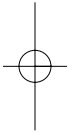


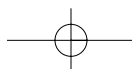
## CHAPTER SEVEN

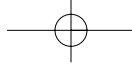
# *Modeling Multiple Ecological Scales to Link Landscape Theory to Wildlife Conservation*

THOMAS C. EDWARDS, JR., GRETCHEN G. MOISEN,  
TRACEY S. FRESCINO, AND JOSHUA J. LAWLER



A successful understanding of linkages between different ecological scales is central to the transition of landscape theory to application (O'Neill et al. 1991; Wiens 1989). Yet as a general rule, ecologists have been unable to combine data collected at multiple scales to explore landscape theory, let alone make the transition from theory to practice. Often landscape data have scale-specific resolutions and extents as well as thematic content resulting from methods of observation, making it difficult to scale measured responses of ecological systems up or down. For example, use of satellite-derived data such as the National Oceanic and Atmospheric Administration's 1.1-km resolution advanced very high resolution radiometer (AVHRR) for mapping animal habitat automatically limits the scale of animal study to a 1.1-km resolution. Any gains in the ability to systematically map habitat over large spatial extents are offset by a loss of resolution relating back to the animals of interest. Similarly, the kinds of ecological characteristics that plants and animals often are associated with (e.g., microclimates, forest structure attributes) often are of such fine resolution that they cannot be systematically



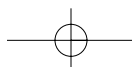
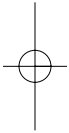


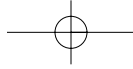
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mapped or modeled over large spatial extents. As before, gains in understanding the ecological processes that may determine species distributions are offset by an inability to map these distributions over large spatial extents. These types of limitations unfortunately limit research aimed at understanding how landscape process and pattern affect the distribution of plants and animals and tend to force research efforts to focus at a single scale. For example, birds have been found to be associated with landscape patterns over large areas (Rosenberg and Raphael 1986; Dunning et al. 1992; Hansen and Urban 1992; Freemark et al. 1995), the composition and structure of vegetation in smaller areas (Cody 1968; James 1971; Wiens and Rotenberry 1981), and localized habitat features such as microclimate and nest substrate (Calder 1973; Walsberg 1981; Rodrigues 1994). Yet each of these studies necessarily focused on the relationship of birds to scale-specific variables (landscape, home range, nest substrate) and therefore was of limited utility for understanding how linkages between the scales affect landscape-level patterns and distributions.

Vegetation modeling suffers similarly, often integrating information having different thematic and spatial resolutions to depict plant and plant community distributions. Numerous studies have demonstrated the ability to integrate environmental data with a variety of remote sensing platforms for vegetation classification (Loveland et al. 1991; Homer et al. 1997), stratification (Franklin 1986), and predictive modeling (Frank 1988; Davis and Goetz 1990; Moisen and Edwards 1999). The underlying satellite data for these analyses had resolutions ranging from the 1.1-km resolution AVHRR to the 30-m, multispectral Landsat thematic mapper (TM) imagery and occurred at a variety of spatial extents. In some cases, satellite information was used to model fine-scaled attributes such as understory components (Stenback and Congalton 1990), basal area and leaf biomass (Franklin 1986), and stand density and height (Horler and Ahern 1986), but results and potential for application to landscape studies seem mixed. However, these studies were focused at single scales and were highly detailed depictions at small spatial extents or coarse depictions at large spatial extents. In particular, those focusing on fine-scaled attributes of vegetation communities (e.g., basal area, leaf biomass, stand density) had limited spatial extrapolation, making it difficult to apply the results to landscape extents.

Differences in variables, explored at different spatial extents and resolutions, limit any systematic exploration of possible linkages between ecological scales for most of these studies. This limitation places serious constraints on the application of landscape theory to conservation issues, such as wildlife

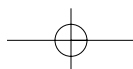
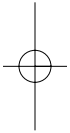


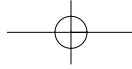


habitat modeling, use and associations, or spatially explicit predictive models for resource management. Only recently have wildlife ecologists begun to investigate habitat associations at multiple spatial scales within a single study (Gutzwiller and Anderson 1987; Morris 1987; Schaefer and Messier 1995; Saab 1999). In part, the impetus for a multiscale approach can be largely attributed to the introduction of hierarchy theory to ecology (Allen and Starr 1982; O'Neill 1989; Lawler 1999).

