CHAPTER 11

Lessons Learned from Using GIS to Model Landscape-Level Wildlife Habitat

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Wildlife-habitat relationships models include spatially explicit models that “keep track of the exact locations of plants and animals” (Kareiva and Wennergren 1995:299) or “have a structure that specifies the location of each object of interest” (Dunning et al. 1995:4). Application of spatially explicit habitat models has been facilitated by readily available aerial and satellite imagery, global positioning systems (GPS), increasingly comprehensive field inventories, and geographic information systems (GIS) (O’Neil et al. 2005; Dijak and Rittenhouse, this volume; Fitzgerald et al., this volume). These tools, particularly GIS, are common in landscape-level habitat assessments (O’Neil et al. 2005), though their use is not without concern (Stoms et al. 1992, Corsi et al. 2000). Numerous GIS-based landscape-level habitat models have been published in the ecological literature, with most authors emphasizing habitat model construction and performance while ignoring how inherent limitations in GIS data, habitat classification schemes, or data processing assumptions may have influenced their findings. It is our goal to increase awareness of these issues when conducting large-scale wildlife-habitat assessments using GIS.

Models benefit wildlife-habitat relationships studies by offering a framework for integrating uncertainty and error and by identifying complex and sometimes obscure relationships (Anderson and Gutzwiller 2005). Model applications are common at all levels of resource decision making ranging from operational, site-specific evaluations to strategic, large-scale evaluations. Modeling wildlife habitat over this range of scales requires many assumptions about the relationships between wildlife population metrics and habitat occurrence, quality, and spatial distribution (Beutel et al. 1999). Standard modeling protocol is to (1) explicitly state all assumptions early in the process; (2) substantiate those assumptions with field data, published information, or expert opinion; (3) hypothesize the relationships among wildlife and their habitat; and (4) use the modeling framework to evaluate sensitivities and produce output.

One critical assumption underlying this protocol is that habitat is accurately characterized at ecologically relevant scales to the organism(s) of interest.

Projects involving the testing of spatially explicit wildlife-habitat models often emphasize wildlife model mechanics and outputs, with less consideration given to how GIS maps and associated attribute information interface with model performance. This is an erroneous approach to understanding model performance. The first question to ask and integrate into spatially explicit wildlife model evaluations is whether supporting GIS data provide an accurate representation of habitat. It is important to remember that GIS data are often derived from models having their own assumptions that influence how data should be interpreted and used. In many cases, wildlife-habitat modelers have little or no involvement in creating GIS data that support their projects and thus may not be aware of data-specific limitations.

The combined experience of the chapter authors as GIS data developers and users in support of wildlife-habitat modeling provides the basis for this chapter. In recounting some of our experiences, we hope to facilitate scientifically rigorous application of GIS to wildlife habitat assessments (also see Corsi et al. 2000 and Bissonette and Storch 2003). We divided our experiences and commentary into six general categories: (1) analysis structure; (2) data abundance; (3) vegetation change analyses; (4) classification systems; (5) spatial and temporal scale issues; and (6) technological considerations. These categories are not independent; rather they are often inseparable in GIS modeling projects. We also stress that our presentation should not be viewed as a complete treatise on GIS's role in characterizing wildlife habitat across landscapes. Textbooks have been written on individual components in our chapter, and the literature cited should help in identifying these sources. Instead, we offer our experiences to stimulate critical thinking during the process of conducting landscape-level habitat assessments using GIS. We suggest that wildlife modelers with GIS skills tend to have a good understanding of ecological issues, but few have a complete understanding of GIS technology and data limits and potential relationships to analysis and interpretation.

ANALYSIS STRUCTURE

At the core of all good wildlife-habitat analyses is a well-thought-out issue or problem statement and an analytical process to address it (Starfield 1997, Morrison et al. 1998:141, Corsi et al. 2000). If the issue statement is erroneous or incomplete, even the best analysis will be inadequate or potentially wrong (Hammond et al. 1999). We have witnessed firsthand how this basic tenet of good decision making and analysis can be compromised by data availability or use restrictions. In most situations, the issue or problem statement retains its integrity and the path to the "best" answer is altered. In extreme situations, even the issue or problem statement can change.

Consider the use of Forest Inventory and Analysis (FIA) plots in wildlife-habitat modeling. The FIA program is a collection of related surveys designed to focus on different aspects of America's forested ecosystems. A portion of this program includes a temporally continuous forest inventory based on a systematic grid of plots across the country. The exact locations of FIA plots are legally protected from the public (U.S. Forest Service 2005). This is not an uncommon practice, as numerous worldwide examples exist of governments restricting access to high-resolution "science-quality" data (Estes and Mooneyhan 1994). Individual landowners can acquire their FIA plot locations through the Forest Service because landscape-level habitat assessments often span multiple ownerships. However, use of geo-referenced FIA data is restricted to those with proprietary permission. Thus, the utility of FIA data is limited for wildlife modelers external to the Forest Service wishing to map habitats across large landscapes using algorithms that require geo-referenced point data (e.g., Frescino et al. 2001). One solution to this limitation has been to work with the Forest Service on using FIA data to attribute habitat classification schemes that hide or blur specific plot locations.

