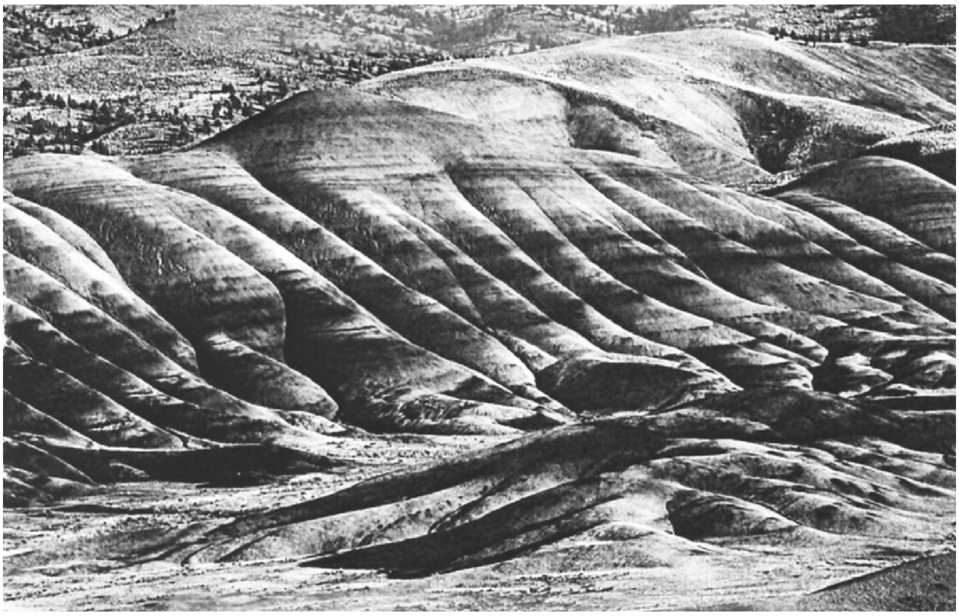
Identifying and Quantifying Landscape Patterns in Space and Time

Janine Bolliger[1*], Helene H. Wagner[1] and Monica G. Turner[2]

[1] Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland
[2] Department of Zoology, University of Wisconsin-Madison, Madison, Wisconsin 53706, U.S.A
[*] Corresponding author: e-mail: janine.bolliger@wsl.ch

Abstract
In landscape ecology, approaches to identify and quantify landscape patterns are well developed for discrete landscape representations. Discretisation is often seen as a form of generalisation and simplification. Landscape patterns however are shaped by complex dynamic processes acting at various spatial and temporal scales. Thus, standard landscape metrics that quantify static, discrete overall landscape pattern or individual patch properties may not suffice when viewing landscapes as gradients or when quantifying spatially dynamic response surfaces resulting from model simulations of landscapes. The spatio-temporal dynamics of patterns can be quantified using various approaches originating in different fields and ranging from geography, geology, engineering, physics, plant community ecology and complex systems theory. This book chapter provides an overview on quantitative measures that may be used as indicators to assess landscape patterns in space and time for discrete and continuous landscape representations and discusses promising avenues for addressing the most pressing needs for spatial analysis of gradient-dominated and dynamic landscapes.

Keywords: landscape analysis, landscape metrics, landscape pattern, spatial pattern, temporal pattern



F. Kienast, O. Wildi & S. Ghosh (eds.), A Changing World. Challenges for Landscape Research, 177–194.

Landscape Patterns

A landscape may be defined as an area that is spatially heterogeneous in at least one factor of interest (Turner *et al.* 2001). This minimum definition stresses heterogeneity as a key concept. In fact, most ecological systems are heterogeneous: environmental factors vary in space and time, and most species are unevenly distributed. Landscape ecology focuses on quantifying heterogeneity and investigating its causes and ecological consequences across ranges of scales (Turner 2005). When dealing with heterogeneity however it is important to discriminate between different types of heterogeneity, to recognise its sources and to consider scale (Levin 1978, 1992; Wiens 2000).

Types of landscape patterns

An ecological system or system property of interest may be heterogeneous in space and in time. In landscape ecology, spatial heterogeneity is usually referred to as landscape pattern or landscape structure, whereas landscape dynamics generally refers to changes in landscape patterns through time. To date, landscape structure has received more attention from landscape ecologists than landscape dynamics (Gustafson 1998).

Both landscape structure and landscape dynamics can be studied using discrete or continuous models of heterogeneity. Many approaches assume that the landscape consists of discrete, non-overlapping objects or patches that belong to mutually exclusive classes or system states. Patches are either embedded in an assumedly homogeneous matrix or form a mosaic (Forman and Godron 1986; Forman 1995). Such discrete landscape representations are widespread and are helpful to simplify and quantify complex landscapes. Discrete landscape representations have been extremely successful in a wide range of landscape ecological topics such as habitat fragmentation (Hargis *et al.* 1998), landscape descriptions (Haines-Young and Chopping 1996), monitoring of landscape change (Lausch and Herzog 2002) or conservation (Thompson and McGarigal 2002). It has been argued however that many natural phenomena may be primarily continuous in character and exist as gradients rather than as features with discrete boundaries (Regan *et al.* 2000; Bolliger and Mladenoff 2005; McGarigal and Cushman 2005). Contrary to discrete boundaries, gradients describe gradual transitions of feature properties. Gradient-based concepts of representing landscape patterns may be more appropriate for many landscape properties than the spatially discrete patch-mosaic concept (Bolliger and Mladenoff 2005; McGarigal and Cushman 2005) as classification of spatially continuous features into discrete units may result in information loss. However, whether a phenomenon appears as relatively discrete or continuous will often depend on the scale of the study, especially the spatial resolution or grain, the measurement resolution and the hierarchical scale (Gosz 1993; McGarigal and Cushman 2005).

Conceptual discussions about whether natural features are of discrete or continuous nature are not new, and date back to Gleason's and Clement's discourses during the first half of the 20th century (Keller and Golley 2000). Methodologically, the continuity of natural features can be assessed using fuzzy logic. The method was originally introduced by Zadeh (1965) and developed further (Bezdek 1981; McBratney and Odeh 1997; Minasny and McBratney 2002). In this approach each unit (e.g., grid cells) may be assigned one or more types and its degree of belonging to each type is expressed as a membership function. Partial memberships are quantified for each type, indicating that some types are compositionally distinct whereas others may share common characteristics. Thus, the membership information may serve as baseline information to assess structural uncertainties, i.e., the degree of certainty with which landscape patterns can be discretised (Brown 1998; Bolliger and Mladenoff 2005).

Pattern-generating processes

Landscape patterns result from various interacting processes (Levin 1978; Forman and Godron 1986; Turner *et al.* 2001; Turner 2005). When modelling landscape dynamics, it is essential to distinguish between biotic and abiotic processes. While both types of processes affect the behaviour of a system, abiotic processes are assumed to depend only on external drivers, whereas biotic processes may themselves be affected by the system (Lischke *et al.* 2007). In empirical studies however the distinction between biotic and abiotic processes is often implicit.

Abiotic processes typically affect landscape patterns via interactions with externally imposed, oftentimes environmental factors, such as climate, soil, topography, or disturbance (fire, wind). For example, climatic parameters play a significant role for spatial distributions of trees. Studies assessing scenarios of elevated temperatures along an altitudinal gradient in the Swiss Alps show that major reorganisation in forests including species shifts are expected along an altitudinal gradient (Kienast *et al.* 1998; Bolliger *et al.* 2000; Bolliger 2002).

