# Chapter 5
# The Gradient Paradigm: A Conceptual and Analytical Framework for Landscape Ecology

**Samuel A. Cushman, Kevin Gutzweiler, Jeffrey S. Evans, and Kevin McGarigal**

## 5.1 Introduction

Landscape ecology deals fundamentally with how, when, and why patterns of environmental factors influence the distribution of organisms and ecological processes, and reciprocally, how the actions of organisms and ecological processes influence ecological patterns (Urban et al. 1991; Turner 1989). The landscape ecologist's goal is to determine where and when spatial and temporal heterogeneity matter, and how they influence processes. A fundamental issue in this effort revolves around the choices a researcher makes about how to depict and measure heterogeneity (Turner 1989; Wiens 1989). Indeed, observed patterns and their apparent relationships with response variables often depend on the scale that is chosen for observation and the rules that are adopted for defining and measuring variables (Wiens 1989; Wu and Hobbs 2000; Wu and Hobbs 2004). Success in understanding pattern–process relationships hinges on accurately characterizing heterogeneity in a manner that is relevant to the organism or process under consideration.

To characterize heterogeneity, landscape ecologists have generally adopted a single approach – the patch-mosaic model of landscape structure (Forman and Godron 1986; Turner 1989; Forman 1995; Turner et al. 1989). In this model a

S.A. Cushman (✉)
US Forest Service, Rocky Mountain Research Station, 800 E Beckwith, Missoula,
MT 59801, USA
e-mail: scushman@fs.fed.us

K. Gutzweiler
Baylor University, Waco, TX, USA

J.S. Evans
Senior Landscape Ecologist, The Nature Conservancy, NACR - Science

K. McGarigal
Department of Natural Resources Conservation, University of Massachusetts,
Amherst, MA, USA

landscape is represented as a collection of discrete patches; major discontinuities in underlying environmental variation are depicted as discrete boundaries between patches, and all other variation is subsumed by the patches and implicitly assumed to be irrelevant. The patch-mosaic model provides a simplifying framework that facilitates experimental design, analysis, and management consistent with established tools (e.g., FRAGSTATS) and methods (e.g., ANOVA). The patch-mosaic model also is the foundation for the major axioms of contemporary landscape ecology (e.g., patch structure matters, patch context matters, pattern varies with scale). Yet, even the most ardent supporters of this model recognize that categorical representation of environmental variables often poorly represents the true heterogeneity of the system, which often consists of continuous multi-dimensional gradients of environmental attributes. We believe that advances in landscape ecology are constrained by the lack of methods and analytical tools for effectively depicting and analyzing continuously varying ecological phenomena at the landscape level.

In the sections that follow, we explain the limitations of categorical map analyses for landscape ecology and then discuss the gradient paradigm, and explain how it can be used to overcome many limitations of the patch-mosaic model. We finish by illustrating specific benefits of gradient approaches using real data. The patch-mosaic model has great heuristic value, and it is the appropriate model to use under many circumstances, such as when natural or anthropogenic forces have created sharp environmental discontinuities. But we argue below that a patch-mosaic model of landscape structure is prone to large errors and distortion of underlying environmental patterns that can obscure true pattern–process relationships and inhibit flexible analysis across scales. We also argue that a gradient based representation of landscape structure is much more consistent with fundamental ecological theory, and that to achieve the full potential of integrating spatial analysis with quantitative ecology the categorical patch-mosaic model should take its rightful place as a special case within a generalized gradient framework.

### 5.1.1 Limitations of Categorical Mapping

Many of landscape ecology's perspectives and techniques have their origins in classical cartographic analysis (Forman and Godron 1986). The first step in most landscape ecology analsyses is to map the system. It has become traditional in geography to abstract the world into non-overlapping regions, or polygons. In terms of observational scale, this kind of mapping truncates the intensity of measured variables into categories. Quantitative information about how variables vary through space and time is lost, leaving rigid, internally homogeneous patches. Though this perspective has been useful for many applications, it is important to recognize how it influences measurements and analyses.

In categorical mapping, discontinuities are presupposed; the world is assumed to be inherently discrete. When quantitative landscape variation is reduced to categories,

four important representation and interpretation problems are generated. First, subjective decisions of what to characterize and how to define boundaries will constrain what patterns can be seen and what relationships can be inferred. Second, patch boundaries based on criteria defined by the observer may not be meaningful or even perceived by the organism in question. Third, once patches are created, all internal variability within and among patches of the same class is eliminated, and all interclass differences are reduced to categorical differences. Fourth, categorical patches define the regions of assumed homogeneity in a single or composite attribute. Once defined, all variability in that attribute not used to define the patch is discarded. The cumulative effect of these issues can result in any number of statistical problems associated with data aggregation including the Modifiable Ariel Unit Problem (Openshaw 1984; Jelinski and Wu 1996; Wu 2007), Ecological Fallacy (Robinson 1950; Wood and Skole 1998; Wu 2007), and misspecification (Guthrie and Sheppard 2001).

Two or more layers of patches can be overlaid and analyzed using map algebra. This is the standard approach to analyzing multi-level categorical map patterns. However, the boundaries of patches in different layers are often poorly related, as they reflect slices through the distributions of independently varying environmental attributes and are based on different classification rules. In the traditional patch-based model, analyzing many layers of patches results in intractably vast numbers of unique map categories. There often are many "sliver" patches resulting from poor matching of edges that are not indicative of any ecological process. This magnitude of this latter problem increases multiplicatively with additional choropleth layers. When a researcher attempts to predict a response variable, such as the habitat suitability for a particular species, as a function of a number of landscape-level attributes across several categorical data layers, prediction can only be based on combinations of categories.

With each combination of categorical data the information loss multiplies, as do the errors of misclassification. No such penalty is incurred for combining quantitatively scaled variables. If the same response variable is predicted on the basis of several layers of quantitative predictor variables, the prediction can be based on how the quantitative landscape-level variables covary along dimensions that are related to the species or process in question (McGarigal and Cushman 2005). In addition, preserving quantitative ecological factors reduces subjectivity. The subjectivity of boundary definition is replaced by the subjectivity of measurement resolution, which often involves less-restrictive assumptions than do decisions about category width and boundary definitions. Retaining the quantitative scale of ecological variables also enables one to analyze many response variables simultaneously, with each responding individually to multiple landscape gradients.

When categorical patch mosaics are derived specifically to correspond to the scale and sensitivities of a particular organism or ecological process, they may represent landscape heterogeneity in an ecologically meaningful way. In most cases, however, little is known about the scale and resolution of landscape variability that are pertinent, and patterns at several scales may simultaneously influence an

organism or process. Reducing a continuous ecological surface to a patch mosaic causes representation and interpretation problems because of inaccuracies in boundary placement and class divisions (Openshaw 1984), or because ecological variation is important across several scale ranges (Wu 2007). Even if a constructed patch mosaic ideally represents an organism's ecological landscape, this mosaic is not likely to do so in an optimal way for a second or third organism, making comparisons between organisms based on a single landscape map questionable (Cushman et al. 2007).

### 5.1.2   Gradient Attributes of Categorical Patterns

Even when categorical data is appropriate, conventional analytical methods often fail to produce unbiased assessments of organism responses. Organisms often experience categorical environments as pattern gradients. For example, consider a species that responds to landscape structure as measured by the density of edges in the landscape weighted by their structural contrast. Traditional landscape pattern analysis would measure the total contrast-weighted edge density for the entire landscape. However, landscape patterns are rarely stationary, and there may be no place in the landscape with a contrast-weighted edge density equivalent to that calculated for the landscape as a whole. If the landscape is large relative to the organism's home range, the organism is unlikely to even experience the global average structure of the landscape. The organism responds to the local structure within its immediate perception, within its daily foraging area, and within its home range. Thus, a more useful description of landscape pattern would be a location-specific measure at a scale relevant to the organism or process of interest (Wiens 2001; Wu 2007). We propose that organisms experience landscape structure as pattern gradients that vary through space according to the distance at which a particular organism perceives or is influenced by landscape patterns. Therefore, instead of analyzing global landscape patterns, it is usually more appropriate to quantify the local landscape pattern across the space delimited by an organism's perceptual abilities.

