Spatial heterogeneity against heteroscedasticity: an ecological paradigm versus a statistical concept

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The scope of the present paper is twofold: first, we want to point out the differences between the concepts of heterogeneity and heteroscedasticity, their partially common etymology being responsible for much confusion; secondly, we will brush over the statistical and ecological perspectives on heterogeneity and its quantification, and will outline the statistical methods of data analysis that are available to ecologists to study it. One widely spread ecological perspective, at least in landscape ecology, is based on the dictionary definition of "heterogeneous": consisting of dissimilar or diverse ingredients or constituents, mixed. From a statistical viewpoint, however, heterogeneity, when applied to the distribution of the values taken by a random variable, is the opposite of homogeneity, which refers to sameness or similarity; the degree of similarity implied by the term "homogeneity" may vary from a minimum of a single common attribute, as in the equality of means, to the extreme of total sameness, that is, equivalence of distributions. In a spatial context, the acceptation given to the word "heterogeneity" primarily depends on the type of spatial pattern of concern; for a point pattern, it refers to density of points and their distribution in space, while for a surface pattern, it concerns instead the values taken by a qualitative or quantitative variable. The ecological and statistical aspects of spatial heterogeneity are compared; in particular, the discussion from an ecological viewpoint will focus on fundamental aspects of spatial heterogeneity and its functional role in ecosystems, combined or not with temporal variability. While heterogeneity is a term commonly used by both ecologists and statisticians, heteroscedasticity is a purely statistical concept which concerns a particular type of heterogeneity restricted to inequality of variances. Difficulties generated by heteroscedastic-

ity in statistical data analyses and solutions taking it into account are briefly reviewed. Finally, a box of statistical tools is assembled to help ecologists quantify spatial heterogeneity.

"Spatial heterogeneity may be viewed from dynamic or static and observer oriented or ecological entity oriented perspectives" (Kolasa and Rollo 1991).

"Synonyms for this condition [equality of variances] are homogeneity of variances or homoscedasticity ... the converse condition (inequality of variances among samples) is called heteroscedasticity" (Sokal and Rohlf 1981).

The importance of heterogeneity in ecology lies in its ubiquity as a feature of ecosystems and in the number of questions it raises, for which answers are not readily available. One of these questions still is: what is heterogeneity? So, the idea of sorting through the often vague concepts of ecological heterogeneity seems to be timely, especially if the competing definitions can be referenced against an ecologically clear and statistically correct operational definition, and even if heterogeneity turns out to have more different aspects than could be covered in a whole book. It follows that our paper primarily intends to clarify the meaning of heterogeneity when compared to heteroscedasticity, their partially common etymology being responsible for much confusion; we will also comment on the implications of these concepts in analysis of variance, experimental design, and other aspects of statistical data analysis, in particular in the spatial context. From a statistical viewpoint, the emphasis will be on the heteroscedasticity problem, which is relevant when discussing how to quantify spatial heterogeneity, because that statistical viewpoint can potentially bring much to the ongoing ecological discussions about patches, scaled pattern, one- and two-dimen-

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Table 1. Results of the bibliographical research carried out into the occurrence of "spatial heterogeneity" and "heteroscedasticity" (and synonyms) in both the ecological and the statistical literatures.

Database	"Spatial"	"Heterogeneity"	"Spatial heterogeneity"	"Heteroscedasticity"	"Inequality of variances" or "Heterogeneity of variances"
BIOSIS, CURRENT CONTENTS and SCISEARCH	64953	41239	837	107	–
MATHSCI	6108	459	28	308	10

sional gradients, predictability, and others. With this in mind, we attempt to relate the statistical and ecological viewpoints, and to review the problem in a way useful and accessible to ecologists interested in quantifying heterogeneity.

We first performed an intensive bibliographic survey, looking for "spatial heterogeneity", "heteroscedasticity", "heterogeneity of variances" or "inequality of variances" in the titles, keywords and abstracts of papers in two sets of journals: ecological, biological and medical on the one hand, mathematical and statistical on the other. The bibliographic databases consulted are: in the biosciences, BIOSIS PREVIOUS (BIOSIS, covering 1969 to the present), CURRENT CONTENTS SEARCH (The Institute for Scientific Information or ISI, covering the current 6 months to 1 year) and SCI-SEARCH (ISI, covering 1974 to the present); and in mathematics, MATHSCI (The American Mathematical Association or AMS, covering 1959 to the present). Results are summarised in Table 1. First, they reveal that, in combination or not, spatial structuring and heterogeneity are crucially relevant to ecologists, while spatial heterogeneity only arouses a mild interest among statisticians. Secondly, "heteroscedasticity" is clearly more frequently used than its synonyms, "heterogeneity of variances" and "inequality of variances", and more in the statistical literature than in the ecological. Among the 107 papers itemised for "heteroscedasticity" in BIOSIS, CURRENT CONTENTS and SCISEARCH, a majority are also listed in MATHSCI as biomathematical or biostatistical contributions. Finally, spatial heterogeneity seems to be nearly as popular in ecology, proportionally to the occurrences of "heteroscedasticity", as heteroscedasticity is in statistics (considering the occurrences of "spatial heterogeneity").

What does "heterogeneity" mean?

Generally speaking, "homogeneity" refers to sameness or similarity, and consequently "heterogeneity" alludes to dissimilarity and unlikeness. This section aims at providing a concise overview of the biological and statistical concepts and views about heterogeneity, and their common, divergent and specific aspects.

Classically in ecology, heterogeneity refers to being composed of parts of different kinds; it is distinct from variability, which indicates changes in the values of a given quantitative or qualitative descriptor (Kolasa and Rollo 1991). This distinction is not as sharp as may appear at first glance, and meanings essentially depend on a choice of approach (e.g., Naeem and Colwell 1991, Shachak and Brand 1991). When compared to homogeneity, viewed as the absence of variation, the concept of ecological heterogeneity is intuitively clear, but as we scrutinise it, our initial impression fractures into complexity. In fact, ecological heterogeneity can be viewed from a wide variety of inclusive, exclusive, complementary, or overlapping perspectives, that are a source of heterogeneity in the definitions of the concept itself (Kolasa and Rollo 1991).

The first major dividing line concerns the spatial and temporal dimensions that are conventionally used for classifying types of heterogeneity in ecology. Temporal heterogeneity and its main differences from spatial heterogeneity are only briefly described here, the next section being devoted to the spatial aspects.

Ecological processes operate at a variety of time scales; for example, forest trees have life spans of decades, annual crops grow during less than a year, and stream insects may have only a few days of adult life (Risser 1987). Formally, temporal heterogeneity is similar to spatial heterogeneity in that it concerns the presence of variation (sometimes opposed to uniformity), except that it refers to many points in time and only one in space. Despite this apparent similarity, temporal heterogeneity is not equivalent to spatial heterogeneity. Actually, if two sites presenting temporal heterogeneity differ in their temporal variation, the result will be spatial heterogeneity; but the reciprocal is not necessarily true: two locations differing at any given moment in time may be either homogeneous or heterogeneous temporally (Kolasa and Rollo 1991; see also Naeem and Colwell 1991).

General measures of heterogeneity are sometimes not widely known (Kolasa and Rollo 1991); this is why

one of the forthcoming sections is devoted to the problem, and aims at proposing a panel of solutions. Available measures fall into the category of absolute measures, objectively defined on statistical grounds without consideration for properties of the (eco)system. The variance associated with a mean abundance estimation, for instance, provides such a primary measure to examine heterogeneity changes across scales (Greig-Smith 1952, Kershaw 1957, Goodall 1974, Ripley 1987); related techniques of blocking quadrats and critiques directed towards them have been compiled by Turner et al. (1990).

These measures are "unidimensional" in the sense that heterogeneity is evaluated as a single value, between some minimum (often zero) and some maximum (Kolasa and Rollo 1991). This does not mean, however, that heterogeneity has to refer to a single variable – although it often does, as when measuring the variance of a single variable over the sampling units. In principal component analysis, for instance, an eigenvalue is a measure of the heterogeneity associated with a principal component, which is a linear combination of different variables. Other multivariate measures of variation are the trace of a multivariate variance-covariance matrix, and Wilks' lambda statistic which measures the heterogeneity among several groups in a multidimensional space.

Measuring heterogeneity through a single synthetic measure does not mean that it cannot be decomposed according to spatial or temporal axes of variation. Two-dimensional correlograms and periodograms have been proposed that allow the spatial autocorrelation or variance to be decomposed between the X and Y geographic axes, in the case of anisotropic spatial phenomena; for the same reason, variograms are often computed in several directions (see Legendre and Fortin 1989 for a review). Spatiotemporal correlograms were also developed for modelling spatiotemporal processes (Cliff and Ord 1981). Finally, Mantel correlograms have been proposed by Sokal (1986) and Oden and Sokal (1986) for measuring the variability associated with multivariate data sets, decomposing it according to distance classes and using Mantel's (1967) statistic as a multivariate autocorrelation coefficient; Mantel correlograms may also be computed in prespecified directions.