Linden (2006) recently used this approach to map habitat for Canada lynx (*Lynx canadensis*) across Michigan's Upper Peninsula. Linden initially proposed using a clustering algorithm (k-means; MacQueen 1967) that required geo-referenced inventory data for mapping forest structure. The k-means approach was selected as the best procedure for fulfilling project objectives because it generated a robust forest structure map based on attributes deemed important to lynx along with classification error estimates. However, to comply with the proprietary FIA data issues, Linden (2006) abandoned the k-means approach and instead, working with the Forest Service, associated FIA plots to strata in a preconceived classification. The preconceived classification was ecologically based but developed for uses other than lynx habitat assessments. Thus, although Linden identified a preferable method for mapping and attributing lynx habitat across Michigan's Upper Peninsula, this methodology was modified because of data use constraints. The effect of using this alternative methodology on lynx habitat assessment accuracy is unknown and, at the study area extent may be negligible. However, Linden's habitat assessment serves as an example of how certain scale(s) (in this case a less resolute classification system) can be forced onto projects by data use restrictions.

Recommendations

Wildlife-habitat modelers should cautiously adjust study designs or analyses in response to available data constraints. One must ensure that the original problem or issue statement can be addressed. A large part of framing appropriate analyses is developing a sound understanding of input data and the intended target scales (e.g., geographic scale, temporal scale, attribute detail). We have experienced situations in which tool or data availability determined how a modeling application proceeds, sometimes compromising the original question. Failure to understand the driving purpose for conducting an analysis can result in inapplicable results, wasted resources, wrong directions of applications, or a combination of these.

Part of developing a sound issue statement and project objectives is consideration of how scale and accuracy affect model outputs. These considerations tend to be ignored during project development stages, and modelers find their results are less useful or corrupted by these factors. We encourage modelers to identify their scalar needs (e.g., data grain, extent, positional accuracy, classification error) while formulating their project objectives. We are not necessarily advocating for explicit inclusion of scalar needs in the issue statement or project objectives. Rather, these needs should be used to evaluate the likelihood of fulfilling project expectations. An early understanding of scalar needs provides one metric for evaluating data set utility.

DATA ABUNDANCE

In the age of Internet data libraries, user-friendly software, desktop computers, and high-speed Internet access, data are abundant and readily available. Thorough data documentation is critical in all analysis situations, but many poorly documented data sets are publicly available, often used, and transferred among colleagues. The tendency for data users to manipulate GIS layers (e.g., change resolution, conduct reclassifications) and not document these manipulations exacerbates potential misuses. In general, data developers tend to provide complete documentation. However, that completeness often erodes as users modify data to fulfill their needs. Improvements in data documentation software (e.g., Earth Systems Research Institute's [ESRI's] metadata management tools) have helped alleviate some documentation issues, but we contend that the majority of GIS users fail to consistently document their data sets. Part of the scientific process associated with using GIS data includes understanding its correct use. Poor or incomplete data documentation hinders this process.

In some situations habitat modelers may simply be overwhelmed by data and be forced to rank the utility of those resources (O'Neil et al. 2005). When available, GIS metadata offer a source of information that can help identify pertinent GIS layers. Metadata are referred to as "data about data" and can be thought of as detailed data descriptions. Users should initially evaluate metadata for publication date, abstract, purpose, use constraints, and positional and attribute accuracy (e.g., significant figures of measurement) statements to ensure that the data are aligned with project objectives. In data selection situations in which metadata are lacking or a quantitative evaluation of available data is needed, we favor exploratory data analyses. Exploratory data analyses are designed to identify important GIS layers, where importance is defined by the layer's association with patterns of wildlife species occurrence, abundance, or habitat use. Numerous tools exist for conducting exploratory data analysis ranging from simple evaluation of statistical distributions and correlation matrices to more complex multivariate analyses (e.g., cluster analysis, factor analysis; Hirzel et al. 2002, Zaniewski et al. 2002, Engler et al. 2004, among others). Tools also are available for determining significance of GIS layers once they are selected including generalized linear models (e.g., Pereira and Itami 1991, Bian and West 1997, Mladenoff et al. 1999, Osborne et al. 2001, Luoto and Seppälä 2002, Brotons et al. 2004), GIS-based simulation (Wu, F., 2004; Wu, J., 2004), and others (see review in Guisan and Zimmerman 2000, Segurado and Araújo 2004).

Although there is often an abundance of data available to support wildlife-habitat modeling, it seems we seldom can find exactly what we need. This leads to another potential problem related to data abundance and the ease with which even novice GIS users can manipulate data. Spatial data are often provided in different data structures, formats, and resolutions (Garbrecht et al. 2001). Data processing and conversion into a consistent spatial reference system, format, and resolution are often needed for practical applications (Garbrecht et al. 2001). Also, because we rarely have exactly what we want, we often manipulate data to meet our needs. Simple GIS processes (such as “intersect”) that generate new combinations of polygons (a map data structure based on areas closed by lines) or rasters (a map data structure based on cells) from multiple input layers are commonly used. These combinations can result in data integrity degradation (e.g., formation of “sliver” polygons, unrealistic attribute combinations) and a divergence from the original metadata. We recognize the value of manipulating data to meet specific project needs; however in doing so users should check the resulting data layers for common errors. These include boundary mismatches (e.g., shorelines between two data sets may not match depending on water levels at the time of original mapping), polygons or patches below the minimum mapping unit, and unrealistic attribute combinations (e.g., a forest cover type that overlays a lake).

