

Chapter 7

Focused Assessment of Scale-Dependent Vegetation Pattern

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7.1 Introduction

Ecological processes frequently occur at multiple spatial scales simultaneously. For example, fires imprint the landscape at a variety of spatial scales, from small areas of high burn intensity due to patchy surface fuels, to large stands within fires that escape conflagration entirely (Fig. 7.1). These types of complex disturbances can increase environmental heterogeneity and thus species diversity by creating a variety of microhabitats and by increasing patch diversity (Romme and Knight 1982; Christensen 1985; Denslow 1985; Pickett and White 1985; Turner et al. 1998). The flow of organisms, genes, and populations provides another excellent example of scale-dependent ecological processes (see Chap. 8).

Because ecological data are scale-specific, any model based on these data will provide inferences at a specific spatial scale. The scale of inference of statistical models is a critical consideration in predictive modeling (see Chap. 4). Some confusion can arise if the variables used to build a model are themselves scaled differently. For example, soils variables and terrain features have different characteristic scales (Urban et al. 2000). As a consequence a regression based on these data would be multi-scaled (Lookingbill and Urban 2004). Peters et al. (2004) refer to this approach to landscape modeling as spatially *implicit*, a non-spatial model built from geospatial data. By far, most models of species distribution are spatially implicit.

By contrast, a spatially *explicit* model would include predictive variables that account for spatial processes explicitly. From a modeling perspective, few approaches are currently available to ecologists to account for scale explicitly. Multi-level modeling (Gelman and Hill 2007) offers a framework for multi-scale

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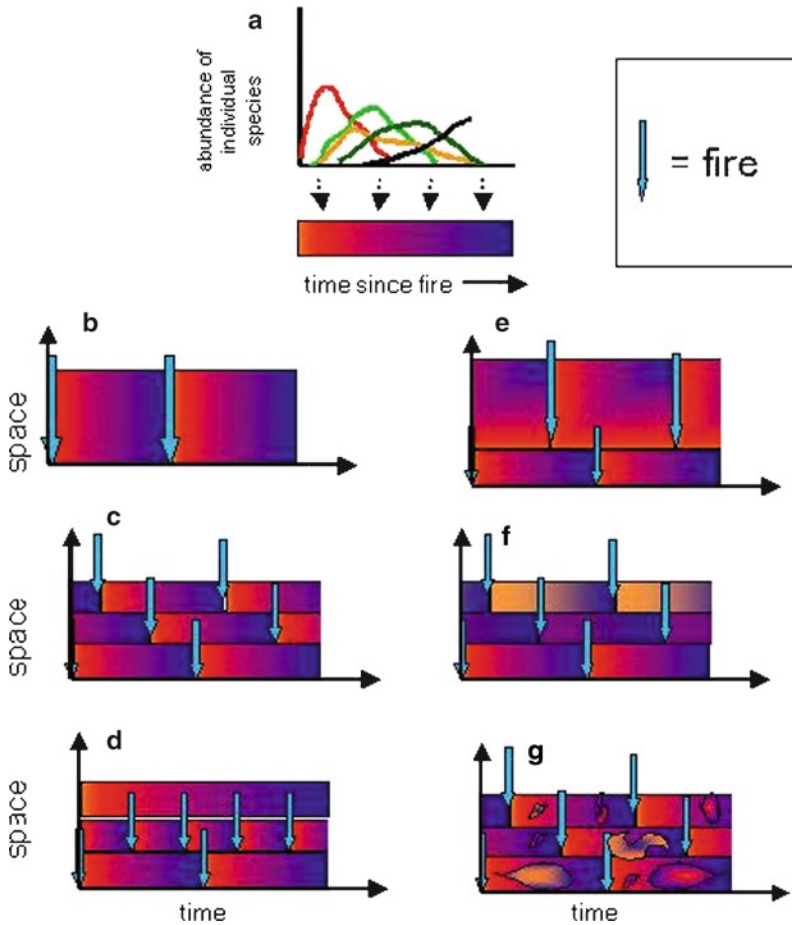


Fig. 7.1 Schematic diagram of different sources of spatial heterogeneity in fire regimes and fire effects. Color gradient represents turnover of species with space (vertical axis) and time (horizontal axis). (a) Red represents an early successional species/post-fire colonizers, blue represents late successional species/competitors, and orange represents the most severely burned areas; (b) uniform landscape with synchronous disturbance; (c) heterogeneity in time-since-fire with uniform fire regime; (d) heterogeneity in fire regime (fire frequency) across the landscape; (e) variable fire size (note dispersal gradients); (f) heterogeneity in season-of burn (top row burned under driest, hottest conditions resulting in orange/high severity; second row burned under mild conditions resulting in little setback of successional clock); (g) within-fire variability in fire intensity (fine-scale patchiness in intensity indicated by small patches with colors ranging from orange to red to blue)

models, if the levels of the nested ANOVA design are explicitly scaled by the user; that is, the levels specified in terms of variables with known characteristic scaling. Thus far, such applications tend to be nested logically (i.e., as treatments nested within blocks) rather than in a spatially explicit manner, but there is no reason why

these models could not be framed across spatial scales. Similarly, hierarchical Bayesian models (Clark 2005; Gelman and Hill 2007) might be constructed to explicitly nest spatial scales, but are a more general construct.

We suggest that the multi-scale nature of ecological processes presents at least two challenges to landscape-scale species distribution modeling: choice of sample design and choice of inferential model. First, to capture landscape variability, fine-grained data need to be collected over a large spatial extent – a task that appears, at first glance, to be difficult if not impossible (Urban et al. 2002). In this chapter, we present a response to this data challenge that identifies and focuses sampling in locations of high resource heterogeneity. Ecologists have tended to focus on homogeneous environments to understand ecological processes (e.g., Whittaker 1956; Peet 1981), deliberately avoiding sampling locations of high local variability. However, locations of fine-scale heterogeneity can be extremely informative of broader-scale vegetation patterns. Ecotone studies provide the opportunity to efficiently collect detailed data on species-environment relationships at the competitive limits of the ecological tolerances of a species (Neilson 1991; Hansen and di Castri 1992; Risser 1995; but see Gosz 1993 for a warning of the dangers of not strictly defining the scale of transition in ecotone studies). Because these regions may be especially sensitive to environmental change, an increasing number of studies have been gathering data at treeline and other potentially sensitive vegetation ecotones (Camarero et al. 2000; Camill and Clark 2000; Fortin et al. 2000; Bunn et al. 2005).

Next, incorporating the data into predictive models presents a second major challenge. Just as it is logistically prohibitive to sample exhaustively at all spatial scales, no model can represent all details of an environmental system simultaneously. Models, by their nature, must simplify. Identification of dominant scales of ecological patterns and processes can be used by modelers to help determine which details are important to retain and which can be safely ignored (Levin 1992; Denny et al. 2004). Borrowing from fields of mathematics and computer science, much attention has been paid to identifying dominant scales of ecological patterns (Greig-Smith 1961; Dale 1999; Fortin and Dale 2005). Relating these patterns to their formative processes requires careful attention to the scale of inference of the statistical model. We provide a review of published approaches for linking pattern to process within a scale-specific framework. The direct assessment of these relationships provides opportunities for improved prediction and management of species responses to environmental change.

In the sections below, we describe methods for collecting landscape data at multiple spatial scales, the models that can be used to interpret these observations of pattern, and example applications of our approach to modeling scale-dependent vegetation pattern for the Sierra Nevada and Cascade Mountains of the western United States. The two examples demonstrate how accounting for spatial autocorrelation, capturing multi-scale pattern, and exploring the causes of pattern at each scale can be used to better predict vegetation shifts in response to changing climate and to improve fire management.