Tools exist to calculate traditional patch based landscape metrics within a moving window (e.g. McGarigal et al. 2002). The window size should be selected such that it reflects the scale at which the organism perceives or responds to pattern. If this is unknown, one can vary the size of the window over several runs and empirically determine to which scale of a landscape variable an organism is most responsive. 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 (Fig. 5.1). 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.
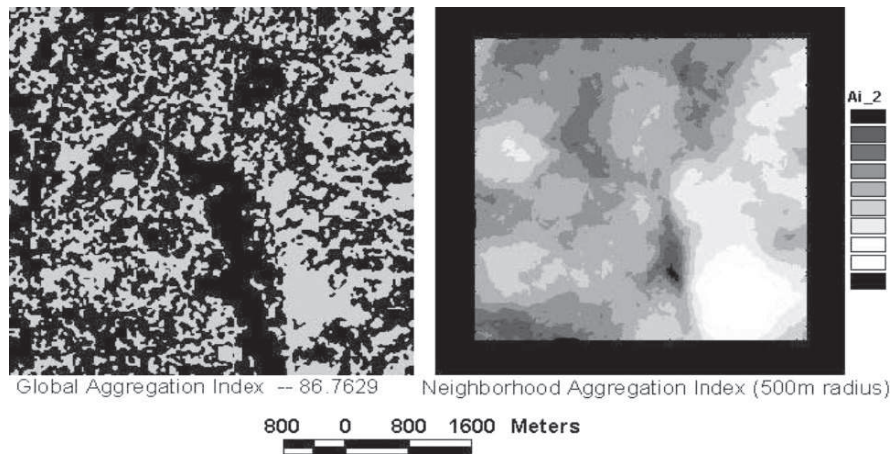
**Fig. 5.1** Comparison of global and neighborhood-based calculation of a landscape metric for a categorical map. The Aggregation Index (AI) was calculated for the "forest" class (grey) in the binary map on the left for the landscape overall, and within 500-m-radius circular windows centered on each pixel. The moving window calculation, shown on the right, produces a surface whose height is equal to the neighborhood AI value. There is a border classified as "no data" around the edge of the landscape to a depth of the selected neighborhood radius. Higher AI values are light, lower values are dark

## 5.1.3   Gradient Analysis of Continuous Field Variables

When patch mosaics are not clearly appropriate as models of the variability of particular environmental factors, there are a number of advantages to modeling environmental variation as individually varying gradients. First, it preserves the underlying heterogeneity in the values of variables through space and across scales. The subjectivity of delimiting boundaries is eliminated. This enables the researcher to preserve in the analysis many variables that vary independently, avoiding the disadvantages of reducing the set to a categorical description of boundaries defined on the basis of one or a few attributes. In addition, the subjectivity of defining cut points for categories is eliminated. With gradient data, scale inaccuracy and boundary sensitivity are not issues because the quantitative representation of environmental variables preserves the entire scale range and the complete gradient. The only real subjectivity is the resolution at which to measure variability.

By tailoring the grain, extent, and intensity of the measurements to the hypotheses and system under investigation, researchers can develop a less equivocal picture of how the system is organized and what mechanisms may be at work. An important benefit is that one can directly assess relations between a continuous response variable for an organism with spatial and temporal patterns in the environment that are continuously scaled. By not truncating patterns of variation in landscape variables to a particular scale and set of categories, one can use a single set of

predictor variables to simultaneously analyze many response variables, be they species responding individually to complex landscape gradients, or ecological processes acting at different scales. Comparison between organisms or processes is not compromised, because each can be optimally predicted by the surface or combinations of surfaces without altering the data in ways that limit its utility for predicting other response variables. Importantly, this facilitates efficient multivariate analyses involving many response and predictor variables simultaneously to test hypotheses about the nature and strength of system control.

## 5.2 The Gradient Paradigm of Landscape Structure

We propose a conceptual shift in spatial ecology that integrates categorical and continuous perspectives. We believe it will be useful for landscape ecologists to adopt a gradient perspective, along with a new suite of tools for analyzing landscape structure and the linkages of patterns and processes under a gradient framework. This framework includes, where appropriate, categorically mapped variables as a special case. In the sections that follow we outline how a gradient perspective can be valuable in several areas of landscape ecological research.

### 5.2.1 Evaluating A Categorical Mapping of Canopy Density

In this example we explore the differences between gradient and categorical representations of an important ecological variable, canopy density. Canopy density is a measure of the amount of canopy photosynthetic material per unit of ground surface area, and is correlated with a number of ecological processes of interest, including net primary productivity, carbon sequestration rate, and is an important habitat attribute for many wildlife species.

#### 5.2.1.1 Mapping Approaches

Lidar

Lidar data was acquired in August of 2006 by Watershed Sciences, Corvallis, Oregon using a Leica-ALS50 sensor with a pulse repetition frequency of 80 kHz, a nominal point-density of ~48 points per/m$^2$, and a maximum scan angle of 14°. Ground measurements were identified using Multiscale Curvature Classification (Evans and Hudak 2007). Canopy density was calculated using the ratio of non-ground to ground measurements (Fig. 5.2a) within a 15 m cell size to make it directly comparison with VMAP. The ratio of non-ground/ground Lidar measurements
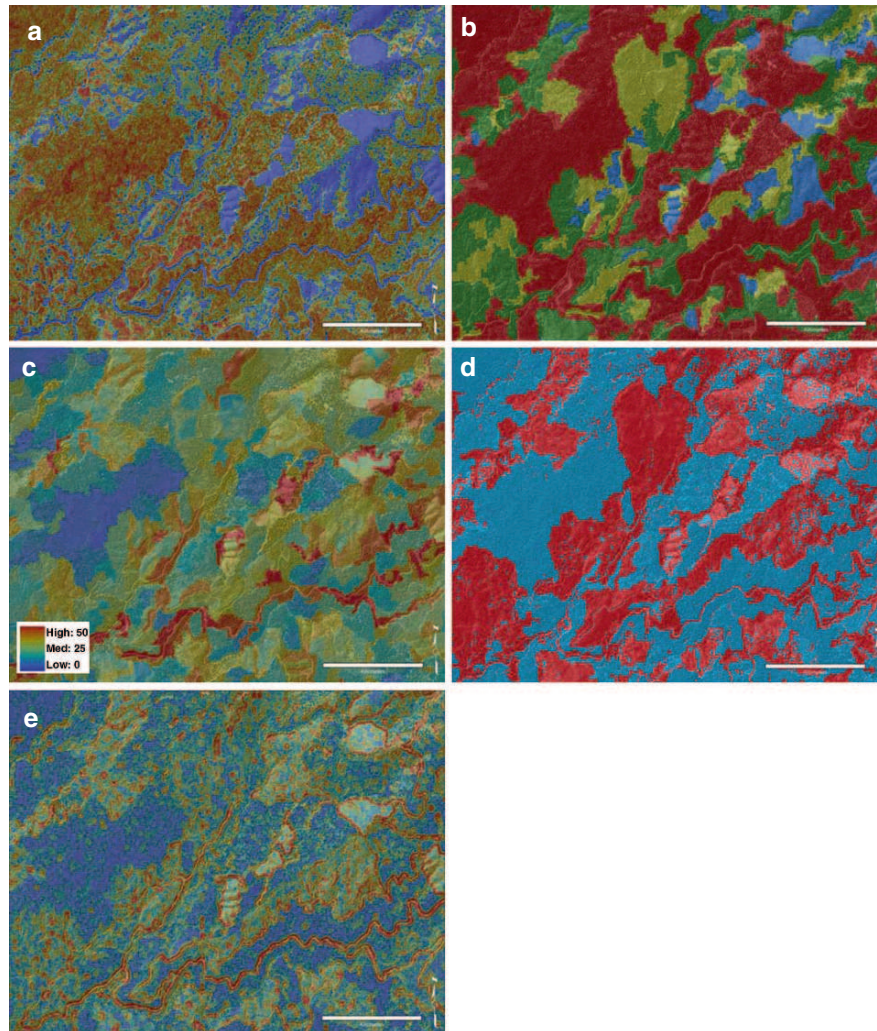
**Fig. 5.2** (**a**) Lidar derived canopy density 15 m. Colors are ramped, blue (0%) to red (100%) using a standard deviation stretch. (**b**) VMAP derived canopy density. Colors are representative of 4 classes, blue (0–10%), green (25–59%), yellow (10–24%), and red (60–100%). (**c**) Standard deviation of lidar canopy density by VMAP polygon (**d**) Non agreement between VMAP and Lidar classification (45% error). Red is an error, blue is correct. (**e**) Maximum Rate of Change, Canopy Density 15 m. Colors are ramped, blue (low change) to red (high change) using a standard deviation stretch

accurately represent the amount of light reaching the ground and are directly comparable to traditional measures of canopy density. Correlation between Lidar derived and field measured canopy cover have been strongly supported (r = 0.97) in several studies.