The full exploration of landscape relationships entails spatially explicit depictions of habitat and other variables at fine resolutions over large spatial extents. Such depictions would allow simultaneous exploration of relationships of variables at small spatial extents (e.g., canopy closure at nest sites) and over large landscapes (e.g., pattern of canopy closure within the home range). Although it is possible to model structural attributes of habitats and vegetation on small regions using satellite imagery, the regional-scale focus of many cover-mapping efforts makes it difficult to build vegetation structure into cover maps. Current efforts provide good maps of broad cover classes at landscape levels (Homer et al. 1997) but typically provide no information on the structure of the cover type or the spatial distribution of structure within the cover type. Recently, emphasis has been placed on linking forest data with satellite-based information not only to improve the efficiency of estimates of forest population totals but also to produce regional maps of forest class and structure and to explore ecological relationships (Moisen and Edwards 1999; Moisen 2000; Frescino et al. 2001; Moisen and Frescino in press). Accuracy of these types of map products is reasonably high (Edwards et al. 1998; Frescino et al. 2001).

Here we describe our collective efforts to develop and apply methods for linking different scales of landscapes for wildlife conservation modeling. Our process includes two steps. The first focuses on methods for modeling habitat that provide fine-grained estimations of habitat type and structure over large spatial extents. The second step is to use these representations of landscapes for modeling habitat use by terrestrial vertebrates at multiple scales. We illustrate how flexible regression techniques, such as generalized additive models (GAMs), can be linked with spatially explicit environmental information to map habitat structure. In this chapter we focus on forested systems. We demonstrate how these techniques can be used to develop spatially explicit probability maps for presence of forest, presence of lodgepole pine, basal area of forest trees, percentage cover of shrubs, and density of snags. We next illustrate how the spatially explicit maps of forest structure can be used to model wildlife habitat, focusing on the prediction of suitable





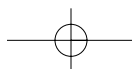
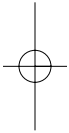
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habitat for cavity-nesting birds in forest systems at landscape scales. We close with discussion of future directions necessary to link multiple scales in landscape ecology.

### *Modeling Vegetation Pattern and Structure*

If a major objective of landscape modeling is to enhance understanding of relationships at multiple scales as a precursor for regional conservation planning, then methods for modeling scale-related ecological parameters are paramount. From a vegetation perspective, the principal question is how to accurately and efficiently model vegetation structure and patterns at multiple scales. Recent advances in statistical modeling techniques (McCullagh and Nelder 1989; Hastie and Tibshirani 1990; Hastie et al. 2001) and geographic tools, such as remote sensing and geographic information systems (GISs), have increased the opportunities for delineating and analyzing vegetation structure and pattern. Numerous studies have demonstrated the use of statistical models to understand and display how plant species are distributed throughout the environment (e.g., Austin and Austin 1980; Davis and Goetz 1990; Austin et al. 1984), yet the unpredictability of natural ecosystems, along with the dramatic influence of human disturbance, has made it difficult to draw conclusions about landscape-level vegetation distribution patterns and relationships to environmental conditions. These limitations result, in part, from past reliance on statistical tools that incorporate classic assumptions of normality (e.g., ordination methods; Austin and Noy-Meir 1971; Austin 1985) rather than other distributions more closely related to underlying ecological processes. Other statistical models, such as GAMs (Hastie and Tibshirani 1990) and so-called data-mining techniques (Hastie et al. 2001), are more flexible and better suited to handle nonlinear relationships of vegetation and environmental gradients (Yee and Mitchell 1991).

In addition to advances in statistical modeling techniques, remote sensing technology has made it possible to identify, analyze, and classify extensive tracts of vegetation using satellite spectral information (e.g., 30-m resolution, multispectral, Landsat TM imagery). Satellite data have been used mainly for constructing vegetation cover type maps (e.g., Loveland et al. 1991; Congalton et al. 1993; Homer et al. 1997), but current studies are also using satellite data to explore ecological factors influencing vegetation patterns (e.g., Horler and Ahern 1986; Franklin 1986; Frank 1988; Congalton et al. 1993). One limitation of classified cover maps is that vegetation typi-



cally is classified into discrete units, thus adding a measure of subjectivity and bias. Recent studies have found that integrating ancillary data, such as elevation, aspect, and slope, with spectral information can enhance the precision of delineation of forest attributes (Strahler and Logan 1978; Woodcock et al. 1980; Frank 1988; Frescino et al. 2001) and reduce the subjectivity of classification procedures. When linked with flexible modeling tools such as GAMs, such spatially explicit ancillary data provide a powerful context for generating fine-resolution depictions of vegetation across landscapes (Fig. 7.1).