7.2 Management Challenge, Ecological Theory, and Empirical Framework

7.2.1 Management Challenge

The decision not to take a spatially explicit, cross-scale approach to environmental assessment can have profound management implications. Managers dealing with rapidly changing systems may not understand how these changes propagate at specific scales and locations on the landscape. A classic example is provided in the area of global climate change. Habitat models using the broad-scale predictions from global climate models as a basis for their predictions have predicted the upslope and northward migration of species in response to increasing temperatures (Peters and Darling 1985). The acquisition and protection of habitat corridors parallel to these gradients has been advised as a potential mitigation strategy (Noss 2001). However, as demonstrated by Halpin (1997) and others, basing management decisions on these coarse-scale models without regard to specific spatial characteristics of a site can be risky and ill-advised. Predictions based on regional variables such as temperature do not capture local-scale factors that drive the water balance (Stephenson 1990, 1998) and therefore may badly predict species physiological responses to future climates. Recent efforts to model species distributions in the context of global change have taken more sophisticated approaches and include more physiologically relevant data. These include the work of Iversen et al. (2004) to estimate potential migration of tree species into suitable habitat using a suite of data on climate, soils, land use, and landscape pattern. Biogeography models such as MAPPS (Neilson 1995) also use multiple soil, climate, and landscape variables to predict vegetation distribution at coarse scales. These models are increasingly linked to biogeochemistry models to provide estimates of major shifts in biomes under projected climate change (Neilson and Drapek 1998; Bachelet et al. 2001). New predictive models that rely heavily on detailed physiological data incorporate factors such as budburst phenology, frost hardiness, and drought tolerance (Morin et al. 2007, 2008). However, these modeling efforts remain largely coarse-scaled relative to the fine-scale variability in soils and climate that are critical to species migration patterns.

Wildland fire provides another example of an area in which managers are faced with making difficult decisions about a complex, multi-scale process. Despite the potential ecological importance of fire-generated heterogeneity at multiple spatial scales to ecosystem health (Davis et al. 1989; Moreno and Oechel 1992; Odion and Davis 2000; Brooks 2002), fire management rarely adopts a spatially explicit perspective that incorporates fine-scale variability. Fire suppression has dominated US natural resource policy and management for a century, and only recently has fire been reintroduced to some fire-adapted landscapes in the form of controlled burning. In many western forest types, especially those that historically experienced frequent low- or moderate-severity fire regimes, fire suppression has led to heavy fuel accumulations and shifts in plant community composition and structure, and has increased the risk of catastrophic wildfire (Agee 1998; Stephenson 1999). In addition to increasing overall loads, the legacy of fire suppression has also acted

to generally homogenize fuel loads in these ecosystems. This homogenization can cause continuous, uniform burn patterns at the fine scale and a larger burn patch or fire size at the landscape scale. Whereas there is considerable variability in the effectiveness of recent fuel reduction efforts across the western US (Schoennagel et al. 2004), many fire-adapted landscapes cannot be restored without active management, nor can fires be entirely controlled (Miller and Urban 1999).

Replicating the full range of natural variability in fire behavior may be critical to maintaining biodiversity and ecosystem functioning. However, this goal has not been fully embraced by practitioners in the field, perhaps because of the difficulty associated with describing multi-scale fire patterns and their ecological effects. As a consequence, fire and mechanical thinning restoration treatments have been widely used without a clear understanding of the influence of fire on species distribution patterns. These applications tend to focus on the temporal domain in attempting to mimic historical disturbance frequency and to restore pre-suppression forest structure, but fire also has an important spatial component that creates heterogeneity in the physical and competitive environment. Spatial considerations have been limited to the among-patch scale (i.e., maintaining a mosaic of patch ages). The importance of reproducing the within-patch fire heterogeneity created by natural burns deserves further consideration in management prescriptions (Gill et al. 2002; Knapp and Keeley 2006; Rocca 2009).

7.2.2 *Ecological Theory*

Ecology has a rich tradition of studying species response to the variability along environmental gradients (Shreve 1922; Austin 1987). In these studies, species or communities of co-occurring species often are projected into a parameter space derived from environmental “proxy” variables. Some of the seminal examples of gradient work are provided by Whittaker (1956, 1960, 1967), who arrayed species abundance as distinct domains along elevation gradients in a variety of montane systems. However, correlations between species abundance and indirect environmental variables, such as elevation, are at best indicative of the underlying relationships driving the physiological responses of species. The importance of replacing indirect gradients such as elevation in vegetation models with direct and resource gradients such as temperature and moisture has been strongly emphasized by Austin and Smith (1989) among others. Vegetation analysis should be more than just correlation analysis, and studies should be geared more towards developing and testing vegetation theory (Austin 1987). This more mechanistic approach to modeling vegetation community pattern is reflected in a number of more recent gradient analyses (Ohmann and Spies 1998; Lookingbill and Urban 2005; Littel et al. 2008).

However, few empirical studies have attempted to link pattern and process in a predictive sense within a framework that explicitly considers the scale of interaction. The importance of scale in ecology has been well documented and is central to the discipline of landscape ecology (Wiens 1989; Wu and Hobbs 2007). According to hierarchy theory, lower levels of organization provide the mechanisms for patterns

observed at higher levels (Allen and Starr 1982). Thus, ecological systems can be viewed as spatially nested hierarchies and understanding (or managing) pattern at the landscape level requires a rather comprehensive understanding of influential processes at finer resolutions. For example, disturbance processes of multiple types and at multiple times create a mosaic of patches of various ages for a given landscape (Pickett et al. 1989). The overlay of these many patch-scale disturbances may be expressed as complex landscape patterns.

Wu and Loucks (1995) argue that spatially explicit *simulation* modeling is the only practical approach to deal effectively with these problems of spatial patchiness, scale and hierarchical structure. Certainly, a new approach is required that develops a more mechanistic understanding of species patterns at landscape extents. We argue that traditional analytic techniques can be adapted to these challenges, but they require data inputs that are carefully selected to describe the multi-scale variability in direct environmental gradients. Conventional empirical methods are poorly suited to gather fine-resolution information on the distribution of these covariates at extents of kilometers to tens of kilometers. Refining landscape models to reflect the relative importance of fine-scale ecological processes requires a daunting field effort. One way to constrain this logistical challenge is to focus field campaigns on areas where we can expect high rather than low plot variability.

7.2.3 *Empirical Framework*

In his classic paper on pattern and scale in ecology, Levin (1992) provides one approach to developing predictive models in light of these issues: (1) describe pattern, (2) look for correlations with pattern to suggest potential mechanisms, and (3) improve understanding of pattern through careful examination of relationships with new ‘mechanistic’ variables. Though a true mechanistic understanding of ecological pattern may not be possible without *in situ* experimentation, well-designed modeling studies can go a long way towards disentangling the complex environmental gradients that are often invoked to explain ecological patterns.

Our approach focuses on the iterative relationship between data and models. The model-guided approach to sampling takes advantage of our ability to model at larger scales than we would reasonably be able to sample (Urban 2000). Preliminary hypotheses can be used to design initial sampling efforts. Field samples are then used to build models, which guide future sampling to answer new hypotheses and build better models. As an example, coarse-scale data available from land cover and digital elevation models can be used to identify areas of high species and environmental turnover on the landscape. Once areas of high variability in pattern over a relatively small space have been identified, those locations can be sampled intensively to attempt to uncover the process that underlies the pattern. The coarse and fine-scale datasets can then be compared to assess whether similar mechanisms are acting at the different spatial scales.

7.3 Data Availability and Suitability

The foundation of any predictive model is the structure of the underlying data, which are often gathered using a simple random sampling design. Unfortunately, random placement of plots can have significant drawbacks for species distribution modeling. There is no guarantee when using a simple random design that sample locations will be spatially balanced; part of the area being studied may be over-sampled and part may have few or no plots at all. This can be particularly troublesome for developing models for rare species, species with highly constrained distributions, or when some parts of a species range are inherently more informative than others for deciphering the ecological mechanisms behind the species distribution.

