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Introduction

Introduction

Processes in natural systems and the patterns that result from them occur in ecological space and time. To study natural structure and to understand the functional processes we need to identify the relevant spatial and temporal scales at which these all occur. While the spatial and temporal dimensions of ecological phenomena have always been an inherent part of the conceptual framework of ecology, it is only recently that they have been incorporated explicitly into ecological theory, sampling design, experimental design and models (Levin 1992). For example, McIntosh (1985), in describing the concepts and theory that form the background of ecological studies, included very little discussion about the spatial aspects of ecological processes. In recent years, however, a growing number of texts have addressed spatial questions by providing both a spatial framework perspective and spatial statistics to perform spatial analyses, for example Cliff & Ord (1973, 1981), Getis & Boots (1978), Ripley (1981), Upton & Fingleton (1985), Anselin (1988), Haining (1990, 2003), Cressie (1991, 1993), Bailey & Gatrell (1995), Manly (1997), Legendre & Legendre (1998), Dale (1999), Fotheringham *et al.* (2000) and O'Sullivan & Unwin (2003).

In this book, we will concentrate on the spatial aspects of ecological data analysis to provide some advice and guidance to practising ecologists. Because all phenomena of ecological interest have both a spatial location, which can be designated by geographic coordinates, and other characteristics, such as measured attributes, we can have different perspectives on how to analyse them:

- their spatial locations can be included explicitly for the purpose of understanding spatial structure and pattern;
- other characteristics of these phenomena can be analysed separately by ignoring, or controlling for, their relative positions (e.g. their topology defined by neighbours) or absolute spatial locations (*x*–*y* coordinates); or

- spatial locations can be incorporated directly into the evaluation of those other characteristics.

Currently, several advanced spatial statistical books are available that cover the formal mathematics of these methods (e.g. Ripley 1981; Cressie 1993), but they may not be readily accessible to most ecologists and may not provide immediate application in the ecological context. In fact, there is a potential for the misapplication of some of these techniques to lead to incorrect inferences. It is our intention to present the concepts needed to perform valid spatial analyses and interpretation. To enhance the presentation (we hope), we use various data sets to illustrate the behaviour of the methods, and the relationships among them.

There is a large number of spatial statistics and new methods are constantly being developed, and so our presentation will not cover all possible approaches but will concentrate on those that we think are key for ecological analysis. We acknowledge that we are omitting several important fields of research and schools of thought. For example, we are not attempting to cover spatial issues related to diversity, information theory and spatio-temporal modelling since these topics would deserve and require a whole book each.

This book aims to guide ecologists through the broad field of spatial analysis by providing the essential basics to perform spatial studies. The intended audience is graduate students and other practising researchers. 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 five main chapters that present spatial methods based on their objectives: population (fully censused) data methods, methods for sampled data, boundary detection, methods dealing with spatial autocorrelation and spatio-temporal analysis. Each chapter includes a description of methods, some examples, an evaluation of the methods' characteristics, and concluding remarks including our advice on the choice of method. The last chapter asks and tries to answer the question 'Where do we go from here?', describing what we see as the direction for future development in this field and the areas where we perceive the need for more work. We also summarize our thoughts on the themes and threads that run through the book and unify it, and we provide some advice to students of ecology on the kinds of skills that we think they need in their future work.

1.1 Process and pattern

In ecological studies, explicit considerations of spatial structure have come to play an important role in efforts to understand and to manage ecological processes. Therefore, in our quest to comprehend the complexity of nature, the description and quantification of ecological patterns, both spatial and temporal, are important