Although new analytical tools have increased our ability to model vegetation over large spatial extents, most research still focuses on modeling dominant vegetation features distinguishable from satellites or climax or seral types strongly associated with environmental factors. But how do we analyze the understory and composition of habitats that are not directly visible from satellites? For example, most assumptions are that stand composition in forested habitats is directly associated with the overstory canopy, yet the density of down, dead material may be a function of slope rather than of canopy cover type. The few studies that have attempted to link reflectance values measured by satellites with understory components (Stenback and Congalton 1990) or stand density and volume (Franklin 1986) have generally been unsuccessful.

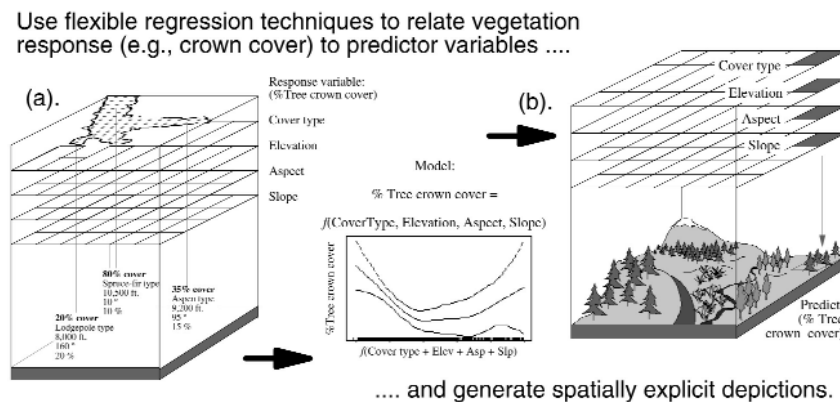


Figure 7.1 Conceptualized process for linking field data and remotely sensed information (A) with flexible statistical tools (B) for creating fine-resolution, large-spatial-extent maps of vegetation attributes.

### *The Context: Modeling Wildlife Pattern and Distribution*

Wildlife habitat relations models (WHR; Salwasser 1982) are one common approach for modeling animal distribution patterns. These models are essentially databases consisting of lists of habitat types, suitability rankings for the different habitat types, range maps, and species notes (Chapter 13, this volume; Verner and Boss 1980). WHR models often are linked with coarse cover maps of general habitat classes to build spatial predictions. They have general application for regional perspectives, but lack local specificity (e.g., gap analysis; Scott et al. 1993). Therefore, they may be accurate for addressing questions of species richness at coarse spatial scales (Raphael and Marcot 1986; Edwards et al. 1996) but are by nature less accurate for addressing questions involving individual species occurrences at fine spatial scales. This is not a failure of this type of model but rather a realized limitation of its applicability.

At finer scales habitat modeling often involves defining relationships between species occurrences or abundances and a set of factors related to vegetation structure and composition. Often called habitat suitability indices (HSIs), these models typically use statistical tools (e.g., regression) to assess the strength and shape of a relationship between species presence or abundance and a suite of ecological predictor variables (Chapter 13, this volume). Data for these models are gleaned primarily from previously published studies (U.S. Fish and Wildlife Service 1981). The fine-scaled nature of HSI-type models may make them more accurate in specific environments at the expense of generality; therefore, different models may be needed for the same species in different habitats (Stauffer and Best 1986). Despite this limitation, HSIs are likely to be more accurate and appropriate for the management of parks and reserves than the coarser-scale WHR models.

