

Chapter 7

Ecosystems and Spatial Patterns

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Glossary

Disturbance	A spatial process or event that reverts forest vegetation to early successional stages typically altering forest structure and composition.
Ecotone	A region of interface between two communities, ecosystems, or biogeographic regions.
Legacy	A persisting spatial feature or pattern that was generated by a historical disturbance. Legacies can constrain the spatial dynamics of contemporary disturbances.
Multi-scale analysis	A method of spatial analysis that looks at the relative contributions of different scales of spatial pattern to a single observed spatial pattern.
Pattern	A repeatable and identifiable feature in a spatial context.
Scale	An attribute of a spatial process or data used to represent that process that describes its spatial dimensions. Scale includes elements of grain, extent, and thematic resolution.
Spatial autocorrelation	The degree of correlation of a variable and itself as a function of the spatial distances among sample points.

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Stationarity	A feature of a spatial process in which the mean and variance of a process is consistent across the extent of a study area.
Variography	A geostatistical modeling tool for describing spatial variance and semivariance as a function of spatial distance among pairs of points.

Definition of the Subject

Ecological processes such as forest disturbances act on ecosystems at multiple spatial and temporal scales to generate complex spatial patterns. These patterns in turn influence ecosystem dynamics and have important consequences for ecosystem sustainability. Analysis of ecosystem spatial structure is a first step toward understanding these dynamics and the uncertain interactions among processes. There are many spatial statistics available to describe and test spatial pattern within ecosystems and to infer the character of the processes that generated them. Indeed, improving understanding of the processes that create spatial pattern is a central objective of spatial pattern analysis. In addition to standard tests of spatial autocorrelation and patch structure, methods for multi-scale decomposition of spatial data and identification of stationarity are necessary to determine the key spatial scales at which the processes operate and affect ecosystems and to identify meaningful spatial subunits within larger contexts. Finally, tools for identifying ecosystem boundaries are also important to monitor boundary movement and changes in local ecosystem characteristics through time.

Introduction

Spatial Patterns in Ecosystems

The spatial structure of ecological systems is important to examine and understand as spatial structure mediates the flows of individuals, materials, and information through space and time [1]. These flows bear on the probabilities of occurrence and persistence of floral and faunal populations which determine local and regional biological diversity as well as ecosystem functioning [2]. Interruptions and alterations of such flows within and among ecosystems in terms of rate, quantity, or both as a result of human interventions or natural dynamics such as disturbance can have important consequences for ecosystem sustainability and long-term population persistence. Quantitative characterization of spatial patterns and their rates of change in natural environments is essential to understanding ecological

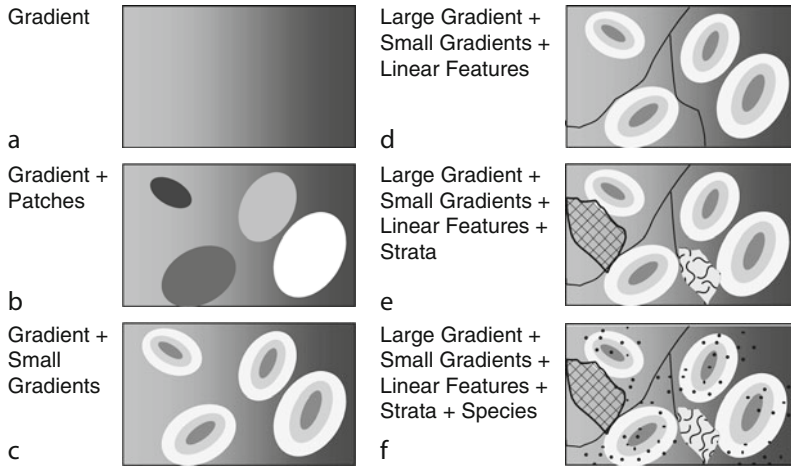


Fig. 7.1 Spatial heterogeneity as a series of additive processes resulting in additive spatial patterns to which individual organisms (here represented points) may respond. Some or all of the different types of spatial heterogeneity may be present in any given landscape

processes and to inform sustainable management techniques that aim to minimize degradation and alteration of ecosystem dynamics [3].

Spatial pattern, or simply spatial structure, refers to a quantifiable attribute of a spatial context. General definitions of the word pattern include a simple definition such as a distinctive or regular “form” or “order,” or a feature that is repeated with some degree of “regularity” [4]. Recently, Wagner and Fortin [5] defined the more general term “spatial heterogeneity” as spatially structured variability in a property of interest. Both exogenous environmental (e.g., edaphic variability, elevation, climate) and endogenous ecological (e.g., species interactions, pollen, and seed dispersal) processes generate spatial structure. Each of these two types of spatial processes can produce spatial pattern in multiple forms and scales (Fig. 7.1). The simplest form of spatial pattern is a simple gradient (Fig. 7.1a). Spatial structure can also be present in the form of patches, linear features, and points and can be superimposed on a gradient (Fig. 7.1b–f). When biological spatial structure is mostly responding to environmental conditions such as those depicted in Fig. 7.1, the resulting spatial structure is said to have spatial dependency to the environmental factors. However, when spatial structure emerges as a result of interactions among ecological processes, the pattern is said to be spatially autocorrelated [5].

Spatial patterns and heterogeneity can also be defined using spatial and topological characteristics. These characteristics can include, but are not limited to, a pattern’s intensity, autocorrelation, degree of clustering, variability, and scale, which itself includes spatial grain and extent [6]. Importantly, a single pattern summarized using different characteristics can result in different interpretations of the processes behind that pattern [7, 8].