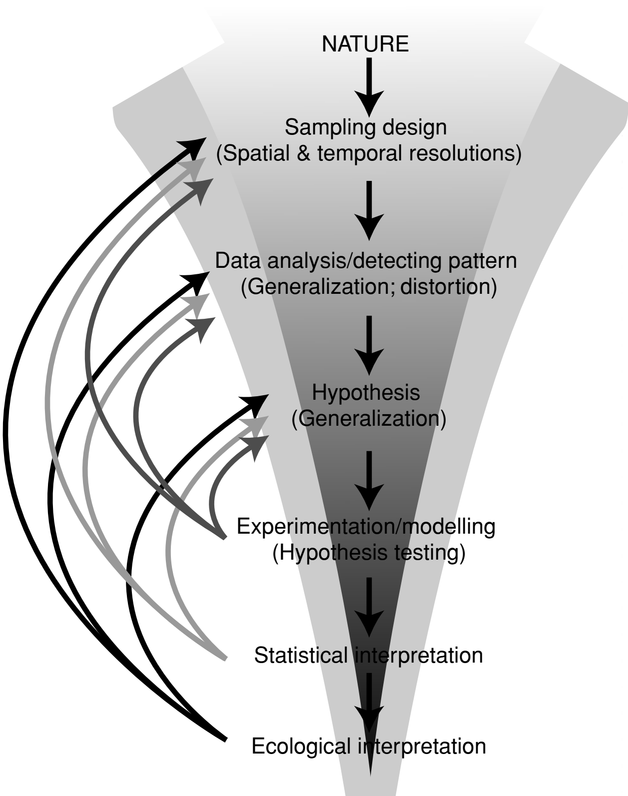

Figure 1.1 Flow of the steps involved in the study of nature and its complexity. As nature acts at several temporal and spatial scales, the selected sampling design narrows down the temporal and spatial limits of the domain under study (as indicated by the funnel effect illustrated in grey). By imposing 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.

first steps. 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 new ecological hypotheses that can be tested either by experiments or by modelling (Figure 1.1). Therefore, ecological research is an iterative process that, at each iteration, provides some insights about the underlying ecological processes through the quantification of ecological patterns. Unfortunately, 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

