., Allen and Hoeks-

Table 1. Data types and methods for quantifying heterogeneity.

Data type	Description	Method	Reference
Non-spatial	No reference to sampling	Variance Interquartile range (IQ) Diversity indices	Sokal and Rohlf 1981 Sokal and Rohlf 1981 Pielou 1975
Spatial	Sampling location as a variable		
Point pattern	Variables or individuals of species distributed at discrete locations	Parameter k of negative binomial Nearest neighbor index Block-size variance statistic	Pielou 1977 Pielou 1977 Greig-Smith 1983
Geostatistical	Continuous variables sampled regularly or irregularly in space	Variogram Correlogram Fractal dimension	Cressie 1991 Rossi et al. 1992 Burrough 1983
Quantitative lattice	Numerical maps	Variogram Correlogram Autocorrelation indices	Cressie 1991 Rossi et al. 1992 Cliff and Ord 1981
Qualitative lattice	Categorical maps	Diversity indices Fractal dimension Patchiness index Contagion index Joint-count statistic	Pielou 1975 O'Neill et al. 1988 Romme 1982 Li and Reynolds 1993 Cliff and Ord 1981

Map A



Map B

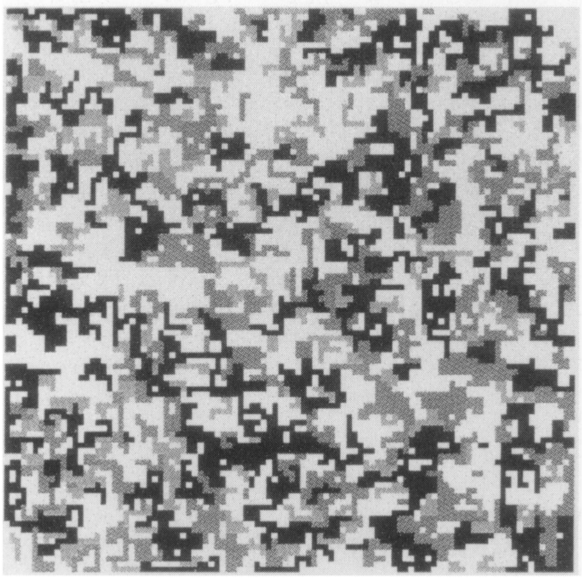


Fig. 2. Heterogeneity in categorical data. The two maps are generated based on the heterogeneity components of categorical data (see Fig. 1 and Table 2). The maps can be regarded as landscape mosaics of cover types.

tra 1992), is a secondary scaling factor. Rescaling may modify grain or extent or both and, hence, plays a role in quantification of heterogeneity (Fig. 1).

Quantification of heterogeneity

Quantitative heterogeneity may be viewed as a continuum of variability and complexity – from low to high – with homogeneity being the low end (i.e., the minimum). Thus, two basic strategies can be used to quantify heterogeneity: (1) *directly*, by measuring complexity and variability and (2) *indirectly*, by measuring departure from homogeneity. For example, heterogeneity in categorical maps can be defined as complexity in number of patch types, proportion, patch shape, and contrast between neighboring patches, and different methods can be used to quantify these aspects of heterogeneity. Moreover, heterogeneity in numerical maps can be measured as degree of departure from randomness when homogeneity is defined as the randomness of the distribution of a system property.

Our definition emphasizes what Allen and Hoekstra (1992) and Dutilleul and Legendre (1993) imply – that quantification of spatial heterogeneity should be based upon data types. In Table 1 we present spatial and non-spatial data types and list examples of methods that can be used to quantify their heterogeneity (also see Turner et al. 1991). Our focus here is on spatial heterogeneity. Each data type has its own characteristic variability and complexity. For point pattern data, spatial heterogeneity can be measured by its variability in *density* and *nearest neighbor distance*. For categorical maps, spatial heterogeneity can be measured by its complexity in *composition* and *configuration* of patches (Fig. 1). Composition includes the number and proportions of patch types, while configuration includes spatial arrangement of patches, patch shape, contrast between neighboring patches, connectivity among patches of the same type, and anisotropy (i.e., variation in different directions). For numerical maps, spatial heterogeneity can be measured by its variability in *trend*, *autocorrelation*, and *anisotropy* (Fig. 1). Trend includes the magnitude of the mean or variance and the deterministic changes of the mean in space (e.g., those defined by trend surface analysis). Autocorrelation includes the degree of autocorrelation, the intensity of autocorrelation (i.e., the rate of change in autocorrelation), and the range of autocorrelation (i.e., the scale beyond which autocorrelation does not exist). Anisotropy is the variation of trend and autocorrelation in different directions. Geostatistical data can be treated similarly to numerical maps. These quantifiable components are specific enough to make quantification of heterogeneity straightforward, and, at the same time, general enough to be applied to the analysis of any data types given in Table 1.

Examples

We present two examples to demonstrate how our operational definition and quantification scheme can be ap-

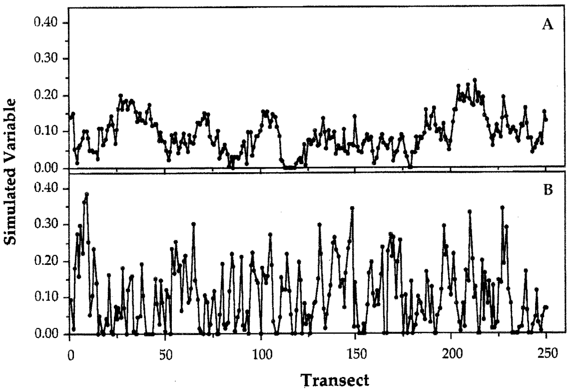


Fig. 3. Heterogeneity in numerical data. The two transects of 1000 points are generated based on the heterogeneity components of numerical data (see Fig. 1 and Table 3). Each transect contains 1000 points; only a quarter of each transect is displayed here for clear presentation. The transects can be regarded as soil nitrogen content in landscapes.

plied to study spatial heterogeneity in practice. We use two data types commonly used in landscape ecology: categorical maps and numerical transects.

