1

Spatial concepts and notions

Introduction

The processes in natural systems and the patterns that result from them occur in ecological space and time. To study natural systems and to understand the functional processes that are related to them, we need to identify the relevant spatial and temporal scales at which these occur. While the spatial and temporal dimensions of ecological phenomena have always been inherent in the conceptual framework of ecology, it is only relatively recently that these spatio-temporal dimensions have been incorporated explicitly into ecological theory, sampling design, experimental design, and formal models (Levin 1992, 2000). Furthermore, all phenomena of ecological interest have both spatial locations, which can be designated by geographic coordinates, and other aspatial characteristics, which are those attributes that do not require location to be meaningful. That being the case, we can have different perspectives on how to proceed with the analysis of these phenomena:

- the spatial locations can be included explicitly for the purpose of understanding spatial structure and pattern;
- the aspatial characteristics can be analysed separately by ignoring, or controlling for, their relative positions, defined by neighbours, or spatial locations, given by x and y in some coordinate system; or
- the spatial locations can be incorporated directly into the evaluation of those aspatial characteristics.

Before getting to the details of spatial statistics, we will review what we mean by spatial analysis, because it has a broad historical base and a wide range of methods included within it. There are several possible classifications of spatial analysis methods, but it is difficult to provide a classification that is 'simultaneously exclusive, exhaustive, imaginative, and satisfying' (Upton & Fingleton 1985, p. 1). A number of authorities on spatial analysis have offered different classifications. For example, Haining (2003) gave a list of three main elements:

(1) cartographic modelling,
(2) mathematical modelling,
(3) statistical methods for spatial data.

Fotheringham & Rogerson (2009) proposed four classes:

(1) summary methods,
(2) exploratory data analysis,
(3) comparisons with randomness, including inference,
(4) mathematical modelling and prediction.

We propose a slightly more detailed classification (see also Box 1.1):

(1) describing and testing spatial structure,
(2) spatial extrapolation and interpolation,
(3) spatial partitioning,
(4) spatial regression and spatial simulation,
(5) spatial interaction,
(6) spatio-temporal analysis and modelling.

A large number of spatial statistics are already available and new methods are constantly being developed in various elements of these classifications. The presentation in this book will not cover all possible approaches, but will concentrate on those that we think are the most important for ecological research. We acknowledge that we are omitting several important fields of research and schools of thought. For example, we do not attempt to cover spatial issues related to information theory and

Box 1.1 Classification of the subjects of spatial analyses

Spatial structure: (a) this can refer to the degree of dependence in the values of a variable between neighbouring locations, usually as a function of distance, Euclidean or otherwise. Most such analyses are 'global' with values of a single statistic to summarize the entire study area (Chapters 4, 5, and 6), but they can be 'local', where subsets of the locations are used to calculate a value for each sampled location (Chapter 6). (b) Spatial structure can also refer to the topology of the system under study, whether due to the physical relationships of the sub-units that constitute the system or the connections that join them one to another.

Spatial extrapolation and interpolation: using the known values from locations that have observations and the degree of spatial autocorrelation based on the distance between locations, the values of the variable can then be estimated for locations that do not have observations. Extrapolation refers to the situation where the unsampled locations of interest are beyond the range of the sampled locations with known values, whether outside the whole sample area or outside a convex hull of the samples; interpolation is where the unsampled locations are within the area covered by the locations with known values.

Spatial partitioning: creates spatial clusters using either clustering methods that group sampling locations together based on the degree of similarity of the variable(s) measured, or boundary detection methods that separate sampling locations by identifying the high rates of change, i.e. possible boundaries, between sampling locations.

Spatial regression and spatial simulation: modelling that includes spatial dependency and spatial location in such a way that closest values have the greatest effect on the result for a specific location. Autoregressive models, autologistic regression, geographically weighted regression, etc., are used to evaluate the relationship of one set of variables to another. A classic example of non-spatial regression is the relationship between the measured plant metabolic rate and ambient temperature; and its spatial version would apply if the relationship was being investigated in the field. Then, the spatial component could appear as autocorrelation in the metabolic rates due to patchy clonal structure of the plants, or through autocorrelation in the temperature regime because of proximity and the topography of the field.

Spatial interaction: examines the flow of material or energy or information among locations and the factors that affect the flow such as distance, density, and resistance. This kind of analysis requires an underlying topology of the connections between locations, and therefore leads into the requirements and possibilities of Graph Theory, the branch of Mathematics that deals with structure in the abstract and also in a spatial context. (We provide a full chapter on Spatial Graph Theory and its applications in spatial analysis: Chapter 3.)