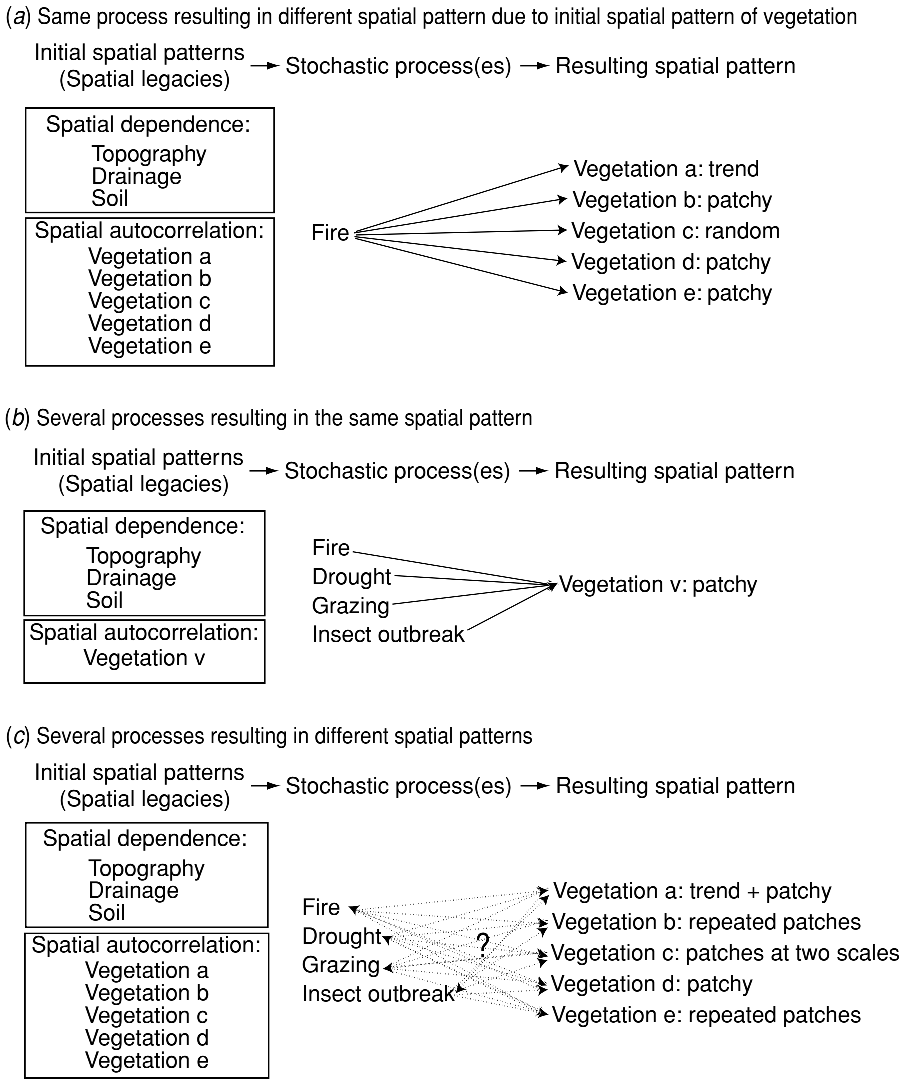

Figure 1.2 Relations between pattern and process. (*a*) Given the initial conditions of the environmental factors and the legacy of the landscape spatial structures, the same intensity of a process can result in different spatial patterns. (*b*) For a given spatial legacy, several processes can generate 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.

pattern signature (Figure 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. The term ‘scale’ is used by ecologists to refer to any of several concepts including the extent of the processes and the spatial and temporal resolution of the data. For a more detailed presentation and discussion of the concepts of scale, we refer readers to Csillag *et al.* (2000) and Dungan *et al.* (2002). When the scale at which the processes are realized is unknown, analysing spatial patterns using different approaches and scales of observation can provide an overall consensus that contributes to our understanding of ecological complexity.

To clarify this discussion we need to define ‘pattern’ exactly and to circumscribe the analytic limits of detecting it accurately. One definition of ‘a pattern’ is ‘a distinctive form’ (Webster 1989), implying that a pattern can be detected and described. Another definition (Fowler & Fowler 1976) is ‘regular form or order’ and hence the term ‘pattern’ is sometimes used as the opposite of ‘random’. Either definition can then be qualified according to whether one is interested in spatial or temporal component of a pattern. These definitions lack the implication that pattern in ecological systems is dynamic, evolving and changing. Indeed, a spatial pattern is usually ‘a single realization’ or ‘snapshot’ of a process or of a combination of processes at one given time (Fortin *et al.* 2003). This is why spatial pattern is so important in ecology and why we emphasize its analysis. Furthermore, 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). Thus, depending on the spatial scale of observations, an area may be considered homogeneous when the extent is small (e.g. one forest stand), or heterogeneous when the extent is large (e.g. a mosaic of forest stands). The physical distances that determine local vs. global can be very different depending on the system studied; just as ‘landscape’ is a level of organization with the distance encompassed determined by the organism of interest: beetle vs. coyote.

Ecological data usually include several kinds of spatial pattern, which are confounded (Figure 1.3): (1) trends at larger scales, (2) patchiness at intermediate and local scales, and (3) random fluctuations or noise at the smallest scale. Therefore, ecological data are the result of embedded and confounded processes and, hence, as ecologists, we are trying 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 main categories (Figure 1.4; Dungan *et al.* 2002): (1) the extent of spatial expression of the processes themselves; (2) the sampling design used to measure ecological data (sample vs. population data; local vs. 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 the following sections we will present the implications of the three components and how they are tied together through the notion of ‘scale’. Indeed,

