# 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



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**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

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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

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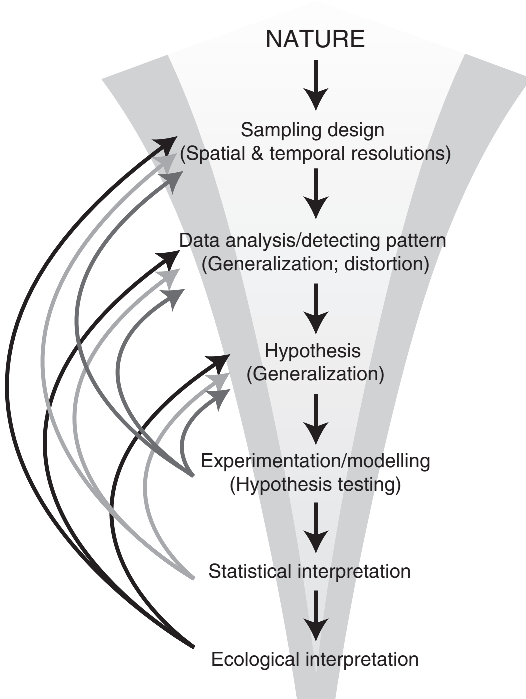


**Figure 1.1** Flow of the steps involved in the study of nature and its complexity. As nature acts at several temporal and spatial scales, the selected sampling design narrows down the temporal and spatial limits of the domain under study (as indicated by the funnel effect illustrated in grey). By imposing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

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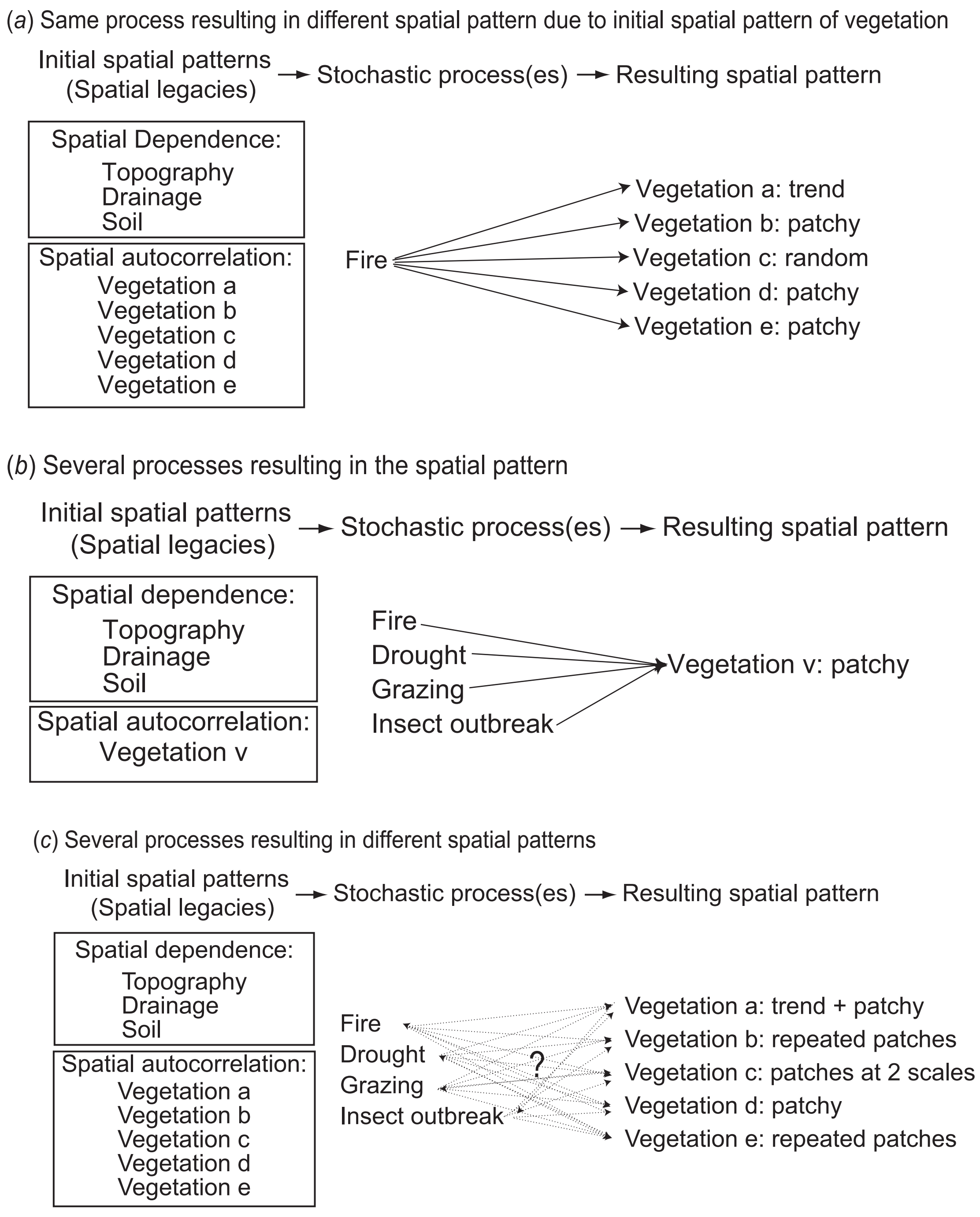


**Figure 1.2** Relations between pattern and process. (*a*) Given the initial conditions of the environmental factors and the legacy of the landscape spatial structures, the same intensity of a process can result in different spatial patterns. (*b*) For a given spatial legacy, several processes can generate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

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**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.

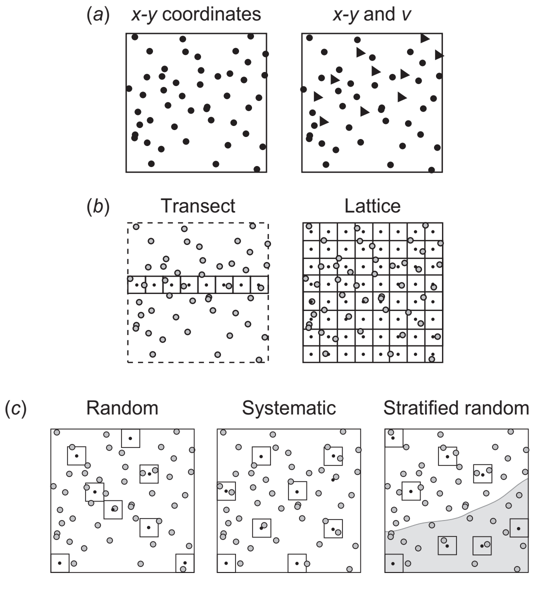


**Figure 1.3** Spatial sampling strategies to collect ecological data: (*a*) point data methods: exhaustive survey of the geographic $x$–$y$ coordinates of all the individuals of a species (left panel) or of more species (right panel; here two species, where $v$ indicates the attribute of each individual – 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.

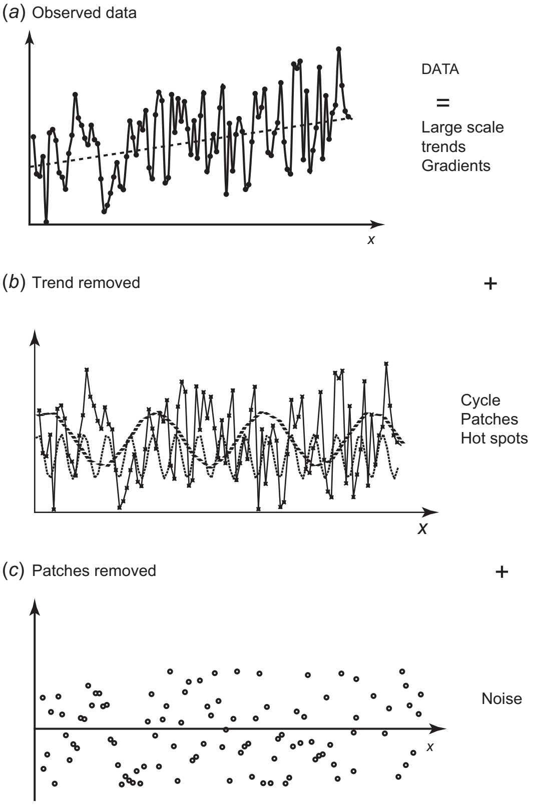


**Figure 1.4** Nested spatial patterns (signals) imbedded in ecological data: (*a*) if the data are gathered along a temperature gradient, tree height can increase in a linear fashion at large scale; (*b*) both topography and spatial dispersal processes can generate patchy patterns at intermediate, landscape,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

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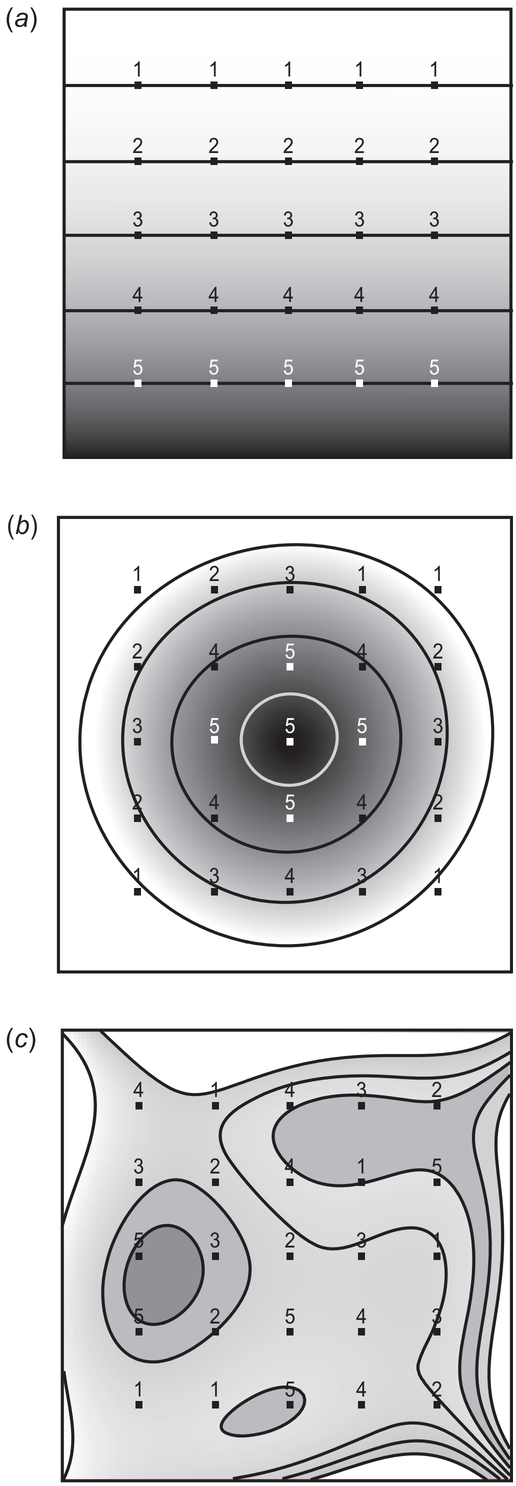


distant things.'(Tobler 1970). In ecological data, the basic structure of similarity that declines with distance may be complicated by patchiness in the system. Indeed the spatial structure of ecological phenomena can take several different forms: (1) a directional *trend* or gradient (Figure 1.4*a*); (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).