Biotic processes include e.g., dispersal or competition between or within species, but also disturbance (insect outbreak). Dispersal and population spread have been of continuing interest (Levin 1979; Webb 1987; Clark 1998; Clark *et al.* 1999), and dispersal in particular has proven to be important in structuring e.g., forest community composition (Jacquemin *et al.* 2001), or governing migration rates (Clark 1998). Biotic processes shape landscape patterns through internal interactions between the individual system components, e.g., organisms that may cause organisation by accumulation of small changes (Bak *et al.* 1987; Bak 1996), generating patchiness even in the absence of environmental heterogeneity.

Processes of both biotic and abiotic nature include disturbance and human impact. Disturbance may be considered abiotic in cases of e.g., fire or wind or biotic if disturbance is caused by e.g., pathogens. Whether human impact is viewed as biotic or abiotic depends on perspective and judgement. If effects of humans on the landscape are perceived as part of an ecosystem, they may be referred to as biotic. If human impacts are perceived as external drivers shaping the ecosystem, they may be referred to as abiotic. Human impact is most important in shaping landscapes and it includes various socio-economic policy- and management driven processes (Bürgi *et al.* 2007).

In most natural systems both biotic and abiotic processes are relevant for shaping landscape patterns. However, system interactions in environmentally extreme habitats e.g., desert, arctic, high/low pH values in soils) are likely to be primarily driven abiotically. Environments with little temporal heterogeneity (e.g., rain forests) are more likely to be dominated by biotic processes (Solé and Manrubia 1995; Solé *et al.* 2002).

As landscapes are the result of interacting biotic and abiotic processes, they pose great challenges for the quantitative assessment of primary processes shaping the patterns. Since the same process may produce many different patterns, two landscape patterns will rarely be identical, making statistical comparison between different landscapes or between different time steps difficult (Fortin *et al.* 2003), and methodological problems arise from the combined effects of several biotic and abiotic processes (Wagner and Fortin 2005).

Process interactions and scale

Processes may interact linearly (unidirectionally), or in nonlinear ways, including mutual, self-reinforcing (positive feedback), and self-inhibiting interactions (negative feedback). Nonlinear interactions may be a primary source of patterns in many systems (Bascompte and Solé 1995; Farkas *et al.* 2002; Green and Sadedin 2005).

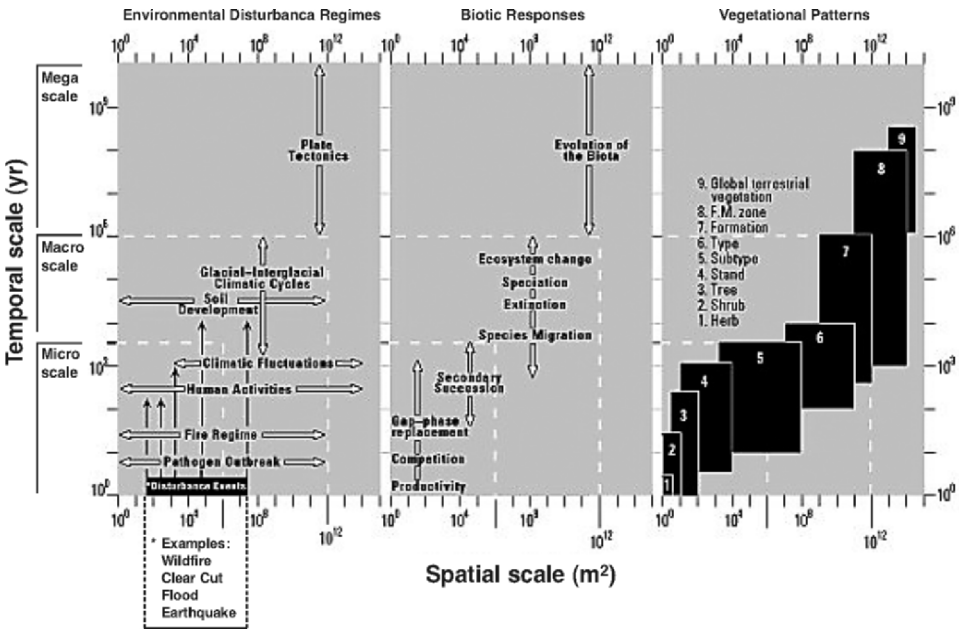


Fig. 1. Relationships between spatio-temporal scales and levels of organization. (Figure redrawn from Turner *et al.* (2001), modified from Delcourt *et al.* (1983)).

Pattern and processes operate on broad ranges of spatial and temporal scales and their characteristics are associated with scale (Levin 1978, 1992; Wu and Loucks 1995). Thus, effects of processes on pattern need to be considered with their characteristic temporal and spatial scale (Levin 1978, 1992; Wu and Loucks 1995). The space-time scaling of many biotic or abiotic processes is such that as a rule, fast processes operate on smaller spatial scales than slow processes (Fig. 1). In order to achieve high predictability, the spatial and temporal scales of a study need to match those of the process (Wiens 1989). For instance, the scale of interest for a research project investigating processes in a grassland that affect individuals of a particular insect species is defined by the organism's home range, and the time scale is identified by its life-history attributes (e.g., reproduction rate, mortality rate; Addicott *et al.* 1987; Wiens 1989).

If one process operates at a much slower rate than the other, an essentially non-linear interaction may appear unidirectional. The faster process is constrained by the quasi-static pattern created by the slower process. For instance, landscape ecological studies often assume the habitat mosaic to be constant in order to study its effect on the movement of organisms, population dynamics, or species distributions.

Indicators

Indicators are qualitative descriptors or quantitative measures that report key information to assess structure, function, or composition of a system (Dale 2001) with the most efficient use of available resources. They identify a system based on selected criteria that are monitored through time or space to inform about the system's state or condition (static), its changes, or trends (dynamic) (Dale 2001). Indicators facilitate decisions about whether intervention is desirable or necessary, which interventions might yield the best results, or how successful interventions have been. Hall and Grinnell (1919) were among the first to use the indicator concept by attributing animal species to specific life zones that are identified by geographical areas with comparable structure and composition.

Indicators are currently widely applied in many areas of research, environmental management, policy and decision making ranging from, for example, environmental pollution (Mal *et al.* 2002) to ecosystem integrity (Grove 2002). Here, we refer to indicators as quantitative measures derived from various methodologies in order to quantify and assess aspects of landscape and landscape-pattern properties.

Ecological indicators: Various types of indicators serve different applications. Ecological indicators, for example, are typically very specific for particular environments or taxonomic groups at specific locations (Fig. 2). They usually rely on expert knowledge and are derived from field observations. Ecological indicators encompass, for example Ellenberg's values (Ellenberg 1988) that benchmark details on specific plant species requirements (e.g., light thresholds), individual species, or communities. They are used to estimate species richness (Duelli and Obrist 1998, 2003), monitor land-use change (Cousins and Lindborg 2002), or assess the influence of disturbance and management (Dale *et al.* 2002a). Other examples of ecological indicators, in particular with respect to biodiversity, are discussed in Duelli *et al.* (2007). Advantages of ecological indicators thus include very specific information of a particular species or population at a particular location (Fig. 2), and are indicative of a process or response that may be too costly or difficult to measure directly. However, the information derived from ecological indicators does not necessarily allow up-scaling or generalisation to larger spatial or temporal scales.