Recommendations

When considering data resources developed external to a project or by others, first and most importantly, one must seek out and read any metadata, supporting reports, or other detailed background information which helps in using the data correctly. Sometimes this assessment requires map displays of source information, and during this phase visualization tools can facilitate understanding (Ramsey and Strong 2000). One needs to pay close attention to issues of scale and accuracy that will influence the ability to make inferences on wildlife-habitat relationships. Failing to conduct this initial step is often the first mistake in a modeling project and will ultimately impact all other steps. When manipulating data, one needs to closely document analysis steps and incorporate processes and decisions into the resulting layer’s metadata (see the Federal Geographic Data Committee metadata standard as reviewed in O’Neil et al.

[2005] or the international standards reviewed by Moellering et al. [2005] for guidance on building or editing metadata). One must ensure that subsequent users of data and analyses can replicate the work. Data abundance offers the opportunity to explore multiple relationships and develop better modeling designs; however, we caution against the tendency to make models overly complex (Burnham and Anderson 1998).

VEGETATION CHANGE ANALYSES

Data limitations in modeling vegetation (or habitat) change over multiple time periods are frequently ignored. Vegetation change analyses often involve comparing GIS data derived from different sources and processes. Our general concern is that classification processes, resolution, and accuracy limitations of time series data are often ignored or downplayed in change analyses. This concern applies to any spatial time series but is perhaps most exemplified by analyses using presettlement vegetation.

It is not uncommon for modelers to rely on presettlement vegetation maps as a baseline for assessing habitat or cover type changes (e.g., Rodgers and Anderson 1979, Van Deelen et al. 1996, Cowell 1998, Radeloff et al. 1999, Farley et al. 2002, Pidgeon et al. 2005, Schulte et al. 2005). These analyses are extremely useful for understanding broad-scale changes in vegetation types and associated ecological processes (Manies and Mladenoff 2000, Delcourt and Delcourt 2006); however, presettlement data have several limitations that influence their utility and proper application (reviewed by Wang 2005). In our experience, modelers often embark on using presettlement data without fully understanding three important limitations related to scale, boundary inaccuracies, and underrepresentation of certain vegetation types.

Scale-Related Limitations

Although presettlement data are most appropriately used for broad-scale, regional assessments (Schulte and Mladenoff 2001, Manies and Mladenoff 2000, Delcourt and Delcourt 2006), the data are frequently used for finer scale change analyses. For example, simulation data from Michigan suggest that inference to scales <65 ha should be avoided when using presettlement vegetation maps derived from the General Land Office (GLO) survey (Delcourt and Delcourt 2006). This scale roughly corresponds to a quarter-section, one of the smallest scales at which GLO data were consistently collected. It is common practice to ignore this scale-related limitation when conducting change analyses between presettlement and current data. For example, a simple change analysis using GLO and more current (circa 2000) satellite-derived data from Michigan suggests a noticeable change in spatial distribution and patch sizes of aspen (*Populus* spp.) (Fig. 11-1). Often, the validity of an analysis like that presented in Fig. 11-1 is not questioned.

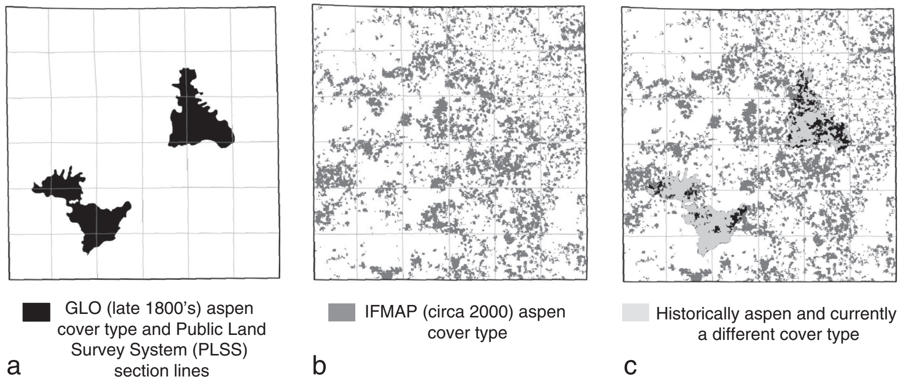


FIG. 11-1

Scale limitation of General Land Office (GLO) settlement data for conducting change analyses on aspen cover type in a northern lower peninsula of Michigan township, Michigan, USA. A) GLO aspen cover type; B) Michigan Department of Natural Resources (MDNR) Integrated Forest Monitoring Assessment and Prescription (IFMAP) aspen cover type for the same township; and C) a change analysis showing historic, current, and areas of overlap.