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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.

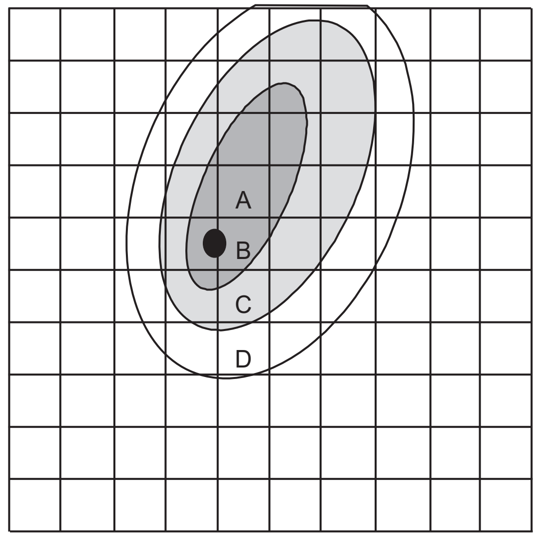


**Figure 1.6** Seed abundance from a tree source. The filled circle indicates the location of the tree source from which seeds are dispersed by wind. As the distance from the tree increases, the amount of seeds decreases (as indicated by the grey-shaded gradient: dark grey for high abundance; light grey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

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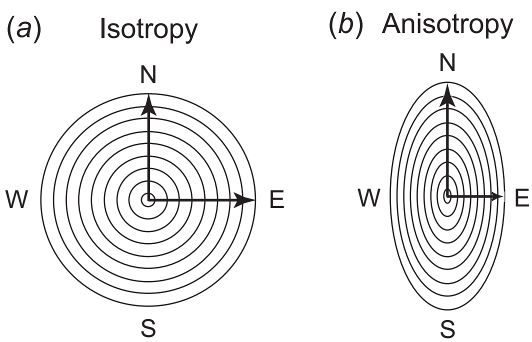


**Figure 1.7** Pattern directionality. (*a*) Isotropic and (*b*) anisotropic spatial patterns. Each isoline indicates the same value of the variable decreasing from the highest value at the centre to the lowest value at the periphery.

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

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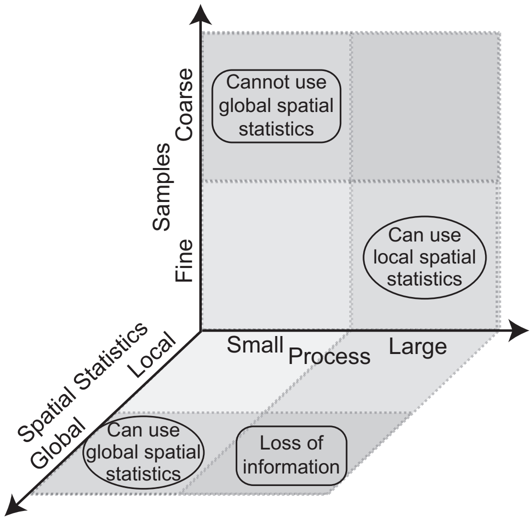


**Figure 1.8** Three main components that interact and affect our ability to identify and characterize spatial patterns accurately: the scale of expression of processes, the sampling design being used at the plot level or landscape level, and the spatial statistics characterizing either the spatial structure 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

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independently and at different scales or locations. Yet, due to political boundaries and differential land-uses, inherent ecological processes may affect spatial disturbance regimes on adjacent regions. Hence several processes may result in multiscale patterns which also differ according to regions. To properly analyse the spatial patterns it is important to first partition the data into spatially homogeneous areas (see Chapter 9).

## 1.5 Sampling design

Any ecological study requires a comprehensive overview of all the components and the steps involved (Figure 1.1). Indeed, once the data are gathered, one cannot obtain more information from the data set than it actually contains. Therefore, determination of the appropriate spatial and temporal domains of the study is one of the most important steps in data analysis from which all subsequent statistical and ecological interpretations will be either meaningful or meaningless. The spatial and temporal scales are therefore important in the definition and testing of ecological hypotheses and we comment about the key components to consider while testing statistically ecological hypotheses given inherent and induced spatial dependency in the data.

Any sampling design for studying ecological processes imposes a template, or filter, with its own specific temporal and spatial units. To be efficient, a sampling design needs to be thought out and crafted carefully by a series of steps to obtain meaningful insights about the ecological processes (see Figures 1.1 and 1.4): (1) define explicitly the spatial and temporal domains of expression of the process(es) under study; (2) determine that the spatial and temporal resolution of the sampling design is able to capture the process under study; and (3) ensure that the spatial and statistical analyses are appropriate for the data type. These three steps interact with each other and must be considered together before conducting any sampling of ecological data in a spatial context (Fortin *et al.* 1989; Dungan *et al.* 2002). In essence, design of an optimal spatial sampling scheme requires a careful balance between samples that are too close to one another, thus not providing enough new information (data highly autocorrelated), and samples that are too sparse, so that processes at other spatial scales introduce too much variability (Haining 1990). To understand better how the sampling can affect the identification of spatial pattern while using different spatial statistics in each chapter, we will review the key spatial aspects that are common to all spatial analysis: the size of the sample, the study area and the sampling unit, the shape of the sampling unit, the spacing between sampling units, and the sampling design.

### 1.5.1 The sample size (the number of observations '*n*')

In any ecological study, the choice of the sample size '*n*' is one of the most important decisions. In the context of spatial analysis, this choice needs to be guided by the minimum requirement for subsequent spatial statistics and analysis (Fortin *et al.* 1989; Legendre & Fortin 1989; Fortin 1999a; Table 1.1). For example, a minimum of 30 sampling locations is recommended to detect significant spatial autocorrelation (Legendre & Fortin 1989). In cases where the spatial pattern is very strong, it may be detected with as few as 20 sampling locations, but this would be exceptional. Reliable estimation of spatial structure and spatial model parameters used in variography (i.e. variogram and Kriging; see Chapter 6) may require 50 to 100 sampling locations.

### 1.5.2 Spatial resolution

The detection of spatial pattern is also directly related to the spatial scale at which ecological data are measured (Figures 1.3 and 1.9). Spatial scale has at least two aspects: the size of the study area, or 'extent', and the size of the sampling unit used to collect the data, the 'sampling grain'. The extent is the total area under consideration and aims to capture the domain of the ecological process under study, while grain refers to the minimum spatial resolution at which information is measured. Several studies have showed that spatial statistics are very sensitive to both of these resolution aspects (Jelinski & Wu 1996; Qi & Wu 1996; Fortin 1999a; Dungan *et al.* 2002; Wu 2004; Hui *et al.* 2010).

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**Table 1.1** Requirements, assumptions and rules of thumb for spatial statistics

| | Requirements | | |
|---|---|---|---|
| Methods | Objectives | Assumption | Rules of thumb or limits |
| Network | Linking locations | Exhaustive mapping of all events | Planar graphs limit the number of edges in a network |
| Aggregation indices | Testing for spatial structure | Stationarity | Cannot differentiate among spatial structures |
| Block variance methods | Computing the intensity and range of spatial structure | Contiguous sampling units | Computed up to $^1/_{10}$ of the length of the transect |
| Ripley's $K$ | Computing and testing the intensity and range of spatial structure | Exhaustive mapping of all events | Extents having rectangular shape are favoured for computation<br>Edge effect needs correction<br>Statistic computed up to $^1/_3$ to $^1/_2$ of the shortest extent |
| Moran's $I$, Geary's $c$ | Description of spatial structure; testing for the presence of spatial autocorrelation | Stationarity | Edge effect needs correction<br>Statistic computed up to $^1/_3$ to $^1/_2$ of the shortest extent<br>Minimum of 20–30 sampling locations |
| Semi-variance | Description of the spatial structure; estimation of spatial parameters | Pseudo-stationarity *[assume stationarity in the search region]* | Edge effect needs correction<br>Statistic computed up to $^1/_3$ to $^1/_2$ of the shortest extent<br>Minimum of 50 sampling locations<br>Search neighbourhood of either the range distance or 12–25 neighbouring sampling locations |
| Mantel and partial Mantel tests | Correlation between spatially autocorrelated variables | Stationarity | Overall, synthetic, value of the linear relationship between distance matrices, not the raw data |
| Wavelets | Description of the spatial structure at multiple scales; Detection of boundaries | Contiguous sampling units and no missing data; Stationarity not required | Multiscale analysis uses powers of 2 ($2^k$); the number of scales $k$ depends on the number of observations |

Furthermore, both the sampling unit size and shape affect the accuracy of spatial pattern detection and using an inappropriate sampling unit may result in detecting less spatial structure than is actually present (Fortin 1999a).

### 1.5.3 The size of the study area: extent

As a guideline in determining the extent of the study area, O'Neill *et al.* (1996, 1999) suggested that it should be at least two to five times larger than the spatial extent of the largest process being studied. If the study area is too small in relation to the ecological process, not enough of the pattern is included, and because it is not measured in the data, it may not be identified. If the extent is too large, different processes or different intensities of process may be affecting the subregions of the study area. This is especially true for remotely sensed images because it is unlikely that the study area corresponds exactly with naturally defined homogeneous areas. Unfortunately, the smaller the extent, the more likely it is that a high proportion of patches will be truncated by the limits of the study area (as illustrated in Figure 1.9*a*).