Unfortunately, HSI models have no spatial component, representing instead quantitative relationships between species presence or abundance and the predictor variables. Although the variables modeled in HSIs usually have relevance to underlying ecological processes that influence the animal's presence or abundance, the lack of spatially explicit depictions of these variables makes it difficult to evaluate how they might be constrained by, or in turn affect, higher-order landscape processes. To the extent that fine-grained predictor variables could themselves be modeled in spatially explicit fashion, opportunity would exist to evaluate links between different landscape scales (Chapter 1, this volume). Spatially explicit depictions of vegetation-based habitat variables (e.g., canopy closure, stem density, species type) linked to wildlife models using the same variables can yield more accurate spatially explicit wildlife models (Fig. 7.2).

Use modern regression techniques (e.g., GAM) to model structure of wildlife variables ....

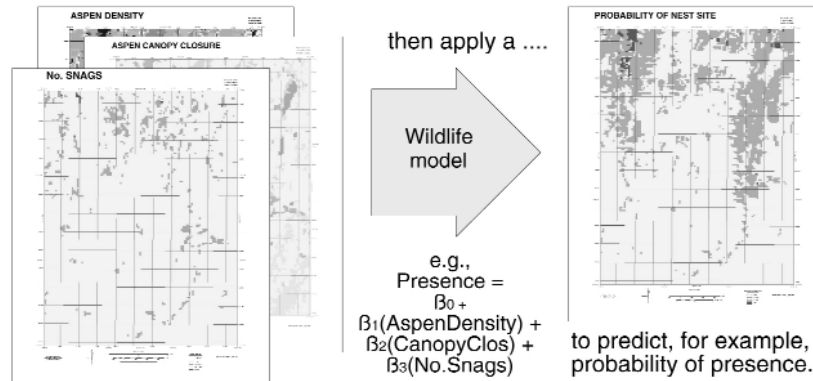


Figure 7.2 Conceptual process linking spatially explicit representations of vegetation type and structure with a wildlife habitat model.

### *The Context: Our Study Areas*

Our work in this arena has focused on forest systems in the intermountain West, principally in the northern Utah mountain ecoregion (hereafter the Uinta Mountains) in the United States. The Uintas have an east–west orientation, an approximate length of 241 km, and a width of 48 to 64 km. Elevation ranges from about 1,700 m to about 4,000 m. The area contains conspicuously deep, V-shaped canyons on the south side of the range and less pronounced canyons on the north side of the range. The climate consists of long winters and high summer precipitation that is mainly a function of elevation, latitude, and storm patterns from the west and the Gulf of Mexico, with local effects from slope exposure or aspect (Mauk and Henderson 1984).

The distribution of vegetation in the Uinta Mountains is highly influenced by topographic position and geographic location. Lodgepole pine (*Pinus contorta*) is the dominant vegetation type, ranging from 1,700 to 3,000 m elevation. At elevations between 2,400 and 3,000 m, lodgepole is mixed with aspen (*Populus tremuloides*), with a few homogenous aspen stands at lower elevations. As elevation increases, lodgepole forests are gradually replaced by spruce–fir (*Picea engelmannii*–*Abies lasiocarpa*) forest types and are often interspersed with large patches of wet and dry meadows. Other forest types include pinyon–juniper (*Pinus edulis*–*Juniperus osteosperma*) at lower elevations on the northeastern slope, Douglas fir (*Pseudotsuga menziesii*) on steep, protected slopes, and ponderosa pine (*Pinus ponderosa*) forests on exposed slopes on the south side of the range (Cronquist et al. 1972).

### *Example Application*

Readers are referred to Moisen and Edwards (1999), Moisen (2000), Frescino et al. (2001), and Moisen and Frescino (in press) for details about the complexities of generating spatially explicit forest structure models. The process is necessarily complex, and only a short overview is presented here. As noted earlier, the GAMs we used for modeling purposes are nonparametric extensions of the more commonly used generalized linear models (GLMs). The GAM, like the GLM, uses a link function to establish a relationship between the mean of the response variables (Table 7.1) and a smoothed function of the explanatory variables (Table 7.2). The main attraction of GAMs for vegetation modeling is their ability to handle nonnormal features in the data such as bimodality or asymmetry. GAMs are best described as data driven rather than model driven, such that the data determine the shape of the response curves rather than fitting a known function to the data. A scatter plot smoother is fit to each predictor variable and then fitted simultaneously in an additive model. The major weakness of GAMs is the danger of overfitting the data (Austin and Meyers 1996).