A systematic sampling design can increase the spatial balance of the sample locations. An even distribution of plots over the entire landscape ensures that no area is over- or under-represented, but is limited by logistical trade-offs in sample grain and extent. Very few studies have the luxury of collecting information using a fine-resolution grid over a large geographic area. Particular sites also may not be suitable for monitoring due to the absence of attributes of interest or due to issues such as safety or accessibility. This can leave a “hole” in the uniform sample. Stratification can be used to spread samples across a full range of conditions and to guarantee minimum sample sizes for different subpopulations. Stratification of samples can also make a field campaign easier to operate. For example, roads can be used as a stratum to improve ease of access for data gathering (Theobald et al. 2007).

We argue that species are rarely distributed randomly or uniformly and these sample designs are inefficient for many modeling efforts. Instead, hybrid designs such as Generalized Random-Tessellation Stratified (Stevens and Olsen 2004) and adaptive clustering (Philippi 2005) have recently become popular among managers interested in gathering spatially sensitive data. Multi-scale designs, in which a subset of plots is sampled at fine resolution, can be highly efficient at collecting data over large areas for intensive spatial analysis (Stohlgren et al. 1995, 1997; Urban et al. 2002). Multi-stage sampling involves completely different kinds of sampling at each stage. Nusser et al. (1998) strongly advocate multi-stage sampling designs for detecting broad-scale ecological patterns and for understanding the dynamics that produce observed changes in pattern. They provide a useful example using the National Resources Inventory (NRI) data.

The NRI sample design was developed to assess natural resource attributes for a broad geographic coverage (nonfederal rural lands of the United States) while acquiring a sufficient density of sample units for local subpopulation management. To accomplish these objectives, a stratified two-stage sample design was used. Stratification was based on small political or geographic areas and one to four primary sample units were located in each stratum during stage one sampling. These typically cover a total of between 2 and 6% of the entire land area. In stage two, a small number of sample points are placed in each primary sample unit. The exact number of sample points depends upon the various demands and constraints at the specific locale.

In addition to sample arrangement, the types of variables sampled at each stage determine the kinds of predictive models that can be used. Early stages typically rely upon indirect, coarse-resolution variables. For example, basic climate, land use, and ownership information is collected in stage one of an NRI sampling. These data are used to determine broad-scale trends and to develop initial weighting for stage two sampling. For our purposes in modeling complex vegetation pattern, these types of coarse variables are less useful than the fine-resolution, resource variables that have a more direct bearing on ecological processes. These types of more mechanistic but logistically more demanding variables can be sampled during later, “focused” stages of a multi-stage design.

7.4 Model and Model Validation Techniques

Spatially explicit, multi-scale data require spatially explicit, scale-specific models. These models can be found sprinkled throughout the literature in community, multi-variate, and spatial ecology. We argue that developing species distribution models from spatially focused sampling schemes proceeds most powerfully from modeling and validation techniques that meet three criteria. First, they should recognize and account for spatial autocorrelation in the data that are used to fit the model. Second, they should identify the dominant spatial scales of species distributions and relate these to the dominant spatial scales associated with the predictor variables. Finally, we propose that techniques that explore quantitative relationships between species occurrences and predictor variables across a range of characteristic spatial scales provide the most mechanistic and insightful understanding of the drivers of species distributions. The first two criteria are well described elsewhere (Cressie 1993; Wagner 2001) and we review them only briefly. The final criterion about exploring scale-specific relationships between predictors and species distributions requires more novel methods that have only recently been explored by ecologists.

Because intensive focus plot sampling, by definition, collects spatially explicit information at fine spatial scales, statistical techniques used to examine species-environment relationships must account for the spatial autocorrelation present in these data as well as in any spatial processes affecting the response (Wagner 2001). In an intensive sampling scheme, data points are located close together so that closer points are likely to be similar to each other (i.e., each data point is not statistically independent). Explanatory variables that are autocorrelated inflate the effective sample size and may bias parameter estimates (Keitt et al. 2002; Dormann 2007). In working with these data, statistical techniques must either (a) remove spatial autocorrelation by averaging or removing data points that are within the spatial range of autocorrelation, or (b) explicitly account for spatial autocorrelation in explanatory variables, perhaps most simply by including a spatial blocking variable in the model design. Habitat modeling approaches include geostatistical methods such as kriging (Chong et al. 2001; Miller 2005), generalized additive models (Hastie and Tibshirani 1990), general estimating equations (Zeger and Liang 1986;

Gumpertz et al. 2000; Underwood et al. 2007), and autoregressive models (Keitt et al. 2002). Bayesian approaches have also been used (Hoeting et al. 2000; Lynch et al. 2006). Several excellent reviews of these methods are available (e.g., Dormann et al. 2007; Miller et al. 2007).

Modeling methods should also account for autocorrelation of residuals caused by spatially contagious processes that affect species distributions. Ecologically important yet many times unmeasured processes, such as propagule dispersal, drive species distributions and result in spatially correlated regression residuals (Legendre 1993; Wagner 2001). It may be difficult to distinguish whether spatial dependence in a response from a species is caused by autocorrelation of environmental variables or by a spatial biological process. Statistical approaches that go beyond consideration of spatial autocorrelation simply as a “nuisance” and instead describe the scales of spatial autocorrelation of both the predictor variables and the response may provide insight. Testing carefully crafted hypotheses and investigating spatial scales in detail can help to address these issues (Fraterrigo and Rusak 2008). In a compelling illustration of this approach, McIntire and Fajardo (2009) use six ecological examples to describe the benefits of using the scales of regression residuals to make statistical inferences about spatial processes.

A useful approach to testing for spatial dependence in explanatory variables takes advantage of the Mantel statistic (Mantel 1967). The statistic is simply calculated as the Pearson correlation between the elements in one distance matrix with the corresponding elements in a second distance matrix (Manly 1991). For a partial Mantel test, control variables are factored out, and the residuals are subsequently correlated with the variables of interest in a manner analogous to partial regression (Smouse et al. 1986). Mantel tests are ideal for testing relationships between species composition and the environment for several reasons. First, the effects of spatial autocorrelation can be tested for explicitly, or partialled out of analyses to detect relationships between variables after controlling for space. Second, the significance of a Mantel statistic is calculated using permutation procedures that eliminate problems associated with independence in parametric regression (Legendre and Fortin 1989). Third, because the correlation is calculated between distance matrices, the multivariate effects of multiple predictor variables (environmental factors) and multiple response variables (species) can be tested for simultaneously, as long as an appropriate distance metric is chosen (McCune and Grace 2002). Mantel tests average over all distances when calculating correlation coefficients. To identify the scales at which the environment and species are spatially autocorrelated, the Mantel correlation between a variable and space can be calculated separately within discrete distance classes (Goslee and Urban 2007). The results are displayed as a multivariate analog to a correlogram (Rossi et al. 1992), with distance class on the *x*-axis and Mantel correlation plotted on the *y*-axis.

Recently, Peres-Neto et al. (2006) have advocated principal coordinates analysis of truncated distance (neighbor) matrices (PCNM) (Legendre et al. 2008) as a means of exploring species turnover at multiple scales. PCNM captures spatial structure in terms of sine waves of varying wavelength, and summarizes species compositional patterns in terms of the compositional variance (dissimilarity)

accounted at different wavelengths (scales). Legendre et al. (2008) argue that this new approach has more statistical power than the Mantel tests they had previously championed for this type of modeling.

