FRAGSTATS Conceptual Foundation

This document provides a brief overview of landscape pattern metrics as they are commonly applied in landscape ecology, as well as some key terms and concepts essential to using FRAGSTATS and quantifying landscape patterns. An understanding of the material in this section is prerequisite to the proper use of FRAGSTATS.

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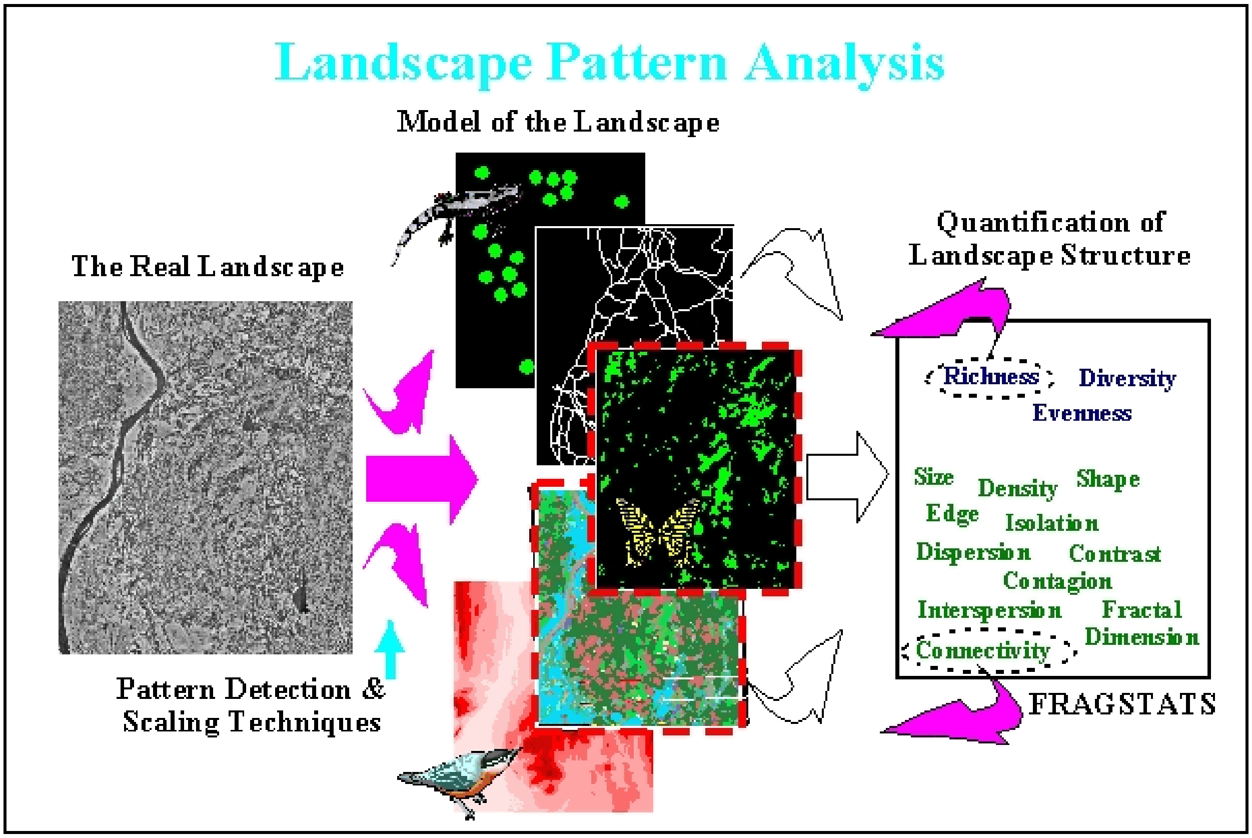
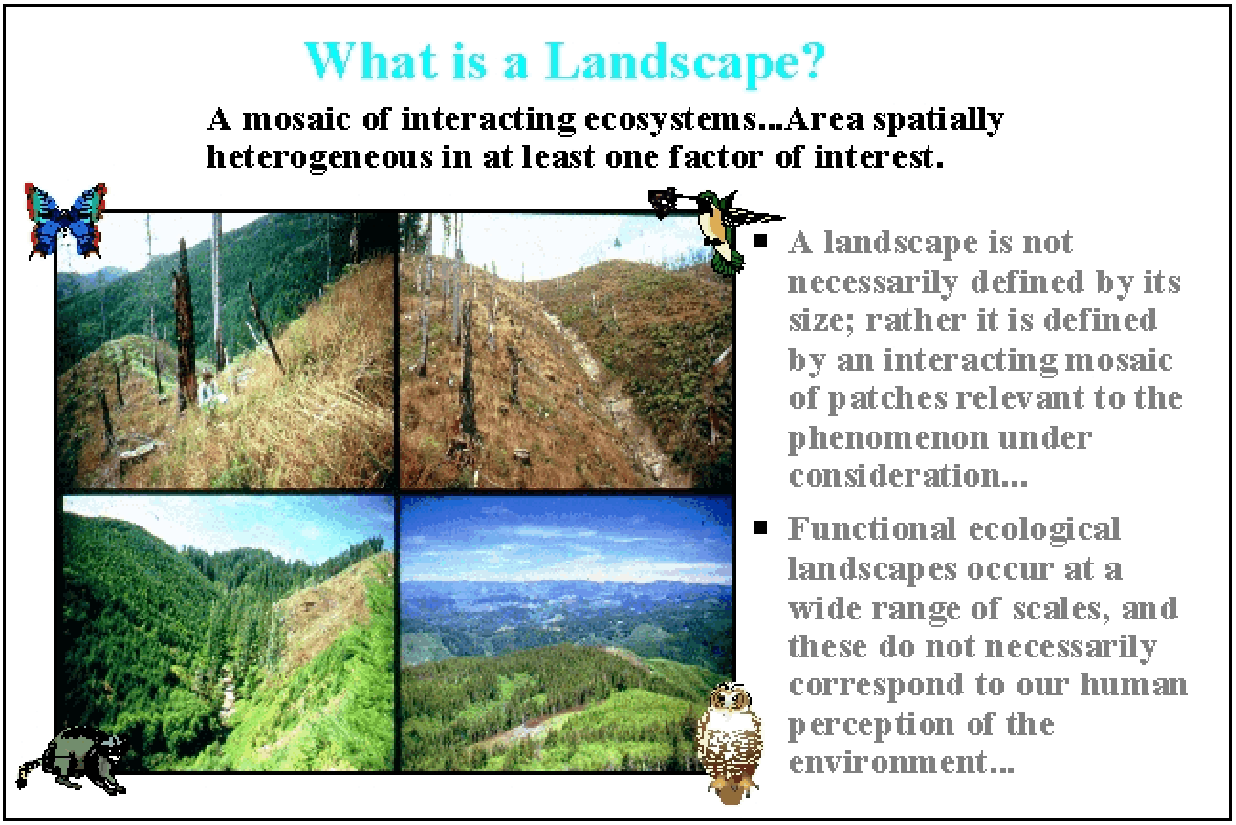


INTRODUCTION

Landscape ecology, if not ecology in general, is largely founded on the notion that environmental patterns strongly influence ecological processes (Turner 1989). The habitats in which organisms live, for example, are spatially structured at a number of scales, and these patterns interact with organism perception and behavior to drive the higher level processes of population dynamics and community structure (Johnson et al. 1992). Anthropogenic activities (e.g. development, timber harvest) can disrupt the structural integrity of landscapes and is expected to impede, or in some cases facilitate, ecological flows (e.g., movement of organisms) across the landscape (Gardner et al. 1993). A disruption in landscape patterns may therefore compromise its functional integrity by interfering with critical ecological processes necessary for population persistence and the maintenance of biodiversity and ecosystem health (With 2000). For these and other reasons, much emphasis has been placed on developing methods to quantify landscape patterns, which is considered a prerequisite to the study of pattern-process relationships (e.g., O'Neill et al. 1988, Turner 1990, Turner and Gardner 1991, Baker and Cai 1992, McGarigal and Marks 1995). This has resulted in the development of literally hundreds of indices of landscape patterns. This progress has been facilitated by recent advances in computer processing and geographic information (GIS) technologies. Unfortunately, according to Gustafson (1998), "the distinction between what can be mapped and measured and the patterns



that are ecologically relevant to the phenomenon under investigation or management is sometimes blurred."

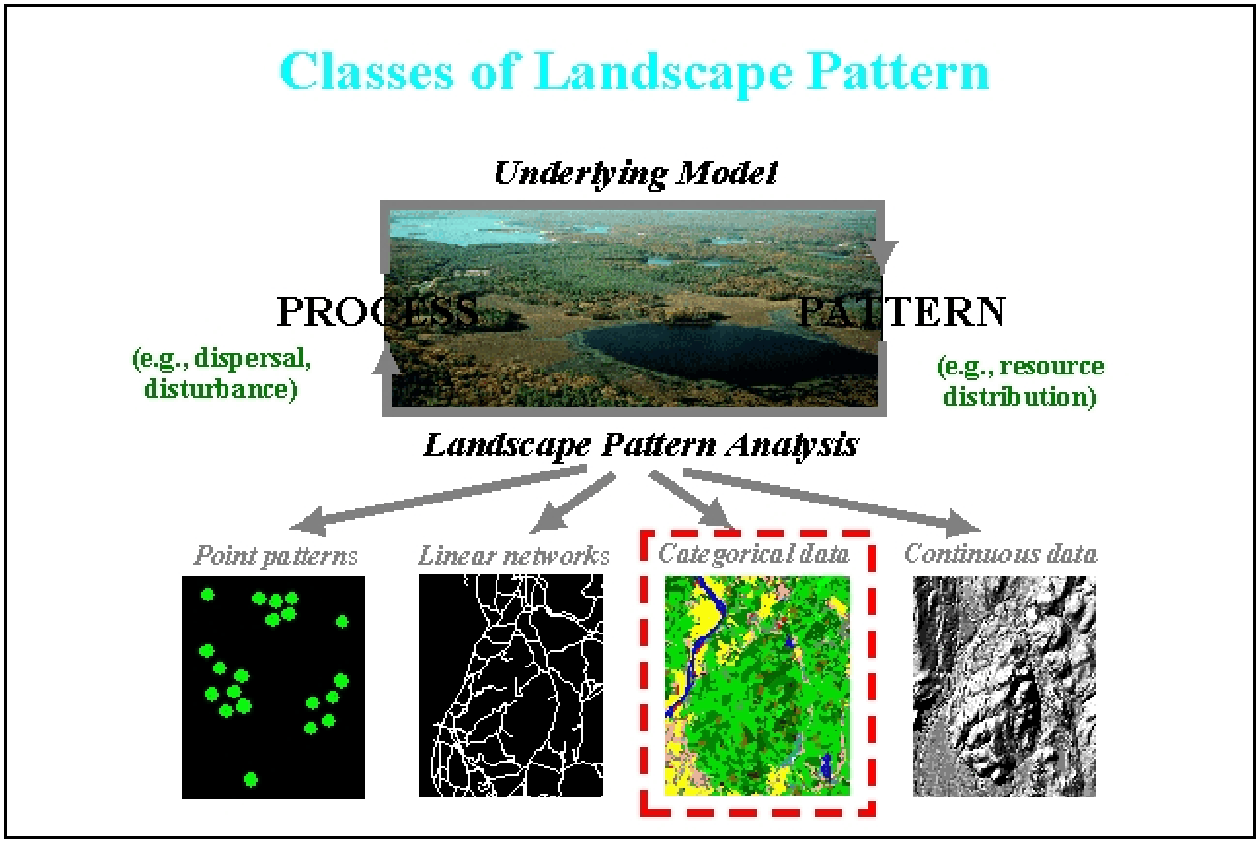
WHAT IS A LANDSCAPE?

Landscape ecology by definition deals with the ecology of landscapes. Surprisingly, there are many different interpretations of the term "landscape." The disparity in definitions makes it difficult to communicate clearly, and even more difficult to establish consistent management policies. Definitions of landscape invariably include an area of land containing a mosaic of patches or landscape elements (see below). Forman and Godron (1986) defined landscape as a heterogeneous land area composed of a cluster of interacting ecosystems that is repeated in similar form throughout. The concept differs from the traditional ecosystem concept in focusing on groups of ecosystems and the interactions among them. There are many variants of the definition depending on the research or management context.

For example, from a wildlife perspective, we might define landscape as an area of land containing a mosaic of *habitat* patches, often within which a particular "focal" or "target" habitat patch is embedded (Dunning et al. 1992). Because habitat patches can only be defined relative to a particular organism's perception and scaling of the environment (Wiens 1976), landscape size would differ among organisms. However, landscapes generally occupy some spatial scale intermediate between an organism's normal home range and its regional distribution. In-other-words, because each organism scales the environment differently (i.e., a salamander and a hawk view their environment on different scales), there is no absolute size for a landscape; from an organism-centered perspective, the size of a landscape varies depending on what constitutes a mosaic of habitat or resource patches meaningful to that particular organism.

This definition most likely contrasts with the more anthropocentric definition that a landscape corresponds to an area of land equal to or larger than, say, a large basin (e.g., several thousand hectares). Indeed, Forman and Godron (1986) suggested a lower limit for landscapes at a "few kilometers in diameter", although they recognized that most of the principles of landscape ecology apply to ecological mosaics at any level of scale. While this may be a more pragmatic definition than the organism-centered definition and perhaps corresponds to our human perception of the environment, it has limited utility in managing wildlife populations if you accept the fact that each organism scales the environment differently. From an organism-centered perspective, a landscape could range in absolute scale from an area smaller than a single forest stand (e.g., a individual log) to an entire ecoregion. If you accept this organism-centered definition of a landscape, a logical consequence of this is a mandate to manage habitats across the full range of spatial scales; each scale, whether it be the stand or watershed, or some other scale, will likely be important for a subset of species, and each species will likely respond to more than 1 scale.

KEY POINT *It is not my intent to argue for a single definition of landscape. Rather, I wish to point out that there are many appropriate ways to define landscape depending on the phenomenon under consideration. The important point is that a landscape is not necessarily defined by its size; rather, it is defined by an interacting mosaic of patches relevant to the phenomenon under consideration (at any scale). It is incumbent upon the investigator or manager to define landscape in an appropriate manner. The essential first step in any landscape-level research or management endeavor is to define the landscape, and this is of course prerequisite to quantifying landscape patterns.*



CLASSES OF LANDSCAPE PATTERN

Real landscapes (at any scale) contain complex spatial patterns in the distribution of resources that vary over time; quantifying these patterns and their dynamics is the purview of landscape pattern analysis. Landscape patterns can be quantified in a variety of ways depending on the type of data collected, the manner in which it is collected, and the objectives of the investigation. Broadly considered, landscape pattern analysis involves four basic types of spatial data corresponding to different representations of landscape pattern. These look rather different numerically, but they share a concern with the relative concentration of spatial variability:

(1) *Spatial point patterns* represent collections of entities where the geographic locations of the entities are of primary interest, rather than any quantitative or qualitative attribute of the entity itself. A familiar example is a map of all trees in a forest stand, wherein the data consists of a list of trees referenced by their geographic locations. Typically, the points would be labeled by species, and perhaps further specified by their sizes (a marked point pattern). The goal of point pattern analysis with such data is to determine whether the points are more or less clustered than expected by chance and/or to find the spatial scale(s) at which the points tend to be more or less clustered than expected by chance (Greig-Smith 1983, Dale 1999).