However, it is important to remember that GLO data were not collected in a manner that would have detected the numerous small aspen patches not intersecting section or quarter-section corners or section lines (Fig. 11-1). Some modelers have explored techniques for extracting finer scale information from the GLO, but these procedures have generally been viewed as qualitative and not easily reproducible (reviewed in Schulte and Mladenoff 2001). The coarse resolution of GLO data makes extrapolation to small-scale vegetation associations problematic except in cases of extremely homogenous vegetation (Cowell 1995).

There are also two issues related to GLO data temporal scale that are relevant to change analyses: survey timing and observed phenomenon age (Wang 2005). Although GLO data collection often spanned several decades (Haines and Sando 1969, Wang 2005), the data are generally accepted as a single ecological period of vegetation development (Brown 1998*b*, Schulte and Mladenoff 2001). GLO surveyors did not specifically record the age of observed events, but they did collect enough information to permit inference on disturbance frequencies and successional processes (reviewed by Wang 2005). For example, in Michigan a commonly used presettlement map is based on GLO survey records dating 1816 to 1856 (Comer et al. 1995). In vegetation change analyses, these 40 years are often viewed as a snapshot in time (e.g., Fig. 11-1). By today's standards of mapping vegetation dynamics, this would not be an acceptable practice, particularly for operational or tactical decision making.

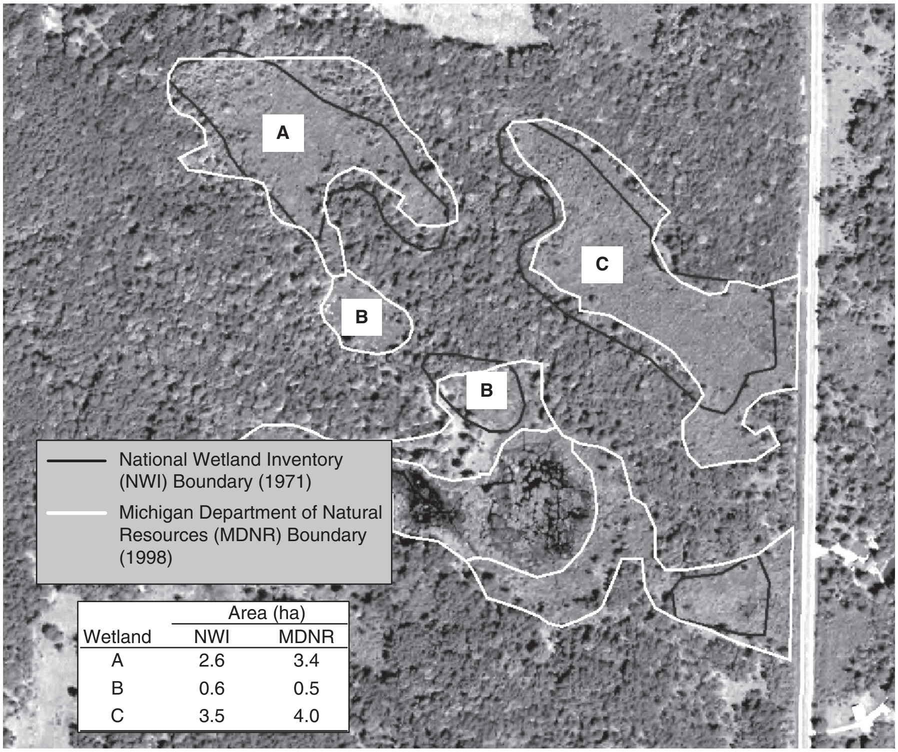
Recommendations.—When conducting vegetation change analyses, GIS users should restrict inference to the coarsest minimal map unit for their input data layers. In Michigan's case, presettlement data patches <65 ha in size are erroneously included in comparisons. A better representation of vegetation change could be derived by simulating GLO data collection processes and patch mapping algorithms on the current vegetation data layer. This would help standardize spatial scales.

We caution modelers conducting vegetation change analyses over multiple time periods to consider how mismatches in temporal scales among data sources may influence their results. For example, understand how vegetation community dynamics, particularly for short-lived communities, relate to the temporal scale of measurement. Consider the temporal scales of disturbance regimes and how disturbances may affect the ability to detect certain vegetation types. Vegetation change analyses are most appropriately conducted on data derived using the same sources (e.g., satellite sensor), techniques, and spatial and temporal scales.

Boundary Inaccuracy Limitation

Boundary mapping errors should be considered when evaluating changes in spatial extent or boundary locations among time periods. For example, Michigan's presettlement vegetation maps were derived from an ecologist's interpretation of GLO surveyor's notes along survey section lines (Public Land Survey System, PLSS). Boundaries between different vegetation types that occurred within section boundaries were interpolated using USGS 7.5 minute quadrangles and should be considered an approximation (Comer et al. 1995). Brown (1998*b*) suggested that presettlement boundaries are best portrayed as fuzzy, indicative of the vagueness associated with the mapping process. Additionally, Wang (2005) noted that many Public Land Survey Records (of which the GLO is a subset in the United States) contain three inherent positional accuracy issues: mislocation of corners, mislocation of landscape features, and incorrect positions of bearing trees. These inaccuracies reinforce the importance of using presettlement data for coarse-level assessments and not inferring an artificial sense of accuracy to the representations.