Ecologists have also begun to use wavelet analysis to identify spatial scaling in variables. Like a Fourier transform, wavelet analysis decomposes a spatial or temporal data series into components at different scales. Wavelets are ideal for ecological data, because they can detect scale-specific patterns without the assumptions of stationarity required by semi-variance analysis or spectral analysis. Wavelet energies represent the proportion of variability in a data series expressed at each spatial scale, for scales in powers of two. Ogden (1997) provides a computational treatment of wavelets, though several attempts have been made to make wavelets more accessible to ecologists (e.g., Dale and Mah 1998; Torrence and Compo 1998; Cazelles et al. 2008; Dong et al. 2008). Most of these ecological treatments focus on using wavelets for time-series analysis, but data from a regularly spaced spatial grid are also appropriate for wavelet analysis (Bradshaw and Spies 1992; Mi et al. 2005; He et al. 2007).

We expect that relationships between environmental variables and species habitat often will change with spatial scale of analysis (Levin 1992; He et al. 2007). Ideally, we would be able not only to describe the scales of spatial variability of predictors and response but also to investigate relationships between variables at each spatial scale (Keitt and Urban 2005; Blanchet et al. 2008). Wavelet analysis can once again prove helpful for meeting this challenge. Wavelet covariance is the covariance between the wavelet coefficients for two variables at a defined spatial scale (Keitt and Urban 2005). Several ecological studies have demonstrated that scale-specific relationships between variables are revealed through analysis of wavelet covariance (Keitt and Fischer 2006; termed “wavelet cross-spectrum” in Cazelles et al. 2008). In a particularly innovative example, Mi et al. (2005) apply a statistical test to compare relationships between two transects.

Keitt and Urban (2005) take scale-specific inference a step further by introducing the concept of wavelet regression. They demonstrate that a linear regression between wavelet coefficients, extracted separately by spatial scale, can identify scale-specific relationships between several predictor variables and a response. Scale-specific regressions using wavelets have not yet caught on in the ecological community, yet we propose that they offer a promising approach for species distribution modeling. Carl and Kuhn (2008) analyze spatial ecological data using wavelet regression, but their objective appears to be to remove the effects of autocorrelation in an attempt to predict habitat for a plant species, rather than using it to extract scale-specific relationships between environmental predictors of habitat and plant occurrence. However, their analysis expands upon the methods of Keitt and Urban (2005) in two ways that are of interest to species distribution modelers: (1) they demonstrate that wavelet regression can proceed in a logistic regression setting, and (2) they take advantage of a two-dimensional (grid) dataset. More work is needed to determine how scale-specific regression analysis can be applied in a predictive mode, as often desired by species distribution modelers.

7.5 Case Studies in Western US Forests

The best species distribution models will incorporate the influence of all the important variables affecting species distributions, from coarse-scale environmental tolerances to fine-scale dispersal and competition processes. We have described the data and modeling challenges presented by the need to consider the influences of variables whose relationship to species may vary depending on spatial scale. In this section, we demonstrate our iterative approach to linking models and data in scale-dependent assessments of vegetation pattern with two examples. For the first, we emphasize the data aspect of developing multi-scale, mechanistic models. We describe how a multi-stage sampling design can be used to create a hierarchical set of models and demonstrate the utility of ecotone focus plots for modeling species distributions in old-growth forest habitats of the Pacific Northwest United States. The second example emphasizes the analytic side of our approach. We use scale-specific modeling approaches – such as wavelet analysis and the Mantel correlogram – to determine whether planned fires in Sequoia National Park appreciably homogenize the environment by burning through heavy, continuous fuel beds, thus leading to altered distributions of herbaceous species within the park.

7.5.1 *Predicting Spatial Shifts in Old-Growth Forest Habitat*

In an effort to develop a predictive model of forest community spatial pattern for the Western Cascades, we conducted intensive field sampling at areas of spatial transition between the *Tsuga heterophylla* (western hemlock) vegetation zone and the *Abies amabilis* (Pacific silver fir) vegetation zone. An improved understanding of this ecotone would better inform the potential impacts of changes in climate or management within these ecologically and economically important forests. For example, an ecotone formed primarily by differences in growth rates associated with temperature may respond linearly to changes in temperature, whereas an ecotone maintained primarily by winter precipitation may not simply migrate up slope in response to increasing temperature. In this study, we considered directly the effect of temperature, snowpack, radiation and moisture on seedling establishment and relative growth rates of trees in an effort to extend our knowledge base beyond the simple correlation of plant communities with the elevation gradient complex.

The multi-stage approach that we followed relies upon a process of successive refinement of the modeled species–environment relationships. The preliminary model (Lookingbill and Urban 2005) was based upon the correlation between species abundance and terrain proxy variables (e.g., elevation) for 164 (20×20 m) vegetation samples stratified across the H.J. Andrews Experimental Forest (HJA). The HJA is a Forest Service Experimental Watershed and a Long-Term Ecological Research site representative of the soils, geology, and climate of the Western Cascades (McKee 1998). Elevation varies from 425 to 1,620 m, and the sampling

for this initial stage extended across the entire range. Variables included measurements of soil nutrients and chemistry, though only terrain variables were significant in the model. The geographic realization of this model identified areas of short but steep gradients in which discrete changes in community type were predicted (Fig. 7.2). A follow-up stage of new field studies at these key locations provided an efficient new set of data to help refine the model and provide a deeper understanding of the fine-scale processes associated with observed vegetation pattern.

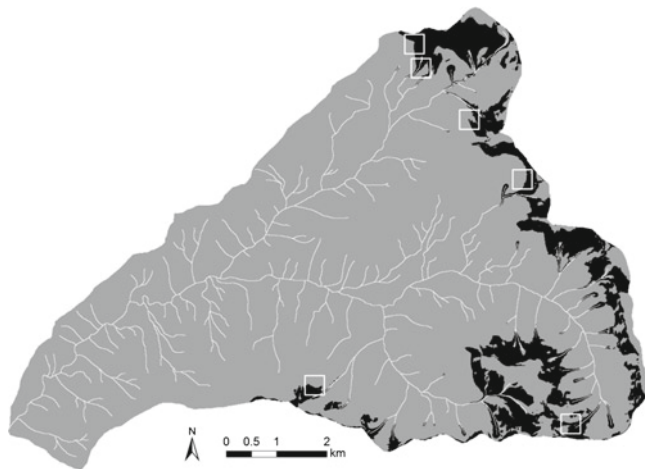


Fig. 7.2 Ecotone plot locations (boxes) within the H.J. Andrews Experimental Forest. Red area represents transition zone as identified by a forest community CART model using temperature, soil moisture and radiation as explanatory variables (described in Lookingbill and Urban 2005)

Six “ecotone focus plots” were designed to explicitly consider fine-scale environmental constraints along this region of active forest community transition. Whereas the preliminary model confirmed the well-documented shift from the *T. heterophylla* vegetation zone to the *A. amabilis* vegetation zone along an elevation gradient (Franklin and Dyness 1988), the second stage of sampling addressed the relative importance of temperature, moisture, radiation, and snowpack as potential drivers of species distributions within the ecotone. Efforts to identify the physiological mechanisms responsible for this transition are surprisingly few, dated, and somewhat contradictory (Krajina 1969; Thornburgh 1969). In this study, we addressed the relationship between regeneration and physical drivers through logistic regression of point measurement and kriged data. We also considered dispersal constraints through bivariate Ripley’s *K*-analysis of seedling and potential dispersed tree data. The Ripley’s *K*-function differs from conventional nearest neighbor analyses in that it considers distances between all observed points and not just the first or second nearest neighbor (Moer 1997; Haase 1995). An advantage of preserving all spatial relationships in the data is that Ripley’s *K*-tests can assess pattern at multiple scales, and can thus be used to evaluate spatial scales of clustering, in a univariate sense, or attraction/repulsion, in a bivariate sense (Haase et al. 1996; Lookingbill and Zavala 2000).