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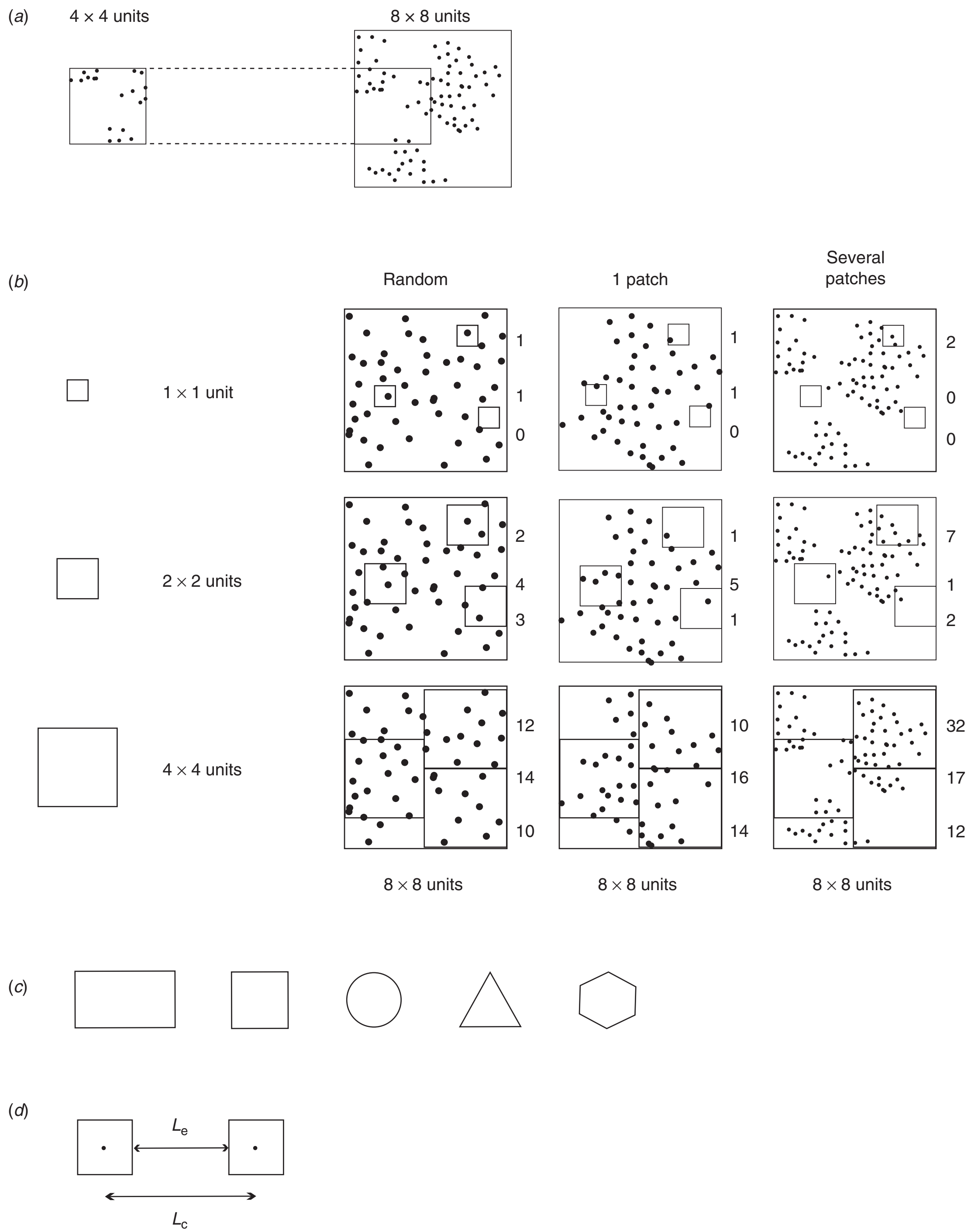


**Figure 1.9** Sampling design: (*a*) spatial extent; (*b*) sampling unit size, where the numbers to the right of each study plot are the count of individuals per sampling unit; (*c*) sampling unit shape; and (*d*) spatial lag ($L_e$ indicates the distance 'edge-to-edge' between the sampling units, $L_c$ indicates the distance 'centroid-to-centroid' between the sampling units). See text for more details.

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### 1.5.4 The location in the landscape

In addition, the location of the study area in the landscape can affect, or even bias, the results of the subsequent spatial analysis (Dungan *et al.* 2002).

(1) If the study area is larger than the process under study, it will be possible to characterize the spatial pattern, but if it is too large, more than one process may affect the area under investigation, creating additional variability in the pattern.
(2) If the study area is smaller than the process, it will be harder to characterize the spatial pattern.
(3) If the process generates repetitive pattern (such as waves or patchiness), then the position of the study area relative to wave crests and troughs will affect the resulting spatial estimation and description of the spatial structure (Plante *et al.* 2004).

### 1.5.5 The size of the sampling or observational units: grain

The size of the sampling unit needs to be considered (Figure 1.9*b*); it sets the smallest spatial resolution at which data can be measured or spatial structure can be characterized. When a landscape is studied using a remotely sensed image, the sampling unit size is the pixel resolution. In such cases, it is unlikely that the pixel resolution matches the ecological process of interest, which affects the spatial pattern detected (Bradshaw & Fortin 2000). Again, O'Neill *et al.* (1996, 1999) suggested that the sampling unit size should be smaller by a factor of two to five than the patch or other features of interest. The sampling unit should be, however, large enough to contain more than one individual, but not so big that there is too much within-unit variability, or that the smallest spatial scale cannot be detected (Figure 1.9*b*). For randomly distributed objects, the size and shape of the sampling unit do not affect our ability to determine the absence of spatial pattern (Figure 1.9*b*). However, when the data are not randomly distributed (Figure 1.9*b*), a sampling unit that is too small (e.g. $1 \times 1$) will increase the variance, and a sampling unit that is too large (e.g. $4 \times 4$) will reduce the variability unless the process is non-stationary. In the illustrated example in Figure 1.9*b*, the optimal sampling unit size is $2 \times 2$. In general, when there is a choice of sampling unit size, we suggest that a smaller sampling unit should be favoured because small units can be aggregated into larger ones without losing information, but the reverse is not true.

### 1.5.6 The shape of the sampling or observational units

When we use a sampling unit that is more-or-less isotropic, such as a square, a circle, a triangle, or a hexagon, the implicit assumption is that the spatial pattern is also isotropic. Ecologists sometimes use rectangular sampling units to reduce within-sampling unit variability along a gradient (Fortin 1999a). Such an anisotropic shape can alter the spatial pattern detected by artificially generating the appearance of an anisotropic spatial pattern (Fortin 1999a). When it is not known in advance whether the pattern is isotropic or anisotropic, we recommend using small isotropic sampling units so that the spatial pattern can be characterized more accurately (more details will be presented about this issue in Chapter 6).

### 1.5.7 The spatial sampling design

Once both the extent and the grain of sampling are defined, there are still important decisions to be made: should we use contiguous or spaced units (Figure 1.10)? Using contiguous sampling units in a transect or a lattice allows a finer description of the spatial pattern because there is no information missing due to space not sampled. In such cases, the extent is exhaustively sampled and the resulting data represent the entire population of sampling units within the extent. This does not guarantee that the data are representative of the entire ecological process being studied, the 'population of inference' as the terms is used in statistics, but rather of the spatial representation of the extent. On the other hand, when we use a different sampling strategy, such as random, systematic or stratified samples, the sampling units are not spatially contiguous; the extent is not completely surveyed and information is missing about the spatial pattern (Stohlgren 2007). We will refer to such a non-contiguous layout of sampling units as 'sparse'.

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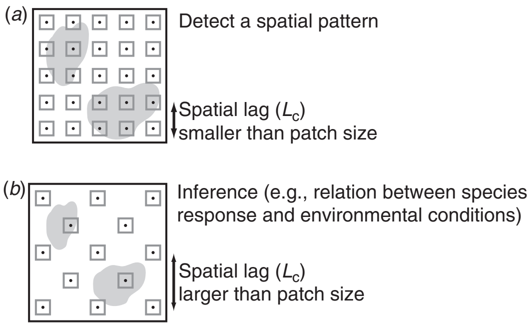


**Figure 1.10** Spatial sampling design. (*a*) Spatial lag must be set according to the objective of the study: to detect a spatial pattern, the spatial lag should be smaller than the patch size; (*b*) to perform inference statistics, the spatial lag should exceed the patch size.

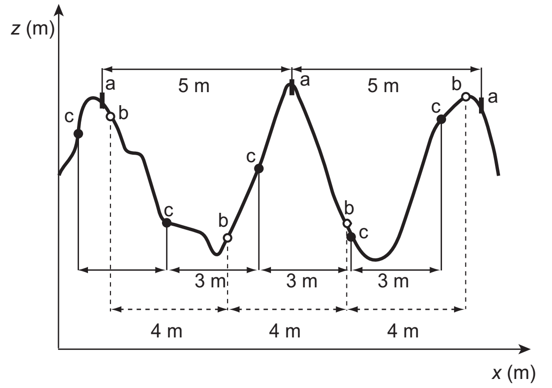


**Figure 1.11** Importance of spatial lag while using a systematic sampling design: when the spatial lag is 5 m ('a' sampling locations) the spatial structure identified is uniform, flat; when the spatial lag is 4 m ('b' sampling locations) high and low periodicity is detected; and when the spatial lag is 3 m ('c' sampling locations), patchiness can be characterized.

## 1.5.8 Spatial lag

The spatial lag between the sampling units is directly related to the previous decisions about the sample size ($n$), the extent and the grain, and about the shape of the sampling unit (Dungan *et al.* 2002): as the $n$ increases, the spatial lag decreases; as the extent increases, the spatial lag increases; and, as the sampling unit size increases, the lag decreases. There are different ways to relate to spatial lag, i.e., the spatial distance among sampling units: (1) non-contiguous sampling units where the spatial lag is measured either from edge to edge ($L_e$) of the sampling units or from centroid to centroid ($L_c$) (Figures 1.9 and 1.10); and (2) contiguous sampling units having no edge-to-edge spatial lag but a non-zero centroid-to-centroid spatial lag equivalent to the length of the sampling unit.

The choice of the spatial lag between the sampling units should also be guided by the goal of the study as follows.

(1) To detect, characterize and quantify spatial pattern in the data to obtain insights about ecological processes (as illustrated in Figure 1.10), so that the aim is primarily to test for significant spatial dependence. In order to detect the spatial pattern, the spatial lag among sampling units needs to be smaller than the size of the patch or the process (e.g. spatial structure or species dispersal ability) that we want to characterize (Figure 1.10). There should be several samples within each patch.

(2) To establish the relationship between two or more kinds of ecological data. Here, we are not so interested in the spatial structure of the ecological data but rather, for example, in the species' response to various environmental conditions, once spatial structure is accounted for. Spatial dependence and autocorrelation are considered a nuisance when using inferential tests that require that the observations are independent (Legendre & Legendre 1998). As Fortin *et al.* (1989) showed, random sampling designs ensure only that each sampling unit is drawn independently from the others and will be representative of the population. It does not guarantee, however, that there is no spatial autocorrelation in the data (see also Fortin & Dale 2009). In fact, in the presence of spatial autocorrelation, it is almost impossible to obtain truly independent data (see Chapter 8).

Furthermore, the choice of the spatial lag is crucial while using systematic sampling design (Fortin *et al.* 1989): when the spatial lag (say 5 m) matches the spatial pattern of the data peak as indicated by sampling locations 'a' (Figure 1.11), the identified pattern

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of the data will be flat (uniform); when the spatial lag is 4 m (indicated by sampling locations 'b'), the periodicity of high and low values of the variable starts to be detected; and when the spatial lag in smaller, say 3 m (indicated by sampling locations 'c'), the spatial pattern detected can better describe the patchiness and periodicity of the data. When the spatial scale of the process is unknown, sampling designs with several spatial lag distances are preferred, so that the spatial pattern can be identified (Fortin *et al.* 1989; Webster & Oliver 2001; Stohlgren 2007). For sparse sampling (a category in addition to the usual categories of random, regular, stratified, clustered, and nested or hierarchical sampling designs), it can be desirable to use an initial round of sampling to inform the choice of positions for sampling in a second round. This is variously known as '2nd phase', 'adaptive', or 'progressive' sampling (Delmelle & Goovearts 2009). One use of this approach is to place additional samples in locations that are identified as high variances associated with local estimates, as in the Kriging approach to interpolation (Chapter 6).