Landscape indicators: Indicators that characterise properties at the landscape scale however supplement ecological indicators by providing information about, e.g., the amount and spatial arrangement of different land-cover types (Jones *et al.* 2000; Gergel *et al.* 2002; Wade *et al.* 2003), or environmental quality (Forman and Alexander 1998). Indicators for landscapes inform on the state of relevant landscape properties or their changes. Since landscapes are higher-level aggregations of individual patch properties, the information quantified by landscape indicators is more general. Indicators at the landscape scale can be derived

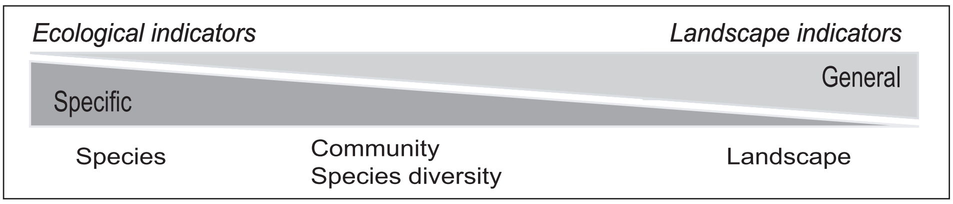


Fig. 2. Ecological indicators and landscape indicators.

from GIS databases, aerial photographs, or remotely sensed images. Advantages thus include that they may be much cheaper and more easily obtained for large areas. Also, they usually rely on standardised approaches and thus allow generalisation at larger spatial and temporal scales. Details on the systems however are usually not accounted for.

A broad variety of landscape characteristics can be quantified with indicators. Primary goals of landscape indicators are to quantify the amount and spatial arrangement of land cover, and to ensure comparability between different landscapes. However, the purpose of quantifying landscape patterns is to capture key features that matter, thus depending on the research question, objectives, allowable errors, and data availability.

Early landscape characterisations relied on two indicators: typology refers to the number of elements, and chorology measures the number of landscape elements or habitat types (Snacken and Antrop 1983). Today, landscapes are commonly described by composition and configuration (Gustafson 1998; Turner *et al.* 2001). Landscape composition can be assessed using indicators such as percent area. Configuration refers to the spatial arrangement of the individual elements. The overall spatial organisation of elements identifies how the landscape types are arranged in relation to each other, involving indicators derived from information theory (O'Neill *et al.* 1988), fractal geometry (Milne 1988; Milne *et al.* 1992; With 1994), or percolation theory (O'Neill *et al.* 1988; Gustafson and Parker 1992; Johnson and Milne 1992; Milne 1998; Wickham *et al.* 1999). Additionally, it has been stressed that the degree and type of interactions (connectivity) between the landscape elements play an important role in shaping ecological systems and landscapes (Taylor *et al.* 1993; With 1997; Bolliger *et al.* 2003; Bolliger 2005; Green and Sadedin 2005).

Landscape Indicators

Landscapes can be characterised discretely or continuously in space and time. Static landscape descriptions are conducted at particular time steps ("snapshots"), whereas dynamic characterisations are performed continuously through time ("movies").

Static, snapshot-like landscape descriptions usually rely on empirical observations (e.g., field measurements, GIS databases, aerial photographs) that represent landscapes at specific time-steps. The state and conditions of smaller-scale systems (e.g., dry meadow) can be reported or monitored through regular visits, e.g., weekly, annually). Empirical observations may provide information that dates back a few years or decades. For larger-scale systems such as landscapes, the system states can be monitored through time series obtained e.g., from temporal series of GIS data, aerial photographs, or remotely sensed images. As a rule however long-term effects of environmental change in the future or the past cannot be assessed with empirical data only. For dynamic, movie-type landscape assessments, models provide a suitable tool to improve the understanding of observed system functions, patterns, or diversity, and to assess consequences of changes of individual system components or of the environment on particular system properties. Models thus allow evaluations of alternative scenarios and help generate hypotheses for states and conditions of systems not only under current, but also under changing future or past conditions (e.g., temperature change, management change) (Lischke *et al.* 2007). Thus, indicators for model simulations inform on the system's state or condition under various scenarios of environmental changes.

In the following sections we present quantitative indicators relying on various methodological approaches that can be used to characterise landscapes or landscape-pattern properties. The indicators include measures to characterise particular periods (static) or time series (dynamic) based on discrete or continuous landscape representations (Fig. 3).

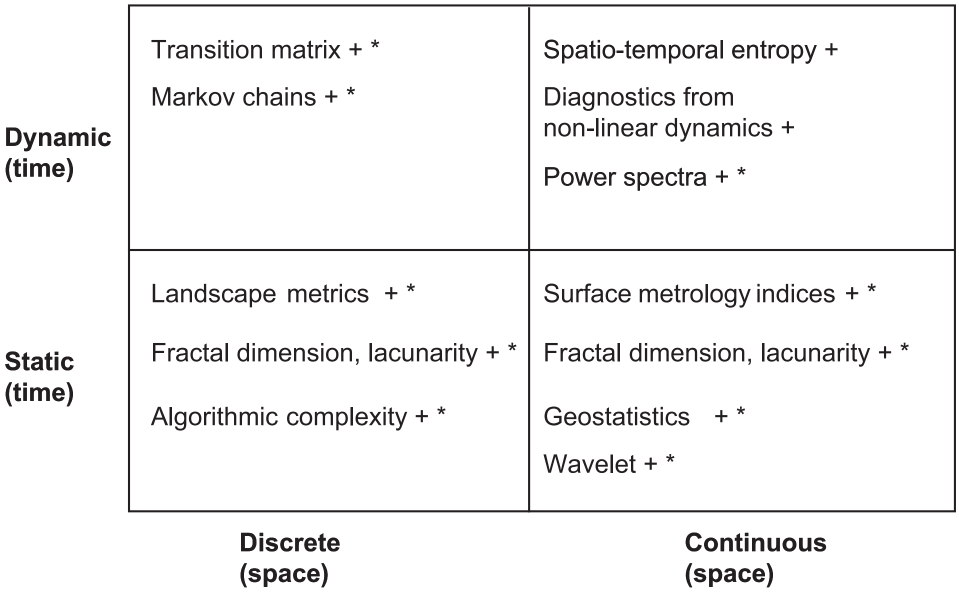


Fig. 3. Quantitative landscape indicators used to characterise landscapes in space and time. Indicators representing landscapes based on empirical (field or GIS) data are labelled with *, whereas + refer to indicators that characterise systems using model simulations.

Static, discrete landscape indicators

Algorithmic complexity: Computers use specific algorithms for the compression of graphic files or images, e.g., of maps representing landscapes. The size of an optimally compressed file or image can be interpreted as the condensation of the entire set of interactions between the digital components of the image or file, e.g., a landscape. The file or image size can thus be interpreted as a measure of landscape complexity based on compression algorithms (Kaspar and Schuster 1987; Manson 2001; Sprott *et al.* 2002; Bolliger *et al.* 2003). Algorithmic complexity is easy to calculate and provides comparability between different images representing, e.g., the same landscape at different times or the results of different simulation runs. The metric however does not provide details on which landscape element contributes more or less to the size of the file, and it is a relative measure.

Landscape metrics: Landscape metrics statistically represent landscapes or individual patch-type properties and are standard tools to analyse questions regarding the composition and configuration of landscapes and individual patches (Turner *et al.* 2001; Cardille and Turner 2002; McGarigal *et al.* 2002).