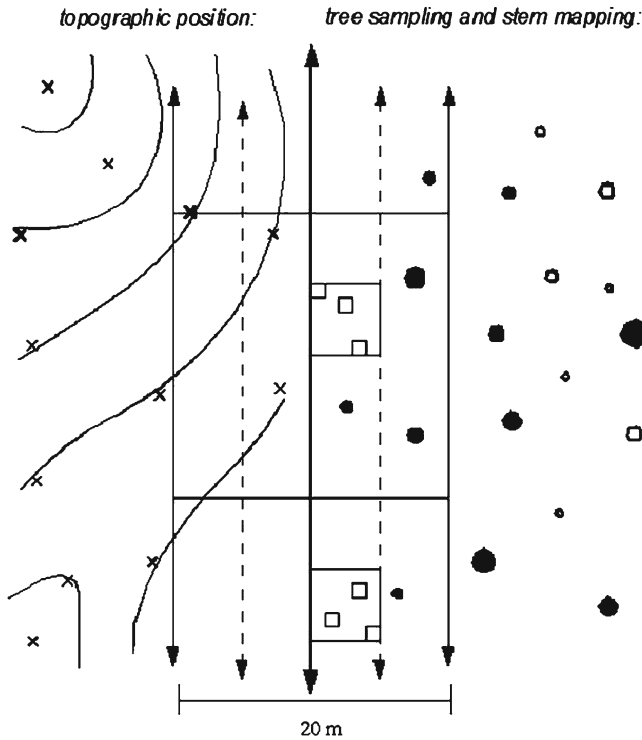


Fig. 7.3 Transect based sampling layout for microtopography (drawn on left side) and vegetation (*right side*) on ecotone focus plots. Transects were 20 m wide by 100–180 m in length. Centerline was paralleled by 5-m bands used for randomly locating seedling (1×1 m) and sapling (5×5 m) quadrats. All seedlings within 1 m of the centerline were mapped. All trees within the transect were mapped. In addition, trees sighted as “in” with a basal area prism were mapped (filled symbols on *right*). Topographic points were surveyed with sufficient density (drawn as x’s) to generate a high-resolution DEM. Direct measures of temperature, soil moisture, snow and radiation also were taken

Our focus plots were 20 m in width and between 100 and 180 m in length. Within each of the plots, all dead and live trees were measured at breast height, cored for age and growth rate analysis, and mapped using a laser surveying system (Fig. 7.3). In addition, potential seed trees outside the transects were identified according to a plotless sampling design using a 2.5-factor basal area prism along the transect centerline. Nested within each transect were 3 (1×1 m) quadrats per every 20 m in which all seedlings were tallied by size class (young of the year, 0–10 cm in height, 10–50 cm in height, and 50–137 cm in height). We also mapped all seedlings within 1 m and all saplings within 5 m of the transect centerline.

Using the laser surveying system, we recorded critical points of topographic change and used these points to interpolate a high-resolution digital elevation model (DEM) of the plots. An average of nearly 40 measurements were taken for every 20 m of transect. Surface soil moisture (0–20 cm in depth) was recorded synoptically at these locations and at all seedling quadrats using a handheld volumetric moisture sampling device (Lookingbill et al. 2004). Three soil depth

measurements also were taken at each of the moisture locations using a 1 m tile probe. Canopy closure was estimated at the seedling quadrats using a concave spherical densiometer. Temperature sensors (Lookingbill and Urban 2003) were located at several key locations along each transect, which recorded temperature at 30-min increments. Several complementary approaches were used to quantify snow levels and melt on the plots. First, we synoptically measured snow depth (up to a maximum depth of 100 cm) in the spring of 2002 at 1 m intervals along the centerline of three of the plots. Lichen height acts as a reasonable proxy for the average maximum snow depth (Winkler and Schultz 2000), and we recorded the average height at which lichens began growing on tree boles for each 20 m plot segment. Finally, we distributed additional temperature sensors at ground level across the plots. These sampling devices allowed remote monitoring of the beginning and end of winter snowcover for specific locations on the plots. When covered with snow, these sensors would consistently record a temperature of 0°C.

For each focus plot, we first looked for geospatial patterns in tree regeneration, growth, and mortality. No significant spatial patterns emerged in the distribution of snags on the plots. The density of dead trees of *A. amabilis* and *A. procera* were highly variable from plot to plot, but consistently greater than for *T. heterophylla*. These findings are consistent with those of Acker et al. (1996) who found low *T. heterophylla* mortality relative to *A. spp* mortality in a 27-year study of a forest stand within the ecotone zone at the HJA. We also found that growth rates were not significantly associated with elevation, temperature, or any of the other environmental variables gathered at this scale (Fig. 7.4). Earlier models relied heavily on these relationships in predicting how this ecotone would respond to changes in climate (Urban et al. 1993). Our models, instead, focus on the importance of regeneration in maintaining observed community patterns.

To evaluate whether dispersal limitations may be constraining the distribution of species, bivariate Ripley's *K*-analysis was conducted using a bivariate label permutation test of seedlings and trees in each of the plots. All tree and seedling locations were held constant, while we randomly reassigned the species labels of the seedlings. The distances from seedlings to conspecific adults for 99 of these randomized trials were then compared with the distances for the actual data ($P < 0.01$). Observations higher than the randomized data were considered to be positively associated. Observations lower than the randomized data were considered to be negatively associated. The scale of positive association should be reflective of species' dispersal capabilities. The point pattern analysis confirmed that the heavier seeded *A. amabilis* and *A. procera* may be more prone to dispersal limitations than *T. heterophylla*, but none of the species were likely constrained by dispersal within the extents of the ecotone plots.

Point measurements of the environmental variables were then kriged to 1 m resolution grids and logistic regression was used to model the presence or absence of seedlings by species as a function of radiation, temperature, soil moisture and snow cover along the 1 × 1 m seedling sample quadrats running up the middle of the plots. Regressions were also conducted using the point measurements of seedling presence/absence, light, soil moisture, and soil depth at each of the 1 × 1 m seedling quadrats. Results of the logistic regression analyses ($n = 653$ *T. heterophylla* seedlings, $n = 603$ *A. amabilis* seedlings, and $n = 232$ *A. procera* seedlings) indicated the

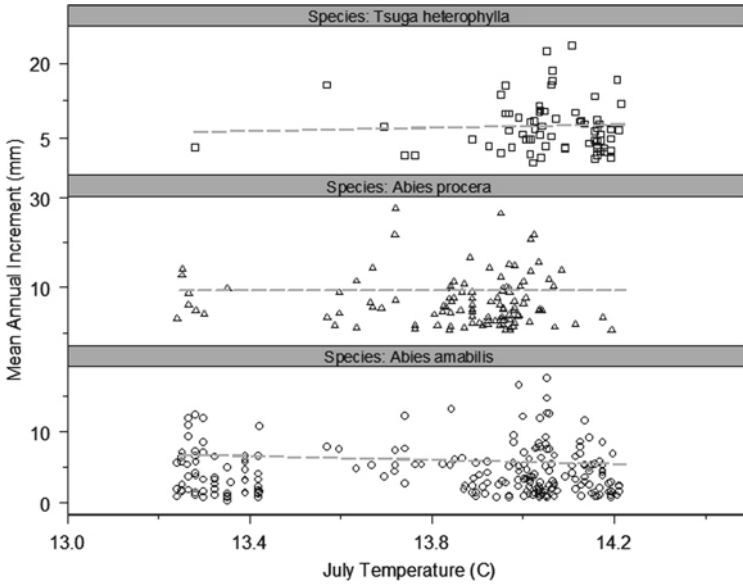


Fig. 7.4 Trends in relative growth rates. In contrast to prior modeling assumptions emphasizing the importance of differences in growth rates to species distributions in this system, growth was not significantly associated with temperature or any of the environmental variables considered at the ecotone scale. Species shown are *A. amabilis*, *A. procera*, and *T. heterophylla*