R1-VMAP

The USDA Forest Service Region 1 VMAP project is a vegetation classification based on hierarchal image segmentation. Multi-temporal Landsat ETM + 7 spectral bands were fused with the panchromatic band (band 8) to create 15 m multispectral images. These images were used to create image object polygons using eCognition. Canopy density was classified into four classes; 1–9%, 10–24%, 25–59%, and 60–100% (Fig. 5.1b). Validation was conducted using photo-interpretation reporting a producer's accuracy based on omission error (65.4%) and a user's accuracy based on commission error (78.7%).

### 5.2.1.2  Analysis and Interpretation

Canopy density is an inherently continuous attribute which varies at scales at least as fine as the canopy width of individual trees. Continuous representation intuitively seems much more appropriate. Lidar effectively represents this continuous variability, given its fine sample resolution (~48 points per/m$^2$) and sensitivity to fine differences in measurement scale (continuous values from 0 to 100% in this case). It has demonstrated very high accuracy in predicting actual canopy density at a fine spatial scale (Leafsky et al. 1999; Means et al. 2000; Hudak et al. 2006). In this example, we will treat the 15 m$^2$ lidar canopy density classification as approximate truth and evaluate the deviation of the classified map from it.

   This example provides a means to test three important questions. First, do the patch boundaries delineated in Fig. 5.2b correspond to discontinuities in the actual patterns of canopy density. In other words, do the patch boundaries correspond to hard boundaries or "breaks" in canopy density. Second, do the patches correspond to areas of homogenous canopy closure, such that categorical representation does not result in severe loss of information about internal variability. Third, is there a strong relationship between the value of canopy density predicted in the VMAP and lidar canopy classifications at the pixel level.

   The patches in Fig. 5.2b do not strongly correspond to discontinuities in actual canopy closure. Visual comparison of Fig. 5.2a and b shows that the patch boundaries in 2b are largely artificial and arbitrary truncations of a continuously varying phenomenon and do not correspond to natural breaks in the pattern. Figure 5.2e further shows that these patches are artificial. The patterns of maximum rate of change of canopy closure in this landscape do not in general suggest the existence of natural boundaries that could meaningfully describe patches, and certainly do not correspond to the patch boundaries shown in Fig. 5.2b

   Second, visual inspection of Fig. 5.2a and b also shows that the patches in 2b do not correspond to areas of homogeneous canopy density. This was more formally evaluated by computing the standard deviation of lidar canopy density by VMAP polygon (Fig. 5.2c). The majority of the landscape is covered by patches that have standard deviation of internal canopy density over 25%. Given the range of this value from 0 to 100%, a 25% standard deviation is very large. Over 15% of the

landscape is occupied by patches with standard deviation over 50%. This analysis shows that the patches delineated by VMAP for canopy closure do not correspond to areas of internal homogeneity, and the internal heterogeneity is so high that the patches are largely meaningless.

The third question is the accuracy of the VMAP classification in representing the degree of canopy closure. In this comparison we evaluate how well the truncated ranges in the classified map correspond to the same artificial ranges imposed on the lidar map. We have already shown that these truncated ranges are artificial and do not represent natural breaks or areas of internal homogeneity. But a remaining question is; do they at least match pixel by pixel to the same range of values in the lidar map with some accuracy? The Lidar canopy density was classified into the same four classes as VMAP. A Boolean equality operation was performed in Workstation ArcInfo between the classified Lidar and VMAP. We conducted two evaluations of accuracy of VMAP in terms of matching lidar. First, a Persons correlation was calculated in R (R Development Core Team 2007) between the classified Lidar and VMAP adjusting for autocorrelation and degrees of freedom (Dutilleul 1993). The value of this correlation was r = 0.329, which indicates that only approximately 10% of the variation in truncated canopy closure values at the pixel level is explainable VMAP. This indicates that VMAP is a very poor predictor of even artificially truncated ranges of canopy closure. Second, we computed the error between the classified map and the lidar prediction (Fig. 5.2d), calculated as the proportion of cells incorrectly classified into the wrong truncated ranges of canopy closure. This analysis indicated that over 45% of the cells in the classified map were incorrectly assigned to one of the four ranges of canopy density.

The classified map fails each of these three critical questions. The patches do not represent discretely bounded discontinuities. Rather, the pattern of canopy density is continuous at a fine scale in a way that does not lend itself to the identification of discrete patch boundaries. Second, the patches do not represent areas of internal homogeneity, but instead subsume a level of heterogeneity that is nearly the same as that between putative patches. The bins used to truncate this continuous variable are artificial and arbitrary. But even if we assumed them to be meaningful, the classified map fails to accurately predict even these artificial truncations, based on the cell correlation and classification accuracy.

This analysis is a comparison of one environmental variable between one classified map product and one continuous representation. However, the classified map product was produced in a multi-million dollar landscape mapping effort using the best available classification techniques and imagery. The published validation reported a producer's accuracy based on omission error (65.4%) and a user's accuracy based on commission error (78.7%). This classified map thus can be considered representative of the upper end of expected quality among the population of such maps available to ecologists and managers. Its failure to represent the important attributes of this variables spatial pattern and cell-level value suggests that efforts to classify inherently variable ecological attributes into categorical maps are questionable. Even if the cell-level classification into truncated bins was highly accurate, it still

would not satisfy questions one and two above, resulting in a distortion of pattern by artificially defining boundaries in a continuous landscape and obliterating the very high degree of internal variability. However, in this case the cell-level accuracy was so low that even if the classification levels were ecologically meaningful, the result is so inaccurate as to be of questionable value.

## 5.3   Multi-scale Gradient Concept of Habitat

In the previous example we considered how well categorical maps represent continuous attributes of vegetation structure. As we noted in that discussion, there are a great many ecological attributes which vary continuously across multiple spatial scales and for which a gradient approach to representing patterns and analyzing pattern-process relationships might be appropriate. One of the most important of these is habitat.

Ecological theory suggests that species exhibit a unimodal response to limiting resources in n-dimensional ecological space (Whittaker 1967; ter Braak 1988; Cushman et al. 2007b). A species not only requires a certain minimum amount of each resource but also cannot tolerate more than a certain maximum amount. Therefore, each species performs best near an optimum value of a necessary environmental variable and cannot survive when the value diverges beyond its tolerance (Shelford 1931; Schwerdtfeger 1977). The relationships between species' performance and gradients of critical resources and conditions describe its fundamental niche (Hutchinson 1957). The composition of biotic communities changes along biophysical gradients because of how the niche relationships of the constituent species interact with the spatial structure of the environment and competing species (Hutchinson 1957; Whittaker 1967; Austin 1985; Rehfeldt et al. 2006).

Most basically habitat is the resources and conditions necessary to allow survival and reproduction of a given organism (Hutchinson 1957). It is organism specific, and characterized as an n-dimensional function of multiple resources and conditions, each operative at particular spatial scales. Habitat relationships often change along a continuum of spatial scale reflecting the hierarchical nature by which animals select resources (Johnson 1980; Cushman and McGarigal 2004). Because relationships at finer scales may reveal mechanisms that are not apparent at broader spatial scales, a multiscaled, hierarchical approach is valuable (Cushman and McGarigal 2002). The volume of ecological space in which the organism can survive and reproduce defines its "environmental niche" (Hutchinson 1957; Rehfeldt et al. 2006).

The environmental gradients comprising the niche are clines in n-dimensional ecological space. In geographical space these gradients often form complex patterns across a range of scales (Wiens 2001; Wu 2007). The fundamental challenge to integrating landscape and community ecology is linking non-spatial niche relationships with the complex patterns of how environmental gradients

overlay heterogeneous landscapes (Austin 1985; ter Braak and Prentice 1988; Cushman et al. 2007). Traditionally there has been a severe disjunction between n-dimensional gradient theory of niche structure and spatial analysis of habitat patterns (McIntyre and Barrett 1992; McGarigal and Cushman 2005). The majority of spatial analyses in habitat ecology have fallen into one of two camps, each of which is conceptually divorced in important ways from gradient theory of niche and habitat structure.

The first paradigm we call the "island biogeographic model" (See Chapter 4). In this model, habitat fragments are viewed as analogues of oceanic islands in an inhospitable sea or ecologically neutral matrix. Under this perspective, discrete habitat patches (fragments) are seen as embedded in a uniform matrix of non-habitat. The key attributes of the model are its representation of the landscape as a binary system of habitat and inhospitable matrix, and that, once lost, habitat remains matrix in perpetuity.