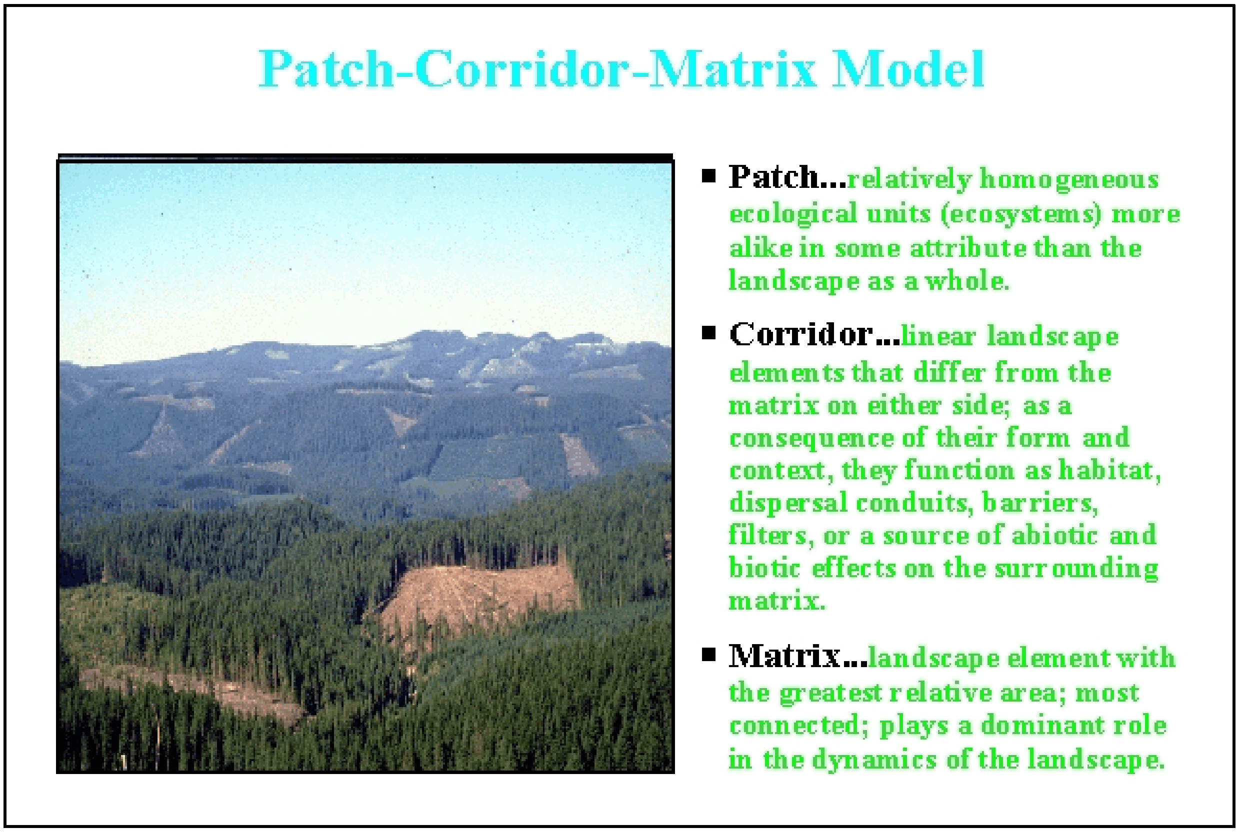
(2) *Linear network patterns* represent collections of linear landscape elements that intersect to form a network. A familiar example is a map of streams or riparian areas in a watershed, wherein the data consists of nodes and linkages (corridors that connect nodes); the intervening area is considered the matrix and is typically ignored (i.e., treated as ecologically neutral). Often, the nodes and corridors are further characterized by composition (e.g., vegetation type) and spatial character (e.g., width). As with point patterns, it is the geographic location and arrangement of nodes and corridors that is of primary interest. The goal of linear network pattern analysis with such data is to characterize the physical structure (e.g., corridor density, mesh size, network connectivity and circuitry) of the network, and a variety of metrics have been developed for this purpose (Forman 1995).

(3) *Surface patterns* represent quantitative measurements that vary continuously across the landscape; there are no explicit boundaries (i.e., patches are not delineated). Here, the data can be conceptualized as representing a three-dimensional surface, where the measured value at each geographic location is represented by the height of the surface. A familiar example is a digital elevation model, but any quantitative measurement can be treated this way (e.g., plant biomass, leaf area index, soil nitrogen, density of individuals). In many cases the data is collected at discrete sample locations separated by some distance. Analysis of the spatial dependencies (or autocorrelation) in the measured characteristic is the purview of geostatistics, and a variety of techniques exist for measuring the intensity and scale of this spatial autocorrelation (Legendre and Fortin 1989, Legendre and Legendre 1999). Techniques also exist that permit the kriging or modeling of these spatial patterns; that is, to interpolate values for unsampled locations using the empirically estimated spatial autocorrelation. These surface pattern techniques were developed to quantify spatial patterns from sampled data (n). When the data is exhaustive (i.e., the whole population, N) over the study landscape, like it is with the case of remotely sensed data, other techniques (e.g., two-dimensional spectral analysis, Ford and Renshaw 1984, Renshaw and Ford 1984, Legendre and Fortin 1989; or two-dimensional wavelet analysis, Bradshaw and Spies 1992) are more appropriate. All surface pattern techniques share a goal of describing the intensity and scale of pattern in the quantitative variable of interest. In all cases, while the location of the data points (or quadrats) is known and of interest, it is the values of the measurement taken at each point that are of primary concern. Here, the basic question is, "Are samples that are close together also similar with respect to the measured variable?" Alternatively, "What is the distance(s) over which values tend to be similar?"

(4) *Categorical (or thematic; choropleth) map patterns* represent data in which the system property of interest is represented as a mosaic of discrete patches. From an ecological perspective, patches represent relatively discrete areas of relatively homogeneous environmental conditions at a particular scale. The patch boundaries are distinguished by abrupt discontinuities (boundaries) in environmental character states from their surroundings of magnitudes that are relevant to the ecological phenomenon under consideration (Wiens 1976, Kotliar and Wiens 1990). A familiar example is a map of land cover types, wherein the data consists of polygons (vector format) or grid cells (raster format) classified into discrete land cover classes. There are a multitude of methods for deriving a categorical map (mosaic of patches) which has important implications for the interpretation of landscape pattern metrics (see below). Patches may be

classified and delineated qualitatively through visual interpretation of the data (e.g., delineating vegetation polygons through interpretation of aerial photographs), as is typically the case with vector maps constructed from digitized lines. Alternatively, with raster grids (constructed of grid cells), quantitative information at each location may be used to classify cells into discrete classes and to delineate patches by outlining them, and there are a variety of methods for doing this. The most common and straightforward method is simply to aggregate all adjacent (touching) areas that have the same (or similar) value on the variable of interest. An alternative approach is to define patches by outlining them: that is, by finding the edges around patches (Fortin 1994, Fortin and Drapeau 1995, Fortin et al. 2000). An edge in this case is an area where the measured value changes abruptly (i.e., high local variance or rate of change). An alternative is to use a divisive approach, beginning with a single patch (the entire landscape) and then successively partitioning this into regions that are statistically homogeneous patches (Pielou 1984). A final method to create patches is to cluster them hierarchically, but with a constraint of spatial adjacency (Legendre and Fortin 1989). Regardless of data format (raster or vector) and method of classifying and delineating patches, the goal of categorical map pattern analysis with such data is to characterize the composition and spatial configuration of the patch mosaic, and a plethora of metrics has been developed for this purpose (Forman and Godron 1986, O'Neill et al. 1988, Turner 1990, Musick and Grover 1991, Turner and Gardner 1991, Baker and Cai 1992, Gustafson and Parker 1992, Li and Reynolds 1993, McGarigal and Marks 1995, Jaeger 2000).

Although a large part of landscape pattern analysis deals with the identification of scale and intensity of pattern, landscape metrics focus on the characterization of the geometric and spatial properties of categorical map patterns represented at a particular scale (grain and extent). Thus, while it is important to recognize the variety of types of landscape patterns and goals of landscape pattern analysis, I will focus on landscape metrics as they are applied in landscape ecology.



PATCH-CORRIDOR-MATRIX MODEL

Landscapes are composed of elements–the spatial components that make up the landscape. A convenient and popular model for conceptualizing and representing the elements in a categorical map pattern is known as the *patch-corridor-matrix model* (Forman 1995). Under this model, three major landscape elements are typically recognized, and the extent and configuration of these elements defines the pattern of the landscape.

(1) *Patch*.--Landscapes are composed of a mosaic of patches (Urban et al. 1987). Landscape ecologists have used a variety of terms to refer to the basic elements or units that make up a landscape, including ecotope, biotope, landscape component, landscape element, landscape unit, landscape cell, geotope, facies, habitat, and site (Forman and Godron 1986). Any of these terms, when defined, are satisfactory according to the preference of the investigator. Like the landscape, patches comprising the landscape are not self-evident; patches must be defined relative to the phenomenon under consideration. For example, from a timber management perspective a patch may correspond to the forest stand. However, the stand may not function as a patch from a particular organism's perspective. From an ecological perspective, patches represent relatively discrete areas (spatial domain) or periods (temporal domain) of relatively homogeneous environmental conditions where the patch boundaries are distinguished by discontinuities in environmental character states from their surroundings of magnitudes that are perceived by or

relevant to the organism or ecological phenomenon under consideration (Wiens 1976). From a strictly organism-centered view, patches may be defined as environmental units between which fitness prospects, or "quality", differ; although, in practice, patches may be more appropriately defined by nonrandom distribution of activity or resource utilization among environmental units, as recognized in the concept of "Grain Response".

Patches are dynamic and occur on a variety of spatial and temporal scales that, from an organism-centered perspective, vary as a function of each animal's perceptions (Wiens 1976 and 1989, Wiens and Milne 1989). A patch at any given scale has an internal structure that is a reflection of patchiness at finer scales, and the mosaic containing that patch has a structure that is determined by patchiness at broader scales (Kotliar and Wiens 1990). Thus, regardless of the basis for defining patches, a landscape does not contain a single patch mosaic, but contains a hierarchy of patch mosaics across a range of scales. For example, from an organism-centered perspective, the smallest scale at which an organism perceives and responds to patch structure is its "grain" (Kotliar and Wiens 1990). This lower threshold of heterogeneity is the level of resolution at which the patch size becomes so fine that the individual or species stops responding to it, even though patch structure may actually exist at a finer resolution (Kolasa and Rollo 1991). The lower limit to grain is set by the physiological and perceptual abilities of the organism and therefore varies among species. Similarly, "extent" is the coarsest scale of heterogeneity, or upper threshold of heterogeneity, to which an organism responds (Kotliar and Wiens 1990, Kolasa and Rollo 1991). At the level of the individual, extent is determined by the lifetime home range of the individual (Kotliar and Wiens 1990) and varies among individuals and species. More generally, however, extent varies with the organizational level (e.g., individual, population, metapopulation) under consideration; for example the upper threshold of patchiness for the population would probably greatly exceed that of the individual. Therefore, from an organism-centered perspective, patches can be defined hierarchically in scales ranging between the grain and extent for the individual, deme, population, or range of each species.

Patch boundaries are artificially imposed and are in fact meaningful only when referenced to a particular scale (i.e., grain size and extent). For example, even a relatively discrete patch boundary between an aquatic surface (e.g., lake) and terrestrial surface becomes more and more like a continuous gradient as one progresses to a finer and finer resolution. However, most environmental dimensions possess 1 or more "domains of scale" (Wiens 1989) at which the individual spatial or temporal patches can be treated as functionally homogeneous; at intermediate scales the environmental dimensions appear more as gradients of continuous variation in character states. Thus, as one moves from a finer resolution to coarser resolution, patches may be distinct at some scales (i.e., domains of scale) but not at others.

KEY POINT *It is not my intent to argue for a particular definition of patch. Rather, I wish to point out the following: (1) that patch must be defined relative to the phenomenon under investigation or management; (2) that, regardless of the phenomenon under consideration (e.g., a species, geomorphological disturbances, etc), patches are dynamic and occur at multiple scales; and (3) that patch boundaries are only meaningful when referenced to a particular scale. It is* *incumbent upon the investigator or manager to establish the basis for delineating among patches and at a scale appropriate to the phenomenon under consideration.*

(2) *Corridor*.--Corridors are linear landscape elements that can be defined on the basis of structure or function. Forman and Godron (1986) define corridors as “narrow strips of land which differ from the matrix on either side. Corridors may be isolated strips, but are usually attached to a patch of somewhat similar vegetation.” These authors focus on the structural aspects of the linear landscape element. As a consequence of their form and context, structural corridors may function as habitat, dispersal conduits, or barriers. Three different types of structural corridors exist: (1) *line corridors*, in which the width of the corridor is too narrow to allow for interior environmental conditions to develop; (2) *strip corridors*, in which the width of the corridor is wide enough to allow for interior conditions to develop; and (3) *stream corridors*, which are a special category.

Corridors may also be defined on the basis of their function in the landscape. At least four major corridor functions have been recognized, as follows:

- Habitat Corridor.--Linear landscape element that provides for survivorship, natality, and movement (i.e., habitat), and may provide either temporary or permanent habitat. Habitat corridors passively increase landscape connectivity for the focal organism(s).

- Facilitated Movement Corridor.–Linear landscape element that provides for survivorship and movement, but not necessarily natality, between other habitat patches. Facilitated movement corridors actively increase landscape connectivity for the focal organism(s).

- Barrier or Filter Corridor.–Linear landscape element that prohibits (i.e., barrier) or differentially impedes (i.e., filter) the flow of energy, mineral nutrients, and/or species across (i.e., flows perpendicular to the length of the corridor). Barrier or filter corridors actively decrease matrix connectivity for the focal process.

- Source of Abiotic and Biotic Effects on the Surrounding Matrix.–Linear landscape element that modifies the inputs of energy, mineral nutrients, and/or species to the surrounding matrix and thereby effects the functioning of the surrounding matrix.

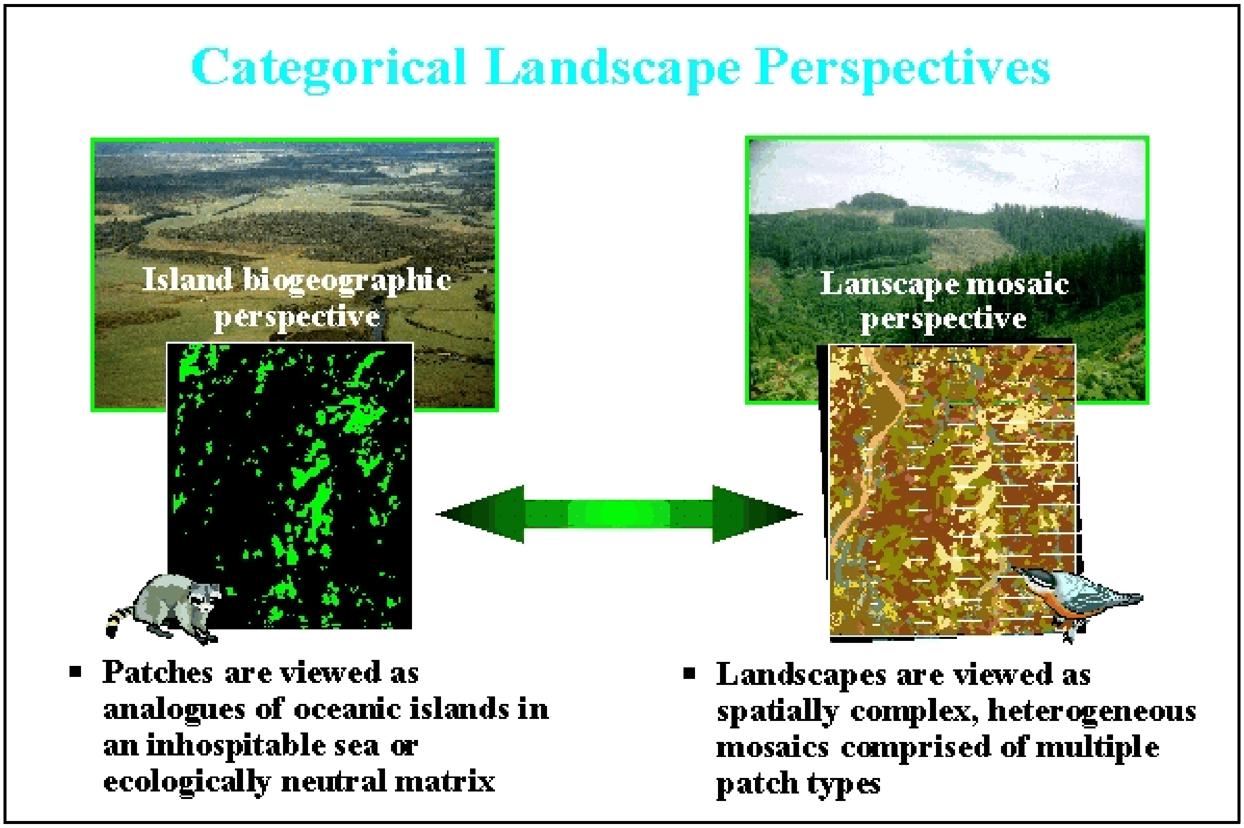
Most of the attention and debate has focused on *facilitated movement corridors*. It has been argued that this corridor function can only be demonstrated when the immigration rate to the target patch is increased over what it would be if the linear element was not present (Rosenberg et al. 1997). Unfortunately, as Rosenberg et al. point out, there have been few attempts to experimentally demonstrate this. In addition, just because a corridor can be distinguished on the basis of structure, it does not mean that it assumes any of the above functions. Moreover, the function of the corridor will vary among organisms due to the differences in how organisms perceive and scale the environment.