**Table 7.1 Summary of response variables for modeling forest attributes in the Uinta Mountains, Utah, USA.**

<i>Forest Attribute</i>	<i>Type</i>	<i>Description</i>	<i>Distribution</i>
Forest presence	Binomial	≥10% tree cover	$P = .77$
Lodgepole pine presence	Binomial	Majority of forest cover	$P = .31$
Basal area (m <sup>2</sup> /ha)	Continuous	Area of trees at 1.37 m basal height (trees >2.5 cm DBH*)	Range: 0–70 Median: 16
Shrubs (%)	Continuous	Sum of total cover from upper, middle, and lower layers	Range: 0–92 Median: 15
Snag density	Continuous	Total salvable and nonsalvable (snags >10.2 cm DBH)	Range: 0–248 Median: 5

\* Diameter Breast Height (DBH)

$P$  = proportion of model-building points defined as forest and lodgepole pine, respectively. See Frescino et al. (2001) for additional details.



**Table 7.2 Summary of explanatory variables used to model forest attributes in the Uinta Mountains, Utah, USA.**

<i>Variable</i>	<i>Type</i>	<i>Resolution</i>	<i>Source</i>
Elevation (m)	Continuous	90 m	DMA <sup>a</sup>
Aspect (°)	Continuous	90 m	Derived from DMA Relative annual solar radiation (Swift 1976)
	Discrete	90 m	Nine categories (see text for descriptions)
	Continuous	90 m	Radiation/wetness index (Roberts and Cooper 1989)
Slope (%)	Continuous	90 m	Derived from DMA
Precipitation (mm)	Continuous	90 m	Downscaled from PRISM <sup>b</sup> ; yearly precipitation climate maps (N. Zimmerman, unpublished data)
Geology	Discrete	1:500,000	Hintze (1980) Time frame (1, Precambrian; 2, Mississippian to Eocene; 3, Alluvium)
	Discrete	1:500,000	Nutrients (1, sandstone and limestone; 2, sedimentary; 3, alluvial)
	Discrete	1:500,000	Rock type (1, sedimentary; 2, alluvial)
Easting	Continuous	—	UTM <sup>c</sup> easting coordinates
Northing	Continuous	—	UTM northing coordinates
District	Discrete	—	National Forest Ranger Districts (1, Evanston; 2, Mountain View; 3, Flaming Gorge; 4, Vernal; 5, Roosevelt; 6, Kamas; 7, Duchesne)
TM-classified	Discrete	90 m	Gap analysis (Homer et al. 1997)
AVHRR	Continuous	1,000 m	NOAA <sup>d</sup> (June 1990)
TM			Landsat TM (June 1990 and August 1991)
	Continuous	30 m	TM band 3 (red)
	Continuous	30 m	TM band 4 (near-infrared)
	Continuous	30 m	TM band 5 (mid-infrared)

<sup>a</sup> Defense Mapping Agency (DMA)<sup>b</sup> Puget Sound Regional Synthesis Model (PRISM); for more information, see [www.prism.washington.edu/](http://www.prism.washington.edu/)<sup>c</sup> Universal Transverse Mercator Map Coordinate System (UTM)<sup>d</sup> National Oceanic and Atmospheric Administration (NOAA)  
See Frescino et al. (2001) for additional details.

### Forest Structure Modeling: The First Link

For forest and lodgepole presence (nominal responses), a logit link was used to transform the mean of the response to a binomial scale (Hastie and Tibshirani 1990). For the continuous variables (basal area, percentage shrubs, snag density), a Poisson link was used to transform the data to the scale of the response (Hastie and Tibshirani 1990). A loess smoothing function (see Venables and Ripley 1997 for description) was chosen to summarize the relationship between the predictors and the response. The loess smoother fits a robust weighted linear function to a specified window of data (Venables and Ripley 1997). One limitation of smoothed functions obtained from GAMs is their inability to extrapolate outside the range of the data used to build the model. To handle this problem, values of the validation data set that were outside the range of the model-building data set were assigned the maximum or minimum value of the respective variable in the data set.