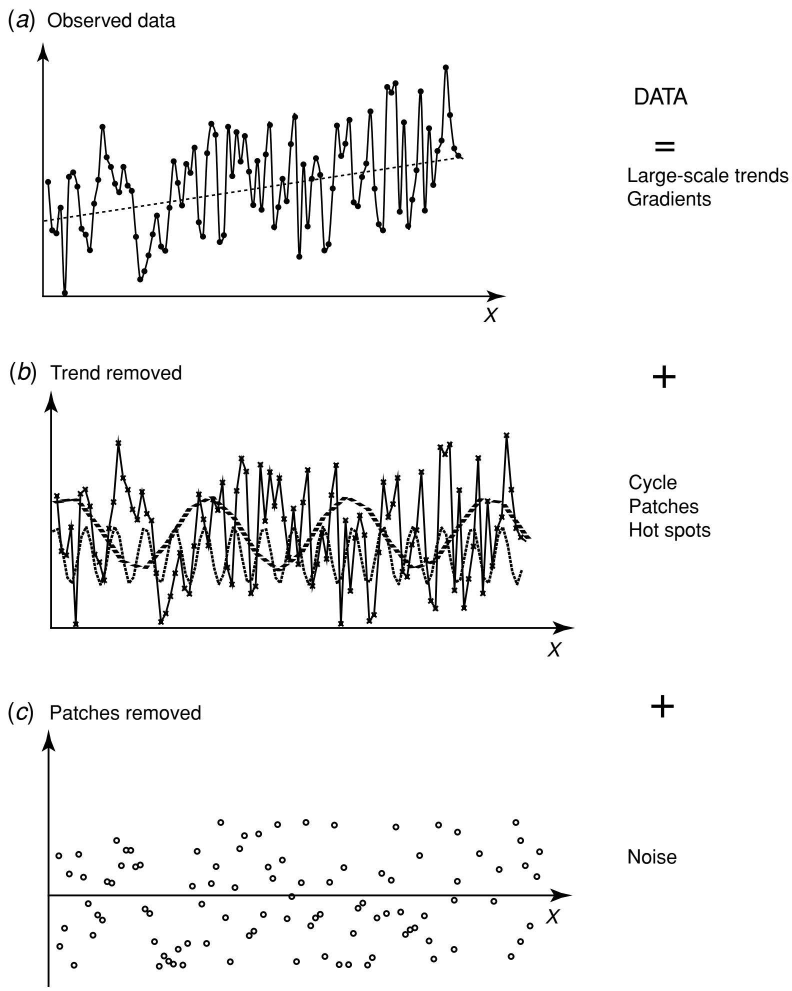

Figure 1.3 Nested spatial patterns (signals) imbedded in ecological data: (*a*) if the data are gathered along a temperature gradient, tree height can increase in a linear fashion at large scale; (*b*) both topography and spatial dispersal processes can generate patchy patterns at intermediate, landscape, scale; and (*c*) there is only random noise at the micro, local, scale.

the identification of ecological processes through the detection of the spatial and temporal patterns that they create vary according to the different aspects of the scale of observation arbitrarily imposed by the sampling design and analytic tools used (Bradshaw & Fortin 2000; Csillag *et al.* 2000; Dungan *et al.* 2002).

1.2 Spatial pattern: spatial dependence versus spatial autocorrelation

Spatial structures and patterns can take several forms: (1) trend, gradient (Figure 1.5*a*); (2) aggregation, clumping, patchy (Figure 1.5*b*); (3) random (Figure 1.5*c*);

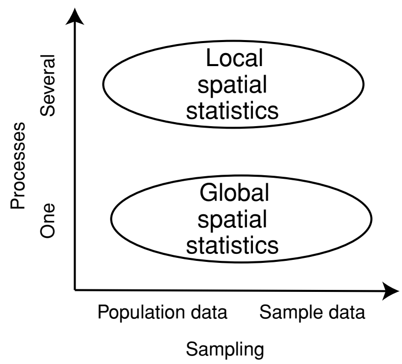

Figure 1.4 Three main components that interact and affect our ability to identify and characterize spatial patterns accurately: the scale of expression of processes, the sampling design being used at the plot level or landscape level, and the spatial statistics characterizing either the spatial structure of each sampling location (local spatial statistics) or the entire study area (global spatial statistics).