KEY POINT *Corridors are distinguished from patches by their linear nature and can be defined on the basis of either structure or function or both. If a corridor is specified, it is incumbent upon the investigator or manager to define the structure and implied function relative to the phenomena (e.g., species) under consideration.*

(3) *Matrix*.--A landscape is composed typically of several types of landscape elements (usually patches). Of these, the matrix is the most extensive and most connected landscape element type, and therefore plays the dominant role in the functioning of the landscape (Forman and Godron 1986). For example, in a large contiguous area of mature forest embedded with numerous small disturbance patches (e.g., timber harvest patches), the mature forest constitutes the matrix element type because it is greatest in areal extent, is mostly connected, and exerts a dominant influence on the area flora and fauna and ecological processes. In most landscapes, the matrix type is obvious to the investigator or manager. However, in some landscapes, or at a certain point in time during the trajectory of a landscape, the matrix element will not be obvious. Indeed, it may not be appropriate to consider any element as the matrix. Moreover, the designation of a matrix element is largely dependent upon the phenomenon under consideration. For example, in the study of geomorphological processes, the geological substrate may serve to define the matrix and patches; whereas, in the study of vertebrate populations, vegetation structure may serve to define the matrix and patches. In addition, what constitutes the matrix is dependent on the scale of investigation or management. For example, at a particular scale, mature forest may be the matrix with disturbance patches embedded within; whereas, at a coarser scale, agricultural land may be the matrix with mature forest patches embedded within.

It is important to understand how measures of landscape pattern are influenced by the designation of a matrix element. If an element is designated as matrix and therefore presumed to function as such (i.e., has a dominant influence on landscape dynamics), then it should not be included as another "patch" type in any metric that simply averages some characteristic across all patches (e.g., mean patch size, mean patch shape). Otherwise, the matrix will dominate the metric and serve more to characterize the matrix than the patches within the landscape, although this may itself be meaningful in some applications. From a practical standpoint, it is important to recognize this because in FRAGSTATS, the matrix can be excluded from calculations by designating its class value as background. If the matrix is not excluded from the calculations, it may be more meaningful to use the class-level statistics for each patch type and simply ignore the patch type designated as the matrix. From a conceptual standpoint, it is important to recognize that the choice and interpretation of landscape metrics must ultimately be evaluated in terms of their ecological meaningfulness, which is dependent upon how the landscape is defined, including the choice of patch types and the designation of a matrix.

KEY POINT *It is incumbent upon the investigator or manager to determine whether a matrix element exists and should be designated given the scale and phenomenon under consideration.*



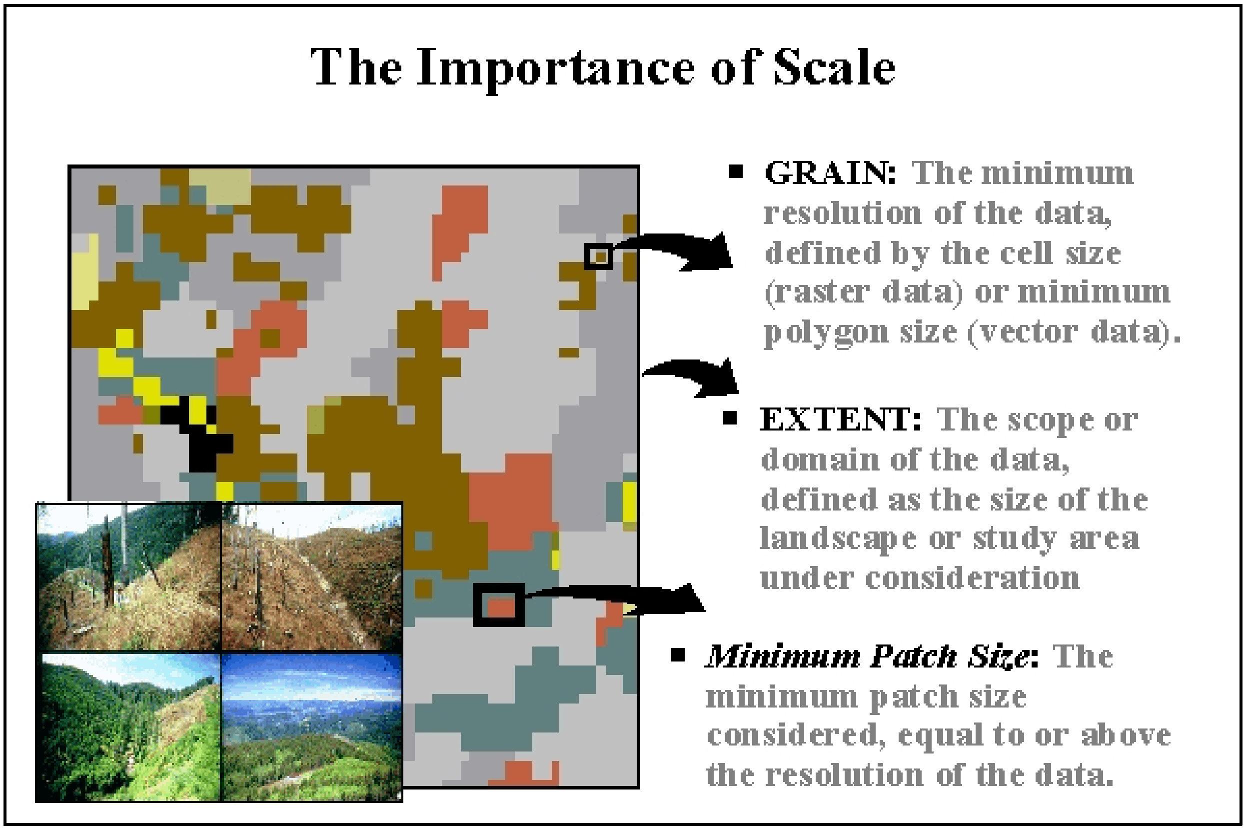
PERSPECTIVES ON CATEGORICAL LANDSCAPES

There are at least two different perspectives on categorical map patterns that have profoundly influenced the development of landscape metrics and have important implications for the choice and interpretation of individual landscape metrics.

(1) *Island Biogeographic Model*.–In the island biogeographic model, the emphasis is on a single patch type; disjunct patches (e.g., habitat fragments) are viewed as analogues of oceanic islands embedded in an inhospitable or ecologically neutral background (matrix). This perspective emerged from the theory of island biogeography (MacArthur and Wilson 1967) and subsequent interest in habitat fragmentation (Saunders et al. 1991). Under this perspective, there is a binary patch structure in which the focal patches (fragments) are embedded in a neutral matrix. Here, the emphasis is on the extent, spatial character, and distribution of the focal patch type without explicitly considering the role of the matrix. Under this perspective, for example, connectivity may be assessed by the spatial aggregation of the focal patch type without consideration of how intervening patches affect the functional connectedness among patches of the focal class. The island biogeography perspective has been the dominant perspective since inception of the theory. The major advantage of the island model is its simplicity. Given a focal patch type, it is quite simple to represent the structure of the landscape in terms of focal patches contrasted sharply against a uniform matrix, and it is relatively simple to devise metrics that quantify this structure.

Moreover, by considering the matrix as ecologically neutral, it invites ecologists to focus on those patch attributes, such as size and isolation, that have the strongest effect on species persistence at the patch level. The major disadvantage of the strict island model is that it assumes a uniform and neutral matrix, which in most real-world cases is a drastic over-simplification of how organisms interact with landscape patterns.

(2) ***Landscape Mosaic Model***.–In the landscape mosaic model, landscapes are viewed as spatially complex, heterogeneous assemblages of patch types, which can not be simply categorized into discrete elements such as patches, matrix, and corridors (With 2000). Rather, the landscape is viewed from the perspective of the organism or process of interest. Patches are bounded by patches of other patch types that may be more or less similar to the focal patch type, as opposed to highly contrasting and often hostile habitats, as in the case of the island model. Connectivity, for example, may be assessed by the extent to which movement is facilitated or impeded through different patch types across the landscape. The landscape mosaic perspective derives from landscape ecology (Forman 1995) and has only recently emerged as a viable alternative to the island biogeographic model. The major advantage of the landscape mosaic model is its more realistic representation of how organisms perceive and interact with landscape patterns. Few organisms, for example, exhibit a binary (all or none) response to habitats (patch types), but rather use habitats proportionate to the fitness they confer to the organism. Moreover, movement among suitable habitat patches usually is a function of the character of the intervening habitats. The major disadvantage of the landscape mosaic model is that it requires detailed understanding of how organisms interact with landscape pattern, and this has delayed the development of additional metrics that adopt this perspective.

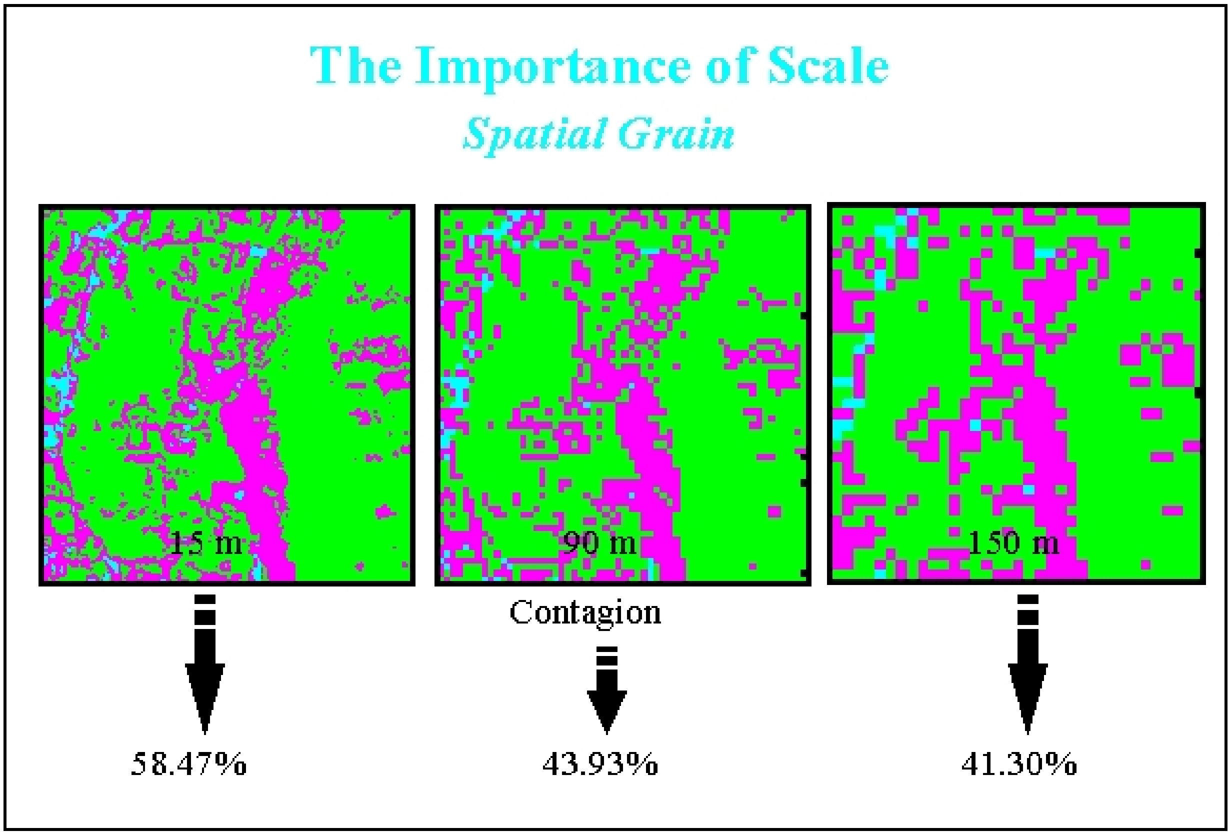


THE IMPORTANCE OF SCALE

Scientists nearly universally recognize the central role that scale plays in determining the outcome of observations (Levin 1992, Schneider 1994, Peterson and Parker 1998). There are at least two different aspects of scale regarding categorical map patterns that have important implications for the choice and interpretation of individual landscape metrics.

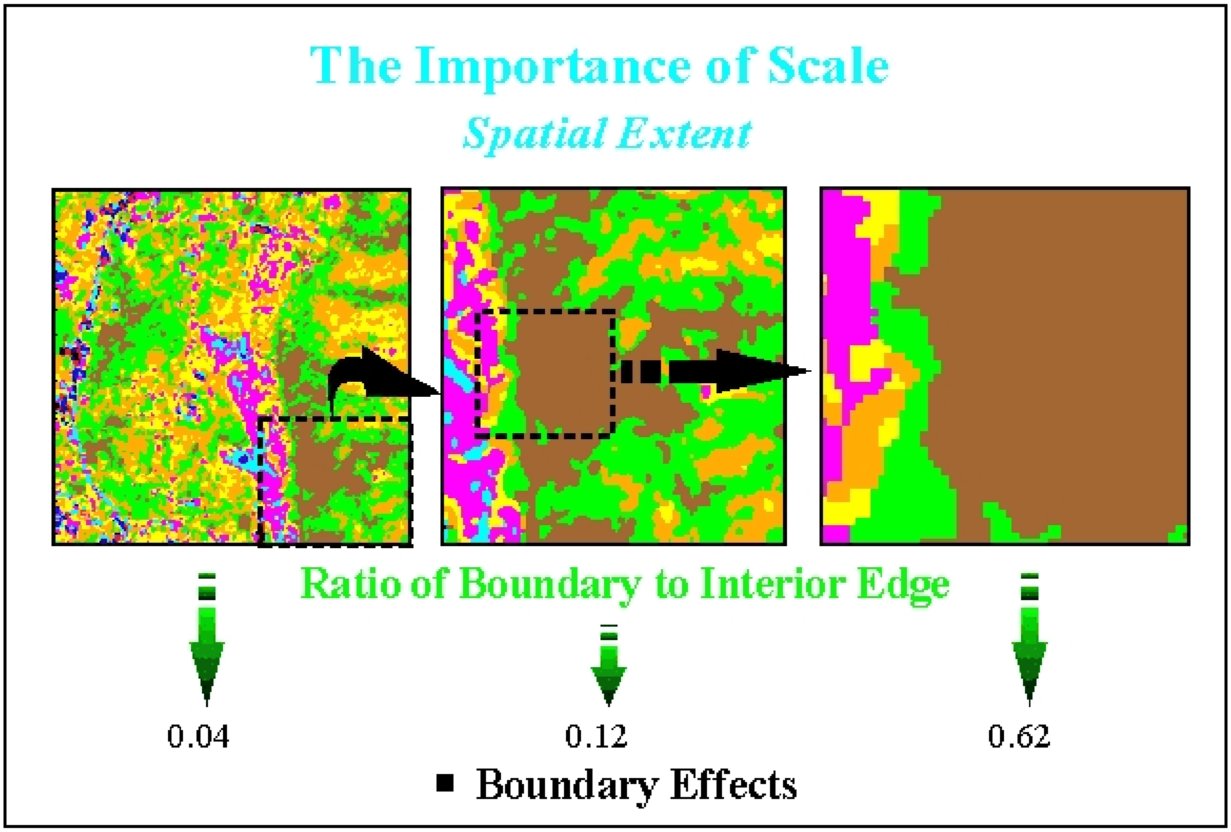
(1) Spatial Scale.--The pattern detected in any ecological mosaic is a function of scale, and the ecological concept of spatial scale encompasses both extent and grain (Forman and Godron 1986, Turner et al. 1989, Wiens 1989). *Extent* is simply the spatial domain over which the system is studied and for which data are available; i.e., the overall area encompassed by an investigation or the area included within the landscape boundary. From a statistical perspective, the spatial extent of an investigation is the area defining the population we wish to sample. *Grain* is the size of the individual units of observation, often denoted as patches or as pixels. The grain defines the smallest entities that can be distinguished. For example, a fine-grained map might structure information into 1-ha units, whereas a map with an order of magnitude coarser resolution would have information structured into 10-ha units (Turner et al. 1989).

Extent and grain define the upper and lower limits of resolution of a study and any inferences about scale-dependency in a system are constrained by the extent and grain of investigation



(Wiens 1989). In other words, extent and grain set the bounds on the generality and scope of inferences. Other processes may be operating in different regions, or at broader or finer scales in the same region, but conclusions must be bound within the extent and grain of the study. From a statistical perspective, we cannot extrapolate beyond the population sampled, nor can we infer differences among objects smaller than the experimental units. Likewise, in the assessment of landscape pattern, we cannot detect pattern or infer processes acting beyond the extent of the landscape or below the resolution of the grain (Wiens 1989).

In practice, extent and grain are often dictated by the scale of the imagery (e.g., aerial photos, Landsat images) being used or the technical capabilities of the computing environment. However, it may be more ecologically meaningful to define scale from the perspective of the organism or ecological phenomenon under consideration. As with the concept of landscape and patch, it may be more ecologically meaningful to define scale from the perspective of the organism or ecological phenomenon under consideration. For example, from an organism-centered perspective, grain and extent may be defined as the degree of acuity of a stationary organism with respect to short- and long-range perceptual ability (Kolasa and Rollo 1991). Thus, grain is the finest component of the environment that can be differentiated up close by the organism, and extent is the range at which a relevant object can be distinguished from a fixed vantage point by the organism (Kolasa and Rollo 1991). Unfortunately, while this is ecologically an ideal way to define scale, it is not very pragmatic.