Spatio-temporal analysis and modelling: include the spatial estimation of parameters and their temporal changes using spatio-temporal statistics and the spatial modelling of variables using spatial regression and spatial ordination (Chapter 7). We have not covered the topic of spatio-temporal analysis fully in this revision; the topic deserves a whole book to itself and that book now exists (Cressie & Wikle 2011), and our book is already too long!

spatio-temporal modelling since these topics deserve and require a whole book each.

In recent years, a very active field of research that rests on spatial analysis has emerged as the broad field of macroecology, which looks at the relationships between organisms and the environment at large spatial scales, focusing on abundance, distribution, and diversity (Brown 1995; Gaston & Blackburn 2000; Marquet 2009). It has evolved out of topics originally included in biogeography. Although there is a clear link between some aspects of what is now included in macroecology and the topics that are dealt with in this book on spatial analysis, such as species-area relationships or spatial turnover of species, there are a large number of topics in macroecology that are less directly linked, such as the relationships between body-size and extinction or between species richness and energy (Gaston & Blackburn (2000) give a partial list of macroecology topics). For that reason, we will concentrate mainly on the inherently spatial aspects and on spatial analysis. The link between the material described in this book and the broad endeavour of macroecology may have been strengthened by popular software packages such as 'Spatial Analysis in Macroecology' (SAM; Rangel *et al.* 2010) and 'PASSaGE' (Rosenberg & Anderson 2010). These provide implementation of many of the methods described in this book through graphical interfaces. Because commentary on software becomes so quickly out-of-date, however, we will not make specific recommendations on software available to carry out the techniques we describe. Instead we suggest that readers seek technical guidance on how to perform spatial analysis in R (see Diggle & Ribeiro Jr. 2007; Bivand *et al.* 2008; Borcard *et al.* 2011; Plant 2012), because the use of R as the environment for analysis seems to be becoming firmly established in ecological research.

There are a number of texts on various aspects of spatial statistics, including Anselin (1988), Haining (1990, 2003), Bailey & Gatrell (1995), Manly (1997), Legendre & Legendre (1998), Dale (1999), O'Sullivan & Unwin (2003), Illian *et al.* (2008), and Fotheringham & Rogerson (2009). Obviously no single book can provide everything that might be needed. Several advanced spatial statistical books cover the mathematics of some of these methods (e.g. Ripley 1981; Cressie 1993; Cressie & Wikle 2011; Dutilleul 2011), but the material may not be easily accessible to most ecologists and may not provide explicit guidance for application in the ecological context. In fact, there is always some potential for the misapplication of these techniques, which can lead to incorrect inferences.

Our intention is to present the concepts needed to perform valid spatial analyses and interpretation. To enhance the presentation, we include various real and simulated data sets to illustrate the behaviour of the methods, and the relationships among them. In this book, we concentrate on the spatial aspects of ecological data analysis to provide some advice and guidance to practising ecologists. The intended audience is graduate students and other practising researchers, who have some familiarity with basic statistics and related approaches to ecological analysis but who are not themselves experts in spatial statistics.

The structure of the book is straightforward. We begin by introducing important terms and concepts, taking the opportunity to clarify how they will be used in subsequent discussion. There are then a number of chapters that present spatial methods based on their objectives, with a few excursions to deal with special topics. Each chapter includes a description of methods, some examples, an evaluation of the methods' characteristics, and advice on the choice of method. The last chapter asks and tries to answer the question: where do we go from here? It describes what we see as the directions for future development in this field and the areas where we perceive the need for more work (and there are lots of these!). We also try to summarize our thoughts on the themes and threads that run through the book and unify it, and we provide some advice on the kinds of skills that we think ecologists will need for future work.

In this introduction chapter, we present a series of concepts and notions that are the foundation needed to understand the spatial statistics presented in the chapters to come.

1.1 The spatial context

In ecological studies, explicit considerations of spatial structure have come to play an important role in our efforts to understand and to manage ecological processes. Therefore, the description and quantification of ecological patterns, both spatial and temporal, are important first steps in our quest to comprehend the complexity of nature. Description is not usually an end in itself, but rather the beginning of a process that leads to insight into natural complexity, and which in turn generates the new ecological hypotheses to be tested (Figure 1.1). Ecological research is an iterative process that can provide, at each stage, some insights about the underlying ecological processes through the quantification of ecological patterns.