Boundary limitations are not unique to comparisons using GLO. We conducted a simple, visual inspection of wetland maps delineated by the Michigan Department of Natural Resources (MDNR; 2001) (based on 1998, 1:12,000 aerial photography) and National Wetlands Inventory (NWI) maps (based on 1971, 1:58,000 scale aerial photography) (Fig. 11-2). The MDNR wetland polygons were digitized by a photo interpreter. In contrast, the NWI maps for Michigan were transformed by hand onto 1:24,000 U.S. Geological Survey (USGS) quadrangles and then scanned to produce a digital form. Even though two significantly different processes were used to generate the wetlands maps, an uninformed user may simply compare the 1971 NWI and 1998 MDNR data to calculate the aerial extent of wetland change over that time period. For wetlands A and C in Fig. 11-2, that analysis would suggest 0.8 and 0.5 ha increases,



Wetland	Area (ha) NWI	Area (ha) MDNR
A	2.6	3.4
B	0.6	0.5
C	3.5	4.0

FIG. 11-2

Boundary delineations for National Wetlands Inventory (NWI) (1971) and Michigan Department of Natural Resources (MDNR) wetlands (1998) overlaid on National Aerial Imagery Program (NAIP); USDA (2000).

respectively. Although the areas of wetland B were similar (0.1 ha difference), note the apparent positional error between the data sources (Fig. 11-2). Boundary discrepancies occurred between the NWI and MDNR data, and from a simple comparison one might conclude that wetlands A and C are increasing in size and all wetland boundaries are dynamic. Is this a real ecological phenomenon or an artifact of boundary delineation processes? Without evaluating the metadata to understand differences in how boundaries were delineated between the two data sets, a modeler may incorrectly attribute the increase in wetland size as an ecologically significant event.

Recommendations.—Evaluate metadata to understand methods for boundary delineation. Quantify potential boundary delineation error among map sources and establish confidence in the boundary locations. Then, if the shifts in boundary locations fall outside confidence estimates, there is more reason to hypothesize that the differences are ecologically based.

Underrepresentation of Vegetation Types Limitation

The third limitation potentially influencing correct use of historical data for vegetation change analysis involves underrepresentation of vegetation communities that historically occurred as small patches (Barbour et al. 1999), such as aspen-birch (*Betula* spp.) and some wetlands in Michigan. Additionally, those vegetation types located on complex topography may not have been as thoroughly surveyed as other areas (Liegel 1982, Manies and Mladenoff 2000, Black and Abrams 2001). Biases in bearing tree selection in the GLO also influence its utility for portraying some vegetation types, but this bias can be somewhat alleviated by also including the section line notes (Wang 2005). Underrepresentation of certain vegetation types and GLO survey biases warrant caution when comparing the frequency and abundance of vegetation types between presettlement data and more recent cover type data acquired through air photo or satellite interpretation.

Recommendations.—It is important to question whether the cover type(s) of interest had similar detection probabilities between the different sampling approaches prior to drawing strong inference from a change analysis. If detection probabilities are unequal due to the scale of source data, then a data bias exists. Recognizing these limitations among data collected using different technologies and from different time periods will increase scientific rigor in conducting vegetation change analyses.

CLASSIFICATION SYSTEMS

Classification Language

Wildlife habitat models rely on a description of habitat. There are two general mapping models used to portray habitat in a GIS environment: (1) a patch-corridor-matrix model and (2) a continuum model. The patch-corridor-matrix model (Forman and Godran 1981, 1986) relies on our ability to denote “patches” of relatively homogenous communities, identify connecting “corridors” between those patches, and map the “matrix” that forms the background for patches and corridors (Forman and Godran 1981). The patch-corridor-matrix model is most commonly used in wildlife applications that can be portrayed in vector or raster data structures in the GIS. This type of discrete vegetation model has been recognized as inadequate where representations of spatial gradients or spatial patterns of boundary uncertainty are desired (Brown 1998*a*), but in terms of practical application, the patch-corridor-matrix model is preferred because it aligns with the ecological community concept and is easier to visualize on the ground. In contrast, the continuum model relies on the fact that gradients often exist among natural communities, and thus, definitive boundaries are difficult to accurately portray (e.g., Brown 1998*a*). The continuum model portrays communities on some continuous gradient (e.g., soil moisture, elevation) and most typically results in raster data structure (e.g., Zhu et al. 2001, Lehmann 2004). The use of continuum models is gaining popularity in wildlife-habitat relationships modeling as statistical techniques evolve, though their interpretation and application are often cumbersome to practitioners.

Patch-corridor-matrix GIS models are often based on some type of ecological classification system (see review in Grossman et al. 1999). A classification system relies on language that describes vegetation or habitat entities. Language resolution becomes an important determinant of predictive capability for any models that use the classification system. By necessity, most classification systems provide a limited vocabulary (or class names) to describe a landscape, and the amount of variability within a class can potentially be high (e.g., Roloff et al. 1994). In some situations we have observed premature rejection of habitat models based on "poor performance" without consideration of how the GIS classification system may have influenced the results. A better approach would be to denote that the model performed poorly in the data environment for which it was applied. A comparison of two systems currently used to support MDNR management decisions will help expose classification limitations of each system for modeling wildlife habitat.