### 1.5.9 Edge effect

The interaction between the extent and the sampling unit size generates an 'edge effect' which can bias the estimation of spatial pattern at small and large distances (Figure 1.12; Haining 1990, 2003; Cressie 1993). Several of the spatial statistics presented in Chapters 4, 5 and 6 evaluate spatial patterns at increasing distances between sampling locations (for example, between A and B, A and C, A and D in Figure 1.6) will therefore be affected by such edge effects. In Figure 1.12, sampling units along the border of the study area (in grey) have fewer neighbours at short distances than at intermediate ones (e.g. at a separation of 1.5 units there are 200 pairs, but almost 600 pairs at 4.5 units) and very few indeed at the largest distances (two pairs at 10.5 units). The appropriate edge effect correction procedure should be selected according to the data type and the spatial statistics used (Cressie 1993; Haase 1995). Some basic 'rules of thumb' can minimize the edge effect either at the sampling design phase or during the analysis phase. For example, during the sampling phase, a buffer zone can be sampled around the study area (Figure 1.13*a*). By doing this, estimation of the spatial pattern at small distances is based on the sampling locations at the border, including sampling locations inside (filled circles) and outside (open circles) the extent of the study area (Figure 1.13*a*). When the extra resources are not available, or when the surroundings of the study area are not homogeneous, calculation of spatial statistics should be limited to the centre of the extent (filled circles), using the samples around the border (open circles) only as neighbours at small distances (Figure 1.13*a*). Another technique that can be used during the analysis, assuming that the extent is a homogeneous area, is the computation of 'torus distances' (Figure 1.13*b*). This can be achieved by 'wrapping' and joining together opposite borders, the north and south as well as the west and the east, to create a doughnut-shaped structure called a torus. The torus distances are computed among all the sampling locations, so that the samples at the northern border are used as near neighbours for the samples at the southern border. The distribution of pairs of sampling locations will then be more uniform, minimizing the edge effects. The torus correction should only be used when the process can be assumed to be stationary. If, for example, the northern edge of the study plot has a patch not occurring at the southern edge, then the torus distances will artificially mix two different spatial patterns, resulting in a distorted spatial structure. (This torus distance approach is closely related to a restricted randomization technique known as the 'toroidal shift'.)

## 1.6 Stationarity

The spatial pattern of a given area is a synthesis of dynamic processes operating at various spatial and temporal scales. Hence the spatial structure at any given time can be viewed as one realization of many potential outcomes of the interactions among these processes (Figure 1.2). To make meaningful ecological

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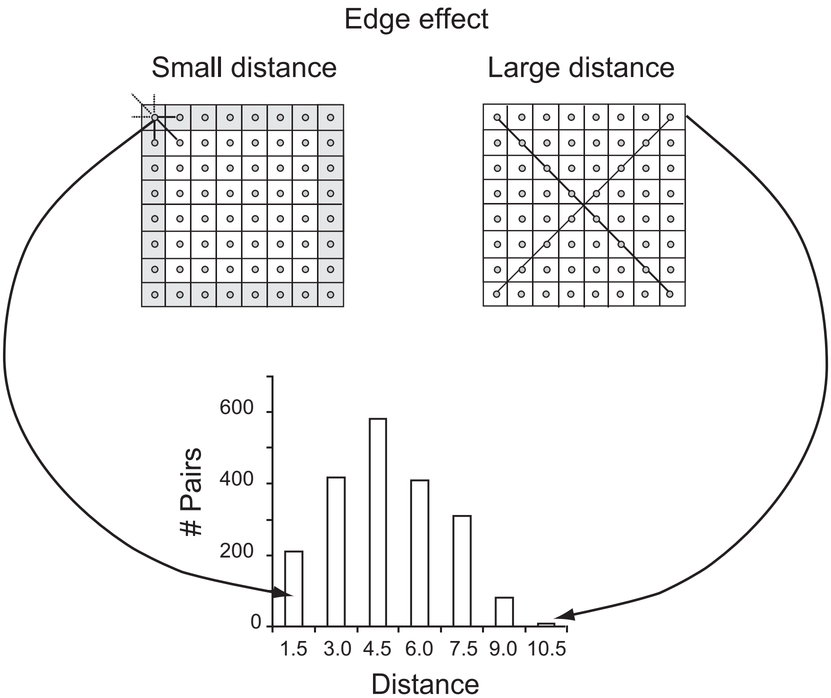


**Figure 1.12** Edge effect affecting the sampling units along the border of the study area (the grey sampling units): at small distance (left panel; 1.5 units apart) and large distance (right panel; say 10.5 units apart), where the number of pairs of sampling locations used to estimate the spatial pattern is lower than for intermediate distances (e.g. 4.5 units apart).

interpretations of the spatial pattern, we need to make some assumptions about the underlying processes (Figure 1.14). Similarly, spatial statistics are usually based on the assumption that the process is stationary (Figure 1.15). In a spatial context, a process or its model, is stationary if its properties are independent of the absolute location and direction in space (Haining 1990); the parameters of the process, such as the mean and the variance, are the same in all parts of the study area. The property of stationarity is required of a model for making inferences about data at locations that are not sampled. This implies that stationarity is a property of the model or the process, and not a property of the data, but a stationary process can generate a spatial pattern that looks non-stationary. If the apparent non-stationarity is because of a trend, the data can be detrended. Furthermore, the property of stationarity is scale dependent, as illustrated in Figure 1.14. When data values vary from place to place, resulting in heterogeneous patterns with changes in both mean and variance, the assumption of stationarity required for spatial statistics is not fulfilled. The implications are that the identified spatial pattern can be distorted and inaccurate (Boots 2002; Fortin *et al.* 2003), so that subsequent spatial inferences may be invalid (see Chapter 8; Legendre 1993; Dale & Fortin 2002, 2009).

Therefore, spatial statistics should be calculated over areas for which stationarity can be assumed (Figures 1.14 and 1.15). Because stationarity is a property of the process, it cannot be tested directly, but we can determine whether or not a landscape is homogeneous by computing the mean and the variance of the data using

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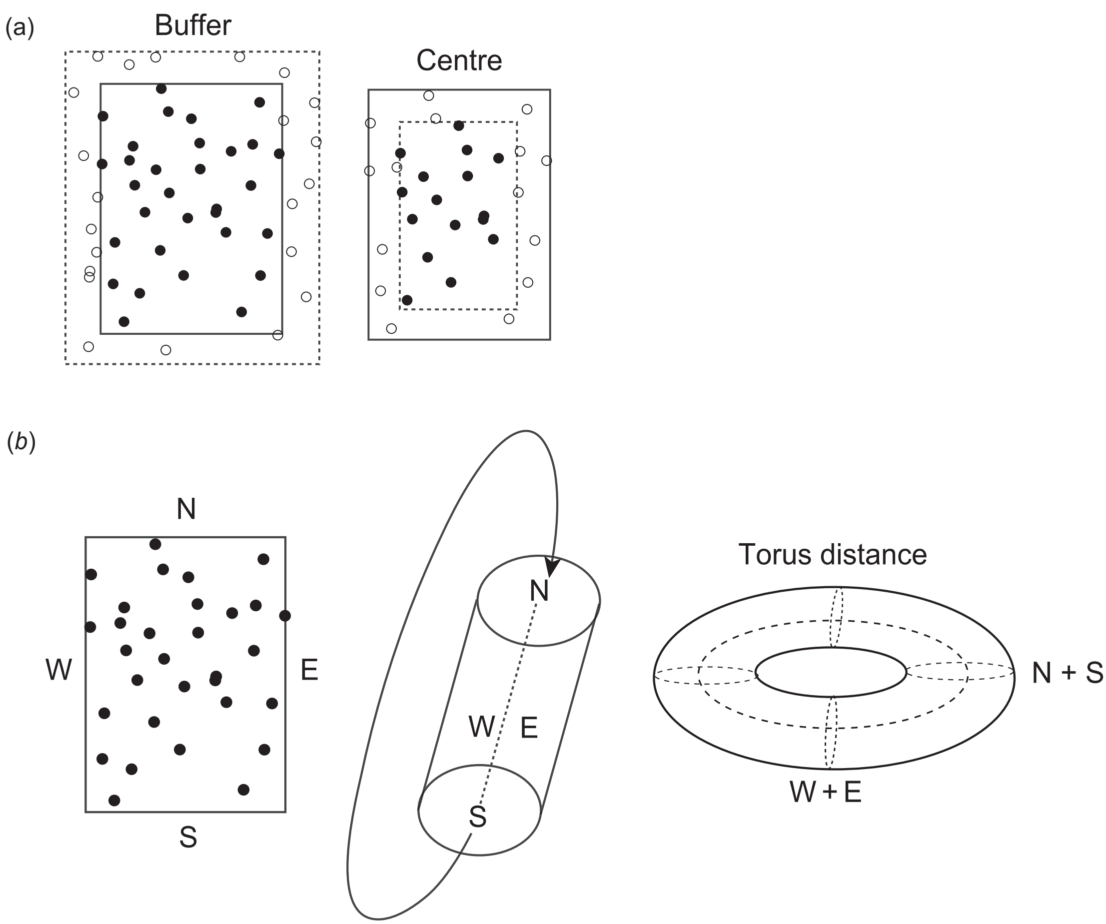


**Figure 1.13** Edge correction techniques during: (*a*) spatial sampling by surveying a buffer area (open circles) around the extent (filled circles) or by analysing only the centre region (filled circles) of the extent; and (*b*) analysis where torus distances are used instead of Euclidean distances. See text for more details.

sliding windows of varying sizes. When processes are obviously not stationary (as illustrated in Figures 1.14 and 1.15*b*, *c*), we need first to identify homogeneous subregions by means of spatial partitioning methods (as presented in Chapter 9).

Depending on the relative scale and the characteristics of a particular realization of a model, a stationary process can give rise to an apparently non-stationary pattern. For example, a Poisson–Poisson or Neyman Type A process gives rise to clumps of events and, given only a few clumps, it is quite possible they will occur in the same part of the plane. For example, Figure 1.16 shows a randomly generated pattern, which appears to exhibit non-stationarity. There are five clumps of events, but they are all on one-half of the plane even though all parts of the plane have an equal probability of a clump occurring there. The probability that all the clumps occur in one-half of the plane is something like $1/2^4 = 0.0625$; so that, while this kind of pattern would be somewhat rare in randomly generated patterns, it is not completely surprising.