The static island biogeography paradigm has been the dominant perspective since its inception. Its major advantage is simplicity. Given a focal habitat, it is quite simple to represent the structure of the landscape in terms of habitat patches contrasted sharply against a uniform matrix. Moreover, by considering the matrix as ecologically neutral, it invites ecologists to focus on those habitat patch attributes, such as size and isolation, that have the strongest effect on species persistence at the patch level. A 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.

The second major conceptual paradigm is the landscape mosaic model. In this paradigm, landscapes are viewed as spatially complex, heterogeneous assemblages of cover types, which can't be simplified into a dichotomy of habitat and matrix (Wiens et al. 1993; With 2000). Connectivity is assessed by the extent to which movement is facilitated or impeded through different land cover types across the landscape. In this model, connectivity is an emergent property of landscapes resulting from the interaction of organisms with landscape structure.

Niether the island biogeographic nor the landscape mosaic model of habitat is consistent with the basic theory that habitat is organism specific, multiple scaled and characterized by a zone in n-dimensional environmental space that consists of resources and conditions necessary and sufficient for the survival and reproduction of the species. Conceptually, patch based models of habitat are Clementsian, in that patches are proposed as discrete entities, analogous to super-organism habitat types (Clements 1916). It seems ironic that modern landscape ecology has adopted this categorical, super-organismal patch based model, when gradient perspectives on species–environment relationships have been dominant in plant and community ecology for nearly 100 years (Gleason 1926; Whittaker 1967). This example will explore several attributes of this inconsistency. We will begin presenting an evaluation of the sufficiency of island biogeographic and patch mosaic representations of habitat for breeding birds in a forest environment. From this analysis

we will argue that habitat quality is a continuous attribute that varies as a function of multiple resources and conditions, across a range of spatial scales, and representations that cast habitat as a categorical attribute in a patch mosaic risk serious error. We then will contrast a categorical representation of habitat with an alternative model in which habitat is represented as a continuous function of multiple variables at several spatial scales, and conclude that a gradient approach is consistent with basic ecological theory and less likely to result in spurious and misleading inferences about habitat amounts and patterns and their relationships with population processes.

The island biogeographic and landscape mosaic approaches implicitly assume that the environmental variation that is important to a species can be accurately represented as a mosaic of categorical patches. The analysis proceeds by proposing a series of landscape element types that are believed to comprise "habitat" for a species. In practice, these are usually represented as vegetation types. These are then classified into "habitat" vs. "nonhabitat" in the island biogeographic perspective, or are left as a mosaic of multiple cover types in the landscape mosaic perspective. We believe this categorical representation of habitat is fundamentally inconsistent with basic ecological theory in that it does not reflect species specific responses to multiple gradients of critical resources or conditions. All variability in environmental attributes is subsumed into a mosaic of patches that may or may not reflect attributes of importance to a species. Importantly, casting habitat as a categorical mosaic makes it very difficult to use the multi-variate and multi-scale methods that have been developed to construct niche-habitat models. This conceptual disjunction provides a major obstacle to linking the methods and theories of niche-relationships to spatial analysis of habitat pattern and its implications to population processes (Urban et al. 2002).

Our example evaluates the sufficiency of categorical representations of habitat patches in comparison to a multi-scale, multivariate approach. It is based on a multi-scale analysis of the habitat relationships of forest birds in the Oregon Coast Range (Cushman and McGarigal 2002, 2004; Cushman et al. 2007). The major question is whether categorical representation of habitat attributes as a patch mosaic is appropriate. For a patch mosaic of vegetation types to serve as an effective proxy for species abundance, Cushman et al. (2007) propose that several conditions must be met simultaneously. The most crucial are: (1) habitat is a proxy for population abundance, and (2) mapped vegetation types provide a proxy for the habitat of multiple species. The first assumption requires that species population sizes are strongly associated with environmental conditions, such that environmental conditions alone are a sufficient proxy for population status and trend. The second assumption states that broadly defined vegetation types provide an effective surrogate for the habitat requirements of each species.

Cushman et al. (2007) assessed habitat relationships across a range of organizational levels, including plot-level measurement of vegetation composition and structure, and the composition and configuration of a classified landscape

mosaic of patches representing vegetation cover types and seral stages. They found that the sufficiency of vegetation community types as proxies for habitat was highly dependent on the classification attributes and spatial scales at which communities were defined, and varied greatly among species. Their multi-scale analysis revealed that a large proportion of the variance in species abundance could not be explained by mapped community types, no matter how they were defined, and that fine-scale measurements of abiotic conditions and vegetation composition and structure were essential predictors of species abundance (Cushman and McGarigal 2004; Cushman et al. 2007). This suggests that the patch mosaic model, in addition to being conceptually distant from fundamental theories of the factors that drive species–environment relationships, also fails in practice to provide a strong predictor of habitat quality. This is primarily because of two factors. First, habitat is a multi-dimensional attribute, uniquely defined for each species, based on the resources it requires and conditions it can tolerate. Second, each of these critical resources or conditions may affect a species at a particular characteristic set of spatial scales. A categorical mosaic is inappropriate for both of these considerations. It is difficult to represent an n-dimensional function of environmental variation as a categorical mosaic. It is likewise difficult to define a unique patch mosaic from the habitat perspective of each individual organism. In addition, it is challenging to integrate environmental variation at several spatial scales into a single categorical representation of habitat quality (McGarigal and Cushman 2005).

The fundamental challenge to integrating the niche theory of habitat with spatial ecology lies in linking non-spatial niche relationships with the complex patterns of how environmental gradients overlay heterogeneous landscapes (Austin 1985; McIntyre and Barrett 1992; Urban et al. 2002; Manning et al 2004; Cushman et al. 2007b). By establishing species optima and tolerances along environmental gradients, researchers can quantify the characteristics of each species' environmental niche. The resulting statistical model can be used to predict the biophysical suitability of each location on a landscape for each species (Rehfeldt et al. 2006; Evans and Cushman 2009) (Fig. 5.3). This mapping of niche suitability onto complex landscapes is the fundamental task required to predict individualistic species responses to complexes of environmental conditions across landscapes. Importantly, it is fundamentally a gradient modelling exercise and the results are predictions of expected probability of occurrence, relative density or some other measure of habitat quality as continuous functions of multiple resources measured at one to many spatial scales. The insufficiency of patch-based representations of environmental structure as surrogates for species habitat relationships and the essential information provided by fine-scale vegetation and abiotic factors (Cushman et al. 2007a), implies that spatial representations of habitat should represent the environmental factors that most strongly predict organism abundance or performance. These factors will likely act across a range of scales, from within stand vegetation structure and composition, to local and landscape biophysical gradients of temperature, water and energy (Cushman et al. 2007b).
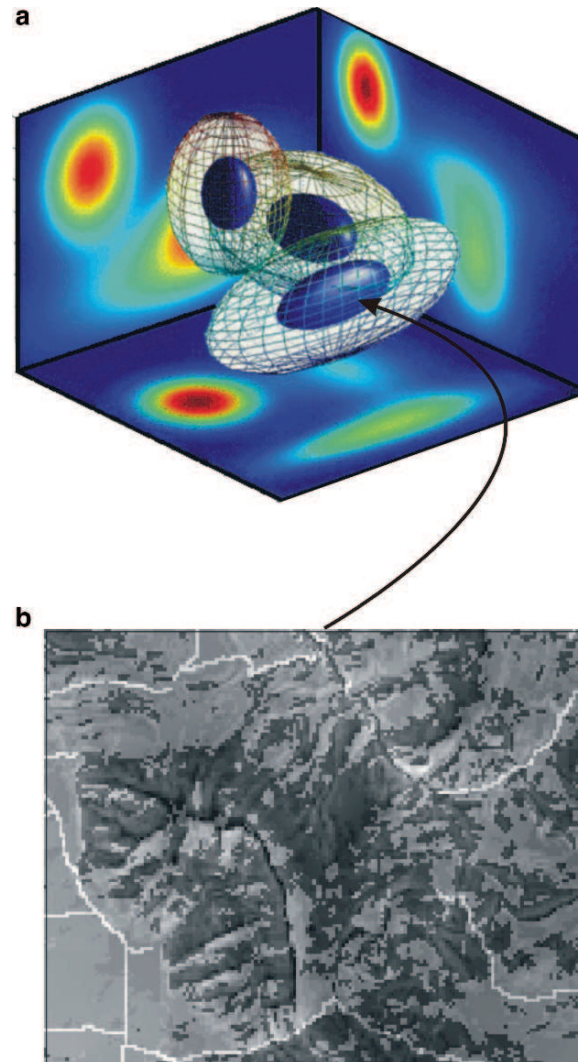
**Fig. 5.3** The habitat niche of an given species describes the range of resources and conditions over which the species can survive and reproduce. The niche is characterized as an n-dimensional hyper-ellipsoid (**a**) in which the species performs optimally within a certain restricted zone (blue core ellipsoids above), and can tolerate a certain wider range (mesh ellipsoids). The factors that comprise the axes of the habitat niche may represent any critical resource or condition, many of which will likely best be described by continous environmental gradients, and may reflect environmental factors from a number of different spatial scales. Given the habitat relationship described by the niche model, it is possible in principle to evaluate the habitat quality each location in a complex landscape, by assessing where the complex of environmental conditions at that location reside within the habitat niche space of the organism (**b**). The map at bottom shows a hypothetical example where habitat quality is a continuous function of multiple environmental attributes. The map shows a grey scale gradient of habitat quality from very low (white) to very high (black)