Because spatial pattern analysis is often interested in inferring the processes that created them, it is important to recognize that any single observed pattern represents but one realization of the stochastic process(es) that generated it [7, 9]. By acknowledging that an observed pattern is but a single “snapshot,” its temporal dimension is recognized and that under different circumstances, the patterns seen may not be exactly the same. Hence, a main objective of studying spatial pattern is to try to tease apart stochastic processes and the patterns they create from their spatiotemporal conditionalities.

In addition to being driven by processes that are stochastic, patterns emerge as a result of multiple processes that operate at different spatial and temporal scales [10, 11]. These processes can be biotic or abiotic and are usually interconnected through dynamic, and occasionally nonlinear, feedback loops. For example, emergent spatial pattern following forest fires is conditional on the initial distribution of forest fuels as well as fire-weather conditions [12]. Similarly, patterns in forest vegetation composition are often related to patterns in abiotic factors such as moisture, drainage, and soil conditions. Patterns in the genetic composition in animal populations have also been shown to be influenced by the environmental variation (e.g., suitable vs. unsuitable habitat) between sampled populations [13]. These relationships are often nonlinear as the patterns that result from the interactions among pattern-generating processes tend to be different than any one process on its own [14, 15].

Novel spatial patterns created by contemporary anthropogenic processes have uncertain consequences for natural ecosystem dynamics. Anthropogenic processes including deforestation, development, land use change, and climate change do not replace natural processes, but have the capacity to interact with and alter them. As such, a significant question in modern ecology and ecosystem science is that of what are the effects of such novel patterns and processes on natural, or historical, system dynamics [16–18]. Not only do new sources of spatial variability influence natural dynamics through changing the patterns to which natural processes respond, but they also can alter the processes themselves. For example, with regard to forest fire dynamics, this is true where forest composition has been changed due to fire suppression and management (pattern change) and fire frequencies are increased due to increased ignitions near roads or changes in local weather patterns (process change). Similarly, with regard to animal population dynamics, movement and dispersal may be impeded through habitat loss and fragmentation (pattern change) and habitat loss can have an absolute effect on effective population size, rates of dispersal, and genetic variability (process change). Sophisticated spatial statistical analyses are required to begin to disentangle the contributions of different processes to observed spatial patterns to understand how best to manage natural systems to safeguard against further habitat-related losses to biodiversity [19].

Here the causes and consequences of spatial patterns in terrestrial forest ecosystems are reviewed with particular emphasis on patterns of forest vegetation generated through landscape level disturbance processes. Spatial patterns in forest vegetation are both ecologically and economically important in that they are directly relevant to wildlife habitat supply, timber supply, future disturbance dynamics,

and represent future challenges to forest and land managers. Uncertainty regarding future disturbance dynamics, in particular fire and insects outbreaks, in the context of global climate change makes investigations into disturbance interactions and potential long-term consequences for ecosystem spatial structure and functioning particularly relevant.

Forest Ecosystems

In North American forests, disturbance processes generally include landscape level fires, insect outbreaks, forest management (i.e., logging), and fine-scale local disturbances such as windthrow and fungal diseases. The patterns created through the interactions among disturbances can have important economic and ecological consequences. For example, Stadler et al. [20] demonstrated that hemlock woolly adelgid (*Adelges tsugae*) infestations in New England can affect both fast and slow ecosystem dynamics, nutrient cycling dynamics in the short term, and landscape-scale patterns of forest composition in the long term. Similarly, compounded disturbances (e.g., fire and logging) in the eastern boreal forest can result in alternate forest states [21], which can have consequences for biodiversity conservation. Economically, it has been clearly demonstrated that forests under risk of disturbance, either through fire or insect outbreaks, required longer rotation periods to accommodate for the losses [22].

Logging, fire, and insect outbreaks represent disturbance processes that revert forest stands to early seral stages. Succession describes processes of forest recovery, regeneration, and change that vary in response to different disturbances. Although multiple processes generate forest spatial heterogeneity, not all influence it in the same way. Spatial disturbance legacies vary in terms of shape, size, intensity, boundary characteristics, influence on forest succession, and effects on forest age structure [18, 23–25]. The interactions among processes, or more properly, interactions among current disturbance and existing spatial legacies, create and maintain heterogeneous forest landscapes. This cascade of effects and constraints creates mutual dynamic feedbacks among patterns (spatial legacies) and spatial processes (disturbances) [26, 27] with important consequences for ecosystem dynamics.

Different forest disturbances create different forms of spatial structure. Indeed, each disturbance imposes its own unique “spatial signature” on the landscape that also has different temporal characteristics contingent on a disturbance’s interaction with succession (Fig. 7.2). Fires, for example, tend to produce relatively discrete patches that occur over a short time frame and vary in terms of the residual forest structure that is left behind [28]. Logging is somewhat similar to fires in that the patches created are discrete and occur over short time frames and forest managers have control over the scale and amount of residual structure. Insect disturbances, such as outbreaks of spruce budworm (*Choristoneura fumiferana*), forest tent caterpillar (*Malacosoma disstria*), and the mountain pine beetle (*Dendroctonus*