Michigan Department of Natural Resources' (2001) Operations Inventory (OI) system for classifying cover types has a limited vocabulary of 26 class names. In contrast, MDNR's Integrated Forest Monitoring Assessment and Prescription (IFMAP) cover-type classification system is hierarchical and at the most resolute level has 137 classes. Both OI and IFMAP rely on remotely sensed imagery interpretation and ground data collection to produce cover type maps, but the decisions that lead to class assignments and polygon boundary locations differ between the two systems. Operations Inventory is based on a forester's interpretation of vegetation composition, structure, and site variables. It is also partially based on future management objectives, which can result in major differences in boundary delineation and class membership. Because OI is based on a qualitative process, it is sometimes difficult to establish the primary determinants of stand boundary location and class membership. Stand polygons in the IFMAP system were delineated based on patterns in aerial imagery. Ground verification was used to verify or edit those boundaries based on specific measurements of vegetation species composition. Class assignments were made using a computer algorithm that interprets these canopy measurements.

What are the ramifications of these classification processes to wildlife modelers using OI and IFMAP? Consider a modeler assessing habitat for a wildlife species that relies on aspen. Aspen communities in Michigan occur in two general forms: (1) as monotypic stands and (2) as associates in a variety of forest types. Aspen is represented in the OI system by a single class and in IFMAP by nine classes. If the modeler wants to identify relatively monotypic aspen stands as important patches for this species, he or she will need to determine which classes from OI and IFMAP are likely to represent this condition. Under the OI scenario, the modeler would likely be forced to accept the lone aspen class and ignore potential bias of management intent (i.e., the forester's perception) in class determination. Using IFMAP, the modeler could evaluate the decision rules associated with multiple aspen classes and determine which were appropriate. Selection of the "correct" data set to use relates back to how the analysis was framed. If the modeler requires quantifiable, repeatable spatial characteristics of aspen stands, then knowledge of the decision rules used for boundary determinations would be important and IFMAP would be preferred. If a modeler were to use OI to address this analysis, he or she may add additional uncertainty and nonrepeatability to habitat model results. Conversely, if the analysis calls for a general assessment of monotypic aspen acreage, the OI may suffice.

The importance of classification system resolution for conducting wildlife habitat assessments cannot be overstated. Results of wildlife-habitat relationships models can vary substantially depending solely on the classification system used (e.g., Lawler et al. 2004). Consider the habitat model results in Fig. 11-3. These results represent brown creeper (*Certhia americana*) habitat suitability, on a scale of 0 (nonhabitat) to 100 (optimal habitat), for a 390 km^2 landscape in central Idaho. Here, a brown creeper habitat suitability index model was applied using three commonly used ecological classification schemes: ecological land units (Haufler et al. 1996), structural stages (Johnson et al. 1994) within a Daubenmire plant series (sensu; Daubenmire 1952), and "alliances" in the National Vegetation Classification (Grossman et al. 1998).

Ecological land units provided the most resolute classification scheme, often used to describe and map combinations of vegetation successional stage and site potential in the context of major disturbance regimes (Haufler et al. 1996).

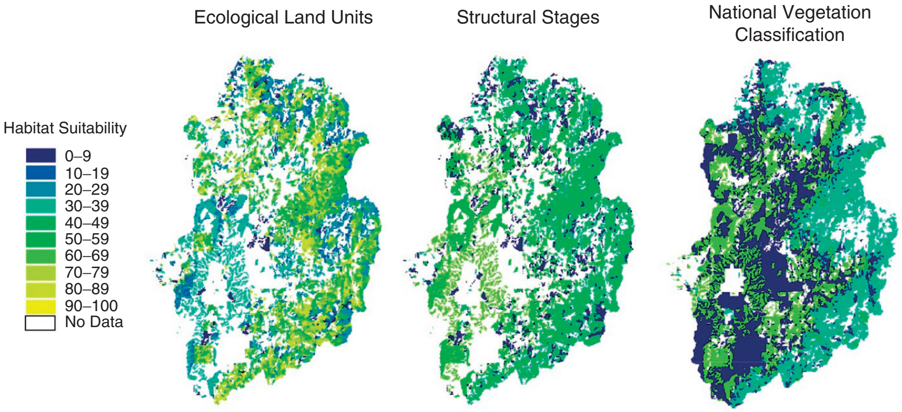


FIG. 11-3

Brown creeper habitat suitability scores on a scale of 0 (nonhabitat) to 100 (optimal) for three ecological classification systems: ecological land units (Haufler 1996), structural stages (Johnson et al. 1994) with Daubenmire plant series (sensu Daubenmire 1952), and the National Vegetation Classification (Grossman et al. 1998).