and (4) for point patterns, uniform, regular or overdispersed patterns. Either exogenous or endogenous processes can generate these patterns. In the case of exogenous pattern generation, the identified spatial pattern is generated by factors independent of the variable or characteristics of interest. Several factors can act at the same time, interacting either additively when the factors are linear, or multiplicatively or otherwise when the factors are non-linear. Several spatial patterns can be identified when the variables of interest, such as species abundances, respond to an exogenous process such as a disturbance or to underlying environmental conditions, such as a moisture gradient on a slope for plants or the spatial configuration of habitats for animals. For example, soil patchiness can result in patches of plants within which the locations of the individual plants are randomly arranged or even overdispersed. In these cases, the values associated with the plants are likely to be similar, not due to internal processes, but rather because the species are responding to external processes which have their own spatial structure; for example, these plants may grow only on a specific type of soil that is itself patchy in its distribution. Hence the spatial structure of plant species is due to the spatial structure of the environmental variables only. On the other hand, when there are endogenous ecological processes involved, such as dispersal, spatial competition or spatial inhibition, plant patchiness is an inherent property of the variable of interest.

In fact, most ecological data have at least some degree of spatial structure, often described by what is known as the first law of geography: ‘Everything is related to everything else, but near things are more related than distant things’ (Tobler 1970). These spatial patterns usually result from a mixture of both exogenous (‘induced’) and endogenous (‘inherent’) processes acting on species spatial structure resulting in spatial dependence among individual organisms (e.g. plants).

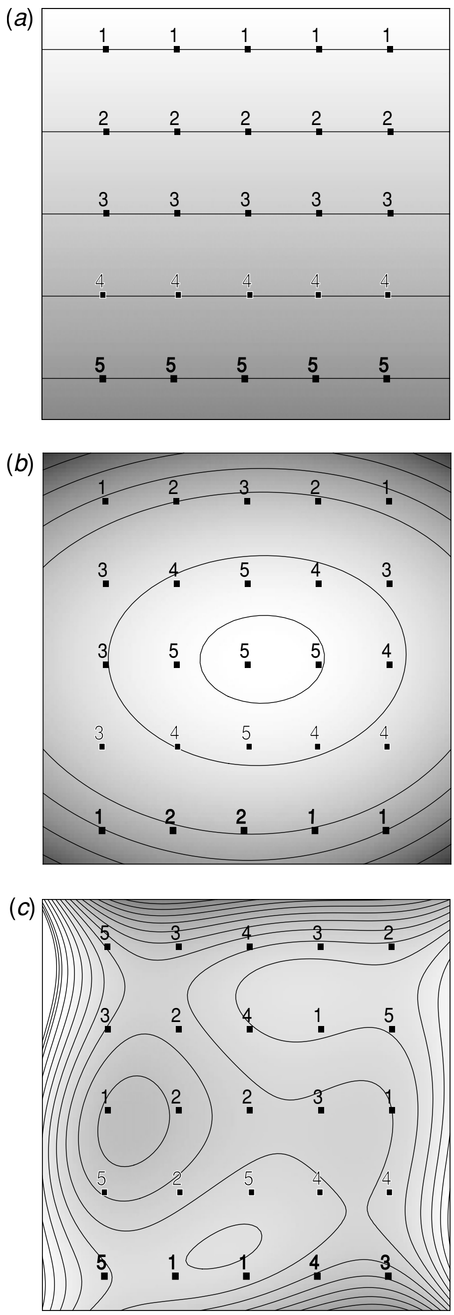

Figure 1.5 Spatial patterns: (*a*) gradient, (*b*) single patch and (*c*) random (although the isolines seem to suggest a patchy pattern). Note that each panel has the same number of sampling locations ($5 \times 5 = 25$), as well as the same frequency distribution of the count of individuals (5 ones;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