The match between pattern and process is far from perfect because changes in process intensity can create different patterns, and because several different processes can generate the same pattern signature

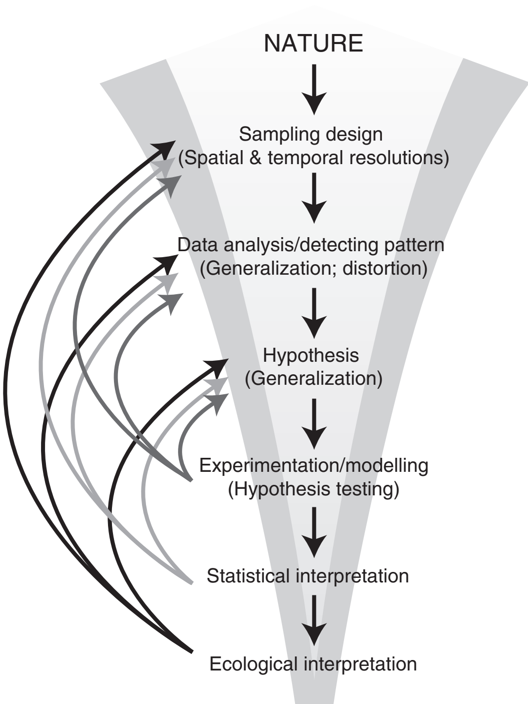


Figure 1.1 Flow of the steps involved in the study of nature and its complexity. As nature acts at several temporal and spatial scales, the selected sampling design narrows down the temporal and spatial limits of the domain under study (as indicated by the funnel effect illustrated in grey). By imposing arbitrary and potentially inappropriate scales by means of the sampling design, the identified spatial patterns can be distorted. From these spatial patterns, generalizations and hypotheses can be drawn about the ecological processes. Then specific experiments or models can be used to test the newly defined hypotheses. And finally, some statistical interpretations and ecological understanding can be reached. At each step, the spatial and temporal domains of inference of the findings diminished.

(Figure 1.2; Box 1.2). Furthermore, the processes may create a mosaic of intermingled and confounded spatial patterns, and the spatial legacy of this heterogeneity affects the intensity and types of ecological processes that act on them through time. These feedback effects between processes and patterns are difficult to distinguish (Figure 1.2*c*). Prior knowledge of the scope of these processes can help to guide the scale chosen for the investigation of spatial patterns.

1.2 Ecological data

Various kinds of measurements can be considered as ecological data, from qualitative records (e.g. taxonomic species), semi-quantitative observations (e.g. non-additive values such as pH), to quantitative measures (e.g. abundance data, height, weight). These measurements can be made for individuals (point data: e.g. discrete objects, events, or organisms), along a line (transect data), over an area (surface data: e.g. within a sampling unit), or in a volume (e.g. phytoplankton productivity in a water column with x, y and z coordinates); see Figure 1.3. When sampling units are used, these can either be spatially adjacent and contiguous to one another or separated by constant or variable distances (Figure 1.3). In either case, the measurements are subject to several precision and accuracy issues. The quality of the measurements are a function of (1) for quantitative measurements, the precision and accuracy of the instrument or of an observer to count species abundance or to estimate per cent cover with the same accuracy over time; (2) for qualitative data, the ability of the observer to identify species correctly; (3) for positional data of either the individuals or sampling units, the precision and accuracy of the instrument used (GPS, telemetry, laser, tape measure, etc.); (4) the precision in data gathering and transfer to digital form (accuracy of transcription); and (5) the appropriate match between the sampling unit size and the variable measured (Fortin 1999a; Bradshaw & Fortin 2000). All these accuracy levels and types of errors will affect the identification and quantification of spatial patterns (Hunsaker *et al.* 2001). All these accuracy problems cannot be eliminated but they can be minimized or at least acknowledged while analysing and interpreting spatial structure.

1.3 Spatial structure: spatial dependence and spatial autocorrelation

Most ecological data have some degree of spatial structure, and at least part of that structure may follow what is known as the first law of geography: ‘Everything is related to everything else, but near things are more related than

