Development and Application of Habitat Suitability Models to Large Landscapes

Chapter · January 2009

DOI: 10.1016/B978-0-12-373631-4.00014-9

Chadwick Damson Rittenhouse
University of Connecticut

CHAPTER

Development and Application of Habitat Suitability Models to Large Landscapes

14

William D. Dijak and Chadwick D. Rittenhouse

Technological advancements in data collection, data processing, analytical procedures, and geographic information systems (GIS) facilitate the use of spatially explicit data for modeling landscape-level wildlife-habitat relationships (Larson et al., this volume; Roloff et al., this volume). Correspondingly, there is a variety of software programs that may be used to model wildlife-habitat relationships. These programs include species presence or probability of occurrence models such as BIOCLIM (Busby 1991), HABITAT (Walker and Cocks 1991), DOMAIN (Carpenter et al. 1993), and BIOMAPPER (Hirzel et al. 2002, 2006). Carpenter et al. (1993), Guisan and Zimmermann (2000), and Hirzel and Arlettaz (2003) reviewed or discussed differences among these programs. An important distinction is made between classification-based approaches (e.g., BIOCLIM, HABITAT) that describe the extent of a species distribution (i.e., niche) based on species' presence-absence information versus multivariate, distance-based approaches that describe both the extent and probability of species occurrence within that extent (e.g., DOMAIN, BIOMAPPER). Habitat Suitability Index (HSI) models provide an alternative approach that quantifies habitat quality, as opposed to species presence or probability of occurrence directly. The suitability relationships may be defined by empirical data, literature review, or expert opinion, or a combination of these. Software programs for HSI models include Landscape Scripting Language (Kushneriuk and Rempel 2007), Landscape HSImodels (Dijak et al. 2007), and VVF (Ortigosa et al. 2000). Also, HSI models have been developed directly within GIS software (Nichols et al. 2000, Juntti and Rumble 2006, Tirpak et al. 2007). Additionally, RAMAS GIS (Akçakaya 1998) provides the means to link wildlife demographic response (i.e., population viability and metapopulation dynamics) to habitat suitability (e.g., Larson et al. 2004; Bekessy et al., this volume). Regardless of which program is used, the goals are similar: to quantify wildlife response in terms of the quality, quantity, or spatial structure of habitat.

Roloff et al. (this volume) discussed some of the issues related to the use of GIS to model landscape-level wildlife habitat. In this chapter, we continue the discussion in the context of habitat suitability model development and application to large landscapes. We refer readers to Beissinger et al. (this volume) and Akçakaya et al. (this volume) for extension of HSI models to viability modeling. We begin with an overview of HSI models and HSI model development, discuss emerging issues regarding data availability and populating landscapes from different data sources, and conclude with a case study that illustrates the use of Landscape HSImodels software to the Hoosier National Forest, Indiana.

HSI MODELS

Habitat Suitability Index modeling is an outgrowth of the Habitat Evaluation Procedures (HEPs) developed during the early 1980s (U.S. Fish and Wildlife Service 1980, 1981). The purpose of HSI models is to numerically quantify wildlife habitat quality. In their original form, HSI models were based on measurements of habitat components at a local scale, which were numerically scored (e.g., suitability indices) and combined into an overall habitat suitability value for selected wildlife species. Collection of detailed local scale information becomes impractical when evaluating habitat at the landscape scale. Surrogates of local scale habitat components may be utilized to provide information about habitat components at the landscape scale. In addition, spatial relationships of habitat components such as area sensitivity, edge sensitivity, the interspersion and quantity of life requisite habitats, and distance to resource become important when modeling wildlife-habitat relationships at the landscape scale (Morrison et al. 1998).

As with any modeling endeavor, the development of HSI models is best accomplished when following an established protocol that outlines the philosophy, assumptions, data sources, analytical approaches, validation procedures, and appropriate applications for the models. The philosophy underlying HSI models is that each species requires a distinctive set of physical environmental factors used for survival and reproduction (e.g., habitat; Block and Brennan 1993). In its most general sense, these factors include food, cover, and, in the case of birds, nest locations for reproduction (Hildén 1965). Often, these environmental factors are associated with specific vegetative communities (e.g., habitat types) and with increasing level of detail, to vegetation structure, species composition, and vegetation age or succession stage. Habitat Suitability Index models hypothesize a functional relationship between the quantity of a resource and its suitability value (or quality). The value of each of these suitability indices (SIs) range from 0 (low or nonsuitable habitat) to 1 (highly suitable) for a specific resource attribute. A composite HSI value is formed by combining multiple SIs in an HSI equation.

Increasingly, HSI models are being developed and applied within a spatial framework (Roseberry and Woolf 1998; Juntti and Rumble 2006; Dijak et al. 2007; Tirpak et al. 2007; Fitzgerald et al., this volume). The application of HSI models to large geographic areas, use of landscape-level data sources, and inclusion of spatial attributes of wildlife-habitat relationships facilitates the transition away from field-based, measurement-intensive HSI models. Large-scale HSI models have a variety of uses, from facilitating evaluation of alternative management strategies in the development of a natural resource management plan (see following description), to identification of priority areas for management activities, and estimation of population viability (Larson et al. 2004). We acknowledge that large-scale HSI models are not immune to some challenges. For example, population density is sometimes used as a surrogate for habitat quality, and some HSI model validations use density as a measure of habitat quality (Duncan et al. 1995, Breininger et al. 1998, Kroll and Haufler 2006). Because HSI models do not account for intra- or inter-specific interactions such as competition and predation, behavioral responses to changes in resource conditions (i.e., changes in space use, movements, or resource selection), nor the error associated with the HSI value (Van Horne 1983, Roloff and Kernohan 1999, Morrison et al. 2006), interpretation and validation of HSI models can be difficult for some species (Shifley et al., this volume). Despite these concerns, the relatively simple conceptual framework of HSI models, availability of GIS data layers, and use of output maps as visual aids elevate the utility of large-scale HSI models and may enhance communication between managers, planners, biologists, and stakeholders.

MODEL DEVELOPMENT

Suitability, Abundance, or Viability?

The first consideration when developing large-scale HSI models is to state the model assumptions. HSI models predict habitat suitability, which is generally assumed to be related to probability of occurrence, population density, or population viability. In other words, habitat with a high suitability value will have high population density or maintain viable wildlife populations. The degree to which this assumption is met can depend on intra- and inter-specific interactions such as competition and predation, seasonal differences in habitat use, and temporal unpredictability in resource distribution or abundance; these factors affect whether abundance is an indicator of viability (Van Horne 1983). Habitat suitability models might also not predict abundance well if regional populations exist well below carrying capacity—that is, if habitat is not limiting. For some species it may be possible to incorporate SIs that explicitly address factors influencing population density or viability. For many species, however, we lack the empirical data or knowledge to support such relationships. When such information is available, an additional consideration is whether or not to mix factors by including suitability relationships for different types of demographic responses. For example, models designed to predict habitat suitability for breeding birds may contain suitability relationships for factors influencing territory density (e.g., patch area) as well as factors affecting nest success (e.g., distance to edge) (Rittenhouse et al. 2007). Habitat Suitability Index models for habitat specialists (e.g., yellow-breasted chat [*Icteris virens*]) may perform better than HSI models for habitat generalists (e.g., wood thrush [*Hylocichla mustelina*]), particularly when the same factors influence density and nest success (Rittenhouse 2008). If HSI models contain suitability relationships for different types of demographic responses, the most appropriate use of the models may be as indicators of probability of occurrence as opposed to specific demographic response(s). We recommend adherence to the most basic assumptions of HSI models: (1) Habitat influences animal distributions; (2) HSI models predict habitat suitability (not occurrence or abundance); and (3) all significant habitat variables are included in the model.