While the previous approach based on "measured heterogeneity" is most accessible and convenient, critics pointed out its low biological relevance. A species' perspective, in which communities result from species' responses to abiotic and biotic constraints imposed onto the landscape (e.g., Milne 1991), is usually biologically much richer. The resulting alternative approach is labelled "functional heterogeneity", which is defined as the "heterogeneity an ecological entity (individual, population, species, or multispecies) perceives and responds to" (Kolasa and Rollo 1991). Whereas measured heterogeneity is a product of the observer's perspective, functional heterogeneity provides the perspective of the

ecological entity and its multidimensionality results from the interaction among scales relevant to the ecological entity and its environment. Thus functional heterogeneity is not the same for different groups of organisms living in the same environment, because processes concerning these different groups act at different temporal or spatial scales: in the sea for instance, the mean time required for doubling the biomass is of the order of 1 day for phytoplankton, 10–40 days for zooplankton, 100–900 days for fish, and 120–500 days for mussels; spatially, the horizontal scale characteristic of patches is of the order of 0.1–1 km for phytoplankton and zooplankton, and 1–100 km for fish (Legendre et al. 1986). The question of perceptual shift at different spatial, temporal, and organisational (individuals, populations) scales is investigated by King (1990), Allen and Hoekstra (1991), and Chesson (1991), among others. Habitat complexity may be an important component of heterogeneity for some ecological entities but does not constitute a class of heterogeneity of its own. Measured heterogeneity converges toward functional heterogeneity as our knowledge of the system increases and with it, our ability to use measures of heterogeneity to reflect its relevant properties (Kolasa and Rollo 1991).

Landscape is yet another facet of heterogeneity. By definition, landscape is heterogeneous, that is, it consists of dissimilar or diverse components or elements; for instance, a typical rural landscape may include several agricultural croplands, pastures, woodlands, streams, farmsteads, and roads (Risser 1987). In addition to that spatial heterogeneity, landscape is also temporally heterogeneous, and the resulting mixture of ecological processes operating at different spatial and temporal scales provides the material that environmental managers act upon. Heterogeneity, landscape and disturbance (anthropic or natural) are related in that a portion of the heterogeneity in the landscape at any one time is caused by disturbance. Heterogeneity may act as a stabilising factor, when environmental heterogeneity increased by a disturbance alters the impact of a later one of the same magnitude; conversely, heterogeneity may also enhance the spread of a disturbance (Risser 1987).

The number of aspects of ecological heterogeneity turns out to be much larger than what can be covered in a paper, or even in a single book, so that the present section only concerns fundamental aspects; illustrations of the interaction between heterogeneity and scale, patchiness, and environmental gradients will be given in the next section. Other ecological issues related with heterogeneity are discussed in detail in the excellent monographs edited by Turner and Gardner (1990) and Kolasa and Pickett (1991), and in the papers of Meentemeyer and Box (1987) and Risser (1987), among others; some salient material from these sources has been used in the present and the next sections.

Another meaning sometimes given to the concept of heterogeneity in community ecology is that of Peet

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(1974), following Good (1953); these authors call "heterogeneity" the mean species diversity, which combines the number of species and their relative abundances. This use is fortunately not widespread and did not take root.

Before switching to the statistical viewpoint, let us mention other meanings that have been associated to homogeneity and heterogeneity in mathematical population ecology and community theory, with a mathematical or statistical, or even a physical connotation; some persist to this time, others have disappeared. For example, models have been described as homogeneous with respect to space and time if their parameters did not vary with respect to the spatial and temporal dimensions. Homogeneity has been used to connote uniformity, constancy, equilibrium, and stability (among others), temporally and spatially. In particular, the Committee on Nomenclature of the Ecological Society of America defined homogeneity to mean "uniform or regular spacing of individual organisms" (McIntosh 1991); we will show in a further section that this definition is restricted to the point pattern aspect of spatial heterogeneity, but does not apply to surface patterns. In yet another perspective, incompatible with the previous one, a distribution of individuals at random, independently of one another, has been called homogeneous in statistical ecology; the absence of spatial association is then the criterion of homogeneity, or lack of pattern, while heterogeneity is assimilated to pattern. McIntosh (1991) gives a full historical account of the terms related to heterogeneity, as indexed in ecology journals since the turn of the century.

From a statistical perspective, heterogeneity is a concept that refers to statistical distributions; there are as many definitions of heterogeneity as there are parameters for a statistical distribution, each of these definitions relating to the object to which heterogeneity applies. A collection of statistical populations is said to be homogeneous with respect to a given characteristic or set of characteristics if the populations are identical with respect to that characteristic or set; for example, homogeneity of means holds if population means are all equal, regardless of whether other population attributes are shared. So, the degree of similarity implied by the term "homogeneity" may vary from the minimum of a single common attribute, as in the equality of means, to the extreme of total sameness, that is, equivalence of the populations. The opposite of homogeneity with respect to a certain characteristic is "heterogeneity" with respect to that characteristic (Glaser 1983).

Mean values (or variability measures, or correlation coefficients, ...) are heterogeneous if they are not all equal, so that heterogeneity and nonstationarity may be confounded, mean values as well as covariance and correlation functions being sometimes called homogeneous for stationary time series or spatial processes (Ripley 1981). The intuitive idea of statistical stationarity (sometimes loosely called uniformity) is that the

statistical properties of the data series or set will not be affected if all the sampling points are moved by some distance over the landscape. Strict stationarity concerns the whole statistical distribution, whose parameters must all remain the same through this translation; it differs from second-order or weak stationarity, which is restricted to constant and finite values for the mean and variance, and (auto)covariance values only depending on the distance between two sampling points. Weak stationarity is required in the analysis of (auto)correlograms; for semi-variance or variogram analysis, the assumption of second-order stationarity can be replaced by a weaker hypothesis known as the intrinsic hypothesis, which says that the increments between all pairs of points located a given distance apart have a zero mean and a finite variance that remains the same in the various parts of the area under study (Jongman et al. 1987, Legendre and Fortin 1989). Semi-variance analysis will be developed in a further section and recommended as a statistical tool for ecologists interested in the quantification of spatial heterogeneity.

Point/Summary: Space and time provide a first dividing line for classifying heterogeneity in ecology, by defining nonequivalent aspects. Measured heterogeneity is a product of the observer's perspective, that somehow simplifies and summarises the organisational aspect or functional heterogeneity, that ecological entities actually perceive, relate to, and respond to. Landscape is heterogeneous in that it consists of dissimilar or diverse components or elements. From a statistical viewpoint, populations are heterogeneous, or homogeneous, with respect to a set of characteristics (or possibly a single one) depending on whether they are different, or not, with respect to that set. In that perspective, stationarity and the intrinsic hypothesis are related to homogeneity in time series and in spatial data analysis.

Spatial heterogeneity: an ecological paradigm

Spatial heterogeneity is a concept whose definition depends on the nature of the underlying pattern. For a point pattern, heterogeneity concerns the distribution or dispersion of individual organisms or ecological entities through space; a point pattern process concerns physical points distributed in space, representing a discontinuous phenomenon, for instance individual plants and animals. In this context, spatial heterogeneity (called infra- or underdispersion, or super- or overdispersion) means density variation, compared to the variation expected from randomly spread organisms; the next section will show that both over- and underdispersion are aspects of heterogeneity, as opposed to homogeneity which means absence of spatial variation in the intensity of the generating point process. For a surface pattern process, which is spatially continuous,

spatial heterogeneity refers to the variability among subregions, for one or several qualitative or quantitative variables taking values in a spatially continuous manner; examples are the geological group to which belongs each map pixel (qualitative), or air temperature (quantitative). The emphasis in the present section will be on the functional aspects of spatial heterogeneity from an ecological perspective, and in the next one, on its measurement from a statistical viewpoint. Their connection will be established in a further section.

Spatial heterogeneity may be associated with ecological information. Actually, high environmental heterogeneity interferes with competition (Powell and Rucherson 1985) and consequently it may allow higher species diversity to be maintained (Hunter 1987, Sogard et al. 1989, Pringle 1990); it reduces the impact of predation (Kaiser 1983, Bryan and Wratten 1984, Gilinsky 1984, Holt 1984, Webb and Willson 1985) and parasitism (Nachman 1981), increases population stability (Weider 1984, Dempster and Pollard 1986, Niemela et al. 1986, Lodge et al. 1988, Williams 1988) and helps maintain intraspecific genetic polymorphism (Pritchettewing 1980, Smith et al. 1983, Desalle et al. 1987, Weider 1989, Bell and Lechowicz 1992, Lechowicz and Bell 1992). Spatial heterogeneity is also functional in ecosystems through its interaction with population dynamics (Cantrell and Cosner 1991) and habitat partitioning within lake communities (Lodge et al. 1988). More fundamental aspects and theoretical models are discussed by Pacala and Roughgarden (1982), Downing (1986), Pacala (1987), and Hastings (1990). In the analysis of earth sciences data, one is often primarily interested in the anomalies in mean values and in the zones of high variability, that will allow to locate the high grade veins in a mineral deposit or the impermeable layers that condition flow in a petroleum reservoir (Isaaks and Srivastava 1989). In all those cases, spatial heterogeneity is undoubtedly of interest per se.

While nature is clearly heterogeneous, the scale at which spatial heterogeneity manifests itself varies widely for different physical and chemical characteristics such as air pressure, irradiation, soil or ionic composition, water temperature, pH, current speed, and so on (Frost et al. 1988, Baker 1989, Allen and Hoekstra 1991); the same applies to different ecological compartments of ecosystems (Legendre et al. 1986: examples given in the previous section). So, scale is a crucial aspect of spatial heterogeneity. Shifts of scale, for an ecological entity, may lead from perceived homogeneity to heterogeneity, and vice versa; the information contained at one level of resolution may look like noise at another. In some cases, there may be a duality in nature between small-scale heterogeneity and large-scale homogeneity, for instance in the distribution of microorganisms in marine ecosystems (Bianchi et al. 1989). The fineness of the scale defines the degree of resolution; following tradition in ecology, scale will be used here in the common meaning of the term, that is, small scale

refers to small measurement units; a geographer's definition is the opposite, scale representing the degree of spatial reduction (ex. 1:250000, Meentemeyer and Box 1987).