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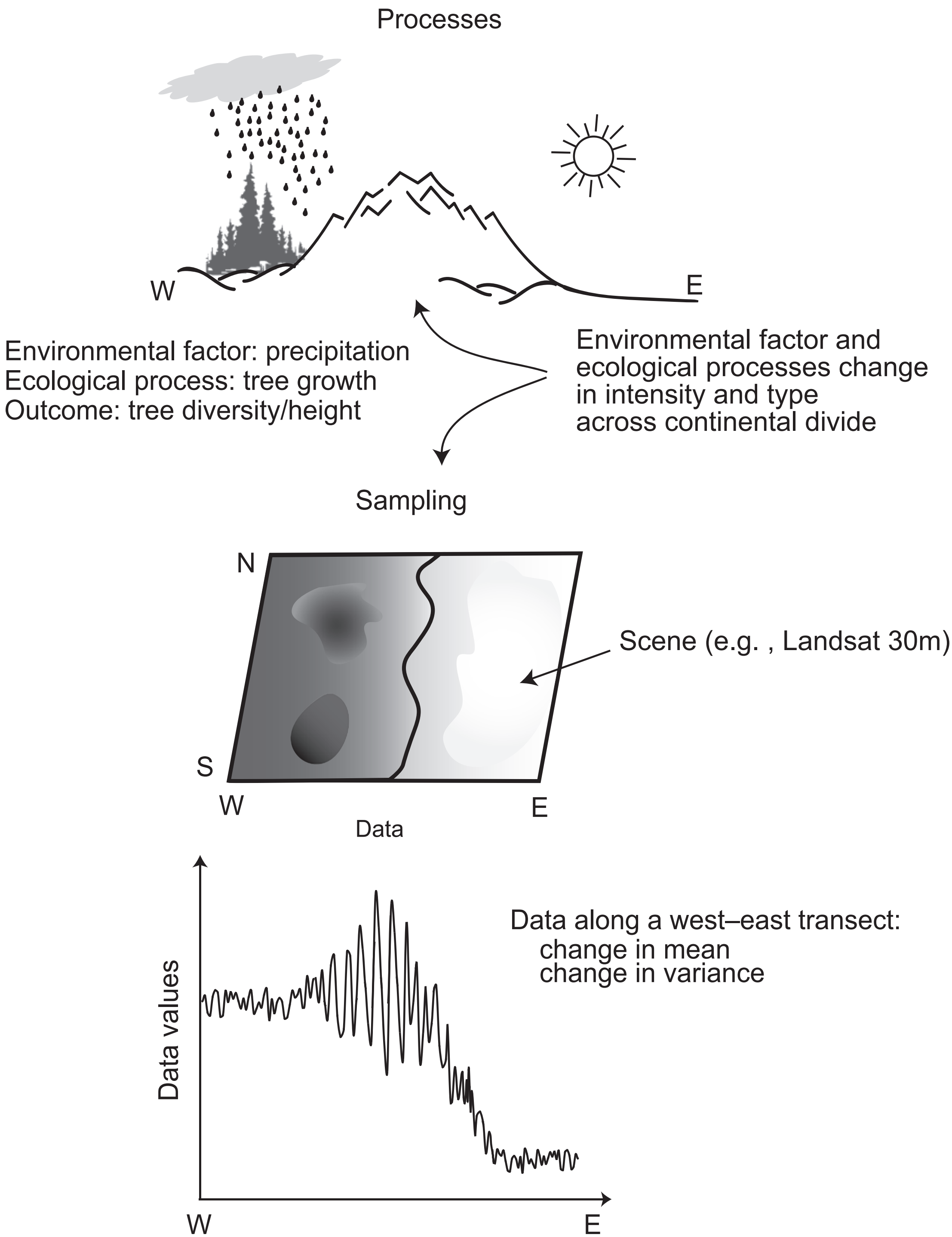


**Figure 1.14** The concept of stationarity: a process level issue. From the west to the east of the continental divide, the amount of precipitation varies, which affects tree growth and diversity. While sampling this region using remotely sensed imagery (a scene) to estimate tree net primary productivity, the extent of the scene includes both sides of the continental divide, which are not under the same process regime. The mean and variance of net primary productivity change along a transect from west to east.

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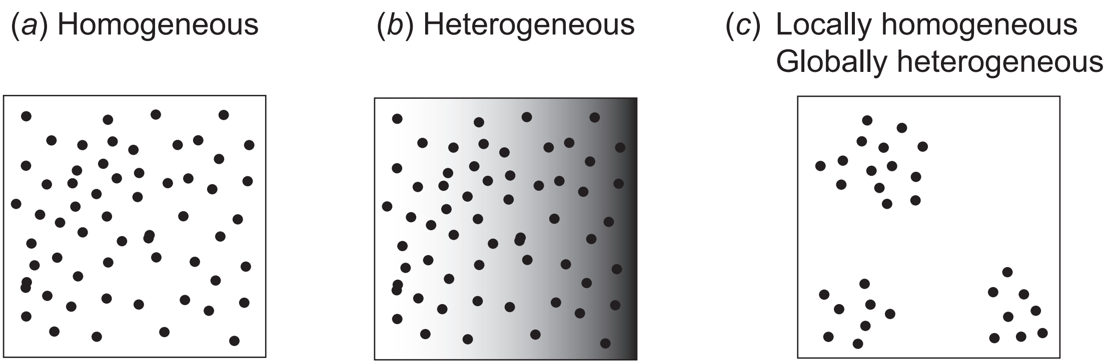


**Figure 1.15** Homogeneous (*a*) versus heterogeneous landscapes (*b*, *c*). In (*b*), the study area includes subregions where plants cannot grow, such as a lake, on rock or in inappropriate soil types. In (*c*) the plants can grow only in subregions where the soil type is appropriate.

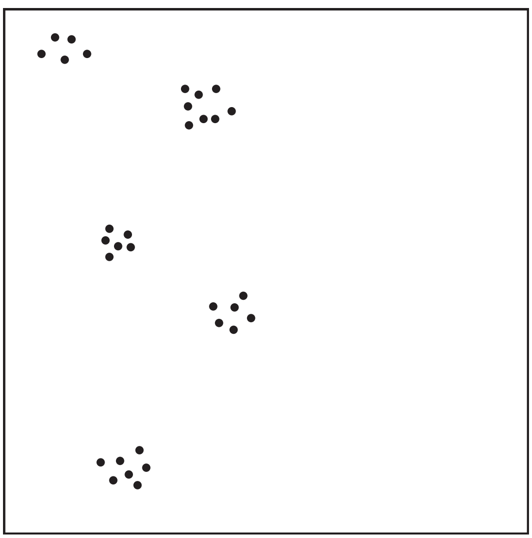

**Figure 1.16** An apparently non-stationary pattern of events (dots) resulting from a stationary underlying process.

A set of data collected from field sampling is, at best, much like a single realization of an underlying model, and apparent inhomogeneity may result from processes that are, in fact, stationary. We need to be concerned, therefore, about the power of our evaluation procedures to reject the null hypothesis of interest, especially the null hypothesis of stationarity. In many instances, a useful exercise is to determine in advance the strength of the spatial pattern that would be required to reject the null hypothesis, given the sample size or effort expended (i.e. the power of the test). Combined with a pilot study to determine some of the characteristics of the spatial structure, this prior knowledge of the magnitude of sample size needed can provide guidance in the study design and in subsequent analysis.

From the plot level to the landscape level, the inherent stationarity needs to be ensured to avoid distorting the identification of spatial pattern and making incorrect inferences, as well as misleading subsequent ecological interpretations. Spatial statistics that summarize the spatial pattern for the entire study area with a single number, referred to as 'global spatial statistics', should not be applied to a study area with non-stationary processes. While it is impossible to test directly whether an underlying process is stationary, it is possible to check whether model residuals appear independent and identically distributed (i.i.d.) across the region of interest. If the covariance structure of the residuals is heterogeneous, it may indicate that the assumption of stationarity is violated. In that case, it may be necessary to subdivide the data into spatially homogeneous subregions so that each subregion can be analysed separately. Another solution is to use 'local spatial statistics' to provide an estimate of the characteristics of the spatial pattern for each sampling

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location (Anselin 1995; Getis & Ord 1996; Boots 2002; see also Chapter 6). In this book, global spatial statistics will be referred to loosely as 'spatial statistics'; local statistics will be designated explicitly.

To sum up: stationarity is the condition that the defining characteristics of the processes underlying spatial patterns are constant across the region of interest, including that the species–environment relationship does not change with location or scale. Most modelling approaches to account for residual spatial structure assume stationarity as a condition for subsequent inference (Chapters 7 and 8 of this book). Of course, the situation and our analysis and interpretation become more 'interesting' when we cannot assume stationarity, or are forced to acknowledge that it may not be obtained.

## 1.7 Spatial statistics

Because natural spatial heterogeneity affects most systems we study, it is not surprising that many kinds of spatial statistics have emerged from a variety of disciplines (plant ecology, human geography, mining engineering, etc.), in order to quantify spatial patterns generated by one or several processes (Figure 1.2). Over the past several decades, a series of 'spatial statistics' approaches (a generic term that includes all statistical methods) have been developed, either building on earlier methods or in parallel by different disciplines, to describe spatial patterns, or to estimate and to predict spatial processes. Not all spatial statistics have exactly the same goal or assume the same kind of underlying spatial processes, nor do they all use the same data type or the same underlying mathematical approach (Dale *et al.* 2002). Therefore, each of these statistics has its own requirements, assumptions, and guidelines for application (Table 1.1).

Our classification of spatial statistics into six elements (presented at the beginning of this chapter) reflects both the historical context in which the methods were developed and their mathematical approach (Dale *et al.* 2002). The first element of our classification (describing and testing the spatial structure) is a very basic step and the goal could be achieved using spatial exploration methods based initially on first-order statistics and more recently on second-order statistics.

### 1.7.1 First-order statistics

First-order spatial statistics are a big family of aggregation indices based on the species abundance data, particularly on the mean of local abundance measures (hence first order). These can detect trends in the data over the entire study area (i.e. the mean value). These aggregation indices can indicate whether there is a spatial pattern or not, but not its magnitude. For example, the variance–mean ratio, based on the Poisson distribution, may distinguish between only three types of spatial pattern: random, when the mean and the variance of species abundance per sampling unit are about equal; patchiness, when the variance is greater than the overall mean; and uniform or regular, when the variance is smaller than the mean (see Dale *et al.* 2002 and Chapter 4 for more detail). As shown in Dale (1999, p. 226), there are some problems with the logic of this approach to point pattern evaluation of the spatial dispersion of point events. In this book, we will not emphasize first-order statistics but we will concentrate on the many second-order statistics commonly used by ecologists.

### 1.7.2 Second-order statistics

Second-order statistics measure local spatial pattern (i.e. the degree of spatial structure) in the data by computing the deviations from values at neighbouring locations (i.e. the spatial variance). Most of the spatial statistics that characterize and test spatial structure in this way are presented in Chapters 4, 5 and 6. At the root of most second-order statistics is the concept of spatial weights to characterize the link between sampling units, which can be used to determine a number of characteristics, including the pairs of sampling units that are spatially adjacent, several search window types, neighbour determination rules, and connectivity algorithms (see also Chapter 3).

These spatial statistics can be further classified according to the type of ecological process to which

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they can be applied. Some processes act on the actual locations of individual organisms and it is the spatial pattern of these locations that is of interest; these are called point pattern processes (see Figure 1.3; Chapter 4). Other processes affect the quantitative values of variables and the spatial pattern is continuous in space, and there are several spatial statistics for studying these continuous processes, such as spatial autocorrelation coefficients (Chapter 6) and spatial variance estimators (block variance methods, lacunarity, and wavelets; Chapter 5). These spatially continuous processes can be sampled using either contiguous sampling units (Figure 1.3*b*) or spatially separated units (Figure 1.3*c*). Then, some processes involve qualitative changes within an area and surface pattern methods are used to analyse them (e.g. join count statistics; Chapter 6). Such categorical processes usually require contiguous sampling units. There are, however, some 'grey zones' in the way these three families of processes can be sampled and analysed. When several processes affect ecological data, they usually have a multiscale spatial structure. Whether such data are univariate or multivariate, multiscale analysis needs to be performed using either wavelets or ordination techniques (see Chapter 7).