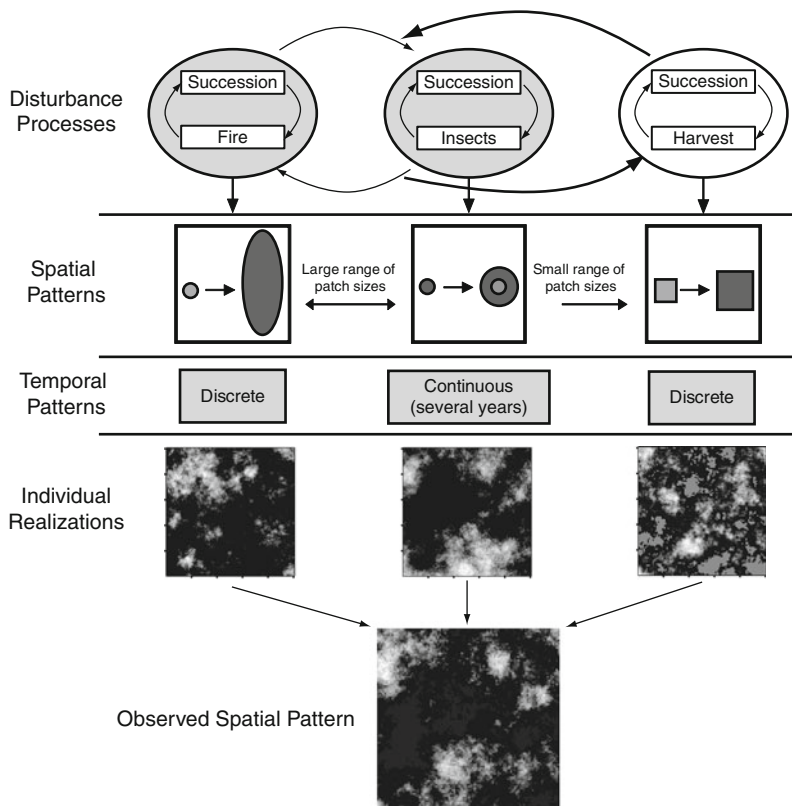


Fig. 7.2 Spatial and temporal scales of forest disturbances. Interactions among disturbances are dependent on the unique successional responses to each disturbance (*row 1*). Historical forest systems were governed by interactions mainly between fire and insects (*arrows*) although presently, logging also interacts with these historical processes. Columns show the unique spatial and temporal attributes of each of the three main boreal forest disturbance agents: fire, insects (i.e., SBW), and harvesting (i.e., logging). These different spatial features result in different realization, or spatial signatures, of each disturbance (*row 4*). Interactions among these different processes produce a single observed spatial realization of spatial structure that contains elements of each of the different processes (*row 5*). Observed patterns contain elements of all three main processes; the objective of spatial analyses is to begin to tease apart the relative contributions of different processes to observed spatial pattern (*row 6*)

ponderosae), are less discrete and tend to produce more complicated spatial structure and continue to affect forest structure at a given location for multiple consecutive years [29].

Each disturbance also has a unique relationship with forest regeneration processes [30] such that forest succession is tightly coupled to the type of disturbance that reinitiates stand development. These relationships determine future forest structure. Historically, fire and insects were the main disturbances in North American forest systems. Adaptations to disturbance such as serotiny in pine species

(e.g., jack pine; *Pinus banksiana*) and advanced regeneration in the understory of spruce (e.g., *Picea spp.*) and balsam fir (*Abies balsamea*) stands that maintain spruce budworm host availability over time [31] are evidence of this dynamic feedback between disturbance and succession. The spatial patterns created through forest management and their influences on forest succession in turn influence future forest disturbances dynamics [32]. Spatial pattern analysis is important to better understand the effects of human activities on natural disturbance dynamics.

Sources of Heterogeneity

Understanding the nature and consequences of spatial heterogeneity in ecosystems requires an understanding of the processes that generate this heterogeneity. In this section, different types of spatial heterogeneity and how different types of processes may give rise to complex spatial patterns are described. The consequences and potential challenges involved in indentifying the relative contributions of these different and frequently interacting processes are discussed next [6].

Levels of Organization

Processes that generate spatial heterogeneity can be classified into a hierarchy of spatial processes that operate at different levels of ecological organization: (1) individual, (2) population, (3) community, and (4) landscape/ecosystem. Individual processes include organism dispersal and habitat selection; population processes can include demographic dynamics as well as immigration/emigration; community level processes are highly relevant to natural disturbance dynamics and can include successional changes and rates of species turnover. Examples of landscape/ecosystem level processes include disturbance, climate change, and migration.

Processes within this organizational hierarchy are not necessarily independent and can influence each other among levels. Such interactions can influence emergent patterns due to potential cross-scale interactions and amplifications [33] and can also further complicate efforts to identify clear cause-and-effect relationships. A recent example of such cross-scale amplification in a forest ecosystem can be found within the mountain pine beetle (*Dendroctonus ponderosae*) system of Western Canada, where the recent outbreaks of the lodgepole pine infesting beetle have affected an unprecedented millions of hectares [34]. Here, the local dynamics of population control by host tree defenses were overcome when population numbers increased dramatically due to persistent warmer temperatures in the early 2000s. The interactions between these local- and landscape-level processes are thought to have led to a positive feedback that allowed the outbreak to expand as much as it did [34].

Interactions Among Spatial Processes

Spatial processes within ecosystems interact with each other directly as well as with the spatial legacies of previous, historical processes. In this way, spatial patterns and processes are connected through a dynamic and persistent feedback loop [32]. Spatial legacies can be thought of as a form of spatiotemporal connectivity among disjunct spatial processes or events that are mediated by forest succession and aging. The legacies of historical processes as represented by contemporary patterns can have long-lasting and significant impacts on biodiversity [16, 35] and efforts to sustainably manage forest ecosystems [23, 36].

Spatial legacies can be defined at different scales and describe persisting features within a stand, landscape, or ecosystem. The term “legacy” can refer to fine-scale structural complexity following windthrow [37], landscape level forest age structure [18, 38], disturbance-mediated seed availability [39], and residual forest structure following fire [39, 40]. Because patterns of historical land use can influence contemporary ecosystem composition, configuration, and ecosystem process dynamics long after the actual event [41], a better understanding of spatial legacies and their influence on ecosystem dynamics and landscape change over time is needed and requires novel spatial and temporal methods of investigation and analysis.