## 5.4 Binary Compared to Multi-scale Gradient Representation of Habitat Quality

In this example we compare a typical categorical representation of habitat based on vegetation seral stage with a multi-variate and multi-scale gradient representation. The example is based on habitat suitability for a hypothetical organism that is associated with mature forests and high elevations, and avoids areas of fragmented forest with high edge density. A typical way to represent habitat for this species in the island biogeographic perspective is as a binary map of habitat vs. nonhabitat (Fig. 5.4a). In this map white areas are mapped late seral forest patches and black areas are covered by various conditions of non-forest and younger seral stages. In this map all locations in late seral forest are given equal quality (1) regardless of their context with respect to edges, elevation or other environmental conditions. Habitat is categorical. Likewise, all locations in non-habitat are given equal value (0) regardless
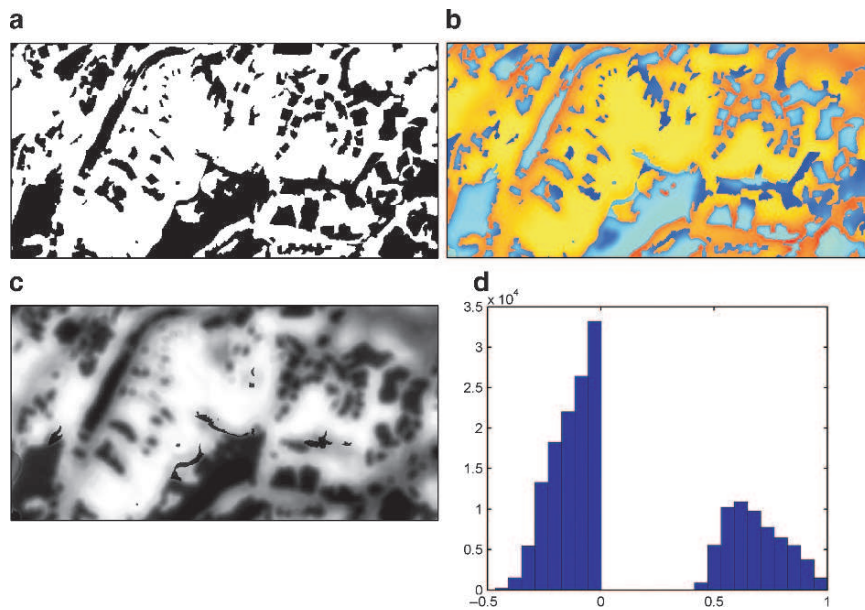


**Fig. 5.4** (**a**) Binary representation of habitat (white) and non-habitat (black) for a late-seral dependent organism. (**b**) Gradient representation of habitat quality for the same organism, including multiple environmental attributes at a range of scales. (**c**) Pixel differences between the two maps, calculated as (**b**)–(**a**). Assuming that the gradient representation more faithfully represents the patterns of habitat suitability, negative values in (**c**) correspond to areas where the binary map overpredicts habitat quality. In the map these are shown as a color ramp from yellow to red. Positive values in (**c**) are areas where the binary map underpredicts habitat quality, and are shown in a scale from dark blue to light blue, with dark blue representing areas with the least difference between the two maps. (**d**) Histogram showing the frequency distribution of differences between the two maps. The histogram shows both extensive areas where habitat quality is over predicted by the binary map (positive values) and extensive areas where habitat quality is underpredicted (negative values)

of whether they are bare rock, young forest or mature forest, or whether they are surrounded by non-habitat or a small island surrounded by quality habitat.

An alternative representation of habitat quality using a multi-scale gradient representation is shown in Fig. 5.4b. In this representation, the organism is also primarily related to late successional forest, but habitat quality is also affected by several other environmental attributes. For example, habitat quality is affected by elevation, with quality decreasing in a Gaussian manner away from a peak at 1,800 m in elevation. Additionally, not all "matrix" patch types are equivalent. Some, such as bare rock and snow, have a 0 quality value, but others, such as young and mature forest, have some habitat value. Further, this organism is sensitive to the density of high contrast edges at the scale of its home range (630 m radius). This example combines categorical, gradient, and neighborhood attributes of habitat quality. In combination these factors produce a surface of hypothetical habitat quality that is continuously varying, without many hard edges (except those around the few patch types with 0 quality), which includes factors from several spatial scales. While this is a hypothetical example, it shows how the gradient perspective allows multi-variate combination of several environmental attributes measured at correct spatial scales with respect to the organism of interest.

A comparison of these two maps will illustrate several points which may be of general value. Figure 5.4c shows the pixel-by-pixel difference between the expected habitat quality (expressed as Binary – Gradient) of the two maps. The color scheme represents the relative deviation of the binary map from the gradient map. Blue colors represent areas where the binary map predicted lower habitat quality than the gradient map. Conversely, yellow to red areas are those in which the binary map over predicted habitat quality. There are two main patterns of interest. First, areas predicted as non-habitat in the binary map are often predicted as suboptimal, but not, nonhabitat in the gradient representation, and the degree of suboptimality varies as function of the vegetation type, elevation and landscape context (with respect to high contrast edges). Second, areas predicted as habitat in the binary map are of varying quality in the gradient map, such that the quality of habitat is overpredicted by the binary map for most locations, particularly those in which there are many high contrast edges and those at relatively lower elevations. This pattern of binary maps systematically over predicting the quality of habitat pixels and under predicting the quality of non-habitat is a general property of categorical patch mosaic representations of habitat and has important implications for assessing effects of landscape patterns on population processes (Fig. 5.4d).

Perhaps the most important implication of the difference between the two maps is how closely they predict habitat quality. If in either case the same general conclusion is reached about habitat amount and pattern then there would be little cost incurred for using a simple binary representation versus a more sophisticated multi-variate, and multi-scale approach. How similar are these two maps in their prediction of habitat quality? A basic measure of this is the pixel-by-pixel correlation between the two maps. The Pearson correlation between the maps is 0.358, which means that only about 13% of variance is shared between them. In other words, 87% of the information in the gradient map cannot be accounted for by the binary

map, even though they are both based on the major influence of late succesional forest on habitat quality. Using one versus the other therefore in evaluating amounts and patterns of quality habitat would yield drastically different results.

## 5.5 Gradient Concept of Population Connectivity

Our final illustration of the gradient concept of landscape analysis centers on the question of population connectivity. One of the more immediate consequences of habitat fragmentation is the disruption of movement patterns and the resulting isolation of individuals and local populations. In the patch mosaic model of landscape structure, as habitat is fragmented, it is broken up into remnants that are isolated to varying degrees. If movement among habitat patches is significantly impeded, then individuals in remnant habitat patches may become reproductively isolated. In the patch mosaic model of categorical landscape structure, connectivity is assessed by the size and proximity of habitat patches and whether they are physically connected via habitat corridors. Patch edges may act as a filter or barrier that impedes or prevents movement, thereby disrupting emigration and dispersal from the patch (Wiens et al. 1985). In addition, the distance from remnant habitat patches to other neighboring habitat patches may influence the likelihood of successful movement of individuals among habitat patches.

However, in the previous example we argued that habitat often should not be represented as categorical patches due to the manner in which multiple environmental attributes combine across scale to influence site quality. Likewise, the factors that impede or facilitate movement may not best be represented as patch edges and inter patch distances. The influences of environmental structure on organism movement and population connectivity are species specific, and reliable inferences about population connectivity in complex landscapes requires assessing relationships between organism movement patterns and multiple environmental features across a range of spatial scales, rather than simplistic representation of habitat patch interiors, edges and inter-patch distances (Cushman 2006).