Spatial heterogeneity has been observed at cell- (Benson et al. 1985, Conway and Weiss 1985, Hall and Yeoman 1986, Franzen et al. 1988, Williford et al. 1990), micro- (Washitani et al. 1989), small- (Smith 1986, Romano and Laborde 1987) and large-scales (Carpenter 1990), in freshwater (Neilson and Stevens 1987, Pinel-Alloul et al. 1988, Horne and Commins 1989), brackish (Legendre and Troussellier 1988) and marine environments (Mukai 1987, Kennely 1989, Mitchell et al. 1990, Perez and Canteras 1990), in botany (Soriano et al. 1987) and forestry (Nunezfarfan and Dirzo 1988, Matlack and Good 1990), in community (Urabe 1989) and landscape ecology (Plowright and Galen 1985, Mader 1988).

To undertake a field study as efficiently as possible, it is necessary to choose its scale thoughtfully (Legendre et al. 1989, Turner et al. 1990). When scale differences are not considered, quantitative and interpretational errors abound (Milne 1991). To avoid them, ecologists have to identify the characteristic scales at which regularities or anomalies are likely to occur, and finally, the dominant scales at which operating processes control the landscape or community (Frost et al. 1988, Legendre et al. 1989). In oceanography for instance, Bianchi et al. (1989) studied the distribution of microorganisms through a biological window whose size depends on such biological processes as growth and predation; Barry and Dayton (1991) point out the importance of the unresolved issue of scale coupling between biotic and abiotic components in marine systems.

A good understanding of the discontinuities and modulations that are associated with spatial heterogeneity, in many forms and combinations, provides an invaluable help to ecologists who are looking for characteristic scales and predictable elements of a system (Allen and Hoekstra 1990). There is a triumvirate of discontinuities that may contribute to spatial heterogeneity; it consists of the deterministic, stochastic, and chaotic components (Kolasa and Rollo 1991). According to these authors, deterministic spatial heterogeneity is geometrically equivalent to design; for instance, a pattern of equally-spaced dots or stripes, all of the same size. The nature of that deterministic heterogeneity is however quite relative with respect to resolution or perception and processing or cognition of environmental signals, because even an absolutely deterministic complex design may appear random to organisms that have cognitive systems too simple to decode them. In such a case, a relative scale that transforms space on the basis of functional relationships would be appropriate, instead of an absolute scale involving distance, direction, shape, and geometry (Meentemeyer and Box 1987). There follows a change of scale during the transition from deterministic to stochastic spatial heterogeneity or vice versa, lead-

ing to a dissipation of information. Geometrically, stochastic spatial heterogeneity is represented as patchiness, characterised by the absence of association of the variation across scales. Among others, Chesson (1991) reviews the effects that among-patch and within-patch heterogeneity may have on ecological systems, and Kotliar and Wiens (1991) use intra-patch and inter-patch information when deciding where to delineate patches. In the analysis of patchy heterogeneity, there is a level of resolution where patch size becomes so fine that an individual or a species stops responding to it; this is the "grain", for that given group of organisms. Finally, spatial heterogeneity may involve chaotic variation, that may look like randomness although it is deterministically generated. In population dynamics for instance, chaos may emerge as an unstable and unpredictable oscillation that corresponds to the solution of the discrete version of the Lokta-Volterra equations for the highest values of growth rate and density dependence, lower values corresponding to equilibrium and stable deterministic cycles. Chaos differs from noise in that it shows the same degree of variation recursively at whatever scale it is examined (Gleick 1987, Glass and Mackey 1988). This property of repeated variation at finer and finer scales has a geometrical analogue known as the fractal dimension (Mandelbrot 1982, Frontier 1987). Fractal geometry may generate complex patterns that can be dissected into infinitely small scales; at each level, the pattern differs but always shows the same relative variability. Among the applications of fractal theory to ecology, Frontier (1987) mentions the contact zones among interacting parts of an ecosystem, and the trips and trajectories of mobile organisms; they respectively result in enhanced fluxes of energy, matter, or information, and diversified contact points between organisms and a heterogeneous environment, and among individuals in predator-prey systems. In particular, fractal strategies (e.g., lake shoreline, tree forest, compound leaves) may have an underlying fractal geometry and the behaviour of organisms living in such environments (fish, birds, caterpillars) may be dominated by this paradigm.

Spatial heterogeneity is not confined to the outdoors. Despite the sophistication of modern growth chambers, growth conditions cannot be uniformly controlled during experiments in vegetation science (Potvin et al. 1990a). The size of the heterogeneous structures varies with species and measured variables. In growth chamber experiments, Potvin and Tardif (1988) recognised as potential sources of variability: the fluctuations over time of the conditions within chambers, the differences among chambers, and the interaction of these two effects.

Point/Summary: The definition of spatial heterogeneity depends on the nature of the underlying pattern: for a point pattern, it refers to the distribution of individuals through space, and means density variation with respect to that expected for randomly spread organisms;

for a surface pattern, it refers to the among-subregion variability, for one or several qualitative or quantitative variables taking values in a spatially continuous manner. Spatial heterogeneity is functional in ecosystems. Scale, defined as measurement units, is a crucial aspect of spatial heterogeneity; shifts of scale may lead from homogeneity to heterogeneity, and vice versa. To undertake a field study in an efficient way, a thoughtful choice of observation scale is necessary; to accomplish this, a good understanding of the deterministic, stochastic and chaotic discontinuities that are associated with the system's spatial heterogeneity is of invaluable help.

Spatial heterogeneity: the statistical perspective

In the present section, we will show that for a point pattern, both ecologists and statisticians agree to define spatial heterogeneity as a density variation among subregions or sites; we will show in particular that under- and overdispersion correspond to well-defined types of variation in the intensity of the underlying point process, while organisms randomly dispersed in space correspond to the absence of such a variation. For a surface pattern, we will illustrate the fact that the diverse facets of spatial heterogeneity, viewed in a statistical perspective, may give interesting insights to ecologists in the observation and measurement of spatial heterogeneity.

The most commonly used statistical model of reference for spatial point patterns is the Poisson process; it is characterised by an intensity, i.e., the occurrence rate (or expected number per area unit) of points in space (for example, the presence or absence of ecological entities in a system), which is constant over the entire plane. It follows that points spatially dispersed at random under the Poisson model correspond to spatial homogeneity: first, by the absence of variation in the intensity of the underlying Poisson process; then, by the absence of variation in the expected number of points in subregions of the same size; and finally, by the corresponding lack of pattern. The other assumptions underlying the Poisson process are: there is no interaction among subareas, and no tendency for neighbouring areas to be similar; and the presence of an object (species) at any point (site) is not influenced by the presence or the absence of objects at nearby locations. Recently, Hurlbert (1990) showed that the variance:mean ratio, which is characteristically equal to 1.0 for the Poisson distribution (based on counts of points in several areas of the same size), is useless as a measure of departure from pure randomness, though it is widely recommended as such (see for instance Greig-Smith 1986); indeed, he showed that computed unicornian distributions (named after the recent discovery of the montane unicorn, whose populations provided the basis for his study) all yield a variance:mean ratio of 1.0, while the

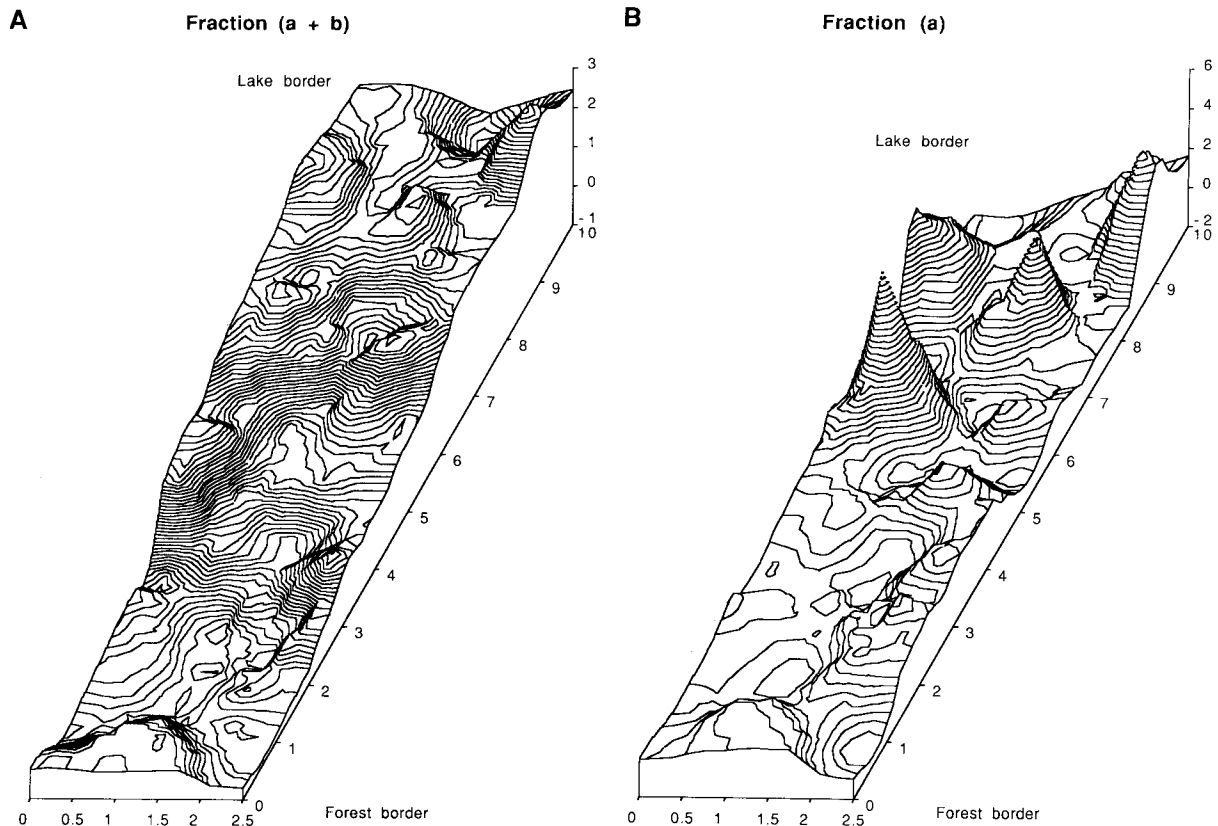**A**   Fraction (a + b)   **B**   Fraction (a)