The functional relationships between each explanatory variable and the respective response variables were analyzed for potential parametric fits following guidelines in Hastie and Tibshirani (1990) and Yee and Mitchell (1991). If a potential parametric fit existed, piecewise and second- and third-order polynomial functions were fit to the data and assessed based on the relative degree of change to the residual deviance (Cressie 1991). All explanatory variables, including all potential parametric fits, were run through a stepwise procedure to determine the best-fit model for prediction (see Chambers and Hastie 1992) using Akaike's information criterion. A percentage deviance reduction ( $D^2$ ) was also calculated for each model, representing the percentage of deviance explained by the respective model (Yee and Mitchell 1991). Once the model fits were derived (see Frescino et al. 2001, Tables 3 and 4), the model was applied to all the explanatory digital layers (Table 7.2) and predictive map surfaces generated. The result was a series of predictive maps of forest attributes having fine resolution (about 0.8 ha) and covering large spatial extents (more than 1 million ha; Fig. 7.3).

Accuracy of the models predicting forest and lodgepole presence was high (86 and 80 percent, respectively). Sixty-seven percent of the basal area validation points fell within  $\pm 15$  percent ( $11.5 \text{ m}^2/\text{ha}$ ) of the true value, 75 percent of the shrub density validation points fell within  $\pm 15$  percent of the true cover, but only 54 percent of the points fell within  $\pm 15$  percent of the true snag count.

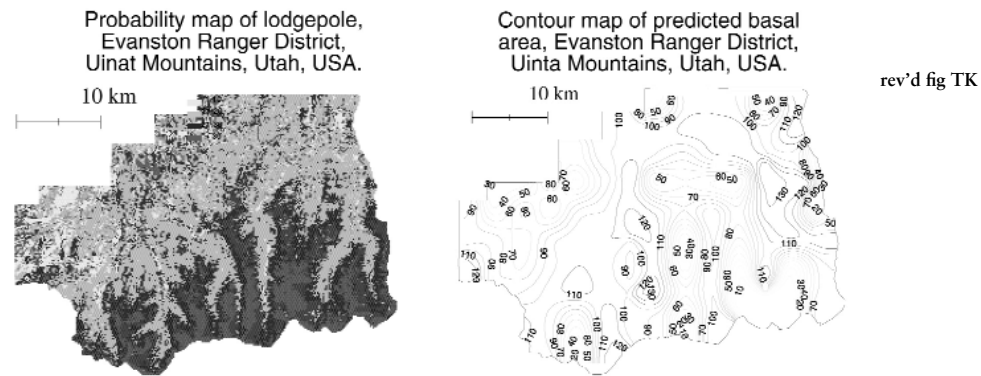


Figure 7.3 Example maps of nominal (lodgepole presence) and continuous (basal area) responses generated for an ~100,000-ha region of the Uinta Mountains, Utah (from Frescino 1998).

### Cavity Bird Nesting Habitat: The Second Link

Once the maps of forest attributes were generated, the next step was to generate models of bird presence based partly on the spatially explicit forest maps. We modeled habitat associations, based on landscape patterns, for four species of cavity-nesting birds nesting in aspen stands in the Uinta Mountains in northeastern Utah. Cavity-nesting birds make up a large part of the avian community in aspen forests in the western United States (Wintertnitz 1980; Dobkin et al. 1995). We modeled habitat of red-naped sapsuckers (*Sphyrapicus nuchalis*), northern flickers (*Colaptes auratus*), tree swallows (*Tachycineta bicolor*), and mountain chickadees (*Parus gambeli*), four common species in the study area. We concentrated on these species because all four species are likely to be associated with landscape patterns. Tree swallows and northern flickers nest on forest-meadow edges (Conner and Adkisson 1977; Rendell and Robertson 1990). Mountain chickadees are arboreal feeders (Ehrlich and Daily 1988) and tend to be associated with forested areas (Wilcove 1985; Yahner 1988). Because they exploit a number of different food resources, including willow bark, tree sap, and insects (Ehrlich and Daily 1988), red-naped sapsuckers may select nest sites in landscapes that provide access to this diverse set of resources.

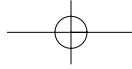
We built habitat models for each of the four species using classification trees (Breiman et al. 1984; Venables and Ripley 1997). Classification trees

are a flexible and simple tool for modeling complex ecological relationships (De'ath and Fabricus 2000). Trees explain the variation in a single response variable with respect to one or more explanatory variables and offer a non-parametric alternative to generalized linear models. Classification trees work by recursive partitioning of the data into smaller and more homogenous groups with respect to the response variable. Each split is made by the explanatory variable and the point along the distribution of that variable that best divides the data.