In practice it has been problematic to develop reliable inferences regarding how multiple environmental features influence movement of organisms across several spatial scales. The two traditional approaches to study animal movement have been mark-recapture and radio-telemetry (Cushman 2006). By quantifying movement rates, distances and routes of dispersing juveniles through complex environments researchers can describe species specific responses to environmental conditions. These methods are suited for incorporation in manipulative field experiments which provide the most reliable inferences about relationships between survival rates, movement and ecological conditions (McGarigal and Cushman 2002). Both of these methods are limited by logistical challenges that reduce their ability to test interactive effects of multiple landscape attributes on organism movements. The challenge in these studies is one of cost and sample sizes. It is very difficult to obtain a large sample size of individuals and then track their movements across

many combinations of environmental conditions to provide data to infer patterns of movement in relation to landscape features.

Recent advances in landscape genetics have greatly facilitated developing rigorous, species-specific, and multi-variate characterizations of habitat connectivity for animal species (Manel et al. 2003; Holderegger and Wagner 2006; Storfer et al. 2007). Landscape genetic approaches largely mitigate the logistical and financial costs of extensive mark-recapture studies. To data, many population and landscape genetic studies have used $F$-statistics (Wright 1943) or assignment tests (Pritchard et al. 2000; Corander et al. 2003; François et al. 2006) to relate genetic differences among well-defined subpopulations to; distance relationships (Michels et al. 2001), putative movement barriers (Manni et al. 2004; Funk et al. 2005) or correlations with landscape features (Spear et al. 2005). This is an explicitly island-biogeographic perspective in which populations are assumed to be discretely bounded and relatively isolated, with no internal structure. Genetic differences are assumed to be a function of group membership entirely, with no effect of internal population structure, or the effects of distance or movement cost between populations.

Once discrete subpopulations have been identified, post hoc analyses are performed, correlating observed genetic patterns with interpopulation distance or putative movement barriers (e.g., Proctor et al. 2005). Populations, however, often have substantial internal structure (Wright 1943), and it is often difficult to rigorously define discrete boundaries between populations. In terrestrial landscapes it is more common to have species that are either continuously distributed or patchily distributed with low densities between populations (Cushman et al. 2006). Thus, in many situations, population structure is better defined as a gradient phenomenon than as a categorical, patch-based entity.

By sampling genetic material from a large number of organisms distributed across large and complex landscapes researchers can quantify neutral genetic variability among individuals (Storfer et al. 2007). Spatial patterns in this neutral variability are indicators of relative connectivity of the population across space (Holderegger and Wagner 2006; Cushman et al. 2006; Storfer et al. 2007). Individual-based analyses that associate genetic distances with alternative models of landscape resistance to gene flow offer a direct and powerful means to assess the affects of multiple landscape features across spatial scales on population connectivity. By comparing the least cost distances among individuals across alternative resistance hypotheses (Fig. 5.5) to genetic distances it is possible to evaluate alternative hypotheses, such as isolation by distance, barriers or landscape resistance gradients (Cushman et al. 2006; Storfer et al. 2007).

For example, Cushman et al. (2006) used least cost path analysis and causal modelling on resemblance matrices to test 110 alternative models of landscape resistance for American black bear (*Ursus americanus*). The approach framed landscape resistance as a gradient phenomenon whose total effect is a weighted combination of multiple landscape factors across a range of spatial scales. Importantly, the analysis framework provided an explicit test of isolation by population patches,
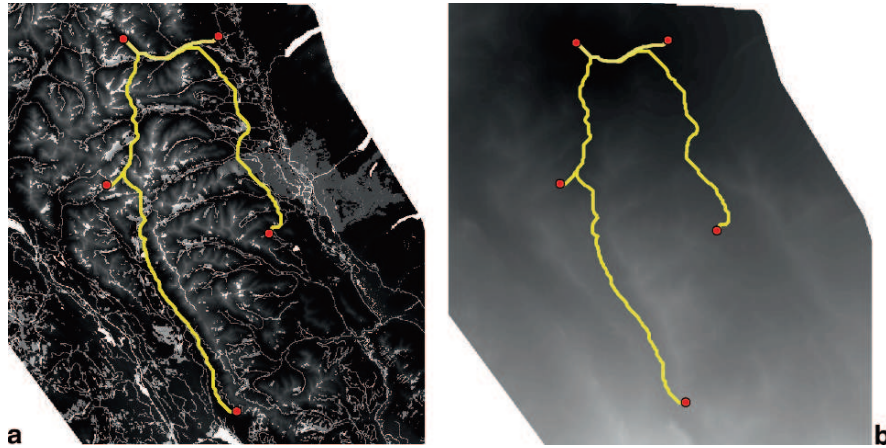
**Fig. 5.5** Example of computing least cost paths to derive cost distances between individuals across a resistance hypothesis. (**a**) landscape resistance is a continuous spatial variable ranging from 1 (black) to approximately 65 (white). The locations of five individual animals are indicated by red dots. (**b**) least cost distance from the upper left individual across the costsurface (**a**). The least cost paths between the upper left individual and the other four animals are shown as yellow lines. Computing cost distances between all pairs of animals on this resistance models will create an independent variable matrix that can be associated with the genetic distances between all pairs of animals. By testing the degree of support for multiple alternative resistance models it is possible to identify the factors that facilitate or inhibit gene flow across complex landscapes

isolation by geographical distance and isolation by landscape resistance gradients. The results indicated that isolation-by-barrier and isolation-by-distance models are poorly supported in comparison to isolation by landscape-resistance gradients. Evaluating multiple competing hypotheses identified land cover and elevation as the dominant factors associated with genetic structure. Gene flow in this black bear population appears to be facilitated by forest cover at middle elevations, inhibited by nonforest land cover, and not influenced by topographical slope. The most supported model produced a map of resistance to gene flow when applied to the landscape (Fig. 5.6). This map shows that landscape connectivity is not a binary function of habitat and matrix, but is best characterized as a gradient of cell-level resistance as a function of several environmental variables.

Most population genetic studies have considered populations to be mutually isolated and internally panmictic. This is often an unrealistic model that imposes an artificial structure on analysis and can distort results. Actual populations usually exhibit continuous gradients of divergence across space and in relation to the resistance of landscape features (e.g. Cushman et al. 2006). Thus, it is often preferable to represent population structure as a gradient phenomenon rather than a categorical, patch-based entity. Representing the population structure in this way preserves internal information about how genetic characteristics vary across space, which would be lost in traditional closed-panmictic population analysis.
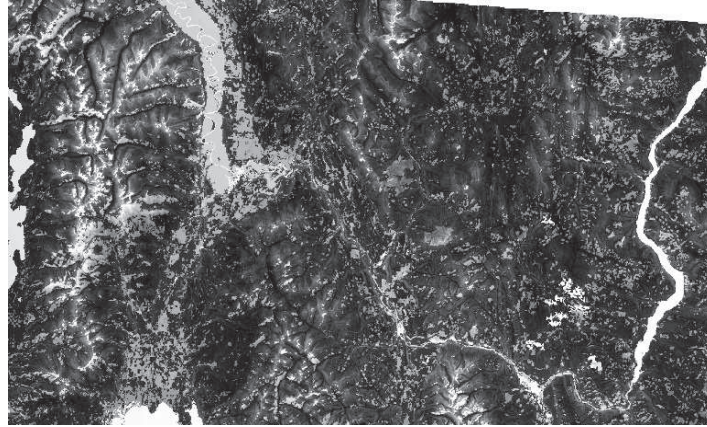
**Fig. 5.6** Continuous landscape resistance map for black bears from Cushman et al. (2006). The most supported model of landscape structure indicated that resistance to gene flow was a continuous function of elevation and landcover. This map represents resistance to gene flow as a color ramp from white (high resistance) to black (low resistance)

Also, by representing population structure as a gradient phenomenon it is possible to compare population gradients with landscape resistance gradients. By representing both the genetic dependent variables and the landscape resistance variables as continuous gradients it is possible to test competing hypotheses of the effects of landscape structure on gene flow, in comparison to isolation by distance and putative barriers in one synthetic analysis. This would not be possible is populations were represented as categorical entities.

## 5.6   Gradient-Based Measures of Landscape Structure

Landscape ecologists often compare the structure of different landscapes, or the structure of the same landscape over time, and relate observed differences to some process of interest. When categorical maps are appropriate, conventional landscape metrics based on the patch-mosaic model are effective, and many metrics for this purpose exist (e.g., Baker and Cai 1992; McGarigal and Cushman 2002). However, when environmental variation is better represented as continuous gradients, it is not as simple to summarize the structure of each landscape in a metric because each landscape is represented as a continuous surface, or several surfaces corresponding to different environmental attributes.