From the perspective of sustainability, spatial disturbance legacies, including those created through human activities, represent future ecosystem patterns and future challenges for sustainable management. Gustafson et al. [42] showed that new forest harvest goals are not easy to achieve due to existing conditions when examining shifting forest management rules. Wallin et al. [38] demonstrated that shifts from a dispersed to an aggregated harvest pattern did not immediately result in a change in forest attributes such as patch size and edge density. Instead, new harvest rules had to work around the legacies of previous patterns, and original patterns were enforced. Similarly, Gustafson and Rasmussen [43] found that when varying parameters in a harvest simulation model, the persistent legacies of previous harvest patterns resulted in timber harvest shortfalls. Using a simulation approach, James et al. [18] demonstrated that legacies in forest age structure created through forest management can persist for over 100 years. Ecologically, the consequences of these legacies interacting with new disturbances can result in greater system variability and gradual ecosystem degradation [43–45] or alternative stable states [21, 46].

Multiple Spatial Scales

Inferring the characteristics of spatial processes through analysis of spatial pattern is a central goal of most ecological studies as it is often very difficult to analyze the processes of interest directly. This can be particularly challenging when several types of pattern (Fig. 7.1) and underlying processes are present (Fig. 7.2). The

challenge resides in the fact that the single observed pattern is an amalgamation of these multiple processes interacting with existing spatial structure and historical legacies; the functional relationships that connect these contributors to pattern are largely uncertain (Fig. 7.2). When analyzing the spatial structure of sampled data, it is not easy to disentangle the key spatial scales, and therefore processes, that act on the data. However, in the last decade, hierarchical decomposition methods (multi-scale ordination [47]; PCNM [48]; wavelets, [49] more detailed below) have been developed to identify the spatial scales at which data are most strongly structured and to decompose the data on the basis of scale-specific variances. Beyond simply describing patterns and the scales at which they are structured, it is also important to have a priori hypotheses about which scales and processes are the most relevant for the questions under study as these methods could reveal many patterns and spatial scales, many of which may not be of relevance [8]. Spatial pattern analysis will be more effective at describing underlying processes when used in an explicit and informed hypothesis testing framework.

Ecological Consequences of Spatial Heterogeneity

The consequences of changes in spatial pattern in forest landscapes are easily confounded by absolute losses in wildlife habitat [19]. That is, although both forest composition and configuration are important, issues related to configuration are only relevant below a critical threshold of forest amount (usually 20–30% of area; [50]). Above the critical threshold, the landscape generally remains “connected” and organisms or disturbances can spread in the landscape [51]. Below such a critical threshold, species’ response to the amount of habitat area is nonlinear as most species do not have enough habitat to meet their needs. Surrounding habitat quality (composition) and configuration become more important for local population persistence in this case. Moreover, fragmented landscapes with various landcover types can impede species abilities to move from habitat patches to another [52]. For example, nesting birds do not cross forest gaps larger than 25 m [53]. Impediments to movement across landscapes can influence population dynamics [54] as well as genetic heterogeneity [55], both of which affect the probability of population persistence.

Spatial Analyses

There are three main approaches to investigating the different aspects and consequences of spatial heterogeneity. Spatial statistics, landscape metrics, and statistical modeling, all approach the question of identifying spatial pattern in ecosystems in a slightly different way [5]. Owing to the varied history of approaches to studying spatial patterns including methods and concepts drawn

from a diverse set of disciplines such as geography, geostatistics, and ecology, only the key concepts related to the most commonly used methods that quantify spatial structure within and among ecosystems are presented. Before describing the different types of analysis, some fundamental issues related to the spatial analysis of data are presented.

Assumption of Stationarity

To infer spatial pattern from samples spatial statistics require that the area under study is governed by the same underlying process (i.e., the assumption of stationarity; [7]). As it is often impossible to be sure that the underlying process is stationary, one needs either to assume it or to determine whether or not the observed data are stationary (i.e., their statistical properties such as mean, variance, isotropy do not vary with spatial distance). Nonstationary processes may arise when more than one process is present and that these multiple processes may be acting at different spatial or temporal scales. Yet, in most forest ecosystems, processes interact with one another, resulting in unique types and scales of spatial pattern which violate the assumption of stationarity. In such circumstances, it is required to first identify stationary subregions within such a larger spatial context. A few spatial analysis methods do not require the stationarity such as lacunarity analysis, local quadrat variance methods, and wavelets [7]. It is worth noting that these types of analyses although different and originating from different developmental histories are quite similar to one another mathematically [56].

Data Type

Spatial pattern within ecosystems can be represented using categorical or continuous data depending on the nature of the variable under investigation. Each type of data requires different methods of analysis (Fig. 7.3; [7]). Categorical data can be described by the amount and configuration of the different discrete types on the landscape. Examples of categorical spatial data include forest type and age, or classified habitat patches. Both amount and configuration can be described in numerous ways using landscape pattern metrics [9, 57, 58]. Continuous data requires more subtlety in describing patterns and can include variables such as soil moisture, forest basal area, or remotely sensed reflectance indices (e.g., NDVI). Composition of continuous variables can be described using the density distribution of the variable and configuration is usually described by a spatial covariance function that captures the strength, directionality, and scale of autocorrelation of the variable [5, 7, 59].