Once the spatial pattern is identified and characterized, we may be interested in either estimating spatial parameters to model the process for prediction or interpolation (the second category in our classification; see Chapter 6), or we may wish to test the relationships among ecological data (the fourth category; see Chapter 8). In the case of estimating parameters or of testing the relation among variables, the goal of the study and prior knowledge about the ecological data should guide the decision whether the spatial structure should be explicitly modelled or detrended before modelling or analysis (see Chapters 6 and 7). For example, we could be interested in the relationship between soil moisture and plant growth. As illustrated in Figure 1.17*a*, both variables have a spatial structure based on multiple regression using the *x* and *y* coordinates of the sampling locations as independent variables. The relationship between the two variables (Figure 1.17*b*) is only significant when the raw data are used (left panel) but not when the spatially detrended data (residual data where the spatial structures are modelled by multiple regression) are used (right panel). This exercise shows that before claiming causality for the relationship between two ecological variables, we should test whether they have significant spatial structure. This investigation falls into the fifth category of the classification we presented at the beginning of this chapter (interactions among variables). In the example, the spatial structure is due to the spatial dependence of both variables on the slope from which the samples were obtained. This may be an instance of spurious correlation. If the residuals from the multiple regressions retain some spatial pattern, the ecological variables could have been both spatially dependent at one spatial scale and spatially autocorrelated at another. Thus, it is important to define adequately the spatial scale of the question asked so that the appropriate spatial statistics can be applied. The remaining elements of our classification are spatial partitioning to create spatially homogeneous areas, using techniques such as spatial clustering, boundary detection, and wavelets analysis (the third category; Chapter 9); and finally spatio-temporal analysis (the sixth in our classification; Chapter 11), where considerations of location in space are augmented by those related to location in time.

## 1.8 Ecological hypotheses and spatial analysis

The relationship between hypotheses and analysis is not a simple one in most ecological studies, and that is certainly true of studies that involve spatial analysis. The hypothesis of interest will determine the kind of data needed and the analysis that is done, and often the way in which the analysis is carried out; but equally, the results of analysis are used to generate hypotheses which will lead, in turn, to further observations and further analysis. Clearly, there may be opportunities for a kind of iterative approach to the use of spatial analysis to evaluate ecological hypotheses (Figure 1.1). Such an iterative sequence can be costly in time and effort, particularly if data

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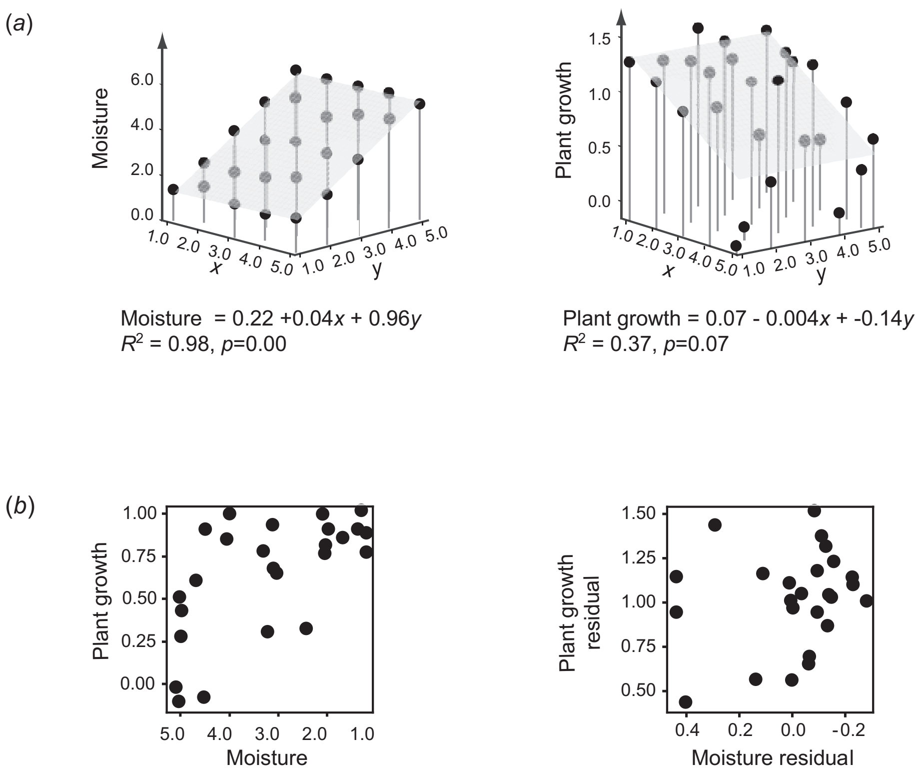


Moisture = 0.22 +0.04$x$ + 0.96$y$
$R^2$ = 0.98, $p$=0.00

Plant growth = 0.07 - 0.004$x$ + -0.14$y$
$R^2$ = 0.37, $p$=0.07

Plant growth = 0.11 - 0.15 (moisture)
$R^2$ = 0.39, $p$ = 0.001

Plant growth res. = -0.00 - 0.29 (moisture res.)
$R^2$ = 0.04, $p$ = 0.312

**Figure 1.17** Example of the relationship between soil moisture and plant growth (artificial data). (*a*) Multiple regressions, using the *x* and *y* coordinates of the sampling locations, as independent variables (soil moisture: left panel; plant growth: right panel). (*b*) Relationship (linear regression) between the two variables using the raw data (left panel) and residuals from the multiple regressions (right panel). Note that the relationship changes from significant to nonsignificant as the data are detrended for the spatial structure.

collection is required at each stage, but in some cases the sequence can be replaced by a well-planned combination of data collection and analysis that takes advantage of a hierarchy of null hypotheses, enabling the study to go beyond the use of the simple null hypothesis of complete spatial randomness (CSR). Rejecting this simple null hypothesis may not provide much useful insight, and so a more knowledge-based approach may be well worth the effort. In that spirit, McIntire & Fajardo (2009) recommended the use of space as a surrogate for unmeasured processes, taking advantage of the combination of a priori hypotheses, background ecological theory or knowledge, and precise spatial analysis to understand pattern and the underlying process better. Yet as space is only a surrogate for unsampled variables or unknown processes, it should be used as last resource. When it is the case, however, knowledge from pilot studies or literature can help to formulate the predicted shape (e.g. trend, or patchiness), degree (e.g. low or high) and range (e.g. species dispersal ability, isolation-by-distance) of the spatial pattern.

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Hierarchical hypothesis framework works best when each level of testing is independent of the previous levels of testing. This independence is not always possible, and we may end up, as we do in the case of a series of scale-specific hypotheses, with a hierarchy of tests that are not mutually independent. Hierarchical structure requires careful consideration of the meaning of the significance levels of test results. Hierarchical analysis may also be closely related to a hierarchy of randomization procedures. For example, Goovaerts & Jacquez (2004) used a typology of null models for the detection of spatial clusters of disease based on (1) risk uniform but spatially independent versus risk uniform but spatially correlated versus risk heterogeneous and spatially correlated; and (2) population size not accounted for (disease incidence) versus population size accounted for (disease prevalence). This classification provides six different null hypotheses for consideration and for simulation. A more familiar example, already alluded to, is the case of spatial data in which are combined a linear trend, regular cyclic behaviour, and random noise.

In the relationship between hypothesis and analysis, one of the most challenging tasks can be the translation of the ecological hypothesis or the theory being investigated into well-formulated and testable spatial or statistical hypotheses. A formal description of how we might proceed is to say that the ecological hypothesis determines the statistical hypothesis to be tested and the data that are required to test it. Together, these provide the choice of the analytical approach that can be used. The results of analysis allow us to decide to reject the statistical hypothesis or not, and this decision is then interpreted in assessing the ecological hypothesis.

As an example, consider the application of point pattern analysis (as described in Chapter 4) to a study of the spatial dynamics of a plant population. One of the most commonly used methods of point pattern analysis is Ripley's $K$ function (Ripley 1981; Chapter 4) and variants upon it; statistically, it determines the spatial scales at which a point pattern is clumped (events underdispersed) and at what scales there is repulsion (events overdispersed). The ecological hypothesis being investigated may be that intraspecific competition increases the spacing of plant stems through time due to nonrandom mortality, so that although seedlings are initially very clumped in patches due to high seed density, moisture, or nutrients, the clumps then self-thin as mortality acts in a local-density-dependent fashion. The translation into spatial hypotheses and the expected results of a spatial analysis might look like the following.

(1) If the population processes proceed as described, an initial spatial analysis should indicate overall clumping at a range of scales, but most evident at distances related to the intervals between the patches of high density. The null hypothesis is just that of complete spatial randomness.

(2) Because the density that causes mortality is very local, small-scale overdispersion develops as the shortest interplant distances are eliminated. Evidence of the underdispersion at the original scale of patchiness will persist, but its magnitude declines because there are fewer plants in those patches. The null hypothesis is still complete spatial randomness.

The ecological hypothesis gives rise to predictions for the results of spatial analysis that contrast with those that would result from complete spatial randomness: initially the Ripley's $K$ analysis will show clumping at all scales but with a maximum corresponding to the distance between patches of high density; the results of later sampling will show overdispersion at short distances and a maximum underdispersion at the same scale as previously, but with decreased magnitude. That seems pretty easy! Having done some appropriate spatial analyses (say Ripley's $K$), we can then determine whether the results of the analysis are consistent with the predictions, as statistical alternative hypotheses. This will allow us to evaluate the original ecological hypothesis, although each step in the chain of logic is inferential. More than one process can give rise to the same spatial pattern, and while results consistent with the hypotheses provide corroboration, alternative explanations for the observed patterns are always possible, even if improbable.

This plant population pattern example gives a rather simple case, the locations of point events in two dimensions, observed at two stages of pattern

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development. Obviously the relationship between ecological hypotheses and spatial analysis can be much more complicated, both in the complexity of the ecological situation and in the number of variables included. Consider, for example, a forest with a high density of fallen logs on the forest floor, and the kinds of questions an ecologist might ask about the relationship between the characteristics and locations of those logs with the small mammal trails through the forest. There is a long list of questions that could be converted into statistical hypotheses for spatial analysis; here are a few.

- Is there a pattern to the locations and other characteristics of the fallen logs? What are the important features of that pattern? Is the pattern isotropic? Is it stationary? Are there edge effects?
- Are the locations of the small mammal trails independent of the locations or other characteristics of the logs? Are the trails apparently random and independent of each other once the dependence on the logs is factored out?
- Is the dependence of trails on logs directionally specific? Is the dependence stationary? Are there edge effects?
- Are big logs more influential on the trails' locations than small logs?

And so on... Obviously the situation and the kinds of questions that can be asked become more complicated as the hypotheses and analysis include more features. Consider this example when we add to the data with the positions of the standing tree boles, the rock outcrops, then streams, then Great Horned Owl nests, and other biological influences.

Although hierarchical hypothesis testing has many features to recommend it for ecological research, it is not as commonly used as it should, in part because it is not always easy to convert what may seem to be an 'easy' ecological hypothesis into clearly defined hypotheses and outcomes for spatial analysis. Finding or collecting the data that will best allow a determination of the competing hypotheses may be difficult or very expensive to obtain. The difficulty is compounded by the fact that different processes can give rise to similar patterns (Figure 1.2), and the alternatives must be carefully explored in order to make the study as convincing as possible. On the other hand, prior knowledge of the physiology, ecology, dispersal ability, and system topology can help to develop and refine suitable null and alternative hypotheses about the shape (trends, cycles, patchiness) and crucial distances (scale of repeats, length of trends) of the spatial structure.