Fig. 1. Three-dimensional maps for two types of spatial heterogeneity for a surface pattern. The data are from Borcard and Legendre (unpubl.); they respectively correspond to fractions (a + b) and (a) from partitioning the variation of Oribatid species abundance data into independent components, as described in Borcard et al. (1992). A – Heterogeneity of means: in this example (gradient type), the mean increases from the bottom (forest border) to the top (lake border) of the figure, while the variance remains relatively constant; fraction (a + b) plotted here corresponds to the environmental component of the species abundance variation. B – Heteroscedasticity, or heterogeneity of variances: in this example (two-level type), the variance is lower in the portion near the forest border than in the part near the lake, while the mean remains relatively constant; fraction (a) plotted here corresponds to the non-spatial part of the environmental component of variation.

montane unicorn populations under study show different patterns of aggregation, none of which corresponding to a Poisson distribution. We will pursue this discussion of aggregation indices in a further section.

During the early decades of the 20th century, many ecologists clung to the 19th century view (Hensen 1884) that ecological communities are homogeneously distributed through space (McIntosh 1991), despite clear demonstrations to the contrary (Moberg 1918, Hanson 1934); nowadays, random patterns resulting from a Poisson process look uninteresting and unlikely ever to occur in nature. The first two major departures from the Poisson scheme result from assuming that the intensity of the process is not a constant but a random variable; they are the true and apparent contagion, or generalised and compound Poisson processes. Because they can yield the same spatial distribution of points, they are hardly distinguishable in practice. Notwithstanding, a generalised Poisson process occurs when the number of objects in observed clusters is assumed to follow a gen-

eralising distribution (for instance a binomial); on the other hand, if the number of objects per quadrat follows a simple Poisson process whose intensity varies from quadrat to quadrat, the final distribution is Poisson compounded with some other distribution specifying its intensity (Cliff and Ord 1981, Upton and Fingleton 1985, Ripley 1987). Related kinds of processes are, among others, the Poisson cluster process, also called centre-satellite, and the doubly stochastic Poisson processes (Matérn 1971).

To complete our demonstration, there remains to show that underdispersion also corresponds to nonconstancy in the intensity of the underlying point process. Actually, the intensity in that case is not a constant, but a function taking either null or infinite values, depending on whether the point at which it is evaluated corresponds, or not, to a point of a predesigned regular grid. Consequently, the expected count of points in any given area is equal to zero, or not, depending on whether the considered subregion contains, or not, at least one point

of the grid. In less extreme regular patterns (Diggle 1983), underdispersion is characterised by points distributed more or less regularly around the nodes of some predesigned grid, because of some associated regulating mechanism operating to encourage their even spatial distribution.

The fit of the Poisson model to data would have to be studied for a whole range of spatial scales before homogeneity could be inferred. One approach to the analysis of point patterns is to sample small zones in the plane and to count the number of individuals occurring in each one. These sample zones are commonly known as quadrats. Quadrats may be contiguous, usually laid at equal intervals, either on a regular grid or more often in transects, or they may be positioned at random in the study area. A risk underlying the use of quadrats is that any detected spatial pattern may be dependent upon quadrat size, although this can be alleviated to some extent for contiguous quadrats (Greig-Smith 1952, Gérard 1970, Diggle 1977, Cliff and Ord 1981, Ripley 1981, Ver Hoef and Glenn-Lewin 1989). To avoid this difficulty, nearest-neighbour distances, which are the distances from each individual to others located nearby, may be studied, when the locations of all individuals in the plane are known. These measurements, and related applications to the analysis of field experiments, may be found in Clark and Evans (1954), Thompson (1956), Bartlett (1978), Freeman (1979), Aplin (1983), Wilkinson et al. (1983), Upton and Fingleton (1985), Besag and Kempton (1986), and Delincé (1986).

For a surface pattern, the ecological and statistical aspects of spatial heterogeneity may be distinguished. In the ecological literature, spatial heterogeneity essentially refers to variation over space of the observed values of a qualitative or quantitative descriptor (e.g., outdoors: Smith 1972, Kolasa and Rollo 1991, Lechowicz and Bell 1992; in controlled experiments: Potvin and Tardif 1988, Potvin et al. 1990a); the environment is considered heterogeneous when that descriptor takes different values at different locations. The statistical viewpoint is somewhat different in that it specifies types of heterogeneity depending on the characteristic or set of characteristics concerned (Glaser 1983). Traditionally, much attention has been devoted to the heterogeneity of distribution parameters such as mean or variance; in particular, the next section will be focused on heterogeneity of variances. To decide statistically between homogeneity and heterogeneity, tests were developed under parametric or nonparametric assumptions (e.g., Sokal and Rohlf 1981): for normally distributed data, the well-known Student's t test of equality of two means with equal but unknown variances, the F test for the homogeneity of variances, Wilks' lambda statistic for the heterogeneity among several groups in a multidimensional space, the comparison of main effects and interactions in the analysis of variance (ANOVA), and the assessment of parallelism or coincidence by ANCOVA between lines or surfaces fitted by regres-

sion. In a spatial context, autocorrelation, when combined with heterogeneity, can alter the conclusions of all the statistical tests above, if they are performed without allowance for it; the effect of spatial autocorrelation is to reduce the number of degrees of freedom that are actually associated to the t or F test statistics, for instance (Cliff and Ord 1981, Dutilleul and Legendre 1991a, b, Dutilleul and Potvin, unpubl., Legendre, in press).

In the statistical analysis of spatial data, Ripley (1981) mixed up homogeneity and stationarity, when defining stationarity under spatial translation, by referring to both the mean and the (auto)covariance functions, and consequently also to the variance; Ripley's definition did not take root, and we highly recommend to specify the type of (spatial) heterogeneity of concern and to distinguish (spatial) heterogeneity of the mean from that of the variance, for example. Fig. 1 illustrates the differences between such types of spatial heterogeneity, the ecological background being that of the Borcard et al. (1992) paper. Both types will be referred to as spatial heterogeneity in an ecological sense, because the observed values are not constant and show the presence of variation across the area under study; from a statistical viewpoint, though, the first type (Fig. 1A) will be called gradient-type heterogeneity of means, and the second (Fig. 1B), two-level heterogeneity of variances or heteroscedasticity. In a sense that we might call biostatistical, "gradient" is used here to mean a spatial structure resulting from the monotonic variation of a variable in space. This acceptation is intermediate between the mathematical sense, that strictly speaking refers to a function of several variables and is defined as the vector of its first derivates corresponding to the slopes of variation; and the ecological gradient, characterising major correlations of the community structure with environmental variable(s) that change monotonically in geographic space (e.g., Whittaker 1967). True gradients in mean (Fig. 1A) are different from false gradients in mean, which are the subject of spatial autocorrelation analysis; Legendre et al. (1990) and Legendre (in press) explain the difference between these two types of gradients. Both of them may also be considered as spatial heterogeneity in the ecological sense.

In practice, the calculation of a few descriptive statistics (mean and variance, for example) within moving windows, which are local neighbourhoods of a given size moving through the area under study, produces smoothed maps which are frequently used to investigate anomalies. A summary of more statistically-oriented methods, allowing to describe spatial patterns in ecological analysis, will be given in a further section, in the form of a statistical toolbox for ecologists.

Point/Summary: For a point pattern, ecologists and statisticians agree to define spatial heterogeneity as density variation among subregions. The most commonly used statistical model of reference for spatial point patterns is the Poisson process. Two major departures from

it, that are in better correspondence with reality, are the true and apparent contagion (generalised and compound Poisson processes), that allow the intensity of the underlying point pattern to vary across space. For a surface pattern, ecological and statistical aspects can be distinguished; the statistical viewpoint specifies different types of spatial heterogeneity depending on the set of characteristics concerned. A panel of tests are available to statistically decide between homogeneity and heterogeneity. From the statistical perspective, there are a multiplicity of facets to spatial heterogeneity for a surface pattern, which can provide potential insight to ecologists in the identification of the ones that are of concern for them, instead of maintaining a global but superficial perception of the concept.