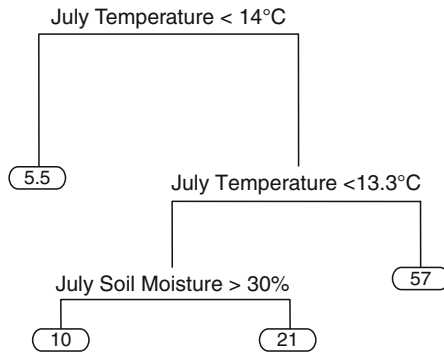


Fig. 7.5 Regression tree model of *T. heterophylla* seedling density on seedling plots. Circles provide mean number of seedlings for the plots described by that end-node. Length of branch corresponds to the amount of variance explained by that variable

importance of temperature and moisture as explanatory variables, but emphasized the high plot-to-plot variability. Temperature differences were highlighted as the strongest predictor of *T. heterophylla* seedling presence/absence across all plots; a finding also supported by regression tree analysis of seedling density in subplots (Fig. 7.5). Relationships were not consistent, however. For example, January temperatures rather than July temperatures were significantly different on Plot 3, for which soil moisture was the strongest predictor variable of seedling abundance.

Radiation was consistently the least important of the potential explanatory variables in the logistic regression and regression tree analyses.

Our results generally suggest that regeneration rather than growth or mortality is likely to be limiting the range of *T. heterophylla* through a combination of snow, temperature, and moisture limitation. Therefore, changes in climate that would alter the competitive dynamics between species would be most apparent in the regeneration niche. Landscape-level management activities such as timber harvesting within the shifting ecotone could result in unattended consequences if these new dynamics were ignored. An interesting observation from the bivariate Ripley's K-analyses was that *T. heterophylla* seedlings were more common under canopies of large trees (of any species) than canopy gaps. One explanation for this finding lies in the shade-tolerance of *T. heterophylla*. However, *A. amabilis*, an equally or even more tolerant competitor in this vegetation zone (Fonda and Bliss 1969; Mitchell et al. 2007), did not show the same spatial patterning. An alternative explanation is suggested by examining the patterns of snowpack on the plots. Snowfall interception by branches and needles can substantially decrease the amount of accumulation under tree crowns. The rate of snowmelt also is modified considerably in the vicinity of large stems that can re-radiate longwave radiation (Anderson 1963). It is possible that *T. heterophylla* establishment in the transition zone, and by extension *T. heterophylla* migration upslope, is aided by these melt cones. The single year of snow sampling that we conducted for this analysis is insufficient to definitively address this issue; however, the model results using these exploratory data do serve as a guide for future work. Targeted data collection to test this hypothesis provides the next round of study in our data gathering → modeling → data framework. In light of the potential interactions between climate and disturbance, experimental studies of montane conifer regeneration under alternative silviculture systems (Mitchell et al. 2007) may be the most efficient way of improving model predictions in this landscape.

7.5.2 Predicting Herbaceous Response to Prescribed Fire

In many ecosystems, fire-adapted landscapes cannot be restored without active management. However, how plant communities respond to prescribed fire and how these responses may differ from responses under natural fire regimes are poorly documented. Some scientists have raised the concern that prescribed fires may be too homogeneous to restore pre-suppression forest structure (Bonnicksen and Stone 1982; Allen et al. 2002). A handful of field-based studies have explored the biodiversity consequences of large-scale, fire-generated, environmental heterogeneity in Yellowstone National Park (Romme and Knight 1982; Turner et al. 1997, 1999). Schoennagel et al. (2008) documented spatial variation in post-fire structure, composition, and ecosystem function at multiple scales following the 1988 Yellowstone fires, but fine-scale heterogeneity under moderate-severity fire regimes have not been thoroughly explored. In the few systems where fine-scale heterogeneity in fire effects and species responses have been reported (Davis et al. 1989; Moreno and

Oechel 1992; Odion and Davis 2000; Brooks 2002), fires have been shown to reinforce already existing patterns, neither increasing nor decreasing spatial pattern and scale of variability. There are few well-studied examples of the effects of fire intensity and spatial patterning in determining post-fire spatial distributions of species.

We tested the role of within-fire variability in fire severity in structuring understory plant communities in a fire-adapted, mixed-conifer forest of the Sierra Nevada, California, USA. We examined the effects of six prescribed fires on plant community structure and spatial distributions, and compared the effects of two management alternatives: early-season prescribed fire (June burn) and late-season prescribed fire (October burn). We collected high-resolution floristic, fuels, and environmental data at every meter along 256-m transects through six prescribed fires (three in each season) and asked whether fire changes the scales of species distributions. If fire creates heterogeneity by subdividing previously homogeneous forest floor patches, we would expect plants to sort along finer-scale environmental gradients after fire and exhibit smaller-scale spatial autocorrelation than they did prior to fire. An increased spatial scale of species turnover, by contrast, would support a model in which fire homogenizes the environment.

Mantel correlograms on species composition show reduced spatial autocorrelation in species distributions after fire with a more pronounced effect observed in the June burns (Fig. 7.6). Before fire, species distributions along all transects exhibited spatial structure at scales up to approximately 150 m. After fire, species distributions on the October burn transects showed autocorrelation at scales similar to pre-fire patterns, whereas June burn transects had a shortened range of approximately 100 m. Perhaps more importantly, after fire the June burns showed a small ($p < 0.05$) but significantly reduced autocorrelation at scales between 5 m and 100 m (the October burns also significantly reduced autocorrelation, but only to a modest degree in a few short portions of the range). These results support a model in which patchy June burns create heterogeneity in the environment, which in turn increases the variability in species distributions at fine-spatial scales. October burns, on the other hand, do not appear to appreciably change the scaling of the environment in a matter that affects understory herbaceous plants.

To further investigate the fire behavior responsible for these results, we used wavelet analysis to examine the spatial scales of burn pattern (for the June and October burns) and fire temperature (for the June burns). Then, we asked whether fire temperature and burn pattern can be predicted with pre-fire site data on fuels and topography, or whether they are affected more by less predictable and difficult to measure features such as ignition, moisture, and local wind patterns. In addition to the fine-scale measurements of fuel and topography taken at every meter along each transect, we recorded maximum fire temperature in the June prescribed burns by installing a “pyrometer” (containing streaks of temperature sensitive paints, which permanently change appearance once their particular melting temperatures are reached) at every meter along the transect.

Our results show that prescribed fires can be remarkably heterogeneous in burn pattern (Fig. 7.7) and fire temperature (Fig. 7.8). It appears possible to create a patchy burn pattern even within methodically ignited prescribed burns through