## 1.9 Randomization tests for spatially structured ecological data

When ecological hypotheses are translated in statistical hypothesis it is crucial to have the appropriate statistic and test procedure to assess significance of the observed data. The general approach to determine significance is to compare the statistic computed from the observed data to an appropriate reference distribution. When this reference distribution is known and can be derived analytically, parametric tests can be used. In using parametric tests, however, ecologists rely on predefined statistical hypotheses, statistics and significance procedures that require the independence of the data and this may be limited in scope.

When the reference distribution is not known from first principles, randomization procedures can be used to generate a reference distribution from the data (Good 1993; Edgington 1995; Manly 2006; Figure 1.18*a*). When inference to the population level is required, bootstrap procedures and Monte Carlo simulations can be used (Figure 1.18*b*; Efron & Tibshirani 1993; Manly 2006). Randomization tests provide an attractive alternative to parametric tests because significance is evaluated based on empirical distributions generated from the observed data. This property is quite appealing to ecologists faced with small data sets that do not meet the assumptions of parametric tests. Randomization tests are based on the hypothesis that the data are independent, so that re-arrangements (such as re-ordering or pairwise exchanges) of the data are all equally likely. Therefore, although randomization tests may have fewer assumptions than other forms of testing, this does not mean that they have no assumptions at all. In a spatial context, this assumption corresponds to a statistical

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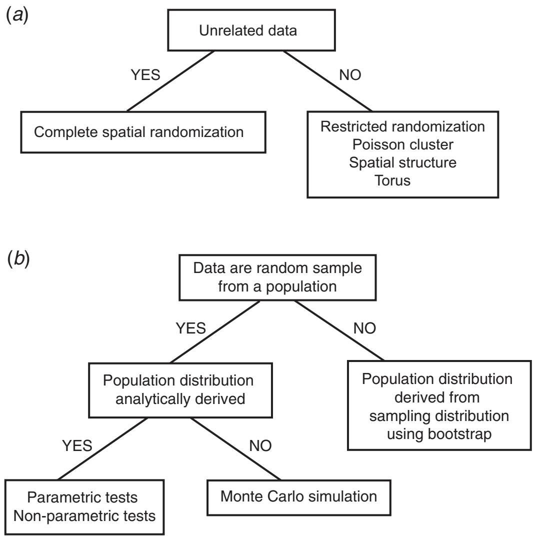


**Figure 1.18** Decision trees to select appropriate significance tests at (*a*) the sample level and (*b*) the population level.

null hypothesis of complete spatial randomness (CSR) of the data.

The basic procedure to generate a reference distribution to which the observed statistic can be compared, is as follows (Figure 1.19):

(1) re-allocate, using a complete simple randomization procedure, all the sample values of the variable, one to each of the sampling locations;
(2) re-compute the statistic; and,
(3) repeat these two steps many times (usually thousands of repeats).
(4) Compare the value from the one observed data set with the distribution of the values derived from the many "data" sets generated in this way, rejecting the null hypothesis is more extreme than a pre-determined proportion of the randomization values (e.g. 499 out of 10 000).

The probability level at which the statistical decision to accept or to reject the null hypothesis is made depends on the number of randomizations performed. When the number of observations is small, all permutations (re-orderings) of the original data can be examined (Good 1993). When the number of observations is large, only a subsample of all possible permutations

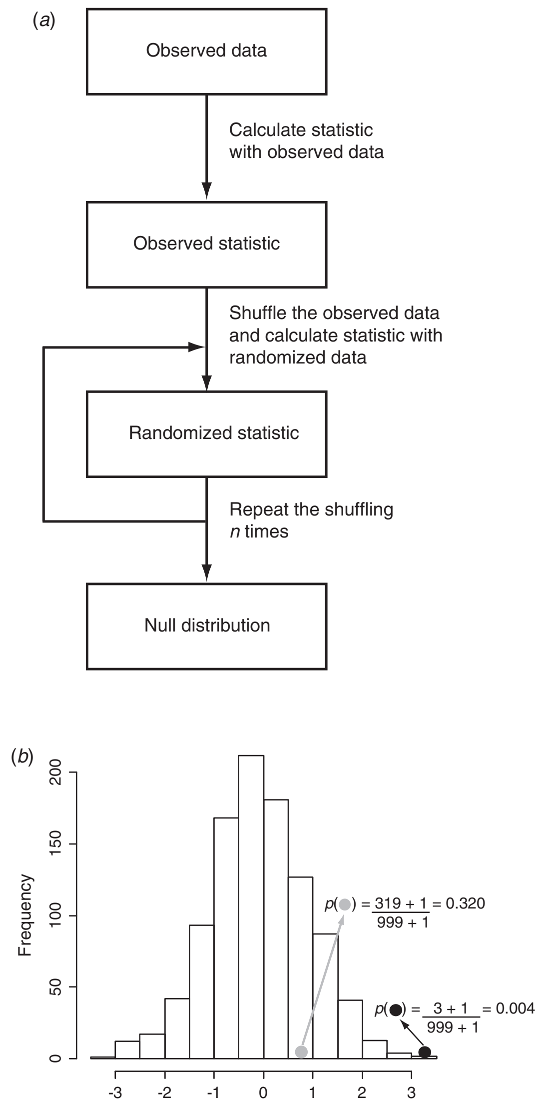


**Figure 1.19** Randomization test. (*a*) Flow chart illustrating the steps involved in generating randomized data from the observed ones. (*b*) Examples on how probabilities are computed from an empirical distribution generated by a randomization procedure.

of the data can be computed and it is recommended that 10 000 or more randomizations should be used (Manly 2006). Then, the reference distribution produced by all these randomizations is used to assess

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the probability of the observed data where the precision of the probability depends on the number of randomizations. As an example, with 1000 values (999 randomized statistics and one observed), the smallest probability that can be calculated is 0.001 (1/1000), but the accuracy of the estimate of the probability will not usually be good; using 10 000 iterations or more is recommended.

Although randomization tests do not offer the apparent security of predefined parametric statistics, their flexibility provides the means to analyse complex ecological data using custom experimental designs for which classical tests have not been developed. Ecologists can also develop their own statistics, opening up the possibility of testing in novel situations. For example, the boundary statistics presented in Chapter 9 were developed to investigate the properties of coherent boundaries. This requires an understanding of how ecological hypotheses can be translated into statistical hypotheses, and especially when formulating randomization tests.

### 1.9.1 Restricted randomizations

Any lack of independence in the data (due to time, space, behaviour, phylogeny, etc.) can impair the usefulness of both parametric and randomization tests. Parametric tests require that the errors are independent, so that each observation or data point brings a full degree of freedom. If the lack of independence is due to spatial relationships, the resulting positive spatial dependence usually makes nearby sampling units more alike and so a spatially autocorrelated sample does not bring a full degree of freedom, but rather a fraction of it, inversely proportional to the strength of autocorrelation in the data (Legendre 1993; Dale & Fortin 2002, 2009). Several techniques in sampling design (see Section 1.5) and in performing the statistical analysis (Legendre & Legendre 1998; Dale & Fortin 2002, 2009) can correct or control for spatial dependence in the data, so that familiar parametric tests can be used, or that can explicitly incorporate the spatial structure into the analysis (see Chapters 7 and 8). This issue, of non-independent errors, is at the core of the analysis of ecological data and will be discussed in detail in Chapter 8. However, as it is applies to the development of randomization procedures for spatially dependent data, complete randomness is not really an appropriate comparator and so forms of randomness which incorporate some degree of spatial structure should be used (Cressie 1993; Venables & Ripley 2002; Figure 1.20). These are *restricted* randomization procedures that include the structure of spatial dependency already in the data (Fortin *et al*. 2002; Manly 2006). There are several different ways to restrict the randomization.

- Randomize only within subsets of the sampling locations, i.e. within subregions, where the data can be considered spatially independent within the subregion despite spatial structure when all the subregions are considered.
- Retain the order within the data. For spatial data, this can be achieved using a two-dimensional torus constructed by connecting the map margins, north edge to south edge and east edge to west edge, and then sliding one variable map over the other (the 'toroidal shift'). This procedure maintains most of the spatial structure of the data. In particular, the relationship between two variables can be tested using this restricted randomization by moving the values of one variable with respect to the other but keeping the spatial structure within each variable intact, and re-computing the statistic of interest. On the whole, this is a good approach but, depending on the number of restricted randomizations performed, and on the shape and size of the study area, this test can end up being too liberal (Fortin *et al*. 1996).
- Generate many realizations of a stochastic process that gives the same spatial structure as the original data (Fortin & Jacquez 2000; Fortin *et al*. 2003; James *et al*. 2010). This can be achieved by first estimating the structure of spatial autocorrelation in the data and then using the estimation of the parameters that will generate simulated data with a similar spatial structure (but not the same spatial pattern). Techniques like 'conditional annealing simulation' (Journel & Huijbregts 1978; Isaaks & Srivastava 1989; Cressie 1993) and 'conditional autoregressive modelling' (Getis & Boots 1978; Cliff & Ord 1981; Haining

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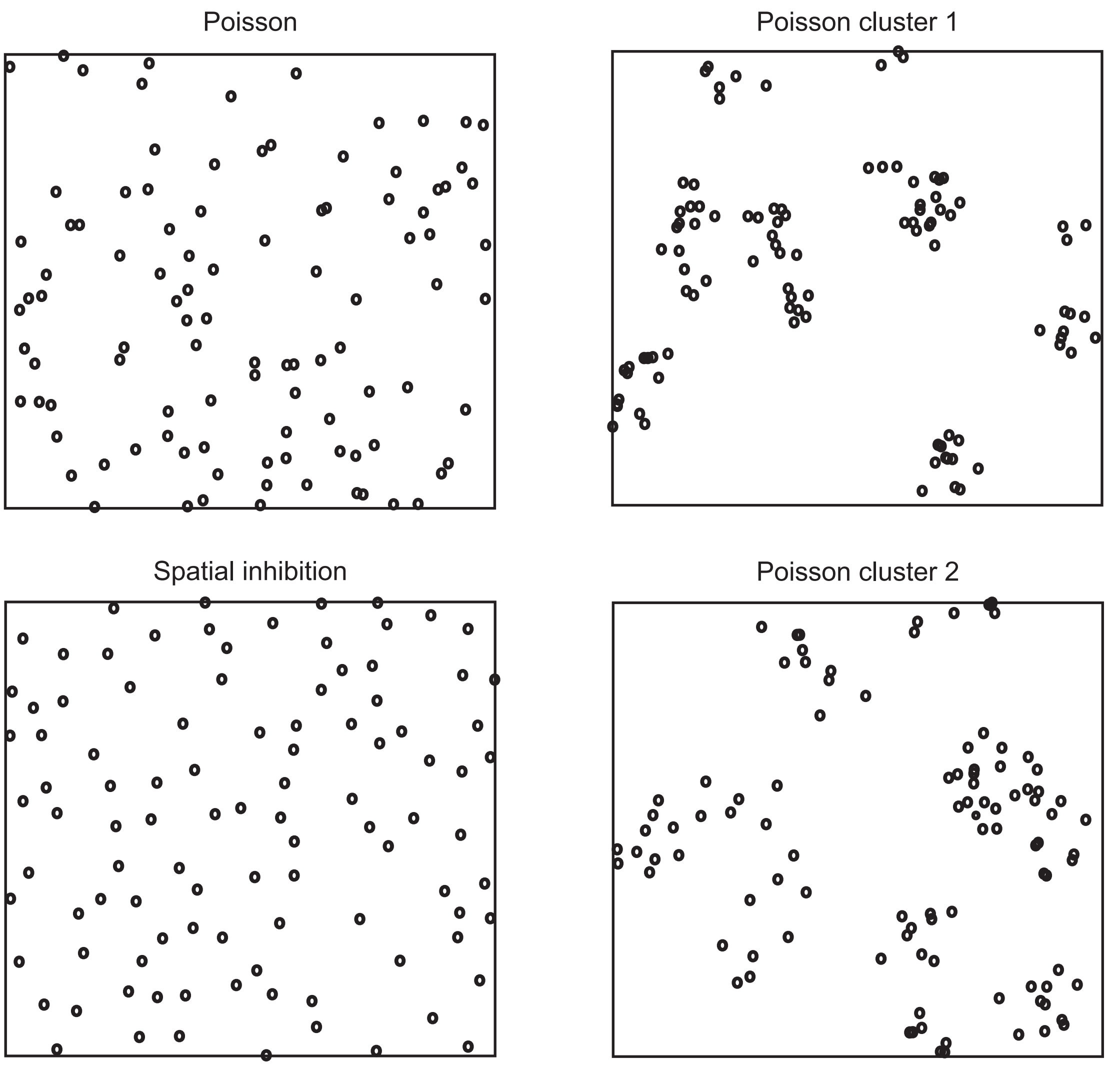