Heteroscedasticity: a purely statistical concept

An important precondition for valid statistical inference is the equality of variances in a set of samples (Scheffé 1959, Winer 1971, Steel and Torrie 1980, Sokal and Rohlf 1981, Mead 1988). It is the case for instance: for a t test of equality of two means (but there is a modified form of the test when the condition is not met); for the F test in a more-than-two-sample analysis of variance; in a spatial context, for the estimation of correlograms and variograms – although in the case of variograms, the "intrinsic hypothesis" is restricted to the constancy (over the study area) of the variance for the variable of interest, for pairs of points located a given distance apart, instead of the "weak stationarity hypothesis" that requires, for the analysis of correlograms, the constancy over space of the variance (and the mean) of the variable itself (Jongman et al. 1987, Legendre and Fortin 1989). Synonyms for the condition of equality of variances are homogeneity of variances or homoscedasticity. The converse condition, that is, the inequality of variances among samples, is called heteroscedasticity (Sokal and Rohlf 1981, Dudewicz 1983, Glaser 1983, Isaaks and Srivastava 1990). Depending on the authors (Table 1), different terms may be used: "inequality of variances" (Box 1954a, b, Scheffé 1959), "heterogeneity of variances" (Winer 1971, Steel and Torrie 1980, Scherrer 1984) or "heteroscedasticity" (Scherrer 1984, Kendall et al. 1987); Kendall et al. (1987) restrict the use of homoscedasticity to the constancy of the conditional variances in the bivariate normal distribution.

Point/Summary: Heteroscedasticity is a purely statistical concept which refers to heterogeneity or inequality of variances. It is an important precondition for valid statistical inference, in particular for the estimation of spatial correlograms and variograms.

Statistical solutions to heteroscedasticity: an outline

Standard techniques of statistical inference are most often concerned with sets of observations drawn from independently and identically distributed random variables, referred to as "random samples". In real-case studies, heteroscedasticity in sample data may impair the validity of tests designed for random samples and can alter the conclusions of statistical analyses performed without allowance for it. It follows that experimenters have often been cautioned that the assumption of equal variability should be investigated prior to assessing treatment effects in their experimentation (Scheffé 1959, Winer 1971, Steel and Torrie 1980, Sokal and Rohlf 1981, Mead 1988). Several univariate tests for homoscedasticity have been proposed (e.g., Winer 1971, Sokal and Rohlf 1981); for instance, the Bartlett (1937) χ^2 test for homogeneity of variances, the Hartley (1950) F_{max} test, and the log-ANOVA or Scheffé's (1959) test. The latter is less sensitive to departures from normality but none is unilaterally more powerful than the others. In the multivariate case, approximate likelihood-ratio χ^2 tests also exist for assessing the homogeneity of variance-covariance matrices among samples of observation vectors prior to performing multivariate ANOVA (MANOVA) and discriminant analysis, under the hypothesis that the multivariate statistical population is normally distributed (e.g., Winer 1971, Morrison 1976).

Standard statistical procedures have trouble dealing with unequal variability among samples. A first alternative would be to perform a variance-stabilising transformation (e.g., logarithmic, square root, or power transformation), or else to combine Bartlett's χ^2 homogeneity-of-variance statistic with the Box-Cox normalising transformation (Sokal and Rohlf 1981). Unfortunately, if one of the original population distributions is normal, a transformation will make it nonnormal; transformation methods do not handle this problem except in special cases (Dudewicz 1983). A second alternative requires the experimenter to have control over the design of his experiment (Hurlbert 1984, Dutilleul, in press), even if such a control may be difficult or impossible at the scale of the landscape (Gardner and Turner 1990). The solution here lies in adequate experimental designs that allow to quantify spatial heterogeneity when it is a characteristic of interest; experimentation in nature adds controlled variability on top of natural heterogeneity, while good experimental designs combined with appropriate analysis of the results help to separate and understand sources of variation such as spatial heterogeneity in mean and variance (Fig. 1, A–B). Recommended designs are reported in the next section for spatial heterogeneity at small scale, patches or mosaics, and one- and two-dimensional gradients. A third alternative is developed at the end of the present

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section; it requires, as a preliminary, a short introduction to the analysis of repeated measures, that follows.

In repeated measurement designs, observations are taken at different times on a given set of experimental units that are plants or animals whose physiological state may be quite different at the beginning and at the end of the measurement period; the transposition from time to space results from the correspondence of repeated measures on the same individual plant or animal, with values observed at neighbouring locations. Thus, the nonrandom assignment of treatment levels across time or over space, which are then considered to be a factor, influences the variances and covariances of the variables observed on the experimental units. Consequently, two of the usual assumptions of ANOVA, that are homoscedasticity and independence of observations, may be violated. Valid statistical inference fortunately does not require them as necessary conditions, and the two alternative approaches, univariate and multivariate, are summarised in Crowder and Hand (1990) and Potvin et al. (1990b), for instance. In particular, a necessary and sufficient condition for valid unmodified F testing in analysis-of-variance models allows for limited forms of heteroscedasticity and autocorrelation (Huynh and Feldt 1970, Rouanet and Lépine 1970, Crowder and Hand 1990). That validity condition, called circularity or H.-F. (named after Huynh and Feldt), is a restriction of the geostatistical intrinsic hypothesis (Dutilleul and Legendre, unpubl.); it applies to repeated measures on the same experimental unit, across time (individual plant or animal) or space (neighbouring locations), and requires the variances to be equal for all pairwise differences between repeated measures on the same individual, or between values observed at different locations, whatever the time interval or distance separating them. For example, in the case of four measures on a 2 × 2 grid, the following covariance matrix is circular:

$$\begin{bmatrix} 1.0 & 0.5 & 1.0 & 1.5 \\ 0.5 & 2.0 & 1.5 & 2.0 \\ 1.0 & 1.5 & 3.0 & 2.5 \\ 1.5 & 2.0 & 2.5 & 4.0 \end{bmatrix}$$

In this matrix, the variance of the difference between the first and second measures (values at two contiguous locations) is the sum of the variances minus twice the covariance, that is, $1.0 + 2.0 - (2 \times 0.5) = 2.0$; this calculation leads to the same result for all pairs.

Finally, when spatial heterogeneity and treatment effects are respectively considered to be a nuisance and the characteristic of interest, the H.-F. condition may not be satisfied while the experimental design has not been accommodated to spatial heterogeneity; an ultimate solution is then provided by the pioneering, multipurpose work of Box (1954a, b) on the effects of heteroscedasticity and autocorrelation on the distribution of ANOVA statistics. Box suggested a conservative test

that uses an F distribution with fewer degrees of freedom than those classically (i.e., without modification) associated to the respective ANOVA sums of squares. Box's correction factor, called epsilon, is a measure of how far a covariance matrix deviates from the H.-F. or circularity condition; it can be estimated as described by Crowder and Hand (1990); this estimation is available in several computer packages, including SAS. In the one-way classification, moderate heteroscedasticity among samples affects the test for unequal sample sizes (Box 1954a); in the two-way classification, moderate inequality of variances among columns (or rows) of the data matrix has but a small effect, and first-order serial correlation within rows (or columns) has a large effect on the comparison of means among rows (or columns) (Box 1954b).

Box's correction technique for ANOVA testing is not widely spread yet among landscape ecologists (see for instance Sklar and Costanza 1990). An example of its application is provided by Dutilleul and Potvin (unpubl.) in the analysis of reaction norms, where the estimation and testing of the stability-variance components used to quantify the genotype-by-environment interaction may be altered by the heterogeneity of environmental variances and genetic correlations. In an ANOVA approach, Dutilleul and Potvin (unpubl.) propose a panel of test corrections based on Box's epsilon, whether genetic correlations are considered to be a nuisance or an interest in the assessment of genotype-by-environment interactions; they also derive related transformations that are based on (the inverse of the square root of) the sample covariance matrix of what they call a "genotypic profile", defined as the vector of mean phenotypic responses of the concerned genotype in various environments. In conclusion, these authors recommend combining a transformation removing environmental heteroscedasticity with testing of the genotype-by-environment interaction, corrected for the genetic correlations.

Point/Summary: Numerous statistical tests of homoscedasticity are available, in both the univariate and the multivariate cases, prior to assessing homogeneity of means. Statistical solutions to heteroscedasticity are provided by transformation methods, experimental design, and corrected testing. Methods developed in the analysis of repeated measures allow to manage both heteroscedasticy and autocorrelation, and help overcome their nuisance.

Quantification of spatial heterogeneity: a statistical toolbox for ecologists

The final part of our review is devoted to relating the ecological and statistical views in order to reach a better quantification of spatial heterogeneity. It is divided in two subsections, corresponding to the main division we

retained for characterising and quantifying spatial heterogeneity: the point and surface patterns. Our first subsection is less developed than the second one, about surface patterns, for which we used the Oribatid data set of the Borcard et al. (1992) paper as our case study. Both subsections are completed by references to a number of statistical textbooks and review papers, in order to reduce the amount of mathematical detail to its simplest expression.

The point pattern case

One can hardly expect a single index to serve well both as a measure of departure from the Poisson distribution (randomness) and as a measure of aggregation, because overdispersion only provides one of the two main alternatives to spatial point-pattern homogeneity; the other, underdispersion, corresponds to regular spacing of the points. In a classical approach (see for instance Downing 1991), organisms that are spatially aggregated are those that show more variability in space than would be expected from either a random or a regular spatial distribution. Hurlbert's (1990) study of unicornian distributions, mentioned above, shows that the variance: mean ratio is of little value as a measure of departure from randomness. The problem is not with the Poisson process itself as a model of reference, but rather with the variance:mean ratio; that this ratio be equal to 1.0 is a necessary condition for a spatial distribution generated under a Poisson process, but it is not a sufficient condition in the sense that other spatial distributions (for instance the unicornian) are also characterised by that property. As an alternative, Hurlbert suggested a simple way of measuring departures from a Poisson distribution, based on an index defined as the degree of overlap or concordance of the observed distribution to a Poisson with same mean; he also showed that this index is not more useful as an index of aggregation than the variance:mean ratio is. The measure of aggregation recommended by Hurlbert (1990) is the Morisita index defined in terms of the probability for two randomly selected individuals to be found in the same quadrat; this definition may be extended to more than two individuals. Hurlbert's conclusion is that a plot of the resulting generalised index as a function of the number of individuals is to be preferred to the condensation of all the information into a single index value.