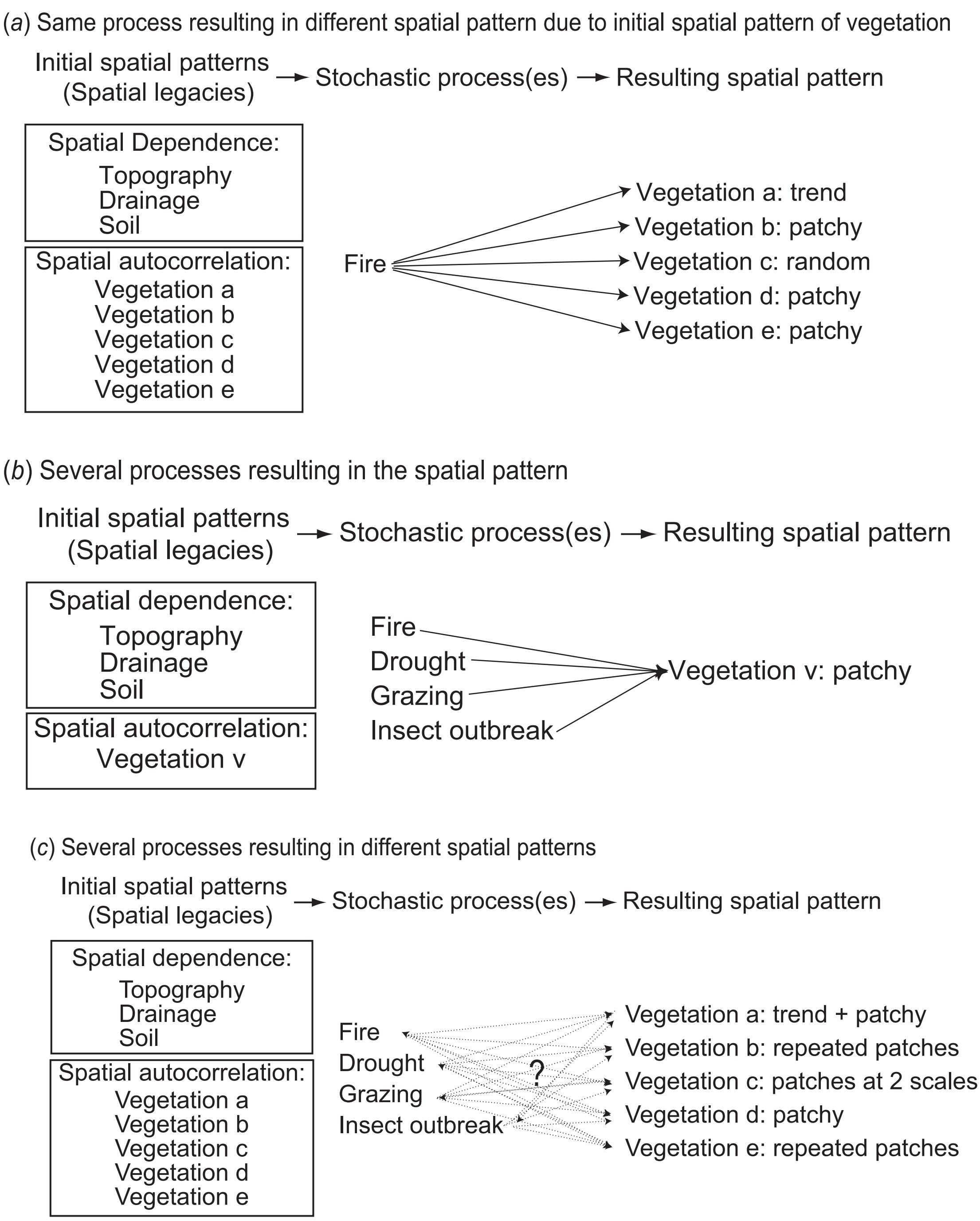


Figure 1.2 Relations between pattern and process. (*a*) Given the initial conditions of the environmental factors and the legacy of the landscape spatial structures, the same intensity of a process can result in different spatial patterns. (*b*) For a given spatial legacy, several processes can generate a given spatial pattern. (*c*) Most of the time there are several spatial legacies nested within each other, which are affected by several processes resulting in several distinct spatial patterns.

Box 1.2 What is a pattern?

For clarity, we need to define 'pattern' and to circumscribe the analytic limits of detecting it accurately. One definition of 'a pattern' is 'a distinctive form' (Webster 1989), and another is 'regular form or order' (Fowler & Fowler 1976) and hence the term 'pattern' is applied to a characteristic of a system that can be detected and described, and is somehow contrasted with 'random'. Either definition can then be qualified according to whether one is interested in the spatial or temporal component of a pattern. The term 'pattern' sometimes has the suggestion that it consists of several repeated units, such as patches and gaps that alternate in a landscape. Throughout the book, we also use the term 'structure' as a close equivalent of pattern in some contexts; again, there is often the implication that a structure consists of identifiable sub-units. These definitions do not suggest sufficiently well that pattern in ecological systems is dynamic, evolving, or changing. Indeed, a spatial pattern that we observe is often 'a single realization' or 'snapshot' of the results of a process or of a combination of processes at one given time in one given place (Fortin *et al.* 2003). This is why spatial pattern is so important in ecology and why we emphasize its analysis as a crucial step toward understanding vital ecological processes.

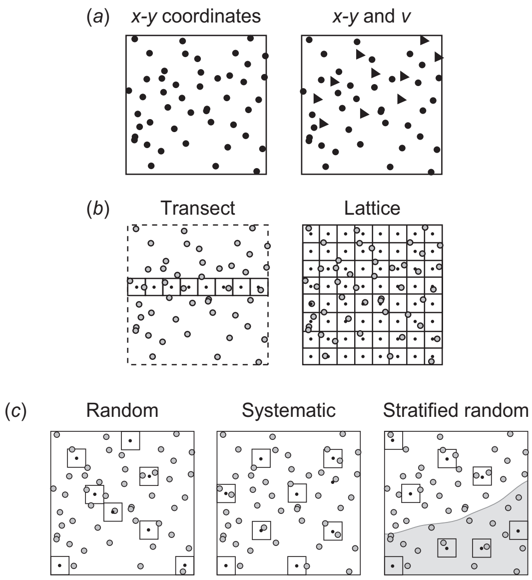


Figure 1.3 Spatial sampling strategies to collect ecological data: (*a*) point data methods: exhaustive survey of the geographic *x–y* coordinates of all the individuals of a species (left panel) or of more species (right panel; here two species, where *v* indicates the attribute of each individual – in this case, the species' name); (*b*) contiguous sampling units: transect (left panel) and lattice (right panel); and (*c*) sparse sampling units (random, systematic, stratified random). See text for more details.