Here, the term 'spatial dependence' is used broadly to include a mix of both the species' response to the underlying (exogenous) processes and the species' spatial autocorrelation due to endogenous processes. The term 'autocorrelation' refers to the degree of correlation of a variable and itself ('auto'). By adding the adjective 'spatial', it implies that the relationship among the values of a given variable is a function of the spatial distances between them or their locations in space. Hence, the notion of spatial dependence implies 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-order moments: a first-order effect is due to variation in the mean value of a process over the study area, corresponding to the large global trend illustrated in Figure 1.3*a*, and second-order effects are due to spatial autocorrelation of the process, implying that deviations of process values from the mean are more alike at neighbouring sampling locations, and hence are equated with localized trends and small-scale patchiness (Figure 1.3*b*).

Therefore, although Legendre (1993) used the term 'false' spatial autocorrelation to refer to species' response to the spatial structure of exogenous processes, we will not use this terminology in this book for clarity and for compatibility with other textbooks on spatial analysis in other fields. Instead, we will refer to this phenomenon as 'induced spatial dependence', which is a more general term that includes species response to spatially structured environmental processes at more than one spatial scale.

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. Such spatial patterns can be modelled by means of regression where the independent variables are themselves spatially structured (Legendre & Legendre 1998). For cases of 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' (Legendre 1993; Legendre & Legendre 1998) or '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.

The degree of spatial dependence can be estimated by comparing the value at one location with those at given distances apart (termed spatial lag or distance interval), say at 1 m, 2 m, and so on. In Figure 1.6, we present a situation where spatial autocorrelation occurs only due to seed dispersal from a tree. Due to the dispersal process, we expect to find fewer and fewer seeds as the distance from the source increases (Figure 1.6). The degree of spatial autocorrelation in space

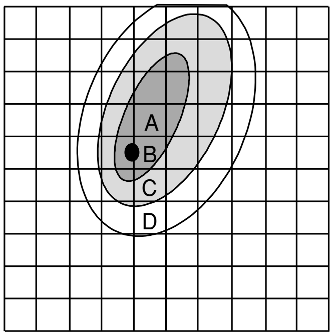

Figure 1.6 Seed abundance from a tree source. The filled circle indicates the location of the tree source from which seeds are dispersed by wind. As the distance from the tree increases, the amount of seeds decreases (as indicated by the grey-shaded gradient: dark grey for high abundance; light grey 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.

will also decrease as the spatial distance increases, for example from locations A to D in Figure 1.6. At short distances from the tree releasing seeds, values of seed abundance should be similar within patches or at nearby locations along a gradient, 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.

The magnitude of the ecological process usually has a direct effect on the degree of spatial autocorrelation in the variable that it influences (e.g. its intensity, spatial range or sign). The intensity of spatial autocorrelation can vary according to direction (Figures 1.6 and 1.7). In the previous example of seed abundance, with the presence of strong directional wind, because seeds are more likely to be dispersed downwind (say northeast–southwest), an elongated, elliptical, patch of seeds results (Figure 1.6). This kind of spatial pattern is said to be ‘anisotropic’, because the intensity and range of spatial autocorrelation vary with the orientation or direction; the opposite is ‘isotropic’ where spatial autocorrelation intensity varies similarly with distance in all directions (Figure 1.7). Various types of internal and external processes can create anisotropic pattern: topography, gradients (e.g. brousse tigrée; see Chapter 2; Lejeune & Tlidi 1999; Wu *et al.* 2000), stream and riparian strips, etc. Anisotropic spatial patterns can appear as artefacts of the shape of the sampling units used to collect the data as will be discussed in more detail in Section 1.4.2 (cf. Fortin 1999a).