In addition to the categorical/quantitative dichotomy of data types, patterns can be described using different geometric topologies of spatial features or units: the

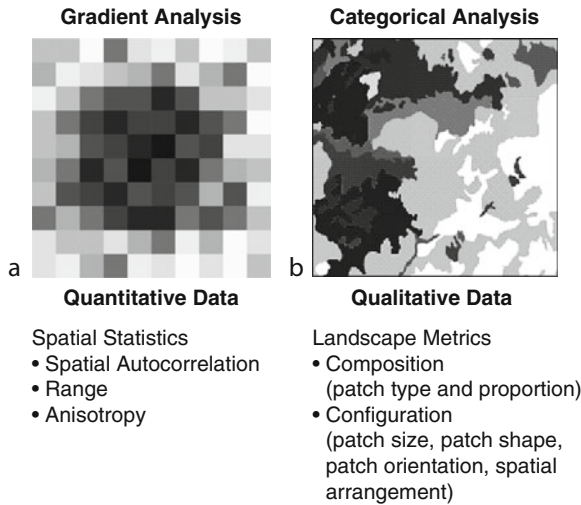


Fig. 7.3 Spatial analysis can be undertaken on different types of spatial data. (a) Raster-based quantitative spatial data (e.g., forest height, basal area, NDVI) that can be analyzed using spatial statistics to determine the intensity, spatial range, and directionality (anisotropy) of the spatial pattern. (b) Categorical and qualitative forest data (e.g., species, stand age) require a different analytical approach that typically includes landscape pattern metrics

vector format (points, lines, polygons) and the raster (i.e., pixel) format [60]. Representation of spatial structure in one form of data does not preclude use of another form. For example, annual polygons of insect defoliation data can be converted into raster form and analyses can be undertaken using time series of raster values at a specific location [61]. Furthermore, binary rasters (presence/absence) can be converted to continuous rasters by increasing the cell size and counting the number of “presence” pixels surrounding a focal pixel using 4-neighbour, 8-neighbour, 16-neighbour rules and assigning this value to the to the new, larger pixel.

Raster data can be used to represent any continuous variable. In contrast to point data, in raster data types, the information fully covers the extent of the study area. There is also a unique grain (or cell size) to each raster “pixel” that determines the subarea of continuous space that is discretized by the raster cell. The selection of raster grain can have important consequences to the results of spatial analyses [6]. Raster data can be used to represent any number of spatial variables relevant to disturbance ecology including, but not limited to, tree species [62], stand age [18, 63], basal area [64], insect damage [61], and number of fire occurrences [65]. The continuous coverage of raster data makes it amenable to many different analytical techniques such local quadrat variance, lacunarity, and wavelets [56].

Spatial Analyses within an Ecosystem

Ecological variables that are geographically distributed in space and time tend to be more similar when compared close together [66]. Autocorrelation is a feature of most data and can be quantified by the degree of self-similarity or dissimilarity in a variable between pairs of locations at a given distance apart (i.e., spatial lag determined in terms of equidistant classes). Note that spatial statistics on their own cannot differentiate between spatial dependence to environmental factors and spatial autocorrelation due to ecological processes; only prior knowledge and multiple testing can differentiate between these two sources of spatial structure.

Spatial Description of the Pattern

The objective of many spatial statistics is often to characterize to what degree spatial data are autocorrelated, if they are oriented in a particular direction (anisotropy), and at what scale. As these spatial statistics have been thoroughly reviewed elsewhere [7, 58], we focus on three topics (1) methods of spatial pattern analysis devoted to identifying structure in point data, (2) methods of spatial analysis that are devoted to identifying structure and pattern in two-dimensional raster (pixel) or polygon data, and (3) methods of spatial analysis explicitly concerned with identifying the scale, or scales of structure that are present in either point or two-dimensional data. Both the data types discussed can be examined in uni-, bi-, and multivariate contexts and can include either categorically or continuously measured variables.

Point Pattern Analysis

Spatial point processes describe phenomena that produce events represented as points in space [67, 68]. The objective of point pattern analysis is to determine whether the distribution of events (points in space) is more or less spatially aggregated than is expected by chance and tests the null hypothesis of complete spatial randomness. The use of complete spatial randomness assumes that the underlying process is the same over the study area (i.e., stationarity). When it is not the case, the study area is said to “inhomogeneous” such that significance cannot be achieved using a single process such as complete spatial randomness. Modified statistics and corrections have been developed to account for inhomogeneity within the study area [69, 70]. Point pattern analysis also assumes complete census of all point occurrences in the study area [7]. Fortin et al. [71] showed that the significance of spatial aggregation estimations is biased only when a subset of sample points is used rather than the entire set of points in the study area.

The most commonly used method of point pattern analysis is Ripley's K statistic [72]. New statistics have also been developed to compute local estimates [68]. Ripley's K statistic, and derived statistics, can be applied in one-, two-, or three-dimensional space to compare the degree of aggregation of points [68]. In cases where two (or more) point processes are operating, it may be of interest to assess whether one process influences the other and whether points of different types tend to cluster together. Examples of ecologically relevant spatial point processes include fire occurrence, plant occurrences [67], or the distribution of animal nesting or denning sites [72]. The bivariate, or cross- K , Ripley's K test assesses whether the co-occurrence of two types of points is clustered together more or less than is expected by chance [58]. Using this technique, Lynch and Moorcroft [73] examined co-occurrence of fire and insect outbreaks and found that contrary to expectation, insect-caused forest mortality does not increase the risk of forest fire.