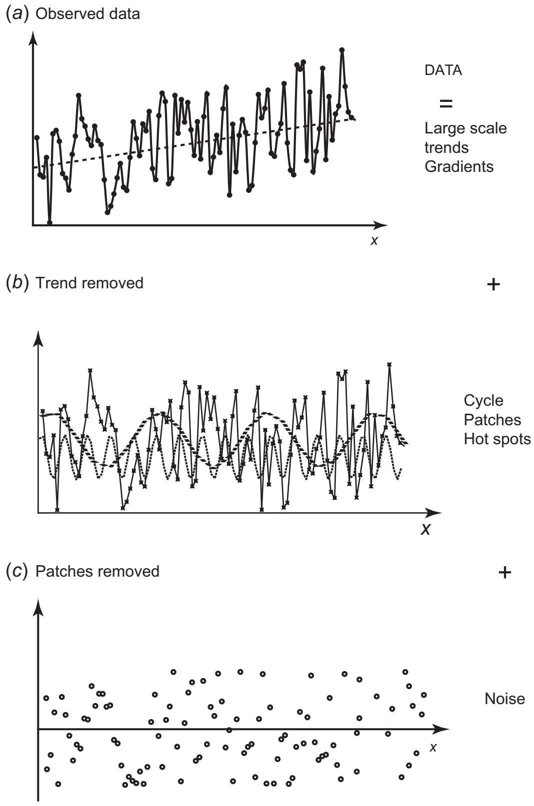
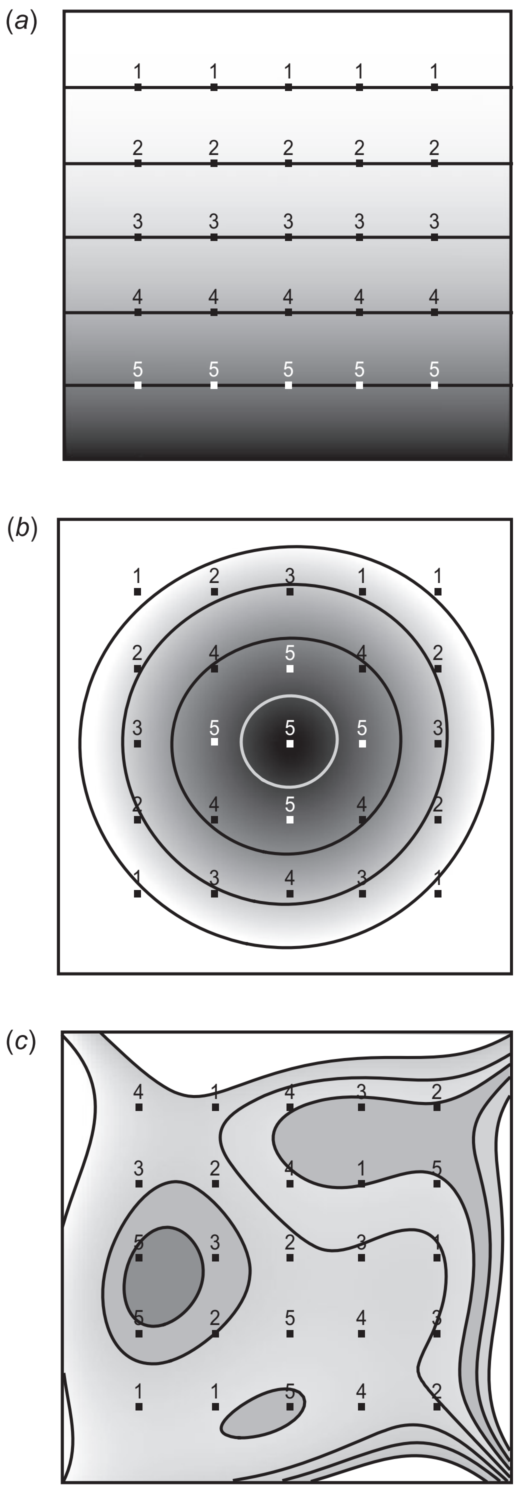