Structural stages provided an intermediate resolution that was based on percent canopy cover in five tree size classes (Johnson et al. 1994). The structural stage classification roughly corresponds to the mid-scale land classification used by the Interior Columbia River Basin Ecosystem Management Process (U.S. Forest Service 1996). The National Vegetation Classification uses both physiognomy and floristics to classify existing vegetation into "alliances" (Grossman et al. 1998). Alliances are roughly equivalent to the Society of American Forester's cover types (Eyre 1980) and were defined as physiognomically uniform groups of plant associations sharing one or more dominant or diagnostic species which are generally found in the upper-most stratum of vegetation (Grossman et al. 1998).

A detailed, geo-referenced vegetation inventory was available for the study area and these data were stratified according to each classification scheme. Average vegetation structure values required by the brown creeper model were calculated by stratum. The results of this analysis demonstrated that habitat model output can vary substantially depending on the classification scheme (Fig. 11-3). Depending on the classification system used, one could draw completely different inferences from the habitat model results. With ecological land units, the model suggests that a relatively broad range of habitat conditions are distributed across the landscape and higher quality patches of habitat are well dispersed (Fig. 11-3). With the National Vegetation Classification, the habitat model suggests that habitat quality is poor to marginal across the landscape, with virtually no high-quality patches (Fig. 11-3).

Recommendations.—Classification language and how map attributes are portrayed can significantly affect wildlife-habitat model output. It is not uncommon for practitioners to dismiss a perfectly good wildlife habitat model on the pretext that "it doesn't do a good job of mapping potential habitat" when in fact the issue resides with classification system resolution and variability. This often raises a dilemma for wildlife modelers. Should we use the model output and describe the sources of error and caveats for use (most typical strategy), should the habitat model be adjusted to accommodate the resolution and errors of available data (less typical strategy), or should new data be collected that directly meet the needs of the habitat assessment (least typical strategy)? Unfortunately, we often tend to ignore error descriptions and caveats associated with habitat maps because of project deadlines and budgetary constraints. Plus, something about a GIS "map" instills a sense of reality and faith in habitat model output. We caution modelers and users of GIS products to understand and convey data limitations to decision makers.

To help account for classification system effects on wildlife habitat model output, we advocate aligning scales of species habitat selection (which are multiscalar; Johnson 1980, Morris 1987) to classification resolution (also see Barry and Elith 2006). Rather than rely on a preconceived classification system and assume that specific vegetation structures are present, we support the recent trend of mapping individual structures as continuous inputs to habitat models

(Edwards et al. 2003, Holmström and Fransson 2003, Tuominen et al. 2003, Lu et al. 2004, Tuominen and Pekkarinen 2005). There are advantages to using continuous versus discrete GIS data in habitat modeling (Conner et al. 2003, Théau et al. 2005, but see Dussault et al. 2005), if the continuous data layers are derived from an adequate set of spatially explicit data. For example, it is a common practice to use geo-referenced sample points (e.g., FIA data) to interpolate continuous data surfaces. We caution that the utility of a continuous data layer depends on the number and distribution of sample points. Users of interpolated continuous data layers should understand the important scales of their project objectives and ensure that the density of supporting data support inference at the correct scale(s).

In regards to using continuous data surfaces in wildlife-habitat modeling, practitioners may argue that they still need to make management decisions based on stands or patches. We contend that stand boundaries that were most likely derived for some purpose (like resource management or planning) other than species habitat modeling can be overlaid on structure-based continuous habitat model output. The issue of classification language resolution is removed in a continuous map, but interpolation errors can be high if few data points are available. Our criticisms of class-based GIS maps should not be used to negate the utility of wildlife-habitat models that rely on this data type as they provide useful conservation information, especially at larger scales (Raphael and Marcot 1986, Edwards et al. 1996, Bolger et al. 1997, Karl et al. 2000, Pearlstine et al. 2002). We encourage modelers to evaluate both continuous and class-based GIS data and use the format that best fulfills their project objectives.

Attribute Variability

Attribute data portray what is known about a spatial location in the GIS. For example, a GIS data layer of vegetation patches may be attributed with vegetation cover type, percent canopy cover, plant species lists, plant structure, area of the patch, and a host of other attributes that explicitly describe an individual patch type. In most situations, attribute data represent field-collected observations, GPS point collections, or GIS-calculated information. In the case of field-collected information, the data contain sample errors. For GIS-calculated information, the data contain potential positional and classification errors. Variation in attribute data should not be ignored when conducting wildlife-habitat assessments using GIS. The concept of fuzzy logic (i.e., a system of logic dealing with the concept of partial truth with values ranging from completely true to completely false) has been incorporated into some habitat modeling efforts (e.g., Silvert 1997, Robinson 2003, Bojórquez-Tapia et al. 2004, Zhang et al. 2004, Cheung et al. 2005) to help account for GIS data uncertainties. Here we focus on GIS attribute data variability as it relates to potential effects on wildlife modeling.