Spatial Autocorrelation

Often, a researcher is interested in determining the scale and strength of spatial autocorrelation of a variable as well as whether there is a directional trend in the data (i.e., anisotropy). This can be achieved using spatial autocorrelation coefficients such as Moran's I which computes the product of the deviations of the values of the variable to its average according to various distance intervals (lags, classes) standardized by the variance at that spatial lag [7]. Moran's I behaves like a Pearson's correlation coefficient such that the null hypothesis is the absence of spatial autocorrelation, positive autocorrelation (mostly a short distance) indicates that values have comparable values, while negative values indicate that the values are very dissimilar. Moran's I assumes that the underlying process is the same over the entire study area (i.e., stationarity). Hence, the spatial autocorrelation coefficients computed at various distance classes are average values. Spatial autocorrelation in this sense can be referred to as a global spatial statistic that describes an attribute of the data over the entire study area [7]. Significance of each coefficient can be computed based on an asymptotic t or randomization procedure. In either case, stationarity is required. Moran's I is very sensitive to skewed data as the mean will be biased and in consequence all the deviations values based on it will also be biased. It is therefore recommended to check the distribution of the data before computing spatial autocorrelation and if needed transform the data to obtain a symmetric distribution.

Measures of spatial autocorrelation are also sensitive to sample size. When autocorrelation is estimated using too few locations, (e.g., <30 positions), spatial patterns may not be detected, even though present. Similarly, depending on the spacing among sampling locations, there will be different numbers of paired comparisons at each lag distance. Typically, there are few pairs at short distances due to the edge effects of the edge of the study area (no locations outside to

compare too), most of the pairs at intermediate distances and very fewer at large distances (because of the overall size of the study area). To mitigate these unequal numbers of pair per distance lag, it is recommended to focus on lags distances equal to the length of the first half (up to two thirds) of the smallest edge of the study area as most spatial autocorrelation occurs at short distances and that the probability of detecting it is also highest in the first spatial lag [7].

A plot of spatial autocorrelation coefficients against distance lags is called a spatial correlogram. If the lags are based on distance only, the correlogram is said to be an omnidirectional correlogram. When the data contain directionality, the omnidirectional correlogram cannot reveal it and may, in fact, “mask” it. To detect the presence of anisotropic spatial pattern (i.e., not having the same sill and range according to direction), the samples need to be divided by distance class as well as direction angle range (usually 0° , 45° , 90° , 135°) to produce a set of directional correlograms.

In areas where several processes influence ecological data, Moran’s I that assumes stationarity cannot be used. Instead, local indicator of spatial aggregation statistics, LISA (e.g., local Moran, local Getis), can be used as they are computed at each sampling location and allow the identification of subareas that have similar high (“hot spots”) or low (“cold spots”) values [7].

Geostatistics

Spatial structure can be determined in terms of spatial autocorrelation as presented above or as spatial variance according to distance as computed using variograms which are part of the family of spatial statistical methods known as geostatistics [7, 58]. Variograms represent a global method of scale-specific analysis that has been used extensively in ecology to analyze spatial patterns [58]. Variograms model the relationship between lag distance and semivariance and can be calculated using continuous raster or point data. Semivariance is calculated as the sum of the squared differences between pairs of locations separated by a given lag distance divided by twice the number of pairs of locations at that particular lag distance [7]. From the observed, or empirical, variogram, three parameters can be estimated to fit a theoretical variogram: (1) range, or scale at which distance does not affect the estimate of variance, (2) sill, or the variance of the data, and (3) nugget effect, which represents the variability in the data that is not accounted for by spatial structure [58]. Theoretical variogram models can identify whether there is a directional trend in the data, that is, anisotropy as the spatial autocorrelation values. In addition to describing the attributes of spatial structure, geostatistical models can be used to “krige” (i.e., spatially interpolate) data [58] and to simulate spatial patterns using a chosen variogram model, process model, and parameter estimates [74].

Spatial Scale and Scaling

In addition to understanding the type (e.g., trend, patch) and strength (e.g., degree and distance) of a spatial pattern, it is useful to identify the spatial scale at which such patterns are present. Because patterns are the result of multiple processes that each have their own unique scales of spatial structure [75], disentangling the relative contributions of these processes and assigning relative importance to them and the scales at which they operate are of fundamental importance to ecology and improving the understanding of complex systems [11, 16]. Furthermore, the identification of the relative contributions of different processes and scales to observed patterns is necessary for understanding cross-scale interactions [33] which is necessary to make reliable predictions of system dynamics, ostensibly the objective of any spatial analysis [76].

As stated above, spatial pattern describes a “quantifiable attribute of a spatial context.” Scale-specific analysis identifies the spatial scale at which that attribute is structured establishes its specific context. With regard to forest disturbance dynamics, for example, individual forest stands may seem unstable through the processes of destruction and renewal through disturbances such as fire, but the larger forest landscape (i.e., collection of stands) is in fact stable with respect to the proportion and relative configuration of the different stand types. This is what is meant when disturbance-mediated forest systems are described as a shifting mosaic [77]. Different conclusions would be drawn about forest stability and resilience (sensu [78]) depending on the spatial or temporal scale of investigation.

Scale generally describes the spatial extent, grain, and thematic resolution of a set of data [6]. However, scale can also be used to refer to a level within an organizational hierarchy to which such data pertain, such as a population, or community, or ecosystem [79]. It is important to note that scale in this latter sense is not directly equivalent to the former; scaling up, that is, increasing from local to a broader extent, or aggregating data from a fine to a coarse scale may move the analysis into another level or an organizational hierarchy, but not necessarily [80]. Although scale is best thought of as a feature of the phenomena of interest, it can also be a feature of sampling scheme imposed by a researcher, or the methods of analysis applied [6]. All of these features can influence a researcher’s ability to identify scales of structure in spatial data and to make meaningful inferences regarding the underlying processes. It is therefore important to distinguish structure that is emergent from the data from those related to sampling or analytic scales (i.e., arbitrary scales; [10]), as such a priori scales may have little to do with the actual scale of structure in the ecological phenomena of interest [76].