Geographic Extent

The second consideration when developing large-scale HSI models is to explicitly define the purpose of the model and the geographic extent of application. Probably the most common purpose of HSI models for avian species is to evaluate breeding habitat suitability, since it is the most studied portion of the avian life cycle. However, many migratory avian species have spatially distinct breeding, migration, and over-wintering habitat that span multiple ecoregional domains (Bailey 1983). For these species, we recommend using an ecoregional classification system such as Bailey (1983, 1996) to establish the geographic area for model application. For example, we developed our large-scale HSI models to predict breeding habitat suitability for the Central Hardwoods Region (Rittenhouse et al. 2007), which we defined as the Hot Continental Division (220) located within the Humid Temperate Domain, excluding the mountainous portions (M220), and including the eastern portion of the Prairie Division (250; Bailey 1996). The forested areas within the Central Hardwoods Region contain primarily oak (*Quercus* spp.) and hickory (*Carya* spp.), with some maple (*Acer* spp.) and beech (*Fagus* spp.), and lesser amounts of pine (*Pinus* spp.) and cedar (*Juniperus virginiana*). This definition restricts the application of our models to the area defined; application to other regions should not occur without modification to site-specific conditions.

Spatial Grain and Extent

The third consideration is to define the spatial scale of model application. Spatial scale has two attributes: grain and extent. Grain defines the lower limit of resolution for the landscape map and is often synonymous with patch or cell size (Wiens 1989). Typically, grain is established by the size of the cells in the available GIS layers, such as the digital elevation model (DEM) or land cover type. The concept of grain may also be used in a biological context. For example, biological grain may be defined as the resolution at which an animal perceives and responds to habitat cues. In large-scale HSI models, biological grain is often expressed at the size of the average home range; however, biological grain may range from micro-habitat to a forest stand to a landscape depending on the habitat cue. Spatial extent refers to the size and location of the study area or landscape (Wiens 1989).

We define large-scale HSI models as those applicable to landscapes >1000 ha in size. Often, the goal is to apply large-scale HSI models to landscapes with high resolution (e.g., small cell size) across large spatial extents. To do this, one needs to define life requisites at multiple spatial scales within a GIS. The ability to do this for a given species is often limited by the data available.

Data Sources

Habitat Suitability Index models are relatively unique among modeling approaches in that they use both empirical data, existing knowledge (based on literature review), and expert opinion. Expert opinion may be invaluable for species with limited empirical data or to describe complex relationships. While expert opinion has great utility, it may be difficult to quantify. For example, many experts and some empirical data support the importance of canopy gaps for cerulean warblers (*Dendroica cerulea*; Burhans et al. 2001). When translating the importance of canopy gaps into a suitability relationship, one needs not only to quantify this relationship in terms of the size, distribution (i.e., random, clumped), density, or position of gaps on the landscape (e.g., bottomland gaps versus upland gaps), but also to associate some metric of cerulean warbler response to canopy gaps (e.g., nest success, population density, or survival during the breeding season). The key is quantifying the resource in terms of its attributes—size, area, quantity, density, age, type, and distribution—and have some metric of animal response to the resource (i.e., demographic, resource use, movements/space use). The transition from a purely qualitative relationship to a quantitative one not only improves the suitability relationship and overall HSI, but also identifies data needs and directions for future studies.

Ideally, empirical data would be available from multiple studies across the geographic extent of interest at multiple spatial scales that affect habitat quality. Literature searches are valuable for identifying data sources, key habitat relationships (factors), and the form of the suitability response (e.g., linear or nonlinear). The context of a study is important: The study design, methods, and analysis should be appropriate for the intended application. One should not assume that the conclusions made from studies conducted at a particular spatial scale are applicable to relationships expressed at a different spatial scale (McCarty et al. 1956). Landscape-level data are often limiting because most empirical studies have been conducted at high resolution for small geographic extents (e.g., micro-habitat or patch-level studies). The strength of the suitability relationship may be improved if it is based on studies conducted at multiple spatial scales or replicated at a single scale across multiple habitat types, study sites, or ecoregions. Another consideration when evaluating empirical data is whether the study was experimental or correlative. Experimental studies are optimal because they can identify the specific mechanisms underlying wildlife-habitat relationships; however, correlative studies are valuable when conducted across habitat gradients.

Suitability Functions

Habitat type and structure.—Landscape-scale HSI models will generally have an SI that is based on a species preference for a habitat type. Habitat types are often inferred from land cover or land use data, classified aerial photography, or stand inventory data where available. For forest species this often includes knowledge of the suitability of tree species, tree species groups (e.g., red oaks, white oaks, pine/cedar, and maple) or forest land cover type (e.g., deciduous, coniferous, mixed). We usually begin HSI models for forest species with an SI that identifies tree species, species groups, forest type, or land cover type associations (Larson et al. 2003, Rittenhouse et al. 2007). For example, we evaluate the dominant tree species (group) for each cell on the landscape and assign SI = 1.0 if the cell contains the resource or SI = 0.0 if it does not. We also typically incorporate successional stage, tree size, or age class, as an indicator of structure, in a second SI or in combination with tree species in the first SI. These functions establish the maximum extent and quantity of potentially suitable habitat.

Area sensitivity.—Additional SIs may be incorporated to address spatial relationships such as area or edge sensitivity, or the composition of habitat within a specified area (e.g., average home range size). Many avian species are considered area sensitive, meaning that a minimum area of contiguous habitat is required before occupancy or breeding occurs. We estimate an SI for area sensitivity using a patch-definition algorithm (Larson et al. 2003, Dijak et al. 2007, Rittenhouse et al. 2007). Prior to applying the algorithm, we assigned suitability based on tree age, tree species, ecological land type, or land cover type as described previously. We used the patch-definition algorithm to join adjacent (i.e., horizontal, vertical, or diagonal) cells of suitable habitat. We then used an SI to assign values to cells based on the size of the habitat patch formed by aggregation. We determined the suitability value by plotting probability of occupancy, density, or nest success on the y-axis and patch size on the x-axis. We assigned the maximum suitability value (SI = 1.0) to the patches with the highest occupancy, density, or nest success and rescaled the y-axis to range from 0 to 1. We assigned the minimum suitability value (SI = 0.0) to patches equal to the cell size (e.g., 0.09 ha for 30 m $\times$ 30 m cells) or the minimum patch size at which occupancy, density, or nest success is nonzero. The form of the function depends on the species response and may be linear or nonlinear. We fit a logistic function to the suitability by patch size data and assigned suitability to all patches using this function.

Distance.—The distance to resources can have a positive or negative effect on habitat quality. For example, bats need water within their home range in order to survive, and roost sites are often clustered around water holes (Adams and

Thibault 2006). As the distance to water increases, the energy expended to utilize the resource increases and the quality of the habitat declines. For black bears (*Ursus americanus*), habitat quality increases as distance from roads increases (Tietje and Ruff 1983). This relationship could be expressed as habitat within 200 m of a road has a value of 0. Between 200 m and 1000 m habitat would gradually increase as expressed by the formula 0.00125 * DISTANCE – 0.25 and habitat greater than 1000 m from a road is assigned a value of 1.0 (Larson et al. 2003).

Edge effects.—Another common spatial relationship is edge sensitivity. Edge sensitivity varies by the type of edge and species' response to edges. We define habitat edges as a change in land cover type (e.g., forest to grassland) or tree age and its associated structure (e.g., early successional forest to mature forest). Species response to edges may be positive if different habitat types are used to meet life requisites. For example, in the Central Hardwoods Region, northern bobwhites (*Colinus virginianus*) nest in grasslands, forage in croplands, and use woody edges for escape cover (Stoddard 1931, Roseberry and Klimstra 1984, Roseberry and Sudkamp 1998, Williams et al. 2001). Suitable habitat contains all three habitat types within a biologically relevant area, such as the average bobwhite home range size. Species response to edges may be negative if the edge decreases the probability of occupancy, survival, or nest success.