The two fundamental attributes of a surface are its height and slope. The patterns in a landscape surface that are of interest to landscape ecologists are emergent properties of particular combinations of surface heights and slopes across the study area. The challenge is to develop metrics that characterize these aspects of surface patterns and that are effective predictors of organismic and ecological processes.

Geostatistical techniques can be used to summarize the spatial autocorrelation of such a surface (Webster and Oliver 2001). Measures such as Moran's I and semi-variance, for example, indicate the degree of spatial correlation in the quantitative variable (i.e., the height of the surface) at a specific lag distance (i.e., distance between points). These statistics are plotted against a range of lag distances to summarize the spatial autocorrelation structure of the landscape. The correlogram and semi-variogram can provide useful indices to quantitatively compare the intensity and extent of autocorrelation in quantitative variables among landscapes. Though these statistics can provide information on the distance at which the measured variable becomes statistically independent, and reveal the scales of repeated patterns in the variable, they do little to describe other important aspects of the surface. For example, the degree of relief, density of troughs or ridges, and steepness of slopes are not measured. Fortunately, a number of gradient-based metrics that summarize these and other important properties of continuous surfaces have been developed in the physical sciences for analyzing three-dimensional surface structures (Stout et al. 1994; Barbato et al. 1995, Villarrubia 1997). In the past 10 years, researchers in microscopy and molecular physics have made tremendous progress in this area, creating the field of surface metrology (Barbato et al. 1995).

*Surface Metrology* – In surface metrology, several families of surface-pattern metrics have become widely used. These have been implemented in the software package SPIP (2001). One such family of metrics quantifies measures of surface amplitude in terms of its overall roughness, skewness and kurtosis, and total and relative amplitude. Another family records attributes of surfaces that combine amplitude and spatial characteristics, such as the curvature of local peaks. Together, these families of metrics quantify important aspects of the texture and complexity of a surface. A third family measures certain spatial attributes of the surface associated with the orientation of the dominant texture. The final family of metrics are based on the surface bearing area ratio curve, also called the Abbott curve (SPIP 2001). The Abbott curve is computed by inversion of the cumulative height-distribution histogram. A number of indices that describe structural attributes of a surface have been developed from the proportions of this curve (SPIP 2001).

Many classic metrics for analyzing categorical landscape structure have ready analogs in surface metrology. For example, the major compositional metrics such as patch density, percent of landscape, and largest patch index correspond respectively to peak density, surface volume, and maximum peak height. Major configuration metrics such as edge density, nearest neighbor index, and fractal dimension index correspond respectively to mean slope, mean nearest maximum index, and surface fractal dimension. Many of the surface metrology metrics, however, measure attributes that are conceptually quite foreign to conventional landscape pattern analysis. Landscape ecologists have not yet explored the behavior and meaning of these new metrics; it remains for them to demonstrate the utility of these metrics, or develop new surface metrics better suited for landscape ecological questions.

*Fractal Analysis* – Fractal analysis provides a vast set of tools to quantify the shape complexity of surfaces. There are many algorithms in existence that can measure

the fractal dimension of any surface profile, surface, or volume (Mandelbrot 1982; Pentland 1984; Barnsely et al. 1988). One such index that is implemented in SPIP calculates the fractal dimension along profiles of the surface from 0° to 180°. A number of other fractal algorithms are available for calculating the overall fractal dimension of the surface, rather than for particular profile directions. Variations on these approaches will yield metrics that quantify important attributes of surface structure for comparison between landscapes, between regions within a landscape, and for use as independent variables in modeling and prediction of ecological processes.

In addition, there are surface equivalents to lacunarity analysis of categorical fractal patterns. Lacunarity measures the gapiness of a fractal pattern (Plotnick et al. 1993). Several structures with the same fractal dimension can look very different because of differences in their lacunarities. The calculation of measures of surface lacunarity is a topic that deserves considerable attention. It seems to us that surface lacunarity, which would measure the 'gapiness' in the distribution of peaks and valleys in a surface rather than holes in the distribution of a categorical patch type, would be a useful index of surface structure.

*Spectral and Wavelet Analysis* – Spectral analysis and wavelet analysis are ideally suited for analyzing surface patterns. The spectral analysis technique of Fourier decomposition of surfaces could find a number of interesting applications in landscape surface analysis. Fourier spectral decomposition breaks up the overall surface patterns into sets of high, medium and low frequency patterns (Kahane and Lemarie 1995). The strength of patterns at different frequencies, and the overall success of such spectral decompositions can tell us a great deal about the nature of the surface patterns and what kinds of processes may be acting and interacting to create those patterns. They also provide potential indices for comparing among landscapes and for deriving variables that describe surface structure at different frequency scales that could be used for prediction and modeling (Kahane and Lemarie 1995; Cho and Chon 2006).

Similarly, wavelet analysis is a family of techniques that has many potential applications in landscape surface analysis (Bradshaw and Spies 1992; Chui 1992; Kaiser 1994; Cohen 1995). Traditional wavelet analysis is conducted on transect data, but the method is easily extended to two-dimensional surface data. Major advances in wavelet applications have occurred in the past several years, with many software packages now available for one- and two-dimensional wavelet analysis. For example, comprehensive wavelet toolboxes are available for R, S-Plus, MATLAB and MathCad. Wavelet analysis has the advantage that it preserves hierarchical information about the structure of a surface pattern while allowing for pattern decomposition (Bradshaw and Spies 1992). It is ideally suited for decomposing and modeling signals and images, and it is useful in capturing, identifying, and analyzing local, multiscale, and nonstationary processes. Because wavelet analyses score a range of kernels they area a robust tool for building multi-scale information directly into an analysis. It can be used to identify trends, break points, discontinuities, and self-similarity (Chui 1992; Kaiser 1994). In addition, the calculation of the wavelet variance enables comparison of the dominant scales of pattern among landscape surfaces or between different parts of a single surface (Bradshaw and Spies 1992).

Thus, wavelet decomposition and wavelet variance have great potential as sources of new surface-pattern landscape metrics and novel approaches to analyzing landscape surfaces.

## 5.7 Conclusions

The patch-mosaic model of landscape structure has provided a valuable operating framework for spatial ecologists, and it has facilitated rapid advances in quantitative landscape ecology, but further advances in spatial ecology are constrained by its limitations. We advocate a gradient-based paradigm of landscape structure that reflects continuously varying heterogeneity and that subsumes the patch-mosaic model as a special case. The gradient paradigm does not presuppose discrete structures, but it will identify them if they exist; it facilitates multi-scale and multivariate analyses of ecological relationships, and provides a flexible framework for conducting organism- or process-centered analyses. Through these advantages, the gradient paradigm of landscape structure will enable ecologists to represent landscape heterogeneity more flexibly in analyses of pattern–process relationships.

## References

Allen TFH, Starr TB (1982) Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, IL

Baker WL, Cai Y (1992) The r.le programs for multiscale analysis of landscape structure using the GRASS geographical information system. Landsc Ecol 7:291–302

Barbato G, Carneiro K, Cuppini D, Garnaes J, Gori G, Hughes G, Jensen CP, Jorgensen JF, Jusko O, Livi S, McQuoid H, Nielsen L, Picotto GB, Wilening G (1995) Scanning tunnelling microscopy methods for the characterization of roughness and micro hardness measurements. Synthesis report for research contract with the European Union under its programme for applied metrology. European Commission Catalogue number: CDNA-16145 EN-C Brussels Luxemburg

Barnsely MF, Devaney RL, Mandelbrot BB, Petigen H, Saupe D, Voss RF (1988) The science of fractal images. Springer, New York

Bradshaw GA, Spies TA (1992) Characterizing canopy gap structure in forests using wavelet analysis. J Ecol 80:205–215

Cho E, Chon T (2006) Application of wavelet analysis to ecological data. Ecol Informat 1:229–233

Chui CK (1992) An introduction to wavelets. Academic, San Diego, CA

Clements FE (1916) The nature and structure of the climax. J Ecol 24:252–284

Cohen A (1995) Wavelets and multiscale signal processing. Chapman & Hall, London

Corander J, Waldmann P, Sillanpää MJ (2003) Bayesian analysis of genetic differentiation between populations. Genetics 163:367–374

Cushman SA, McGarigal K (2004) Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. Ecological Applications. 14(4):1090–1105.

Cushman SA, McKenzie D, Peterson DL, Littell J, McKelvey KS (2007) Research agenda for integrated landscape modelling. USDA For. Serv. General Technical Report RMRS-GTR-194.