The ability to identify meaningful scales of spatial structure depends on the methods used and the type of data being analyzed [77, 81]. Methods differ in their ability to identify local vs. global scales of pattern. Global methods of scale-specific analysis summarize spatial pattern at a single scale and generally assume that the underlying processes are stationary. Examples of global methods of analysis include variography [58], spectral (i.e., Fourier) analysis [82], and global measures

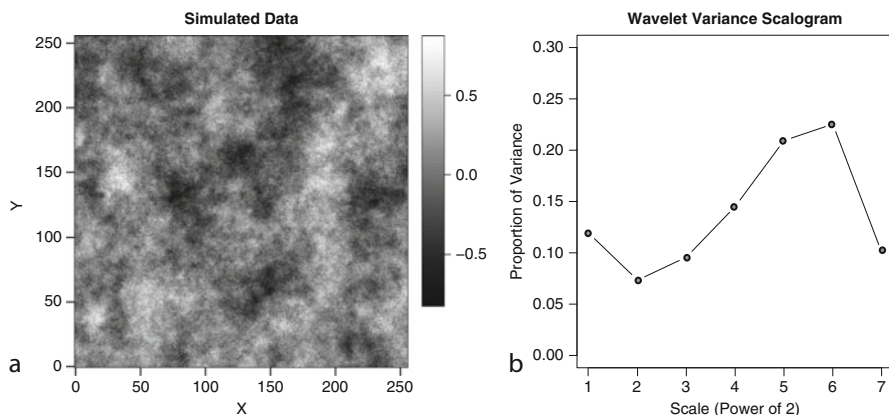


Fig. 7.4 Example of a hierarchical multi-scale decomposition of two-dimensional, quantitative data using wavelets. (a) Simulated spatial data. (Data were simulated using an exponential variogram model with the following parameters: Sill = 1; Range = 40; Nugget = 0.1). (b) Scalogram that summarizes the proportion of total variance in the original data associated with each scale of the decomposition. Wavelet decomposition was accomplished using a maximal-overlap discrete wavelet transform (MODWT; Percival and Walden [109])

of spatial autocorrelation such as Moran's I and Geary's c [7]. Multi-scale methods of analysis identify both global and local scales of structure, can assign relative importance to different scales, and do not assume stationarity. Instead, such methods can be used to identify boundaries and scale-specific stationary subregions within a larger spatial context [7, 74]. Multi-scale methods of analysis include lacunarity analysis [83], wavelets [74, 81, 84], distance-based Eigenvector methods (e.g., PCNM; [85]), and local spatial statistics [86].

Wavelet analysis is a particularly powerful method of local spatial analysis that can be used to decompose continuous data into its scale-specific components [87, 88]. A proportion of the total variance in the data set is associated with each level of the decomposition through use of the wavelet variance [84] and the relative contributions of different scales to overall structure can be assessed and visualized as a scalogram (Fig. 7.4b). Each of these scales of pattern can then be isolated using a multi-resolution decomposition (Fig. 7.5; [88]). Under conditions where observed spatial pattern is assumed to be the result of multiple interacting processes, such data decomposition provides an opportunity to assess the relationship among processes and individual scales of spatial structure present in the data. In combination with the scalogram (Fig. 7.4b), the relative importance of these different scales can also be determined and further analyses can be restricted to only those spatial layers that correspond to the scales of interest. Isolated scales of spatial pattern can then be examined independently or used as scale-specific predictors in further statistical analyses [89].

Whereas Fourier analysis assumes that observed patterns can be described as a sum of sine waves of different frequencies, wavelet analysis identifies global and local structure at different scales using a local wavelet template that can take on

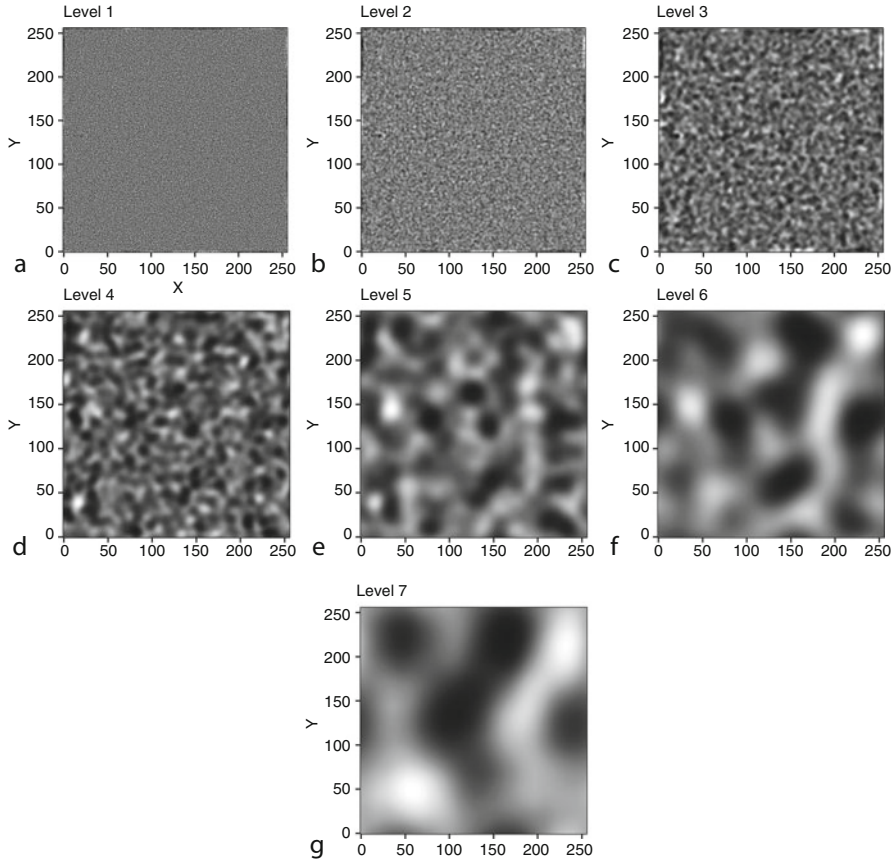


Fig. 7.5 Back-transformed images from the decomposition of the data in Fig. 7.4a. Each panel shows the spatial structure at an individual isolated scale