A moving window approach can be used to model edge effects. The size of the neighborhood of cells represents the distance to which an edge effect penetrates the interior of a habitat. For example, if we have a 5 cell × 5 cell circular moving window and the raster cells are 30 m × 30 m resolution, the edge effect would extend a distance of 60 m, the maximum distance any cell in the neighborhood is away from the center cell. If any of the cells within the moving window create an edge that increases or decreases the value of the habitat represented by the center cell, the center cell value of the SI would be assigned the increase or decrease in habitat quality.

Landscape composition.—We quantify the landscape context through a more computationally and data-intensive approach. We compute the percent of a particular cover type (i.e., forest) within a moving window (Larson et al. 2003, Dijak et al. 2007, Rittenhouse et al. 2007). A moving window approach requires knowledge of habitat quality as a function of percent cover type and the effective landscape size in which to evaluate the percent cover type. The size of the moving window may be based on the biology of the species (e.g., maximum dispersal or movement distance) or a large value based on landscape size or attributes needed to support a population (e.g., 1, 5, or 10 km).

Landscape composition is the relative amount of individual habitat components found within a biologically relevant area, such as an animal's home range. The habitat components must be available in the correct proportions within the specified area to achieve optimal habitat. As the proportions deviate from the ideal, habitat quality declines. We use a circular moving window to process portions of the landscape equal in size to a typical home range for a species as the area within which habitat composition would be evaluated (Fig. 14-1). The moving window for a raster cell operates by evaluating the neighboring cells

1	1	2	4	1	2	1
1	4	1	2	3	3	3
3	3	2	1	1	1	4
4	3	3	3	1	1	4
2	3	2	2	1	1	4
2	2	2	2	1	1	3
2	2	1	2	1	1	3

FIG. 14-1

Habitat composition determined through the use of a circular moving window. Numbers represent one of four habitats located at each raster cell. Composition of this window is 0.43 habitat 1, 0.28 habitat 2, 0.28 habitat 3, and 0.00 habitat 4.

within a given area, in this case the area of a home range, and calculates the proportion of the neighboring cells for each habitat. These proportions are then compared to proportions thought to provide the best habitat, and an SI value determined from the comparison is then assigned to the center cell and the process continues by moving to the next adjoining cell and repeating the process. Optimum landscape composition receive a value of 1.0, and values decline as composition deviates from the optimum. In the example shown in Table 14-1,

Table 14-1 Habitat Composition Table for Two Habitat Components, A and B. Axes Represent the Observed Proportions of Habitats A and B. Table Values are the Suitability Index Values Resulting from Differences Between the Observed and Ideal Compositions of Habitats A and B. Optimum Suitability would be Achieved with Observed Proportion of A at 0.2 and Proportion of B at 0.8

Proportion of Habitat Component B	Proportion of Habitat Component A										
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
0.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.1	0.00	0.27	0.30	0.27	0.24	0.21	0.18	0.15	0.12	0.09	
0.2	0.00	0.36	0.40	0.36	0.32	0.28	0.24	0.20	0.16		
0.3	0.00	0.45	0.50	0.45	0.40	0.35	0.30	0.25			
0.4	0.00	0.54	0.60	0.54	0.48	0.42	0.36				
0.5	0.00	0.63	0.70	0.63	0.56	0.49					
0.6	0.00	0.72	0.80	0.72	0.64						
0.7	0.00	0.81	0.90	0.81							
0.8	0.00	0.90	1.00								
0.9	0.00	0.81									
1.0	0.00										

the optimum composition would be 20% component A and 80% component B. The values derived for the table values not equal to 0 use the equation (1-|optimum proportion A – observed proportion A|) * (1-|optimum proportion B – observed proportion B|). Both habitat components must be present to be considered suitable habitat, so if the proportion of either component equals 0, the composition is equal to 0. If the decline in habitat quality is thought to be more severe as the proportions deviate from the ideal, one or both terms can be squared or cubed. Other formulas are possible including the geometric or arithmetic mean of the two terms.

INPUT DATA LAYERS

Various data layers are used to provide information on landscape characteristics such as landform, land cover, and DEMs, which are important in defining habitat suitability. A basic landform map (Fig. 14-2) can be derived from a DEM using a topographic position index (Jenness 2006, Tirpak et al. 2007). Topographic position index is calculated as the elevation of a particular cell minus the mean elevation of cells in a moving window neighborhood divided by the standard deviation of the mean cell elevation within the window. Slope and aspect layers are created from the DEM. The slope layer and two moving windows of different sizes representing a large and small scale are used to evaluate a cell's elevation compared to the large-scale variation and small-scale variation in elevation to define landform classes. Decision rules (Table 14-2) provide an example of how different landform classes are determined. Landform in some instances can be used to identify ecological land types (ELTs; Van Kley 1994).

Input layers that we commonly use for forest species include a general land cover map (i.e., forest, croplands, water, etc.), a landform map (i.e., ridge, bottomlands, etc.), a dominant tree species map (i.e., white oak, maple, etc.), and a dominant tree age class map. Age class maps can be replaced with maps defining areas of similar forest structure if age classes are unavailable. Land cover maps are available from a variety of sources. The national land cover data (NLCD) map provides land cover based on classified satellite imagery with a resolution of 30 m that spans the United States. Many states have developed their own land cover classification as part of the national Geographic Approach to Planning for Biological Diversity (GAP) project. Some states have classified satellite imagery from the National Agriculture Statistics Service (NASS). Most states have National Aerial Imagery Program (NAIP) data that can be used as the basis to digitize land cover layers for smaller regions of interest. These land cover data layers offer general land cover classes that can be the foundation of land cover data used in HSI modeling.

The land cover data can be augmented with data from Forest Inventory and Analysis (FIA) data (Miles et al. 2001) and landform data to create spatially representative forest type maps, forest species composition maps, and forest age class