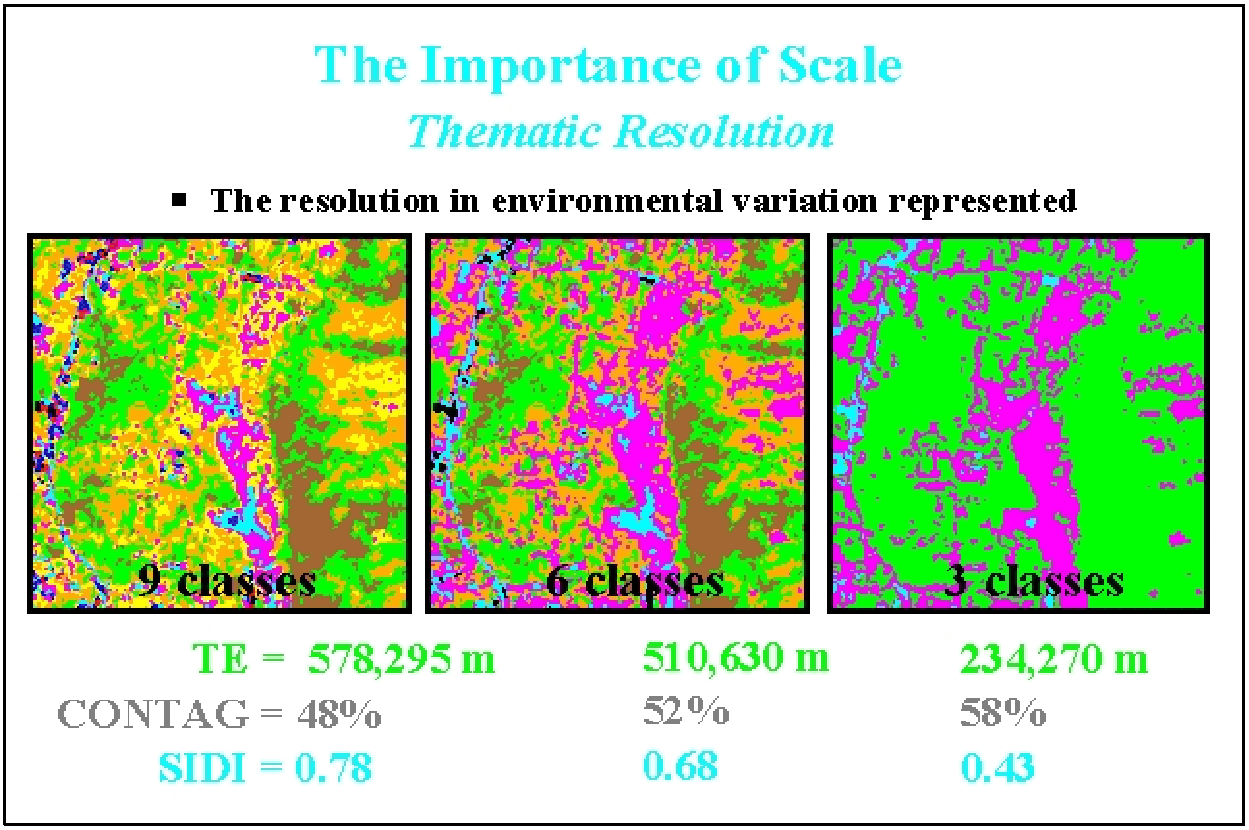


It is critical that extent and grain be defined for a particular study and represent, to the greatest possible degree, the ecological phenomenon or organism under study; otherwise, the landscape patterns detected will have little meaning and there is a good chance of reaching erroneous conclusions. For example, it would be meaningless to define grain as 1-ha units when the organism under consideration perceives and responds to habitat patches at a resolution of 1-m^2. A strong landscape pattern at the 1-ha resolution may have no significance to the organism under study. Similarly, it would be meaningless to define the landscape extent as 1-km^2 when the organism under consideration has a home range size several times that size. Typically, however, we do not know what the appropriate resolution should be. In this case, it is much safer to choose a finer grain than is believed to be important because the grain sets the minimum resolution of investigation. Once set, we can always resample to a coarser grain. In addition, we can always specify a minimum mapping unit that is coarser than the grain. That is, we can specify the minimum patch size to be represented in a landscape, and this can easily be manipulated above the grain size. Indeed, it may be useful to reanalyze the same landscape using progressively coarser minimum patch sizes to better assess landscape heterogeneity across a range of potentially relevant scales. Thompson and McGarigal (2002) used this approach successfully to define the "best" scale (grain and extent) for representing bald eagle habitat along the Hudson River, New York.

It is important to recognize the practical implications of the choice of grain and extent for a particular application. Many of the landscape metrics are particularly sensitive to grain. Metrics involving edge or perimeter will be affected; edge lengths will be biased upwards in proportion to the grain size–larger grains result in greater bias. Edge lengths can vary by as much as 25-50% over vector calculations depending on grain size. Metrics based on cell adjacency information such as the contagion index of Li and Reynolds (1993) will be affected as well, because grain size effects the proportional distribution of adjacencies. In this case, as resolution is increased (grain size reduced), the proportional abundance of like adjacencies (cells of the same class) increases, and the measured contagion increases. Similarly, the measured landscape patterns will often vary with extent. Intuitively this makes sense, because as the landscape extent increases, new patch types may be encountered and habitat configurations may change in response to underlying environmental or land use gradients.

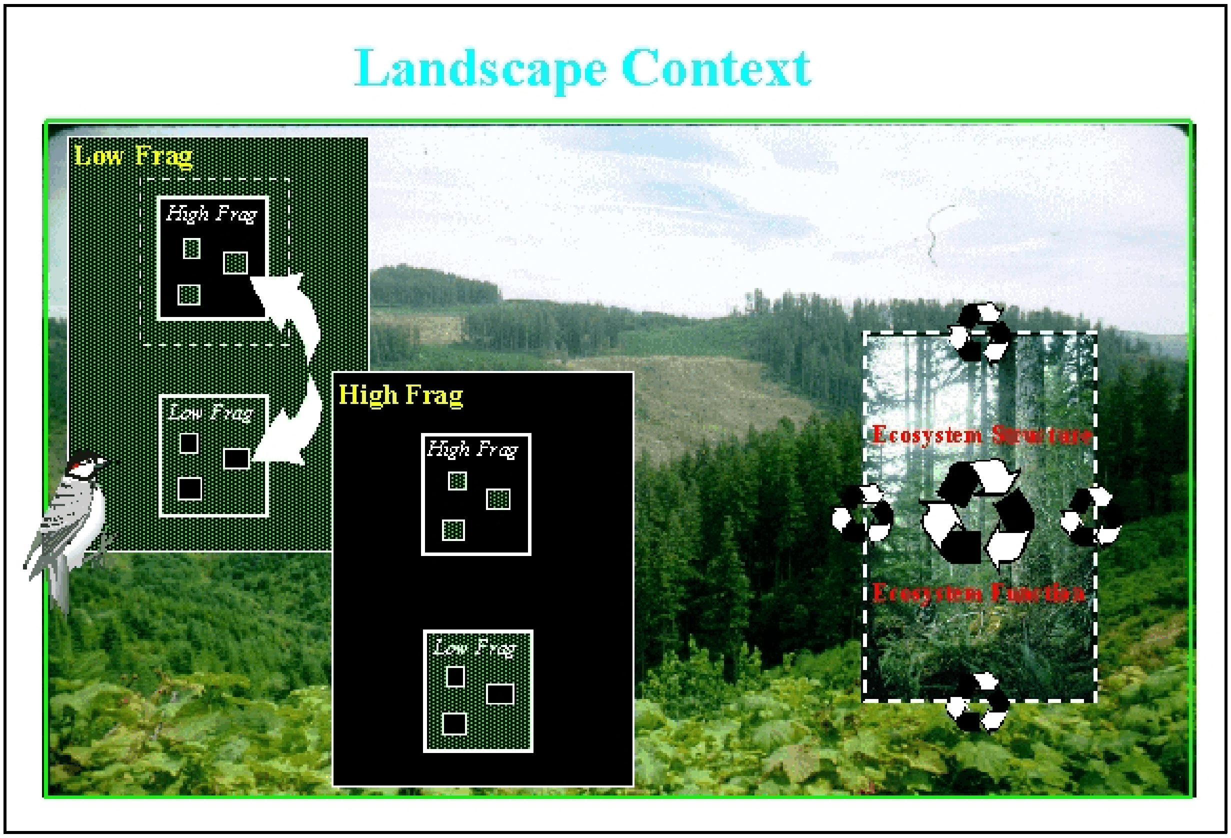
The ratio of grain to extent for a particular analysis warrants consideration as well. If the ratio is very small (i.e., a coarse-grained map), then the landscape dynamics are likely to be dominated by boundary effects, analogous to the bias associated with small sample size in statistics. Moreover, the boundary of the landscape can have a profound influence on the value of certain metrics. Landscape metrics are computed solely from patches contained within the landscape boundary. If the landscape extent is small relative to the scale of the organism or ecological process under consideration and the landscape is an “open” system relative to that organism or process, then any metric will have questionable meaning. Metrics based on nearest neighbor distance or employing a search radius can be particularly misleading. Consider, for example, a local population of a bird species occupying a patch near the boundary of a somewhat arbitrarily defined landscape. The nearest neighbor within the landscape boundary might be quite far away; yet, in reality, the closest patch might be very close but just outside the designated landscape boundary. In addition, those metrics that employ a search radius (e.g., proximity index) will be biased for patches near the landscape boundary because the searchable area will be much less than a patch in the interior of the landscape. In general, boundary effects will increase as the landscape extent decreases relative to the patchiness or heterogeneity of the landscape. The key point is that some landscape metrics are likely to be very sensitive to this ratio (e.g., those based on nearest-neighbor distances such as the mean proximity index; Gustafson and Parker 1992).

Information may be available at a variety of scales and it may be necessary to extrapolate information from one scale to another. In addition, it may be necessary to integrate data represented at different spatial scales. It has been suggested that information can be transferred across scales if both grain and extent are specified (Allen et al. 1987), yet it is unclear how observed landscape patterns vary in response to changes in grain and extent. The limited work on this topic suggests that qualitative and quantitative changes in measurements across spatial scales will differ depending on how scale is defined (Turner et al. 1989) and that metrics vary markedly in their sensitivity to scale and the nature of the scaling relationships (Wickham and Riitters 1995, O'Neill et al. 1996, Saura and Martinez-Millan 2001, Saura 2002, Wu et al. 2002). In investigations of landscape structure, until more is learned, any attempts to compare landscapes measured at different scales should be done cautiously.



(2) <u>*Thematic Resolution*</u>.–Another critical, but often overlooked, nonspatial aspect of scale in categorical landscapes is the thematic resolution, representing the degree of environmental variation discriminated by a given classification variable. A single variable may be recorded at any number of resolutions. For example, land cover may be classified as either forest or nonforest, or as conifer, hardwood, mixed forest, shrubland, grassland, etc., or into even finer classifications. The choice of thematic resolution has dramatic influences on the types of associations that can be made and on the nature of the patterns that can be mapped from that variable.

KEY POINT *The key point here is that any model of landscape structure requires an explicit identification of scale. Unfortunately, in many applications, scale is selected arbitrarily or defined by technical considerations and the ecological significance of the scale-imposed limitations are dismissed or not recognized. In any landscape structural analysis, it is incumbent upon the investigator or manager (1) to select a scale (i.e., extent, grain, minimum mapping unit, thematic resolution) that is appropriate to the phenomenon under consideration, because any interpretation of landscape structure is ultimately constrained by the scale; (2).to describe any observed patterns or relationships relative to the scale of observation; and (3) to be especially cautious when attempting to compare landscapes measured at different scales.*

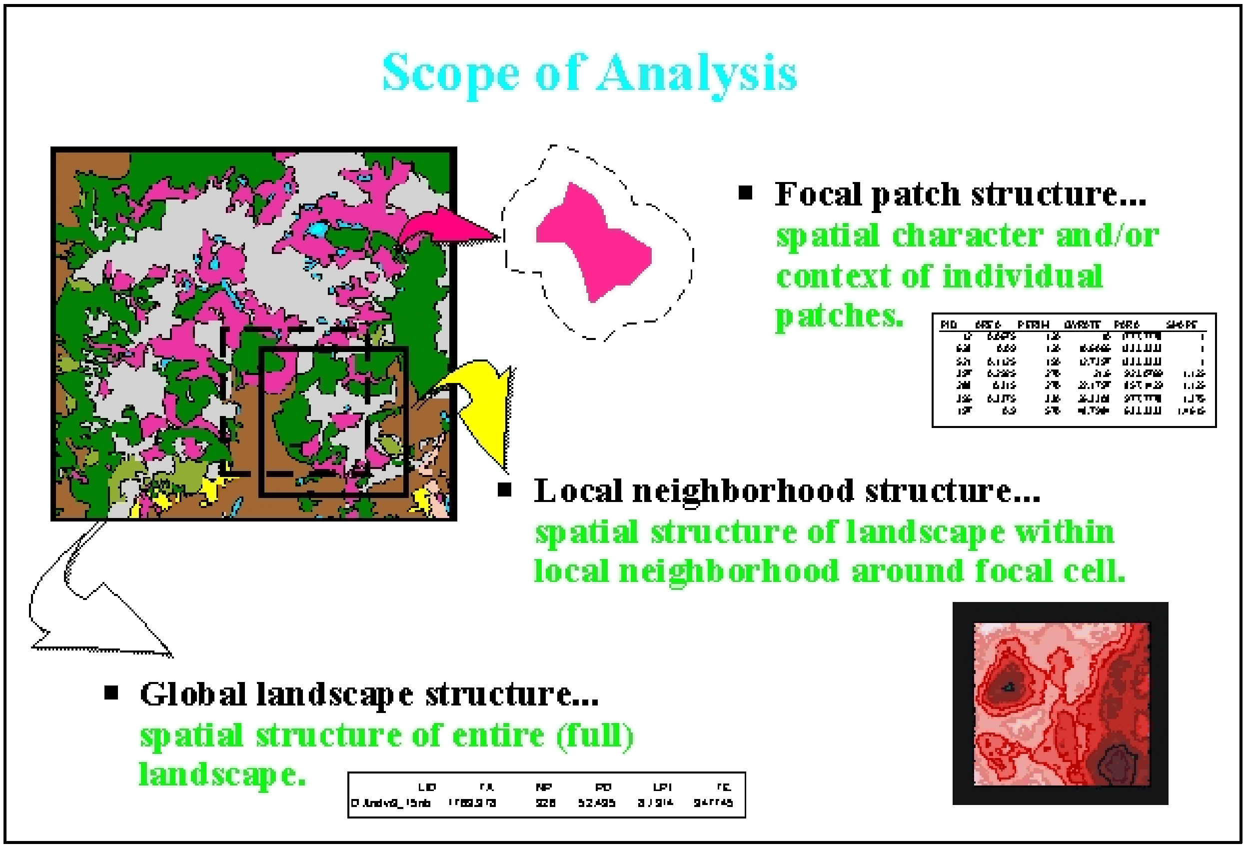


LANDSCAPE CONTEXT

Landscapes do not exist in isolation. Landscapes are nested within larger landscapes, that are nested within larger landscapes, and so on. In other words, each landscape has a context or regional setting, regardless of scale and how the landscape is defined. The landscape context may constrain processes operating within the landscape. Landscapes are "open" systems; energy, materials, and organisms move into and out of the landscape. This is especially true in practice, where landscapes are often somewhat arbitrarily delineated. That broad-scale processes act to constrain or influence finer-scale phenomena is one of the key principles of hierarchy theory (Allen and Star 1982) and 'supply-side' ecology (Roughgarden et al. 1987). The importance of the landscape context is dependent on the phenomenon of interest, but typically varies as a function of the "openness" of the landscape. The "openness" of the landscape depends not only on the phenomenon under consideration, but on the basis used for delineating the landscape boundary. For example, from a geomorphological or hydrological perspective, the watershed forms a natural landscape, and a landscape defined in this manner might be considered relatively "closed". Of course, energy and materials flow out of this landscape and the landscape context influences the input of energy and materials by affecting climate and so forth, but the system is nevertheless relatively closed. Conversely, from the perspective of a bird population, topographic boundaries may have little ecological relevance, and the landscape defined on the basis of watershed boundaries might be considered a relatively "open" system. Local bird abundance patterns may be produced not only by local processes or events operating within the designated landscape, but also by the dynamics of regional populations or events elsewhere in the species' range (Wiens 1981, 1989b, Vaisanen et al. 1986, Haila et al. 1987, Ricklefs 1987).