Tree models have several advantages for analyzing ecological data. First, decision trees are nonparametric and assume no underlying distribution in the data. Consequently the exact form of the relationship between the response variable and the explanatory variables (e.g., normal, logit) does not have to be known. Second, tree-based models readily capture nonadditive behavior and complex interactions. This ability to deal with complex interaction better mirrors ecological reality and can lead to superior models of ecological systems. Third, tree models are capable of modeling a large number and mixture of categorical and continuous explanatory variables. These types of data are very common in ecological studies, and the application of traditional linear statistical models can lead to erroneous conclusions. Finally, because their structure is easy to conceptualize and graphically represent, they usually are somewhat easy to interpret and explain. This latter point in particular is a critical aspect of building useful habitat models. See De'ath and Fabricus (2000) and Lawler and Edwards (2002) for a more thorough discussion of the use of classification trees in ecological modeling.

The four species models included a number of variables pertaining to the amount and configuration of aspen forest and open area (Fig. 7.4) (see Lawler 1999, and Lawler and Edwards 2002, for model specifics). We used these models to produce maps of predicted nesting habitat for each of the four species (Fig. 7.5). The spatial configuration of predicted suitable habitat differed between the four species. Red-naped sapsucker nesting habitat often was spread throughout the sites but tended to be concentrated at meadow edges. Tree swallow and northern flicker nesting habitat was even more closely associated with meadow edges and riparian areas, whereas mountain chickadee nesting habitat was patchily distributed and not necessarily associated with aspen–meadow edges.

We tested these models by searching new field sites for nests. We then mapped the nests on the prediction maps and assessed the accuracy of the maps for predicting the nests (Lawler and Edwards 2002). The northern flicker model was the most accurate (84 percent of nests correctly classified).



### CART model Red-naped sapsucker

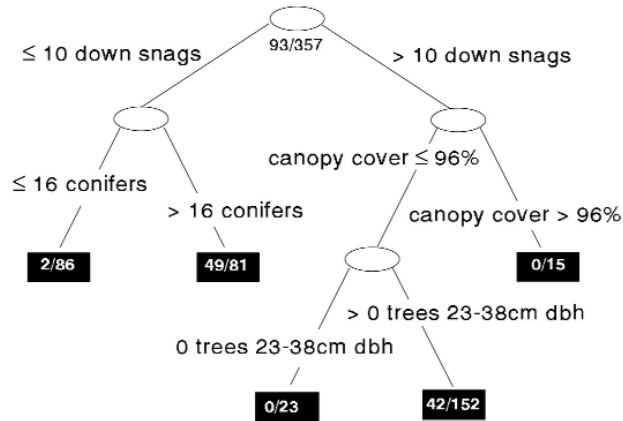


Figure 7.4 Classification and regression tree (CART) model predicting nesting habitat for red-naped sapsuckers. Models for the other species were similar in structure, varying only in the predictor variables and tree complexity (see Lawler and Edwards 2002).

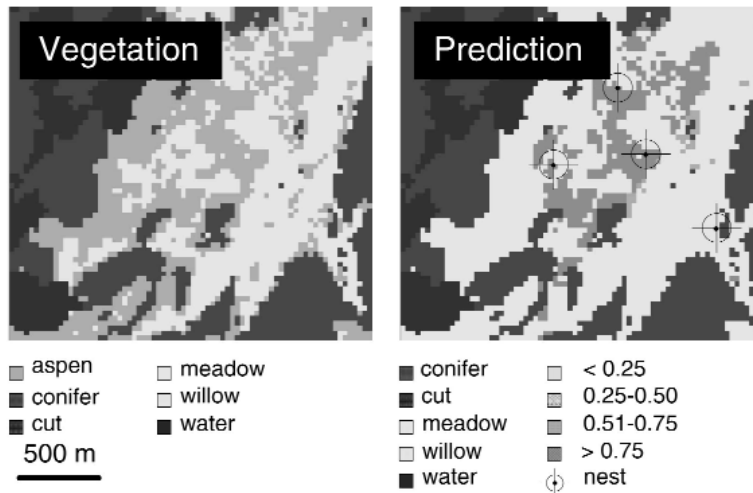
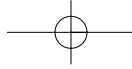


Figure 7.5 Vegetation and spatially explicit prediction maps for northern flicker nesting habitat. Medium gray in the vegetation map represents suitable nesting habitat and is based on classic WHR approaches (see text). Note how the amount and distribution of gray is reduced under the refined vegetation models, which then are incorporated in the wildlife models as described in the text. Nests are represented as circles with crosshairs.