a wide variety of shapes and forms [90]. The majority of wavelet applications have been in the analysis of temporal signals to identify periodicity in things such as climatic variability [91] and epidemiological time series [92, 93]. However, spatial applications of wavelet analysis in ecology continue to be developed and have been used to investigate one-dimensional forest canopy gap structure [87], vegetation reflectance [89], two-dimensional structure in grassland productivity [81], tree crown identification [94], and the significance of spatial structure in forest basal area [74].

When data are not sampled in a continuous way (i.e., they are irregularly spaced), multi-scale decompositions can be performed using spatial eigenfunction analyses such as principal coordinate analysis of neighbor matrices (PCNM) and Moran's eigenvector maps (MEM) [48, 95, 96]. These methods model spatial structure in a multivariate framework using distance matrices where the spatial coordinates of the sampled sites are converted into a set of synthetic spatial variables that represent

spatial structure at different spatial scales. These synthetic variables can then be used in combination with constrained ordination methods (e.g., canonical correspondence analysis and redundancy analysis; [95]) to identify the spatial scales at which data are dominantly structured. Jombert et al. [97] also proposed a multi-scale pattern analysis (MSPA) to determine which of these many scales are the most relevant to use as spatial predictors in subsequent analyses such as partial ordination or multiple regression [85].

Spatial Analyses Among Ecosystems

The ecotonal interfaces between ecosystems are important to delineate as they are the locations where the exchange of nutrients and species turnover occurs [7]. It is also important to determine not only the boundary location between ecosystems, that is, where one system begins and another ends, but also its width (i.e., sharp/line or gradual/zone) [98]. There are two different types of methods that can be used to determine the interface between ecosystems: by creating spatial clusters or by detecting boundaries [99]. In either case, the sampling design used to collect the data is crucial: The determination of a boundary (i.e., area of high rate of changes in the values of variables, hence a heterogeneous area) is relative to the two adjacent spatially homogeneous ecosystems. Therefore, the sampled data should cover enough of both ecosystems such that their interface can be detected.

Spatial Clustering

To delimit boundaries between ecosystems, spatially homogeneous clusters can be determined based on the degree of similarity of sample attributes and their spatial adjacencies [66, 99, 100]. The degree of similarity can be based on commonly used clustering algorithms (agglomerative, k -means, fuzzy logic, etc.) and adjacency can be based on network connectivity algorithms (e.g., nearest neighbors, minimum spanning tree, Gabriel network, Delaunay network; [7]). Spatial clustering provides the membership of each location to a spatial cluster and therefore, as a by-product, identifies boundaries among clusters. However, clustering procedures do not provide any information about the location and width of the identified boundaries between clusters. When information about location and width are needed, other methods should be used such as boundary detection methods ([99]; but see [101]).

Spatial Boundary Analyses

Ecological boundaries can be defined as areas of high rates of change or large absolute differences between adjacent locations [102]. Boundary detection methods [98] include edge detection algorithms (Laplacian, Canny, Sobel, Monomier, etc.),

wavelet analysis [74, 81], and wombling (lattice, triangulation, categorical). The two former families of methods require the data to be in a contiguous fashion (grid) without any missing values while the latter one can either be used with contiguous or irregularly sampled data. All methods compute the magnitude of rate of change between adjacent locations over the entire extent of the study area. To determine which rates of changes are significantly higher than the others, different statistics and significance tests having been developed. Wombling typically uses arbitrary percentile thresholds of boundary elements to identify significant boundaries [7]. James et al. [74] proposed a series of restricted randomization procedures to test the significance of wavelet boundaries using variogram-based spatial null models. Oden et al. [103] developed boundary statistics to test the cohesiveness properties of the boundaries. Once cohesive boundaries have been detected and tested, subsequent hypothesis testing can be performed by comparing the spatial overlap and movement of boundaries using spatial overlap statistics [7, 104, 105] or polygon change analysis [106].

Future Directions

The detection and characterization of spatial structure is necessary for developing the understanding of ecosystem function and for ensuring sustainable management and use of landscape resources. Indeed, the current scale and pace of anthropogenic influence on the natural environment is without precedent and the ways in which novel human-created spatial patterns interact with and influence natural processes are uncertain. Even more uncertain are the relationships among different scales of spatial and temporal pattern and what such cross-scale interactions may mean to ecosystem dynamics [107]. Future directions in the analysis of spatial pattern will require approaches and methods that can begin to tease apart the separate scales, both spatial and temporal, of processes that contribute to spatial patterns both within and among ecosystems. These methods should include multi-scale approaches such as the wavelet-based methods described above, tools to assess statistically significant changes over time, and methods that can identify local spatially significant subregions within larger spatial contexts [74]. Meaningful inference in these regards will only be possible if the spatial pattern analysis is applied within a hypothesis testing framework, where competing notions of how individual processes percolate through the landscape to produce pattern can be tested statistically [8]. Finally, increasing availability of remotely sensed data (e.g., NDVI, LiDAR, Quickbird, LANDSAT, MODIS) will allow people to detect spatial patterns at finer spatial and temporal scales over much larger spatial extents than has been previously possible. These huge amounts of data will also require focused, hypothesis-driven questions, the use of data-mining tools [108], and the further development of spatiotemporal statistics.

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