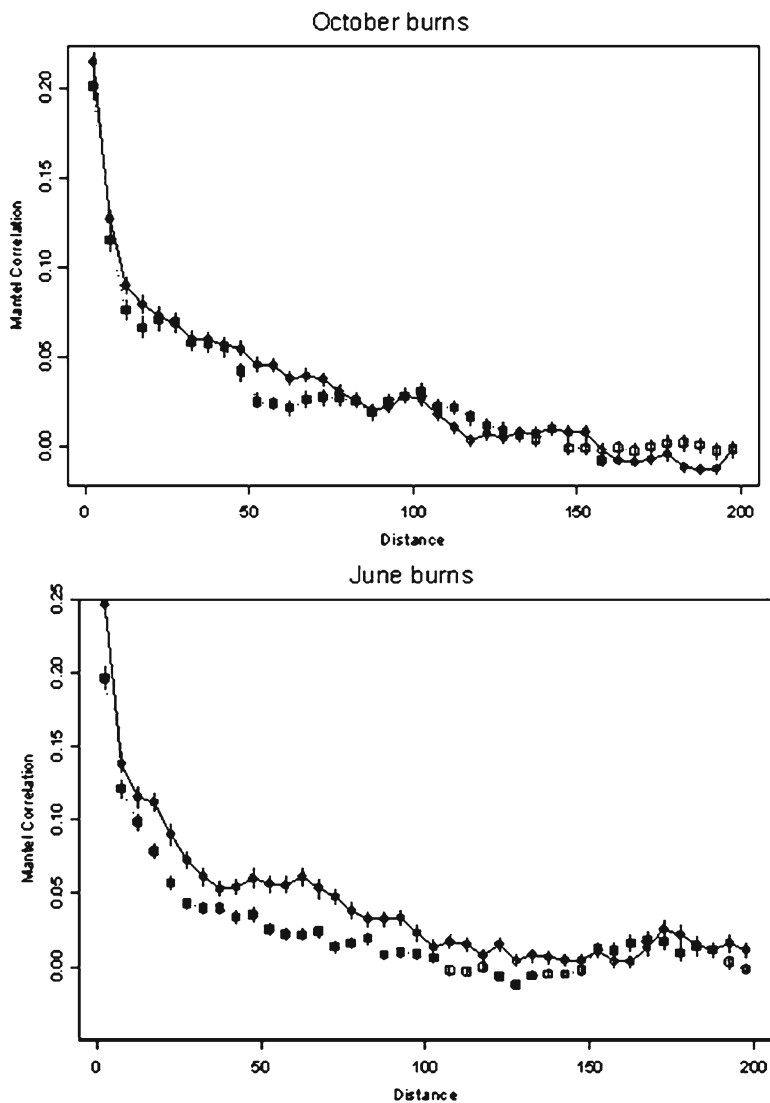


Fig. 7.6 Mantel correlograms of pre-fire (*circles connected by solid lines*) and post-fire (*squares*) species distributions, calculated using the Bray and Curtis (1957) index of dissimilarity. Filled symbols represent correlation significantly different than zero, and error bars represent 95% confidence intervals

fire-suppressed forest understories. In this experiment, four out of six management burns displayed significantly more variability in burn pattern and fire temperature than might have been expected, given high fuel continuity. The four heterogeneous fires included all three of the early season (June) burns and one October burn (plot 2). Plot 2 spans a relatively wet, level area, and was burned under rather humid weather conditions for the time of year. Plots 5 and 6, the other two October burns were

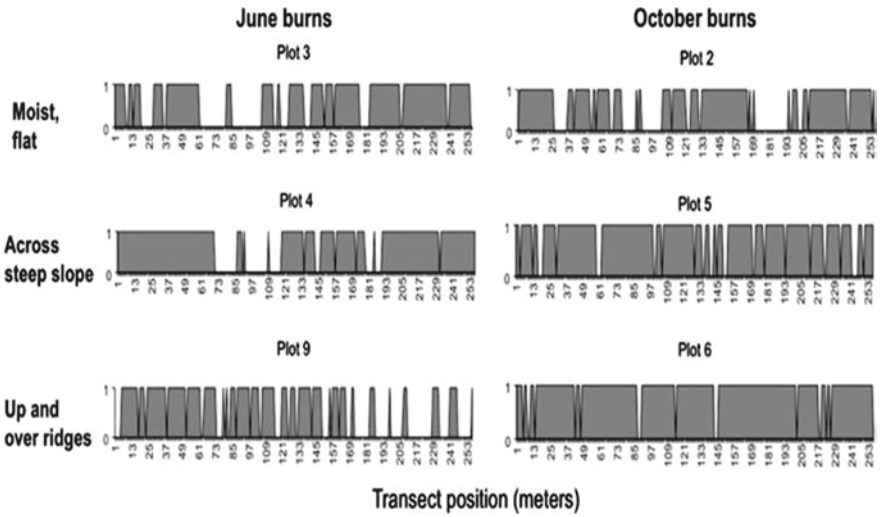


Fig. 7.7 Meters burned along each transect for spring and fall burns (1 = burned, 0 = unburned)

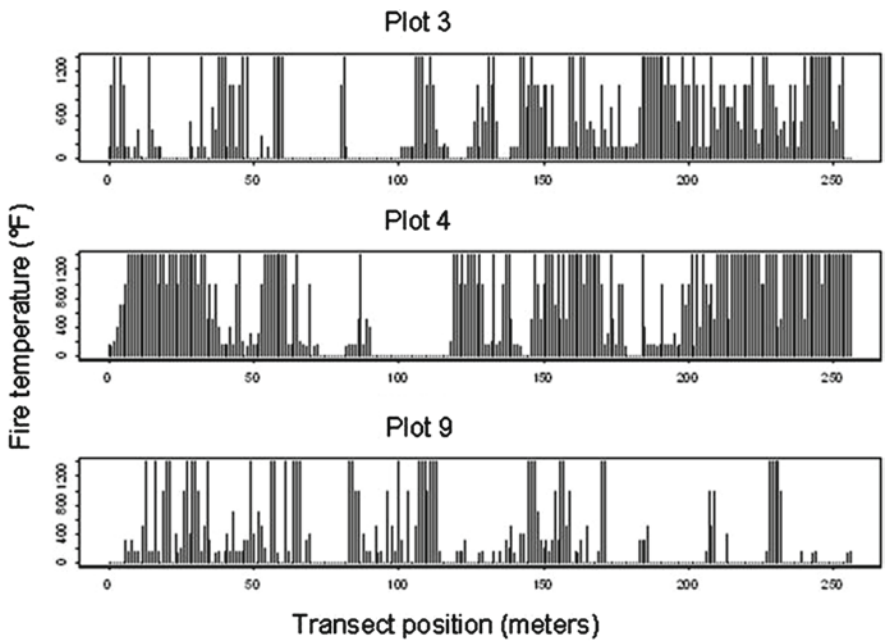


Fig. 7.8 Maximum fire temperatures along the three June transects

considerably more homogeneous in their fire effects. In comparison with the fuels in plot 2, fuels in plots 5 and 6 units were uniformly dry, with no areas of moisture accumulation encountered along the transect.

The wavelet energies for burn pattern showed a complex relationship in which the dominant spatial scales of variability are not easily categorized based on season

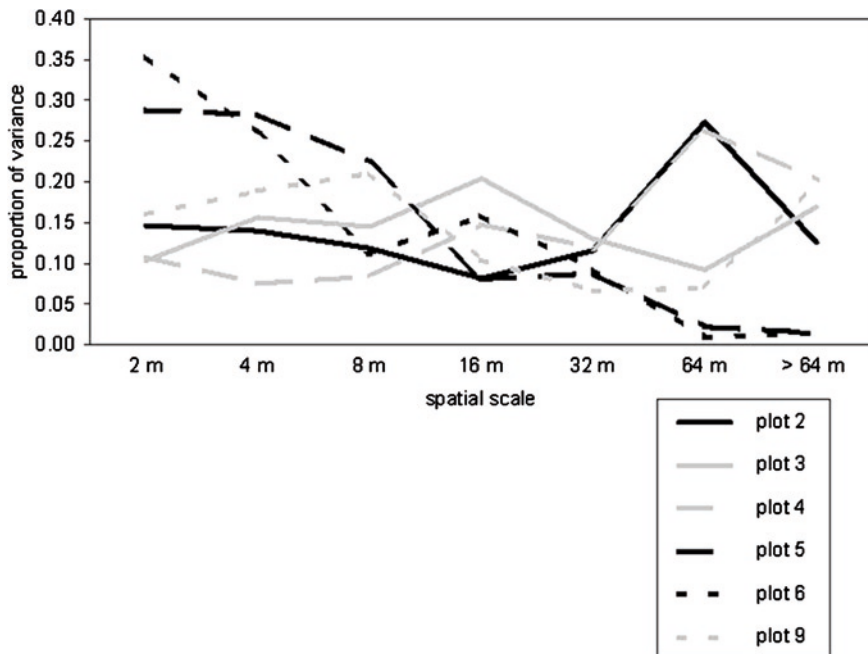


Fig. 7.9 Wavelet energies for burn pattern in the three June burn transects (*gray*) and the three October burn transects (*black*)

(Fig. 7.9). Plots 5 and 6, October burns that burned almost completely, expressed most of their (nominal) variability at the finest spatial scales. Plots 2 and 4 showed maximum variability at the 64 m scale. Plots 3 and 9, both highly patchy June burns, expressed their spatial variability in burn pattern across a wide range of scales.