Figure 1.4 Nested spatial patterns (signals) imbedded in ecological data: (*a*) if the data are gathered along a temperature gradient, tree height can increase in a linear fashion at large scale; (*b*) both topography and spatial dispersal processes can generate patchy patterns at intermediate, landscape, scale; and (*c*) there is only random noise at the micro, local, scale.



distant things.'(Tobler 1970). In ecological data, the basic structure of similarity that declines with distance may be complicated by patchiness in the system. Indeed the spatial structure of ecological phenomena can take several different forms: (1) a directional *trend* or gradient (Figure 1.4*a*); (2) nonrandom dispersion of objects that is *aggregated*, clumped, or patchy (Figure 1.4*b*); (3) dispersion that is apparently *random* (Figure 1.4*c*); and (4) for discrete objects like point events, nonrandom dispersion that is *uniform*, also called regular or overdispersed. Either exogenous or endogenous processes can generate any of these patterns. In addition several factors can act together, either additively, or multiplicatively or otherwise when the factors are nonlinear (for example, a threshold response to habitat fragmentation). Hence numerous spatial patterns can be identified when the variables of interest (say, species abundances) respond to an exogenous process (such as disturbance) or to underlying environmental conditions (such as the spatial configuration of heterogeneity). For example, soil patchiness can produce regions of high plant density, within which the locations of the individuals are either apparently random or overdispersed. In these cases, any local similarity is due to the species responding to external processes, which have their own spatial structure. On the other hand, when endogenous processes (like dispersal or spatial inhibition) are dominant, the observed pattern of the plants is an inherent property of the variable of interest.

Spatial patterns usually result from a mixture of both exogenous ('induced') and endogenous ('inherent') processes, resulting in spatial dependence among organisms. Here, the term 'spatial dependence' is broadly interpreted as including both the species' response to underlying exogenous processes and the species' spatial autocorrelation due to endogenous processes (Wagner & Fortin 2005). The term 'autocorrelation' refers to correlation among values of a single variable. The adjective 'spatial' indicates that the correlation is a function of locations in space or the distances between locations.

Figure 1.5 Spatial patterns: (*a*) gradient, (*b*) single patch and (*c*) random (although the isolines seem to suggest a patchy pattern). Note that each panel has the same number of sampling locations ($5 \times 5 = 25$), as well as the same frequency distribution of the count of individuals (5 ones; 5 twos; 5 threes; 5 fours and 5 fives).

Spatial dependence means that there is a lack of independence among data from nearby locations. This definition of spatial dependence is the most widely used by spatial statisticians and geographers (Cressie 1993; Haining 2003).

Bailey & Gatrell (1995, p. 32) defined spatial dependence using an analogy to first and second moments: a first-order effect is due to variation in the mean value of a process over the study area, corresponding to the global trend illustrated in Figure 1.5*a*, and second-order effects are due to spatial autocorrelation of the process, implying that deviations from the mean are more alike at neighbouring sampling locations, and hence are equated to localized trends and small-scale patchiness (Figure 1.5*b*). In describing spatial dependence of plants, where exogenous processes predominate, we would say that the spatial dependence is 'induced' by the underlying variable that is itself spatially autocorrelated. Therefore, although Legendre (1993) used the term 'false' spatial autocorrelation to refer to species' response to the spatial structure of exogenous processes, we refer to this phenomenon as 'induced spatial dependence'.

These spatial patterns can be modelled by regression where the independent variables are themselves spatially structured (Legendre & Legendre 1998). For endogenous processes, individuals of a species are more likely to be spatially adjacent in a patchy fashion, related to what is referred to as 'true' spatial autocorrelation (Legendre 1993; Legendre & Legendre 1998) or, as we will recommend, 'inherent' spatial autocorrelation. This means that nearby values of a variable are more likely to be similar than they would be by chance. The spatial structure can therefore be modelled with second-order statistics (e.g. spatial covariance rather than just mean value) that characterize the local spatial variability of the variable. In some ecological applications, high similarity at small scales declines with distance, and so the equation that describes this decline is often a decay function, and the phenomenon is described as the 'distance decay' of similarity.

In general, spatial dependence is estimated by comparing the value at one location with those values at given distances away (termed spatial lag or distance interval), say at 1 m, 2 m, 3 m, and so on. In Figure 1.6, spatial autocorrelation occurs only due to seed dispersal from a tree and we expect to find fewer and fewer seeds as the distance from the source increases. The degree of spatial autocorrelation also decreases with distance, for example from locations A to D in Figure 1.6. At short distances from the tree, values of seed abundance should be similar at nearby locations, giving positive autocorrelation, and as the distance at which the comparison is made increases, the values are less likely to be similar. They can become either independent, with no spatial autocorrelation, or dissimilar, with negative autocorrelation. Over large areas, plants can have a patchy pattern that repeats itself to create spatial structure at two scales: (1) a within-patch scale of plants and (2) a between-patch scale of patches in their landscape.