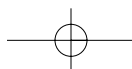
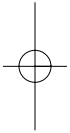
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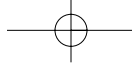
The red-naped sapsucker and tree swallow models were also accurate (80 percent and 75 percent of the nests correctly classified, respectively). The mountain chickadee model was far less accurate, correctly predicting only 50 percent of the nests at the test sites.

### *Discussion*

The ability to create spatially explicit depictions of vegetation type and structure depends, in part, on the flexibility and capability of the analytical procedures used to model vegetation. GAMs, in contrast to some analytical procedures (e.g., ordination and linear regression models), do not make a priori assumptions about underlying relationships, thus allowing the data to drive the fit of the model instead of the model driving the data. The graphic nature of GAMs also allows a visualization of the additive contribution of each variable to the respective response using smoothed functions. Smoothed functions are capable of fitting unusual variance patterns such as skewness and bimodality that are often overlooked with standard linear models (Austin and Noy-Meir 1971). One limitation of GAMs is the uncertainty associated with extrapolation of the smoothed functions, particularly at the tails of the distribution. As suggested by Hastie and Tibshirani (1990) and Yee and Mitchell (1991), we fitted parametric functions to the model whenever statistically allowable, thus constraining the behavior of the functions in the extreme ranges of the data. Often this involved a subjective interpretation based on visual inspection of the data.

Once the vegetation type and structure are modeled, the resultant maps can be linked with wildlife models and used to create predictive maps. We have demonstrated the potential for a linkage between habitat models and models of vegetation at large spatial extents. Although predictive models based on landscape patterns may prove to be accurate, models built solely at coarse spatial scales will be less accurate when fine-scale associations with structural attributes are strong. Cavity-nesting birds have been shown to respond to patterns of vegetation at several spatial scales finer than those modeled in our study. For example, nest tree size and condition (Dobkin et al. 1995; Schepps et al. 1999), snag and tree density (Flack 1976; Raphael and White 1984), and cavity availability (Brawn and Balda 1988) may all influence nest site selection decisions. To improve the predictive capability of coarser-scale habitat models, they must be linked with models of finer-scale habitat associations. Until now, making predictions with finer-scale models has been limited by the availability of fine-scale data over large spatial extents. Our vegetation modeling





approach, which includes techniques capable of predicting fine-scale attributes (e.g., canopy closure, stem density) at fine resolutions, overcomes this problem and generally increases model predictive capabilities.

### *Summary*

In general, ecologists have been unsuccessful in attempts to link information collected at multiple scales to explore landscape theory. Often these data have different resolutions and thematic content, making it difficult to scale measured responses of ecological systems up or down. This chapter explores our collective efforts to develop and apply methods for linking different scales of landscapes. Research focus has been at two levels. The first is approaches to modeling habitat that provide fine-grained estimations of landscape patterns at large spatial extents. The second is using these representations of landscapes to explore habitat use by terrestrial vertebrates at multiple scales. Current vegetation modeling efforts provide good maps of broad cover classes at landscape levels but typically provide no information on the structure of the cover type or the spatial distribution of structure within the cover type. Our work demonstrates how flexible regression techniques, such as generalized additive models, can be linked with spatially explicit environmental information for mapping forest structure. We demonstrated how these techniques can be used to develop spatially explicit probability maps for presence of forest, presence of lodgepole pine, basal area of forest trees, percentage cover of shrubs, and density of snags. We illustrated how these spatially explicit maps of forest structure can be used to model wildlife habitat, focusing on the prediction of suitable habitat for cavity-nesting birds in forest systems. We closed with discussion of future directions necessary to link multiple scales in landscape ecology.

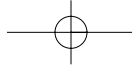
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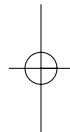
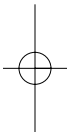
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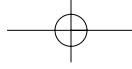


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