**Figure 1.20** Different point pattern processes generating different types of random patterns: Poisson process (i.e. complete simple randomness); Poisson clusters (1 and 2 using different parameter values for spacing among clusters); spatial inhibition.

1990) are available to do so (Fortin *et al.* 2003). Such restricted randomization tests assume that the underlying process is stationary within the study area. If this is not the case, then this approach is not appropriate and other kinds of modelling of the ecological processes will be required.

One of the themes of this book is the suggestion that a single simple null hypothesis, such as complete spatial randomness of events, may not be particularly interesting or particularly useful in an ecological context. In many instances, a hierarchy of null hypotheses of increasing restriction and sophistication will be much more informative. In parallel, when we consider the use of randomization techniques for testing these hypotheses, a series of increasingly restricted randomization schemes may provide more

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**Table 1.2** The abundance of a given species in 32 plots arranged in eight transects

| | Transect | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Condition | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Unburned | 10 | 10 | 6 | 6 | 6 | 6 | 2 | 2 |
| Unburned | 10 | 10 | 6 | 6 | 6 | 6 | 2 | 2 |
| Unburned | 10 | 10 | 6 | 6 | 6 | 6 | 2 | 2 |
| Burned | 7 | 7 | 5 | 5 | 5 | 5 | 3 | 3 |

meaningful results than a single unrestricted randomization. In designing randomization procedures, it is also important to think through the worst possible case, the 'pathological' data set, and how the proposed procedure would respond to it. We may be able to resolve our concerns about a particular randomization procedure by finding a counter-example that shows its faults.

As an example of this thinking, consider a sampling design of eight transects of four sample plots each, three in unburned forest and one in an adjacent burned area. The abundance of a particular species was determined in each plot and the question of interest is whether the abundance is different between the burned and unburned areas. The analysis first proposed was to use 1000 iterations to create a reference distribution of the density in the unburned forest, by taking only one of the three 'unburned' values in each transect and calculating the average. These averages were then to be used to create a distribution of mean densities, and the mean density of the burned area plots (calculated once) was to be compared to the distribution. This mean was to be declared significantly different from the unburned area mean if it fell above the 97.5% value of the distribution or below 2.5%. This initial proposal seems straightforward, but Table 1.2 gives a counter-example of why the proposed analysis is not the best approach.

The mean value for the intact forest is 6.0 in every iteration, and so the distribution is very narrow. The burned area has a mean of 5.0, which is outside the distribution, leading to the conclusion that it is significantly low. An examination of the distributions of the two sources of data suggests that they overlap greatly, and that the conclusion may be mistaken.

This example provides a good illustration of the close relationship between the null hypothesis and the randomization method used to test it. What was actually tested here was the hypothesis: 'The burned area mean is not different from the unburned area mean (which can be treated as a given)'. A better version of the null hypothesis is that the densities in the two areas are the same, so that the observed values in the two areas provide an estimate of a common mean. This logic leads to a different randomization method: the observed difference in mean density between the two areas ($6.0 - 5.0 = 1.0$) is compared to the distribution of the difference when all 32 observations are randomized. When that approach is used, the difference is not significant: 155 of 1000 trials have an observed difference greater than 1.0. That is the result of a complete randomization, which destroys all the spatial structure in the data. Given the obvious trend in overall densities in the transects, a restricted randomization, within transects, should be considered. Then the null hypothesis is: 'Given the overall density within each transect, the burned and unburned densities do not differ.' Randomizing within transects produces a significant result, with only 4 of 1000 trials giving a greater difference between the means than that observed.

In addition to showing the close relationship between the hypothesis being tested and the randomization technique used, this example also shows the potentially very important difference between complete and restricted randomizations. The type of restriction appropriate for the randomization technique is directly related to the null hypothesis under consideration. One conclusion is that randomization and restricted randomization tests can free ecologists from parametric

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tests that were not designed to accommodate their novel questions and the inherent spatial structure of ecological data.

However, restricted randomization is not without its own drawbacks, and we should provide an example of potential problems with randomization procedures. Consider the following situation: in a transect of 100 contiguous sampling units, we have recorded the presence or absence of tree canopy and the presence or absence of a shrub layer. By amazing coincidence, only 10 sampling units have no tree canopy (all in a row) and only 10 have a shrub layer (also all in a row). Interestingly, the canopy gap and the shrub patch are offset somewhat, so that only 7 sampling units have shrubs and no canopy. By a restricted randomization test (the one-dimensional torus method, also known as sequential or caterpillar randomization), this is not a significant match (with $\alpha = 0.05$) because there are 7 of 100 random relative positions that have an overlap as great, with overlaps of 7, 8, 9, 10, 9 and 8, and 7 sampling units. If the transect were just a little longer, and the pattern was maintained, the result would be significant!

We must be careful that the null hypothesis implicit in the restricted randomization is ecologically tenable. Randomization and restricted randomization tests in ecology are particularly prone to mis-specification of the null hypothesis, primarily because the null hypothesis is embedded in the randomization procedure and is not made explicit. A clear understanding of the null and alternative hypotheses of the chosen randomization test is required to ensure our biological and ecological questions are correctly addressed. Furthermore, the null hypotheses and the randomization procedures that follow from them must not include the key process being tested. Indeed, if all the processes are included in the null hypothesis, there is nothing left to test! For example, in Chapter 9, the overlap statistics have been developed to test whether or not the spatial locations of two boundaries, based on two different data sets (e.g. plant species and animal species), spatially overlap. In such a case, the null hypothesis is that there is no spatial relationship between the plant and animal boundaries: $H_0$ = no spatial association between the boundaries. The alternatives are: $H_{1a}$ = the boundaries are spatially positively associated, and $H_{1b}$ = the boundaries are spatially negatively associated (i.e. spatial repulsion). The null and alternative hypotheses are at the boundary level. Consequently, the randomization procedure should also be at the boundary level. There are several ways to do so: for example by the toroidal shift (Fortin *et al.* 1996) or by randomly placing the boundaries (location and orientation) within the study area (Sokal *et al.* 1988). We might be interested, however, in testing which ecological processes are involved in the actual location of the boundaries. In that case, the randomization should be at the species level. Then we could examine two ecological processes:

(1) the spatial structure (spatial dependence and spatial autocorrelation) of each species; and,
(2) the spatial interaction among species in the structure of the community.

If only the spatial structure of the species is of interest, then each species can be spatially randomized separately; if both the species and the community spatial structures are of interest then the spatial randomization of each species needs to be linked to the randomization procedure of the other species. These randomizations can be trickier to implement and they require a clear understanding of the ecological processes of species interactions (facilitation, competition, mutualism, etc.) and their spatial implications as reviewed in Chapter 2.

We will be discussing particular examples of randomization and restricted randomization in other sections of this book, but the general comments introduced here will provide useful background to the specific applications.

## 1.10 In conclusion: what is space?

A key purpose in performing spatial analysis is to determine the characteristics of the spatial structure of the data. Possibilities include the usual null hypothesis of independence (spatial, temporal, genetic, phylogenetic, etc.), and several forms of lack of independence. These include aggregation or overdispersal of events, spatial dependence of one variable on another in a spatial context, and spatial autocorrelation within a single variable.

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Only when the data are spatially independent can we interpret parametric and randomization tests with any confidence. Yet, there are several ways in which the detection of significant spatial structure (spatial aggregation, spatial dependence, spatial autocorrelation) provides meaningful insights about ecological data and their underlying processes (Griffith 1992). Space effects can be interpreted as any one of the following.

(1) A statistical nuisance: the presence of spatial autocorrelation is a problem for applying parametric and randomization tests that require independent errors (Cliff & Ord 1981).
(2) A diagnostic indicator: when using linear or multiple regressions, the presence of spatial autocorrelation in residuals can indicate that one or more processes and their associated variables were not included in the model or were not parameterized adequately (Fortin & Melles 2009; Melles *et al.* 2010).
(3) A useful surrogate for unmeasured processes or factors that are too expensive or too difficult to measure, or of which the researchers are unaware.
(4) A predictor variable that can be used in a regression or ordination framework using the relative spatial location of sample (Dray *et al.* 2006; see Chapters 7 and 8) or the spatial neighbouring effects of the environmental factors or response variables (Dormann 2009; see Chapters 7 and 8). Yet space should be used as a predictor variable only as a last resource as it does not provide any insights about the causality relationships.
(5) A confounding variable that produces confusing or spurious results when a system is analysed; it should be used as a covariable (Dray *et al.* 2006).

The degree and the sign of the spatial coefficient values can also be informative about the structure.

(1) Negative spatial autocorrelation can indicate that the sampling unit size or shape is inappropriate to capture the scale of the process adequately.
(2) Weak or absent significant spatial autocorrelation at small distances may indicate that some characteristic may be poorly chosen: the sampling unit size and shape, the spatial lag among the sampling locations, or the spatial distance classes used to estimate spatial autocorrelation are inappropriate to capture the scale of the process.

In the chapters that follow, we are going to address the different components of 'space' and how they affect statistical analyses of ecological data and the interpretation of the results. Clearly there is a broad range of phenomena in ecology that have a spatial component to be understood, as well as a broad range of approaches to their analysis. This current chapter has focused on the various and complex processes in ecological systems that give rise to or affect the expression of spatial structure and spatial pattern. Although we have not emphasized the detailed mechanisms of these processes, the possibilities of factors such as landscape memory, feedback switches, and chaos, and the conceptual frameworks of mosaic cycles or patch–gap alternation, are critical background knowledge for the interpretation of the results of spatial analysis. As always, the interplay of pattern and process is the subject for further investigation and the theme that informs this book. It is an investigation that should prove both intriguing and worthwhile.

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