Metrics for landscape composition identify and describe the landscape pattern, whereas landscape configuration refers to their spatial arrangement of the landscape elements. Landscape composition is assessed using metrics such as landscape diversity (Shannon-Weaver diversity), or the proportion of area occupied by habitat types (Turner *et al.* 2001). Metrics for landscape configuration involve e.g., probabilities of patch adjacency, patch shape, or connectivity between patches (Turner *et al.* 2001). Such metrics are of great value to investigations dealing with habitat fragmentation, where patch isolation may cause extinction of entire populations because dispersal or colonisation rates are reduced (With 1997, 2002), or where disaggregation of landscapes may foster persistence of populations in reducing the probability of some disturbances such as fire (Franklin and Forman 1987). Patch size and shape may influence a variety of ecological properties, e.g., flows between patches in animal foraging strategies (Zollner and Lima 1997). The shape characteristics can be directly related to the overall heterogeneity of the landscape, whereas the area of an individual patch is of great ecological relevance in that it determines the space to support viable populations.

Advantages of landscape metrics include that many metrics are easily calculated and widely known to landscape ecologists (e.g., FRAGSTATS, McGarigal *et al.* 2002). However, the ecological relevance of the broad range of available metrics may be difficult to asses and may lead to misleading conclusions if not analysed carefully regarding concept and limitations (Li and Wu 2004). For example, it has been shown that some metrics, though calculated differently, are highly correlated (Riitters *et al.* 1995; Gustafson 1998; Turner *et al.* 2001; Neel *et al.* 2004). Other studies have shown that the comparability of metrics across scales may be problematic (Wu *et al.* 2002), so that different conclusions are drawn on the ecology depending on the scale of the study (Turner *et al.* 2001; Greenberg *et al.* 2002; Thompson and McGarigal 2002; Li and Wu 2004). Furthermore, it has been stressed that current methods to quantify landscape properties are more advanced in comparison to our ability to interpret the landscape properties with respect to ecologically relevant processes (Turner *et al.* 2001). Thus, the search for relationships between patterns and processes requires careful evaluation (Turner *et al.* 2001; Li and Wu 2004), especially since we are currently lacking thorough understanding of the required degree of landscape change to provoke ecologically relevant implications (Turner *et al.* 2001; Wu and Hobbs 2002).

Static, continuous landscape indicators

Indicators derived from geostatistics: Geostatistics is a method to quantify continuous surfaces (e.g., landscapes) and to assess the degree and extent of spatial autocorrelation. Spatial autocorrelation is an indicator that measures the common phenomenon that nearby observations tend to be more similar than distant ones. The distance at which spatial autocorrelation levels off indicates the spatial scale of organisation in a system, e.g., the size of an ecological neighbourhood, so that observations beyond this distance may be considered as ecologically and statistically uncorrelated. Positive spatial autocorrelation is assumed to result from a spatial process, e.g., dispersal. The major approaches to quantify spatial autocorrelation differ in their practical objectives: geostatistical methods focus on the estimation of the spatial covariance structure of a variable (e.g., variogram modelling) in order to estimate population parameters from spatially dependent observations (block kriging) or to interpolate values at unobserved locations (e.g., kriging). Spatial statistics developed in geography on the other hand, aim at testing for the presence of a spatial process in order to model this process or to account for spatial autocorrelation when assessing the correlation between spatially structured variables (Cliff and Ord 1981; Fortin *et al.* 2001; Liebhold and Gurevitch 2002).

However, all these methods require an assumption of stationarity, i.e., the spatial autocorrelation structure must be the same throughout the study area. It is often sufficient to assume weak or second-order stationarity, where the mean is constant, the autocorrelation depends only on the geographic distance between sampling units, and the variance is finite and constant (Burrough 1995). Local spatial statistics can be calculated within a moving-window, thus assuming stationarity only within the extent of the window, in order to identify anomalous subareas or delimit boundaries (Boots 2002; Pearson 2002).

Variogram modelling is widely used for assessing the spatial structure of a continuous variable (Isaaks and Srivastava 1989; Haining 1997). An empirical variogram is a plot of the semivariance between pairs of observations, averaged for each distance class, against geographic distance. The plot can be interpreted visually to assess how the variance of the variable changes with distance and, possibly, direction in space. This spatial covariance structure can then be summarised by fitting a theoretical variogram model. More complicated cases require the fitting of model parameters as a function of direction or the combination of several basic variogram functions, and the spatial cross-correlation between pairs of variables can be modelled in a similar way to allow for multivariate analysis (Wackernagel 1998).

Any variance can be partitioned by the distance between observations (Wagner 2004) so that, e.g., the results of multivariate analysis such as ordination can be plotted in variogram form. This allows additional insights into the spatial structure due to different processes, e.g., the spatial structure of a community that is induced by a specific environmental factor or the scale of patchiness of the residual variance after accounting for environmental heterogeneity (Wagner 2004; Wagner and Fortin 2005).

Indicators derived from spectral analysis: Spectral analysis is probably among the best known methods to characterise temporal data. When analysing time-series, spectral analysis using Fourier transform subdivides the series into individual sine and cosine waves, assuming an overlay of periodic structures with different wave lengths (frequencies) and amplitudes. To examine the spectrum, the logarithm of the squared amplitude is plotted against the logarithm of the frequency. The analysis of spatial surfaces relies on the periodogram, where a measure of variance (instead of amplitude) is plotted against distance (instead of frequency) (Dale 2000).

Results from spectral analysis can be graphically displayed by periodograms. These can be used as indicators to assess whether any particular time or space scale is singled out. For example, if the log-log spectrum exhibits straight lines (power laws), no particular spatial or temporal scale is singled out, and the properties of a given frequency or distance stand for all frequencies or distances. The phenomenon is referred to as scale invariance and has been observed throughout a broad range of natural phenomena and research fields including earthquakes (Ceva 1998), avalanches in sand piles (Bak *et al.* 1987; Bak 1996), chemical reactions (Simoyi *et al.* 1982), population dynamics (Solé *et al.* 1993; Perry 1995), landscape pattern (Milne 1998; Bolliger *et al.* 2003; Bolliger 2005), or evolutionary ecology (Solé *et al.* 1999).

Applied to landscape ecology, spectral analysis may help to identify particular spatial or temporal scales that are typical for a landscape. However, although scaling relationships offer clues to how the fundamental processes of biology give rise to empirical evidence is still largely missing (Levin 1998). Also, the indicator is likely most suitable to analyse model simulations since long time series are required that may not be empirically available.

Fractals and lacunarity: Fractals (Mandelbrot 1982) are mathematical representations of the complexity. Many objects relevant to landscape ecological research have fractal qualities either in two or three dimensional space (e.g., coastlines).

Fractals have many properties (Hastings and Sugihara 1993; Sprott 2003). For example, they have geometries that are too irregular to be represented by ordinary geometry, or they are self-similar, meaning that individual elements of the object are similar to the whole. Infinite copies of the elements make up the landscape. Self-similarity implies that the object is independent of the scale of observation (scale invariance), i.e., no characteristic scale is singled out and large-scale patterns can be predicted from small-scale pattern properties and vice versa. The upper boundary of the scale is determined by the extent of the object itself (e.g., landscape). The lower boundary is identified by the grain of the data. In landscape research, fractal geometry can be used to quantify the spatial complexity apparent in landscapes (Mandelbrot 1982; Gardner *et al.* 1987; Milne 1988, 1991; Milne *et al.* 1992; With 1994; Sprott *et al.* 2002; Bolliger *et al.* 2003).