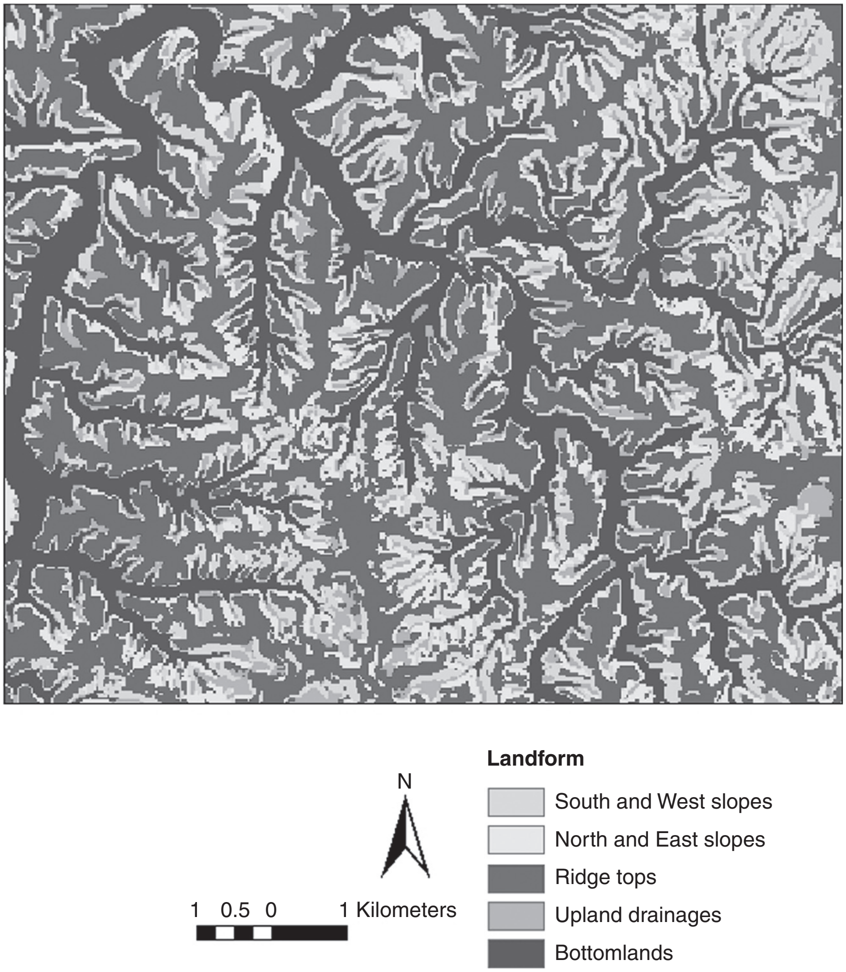

FIG. 14-2

Map of landforms created using topographic position index calculated from a digital elevation map.

maps. These maps will not be spatially accurate (i.e., placing a tree of specific age and species on an exact point in the landscape) but will be spatially representative of forests within a region. Tree species and age maps are created using land cover maps to separate forested lands from nonforested lands. If information in the land cover maps also separates deciduous, coniferous, and mixed forests, location of forest types within those land covers becomes more spatially representative of the true condition. The land cover data are combined with landform data to create patches representing the different combinations of forest land covers and landforms. These patches are surrogates for forest stands. Forest Inventory Analysis data from each state is broken up into geographic regions

Table 14-2 Criteria used to Assign Landform Classes for Landscape-Scale Habitat Suitability Models Based on Topographic Position Index

	Topographic Position Index (TPI)			
Landform	**240 m Radius Window**	**750 m Radius Window**	**% slope**	**Aspect**
Bottomland	TPI $<$ 1 SD	TPI $\leq$ –1 SD		
Upland drainage	TPI $\leq$ –1 SD	–1 SD $<$ TPI		
S&W slopes	–1 SD $<$ TPI $<$ 1 SD	–1 SD $<$ TPI $<$ 1 SD	slope $>$ 5%	135 $>$ aspect $<$ 315
N&E slopes	–1 SD $<$ TPI $<$ 1 SD	–1 SD $<$ TPI $<$ 1 SD	slope $>$ 5%	135 $\leq$ aspect $\geq$ 315
Ridges	–1 SD $<$ TPI	–1 SD $<$ TPI	slope $\leq$ 5%	
Ridges	TPI $\geq$ 1 SD			

called units; FIA data should be used from the unit that corresponds to the geographic extent of the landscape being created. Forest Inventory Analysis data for the unit is summarized to represent the proportions of forest types and age classes by landform and forest land cover (deciduous, coniferous, etc.). Forest Inventory Analysis age classes are converted to size classes, and a forest type and forest size class are randomly assigned to each patch based on the proportions of forest types and size classes found in the FIA data. The next step is to create the tree species and tree age maps. All subplots are pooled for each combination of landform, forest type, and size class plots. Subplots are assigned to a raster cell based on the raster cells' landform, forest type, and size class. The subplot data contain the list of tree species and diameters found on the subplot. The tree diameters are converted to tree ages, and the dominant tree species and age are assigned to cells in the dominant tree species and age maps. Though this process is tedious, it retains the patchy nature of forest stands by first assigning forest types and size class but includes the heterogeneity of species and age classes found within forest stands.

Another source of base map information is forest stand inventory data collected by national and state forests. These inventory data layers provide information about the forest type, forest structure, size class, and/or age of forest stands within sampling areas within a state. Using FIA subplot data and a land form data layer as in our previous example, one can create tree composition data layers that reflect the tree species and ages of trees typical to the forest stands. Similar methods of assigning forest structure parameters from FIA to forest patches are discussed by Tirpak et al. (2007).

The methods discussed in the preceding paragraphs describe ways to develop spatially representative data layers of forest tree species and structure.

Advancements are being made to directly measure these landscape attributes to create spatially exact rather than spatially representative landscapes.

Light Detection and Ranging (LiDAR) technology is leading the way in providing direct structural measurement of forests from remotely sensed technology. Forest structure has been shown to be important to a variety of species of birds (MacArthur and MacArthur 1961, James 1971, Rotenberry and Wiens 1980). LiDAR uses a pulsed laser beam emitted from an airplane or helicopter flying a specified route. The time it takes the light beam to reflect back to the aircraft can be used to determine the elevation of an object on the ground. Light beams that pierce the canopy and reflect from the ground are used to determine surface elevation. LiDAR data are often collected at submeter resolution and can have a vertical accuracy of 15 cm. Forest structure such as mean tree canopy height, dominant tree height, mean diameter, stem number, basal area, timber volume (Naesset 2002), canopy density (Lefsky et al. 1999, Maier et al. 2006), and quadratic mean canopy height (Lefsky et al. 1999) can be calculated from LiDAR in certain forest types. As the costs of acquiring LiDAR declines and the potential of the data to solve questions increases, LiDAR is becoming an essential data layer in many projects. For example, the U.S. Army Corps of Engineers and the U.S. Natural Resources Conservation Service are in the process of acquiring 2900 square miles of LiDAR data along the Missouri River for preliminary design of agricultural practices such as terracing, grade stabilization, and vegetative condition. It is expected that the data will enable them to perform detailed land cover mapping and vegetative species identification along the flood plain. Similar acquisitions of data are occurring across the United States. In an effort to expand the availability and utilization of LiDAR, the first U.S. National LiDAR Initiative meeting was held in February 2007 in Reston, Virginia.

Advancements are also being made in image classification of remotely sensed data for nondiscrete habitat classes. For example, texture analysis allows for the classification of habitats where there is high structural diversity but little distinct change from one habitat type to the next, such as what might occur in semi-arid regions and grasslands. The process evaluates more than the values of an individual raster cell. It bases the classification on repeated patterns occurring in a neighborhood of raster cells. Texture is defined by Hawkins (1969, p. 347) as (1) "some local 'order' is repeated over a region, which is large in comparison to the order's size"; (2) "the order consists in a nonrandom arrangement of elementary parts"; and (3) "the parts are roughly uniform entities having approximately the same dimensions everywhere within the textured region." For other definitions of texture and methods to determine texture, see Haralick et al. (1973) and Tuceryan and Jain (1998). Applications of image texture analysis include predicting avian species richness (Hepinstall and Sader 1997, Knick and Rotenberry 2000, St-Louis et al. 2006) and mapping nesting habitat (Pasher et al. 2007).

Software has been developed to perform object-oriented classification of imagery and LiDAR data including textured areas through a process known as segmentation. One such software, Definiens eCognition software (Definiens 2003), has been used to classify satellite and LiDAR data simultaneously to create land cover polygons of agricultural lands (Manakos et al. 2000). Their object-oriented classification outperformed the traditional ISODATA pixel classification approach. Levick and Rogers (2006) used object-oriented classification of color aerial photography and LiDAR data to monitor the spatio-temporal changes of savanna woody vegetation in Kruger Park, South Africa.

HSI EQUATIONS

An HSI value is a combination of individual SIs. The functional response by a species to a resource attribute can take many forms, but the most commonly used form for SIs is a linear relationship. More complex forms may be appropriate when supported by empirical data or expert opinion. These include sigmoid, exponential, and piecewise-regression functions. We recommend using a sigmoid function when there is uncertainty about the endpoints of the hypothesized relationship. Piecewise regression may be used to estimate the breakpoints (i.e., thresholds) of nonlinear suitability relationships, such as a species' response to edge effects (Toms and Lesperance 2003). However, these equations are data hungry and computationally intensive.