The causes of these patterns in burn pattern were explored using a logistic regression on pre-fire variables related to fuels and topography. Because many of the explanatory variables taken prior to the burns are highly correlated, we first conducted a factor analysis on the pre-fire variables to create orthogonal “factors” that represent the major components of variability along the transect prior to fire, then used the resulting factors as the explanatory variables in the logistic regression models to predict burn pattern. The six factors identified through factor analysis together account for 61% of the original variability in the environmental dataset (Table 7.1).

Surprisingly, the important explanatory variables for predicting burn pattern depended on transect orientation more than burn season (Table 7.2). Plots 4 and 5, the two transects crossing across hillslopes, had burn patterns driven by fuel load (e.g., litter/canopy, woody fuel, and CWD). Burn patterns in the gently sloping, moist transects (plots 2 and 3), were also affected by fuel loads, with moisture and elevation decreasing the probability of burning. Plots 6 and 9, whose transects go over small ridges, depend on fuel to explain their burn pattern. The topographic factors insolation and elevation affected probability of burning, but only for the June burn (plot 9). Pre-burn factors account for between 14 and 36% of the variation in burn pattern.

Table 7.1 Variable loadings from factor analysis

Original variables	Factors					
	“Insolation”	“Woody fuel”	“Moisture”	“CWD”	“Litter/canopy”	“Elevation”
Elevation			0.51			0.65
Slope			-0.75			
T-aspect	0.96					
Radiation	0.94					
Soil moisture			0.56			
Light					-0.57	
Litter cover					0.39	
Litter depth					0.56	
1-h fuel		0.67				
10-h fuel		0.98				
100-h fuel		0.26				
CWD				1.00		
% variability	16.0	13.0	10.2	9.6	7.6	4.5
Cum % variability	16.0	29.0	39.2	48.8	56.4	60.9

Factors are combinations of variables that tend to correlate with each other, and loadings are the correlation coefficients between the original variable and the factors. We gave factors names to make the results easier to interpret. The percent variability in the original dataset that is explained by each factor is also provided

Table 7.2 Results of stepwise logistic regression on burn pattern

	Factors						% Variance in burn pattern explained	<i>n</i>
	“Insolation”	“Woody fuel”	“Moisture”	“CWD”	“Litter/canopy”	“Elevation”		
<i>June burns</i>								
Plot 3		(+)	-	+	+	-	17	242
Plot 4				+	+	(+)	36	254
Plot 9	+	+		+	+	+	33	242
<i>October burns</i>								
Plot 2		(+)	-	+	+	-	14	236
Plot 5		+		+	+		21	192
Plot 6		+		(+)	+	(+)	23	242

Positive factors increase probability of burning while negative factors reduce probability of burning. Signs in parentheses indicate factors that were included in the optimal model, but were not statistically significant at the 0.05 level. Percent of variance in burn pattern explained by each model (pseudo R^2) and sample size (n) are also provided

This case study demonstrates that prescribed fires can generate remarkable variability in fire temperature when conducted under particular conditions, and this variability can, in turn, play a pivotal role in shaping the distribution of flora. The factors that affect burn pattern depend on topographic context more than season. In particular, moisture patterns driven by topographic variability had a stronger

influence on burn pattern than did seasonal differences (i.e., early summer vs. late-season burns). Despite the large amounts of data collected for this analysis, burn pattern and fire temperature were approximately 25% ($\pm 15\%$) predictable, suggesting that random or unmeasured factors (e.g., wind, ignition pattern) have an important influence on fire behavior and fire effects. Even so, this improved predictive ability translates directly into management recommendations about how prescriptions might be tailored to create within-burn heterogeneity. If fuel loads are continuous and homogeneous, as they typically are for first-entry burns in much of the Sierra Nevada, heterogeneity in fuel moisture due to topographic drainage patterns (which influence seasonal soil moisture patterns) or aspect and elevation (which influence diurnal fuel drying) can create heterogeneity. Heterogeneity associated with either drainage or diurnal drying occurs more often during the early season, before fuels are uniformly dry, but may extend later into the summer on moist sites. If fuels are distributed heterogeneously, either because of large tree gaps or because of previous fuel reduction burns, heterogeneous fuels will probably simulate a more natural burn pattern, even in uniformly dry conditions. In areas where both fuel and topography are homogeneous, then the possibility of altering ignition pattern should be explored in an effort to ensure heterogeneity.

7.6 Conclusions

The multi-scale nature of many ecological processes presents a challenge to modelers projecting species distributions across large geographic extents. Our approach of coupling focused sample plots with analytic models that explicitly account for variability in space and scale is appropriate when any one of the following is true:

1. The ecological process in question occurs at a fine spatial scale, but the manifestations of that process influence large-scale patterning. In these situations, a more traditional sampling scheme may capture the pattern, but it will not distinguish between alternative mechanisms for the fine-scale process that creates the pattern.
2. Data are expensive in terms of time or money. Focusing on areas of high heterogeneity may be necessary when the costs of travel across a research area are high or when field equipment – such as dataloggers or sensors – are in limited supply relative to the size of the study area. Given these restrictions, the most statistically powerful placement of samples may be in areas of high contrast in one variable, controlling for as many other influences as possible.
3. The ecology of areas of contrast, such as ecotones or edges, is the focus of the project. Examples might include tree-line studies of climate change effects or studies of the spread of invasive species across land-use boundaries in mixed-use landscapes.
4. Describing the scales and/or magnitudes of spatial variability of a pattern or process is an explicit goal of the study. In many cases, spatially averaged results are not adequate for answering a research question. Alternate hypotheses generated around ideas of scale can only be tested when spatial scale is explicitly explored.

Our second case study provides an example of this latter criterion. A better understanding of the scale of variability in burn pattern and intensity imposed by human prescriptions of fire can provide important insights into the influence of disturbance on species distributions. To capture this variability, fine-scale data need to be collected over a large sample area. This can be a daunting task that is often most efficiently accomplished by selecting sample locations of high, rather than low, plot heterogeneity as demonstrated in our initial case study. Whereas data collected at these sites are noisy and may be somewhat limited by small sample sizes, they offer the advantage that the environmental variables and demographic processes can be measured directly and thoroughly rather than inferred from larger-scale correlations.

Once these data are in hand, they can be analyzed using emerging statistical techniques to create powerful predictive models. The challenges of spatial patchiness, scale, and hierarchical structure need not demand a spatially explicit *simulation* modeling approach. Purely *statistical* approaches may suffice given that they (1) recognize and account for spatial autocorrelation in the data, (2) identify the dominant spatial scales of species distributions and of potential predictor variables, and (3) explore quantitative relationships between species distributions and predictor variables across the range of characteristic spatial scales.

In general, more landscape studies are needed that attempt to link pattern and process in a predictive sense within a framework that explicitly considers the scale of interaction (i.e., providing a more mechanistic understanding of species patterns and informing specific scales of management). We attempt to address this challenge in our work by maintaining a tight link between the data, hypotheses and models. The results are often fine-scale field studies that can be scaled up to their landscape-scale management implications.

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