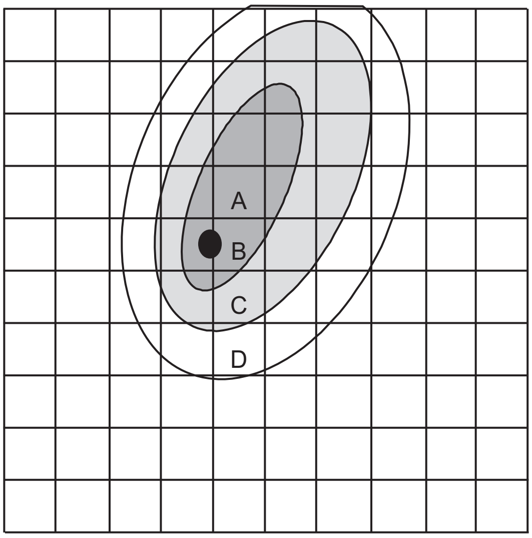


Figure 1.6 Seed abundance from a tree source. The filled circle indicates the location of the tree source from which seeds are dispersed by wind. As the distance from the tree increases, the amount of seeds decreases (as indicated by the grey-shaded gradient: dark grey for high abundance; light grey for low abundance; white for no seeds). Positive spatial autocorrelation exists between adjacent sampling units A and B; no significant spatial autocorrelation exits between A and C; and negative spatial autocorrelation exists between A and D.

The magnitude of the ecological process usually has a direct effect on the degree of spatial autocorrelation in the variable that it influences. The degree and

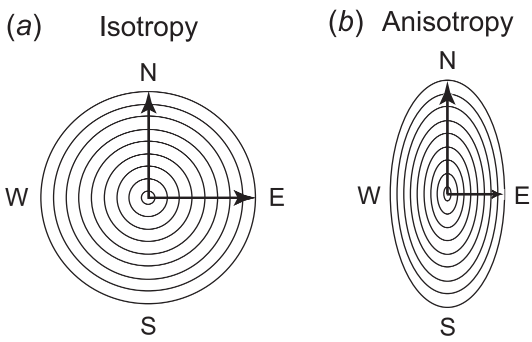


Figure 1.7 Pattern directionality. (*a*) Isotropic and (*b*) anisotropic spatial patterns. Each isoline indicates the same value of the variable decreasing from the highest value at the centre to the lowest value at the periphery.

shape of spatial autocorrelation can vary with direction (Figures 1.6 and 1.7). In the previous example, with the presence of strong directional wind, seeds are more likely to be dispersed downwind (say northeast), an elongated, elliptical, patch of seeds results (Figure 1.6). This kind of spatial pattern is said to be 'anisotropic', because the magnitude and range of spatial autocorrelation vary with direction; the opposite is 'isotropic' where spatial autocorrelation magnitude varies similarly with distance in all directions (Figure 1.7). Various types of internal and external processes can create anisotropic pattern: topography, gradients, streams and riparian strips, etc. A favourite example of anisotropic pattern in vegetation is the 'brousse tigrée' striped scrubland that develops on gentle slopes in arid regions (see Lejeune & Tlidi 1999; Wu *et al.* 2000), but string bogs (Koutaniemi 1999; Rietkerk *et al.* 2004; Couwenberg & Joosten 2005), and wave-regenerated forests (Sprugel 1976; Ichinose 2001) are other examples that are equally well-known. Anisotropic spatial patterns can also appear as artifacts of the shape of the sampling units used to collect the data (cf. Fortin 1999a).

1.4 Spatial scales

Without processes, there would obviously be no pattern, but it is also clear that spatial pattern has its own effects on processes, including those that give rise to the pattern. When the scale at which the processes are realized is unknown, analysing spatial pattern using different approaches and scales of observation can provide a consensus that contributes to our understanding of the ecological complexity. To clarify this discussion we have defined 'pattern' in Box 1.2. Spatial pattern in ecological systems refers to a certain degree of predictability for characteristics, based on the spatial location. In these systems, spatial pattern is rarely static, but dynamic and changing in response to processes internal to the system itself or imposed by external forces.

The concept of spatial pattern ranges from obvious structure such as windfall gaps in a forest canopy, to more diffuse spatial heterogeneity, such as the patchiness of species on a level prairie. In either case, spatial pattern is the nonrandom arrangement of quantitative or qualitative characteristics, often repetitive, as a form of spatial heterogeneity. The most obvious contrast to spatial heterogeneity is spatial homogeneity, but true homogeneity is most frequently a conceptual null model and is very rare in reality (Fischer & Lindenmayer 2007). Spatial heterogeneity depends on scale: at a large extent and coarse resolution, a pattern may appear to be homogeneous, but at a small extent and finer spatial resolution, heterogeneity emerges. Ironically, in the absence of pattern, there really is no scale to be detected and so an examination of the results of a process, the spatial pattern, is required to determine the spatial scale of that process (Dungan *et al.* 2002).