The form of the HSI equation varies depending on whether an SI represents a critical or limiting resource, or modifies a resource based on a spatial attribute such as size, proximity to edge, or composition. We used geometric, arithmetic, and logical relationships to calculate HSI scores depending on the number and type of species' life requisites (Larson et al. 2003, Dijak et al. 2007, Rittenhouse et al. 2007). We used a geometric mean when all habitat characteristics were necessary for habitat suitability:

$$HSI = \sqrt[3]{SI_1 \times SI_2 \times SI_3}.$$

With a geometric mean, the HSI value is zero if any suitability index is zero. We used an arithmetic mean when habitat characteristics were substitutable. In other words, the HSI value is greater than zero when at least one SI is nonzero.

Suitability indexes may be included as modifiers to decrease habitat quality. For example, we included an SI for fire in our worm-eating warbler (*Helmitheros vermivorum*) HSI model (Rittenhouse et al. 2007). The final habitat suitability value was the geometric mean of deciduous habitat (SI_1), tree age by ELT (SI_2), and deciduous patch size (SI_3), multiplied by SI_4 to account for reduced suitability due to fire:

$$HSI = (\sqrt[3]{SI_1 \times SI_2 \times SI_3}) \times SI_4.$$

Logical relationships are useful when a species' life requisites cannot occur in a single cell. Recall the northern bobwhite example earlier, where bobwhites use woody edges for escape cover, grasslands for nesting, and croplands for forage.

In this situation, the suitability value of a given cell represents only one of the life requisites. We used a maximum function to identify the greatest contribution to habitat suitability among the three requisites (Rittenhouse et al. 2007). The final habitat suitability value was the sum of (1) the maximum value of grassland (SI_1), cropland (SI_2), and woody cover (SI_3); and (2) the product of habitat composition (SI_4) and a modifier to reduce the suitability of roads and urban areas within the moving window for habitat composition (SI_5):

$$HSI = Maximum(Maximum(SI_1, SI_2), SI_3) + (SI_4 \times SI_5).$$

We used an additive HSI equation instead of a geometric mean because we recognized that grassland, cropland, or woody cover provided bobwhite habitat; however, the highest suitability value occurred when at least two of the three habitat types were present within a bobwhite's home range. Alternatively, a minimum function can be used when a suitability index represents a limiting factor.

LANDSCAPE HSImodels SOFTWARE

We developed Landscape HSImodels software (Dijak et al., 2007) to provide a user-friendly interface to evaluate the spatial relationships of wildlife habitat at the landscape scale. Version 2.1.1 contains models for 21 species of wildlife, including American woodcock (*Scolopax minor*), black bear, bobcat (*Lynx rufus*), cerulean warbler, eastern wild turkey (*Meleagris gallopovo silvestris*), gray squirrel (*Sciurus carolinensis*), Henslow's sparrow (*Ammodramus henslowii*), hooded warbler (*Wilsonia citrina*), Indiana bat (*Myotis sodalis*), northern bobwhite, northern long-eared bat (*Myotis septentrionalis*), ovenbird (*Seiurus aurocapilla*), pine warbler (*Dendroica pinus*), prairie warbler (*Dendroica discolor*), red bat (*Lasiurus borealis*), ruffed grouse (*Bonasa umbellus*), southern redback salamander (*Plethodon serratus*), Timber rattlesnake (*Crotalus horridus*), wood thrush, worm-eating warbler, and yellow-breasted chat. A generic model is also included so that suitability relationships from different species models can be recombined into models for a species not represented in the software. We created models using literature review, expert opinion, and from previous local-scale models (see Larson et al. [2003] and Rittenhouse et al. [2007]). Each species model contains an interface that guides the user through the calculation of each SI (Fig. 14-3). The individual SIs are combined into an overall HSI by an equation specified by the user (Fig. 14-3). All models come with default parameters and equations developed for the Central Hardwoods Region of the United States (Larson et al. 2003, Rittenhouse et al. 2007) but can be modified to fit habitat relationships that occur in other parts of a species range.

Input and output data formats are ASCII rasters, which may be created in ArcView 3.x by exporting a data source, in ArcGIS using ArcToolBox, and in ArcInfo by issuing the gridascii command. ASCII rasters created in other GIS software packages need to follow the Environmental Systems Research Institute (ESRI, Redlands, California, USA) format for header lines (ESRI, ArcGIS, ArcView,

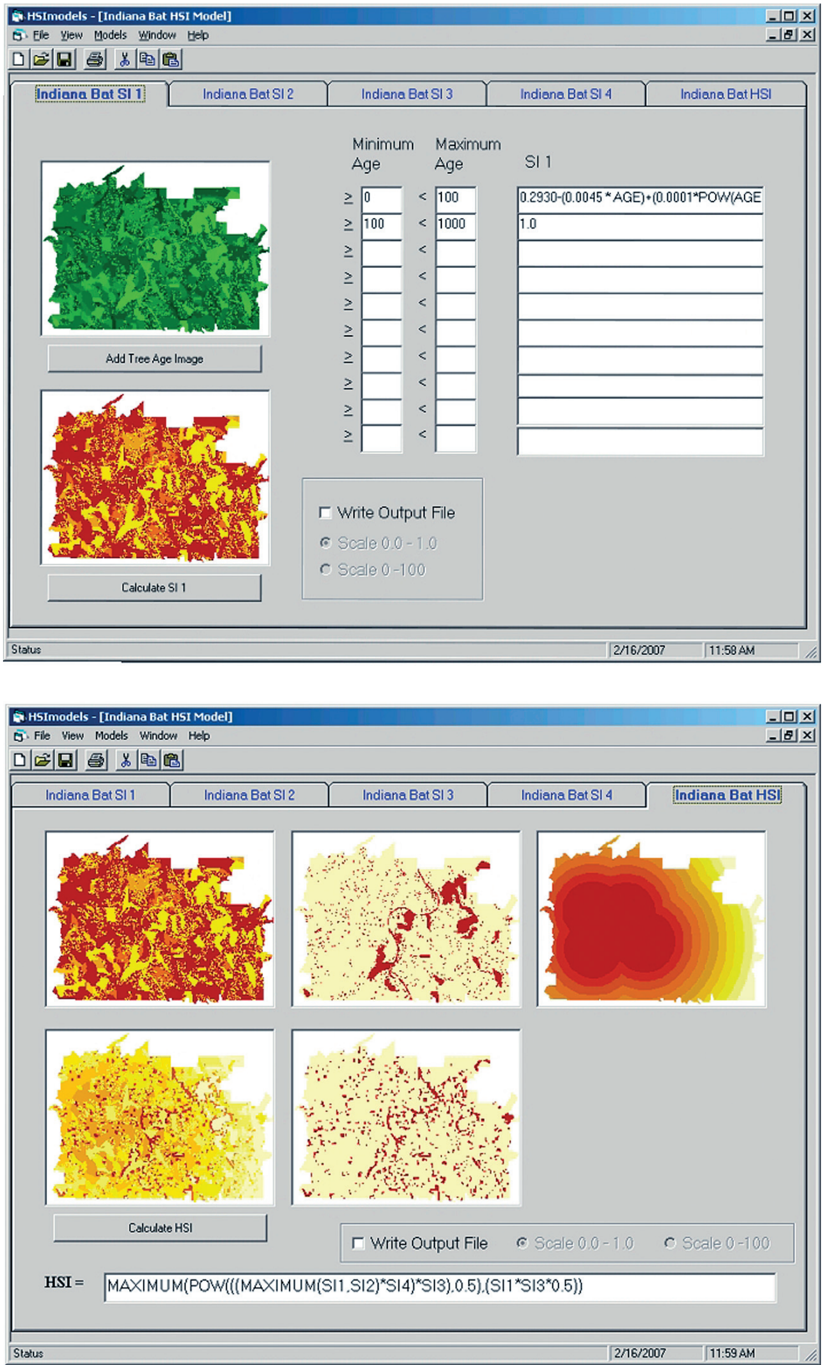

FIG. 14-3

Examples of the Indiana bat model in Landscape HSImodels software. The top window is a map of tree age (light green for young forest and dark green for older forest) and the resulting suitability index values ranging from light yellow (SI 1 = 0.0) to dark red (SI 1 = 1.0). The lower window is a map of the overall Habitat Suitability Index (lower, left map) and four suitability index maps.