Landscape metrics quantify the pattern of the landscape within the designated landscape boundary only. Consequently, the interpretation of these metrics and their ecological significance requires an acute awareness of the landscape context and the openness of the landscape relative to the phenomenon under consideration. These concerns are particularly important for nearest-neighbor metrics. Nearest-neighbor distances are computed solely from patches contained within the landscape boundary. If the landscape extent is small relative to the scale of the organism or ecological processes under consideration and the landscape is an "open" system relative to that organism or process, then nearest-neighbor results can be misleading. Consider a small subpopulation of a species occupying a patch near the boundary of a somewhat arbitrarily defined (from the organism's perspective) landscape. The nearest neighbor within the landscape boundary might be quite far away, yet in reality the closest patch might be very close, but just outside the landscape boundary. The magnitude of this problem is a function of scale. Increasing the size of the landscape relative to the scale at which the organism under investigation perceives and responds to the environment will generally decrease the severity of this problem. In general, the larger the ratio of extent to grain (i.e., the larger the landscape relative to the average patch size), the less likely these and other metrics will be dominated by boundary effects.

KEY POINT *The important point is that a landscape should be defined relative to both the patch mosaic within the landscape as well as the landscape context. Moreover, consideration should always be given to the landscape context and the openness of the landscape relative to the phenomenon under consideration when choosing and interpreting landscape metrics.*



SCOPE OF ANALYSIS

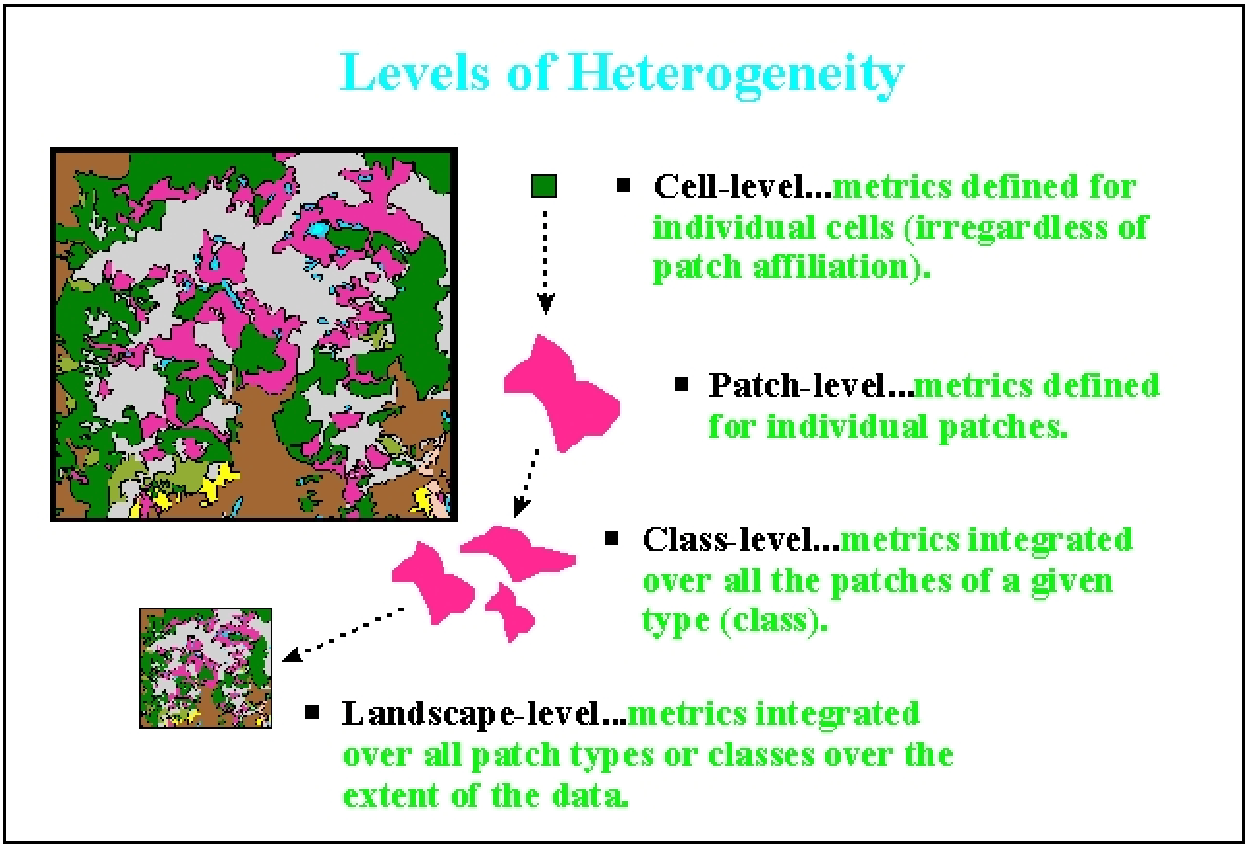
The scope of analysis pertains to the scale and or focus of the investigation. There are three levels of analysis that represent fundamentally different conceptualizations of landscape patterns and that have important implications for the choice and interpretation of individual landscape metrics and the form of the results.

(1) *Focal patch analysis*.–Under the patch mosaic model of landscape structure the focus of the investigation may be on individual patches (instead of the aggregate properties of patches); specifically, the spatial character and/or context of individual focal patches. This is a "patch-centric" perspective on landscape patterns in which the scope of analysis is restricted to the characterization of individual focal patches. In this case, each focal patch is characterized according to one or more patch-level metrics (see below). The results of a focal patch analysis is typically given in the form of a table, where each row represents a separate patch and each column represents a separate patch metric.

(2) *Local landscape structure*.–In many applications it may be appropriate to assume that organisms experience landscape structure as local pattern gradients that vary through space according to the perception and influence distance of the particular organism or process. Thus, instead of analyzing global landscape patterns, e.g., as measured by conventional landscape

metrics for the entire landscape (see below), we would be better served by quantifying the local landscape pattern across space as it may be experienced by the organism of interest, given their perceptual abilities. The local landscape structure can be examined by passing a “moving window” of fixed or variable size across the landscape one cell at a time. The window size and form should be selected such that it reflects the scale and manner in which the organism perceives or responds to pattern. If this is unknown, the user can vary the size of the window over several runs and empirically determine which scale the organism is most responsive to. The window moves over the landscape one cell at a time, calculating the selected metric within the window and returning that value to the center cell. The result is a continuous surface which reflects how an organism of that perceptual ability would perceive the structure of the landscape as measured by that metric. The surface then would be available for combination with other such surfaces in multivariate models to predict, for example, the distribution and abundance of an organism continuously across the landscape.

(3) *Global landscape structure*.–The traditional application of landscape metrics involves characterizing the structure of the entire landscape with one or more landscape metrics. For example, traditional landscape pattern analysis would measure the total contrast-weighted edge density for the entire landscape. This would be a global measure of the average property of that landscape. This is a “landscape-centric” perspective on landscape patterns in which the scope of analysis is restricted to the characterization of the entire patch mosaic in aggregate. In this case, the landscape is characterized according to one or more landscape-level metrics (see below). The results of a global landscape structure analysis is typically given in the form of a vector of measurements, where each element represents a separate landscape metric.



LEVELS OF HETEROGENEITY

Patches form the basis (or building blocks) for categorical maps. Depending on the method used to derive patches (and therefore the data available), they can be characterized compositionally in terms of variables measured within them. This may include the mean (or mode, central, or max) value and internal heterogeneity (variance, range). However, in most applications, once patches have been established, the within-patch heterogeneity is ignored. Landscape pattern metrics instead focus on the spatial character and distribution of patches. While individual patches possess relatively few fundamental spatial characteristics (e.g., size, perimeter, and shape), collections of patches may have a variety of aggregate properties, depending on whether the aggregation is over a single class (patch type) or multiple classes, and whether the aggregation is within a specified subregion of a landscape or across the entire landscape. Thus, the common hierarchical organization of categorical maps is patch→class→landscape. However, the fundamental spatial unit in a grid or raster data model is the cell. Therefore, for grid representations of categorical patterns, the cell represents an additional (and finest) level of heterogeneity.

(1) *Cell-level metrics* are defined for individual cells, and characterize the spatial context or ecological neighborhood of each cell without explicit regard to any patch or class affiliation. In other words, cell metrics are not patch-centric. Cell metrics provide the finest spatial unit of

resolution for characterizing spatial patterns. Each cell has a spatial context defined by the composition and configuration of its neighborhood, and that context may influence the ecological properties of the focal cell. For example, an individual organism dispersing from its natal habitat interacts with the structure of the landscape in the neighborhood surrounding that initial location. Thus, the ability to traverse across the landscape from that location may be a function of the landscape character within some ecological neighborhood defined by dispersal distance. Cell metrics may be computed for a targeted set of focal cells representing specific locations of interest (e.g., nest sites, capture locations, etc.), in which case the standard output would consist of a vector of cell-based measurements reported in tabular form (i.e., one record for each focal cell). Cell metrics may also be computed exhaustively for every cell in the landscape, in which case the standard output would consist of a continuous surface grid or map.

(2) *Patch-level metrics* are defined for individual patches, and characterize the spatial character and context of patches. In most applications, patch metrics serve primarily as the computational basis for several of the landscape metrics, for example by averaging patch attributes across all patches in the class or landscape; the computed values for each individual patch may have little interpretive value. However, sometimes patch indices can be important and informative in landscape-level investigations. For example, many vertebrates require suitable habitat patches larger than some minimum size (e.g., Robbins et al. 1989), so it would be useful to know the size of each patch in the landscape. Similarly, some species are adversely affected by edges and are more closely associated with patch interiors (e.g., Temple 1986), so it would be useful to know the size of the core area for each patch in the landscape. The probability of occupancy and persistence of an organism in a patch may be related to patch insularity (sensu Kareiva 1990), so it would be useful to know the nearest neighbor of each patch and the degree of contrast between the patch and its neighborhood. The utility of the patch characteristic information will ultimately depend on the objectives of the investigation.

(3) *Class-level metrics* are integrated over all the patches of a given type (class). These may be integrated by simple averaging, or through some sort of weighted-averaging scheme to bias the estimate to reflect the greater contribution of large patches to the overall index. There are additional aggregate properties at the class level that result from the unique configuration of patches across the landscape. In many applications, the primary interest is in the amount and distribution of a particular patch type. A good example is in the study of habitat fragmentation. Habitat fragmentation is a landscape-level process in which contiguous habitat is progressively sub-divided into smaller, geometrically more complex (initially, but not necessarily ultimately), and more isolated habitat fragments as a result of both natural processes and human land use activities (McGarigal and McComb 1999). This process involves changes in landscape composition, structure, and function and occurs on a backdrop of a natural patch mosaic created by changing landforms and natural disturbances. Habitat loss and fragmentation is the prevalent trajectory of landscape change in several human-dominated regions of the world, and is increasingly becoming recognized as a major cause of declining biodiversity (Burgess and Sharpe 1981, Whitcomb et al. 1981, Noss 1983, Harris 1984, Wilcox and Murphy 1985, Terborgh 1989, Noss and Cooperrider 1994). Class indices separately quantify the amount and spatial configuration of each patch type and thus provide a means to quantify the extent and

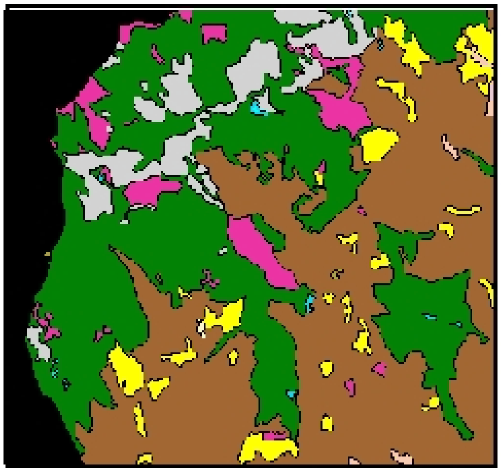
fragmentation of each patch type in the landscape.

(4) ***Landscape-level metrics*** are integrated over all patch types or classes over the full extent of the data (i.e., the entire landscape). Like class metrics, these may be integrated by a simple or weighted averaging, or may reflect aggregate properties of the patch mosaic. In many applications, the primary interest is in the pattern (i.e., composition and configuration) of the entire landscape mosaic. A good example is in the study of wildlife communities. Aldo Leopold (1933) noted that wildlife diversity was greater in more diverse and spatially heterogenous landscapes. Thus, the quantification of landscape diversity and heterogeneity has assumed a preeminent role in landscape ecology. Indeed, the major focus of landscape ecology is on quantifying the relationships between landscape pattern and ecological processes. Consequently, much emphasis has been placed on developing methods to quantify landscape pattern (e.g., O'Neill et al. 1988, Li 1990, Turner 1990, Turner and Gardner 1991) and a great variety of landscape-level metrics have been developed for this purpose.

It is important to note that while most metrics at higher levels are derived from patch-level attributes, not all metrics are defined at all levels. In particular, collections of patches at the class and landscape level have aggregate properties that are undefined (or trivial) at lower levels. The fact that most higher-level metrics are derived from the same patch-level attributes has the further implication that many of the metrics are correlated. Thus, they provide similar and perhaps redundant information (see below). Even though many of the class- and landscape-level metrics represent the same fundamental information, naturally the algorithms differ slightly (see below).

In addition, while many metrics have counterparts at all levels, their interpretations may be somewhat different. Patch-level metrics represent the spatial character and context of individual patches. Class-level metrics represent the amount and spatial distribution of a single patch type and may be interpreted as fragmentation indices. Landscape-level metrics represent the spatial pattern of the entire landscape mosaic and may be interpreted more broadly as landscape heterogeneity indices because they measure the overall landscape structure. Hence, it is important to interpret each metric in a manner appropriate to its level (patch, class, or landscape).

Components of Landscape Structure

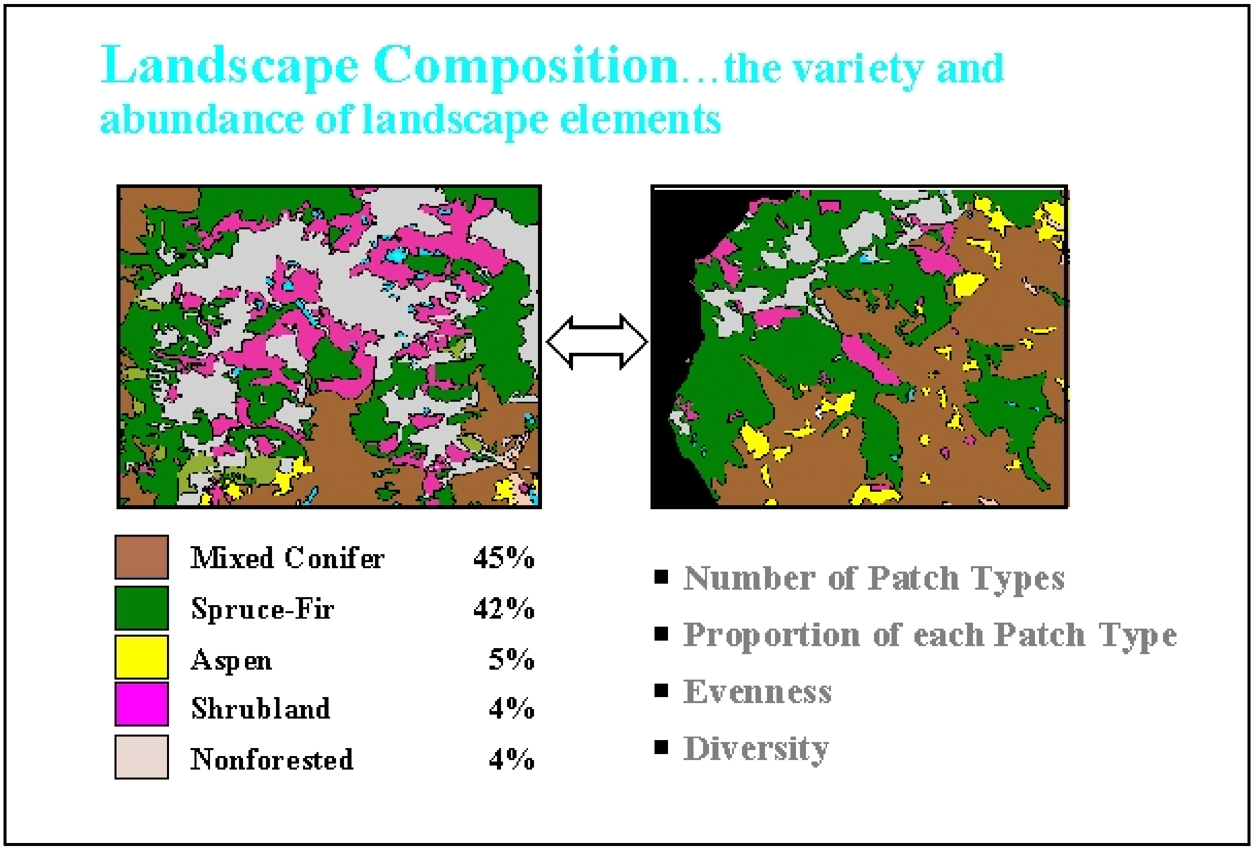


- **Landscape Composition...**the variety and abundance of landscape elements.
- **Landscape Configuration...**the spatial characteristics and distribution of landscape elements.