There exists a plethora of indices of spatial aggregation, that were primarily defined as simple ratios of either the sample standard deviation or variance of quadrat counts to their sample mean (with the Poisson process as reference), and whose variants (the Morisita and Lloyd indices among others, and the parameter of the negative binomial distribution as an alternative to the Poisson distribution) try to compensate for some systematic variation of the sample mean across space

(e.g., Ripley 1981, Downing 1991). What would constitute a widely applicable index of spatial aggregation, providing both a measure that actually corresponds to the definition of spatial aggregation, and reliable values that can be compared among populations? Except for the one advocated by Hurlbert (1990), the answer to this fundamental question remains unclear. Few indices work generally enough to allow comparisons; some of them lead to directly conflicting interpretations (Downing 1991); and without exception, they failed to survive close examination (Ripley 1987).

The use of aggregation indices may be completed by the analysis of nearest-neighbour distances, although these concern more specifically the detection of scale. Even if scale is a crucial aspect of spatial heterogeneity, one may argue that nearest-neighbour distances do not provide, as such, a direct quantification of spatial heterogeneity; this is why they are not discussed in detail here. Blocking of quadrats and looking at how the variability of counts varies with the size of the quadrats also provide fruitful information about spatial scales. Good presentations and criticisms of both methods are given by Pielou (1977), Upton and Fingleton (1985), Ripley (1987), and Turner et al. (1990). Methods based on distances among individual organisms are useful only under particular circumstances (Pielou 1977). On the contrary, quadrat counts can always be used, and more information on the spatial pattern can be extracted if several quadrat sizes are used, although it is negligible compared to the information lost when the position of the quadrats is ignored (Ripley 1987); Ripley also demonstrated that L-plots, that he defined, are very useful in describing the ecologically features of a spatial pattern, where L is a function of scale on the basis of distances between all pairs of points.

The surface pattern case

Among the statistical methods that we recommend for quantifying spatial heterogeneity, we will distinguish the ones that apply whether the heterogeneity concerns the mean or the variance of the variable of interest, from those that are specifically designed for one of these two types of heterogeneity. The methods discussed below are essentially relevant for quantitative or semi-quantitative variables; only a few apply to qualitative variables.

Mapping
If we are interested in fitting nonperiodic large-scale spatial heterogeneity in the mean (see for example Fig. 1A), trend surface analysis is perhaps the simplest and oldest method used by ecologists (for a review, see Jongman et al. 1987, Legendre and Fortin 1989, or Turner et al. 1990); it consists of separating, by regres-

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Table 2. Experimental designs to accommodate three types of spatial heterogeneity, when spatial heterogeneity is a characteristic of interest or a nuisance. Modified from Dutilleul (in press).

Type of spatial heterogeneity	In the absence of treatment assignment	In the presence of treatment assignment	
	Spatial heterogeneity is of interest	Spatial heterogeneity and treatment effects are both of interest	Spatial heterogeneity is a nuisance and treatment effects are of interest
Small-scale	1 classification factor (plots)	Complely randomised design	
		with more than 1 observation per plot	with 1 observation per plot
Patches	cf. Small-scale	Randomised complete block design	
		with more than 1 block per patch	with 1 or more than 1 block per patch
Environmental gradient: – one-dimensional	cf. Small-scale	Randomised complete block design	
		with more than 1 observation per treatment per block	with 1 observation per treatment per plock
– two-dimensional	cf. Small-scale	Latin square design	
		with more than 1 observation per cell or multiple Latin squares	with 1 observation per cell

sion, the large-scale trend (that we called "true gradient" in mean in a biostatistical sense, above) from the residual variation. The trend is then represented in the model by a deterministic function of the geographic coordinates of the sampling locations, that may be linear or a polynomial of higher degree in the simplest cases, an orthogonal polynomial or a spline function in more sophisticated cases; in the case of Fig. 1A, a polynomial function of the second or third degree would be sufficient. Interpolated mapping, either by linear interpolation among nearest neighbours using methods such as locally weighted averaging, by techniques based on Dirichlet tessellations or Delaunay triangulations, by kriging or by kernel estimation, is more appropriate to fit small-scale spatial heterogeneity in mean ("false gradient" in mean). All those methods and others are reviewed by Ripley (1981), Upton and Fingleton (1985), Jongman et al. (1987), Isaaks and Srivastava (1989), among others. In the very special case of periodic large-scale spatial heterogeneity in mean, trend surface analysis, using cosine and sine waves as explanatory functions in the regression model instead of a polynomial, provides a Fourier series modelling that can be represented by a two-dimensional periodogram (described for instance by Legendre and Fortin 1989, and Turner et al. 1990). If the periodic spatial heterogeneity of concern is on the variance instead of the mean, spectral analysis and the estimation of a two-dimensional spectral density function, whose integration over a range of frequencies provides the associated variance, are recommended here, as their one-dimensional versions are in time series analysis (e.g., Priestley 1981).

Experimental design

There are different meanings associated with the expression "experimental design". The meaning retained here is the one commonly used in experimentation (Winer 1971, Steel and Torrie 1980, Mead 1988). It differs from that of Fahrig (1990) in simulation experiments, who studied by simulation the effects of each parameter over its plausible range in the model.

Spatial heterogeneity of the landscape (or greenhouse, etc.) must be studied before treatments are assigned in a controlled experiment, so that the constancy of the system's properties over space can be evaluated. The information collected, when combined with the a priori knowledge of the experimenter about his experimental material, helps design the experiment, or validate or invalidate a preexisting design. On the other hand, the variability due to spatial heterogeneity may be of interest, aside from any field experiment concerning treatment effects.

We illustrate hereafter how experimental design can be accommodated to spatial heterogeneity in nature, whether it is a nuisance or a characteristic of interest, combined or not with assessment of treatment effects. There are obviously no recipes to accomplish this; no single design can best accommodate all experiments, and judgment must be exercised every time. Dutilleul (in press) gives an overview of the kind of considerations that must be taken into account and of the compromises entailed by those considerations; his analysis-of-variance approach to the quantification of spatial heterogeneity is based on the adequate design of ecological field experiments, according to the type of heter-

A   Fraction (a + b)

B   Fraction (a)