ArcToolBox, ArcInfo are trademarks, registered trademarks, or service marks of ESRI in the United States, the European Community, or certain other jurisdictions, Environmental Services Research Institute, Redlands, California, USA). Input layers as well as SI and HSI layers are displayed as the user works through the model. All SI and HSI layers can be exported from the software and imported back into GIS software for further analysis.

The minimum computer system recommended is a PC with a 1.7 gigahertz (GHz) processor and 500 megabytes of random access memory (RAM). We also recommend using a 17-inch or larger monitor. Computers with faster processors and more RAM will reduce model processing time. A computer with the above configuration was successfully used to process a 1200 row by 1200 column landscape. A landscape with 2000 rows and 3000 columns was modeled on a computer with a 3.0 GHz processor and 2 gigabytes of RAM. The maximum size of a landscape that can be processed will vary from model to model based on the number of individual suitability indices incorporated into the model and the complexity of the calculations that need to be processed within the model. Models using large moving windows on large landscapes take several hours to complete. The limitation in landscape size is controlled by the amount of RAM the operating system is capable of utilizing. At the time of this printing, none of the HSI models have been validated, and the authors recognize the importance of validation. The software has been applied to districts of the Hoosier and Mark Twain National Forests (Shifley et al. 2006).

HOOSIER NATIONAL FOREST CASE STUDY

Working cooperatively with the personnel of the Hoosier National Forest (HNF) (Fig. 14-4), and in support of the HNF management plan, we applied Landscape HSI-models to five proposed forest management plan alternatives. Alternative 1 was the current plan and was mostly focused on uneven-aged management using single tree and group selection harvesting of timber with only a small percentage of the forest being harvested per decade. Alternative 2 had no harvesting, no maintenance of openings, and no prescribed burning. Alternative 3 had greater levels of uneven-aged management than alternative 1 and included a moderate amount of prescribed burning. Alternative 4 had even-aged management and a high level of prescribed burning. Alternative 5 was similar to alternative 1 but provided for a focal area that used even-aged management to provide for wildlife species needing early successional forest. Alternatives 3 and 4 also included this focal area for early successional species. The alternative plans were first modeled through LANDIS, a forest landscape simulation model (Mladenoff et al. 1996, He et al. 1999, Mladenoff and He 1999) that applies forest management practices and natural disturbance to current conditions to produce maps of future forest age class patterns and forest species composition. Methods similar to those described above were used to build input layers for LANDIS with the exception that multiple species and age cohorts were

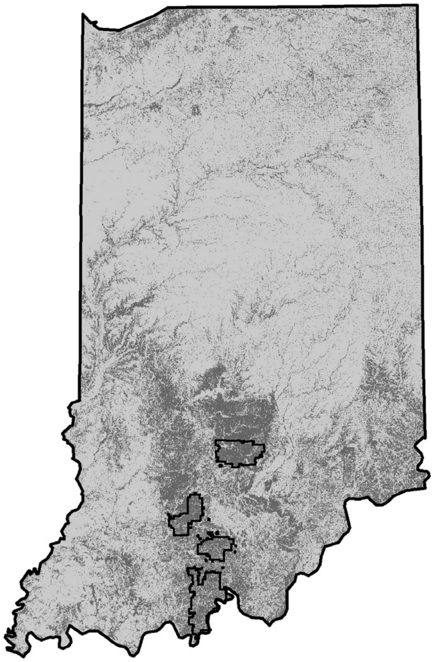

FIG. 14-4

Hoosier National Forest (outlined in black) located in south central Indiana, USA. Dark gray depicts forested; and light gray, nonforested areas of the state.

assigned to each cell of the current condition map, since LANDIS uses this information in forecasting future forest landscapes. Landscapes were modeled at 10 m resolution representing the size of a mature tree crown so that single tree selection harvesting could be modeled. The forest landscapes were modeled through 15 decades of each management alternative producing sets of forest landscape maps at each decade. LANDIS output maps were converted to ASCII rasters, and nine wildlife models were then applied to the current conditions as well as maps forecasting forest conditions at 10, 50, and 150 years of age.

We modeled the effects of alternatives on American woodcock, cerulean warbler, Henslow's sparrow, Indiana bat, northern bobwhite, ruffed grouse, wood thrush, worm-eating warbler, and yellow-breasted chat; these represented species that were disturbance dependent, area sensitive, edge sensitive, fire sensitive, mast dependent, game species, species dependent on specific forest ages or structures, and species of special concern. By selecting a suite of species that respond in different ways to varying management methods, we were able to evaluate the trade-offs in habitats for each species. Changes from current condition HSI values occurred over time and between competing alternatives. Habitat Suitability Index maps (Fig. 14-5) were produced as well as tabular summaries and charts (Fig. 14-6). Alternatives 1 and 2 did not

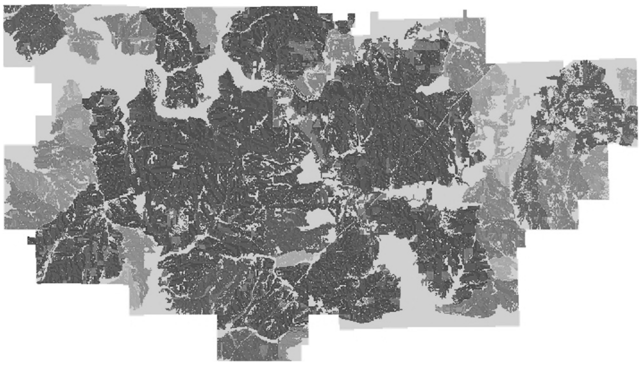

FIG. 14-5

Worm-eating warbler Habitat Suitability Index map for current condition on the Pleasant Run district of the Hoosier National Forest, Indiana, USA. Values range from 0.0 (light gray) to 1.0 (dark gray).

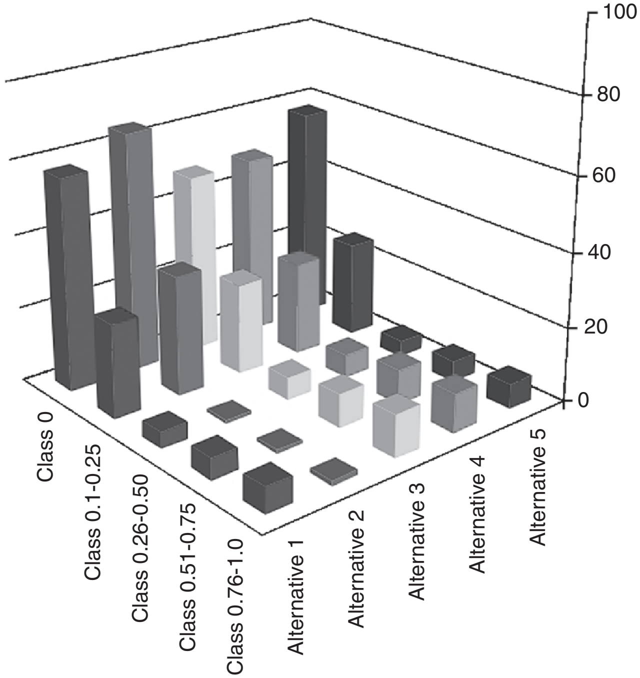

FIG. 14-6

The proportion of the Hoosier National Forest, Indiana, USA, that falls within five different habitat suitability classes for ruffed grouse after 50 years of forest management under five different management alternatives.

provide adequate habitat for American woodcock, ruffed grouse, and yellow-breasted chat. Alternative 2 did not provide adequate habitat for Henslow's sparrow. Alternatives 3, 4, and 5 all provided adequate habitat in varying degrees to all species. This information was included with the proposed plan alternatives to provide managers and stakeholders with information on the cumulative effects over time of all the proposed management alternatives.