Fractals may be described using algorithms that quantify the proportion of the geometrical space that is occupied by the fractal and are expressed as fractal dimensions. Fractals with identical fractal dimension may have greatly different appearances (Plotnick *et al.* 1993). In discrete patterns these differences are determined by the size of the gaps. The gaps in geometric structures can be measured using lacunarity indices (Mandelbrot 1982; Plotnick *et al.* 1993) to quantify the texture associated with patterns of spatial dispersion. Lacunarity is a useful index of surface structure for continuous landscape data where it measures the distributions of local maxima (peaks) and minima (valleys) of continuous landscape data (McGarigal and Cushman 2005). Additionally, lacunarity captures multiple dimensions of segregation across multiple scales (Wu and Sui 2001). First developed by Mandelbrot (1982), a variety of algorithms to calculate lacunarity are available (Allain and Cloitre 1991).

Indicators derived from wavelet analysis: Wavelet analysis is similar to spectral analysis, but instead of representing a pattern by a linear combination of sinusoid functions at different scales, it uses more flexible wavelet functions (Percival 2001). Wavelet analysis provides a promising alternative for characterising and partitioning landscapes in the presence of multiple, overlapping processes, and the method can easily handle large data sets such as remote sensing data (Bradshaw and Spies 1992; Csillag and Kabos 2002; McGarigal and Cushman 2005). Wavelet analysis has the advantage that it preserves the hierarchical information about the structure of a surface and allows pattern decomposition at the same time (Bradshaw and Spies 1992). The results can be interpreted in two ways: the wavelet variance identifies the scales that contribute most strongly to the pattern (similar to a periodogram in spectral analysis), whereas the degree of matching of the wavelet function can be mapped directly onto the data, thus identifying the spatial location of a specific structure (similar to local spatial statistics). Wavelets can thus be used as explanatory variables to predict a biotic response (Keitt and Urban 2005).

Surface metrology indices: Continuous surfaces have more properties than can be assessed using for example geostatistical approaches that quantify correlation distances, or spectral analysis that identifies particular spatial or temporal scales of periodic structures. Additional properties of continuous surfaces include e.g., roughness, skewness, curvature, or local peaks. These characteristics can be assessed by surface metrology indices based on methods that have been developed in microscopy and molecular physics (Barbato *et al.* 1995; SPIP 2001). The indices have recently become of interest to the landscape ecological community (McGarigal and Cushman 2005) and offer promising grounds for exploring their use and limitation for landscape ecological research.

Dynamic, discrete landscape indicators

The first step towards an empirical quantification of landscape dynamics is often a comparison between at least two time steps (Fig. 3). For instance, land-use/land-cover classifications derived from remote sensing may be available for different years. The resulting transition frequencies may be referred to as an indicator of landscape change representing the degree and spatial location of change. Obviously, such a comparison is only valid if the methodology is comparable between classifications, i.e., the same georeferencing, resampling and classification algorithms or rules were applied. Comparison may be based on map properties (comparison of landscape metrics that quantify composition or configuration for each time step) or on pixels (assessment of transitions from one state to another) (Jenerette and Wu 2001).

With transition matrices and Markov chains, the change of each pixel state between two time steps can be summarised in a transition probability matrix (Dale *et al.* 2002b) (Fig. 3). This is a square matrix with as many rows and columns as there are states (e.g., land-use/land-cover classes). A cell in row A and column B contains the estimated transition probability for a pixel with initial state A to switch to state B in one time step, thus representing an indicator of the likelihood of change. The transition probability is estimated by the observed number of transitions from A to B divided by the number of pixels with initial state A. For a series of *k* time steps with constant interval, *k-1* transition matrices can be estimated. If the underlying process is assumed constant (stationary), the *k-1* matrices are expected to be identical and may be averaged. The pooled transition matrix summarises the amount of change between all land-use types per average time step. The equilibrium state of the system, if such a state exists, is defined by a vector that, when multiplied by the transition matrix, yields the same vector again (eigen vector of the transition matrix; Usher 1992).

Under the assumption that the transition of a pixel between time steps $t_1 < t_2$ depends solely on the state of the pixel in t_1, the transition probability matrix describes a first-order Markov chain (Nicheva 2001). In ecology, this assumption is sometimes replaced by introducing holding-time requirements, i.e., a pixel needs to persist in state A for at least x time steps before transition to state B is possible (Acevedo *et al.* 1995; Yemshanov and Perera 2002). In some situations, a Markov chain will converge to an equilibrium state, independent of initial conditions (Usher 1992). A traditional Markov chain represents a spatially implicit temporal process. The explicit introduction of a spatial dimension results in spatio-temporal Markov chains (STMC), which combine a Markov chain with a cellular automaton (Balzter *et al.* 1998).

Dynamic, continuous landscape indicators

Indicators for continuous, dynamic landscapes can be found in dynamic systems or information theory. Currently, they rely on model simulations since empirical data (e.g., field-derived, aerial photographs) rarely provide long time series. One example of a dynamic, continuous indicator is spatiotemporal complexity that quantifies patchy vegetation dynamics (Parrott 2005). The indicator is similar to the information-based Shannon entropy and distinguishes between ordered, random, and aggregated patchiness (Parrott 2005). Other examples of dynamic, continuous indicators include measures to assess equilibria and their stability to gain impressions on how a trajectory of a continuous-time differential equation behaves throughout the entire state space (e.g., landscape) (Lischke *et al.* 2007). If the trajectory spirals around a point equilibrium, a spiral point is observed. Saddle points are found where some trajectories are attracted to equilibria, and others are repelled from them. In non-linear dynamics, periodic attractors (or repellors) are referred to as limit cycles. For example, the size of a basin of attraction of some equilibrium and its limits, within which the state variable may be perturbed before the system switches to other basins of attraction, may provide measures of system resilience (Pykh 2002).

Lyapunov exponents are indicators to assess the predictability of a system by measuring the extent to which small changes are amplified. It thus quantifies how sensitive a system is to perturbations (changes). In most cases perturbations tend to be amplified until they grow large, no matter how tiny the initial perturbations were. This behaviour, where small perturbations are amplified, is called sensitivity dependence on initial conditions. The Lyapunov exponents reflect the average rate at which perturbations increase or decrease. There are as many Lyapunov exponents as there are dimensions of the state space, and each exponent indicates whether the perturbation will increase or decrease in a particular direction

(Eckmann and Ruelle 1985). Applications of Lyapunov exponents in landscape ecology may thus involve assessments on the predictability of models. Additionally, since dependence on initial conditions is one of the hallmarks of chaos (Sprott 2003), Lyapunov exponents can be used to assess whether a system is chaotic or not.

Assessments of the aesthetic appeal of art and nature (Hunziker *et al.* 2007) reveal that a balance of simplicity and complexity, order and unpredictability, is preferred by humans (Aks and Sprott 1996). Results showed that the correlations between Lyapunov exponents (representing the unpredictability of the dynamic process) and people's aesthetical preferences for patterns had on average Lyapunov exponents that corresponded to those of many natural objects (Aks and Sprott 1996).

Conclusions and Challenges

Identifying and quantifying the structure and dynamics of landscape patterns is central to many questions in basic and applied research, and indicators provide a useful framework to assess key properties of landscapes in space and time at most efficient use of the available resources. Selection of the appropriate suite of indicators with respect to the research objective and scale is a key to successful application. Ideally, indicators should inform about a system as comprehensively as possible with respect to the research question of interest. It is thus necessary to choose appropriate indicators that mirror adequately the system's structure, function, and composition including assessments on the indicator's use and limitation.