Dutilleul P (1993) Modifying the t-test for assessing the correlation between two spatial processes. Biometrics 49:305–314

Evans JS, Hudak AT (2007) A multiscale curvature algorithm for classifying discrete return lidar in forested environments. IEEE Transactions on Geoscience and Remote Sensing, 45:1029–1038

Evans JS, Cushman SA (2009) Gradient modeling of conifer species using random forests. Landscape Ecology 24:673–683.

Ewe HT, Au WC, Shin RT, Kong JA (1993) Classification of SAR images using a fractal approach. Proceedings of Progress in Electromagnetic Research Symposium (PIERS) Los Angeles

Forman RTT (1995) Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge

Forman RTT, Godron M (1986) Landscape ecology. Wiley, New York

François O, Ancelet S, Guillot G (2006) Bayesian clustering using hidden Markov random fields in spatial population genetics. Genetics 174:805–816

Funk WC, Blouin MS, Corn PS, Maxell BA, Pilliod DS, Amish S, Allendorf FW (2005) Population structure of Columbia spotted frogs (Rana luteiventris) is strongly affected by the landscape. Mol Ecol14:483–496

Gleason HA (1926) The individualistic concept of the plant association. Bull Torr Bot Club 53:7–26

Guthrie KA, Sheppard L (2001) Overcoming biases and misconceptions in ecological studies. J Roy Stat Soc Stat Soc 164:141–154

He HS, DeZonia BE, Mladenoff DJ (2000) An aggregation index (AI) to quantify spatial patterns of landscapes. Landsc Ecol 15:591–601

Holderegger R, Wagner HH (2006) A brief guide to landscape genetics. Landsc Ecol 21:793–796

Hutchinson GE (1957) Concluding remarks. Cold Spring Harbor Symp Quantitative Biol 22:415–427

Jelinski DE, Wu J (1996) The modifiable areal unit problem and implications for landscape ecology. Landsc Ecol 11:129–140

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kahane JP, Lemarie PG (1995) Fourier series and wavelets.Studies in the Development of Modern Mathematics, vol 3. Gordon and Research Publishers

Kaiser G (1994) A friendly guide to wavelets. Birkhauser

Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253–260

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Mandelbrot BB (1982) The fractal geometry of nature. W.H. Freeman, New York

Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: the combination of landscape ecology and population genetics. Trends in Ecol Evol 18:189–197

Manni F, Guerard E, Heyer E (2004) Geographic patterns of (genetic, morphologic, linguistic) variation: how barriers can be detected by using Monmonier's algorithm. Hum Biol 76:173–190

Manning AD, Lindenmayer B, Nix HA (2004) Continua and umwelt: novel perspectives on viewing landscapes. Oikos 104:621–628

McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation. Ecol Appl 12:335–345

McGarigal K, Cushman SA (2005) The gradient concept of landscape structure. In: Wiens J, Moss M (eds) Issues and Perspectives in Landscape Ecology. Cambridge University Press, Cambridge

McGarigal K, Marks BJ (1995) FRAGSTATS: spatial analysis program for quantifying landscape structure. USDA For Serv Gen Tech Rep PNW-GTR-351

McGarigal K, Cushman SA, Stafford S (2000) Multivariate statistics for wildlife and ecology research. Springer, New York

McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst www.umass.edu/landeco/research/fragstats/fragstats.html

McIntyre S, Barrett GW (1992) Habitat variegation, an alternative to fragmentation. Conservat Biol 4:197–202 McGarigal K, Cushman SA (2005) The gradient concept of landscape structure. In: Wiens J, Moss M (eds) Issues and Perspectives in Landscape Ecology. Cambridge University Press, Cambridge

Michels E, Cottenie K, Neys L, DeGalas K, Coppin P, DeMeester L (2001) Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modeling of the effective geographical distance. Mol Ecol 10:1929–1938

Moore ID, Gryson RB, Ladson AR (1991) Digital terrain modeling: a review of hydrological, geomorphological, and biological applications. Hydrolog Process 5:3–30

Murphy MA, Evans JS, Cushman SA, Storfer A (2008) Representing genetic variation as continuous surfaces: An approach for identifying spatial dependency in landscape genetic studies. Ecography 31:685–697

Ohmann JL, Gregory MJ (2002) Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. Canadian Journal of Forest Resources 32:725–741.

O'Neill RV, DeAngelis DL, Waide JB, Allen TFH (1986) A hierarchical concept of ecosystems. Princeton University Press, Princeton, NJ

O'Neill RV, Johnson AR, King AW (1989) A hierarchical framework for the analysis of scale. Landsc Ecol 3:193–205

Openshaw S (1984) The modifiable areal unit problem. Norwich: Geo Books. ISBN 0–86094–134–5

Pentland AP (1984) Fractal-based description of natural scenes. IEEE Trans Patt Anal Mach Intel 6:661–674

Peterson DL, Parker VT (1998) Ecological scale: theory and applications. Columbia University Press, New York

Plotnick RE, Gardner RH, O'Neill RV (1993) Lacunarity indices as measures of landscape texture. Landsc Ecol 8:201–211

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

Proctor MF, McLellan BN, Strobeck C, Barclay RMR (2005) Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerability by small populations. Proceedings of the Royal Society B: Biological Sciences 272:2409–2416

Rehfeldt GE, Crookston NL, Warwell MV, Evans JS (2006) Empirical analyses of plant-climate relationships for the western United States. Int J Plant Sci 167:1123–1150

Robinson WS (1950) Ecological correlations and the behavior of individuals. Am Socio Rev 15:351–357

Spear SF, Peterson CR, Matacq M, Storfer A (2005) Landscape genetics of the blotched tiger salamander (*Ambystoma tigrinum melanostictum*). Mol Ecol 14:2553–2564

SPIP (2001) The scanning probe image processor. Image Metrology APS, Lyngby, Denmark

Schneider DC (1994) Quantitative ecology: spatial and temporal scaling. Academic, San Diego, CA.

Stout KJ, Sullivan PJ, Dong WP, Mainsah E, Lou N, Mathia T, Zahouani H (1994) The development of methods for the characterization of roughness on three dimensions. Publication no EUR 15178 EN of the Commission of the European Communities, Luxembourg

Storfer A, Murphy MA, Evans JS, Goldberg CS, Robinson S, Spear SF, Dezzani R, Delmelle E, Vierling L, Waits LP (2006) Putting the 'landscape' in landscape genetics. Heredity 2006:1–15

ter Braak CJF (1988) Partial canonical correspondence analysis. In: Bock HH (ed.) Classification and related methods of data analysis. North-Holland, Amsterdam

Turner MG (1989) Landscape ecology: the effect of pattern on process. Annl Rev Ecol System 20:171–197

Turner MG, O'Neill RV, Gardner RH, Milne BT (1989) Effects of changing spatial scale on the analysis of landscape pattern. Landsc Ecol 3:153–162

Urban DL, O'Neill RV, Shugart HH (1991) Landscape ecology. BioScience 37:119–127

Urban DL, Goslee S, Pierce K, Lookingbill T (2002) Extending community ecology to landscapes. Ecoscience 9:200–212

Villarrubia JS (1997) Algorithms for scanned probe microscope, image simulation, surface reconstruction and tip estimation. J Nat Inst Stand Tech 102:435–454

Webster R, Oliver M (2001) Geostatistics for environmental scientists. Wiley, Chichester

Whittaker RH (1967) Gradient analysis of vegetation. Biol Rev 42:207–264

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397

Wiens JA (2001) Understanding the problem of scale in experimental ecology. In: Gardner RH, Kemp WM, Kennedy VS, Petersen JE (eds) Scaling relations in experimental ecology. Columbia University Press, New York

Wiens JA, Stenseth NC, Van Horne B, Ims RA (1993) Ecological mechanisms and landscape ecology. Oikos 66:369–380

Wood CH, Skole D (1998) Linking satellite, census, and survey data to study deforestation in the Brazilian Amazon. In: Liverman D, Moran EF, Rindfuss RR, Stern PC (eds) People and pixels: linking remote sensing and social science. National Academy Press, Washington, DC

Wright S (1921) Correlation and causation. J Agric Res 20:557–585

Wright S (1943) Isolation by distance. Genetics 28:114–138

Wright S (1960) Path coefficients and path regressions: alternative or complementary concepts? Biometrics 16:189–202

Wu J (2007) Scale and scaling: a cross-disciplinary perspective. In: Wu J, Hobbs RJ (eds) Key topics in landscape ecology. Cambridge University Press, Cambridge

Wu J, Hobbs R (2002) Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landsc Ecol 17:355–365