C   Fraction (a), near the forest

D   Fraction (a), near the lake

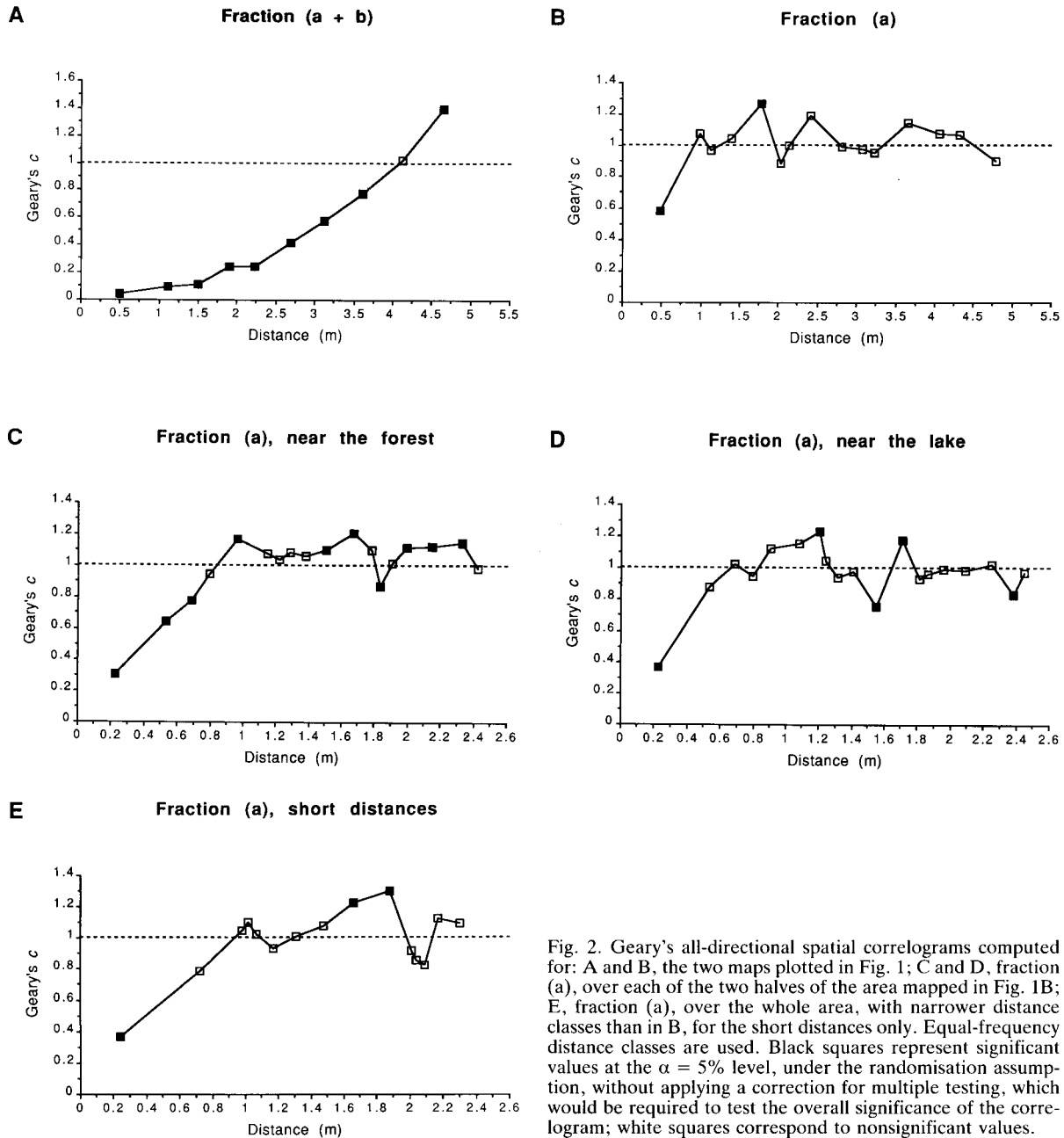**E**   Fraction (a), short distances

Fig. 2. Geary's all-directional spatial correlograms computed for: A and B, the two maps plotted in Fig. 1; C and D, fraction (a), over each of the two halves of the area mapped in Fig. 1B; E, fraction (a), over the whole area, with narrower distance classes than in B, for the short distances only. Equal-frequency distance classes are used. Black squares represent significant values at the $\alpha = 5\%$ level, under the randomisation assumption, without applying a correction for multiple testing, which would be required to test the overall significance of the correlogram; white squares correspond to nonsignificant values.

ogeneity of concern (at small scale, patches, one- or two-dimensional gradients). Our purpose here is to summarize the basic guidelines of Dutilleul's paper, to which we refer for detail.

When spatial heterogeneity in nature is of interest, it can be taken into account by one or several, fixed or random classification factors in an ANOVA model, depending on whether it concerns the mean or the variance of the variable under study. Accurate estimations of that spatial heterogeneity are then provided by the

sums of squared differences between sample means at different levels of the classification factors, or by the variance components associated with the classification factors; absence of spatial heterogeneity can be tested by assessing the absence of effects of the classification factor concerned, eventually correcting the test for spatial autocorrelation. In the presence of treatment assignment, spatial heterogeneity in nature can be told apart from controlled spatial heterogeneity in mean, represented by treatment effects. Spatial heterogeneity
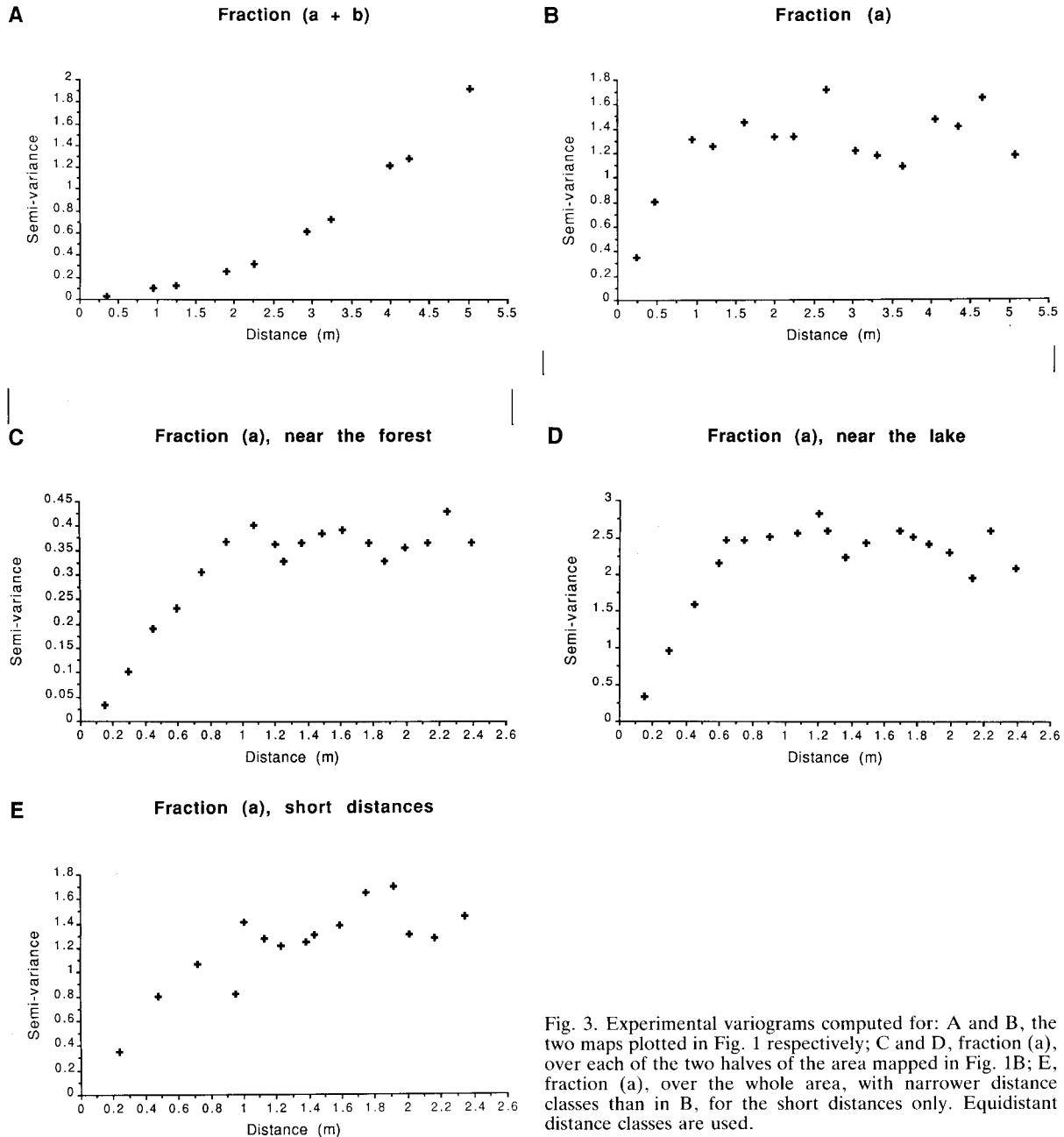
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A   Fraction (a + b)

Semi-variance

Distance (m)

B   Fraction (a)

Semi-variance

Distance (m)

C   Fraction (a), near the forest

Semi-variance

Distance (m)

D   Fraction (a), near the lake

Semi-variance

Distance (m)

E   Fraction (a), short distances

Semi-variance

Distance (m)

Fig. 3. Experimental variograms computed for: A and B, the two maps plotted in Fig. 1 respectively; C and D, fraction (a), over each of the two halves of the area mapped in Fig. 1B; E, fraction (a), over the whole area, with narrower distance classes than in B, for the short distances only. Equidistant distance classes are used.

in nature is seen as a nuisance to the assessment of the absence of treatment effects, which are the characteristics of interest, when the associated variability is not adequately removed from the effective error of the model, resulting in the inflation of the error mean square used in F testing and the undervaluation of the associated power.

Recommended designs are summarised in Table 2. For patches and one- or two-dimensional gradients, and in the presence of treatment assignment, they require a

principle called blocking, that differs from quadrat blocking and whose application criteria are more restricting; it allows avoiding spurious treatment effects and inflated error mean square. Blocking results from the a priori idea most experimenters have of which experimental units are likely to behave similarly, and the exploitation of that knowledge to allocate the treatments to experimental units more fairly; groups of similar experimental units or "blocks" should essentially include a roughly equal number of experimental units

for each treatment. The simplest and most frequently used blocking is the randomised complete block design (Winer 1971, Steel and Torrie 1980, Sokal and Rohlf 1981, Mead 1988), in which each block is divided into as many subblocks of equal size as there are treatments; within each block, treatments are randomly assigned to the subblocks. When the underlying spatial pattern is clearly patchy, or has been detected to be so, the plots must be matched as far as possible with the patches, and the number of subplots per plot must be adapted to the physical size of the patches. When spatial heterogeneity due to a one-dimensional "true gradient" in nature and treatment effects are both of interest, the various plots or blocks of subplots must cover the whole gradient in order to capture the systematic change. In the case of a two-dimensional gradient, it is recommended to divide the experimental field into row and column blocks of subplots in order to account for changes along its two axes; the resulting design is the Latin square (Sokal and Rohlf 1981, Mead 1988).

Variograms and correlograms

Two final quantification methods essentially concern spatial heterogeneity in variance; they are outlined hereafter, and illustrated using the Oribatid data set of the Borcard et al. (1992) paper. Both of these methods are based on the same statistical function, defined, over each given distance class or over the average distance within each class, as the sum of squared differences between all pairs of observations belonging to the class under consideration:

$$\sum_{(i,j)\,\in\,\text{distance class d}} (y_i - y_j)^2$$

where y_i and y_j respectively represent the observed values of the variable under study for sampling locations i and j, separated by a distance belonging to distance class d. Under the intrinsic hypothesis (zero mean and constant variance of the increments $y_i - y_j$), the sum of squares above provides, up to a multiplicative constant $\frac{1}{n_d}$ or $\frac{1}{n_{d-1}}$, an estimation of the variance of the increments between sites located the said distance apart.