There are several important challenges:

1. *Characterising landscapes dynamically:* To date, landscapes have been characterised mostly spatially. However, it is widely recognised that many landscape elements exhibit non-equilibrium dynamic-transient behaviour (Lischke *et al.* 2007). Thus, future challenges in landscape ecology include increasing focus on dynamic assessments of landscapes and landscape change, especially since appropriate data will be increasingly available through remote sensing (Zimmermann *et al.* 2007).
2. *Characterising landscapes continuously:* Approaches to assess landscapes continuously include geostatistical approaches that indicate distances of correlation, spectral analysis to assess whether there are any particular spatial or temporal scales, and fractals allow analysis of the spatial complexity of a surface. However, continuous surfaces exhibit many more properties. Surface metrology indices and wavelets are promising tools to overcome this shortcoming, although their suitability for application in landscape ecology remains to be tested.
3. *Comparability of landscape indicators across scales and statistical tests:* Use of indicators for landscape ecological questions involves thorough testing to ensure comparability within and across different landscapes and scales. Quantifying and interpreting differences between landscapes/landscape patterns is a future challenge, since routine statistical tests are hardly applicable. Furthermore, not only pattern, but also driving processes need to be compared (Fortin *et al.* 2003).

Acknowledgements

We would like to thank the three editors of this book Felix Kienast, Rita Ghosh and Otto Wildi and two anonymous reviewers for their helpful and constructive suggestions and comments.

References

Acevedo M.F., Urban D.L. and Ablan M. 1995. Transition and gap models of forest dynamics. Ecological Applications 5: 1040–1055.
Addicott J.F., Aho J.M., Antolin M.F., Padilla D.K., Richardson J.S. and Soluk D.A. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49: 340–346.
Aks D.J. and Sprott J.C. 1996. Quantifying aesthetic preference for chaotic patterns. Empirical Studies of the Arts 14: 1–16.
Allain C. and Cloitre M. 1991. Characterising the lacunarity of random and deterministic fractal sets. Physical Review A 44: 3552–3558.
Bak P. 1996. How nature works. Springer Verlag, New York.
Bak P., Tang C. and Wiesenfeld K. 1987. Self-organised criticality: an explanation of 1/f noise. Physical Review Letters 59: 381–384.
Balzter H., Braun P.W. and Kohler W. 1998. Cellular automata models for vegetation dynamics. Ecological Modelling 107: 113–125.
Barbato W.L., Carneiro K., Cuppini D., Garnaes J., Gori G., Hughes G., Jensen C.P., Jorgensen J.F., Jusko O., Livi S., McQuoid H., Nielsen L., Picotto G.B. and Wilening G. 1995. Scanning tunnelling microscopy methods for the characterisation for roughness and micro hardness measurements. Synthesis report for research contract with the European Union under its programme for applied metrology. In: European Commission Catalogue number, Brussels, Luxemburg.
Bascompte J. and Solé R.V. 1995. Rethinking complexity – modelling spatiotemporal dynamics in ecology. Trends in Ecology & Evolution 10: 361–366.
Bezdek J.C. 1981. Pattern recognition with fuzzy objective function algorithms. Plenum Press, New York.
Bolliger J. 2002. Schweizer Wälder und Klimaveränderungen: Vergleich von Simulationen quantitativer Vegetationsmodelle. Schweizerische Zeitschrift für Forstwesen 153: 167–175.
Bolliger J. 2005. Simulating complex landscapes with a generic model: sensitivity to qualitative and quantitative classifications. Ecological Complexity 2: 131–149.
Bolliger J., Kienast F. and Zimmermann N.E. 2000. Risks of global warming on montane and subalpine forests in Switzerland. Regional Environmental Change 1: 99–111.
Bolliger J. and Mladenoff D.J. 2005. Quantifying spatial classification uncertainties of the historical Wisconsin landscape (U.S.A). Ecography 28: 141–156.
Bolliger J., Sprott J.C. and Mladenoff D.J. 2003. Self-organisation and complexity in historical landscape patterns. Oikos 100: 541–553.
Boots B. 2002. Local measures of spatial association. Ecoscience 9: 168–176.
Bradshaw G.A. and Spies T.A. 1992. Characterising canopy gap structure in forests using wavelet analysis. Journal of Ecology 80: 205–215.
Brown D.G. 1998. Classification and boundary vagueness in mapping presettlement forest types. International Journal of Information Science 12: 105–129.
Bürgi M., Hersperger A., Hall M., (Russell) Southgate E.W.B. and Schneeberger N. 2007. Using the past to understand the present land use and land cover. In: Kienast F., Wildi O. and Ghosh S. (eds.). A Changing World. Challenges for Landscape Research, Vol. 8: 133–144. Springer Landscape Series, Dordrecht.
Burrough P.A. 1995. Spatial aspects of ecological data. In: van Tongeren O.F.R. (ed.), Data Analysis in Community and Landscape Ecology, pp. 213–251. Cambridge University Press, Cambridge.
Cardille J.A. and Turner M.G. 2002. Understanding landscape metrics I. In: Gergel S.E. and Turner M.G. (eds.). Learning landscape ecology, pp. 85–100. Springer, New York.

Ceva H. 1998. On the asymptotic behvaieur for an earthquake model. Physics Letters A 245: 413–418.
Clark J.S. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. American Naturalist 152: 204–224.
Clark J.S., Kern R., Macklin E. and HilleRisLambers J. 1999. Seed dispersal near and far: Patterns across temperate and tropical forests. Ecology 80: 1475–1494.
Cliff A.D. and Ord J.K. 1981. Spatial Processes: Models and Applications. Pion, London.
Cousins S.A.O. and Lindborg R. 2002. Assessing changes in plant distribution patterns – indicator species versus plant functionl types. Ecological Indicators 1: 17–27.
Csillag F. and Kabos S. 2002. Wavelets, boundaries, and the spatial analysis of landscape pattern. Ecoscience 9: 177–190.
Dale M.R.T. 2000. Spatial pattern analysis in plant ecology. Cambridge University Press, Cambridge.
Dale V.A. 2001. Challenges in the development and use of ecological indicators. Ecological Indicators 1: 3–10.
Dale V.A., Beyeler S.C. and Jackson B. 2002a. Understory vegetation indicators of anthropogenic disturbance in longleaf pine forests at Fort Benning, Georgia, U.S.A. Ecological Indicators 1: 155–170.
Dale V.H., Fortes D.T. and Ashwood T.L. 2002b. A landscape transition matrix approach for land management. In: Liu J. and Taylor W. (eds.). Integrating Landscape Ecology into Natural Resource Management, pp. 265–293. Cambridge University Press, Cambridge.
Duelli P., Baur P., Buchecker M., Gugerli F., Holderegger R. and Wohlgemuth T. 2007. The role of value systems in biodiversity research. In: Kienast F., Wildi O. and Ghosh S. (eds.). A Changing World. Challenges for Landscape Research, Vol. 8: 27–34. Springer Landscape Series, Dordrecht.
Duelli P. and Obrist M.K. 2003. Biodiversity indicators: the choice of values and measures. Agriculture Ecosystems and Environment 98: 87–98.
Duelli P. and Obrist M.K. 1998. In search of the best correlates for local organismal biodiversity in cultivated areas. Biodiversity and Conservation 7: 297–309.
Eckmann J.-P. and Ruelle D. 1985. Ergodic theory of chaos and strange attractors. Rev. Mod. Phys 57: 617–656.
Ellenberg H. 1988. Vegetation ecology of Central Europe, 4th ed. Cambridge University Press.
Farkas I., Derenyi I., Jeong H., Neda Z., Oltvai Z.N., Ravasz E., Schubert A., Barabasi A.-L. and Vicsek T. 2002. Networks in life: scaling properties and eigenvalue spectra. Physica A 314: 25–34.
Forman R.T.T. 1995. Land mosaic: the ecology of landscapes and regions. Cambridge University Press, Cambridge, UK.
Forman R.T.T. and Alexander I.F. 1998. Roads and their major ecological effects. Ann. Rev. Ecol. Syst. 29: 207–231.
Forman R.T.T. and Godron M. 1986. Landscape Ecology. John Wiley & Sons, New York.
Fortin M.J., Boots B., Csillag F. and Remmel T.K. 2003. On the role of spatial stochastic models in understanding landscape indices in ecology. Oikos 102: 203–212.
Fortin M.-J., Dale M.R.T. and ver Hoef J. 2001. Spatial analysis in ecology. In: Piegorsch W.W. (ed.). The Encyclopedia of Environmetrics, pp. 2051–2058. John Wiley and Sons Ltd.
Franklin J.F. and Forman R.T.T. 1987. Creating landscape patterns by forest cutting: Ecological consequences and principles. Landscape Ecology 1: 5–18.
Gardner R.H., Milne B.T., Turner M.G. and O'Neil R.V. 1987. Neutral models for the analysis of broad-scale landscape pattern. Landscape Ecology 1: 19–28.
Gergel S.E., Turner M.G., Miller J.R., Melack J.M. and Stanley H.E. 2002. Landscape indicators of human impacts to riverine systems. Aquatic Science 64: 118–128.
Gosz J.R. 1993. Ecotonoe hierarchies. Ecological Applications 3: 369–376.
Green D.G. and Sadedin S. 2005. Interactions matter – complexity in landscapes and ecosystems. Ecological Complexity 2: 117–130.
Greenberg J.D., Gergel S.E. and Turner M.G. 2002. Understanding landscape metrics II. In: Gergel S.E. and Turner M.G. (eds.). Learning landscape ecology, pp. 101–111. Springer, New York.