COMPONENTS OF LANDSCAPE STRUCTURE

The common usage of the term “landscape metrics” refers to indices developed for categorical map patterns. Landscape metrics are algorithms that quantify specific spatial characteristics of patches, classes of patches, or entire landscape mosaics. A plethora of metrics has been developed to quantify categorical map patterns. An exhaustive review of all published metrics, therefore, is beyond the scope of this chapter. These metrics fall into two general categories: those that quantify the *composition* of the map without reference to spatial attributes, and those that quantify the *spatial configuration* of the map, requiring spatial information for their calculation (McGarigal and Marks 1995, Gustafson 1998).

Composition is easily quantified and refers to features associated with the variety and abundance of patch types within the landscape, but without considering the spatial character, placement, or location of patches within the mosaic. Because composition requires integration over all patch types, composition metrics are only applicable at the landscape-level. There are many quantitative measures of landscape composition, including the proportion of the landscape in each patch type, patch richness, patch evenness, and patch diversity. Indeed, because of the many ways in which diversity can be measured, there are literally hundreds of possible ways to quantify landscape composition. Unfortunately, because diversity indices are derived from the indices used to summarize species diversity in community ecology, they suffer the same



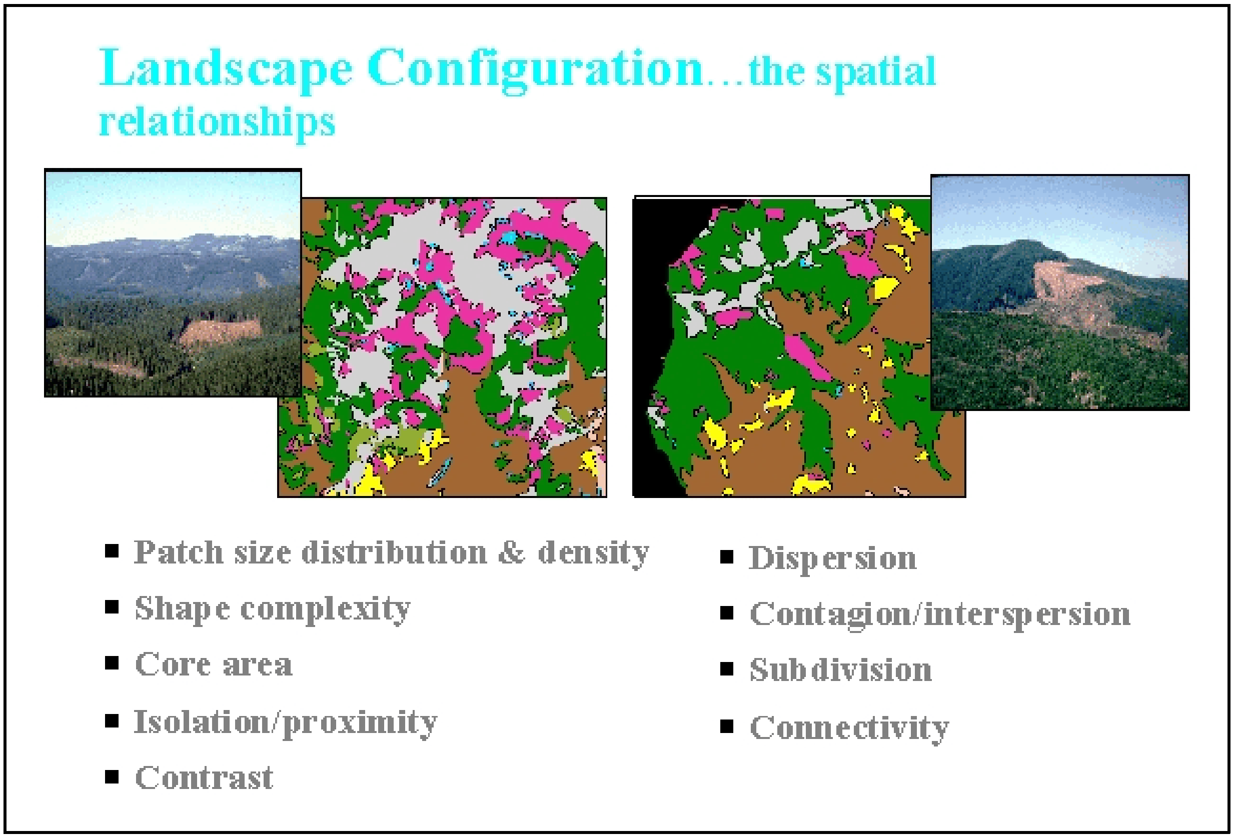
interpretative drawbacks. It is incumbent upon the investigator or manager to choose the formulation that best represents their concerns. The principle measures of composition are:

- *Proportional Abundance of each Class*.–One of the simplest and perhaps most useful pieces of information that can be derived is the proportion of each class relative to the entire map.

- *Richness*.--Richness is simply the number of different patch types.

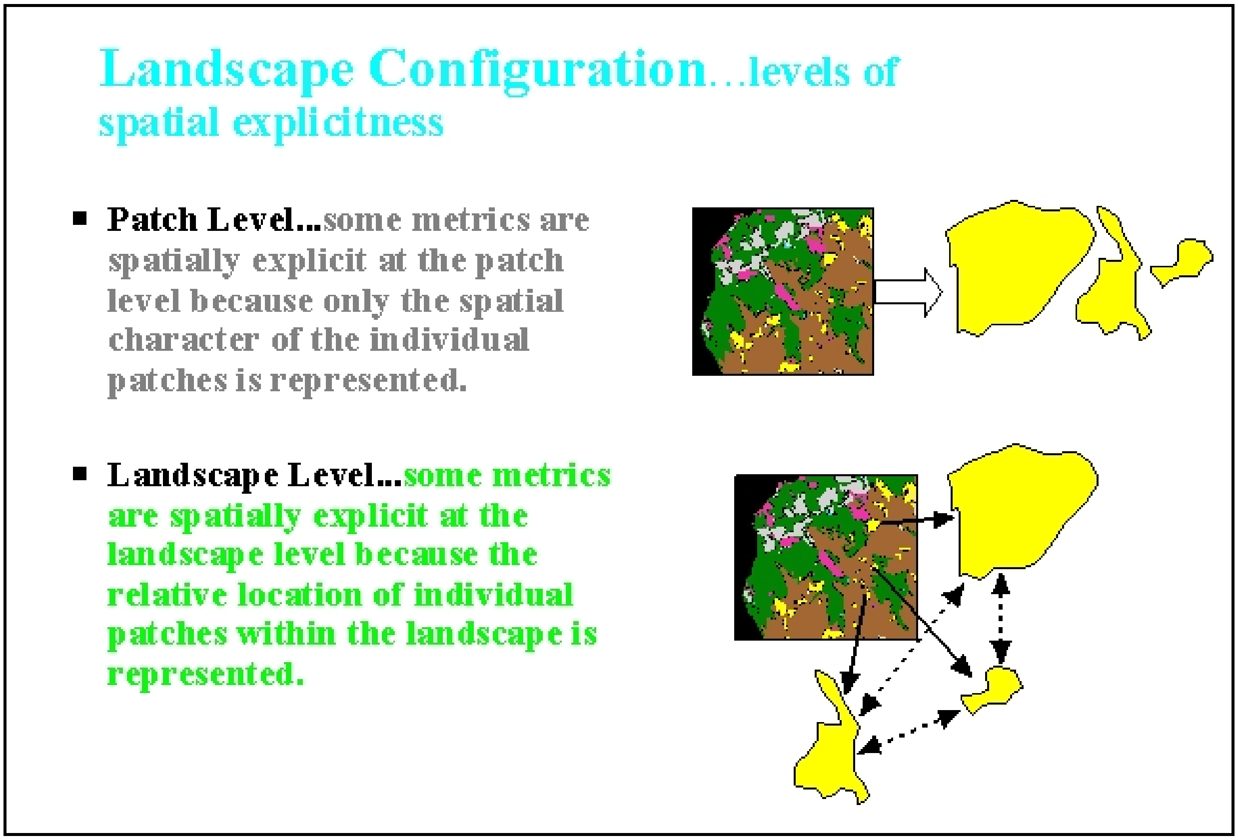
- *Evenness*.--Evenness is the relative abundance of different patch types, typically emphasizing either relative dominance or its compliment, equitability. There are many possible evenness measures corresponding to the many diversity measures. Evenness is usually reported as a function of the maximum diversity possible for a given richness; i.e., evenness is given as 1 when the patch mosaic is perfectly diverse given the observed patch richness, and approaches 0 as evenness decreases. Evenness is sometimes reported as its complement, dominance, by subtracting the observed diversity from the maximum for a given richness. In this case, dominance approaches 0 for maximum equitability and increases >0 for higher dominance.

- *Diversity*.--Diversity is a composite measure of richness and evenness and can be computed in a variety of forms (e.g., Shannon and Weaver 1949, Simpson 1949), depending on the relative emphasis placed on these two components.



Spatial configuration is much more difficult to quantify and refers to the spatial character and arrangement, position, or orientation of patches within the class or landscape. Some aspects of configuration, such as patch isolation or patch contagion, are measures of the placement of patch types relative to other patches, other patch types, or other features of interest. Other aspects of configuration, such as shape and core area, are measures of the spatial character of the patches. There are many aspects of configuration and the literature is replete with methods and indices developed for representing them (see previous references).

Configuration can be quantified in terms of the landscape unit itself (i.e., the patch). The spatial pattern being represented is the spatial character of the individual patches, even though the aggregation is across patches at the class or landscape level. The location of patches relative to each other is not explicitly represented. Metrics quantified in terms of the individual patches (e.g., mean patch size and shape) are spatially explicit at the level of the individual patch, not the class or landscape. Such metrics represent a recognition that the ecological properties of a patch are influenced by the surrounding neighborhood (e.g., edge effects) and that the magnitude of these influences are affected by patch size and shape. These metrics simply quantify, for the class or landscape as a whole, some attribute of the statistical distribution (e.g., mean, max, variance) of the corresponding patch characteristic (e.g., size, shape). Indeed, any patch-level metric can be summarized in this manner at the class and landscape levels. Configuration also can be quantified in terms of the spatial relationship of patches and patch types (e.g., nearest



neighbor, contagion). These metrics are spatially explicit at the class or landscape level because the relative location of individual patches within the patch mosaic is represented in some way. Such metrics represent a recognition that ecological processes and organisms are affected by the overall configuration of patches and patch types within the broader patch mosaic.

A number of configuration metrics can be formulated either in terms of the individual patches or in terms of the whole class or landscape, depending on the emphasis sought. For example, perimeter-area fractal dimension is a measure of shape complexity (Mandelbrot 1982, Burrough 1986, Milne 1991) that can be computed for each patch and then averaged for the class or landscape, or it can be computed from the class or landscape as a whole by regressing the logarithm of patch perimeter on the logarithm of patch area. Similarly, core area can be computed for each patch and then represented as mean patch core area for the class or landscape, or it can be computed simply as total core area in the class or landscape. Obviously, one form can be derived from the other if the number of patches is known and so they are largely redundant; the choice of formulations is dependent upon user preference or the emphasis (patch or class/landscape) sought. The same is true for a number of other common landscape metrics. Typically, these metrics are spatially explicit at the patch level, not at the class or landscape level.

The principle aspects of configuration and a sample of representative metrics are:

- *Patch size distribution and density*.–The simplest measure of configuration is patch size, which represents a fundamental attribute of the spatial character of a patch. Most landscape metrics either directly incorporate patch size information or are affected by patch size. Patch size distribution can be summarized at the class and landscape levels in a variety of ways (e.g., mean, median, max, variance, etc.), or, alternatively, represented as patch density, which is simply the number of patches per unit area.

- *Patch shape complexity*.--Shape complexity relates to the geometry of patches--whether they tend to be simple and compact, or irregular and convoluted. Shape is an extremely difficult spatial attribute to capture in a metric because of the infinite number of possible patch shapes. Hence, shape metrics generally index overall shape complexity rather than attempt to assign a value to each unique shape. The most common measures of shape complexity are based on the relative amount of perimeter per unit area, usually indexed in terms of a perimeter-to-area ratio, or as a fractal dimension, and often standardized to a simple Euclidean shape (e.g., circle or square). The interpretation varies among the various shape metrics, but in general, higher values mean greater shape complexity or greater departure from simple Euclidean geometry. Other methods have been proposed--radius of gyration (Pickover 1990), contiguity (LaGro 1991), linearity index (Gustafson and Parker 1992), and elongation and deformity indices (Baskent and Jordan 1995)–but these have not yet become widely used (Gustafson 1998).

- *Core Area*.--Core area represents the interior area of patches after a user-specified edge buffer is eliminated. The core area is the area unaffected by the edges of the patch. This “edge effect” distance is defined by the user to be relevant to the phenomenon under consideration and can either be treated as fixed or adjusted for each unique edge type. Core area integrates patch size, shape, and edge effect distance into a single measure. All other things equal, smaller patches with greater shape complexity have less core area Most of the metrics associated with size distribution (e.g., mean patch size and variability) can be formulated in terms of core area.

- *Isolation/Proximity*.--Isolation/proximity refers to the tendency for patches to be relatively isolated in space (i.e., distant) from other patches of the same or similar (ecologically friendly) class. Because the notion of “isolation” is vague, there are many possible measures depending on how distance is defined and how patches of the same class and those of other classes are treated. If d_{ij} is the nearest-neighbor distance from patch i to another patch j of the same type, then the average isolation of patches can be summarized simply as the mean nearest-neighbor distance over all patches. Alternatively, isolation can be formulated in terms of both the size and proximity of neighboring patches within a local neighborhood around each patch using the isolation index of Whitcomb et al. (1981) or proximity index of Gustafson and Parker (1992), where the neighborhood size is specified by the user and presumably scaled to the ecological process under consideration. The original proximity index was formulated to consider only patches of the same class within the specified neighborhood. This binary representation of the landscape reflects an island biogeographic perspective on landscape pattern. Alternatively, this metric can be formulated to consider the contributions of all patch types to the isolation of the focal patch, reflecting a landscape mosaic perspective on landscape patterns.

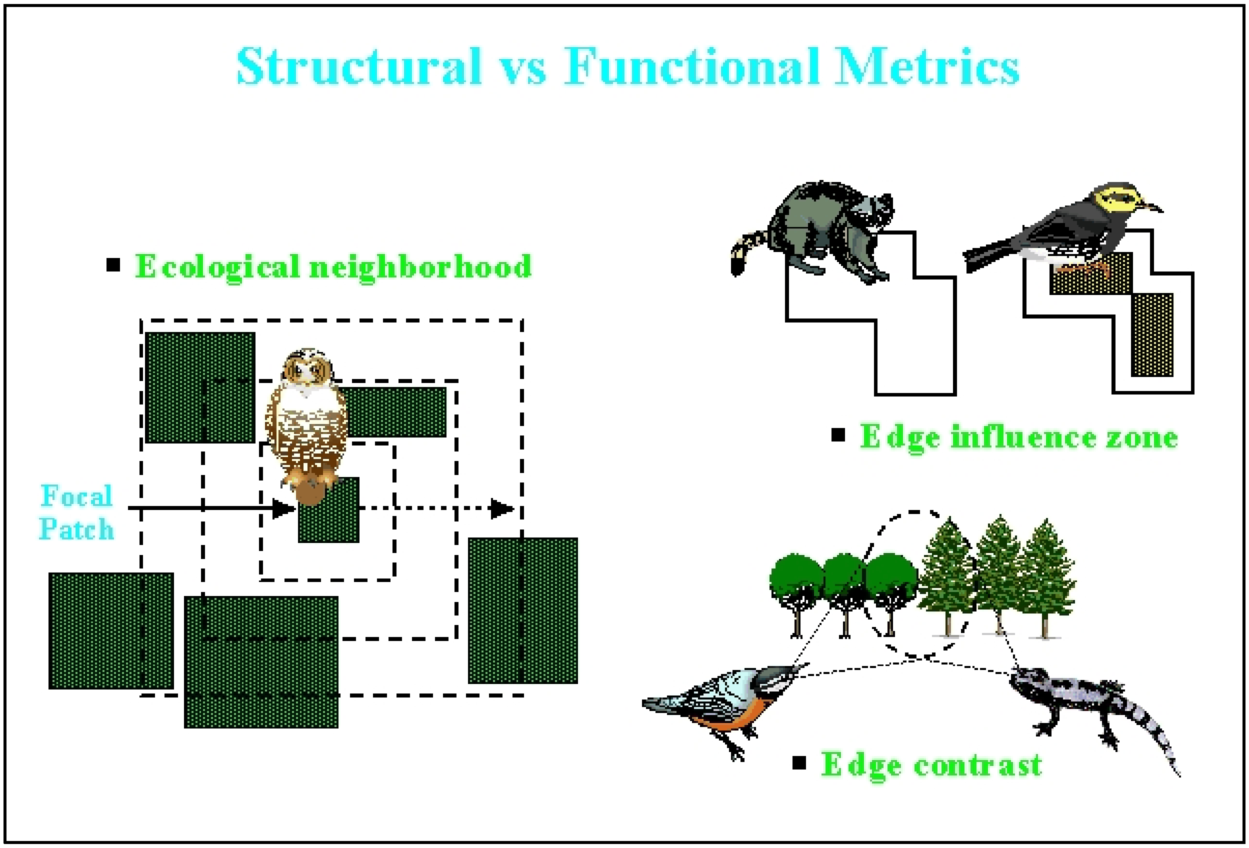
- *Contrast*.–Contrast refers to the relative difference among patch types. For example, mature forest next to younger forest might have a lower-contrast edge than mature forest adjacent to open field, depending on how the notion of contrast is defined. This can be computed as a contrast-weighted edge density, where each type of edge (i.e., between each pair of patch types) is assigned a contrast weight. Alternatively, this can be computed as a neighborhood contrast index, where the mean contrast between the focal patch and all patches within a user-specified neighborhood is computed based on assigned contrast weights. Relative to the focal patch, if patch types with high contrast lead to greater isolation of the focal patch, as is often the case, then contrast will be inversely related to isolation (at least for those isolation measures that consider all patch types).