SUMMARY

Extending HSI modeling to the landscape scale allows for the evaluation of habitat quality for larger geographic areas based on our knowledge of spatial wildlife-habitat relationships. When used with landscape forest simulation models, they provide a method of evaluating temporal changes, including proposed management activities. Landscape-level planning and management of populations requires knowledge of habitat quality at the landscape scale.

Suitability indices can be developed to represent habitat relationships based on habitat type and structure and landscape patterns such as patch size, distance to features, edge effects, and landscape composition. Input layers in the form of GIS layers can be developed from a variety of remote sensing products or large-scale field inventories to calculate suitability index values based on landform, land cover, forest type or tree species, forest age class, etc. By varying the values of SIs and varying the methods used to combine SIs into an HSI, we can examine the effects of individual habitat components on overall habitat suitability to help us to determine which habitat components are most lacking for a species.

Methods of deriving landscape information and monitoring landscape changes are improving quickly, and the availability of software such as Landscape HSImodels (Dijak et al. 2007) further facilitates the use of large-scale HSI models. Better and more concise models can be developed as our knowledge of habitat components increases at the landscape scale, but management cannot and should not wait for the perfect model. We contend that applying the best current knowledge is better than waiting until all wildlife-habitat relationships are thoroughly defined.

ACKNOWLEDGMENTS

We wish to thank Michael Larson, Joshua Millspaugh, and Frank Thompson for their insightful comments on this chapter.

LITERATURE CITED

Akçakaya, H. R. 1998. *RAMAS GIS: Linking landscape data with population viability analysis. Version 3.0.* Applied Biomathematics, Setauket, New York, USA.

Adams, R. A., and K. M. Thibault. 2006. Temporal partitioning by bats at water holes. *Journal of Zoology* 270:466–472.

Bailey, R. G. 1983. Delineation of ecosystem regions. *Environmental Management* 7:365–373.

Bailey, R. G. 1996. *Ecosystem geography.* Springer-Verlag, New York, New York, USA.

Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology: Theory and applications. Pages 35–91 *in* D. M. Powers, editor. *Current ornithology.* Volume 11. Plenum Press, New York, New York, USA.

Breininger, D. R., V. L. Larson, B. W. Duncan, and R. B. Smith. 1998. Linking habitat suitability to demographic success in Florida scrub-jays. *Wildlife Society Bulletin* 26:118–128.

Burhans, D. E., W. D. Dijak, and F. R. Thompson, III. 2001. *Conservation assessment: Cerulean warbler* Dendroica cerulea. USDA Forest Service, North Central Research Station, Columbia, Missouri, USA.

Busby, J. R. 1991. BIOCLIM—a bioclimate analysis and prediction system. Pages 64–68 *in* C. R. Margules and M. P. Austin, editors. *Nature conservation: Cost effective biological surveys and data analysis.* CSIRO, Melbourne, Australia.

Carpenter, G., A. N. Gillison, and J. Winter. 1993. DOMAIN—A flexible modeling procedure for mapping potential distributions of plants and animals. *Biodiversity and Conservation* 2:667–680.

Definiens. 2003. *Definiens, eCognition, object oriented image analysis, Version 3*. Definiens Imaging, Munich, Germany.

Dijak, W. D., C. D. Rittenhouse, M. A. Larson, F. R. Thompson, III, and J. J. Millspaugh. 2007. Landscape habitat suitability index software. *Journal of Wildlife Management* 71:668–670.

Duncan, B. W., D. R. Breininger, P. A. Schmalzer, and V. L. Larson. 1995. Validating a Florida scrub-jay habitat suitability model, using demography data on Kennedy Space Center. *Photogrammetric Engineering & Remote Sensing* 61:1361–1370.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.

Haralick, R. M., K. Shanmugan, and I. Dinstein. 1973. Textural features for image classification. *IEEE Transactions on Systems, Man, and Cybernetics SMC* 3:610–621.

Hawkins, J. K. 1970. Textural properties for pattern recognition. *In* B. S. Lipkin and A. Rosenfeld, editors. *Picture processing and psychopictorics* pp. 347–370. Academic Press, New York, New York, USA.

He, H. S., D. J. Mladenoff, and J. Boeder. 1999. An object-oriented forest landscape model and its representation of tree species. *Ecological Modelling* 119:1–19.

Hepinstall, J. A., and S. A. Sader. 1997. Using Bayesian statistics, thematic mapper satellite imagery, and breeding bird survey data to model bird species probability of occurrence in Maine. *Photogrammetric Engineering & Remote Sensing* 63:1231–1237.

Hildén, O. 1965. Habitat selection in birds, a review. *Annales Zoologici Fennici* 2:53–75.

Hirzel, A. H., and R. Arlettaz. 2003. Modelling habitat suitability for complex species distributions by the environmental-distance geometric mean. *Environmental Management* 32:614–623.

Hirzel, A. H., J. Hausser, and N. Perrin. 2002. *Biomapper 2.0.* Division of Conservation Biology, University of Switzerland, Bern. <http://www.unil.ch/biomapper>.

Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199:142–152.

James, F. C. 1971. Ordination of habitat relationships among breeding birds. *Wilson Bulletin* 83:215–236.

Jenness, J. 2006. Topographic Position Index (tpi_jen.avx) extension for ArcView 3.x version 1.2. Jenness Enterprises website. <http://www.jennessent.com/arcview/tpi.htm>. Accessed 15 January 2008.

Juntti, T. M., and M. A. Rumble. 2006. *Arc habitat suitability index computer software*. U.S. Forest Service, Rocky Mountain Research Station. General Technical Report RMRS-GTR-180WWW, Fort Collins, Colorado, USA.

Knick, S. T., and J. T. Rotenberry. 2000. Ghosts of habitats past: Contribution of landscape change to current habitats used by shrubland birds. *Ecology* 81:220–227.

Kroll, A. J., and J. B. Haufler. 2006. Development and evaluation of habitat models at multiple spatial scales: A case study with the dusky flycatcher. *Forest Ecology and Management* 229:161–169.

Kushneriuk, R. S., and R. S. Rempel. 2007. *LSL: Landscape Scripting Language*. Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources, Thunder Bay, Ontario, Canada.

Larson, M. A., W. D. Dijak, F. R. Thompson, III, and J. J. Millspaugh. 2003. *Landscape-level habitat suitability models for 12 wildlife species in southern Missouri*. U.S. Forest Service, North Central Research Station, General Technical Report NC-233, St. Paul, Minnesota, USA.

Larson, M. A., F. R. Thompson, III, J. J. Millspaugh, W. D. Dijak, and S. R. Shifley. 2004. Linking population viability, habitat suitability and landscape simulation models for conservation planning. *Ecological Modelling* 180:103–118.