Grove S.J. 2002. Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. Ecological Indicators 1: 171–188.
Gustafson E.J. 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems 1: 143–156.
Gustafson E.J. and Parker G.R. 1992. Relationship between landcover proportion and indices of landscape spatial pattern. Landscape Ecology 7: 101–110.
Haines-Young R. and Chopping M. 1996. Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. Progress in Physical Geography 20: 418–445.
Haining R. 1997. Spatial Data Analysis in the Social and Environmental Sciences. Cambridge University Press, Cambridge.
Hall H.M. and Grinnell J. 1919. Life-zone indicators in California. Proc. Calif. Acad. Sci 37–67.
Hargis C.D., Bissonnette J.A. and David J.L. 1998. The behaviour of landscape metrics commonly used in the study of habitat fragmentation. Landscape Ecology 13: 167–186.
Hastings H.M. and Sugihara G. 1993. Fractals: a User's Guide for the Natural Sciences. Oxford University Press, Oxford.
Hunziker M., Buchecker M. and Hartig T. 2007. Space and place – two aspects of the human-landscape relationship. In: Kienast F., Wildi O. and Ghosh S. (eds.). A Changing World. Challenges for Landscape Research, Vol. 8: 47–62. Springer Landscape Series, Dordrecht.
Isaaks E.H. and Srivastava R.M. 1989. Applied Geostatistics. Oxford University Press, New York.
Jacquemin H., Butaye J. and Hermy M. 2001. Forest plant species richness in small, fragmented mixed deciduous forest patches: The role of area, time and dispersal limitations. Journal of Biogeography 28: 801–812.
Jenerette G.D. and Wu J.G. 2001. Analysis and simulation of land-use change in the central Arizona-Phoenix region, U.S.A. Landscape Ecology 16: 611–626.
Johnson A.R. and Milne B.T. 1992. Diffusion in fractal landscapes: simulations and experimental studies of tenebrionid beetle movement. Ecology 73: 1968–1983.
Jones K.B., Neale A.C., Nash M.S., Riitters K.H., Wickham J.D., O'Neill R.V. and Van Remortel R.D. 2000. Landscape correlates of breeding bird richness across the United States mid-atlantic region. Environmental Monitoring and Assessment 63: 159–174.
Kaspar F. and Schuster H.G. 1987. An easily calculable measure for the complexity of spatio-temporal patterns. Phys. Rev. A 36: 842.
Keitt T.H. and Urban D. 2005. Scale-specific inference using wavelets. Ecology 86: 2497–2504.
Keller D.R. and Golley F.B. 2000. The philosophy of ecology. The University of Georgia Press, Athens GA, U.S.A.
Kienast F., Wildi O. and Brzeziecki B. 1998. Potential impacts of climate change on species richness in mountain forests – an ecological risk assessment. Biological Conservation 83: 291–305.
Lausch A. and Herzog F. 2002. Applicability of landscape metrics for the monitoring of landscape change: Issues of scale, resolution and interpretability. Ecological Indicators 2: 3–15.
Levin S.A. 1998. Ecosystems and the bioshpere as complex adaptive systems. Ecosystems 1: 431–436.
Levin S.A. 1978. Pattern formation in ecological communities. In: Steele J.H. (ed.), Spatial pattern in plankton communities, pp. 433–465. Plenum Press, New York.
Levin S.A. 1979. Non-uniform stable solutions to reaction-diffusion equations: applications to ecological pattern formation. In: Haken H. (ed.). Pattern formation by dynamic systems and pattern recognition, pp. 210–222. Springer Verlag, Heidelberg, New York.
Levin S.A. 1992. The problem of pattern and scale in ecology. Ecology 73: 1943–1967.
Li H. and Wu J. 2004. Use and misuse of landscape indices. Landscape Ecology 19: 389–399.
Liebhold A.M. and Gurevitch J. 2002. Integrating the statistical analysis of spatial data in ecology. Ecography 25: 553–557.
Lischke H., Bolliger J. and Seppelt R. 2007. Dynamic spatio-temporal landscape models. In: Kienast F., Wildi O. and Ghosh S. (eds.). A Changing World. Challenges for Landscape Research, Vol. 8: 273–296. Springer Landscape Series, Dordrecht.
Mal T.K., Uveges J.L. and Turk K.W. 2002. Fluctuating asymmetry as an ecological indicator of heavy metal stress in *Lythrum salicaria*. Ecological Indicators 1: 189–195

Mandelbrot B. 1982. The fractal geometry of nature. Freeman.

Manson S.M. 2001. Simplifying complexity: a review of complexity theory. Geoforum 32: 405–414.

McBratney A.B. and Odeh I.O.A. 1997. Application of fuzzy sets in soil science: fuzzy logic, fuzzy measurements, and fuzzy decisions. Geoderma 77: 85–113.

McGarigal K. and Cushman S.A. 2005. The gradient concept of landscape structure. In: J. Wiens and Moss M. (eds.). Issues and perspectives in landscape ecology, pp. 112–119. Cambridge University Press, Cambridge.

McGarigal K., Cushman S.A., Neel M.C. and Ene E. 2002. FRAGSTATS: Spatial pattern analysis program for categorial maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, MA, U.S.A. http://www.umass.edu/landeco/research/fragstats/fragstats.html.

Milne B.T. 1991. Lessons from applying fractal models to landscape patterns. In: Turner M.G. and Gardner R.H. (eds.). Quantiative methods in landscape ecology, pp. 199–235. Springer.

Milne B.T. 1988. Measung the fractal geometry of landscapes. Appl. Math. Computation 27: 67–79.

Milne B.T. 1998. Motivation and benefits of complex systems approaches in ecology. Ecosystems 1: 449–456.

Milne B.T., Turner M.G., Wiens J.A. and Johnson A.R. 1992. Interactions between the fractal geometry of landscapes and allometric herbivory. Theoretical Population Biology 41: 337–353.