- *Dispersion*.--Dispersion refers to the tendency for patches to be regularly or contagiously distributed (i.e., clumped) with respect to each other. There are many dispersion indices developed for the assessment of spatial point patterns, some of which have been applied to categorical maps. A common approach is based on nearest-neighbor distances between patches of the same type. Often this is computed in terms of the relative variability in nearest-neighbor distances among patches; for example, based on the ratio of the variance to mean nearest neighbor distance. Here, if the variance is greater than the mean, then the patches are more clumped in distribution than random, and if the variance is less than the mean, then the patches are more uniformly distributed. This index can be averaged over all patch types to yield an average index of dispersion for the landscape. Alternative indices of dispersion based on nearest neighbor distances can be computed, such as the familiar Clark and Evans (1954) index.

- *Contagion & Interspersion*.–Contagion refers to the tendency of patch types to be spatially aggregated; that is, to occur in large, aggregated or "contagious" distributions. Contagion ignores patches *per se* and measures the extent to which cells of similar class are aggregated. Interspersion, on the other hand, refers to the intermixing of patches of different types and is based entirely on patch (as opposed to cell) adjacencies. There are several different approaches for measuring contagion and interspersion. One popular index that subsumes both dispersion and interspersion is the contagion index based on the probability of finding a cell of type i next to a cell of type j (Li and Reynolds 1993). This index increases in value as a landscape is dominated by a few large (i.e., contiguous) patches and decreases in value with increasing subdivision and interspersion of patch types. This index summarizes the aggregation of all classes and thereby provides a measure of overall clumpiness of the landscape. McGarigal and Marks (1995) suggest a complementary interspersion/juxtaposition index that increases in value as patches tend to be more evenly interspersed in a "salt and pepper" mixture. These and other metrics are generated from the matrix of pairwise adjacencies between all patch types, where the elements of the matrix are the proportions of edges in each pairwise type. There are alternative methods for calculating class-specific contagion using fractal geometry (Gardner and O'Neill 1991). Lacunarity is an especially promising method borrowed from fractal geometry by which contagion can be characterized across a range of spatial scales (Plotnick et al. 1993 and 1996, Dale 2000). The technique involves using a moving window and is concerned with the frequency with which one encounters the focal class in a window of different sizes. A log-log plot of lacunarity against window size expresses the contagion of the map, or its tendency to aggregate into discrete patches, across a range of spatial scales.

- *Subdivision*.--Subdivision refers to the degree to which a patch type is broken up (i.e., subdivided) into separate patches (i.e., fragments), *not* the size (per se), shape, relative location, or spatial arrangement of those patches. Because these latter attributes are usually affected by subdivision, it is difficult to isolate subdivision as an independent component. Subdivision can be evaluated using a variety of metrics already discussed; for example, the number, density, and average size of patches and the degree of contagion all indirectly evaluate subdivision. However, a suite of metrics derived from the cumulative distribution of patch sizes provide alternative and more explicit measures of subdivision (Jaeger 2000). When applied at the class level, these metrics can be used to measure the degree of fragmentation of the focal patch type. Applied at the landscape level, these metrics connote the graininess of the landscape; i.e., the tendency of the landscape to exhibit a fine- versus coarse-grain texture. A fine-grain landscape is characterized by many small patches (highly subdivided); whereas, a coarse-grain landscape is characterized by fewer large patches.

- *Connectivity*.--Connectivity generally refers to the functional connections among patches. What constitutes a "functional connection" between patches clearly depends on the application or process of interest; patches that are connected for bird dispersal might not be connected for salamanders, seed dispersal, fire spread, or hydrologic flow. Connections might be based on strict adjacency (touching), some threshold distance, some decreasing function of distance that reflects the probability of connection at a given distance, or a resistance-weighted distance function. Then various indices of overall connectedness can be derived based on the pairwise connections between patches. For example, one such index, *connectance*, can be defined on the number of functional joinings, where each pair of patches is either connected or not. Alternatively, from *percolation theory*, connectedness can be inferred from patch density or be given as a binary response, indicating whether or not a spanning cluster or percolating cluster exists; i.e., a connection of patches of the same class that spans across the entire landscape (Gardner et al. 1987). Connectedness can also be defined in terms of *correlation length* for a raster map comprised of patches defined as clusters of connected cells. Correlation length is based on the average extensiveness of connected cells. A map's correlation length is interpreted as the average distance one might traverse the map, on average, from a random starting point and moving in a random direction, i.e., it is the expected traversibility of the map (Keitt et al. 1997).



STRUCTURAL VERSUS FUNCTIONAL METRICS

Landscape metrics can also be classified according to whether or not they measure landscape patterns with explicit reference to a particular ecological process. *Structural metrics* can be defined as those that measure the physical composition or configuration of the patch mosaic without explicit reference to an ecological process. The functional relevance of the computed value is left for interpretation during a subsequent step. Most landscape metrics are of this type. *Functional metrics*, on the other hand, can be defined as those that explicitly measure landscape pattern in a manner that is functionally relevant to the organism or process under consideration. Functional metrics require additional parameterization prior to their calculation, such that the same metric can return multiple values depending on the user specifications. The difference between structural and functional metrics is best illustrated with an example. As conventionally computed, mean nearest neighbor distance is based on the distances between neighboring patches of the same class. The mosaic is in essence treated as a binary landscape (i.e., patches of the focal class versus everything else). The composition and configuration of the intervening matrix is ignored. Consequently, the same landscape can only return a single value for this metric. Clearly, this is a structural metric because the functional meaning of any particular computed value is left to subsequent interpretation. Conversely, connectivity metrics that consider the permeability of various patch types to movement of the organism or process of interest are functional metrics. Here, every patch in the mosaic contributes to the calculation of the metric. Moreover, there are an infinite number of values that can be returned from the same landscape, depending on the permeability coefficients assigned to each patch type. Given a particular parameterization, the computed metric is in terms that are already deemed functionally relevant.

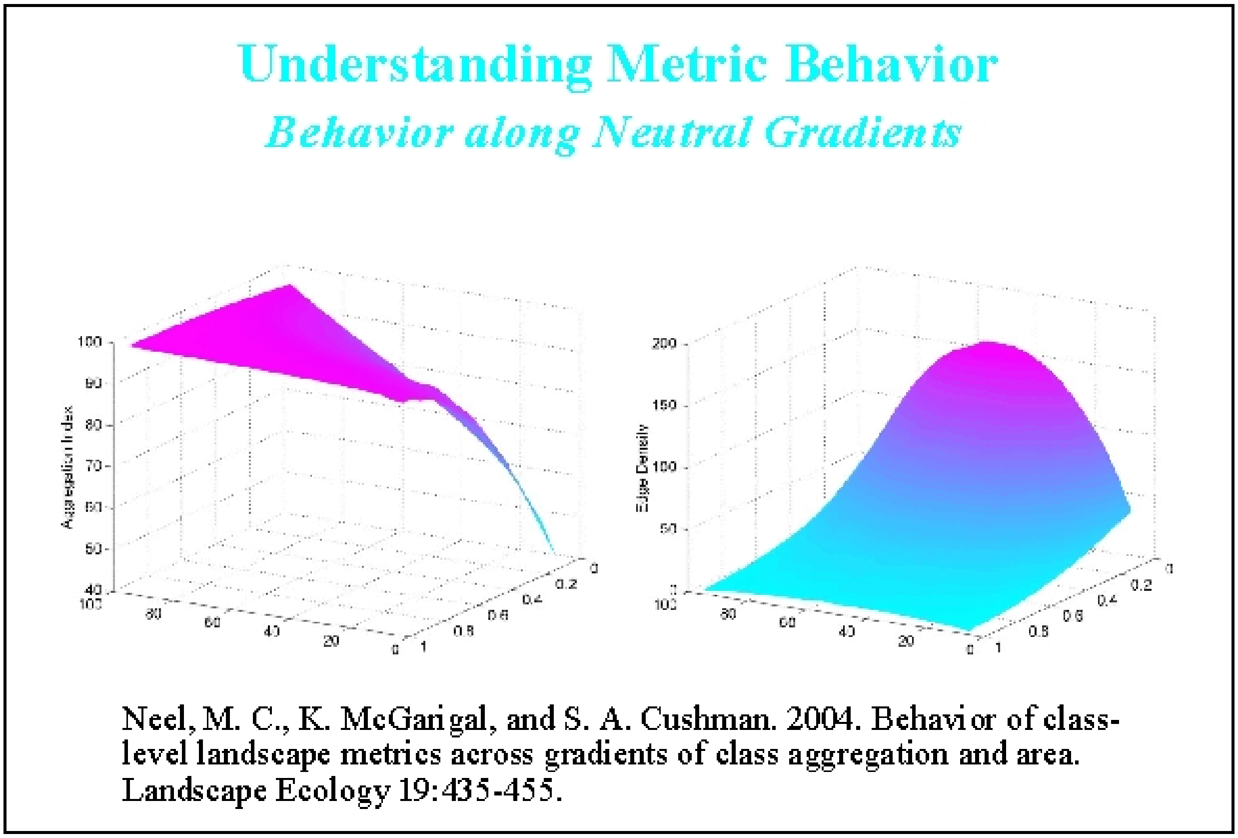
LIMITATIONS IN THE USE AND INTERPRETATION OF METRICS

The quantitative analysis of landscape patterns is fraught with numerous difficult issues. Four broad issues that currently limit the effective use and interpretation of landscape metrics are considered here.

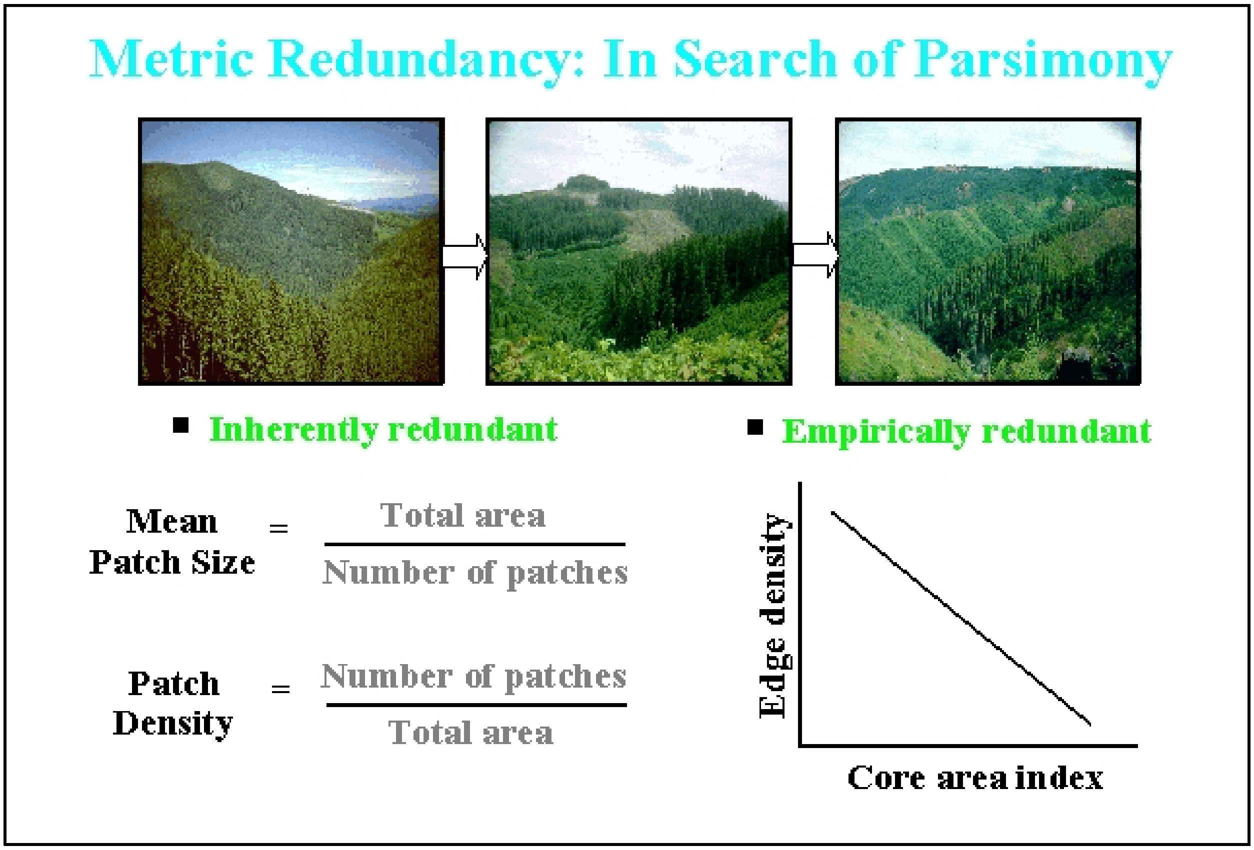
(1) ***Defining a relevant landscape***.--All landscape metrics represent some aspect of landscape pattern. However, the user must first define the landscape, including its extent and grain and the patches that comprise it, before any of these metrics can be computed. In addition, for many of the metrics, the user must specify additional input parameters such as edge effect distance, edge contrast weights, and search distance. Hence, the computed value of any metric is merely a function of how the investigator chose to define and scale the landscape. If the measured pattern of the landscape does not corresponding to a pattern that is functionally meaning for the organism or process under consideration, then the results will be meaningless. For example, the criteria for defining a patch may vary depending on how much variation will be allowed within a patch, on the minimum size of patches that will be mapped, and on the components of the system that are deemed ecologically relevant to the phenomenon of interest (Gustafson 1998). Ultimately, patches occur on a variety of scales, and a patch at any given scale has an internal structure that is a reflection of patchiness at finer scales, and the mosaic containing that patch has a structure that is determined by patchiness at broader scales (Kotliar and Wiens 1990). Thus, regardless of the basis for defining patches, a landscape does not contain a single patch mosaic, but contains a hierarchy of patch mosaics across a range of scales. Indeed, patch boundaries are artificially imposed and are in fact meaningful only when referenced to a particular scale (i.e., grain size and extent). It is incumbent upon the investigator to establish the basis for delineating among patches and at a scale appropriate to the phenomenon under consideration. Extreme caution must be exercised in comparing the values of metrics computed for landscapes that have been defined and scaled differently.

Given the subjectivity in defining patches, surface pattern techniques can provide an objective means to help determine the scale of patchiness (Gustafson 1998). In many studies, the identification of patches reflects a minimum mapping unit that is chosen for practical or technical reasons and not for ecological reasons. Surface pattern analysis can provide insight into the scale of patchiness and whether there are hierarchies of scale. This information can then provide the empirical basis for choosing the scale for mapping patches, rather than relying on subjective and somewhat arbitrary criteria. Despite the complimentary nature of surface pattern and categorical map pattern techniques, few studies have adopted this approach.