Both methods use the above statistic as their numerator. When computing the semi-variance, that statistic is divided by $2n_d$, where n_d represents the number of pairs in the given distance class; a semi-variogram, often called "variogram" for convenience (Jongman et al. 1987, Isaaks and Srivastava 1989), is a plot of the semi-variance statistic against the various distance classes or against the average distance within each class. In Geary's c autocorrelation coefficient (Cliff and Ord 1973, 1981, Legendre and Fortin 1989), the semi-variance statistic is further divided by the variance of all the observed values in the study. We preferred using

Geary's c coefficient instead of another well-known autocorrelation coefficient, Moran's I, because the former represents a standardised variance, while the latter measures a correlation (Legendre and Fortin 1989). Autocorrelation coefficients are also available for nominal data (Cliff and Ord 1973, 1981, Sokal and Oden 1978a, b) and for multivariate data (Oden and Sokal 1986, Sokal 1986). Geary's c correlograms and the experimental variograms for the data mapped in Fig. 1A and B are plotted in Fig. 2A and B and in Fig. 3A and B, respectively; the "R package" (Legendre and Vaudor 1991) was used for computing Geary's c statistics, and GEO-EAS (Englund and Sparks 1988) for the semi-variances.

Although they are built from the same variance statistic, semi-variance and Geary's c analyses require to be valid somewhat different assumptions about the underlying surface pattern. As mentioned above, the intrinsic hypothesis of variogram analysis is weaker than the second-order stationarity condition required by spatial correlogram analysis. In the case of Geary's c autocorrelation coefficient, second-order stationarity is required because an overall estimation of the variance is used in the denominator of the coefficient, and it appears again in the formula for estimating the variance of c when performing the test of significance (which is not available in variogram analysis). The result is a greater validity of variogram analysis, compared to correlograms; this is counterbalanced by the ability of testing the significance of the semi-variance in Geary's c analysis. In Fig. 1, fractions (a + b) and (a) clearly do not satisfy the second-order stationarity condition, so that the corresponding correlograms in Fig. 2 suffer from lack of statistical confidence in the significance of the observed values; in the case of fraction (a + b), the pattern of both statistics (Figs 2A and 3A) is however typical of a gradient in mean. Even the intrinsic hypothesis is violated by the increments, because of the nonzero mean for fraction (a + b), and a nonconstant variance for fraction (a). Spatial heterogeneity in the variance of fraction (a) motivates further discussion below.

Concerning the statistical assessment of the significance of correlogram ordinates, both Moran's I and Geary's c are asymptotically normally distributed as the number of observations increases, as originally demonstrated by Cliff and Ord (1973), followed by Sokal and Oden (1978a, b), Cliff and Ord (1981), and Legendre and Legendre (1983) among others; I and c are tested for significance as standard normal deviates; and these properties approximately hold for regular grids of moderate size. Moments of I and c may be evaluated under either of two assumptions: normality, where observations are supposed to be independently drawn from a normal population; randomisation, under which the observed value of I or c is considered relative to the set of all possible values which I and c could take on if the indices identifying observations were repeatedly ran-

domly permuted, whatever the underlying distribution of the population. For instance, the significance of the sample autocorrelation values of Geary's c (and Moran's I), as computed in the computer package that we used, is based on the randomisation assumption, that Sokal and Oden (1978a) argued to be more reasonable for most applications in systematics. There is no constraint of equal spacing of the data to the use of I and c.

We complete this section with the rules concerning the interpretation of Geary's c spatial correlogram and the variogram, and their application to Figs 2 B-E and 3 B-E. The first rule concerns the interpretation to give to the statistics themselves: Geary's c and the semi-variance. By definition, they are based on the sample variance of increments, so that they are functions of spatial autocorrelation, and the weaker spatial autocorrelation is for all distance classes, the more constant both statistics are expected to be over the distance range; they also provide measures for quantifying spatial heterogeneity by partitioning variance into distance classes, in a way similar to that by which the spectral density function allows a variance partitioning of a time series in the frequency domain (Priestley 1981). The second rule results from the first, at least for Geary's c. For this coefficient, the more distant the correlogram ordinate is from the 1.0 value, the more significant it is; c's values smaller (greater) than 1.0 correspond to positive (negative) spatial autocorrelation. For the semi-variance, there are three parameters that are important in the adjustment of a theoretical model to an experimental variogram, required for kriging; for a full description of these models and of kriging itself, that falls beyond the scope of this paper, we refer to the monographs of Cicéri et al. (1977), Journel and Huijbregts (1978), Jongman et al. (1987), Isaaks and Srivastava (1989), and the review paper of Legendre and Fortin (1989). We limit our description to the basic parameters that are: the "range" of influence of the spatial structure, which is the distance where the variogram stops increasing; the "sill", which is the ordinate value of the flat portion of the variogram (if any), where the semi-variance is no longer a function of distance and corresponds to the sample variance; and eventually, the "nugget effect", that refers to variograms that do not go through the origin of the graph, but display some amount of variance even at distance zero. This last effect may be caused by the sampling variance, or it may suggest that sampling has not been performed at the right spatial scale. In view of Figs 2 B-E and 3 B-E, a great similarity of pattern is observed, as expected, between each Geary's c correlogram and the corresponding variogram. The only difference lies in the distance classes used for the computations: equidistant classes for the variograms (an average distance is finally used by GEO-EAS for each class) and equifrequential classes for Geary's correlogram; although the correlogram could have been computed from equidistant classes, we chose equal-frequency classes here to retain

the same power for the statistical tests throughout the range of distance classes. In order to overcome spatial heterogeneity in variance of fraction (a), we divided the studied area in two parts: the portion near the forest and the one near the lake. The resulting Geary's correlograms and variograms (Figs 2 C-D and 3 C-D) show the following: the "range" of fraction (a) near the lake is about 0.6 m, which is smaller than for the part near the forest, around 1.0 m; the magnitude of the variogram ordinates, and in particular the "sill", is in direct relation with the heterogeneity of the variances (Figs 3 C-D); in concordance with the observations about the "range", spatial autocorrelation is significant up to approximately 0.75 m near the forest, but only for the very first distance class near the lake (Figs 2 C-D); significant autocorrelation at further distance classes, in relation with semi-variance values observed above or below the sill, corresponds to the association, negative or positive, between peaks and troughs, providing some pseudo-periodicity (Cicéri et al. 1977, Jongman et al. 1987); this last feature was clearly visible near the lake, but not near the forest (Fig. 1B). The presence of a mixture of two spatial structures is reflected in Figs 2B and 3B, and also in Figs 2E and 3E, for a refined range of short distances. One should finally note that all these variograms are characterised by the absence of nugget effect; if a trend surface had to be fitted to fraction (a) over the whole area, a weighted least squares method of estimation (Draper and Smith 1981, Montgomery and Peck 1982), using as weights the inverse of the sample variances computed over each half of the area, would be recommended. An ecological interpretation of the spatial structure of this Oribatid community in relation with environmental gradients is given in Borcard and Legendre (unpubl.).

Point/Summary: For a point pattern, measures of departure from randomness are distinguished from measures of spatial aggregation; while there exists a plethora of aggregation indices, only a few, and perhaps only one, are approved unanimously; the use of aggregation indices may be completed by the analysis of nearest-neighbour distances and quadrat blocking, but even these methods are subject to criticism. For a surface pattern, quantification methods of spatial heterogeneity in mean are provided by trend surface and spectral analysis, and more or less sophisticated interpolation methods such as moving average or kriging, depending on the scale – large or small – of the heterogeneity; the experimenter's knowledge about his experimental material, combined with premanipulation or control, must be an important source of information during the design of an experiment; no single design can best accommodate all experiments and judgment must be exercised every time. Quantification methods of assessing spatial heterogeneity in variance are provided by the analysis of semi-variance and of Geary's c spatial autocorrelation coefficient; they are built on the same variance statistic but require somewhat different validity assump-

tions, allowing or not significance testing of their ordinates.

Conclusion

Heterogeneity is a contemporary subject of concern for ecologists, that one can view from a variety of perspectives; some of them have been thoroughly explored, while many others have not. A good understanding of the concept and of its chief aspects are required, either for its fruitful study when spatiotemporal heterogeneity is a characteristic of interest, or for removing it efficiently when it is a nuisance. The primary objective of our paper was to review the ways heterogeneity is construed in both the ecological and statistical literatures with emphasis on space; in particular, we wanted to understand its structural and dynamic aspects in ecosystems, and describe the various forms it can take in a statistical perspective. Our contribution has been in the distinction between the point and surface patterns of spatial heterogeneity, the relation between the ecological perspective of spatial heterogeneity for a point pattern and the statistical Poisson model, and the enlightenment of the multiple facets spatial heterogeneity can present for a surface pattern.

The confusion between heterogeneity and heteroscedasticity, induced by a partially common etymology, has motivated to pursue our review and synthesis of the statistical and ecological perspectives of spatial heterogeneity, and to discuss the problems of its quantification. First, we emphasised the purely statistical nature of heteroscedasticity, strictly defined as the inequality or heterogeneity of variances. Secondly, we outlined the statistical solutions to heteroscedasticity: transformation methods, experimental design, and corrected testing, with emphasis on space for the latter. We also argued that, combined or not with dependence of observations or autocorrelation, heteroscedasticity does not always impair our ability to perform, without modification nor lack of validity, standard methods of statistical inference. We completed the connection of the ecological and statistical views with a statistical toolbox for ecologists interested in quantifying spatial heterogeneity, whose key tools are a panel of aggregation indices for point patterns; and mapping, experimental designs, variograms, and correlograms for surface patterns.

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