Minasny B. and McBratney A.B. 2002. FuzME Version 3.0 http://www.usyd.edu.au/su/agric/acpa/fkme/program.html. The University of Sydney, Sydney, Australia, http://www.usyd.edu.au/su/agric/acpa.

Neel M.C., McGarigal K. and Cushman S.A. 2004. Behaviour of class-level landscape metrics across gradients of class aggregation and area. Landscape Ecology 19: 435–455.

Nicheva D. 2001. Encyclopedia of Environmetrics. In: El-Shaarawi A.H. and Piegorsch W.W. (eds.). Markov chains, pp. 1207–1208. John Wiley & Sons, Chichester.

O'Neill R.V., Milne B.T., Turner M.G. and Gardner R.H. 1988. Resource utilisation scales and landscape pattern. Landscape Ecology 2: 63–69.

Parrott L. 2005. Quantifying the complexity of simulated spatiotemporal population dynamics. Ecological Complexity 2: 175–184.

Pearson D.M. 2002. The application of local measures of spatial autocorrelation for describing pattern in north Australian landscapes. Journal of Environmental Management 64: 85–95.

Percival D.B. 2001. Wavelets. In: Piegorsch W.W. (ed.). The Encyclopedia of Environmetrics, pp. 2338–2351. John Wiley and Sons Ltd., New York.

Perry D.A. 1995. Self-organising systems across scales. Trends in Ecology and Evolution 10: 241–244.

Plotnick R.E., Gardner R.H. and O'Neill R.V. 1993. Lacunarity indices as measures of landscape texture. Landscape Ecology 8: 201–211.

Pykh Y.A. 2002. Lyapunov functions as a measure of biodiversity: Theoretical background. Ecological Indicators 2: 123–133.

Regan H.M., Colyvan M. and Burgman M.A. 2000. A proposal for fuzzy International Union for the Conservation of Nature (IUCN) categories and criteria. Biological Conservation 92: 101–108.

Riitters K.H., O'Neill R.V., Hunsaker C.T., Wickham J.D., Yankee D.H., Timmins S.P., Jones K.B. and Jackson B.L. 1995. A factor analysis of landscape pattern and strucutre metrics. Landscape Ecology 10: 23–39.

Simoyi R.H., Wolf A. and Swinney H.L. 1982. One-dimensional dynamics in a multicomponent chemical reaction. Physical Review Letters 49: 245–248.

Snacken F. and Antrop M. 1983. Structure and dynamics of landscape systems. In: Drdos J. (ed.). Landscape synthesis: geoecological foundations of the complex landscape management, pp. 10–30. Veda Publishing House of the Slovak Academy of Sciences, Bratislava.

Solé R.V., Alonso D. and McKane A. 2002. Self-organised instability in complex ecosystems. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 357: 667–681.

Solé R.V. and Manrubia S.C. 1995. Are rainforests self-organised critical? Journal of Theoretical Biology 173: 31–40.

Solé R.V., Manrubia S.C. and Benton M. 1999. Criticality and scaling in evolutionary ecology. Trends in Ecology and Evolution 156–160.

Solé R.V., Miramontes O. and Goodwin B.C. 1993. Oscillations and chaos in ant societies. Journal of Theoretical Biology 161: 343–357.
SPIP 2001. The scanning probe image processor. Image metrology APS. Lyngby, Denmark.
Sprott J.C. 2003. Chaos and time-series analysis. Oxford University Press, Oxford.
Sprott J.C., Bolliger J. and Mladenoff D.J. 2002. Self-organised criticality in forest-landscape evolution. Physics Letters A 297: 267–271.
Taylor P.D., Fahrig L., Henein K. and Merriam G. 1993. Connectivity is a vital element of landscape structure. Oikos 68: 571–573.
Thompson C.M. and McGarigal K. 2002. The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (U.S.A). Landscape Ecology 17: 569–586.
Turner M.G. 2005. Landscape ecology in North America: past, present, and future. Ecology 86: 1967–1974.
Turner M.G., Gardner R.H. and O'Neill R.V. 2001. Landscape ecology in theory and practice: pattern and process. Springer Verlag, New York, U.S.A.
Usher M.B. 1992. Statistical models of succession. In: Glenn-Lewin D.C., Peet R.K. and Veblen T.T. (eds.), Plant succession: theory and prediction, pp. 215–248. Chapman and Hall, London.
Wackernagel H. 1998. Multivariate Geostatistics. 2nd, completely revised. Springer, Berlin.
Wade T.G., Wickham J.D., Nash M.S., Neale A.C., Riitters K.H. and Jones K.B. 2003. A comparison of vector and raster GIS methods for calculating landscape metrics used in environmental assessments. Photogrammetric Engineering and Remote Sensing 69: 1399–1405.
Wagner H.H. 2003. Spatial covariance in plant communities: an integration of ordination, variogram modelling and the variance test of species richness. Ecology 84: 1045–1057.
Wagner H.H. 2004. Direct multiscale ordination with canonical correspondence analysis. Ecology 85: 342–351.
Wagner H.H. and Fortin M.J. 2005. Spatial analysis of landscapes: concepts and statistics. Ecology 86: 1975–1987.
Webb S.L. 1987. Beech range extension and vegetation history: pollen stratigraphy of two Wisconsin, U.S.A lakes. Ecology 68: 1993–2005.
Wickham J.D., Jones K.B., Riitters K.H., Wade T.G. and O'Neill R.V. 1999. Transitions in forest fragmentation: implications for restoration opportunities at regional scales. Landscape Ecology 14: 137–145.
Wiens J.A. 1989. Spatial scaling in ecology. Functional Ecology 3: 385–397.
Wiens J.A. 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. In: Hutchings M.J., John E.A. and Stewart A.J.A. (eds.). The ecological consequences of heterogeneity, pp. 9–31.
With K.A. 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecology 9: 25–36.
With K.A. 1997. The application of neutral landscape models in conservation biology. Conserv Biol 11: 1069–1080.
With K.A. 1997. The theory of conservation biology. Conserv Biol 11: 1436–1440.
With K.A. 2002. Landscape connectivity and metapopulation dynamics. In: Gergel S.E. and Turner M.G. (eds.), Learning landscape ecology, pp. 208–227. Springer, New York.
Wu J. and Hobbs R. 2002. Key issues and research priorities in landscape ecology: An idiosyncratic synthesis. Landscape Ecology 17: 355–365.
Wu J. and Loucks O.L. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. The Quarterly Review of Biology 70: 439–466.
Wu J., Shen W., Sun W. and Tueller P.T. 2002. Empirical patterns of the effects of changing scale on landscape metrics. Landscape Ecology 17: 761–782.
Wu X.B. and Sui D.Z. 2001. An initial exploration of a lacunarity-based segregation measure. Environment and Planning B: Planning and Design 28: 433–446.
Yemshanov D. and Perera A.H. 2002. A spatially explicit stochastic model to simulate boreal forest cover transitions: general structure and properties. Ecological Modelling 150: 189–209.
Zadeh L.A. 1965. Fuzzy sets. Information Control 8: 338–353.

Zimmermann N.E., Washington-Allen R.A., Ramsey R.D., Schaepman M.E., Mathys L., Kötz B., Kneubühler M., and Edwards T.C. 2007. Modern remote sensing for environmental monitoring landscape states and trajectories. In: Kienast F., Wildi O. and Ghosh S. (eds.). A Changing World. Challenges for Landscape Research, Vol. 8: 65–91. Springer Landscape Series, Dordrecht.

Zollner P.A. and Lima S.L. 1997. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. Oikos 80: 51–60.