The format (raster versus vector) and scale (grain and extent) of the data can have a profound influence on the value of many metrics. Because vector and raster formats represent lines differently, metrics involving edge or perimeter will be affected by the choice of formats. Edge lengths will be biased upward in raster data because of the stair-step outline, and the magnitude of this bias will vary in relation to the grain or resolution of the image. In addition, the grain-size of raster format data can have a profound influence on the value of certain metrics. Metrics involving edge or perimeter will be affected; edge lengths will be biased upwards in proportion to the grain size–larger grains result in greater bias. Metrics based on cell adjacency information such as the contagion index of Li and Reynolds (1993) will be affected as well, because grain size effects the proportional distribution of adjacencies. In this case, as resolution is increased (grain size reduced), the proportional abundance of like adjacencies (cells of the same class) increases, and the measured contagion increases. Finally, the boundary of the landscape can have a profound influence on the value of certain metrics. Landscape metrics are computed solely from patches contained within the landscape boundary. If the landscape extent is small relative to the scale of the organism or ecological process under consideration and the landscape is an "open" system relative to that organism or process, then any metric will have questionable meaning. Metrics based on nearest neighbor distance or employing a search radius can be particularly misleading. Consider, for example, a local population of a bird species occupying a patch near the boundary of a somewhat arbitrarily defined landscape. The nearest neighbor within the landscape boundary might be quite far away; yet, in reality, the closest patch might be very close but just outside the designated landscape boundary. In addition, those metrics that employ a search radius (e.g., proximity index) will be biased for patches near the landscape boundary because the searchable area will be much less than a patch in the interior of the landscape. In general, boundary effects will increase as the landscape extent decreases relative to the patchiness or heterogeneity of the landscape.

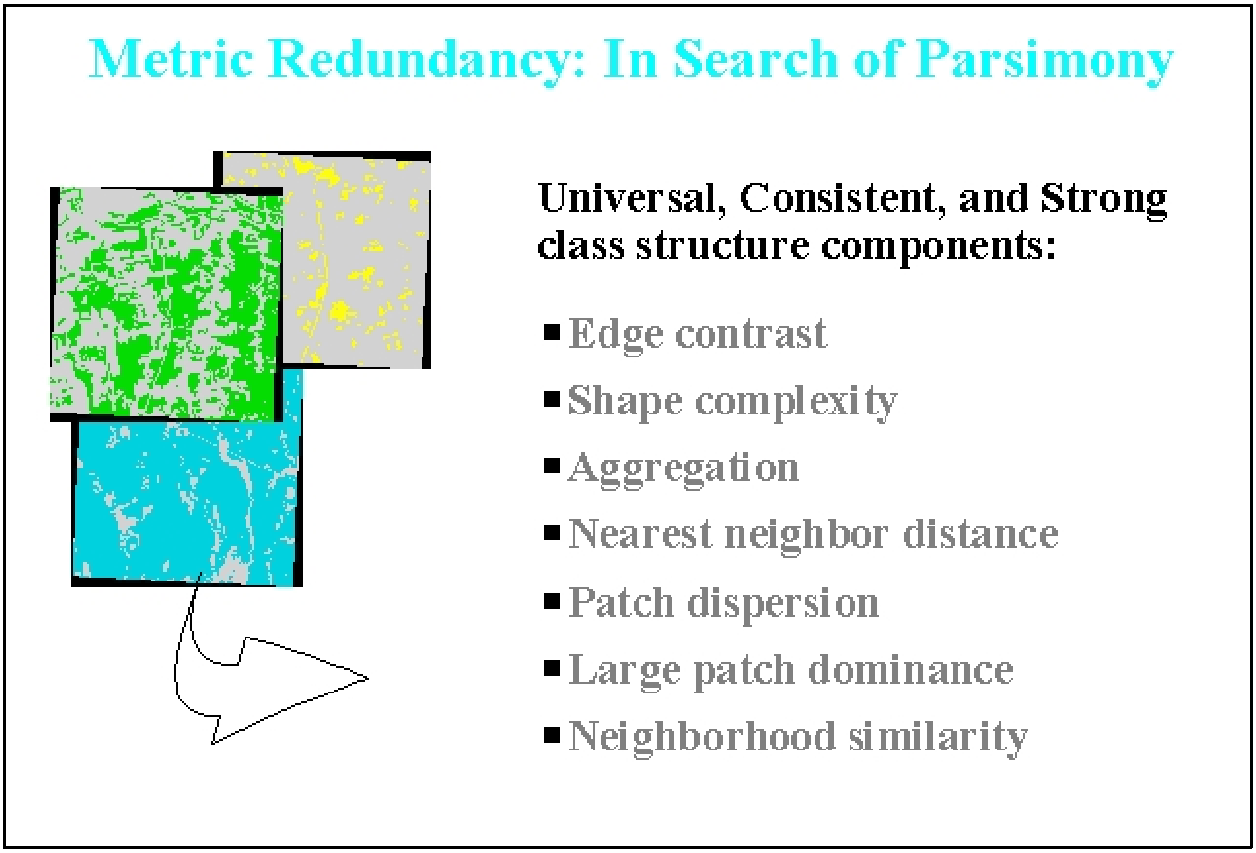


(2) <u>*Understanding metric behavior*</u>.--In addition to these technical issues, current use of landscape metrics is constrained by the lack of a proper theoretical understanding of metric behavior. The proper interpretation of a landscape metric is contingent upon having an adequate understanding of how it responds to variation in landscape patterns (e.g., Gustafson and Parker 1992, Hargis et al. 1998, Jaeger 2000, Neel et al. 2004). Failure to understand the theoretical behaviour of the metric can lead to erroneous interpretations (e.g., Jaeger 2000). Neutral models (Gardner et al. 1987, Gardner and O'Neill 1991, With 1997) provide an excellent way to examine metric behaviour under controlled conditions because they control the process generating the pattern, allowing unconfounded links between variation in pattern and the behaviour of the index (Gustafson 1998). Unfortunately, existing neutral models are extremely limited in the types of patterns that can be generated, so developing a better theoretical understanding of metric behaviour through the use of neutral models is somewhat limited at this time.

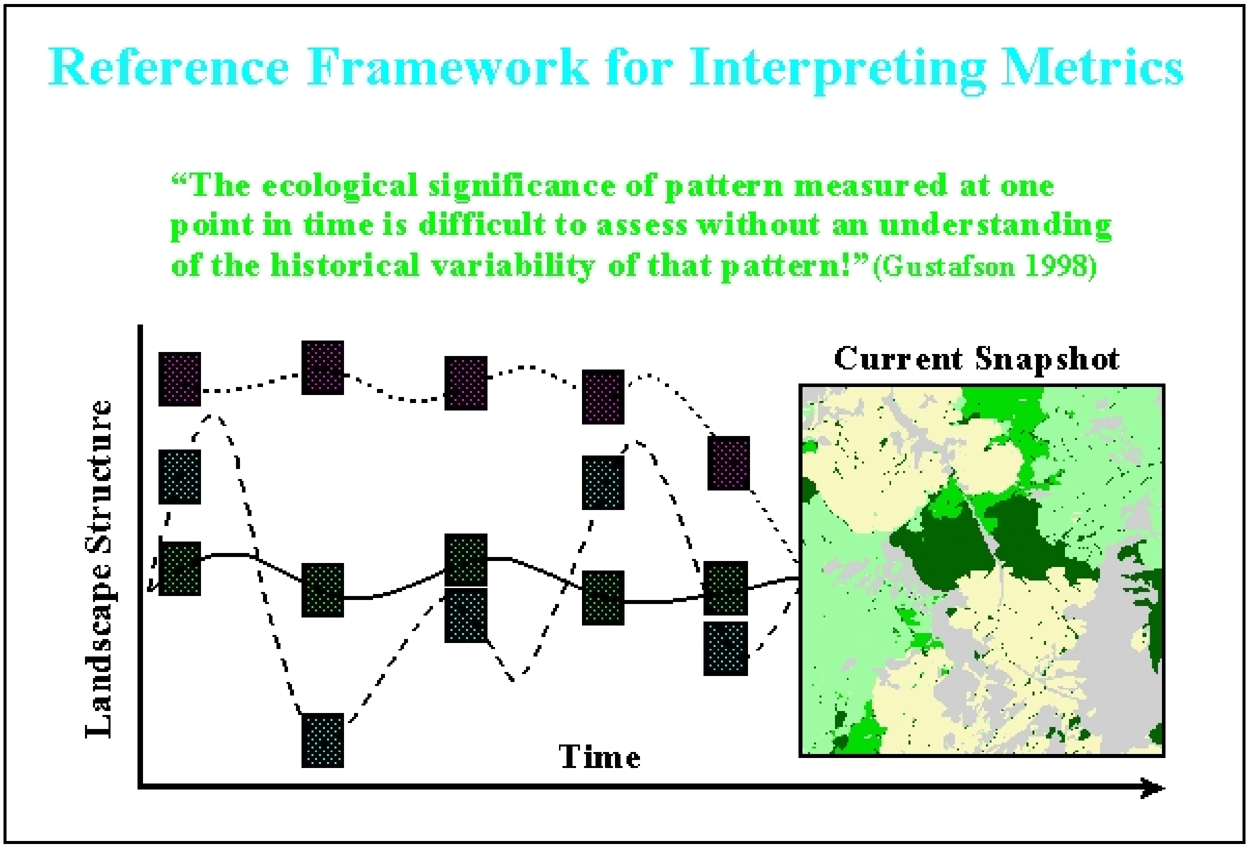


(3) *Metric redundancy: In search of parsimony*.--Although the literature is replete with metrics now available to describe landscape pattern, there are still only two major components–composition and configuration, and only a few aspects of each of these. Metrics often measure multiple aspects of this pattern. Thus, there is seldom a one-to-one relationship between metric values and pattern. Most of the metrics are in fact correlated among themselves (i.e., they measure a similar or identical aspect of landscape pattern) because there are only a few primary measurements that can be made from patches (patch type, area, edge, and neighbor type), and most metrics are then derived from these primary measures. Some metrics are inherently redundant because they are alternate ways of representing the same basic information (e.g., mean patch size and patch density). In other cases, metrics may be empirically redundant; not because they measure the same aspect of landscape pattern, but because for the particular landscapes under investigation, different aspects of landscape pattern are statistically correlated.

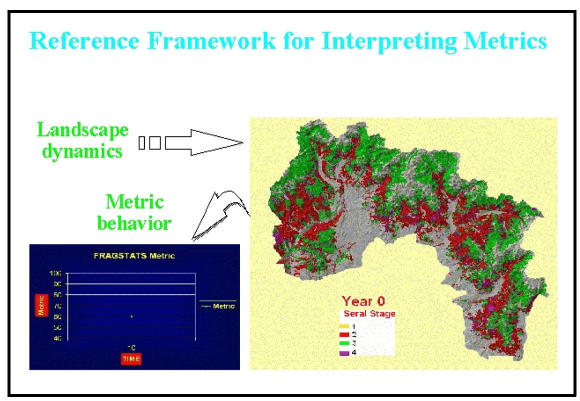
Several investigators have attempted to identify the major components of landscape pattern for the purpose of identifying a parsimonious suite of independent metrics (e.g., Li and Reynolds 1995, McGarigal and McComb 1995, Ritters et al. 1995). Although these studies suggest that patterns can be characterized by only a handful of components, consensus does not exist on the choice of individual metrics. These studies were constrained by the pool of metrics existing at the time of the investigation. Given the expanding development of functional metrics, particularly those based on a landscape mosaic perspective, it seems unlikely that a single

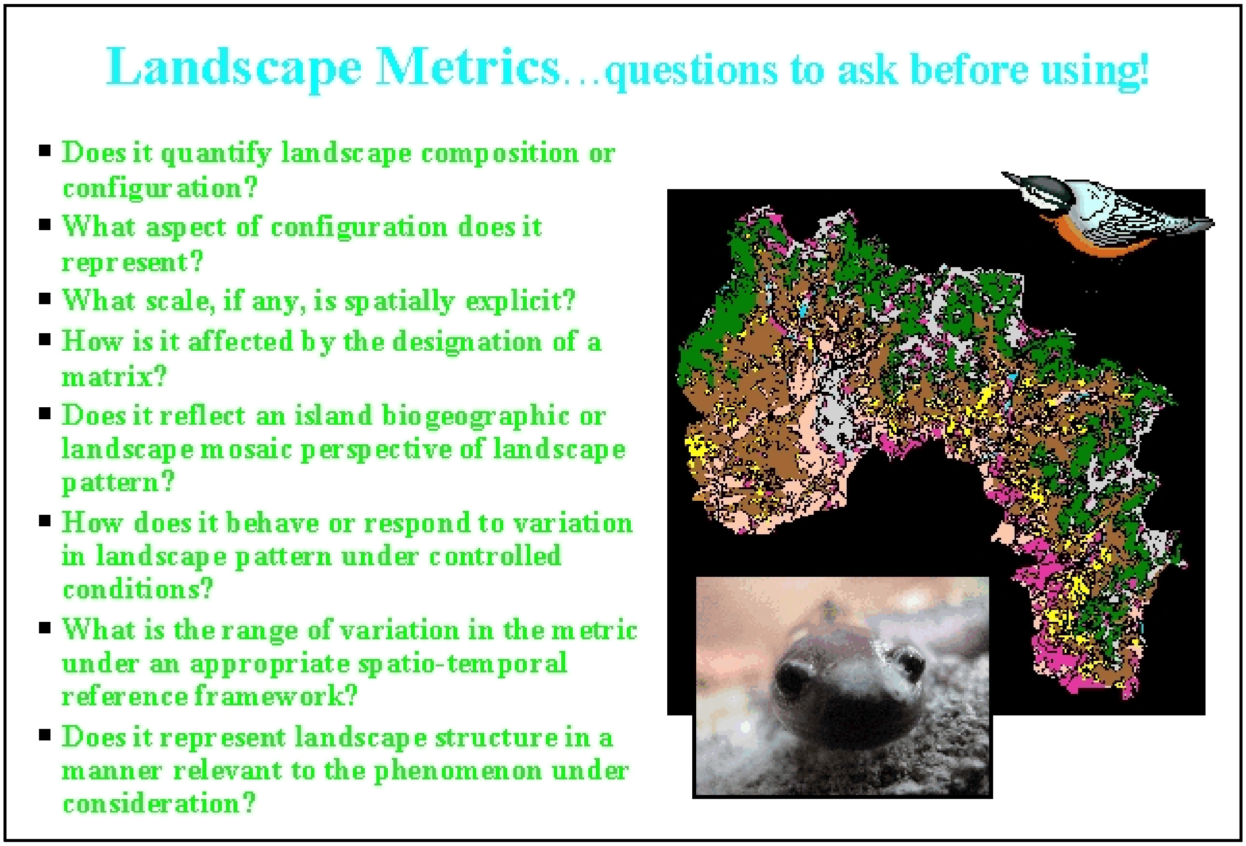


parsimonious set exists. Ultimately, the choice of metrics should explicitly reflect some hypothesis about the observed landscape pattern and what processes or constraints might be responsible for that pattern.



(4) <u>*A reference framework for interpreting landscape metrics*</u>.--The interpretation of landscape metrics is further plagued by the lack of a proper spatial and temporal reference framework. Landscape metrics quantify the pattern of a landscape at a snapshot in time. Yet it is often difficult, if not impossible, to determine the ecological significance of the computed value without understanding the range of natural variation in landscape pattern. For example, in disturbance-dominated landscapes, patterns may fluctuate widely over time in response to the interplay between disturbance and succession processes (e.g., Wallin et al. 1996, He and Mladenoff 1999, Haydon et al. 2000, Wimberly et a. 2000). It is logical, therefore, that landscape metrics should exhibit statistical distributions that reflect the natural spatial and temporal dynamics of the landscape. By comparison to this distribution, a more meaningful interpretation can be assigned to any computed value. Unfortunately, despite widespread recognition that landscapes are dynamic, there is a dearth of empirical work quantifying the range of natural variation in landscape pattern metrics. This remains one of the greatest challenges confronting landscape pattern analysis.





In summary, the importance of fully understanding each landscape metric before it is selected for interpretation cannot be stressed enough. Specifically, these questions should be asked of each metric before it is selected for interpretation:

- Does it represent landscape composition or configuration, or both?
- What aspect of composition or configuration does it represent?
- Is it spatially explicit, and, if so, at the patch-, class-, or landscape-level?
- How is it effected by the designation of a matrix element?
- Does it reflect an island biogeographic or landscape mosaic perspective of landscape pattern?
- How does it behave or respond to variation in landscape pattern under controlled conditions?
- What is the range of variation in the metric under an appropriate spatio-temporal reference framework?

Based on the answers to these questions, does the metric represent landscape pattern in a manner and at a scale ecologically meaningful to the phenomenon under consideration? Only after answering these questions should one attempt to draw conclusions about the pattern of the landscape.

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