Lefsky, M. A., D. Harding, W. B. Cohen, G. Parker, and H. H. Shugart. 1999. Surface LiDAR remote sensing of basal area and biomass in deciduous forests of eastern Maryland, USA. *Remote Sensing of the Environment* 67:83–98.

Levick, S. R., and K. H. Rogers. 2006. LiDAR and object-based image analysis as tools for monitoring the structural diversity of savanna vegetation. *In* S. Lang, T. Blaschke, and E. Schöpfer, editors. *Proceedings of the 1st International Conference on object-based image analysis.* International Archives of Photogrammetry, Remote Sensing and Spatial Information Sciences, Volume 34, Part XXX.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594–598.

Maier, B., D. Tiede, and L. Dorren. 2006. Assessing mountain forest structure using laser scanning and landscape metrics. *In* S. Lang, T. Blascbke, and E. Schöpfer, editors. *Proceedings of the 1st International Conference on object-based image analysis*. International Archives of Photogrammetry, Remote Sensing and Spatial Information Sciences, Volume XXX VI4/C42, Saizburg, Austria.

Manakos, I., T. Schneider, and U. Ammer. 2000. A comparison between the ISODATA and the eCognition classification methods on basis of field data. *International Archives of Photogrammetry, Remote Sensing and Spatial Information Sciences,* Volume XXXIII (Supplement B7): 133–139.

McCarty, H. H., J. C. Hook, and D. S. Knos. 1956. *The measurement of association in industrial geography.* Department of Geograpy Report 1, State University of Iowa, Iowa City, USA.

Miles, P. D., G. J. Brand, C. L. Alerich, L. F. Bednar, S. W. Woudenberg, J. F. Glover, and E. N. Ezell. 2001. *The forest inventory and analysis database: Database description and users manual version 1.0*. U.S. Forest Service, North Central Research Station, General Technical Report NC-218, St. Paul, Minnesota, USA.

Mladenoff, D. J., and H. S. He. 1999. Design, behavior and application of LANDIS, an object-oriented model of forest landscape disturbance and succession. Pages 125–162 *in* D. J. Mladenoff and W. L. Baker, editors. *Spatial modeling of forest landscape change: Approaches and applications.* Cambridge University Press, Cambridge, United Kingdom.

Mladenoff, D. J., G. E. Host, J. Boeder, and T. R. Crow. 1996. LANDIS: A spatial model of forest landscape disturbance, succession, and management. Pages 175–180 *in* M. F. Goodchild, L. T. Steyaert, B.O Parks, C. Johnston, D. Maidment, M. Crane, and S. Glendinning, editors. *GIS and environmental modeling: Progress and research issues.* GIS World Books, Fort Collins, Colorado, USA.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1998. *Wildlife-habitat relationships: Concepts and applications*. Second edition. University of Wisconsin Press, Madison, Wisconsin, USA.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 2006. *Wildlife-habitat relationships: Concepts and applications*. Third edition. Island Press, Washington, D.C., USA.

Naesset, E. 2002. Predicting forest stand characteristics with airborne scanning laser using a practical two-stage procedure and field data. *Remote Sensing of Environment* 80:88–99.

Nichols, J. M., S. A. Husain, and C. Papadas. 2000. *Integrating GIS technology with forest management and habitat assessment efforts on our national forests.* U.S. Forest Service, North Central Research Station, General Technical Report NC-205, St. Paul, Minnesota, USA.

Ortigosa, G. R., G. A. De Leo, and M. Gatto. 2000. VVF: Integrating modelling and GIS in a software tool for habitat suitability assessment. *Environmental Modelling & Software* 15:1–12.

Pasher, J., D. King, and K. Lindsay. 2007. Modelling and mapping potential hooded warbler (*Wilsonia citrina*) habitat using remotely sensed imagery. *Remote Sensing of Environment* 107:471–483.

Rittenhouse, C. D., W. D. Dijak, F. R. Thompson, III, and J. J. Millspaugh. 2007. *Development of landscape-level habitat suitability models for ten wildlife species in the Central Hardwoods Region*. U.S. Forest Service, Northern Research Station, General Technical Report NRS-4, Newtown Square, Pennsylvania, USA.

Roloff, G. J., and B. J. Kernohan. 1999. Evaluating reliability of habitat suitability index models. *Wildlife Society Bulletin* 27:973–985.

Roseberry, J. L., and W. D. Klimstra. 1984. *Population ecology of the bobwhite*. Southern Illinois University Press, Carbondale, Illinois, USA.

Roseberry, J. L., and S. D. Sudkamp. 1998. Assessing the suitability of landscapes for northern bobwhite. *Journal of Wildlife Management* 62:895–902.

Roseberry, J. L., and A. Woolf. 1998. Habitat-population density relationships for white-tailed deer in Illinois. *Wildlife Society Bulletin* 26:252–258.

Rotenberry, J. T., and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: A multivariate approach. *Ecology* 61:1228–1250.

Shifley, S. R., F. R. Thompson, III, W. D. Dijak, M. A. Larson, and J. J. Millspaugh. 2006. Simulated effects of forest management alternatives on landscape structure and habitat suitability in the Midwestern United States. *Forest Ecology and Management* 229:361–377.

St-Louis, V., A. M. Pidgeon, V. C. Radeloff, T. J. Hawbaker, and M. K. Clayton. 2006. High-resolution image texture as a predictor of bird species richness. *Remote Sensing of Environment* 105:299–312.

Stoddard, H. L. 1931. *The bobwhite quail: Its life history and management*. Charles Scribner's Sons, New York, New York, USA.

Tietje, W. D., and R. L. Ruff. 1983. Responses of black bears to oil development in Alberta. *Wildlife Society Bulletin* 11:99–112.

Tirpak, J. M., D. T. Jones-Farrand, F. R. Thompson, III, D. J. Twedt, M. D. Nelson, and W. B. Uihlein, III. 2008. Predicting bird habitat quality from a geospatial analysis of FIA data. Pages xx–xx *in* R. E. McRoberts, G. A. Reams, P. C. Van Duesen, and W. H. McWilliams, eds. *Proceedings of the 8th annual forest inventory and analysis symposium.* U.S. Forest Service, General Technical Report WO-xx, Newtown Square, Pennsylvania, USA.

Toms, J. D., and M. L. Lesperance. 2003. Piecewise regression: A tool for identifying ecological thresholds. *Ecology* 84:2034–2041.

Tuceryan, M., and A. K. Jain. 1998. Texture analysis. Pages 207–248 *in* C. H. Chen, L. F. Pau, and P. S. P. Wang, editors. *The handbook of pattern recognition and computer vision.* Second edition,. World Scientific Publishing, River Edge, New Jersey, USA.

U.S. Fish and Wildlife Service. 1980. *Habitat evaluation procedures (HEP).* U.S. Fish and Wildlife Service, Division Ecological Services, Manual 102, Washington, D.C., USA.

U.S. Fish and Wildlife Service. 1981. *Standards for development of habitat suitability index models for use in the habitat evaluation procedure.* U.S. Fish and Wildlife Service, Division Ecological Services, Manual 103, Washington, D.C., USA.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.

Van Kley, J. E., G. R. Parker, D. P. Franzmeier, and J. C. Randolph. 1994. *Field guide: Ecological classification of the Hoosier National Forest and surrounding areas of Indiana*. U.S. Department of Agriculture, Forest Service, Hoosier National Forest, Bedford, Indiana, USA.

Walker, P. A., and K. D. Cocks. 1991. HABITAT—A procedure for modeling a disjoint environmental envelope for a plant or animal species. *Global Ecology and Biogeography Letters* 1:108–118.

Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2001. *Analysis and management of animal populations*. Academic Press, San Diego, California, USA.