The term 'scale' is used by ecologists to refer to several concepts, including the physical extent of the processes (the 'range') and the spatial and temporal resolution of the data ('grain'). Our perception of the spatial structure of an area is directly related, and limited, to both the study area or 'extent' and sampling unit size or 'grain' at which we analyse it (Wiens 1989). The physical distances that determine what is considered local versus global can vary depending on the system; just as 'landscape' is a level of organization with the distance it encompasses being determined by the characteristics of the organism of interest: such as earthworm versus coyote.

Ecological data usually include several spatial scale patterns which are confounded (Figure 1.4): (1) trends at larger scales, (2) patchiness at intermediate and local scales, and (3) random fluctuations or noise at the

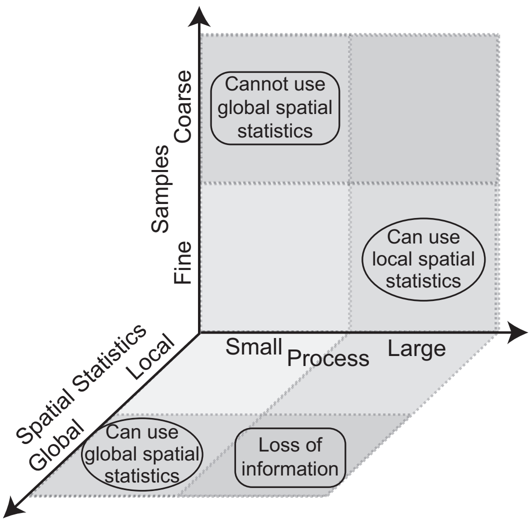


Figure 1.8 Three main components that interact and affect our ability to identify and characterize spatial patterns accurately: the scale of expression of processes, the sampling design being used at the plot level or landscape level, and the spatial statistics characterizing either the spatial structure of each sampling location (local spatial statistics) or the entire study area (global spatial statistics).

smallest scale. Therefore, ecological data are the result of embedded and confounded processes; hence, as ecologists, we try to disentangle the spatial scales of these processes using spatial analysis. The components that affect our ability to identify spatial patterns and their underlying processes accurately are numerous, but they can be organized into three categories (Figure 1.8; Dungan *et al.* 2002): (1) the extent of spatial expression of the processes themselves; (2) the sampling design used to measure ecological data (sample versus population data; local versus global level); and (3) the statistical tools used to characterize the spatial pattern of either the entire sampling area (i.e. global spatial statistics) or each sampling location (i.e. local spatial statistics).

In studies where the scale of observation is a large heterogeneous area in which many processes may occur, data cannot be collected as intensively as at the plot level. Hence, the data are usually obtained by remote sensing or as inventory maps created from air photo interpretation. Such information provides mostly coarse categorical data, such as forest versus urban, or mature mixed forest versus peatland. Therefore, while spatial statistics are used to characterize spatial pattern from quantitative data at the plot level (Haining 1990; Cressie 1993), various landscape indices are commonly used to summarize the spatial configuration of categorical data at the landscape level (O'Neill *et al.* 1988; Baker & Cai 1992; McGarigal & Marks 1995; Gustafson 1998; Leitão *et al.* 2006).

When several processes act together, they can combine in different ways to produce the observed spatial pattern (Figures 1.2 and 1.4). In the simplest case, the combination is additive and the resulting pattern is the sum of patterns generated by the individual processes acting independently. Additive combination is illustrated in Figure 1.4; a large-scale trend due to an environmental gradient is augmented by patchiness caused by limited species dispersal, and a random component ('noise'). Additive spatial pattern can be analysed by removing each contributing pattern, and then quantifying the characteristics of the residual. For example, a linear trend can be removed by linear detrending, and if some pattern remains in the residuals, a second detrending with another type of structure (quadratic, cubic, etc.) can be applied. While, in theory, detrending is an elegant solution, in practice it is difficult to be certain that only the targeted trend is removed and no other information of importance from the other scales. This is why, in the absence of prior knowledge or a hypothesis about the underlying process and its resulting pattern, several authors recommend not detrending data at all (Osborne & Suarez-Seoane 2002).

Nowadays, current global change studies are usually carried out at the regional level where multiple processes occur at different spatial scales. In such conditions, processes interact in different ways to create non-additive spatial patterns, which may appear to be characteristic of non-stationary processes. Patterns can combine multiplicatively and this may be particularly obvious in the case of presence : absence data (see Dale 1999, fig. 3.5). Multiplicative combination can occur where different factors in the environment, each of which can cause a species to be absent, act