The two maps of landscape mosaics of cover types (Fig. 2) were generated by SHAPC, which has been described elsewhere (Li and Reynolds 1994). SHAPC generates categorical landscape maps based on complexity in number of patch types, proportion of each type, patch distribution, patch shape, patch size distribution, and several other parameters. The two transects of soil nitrogen content (Fig. 3) were generated by SHAPN, which is a model of the autoregressive-moving-average (ARMA) type (e.g., Bras and Rodriguez-Iturbe 1985). ARMA is often used in time series analysis. SHAPN generates transects (or numerical maps) based on variability in magnitude, trend surface, degree of autocorrelation, and anisotropy. The parameters used in the simulation are given in Tables 2 and 3. Simulated data were used because the results could be compared with certainty (i.e., heterogeneity of these maps and transects were fixed).

Spatial heterogeneity of the maps and the transects were analyzed by methods commonly used in landscape ecology. For the categorical maps, the indices of evenness, contagion, fractal dimension, and patchiness were calculated. They represent the number and proportions of patch types, spatial arrangement of patches, patch shape, and contrast between neighboring patches (Pielou 1975, Romme 1982, O'Neill et al. 1988, Li and Reynolds 1993, 1994). We have discussed these four indices and their effectiveness (Li and Reynolds 1994). For the numerical transects, we calculated the coefficient of variation (CV), Moran's I index, the fractal dimension, and the relative heterogeneity (SH%). CV is a common statistic for non-spatial data (e.g., Sokal and Rohlf 1981) and was used to represent the zero-order heterogeneity (i.e., magnitude of variance). Moran's I was calculated for adjacent points along transects (see Cliff and Ord 1981, Legendre and Fortin 1989) and was used to represent the first-order spatial heterogeneity (i.e., degree of autocorrelation). To calculate the fractal dimension and SH%, semivariograms of the numerical transects were constructed (see Cressie 1991, Rossi et al. 1992). The fractal dimension is a negative function of the slope of logarithm-transformed semivariograms (Burrough 1983). Slope expresses the rate of change in semivariance with the lag distance, and high slope values indicate high degrees of heterogeneity. Thus, the fractal dimension is a measure of spatial homogeneity; it attains its highest value of 2 with a random (i.e., homogeneous) landscape. This fractal dimension is called stochastic fractal and differs from the fractal of patch shape used in the analysis of the categorical maps (Carr and Benzer 1991). SH% was calculated from the nugget variance and sill (i.e., two of the semivariogram parameters). SH% is defined by: *SH%=(sill-nugget)/sill.* In semivariogram analysis, sill represents the maximum (total) variation, and nugget represents the random variation (i.e., homogeneity). Subtraction of the random variation from the total variation results in the autocorrelated variation (i.e., heterogeneity). Thus, SH% represents the proportion of the autocorrelated spatial heterogeneity in the total variation.

The two maps and the two transects were contrasted for their differences in spatial heterogeneity. For the categorical data, map A shows higher values in evenness and fractal dimension, while map B shows higher values in contagion and patchiness (Table 2). These results are expected given the parameter settings used in simulation (Table 2). The results indicate that map A represents a landscape that is more diverse and has more irregularly shaped patches, and that map B represents a landscape that has larger patches and higher contrast. Whether map A or B is "more" heterogeneous depends on the aspect of spatial heterogeneity of interest. This does not imply a conflict because each heterogeneity component characterizes a distinct aspect of spatial heterogeneity. However, this result does support our argument that one must explicitly define the component of heterogeneity of interest. More detailed discussion of this subject can be found in Li and Reynolds (1994).

Table 2. The simulation parameters and the heterogeneity measures for the categorical maps in Fig. 2.

	Map A	Map B
Map characteristics (Simulation)		
No. of patch types	6	6
Proportion	Even	Uneven
Spatial arrangement	Aggregated	Random
Patch shape	Random	Regular
Heterogeneity measures		
Evenness	1.000	0.819
Contagion	0.152	0.196
Fractal dimension	1.640	1.603
Patchiness	0.296	0.550

Table 3. The simulation parameters and the heterogeneity measures for the numerical transects in Fig. 3.

	Transect A	Transect B
Transect characteristics (Simulation)		
Mean	0.10	0.10
Standard deviation (% of Mean)	0.05 (50%)	0.10 (100%)
Autocorrelation	0.8	0.5
Heterogeneity measures		
CV	0.483	0.812
Moran's I	0.798	0.450
Fractal dimension	1.715	1.817
SH%	80.74%	62.88%

For the numerical data, transect A shows higher values in Moran's I and SH% and a lower value in fractal dimension, while transect B shows a higher value for CV (Table 3). These results are also expected because of the parameters used in simulation (Table 3). The results indicate that transect A is "more" heterogeneous in most aspects (e.g., higher autocorrelation, higher intensity, and higher relative heterogeneity), except for the zero-order, non-spatial heterogeneity.

These two examples illustrate that the operational definition and the quantification scheme of heterogeneity we propose are easy to apply in practice. When the specific components of heterogeneity are identified (e.g., Fig. 1), quantification is straightforward, which enables us to unambiguously characterize and compare heterogeneity and its effects on ecological systems.

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