As demonstrated in the analysis conducted to produce Fig. 11-3, habitat elements are often portrayed using map stratum averages. Within-stratum variability is frequently ignored in wildlife-habitat modeling (Roloff and Kernohan 1999), even though it can have significant effects on model interpretation (e.g., Verbyla and Litvaitis 1989, Bender et al. 1996, Hess and Bay 2004). Linden (2006) examined the effects of simulating within-stratum variability in habitat attributes for an ecological land classification as an alternative to using stratum averages. Frequency distributions of habitat characteristics were estimated from field surveys for each stratum and linked to the occurrence of cell values in a GIS raster. The spatial distribution of cell values within each stratum was randomized through multiple iterations, and habitat quality for Canada lynx and snowshoe hare (*Lepus americanus*) was examined. This evaluation indicated a significant effect on modeled habitat quality for those strata with high attribute variability. In these highly variable strata, habitat quality would have been inaccurately portrayed by the use of averages. Linden (2006) noted that as the scale of analysis increased, differences in habitat quality decreased. This observation is consistent with known relationships on how variance responds to changes in map extent, with larger areas tending to dampen the variance extremes (Stoms 1994, Wolock and Price 1994, Wu, F., 2004; Wu, J., 2004). Linden (2006) concluded that the decision to explicitly include attribute variability in a habitat modeling project depends on map data resolution and how it relates to the scale at which focal organisms perceive their habitats and the spatial extent of the landscape. In Linden's example, raster cell variability between iterated maps was less important for Canada lynx than for snowshoe hare because the scales of modeled habitat selection behavior (i.e., the probability that habitat would support a home range) substantially differed between the species. In other words, habitat suitability for snowshoe hare home ranges was modeled as more sensitive to the habitat structure of an individual patch compared to lynx, which was modeled as less sensitive to individual patches. Linden's analysis demonstrates the importance of understanding the effects of scale and attribute variability on habitat model output.

Recommendations.—Attribute error should be incorporated into habitat models. Recent advances in resampling statistics (Manly 1997, Simon 1997) and computing capabilities have offered mechanisms for bounding habitat model outputs with confidence estimates, but computer processing time across large landscapes still prohibits incorporation of these tools into many projects. It is important not to confuse this source of habitat model error with that portrayed by some quantitative modeling procedures. In quantitative models, the error estimates represent a composite of system errors (e.g., error in animal location and perhaps the variation in land classification system, particularly if the continuum GIS data model is used). A quantitative model derived from GIS layers based on stratum averages (e.g., a cover type map with average tree densities per class) does not account for within-stratum variability in model error estimates. As Bender et al. (1996) demonstrated, ignoring this source of error in wildlife-habitat relationships modeling can lead to erroneous conclusions.

SPATIAL AND TEMPORAL SCALE ISSUES

Correct determination of the appropriate scale is the cornerstone of habitat analysis and model development (Morrison et al. 1998:141, Morrison 2002). Here, we offer advice on some common spatial scale issues that we have encountered in our habitat modeling efforts. Readers should refer to Turner et al. (1989), Wiens (1989), Levin (1992), and Hunsaker et al. (2001) for more complete treatises of this topic.

Spatial Scale Considerations

There are at least four meanings of spatial scale in remote sensing and GIS (partially taken from Cao and Lam [1997], also see Morrison et al. [1998:241]):

1. *Cartographic (or map) scale:* the relationship (proportion) of map distance to ground distance (e.g., 1 cm on the map = 1 km on the ground);
2. *Geographic (or observational) scale:* the size or spatial extent of a study;
3. *Operational scale:* the geographic extent at which certain processes operate within the environment. This could be the scale associated with nutrient-cycling in a wetland;
4. *Measurement scale:* the smallest distinguishable part of an object. Examples include the cell size in a remotely sensed image or the sampling interval in an ecological study.

In wildlife-habitat modeling, most explicit references to scale use the second (geographic or observational) or third (operational) meanings of the term. The phenomena of interest in most ecological studies are observed at operational scale (s). One of the basic challenges in using GIS data to model wildlife habitats across landscapes is to understand how observations at the operational scale(s) are influenced by observational and measurement scales.

Observational Scale.—It is not uncommon for significant ecological information to be lost or compromised because habitat modelers are forced to use data from some arbitrarily determined study area boundary (Johnson 1980, Porter and Church 1987, Morrison 2002). Other authors have documented the importance of identifying an appropriately scaled study area (Brennan et al. 2002, Morrison 2002), especially in the context of resource selection studies (e.g., Aebischer et al. 1993, Erickson et al. 2001). The recommended approach is to ensure that phenomena measured at operational scales can be fully encompassed by the observational scale (i.e., the study area boundary; Brennan et al. 2002). Morrison (2002) concluded that study area size and its relationship to wildlife population data and how the location of a study area fits the geographic range of species are seldom studied or incorporated into analyses. Unfortunately, the scale(s) at which ecological processes operate may not become evident until data are collected. This was the case in Roloff et al. (2001) in which radio-collared elk (*Cervus elaphus*) were used to test the reliability of a habitat potential model. Detailed habitat maps were generated for the study area, which was defined by the boundary of Custer State Park, South Dakota. All radio-tagged elk were located within the study area boundary, but one sub-herd tended to seasonally use habitats outside this area. As a result, Roloff et al. (2001) needed to censor that sub-herd from the habitat model evaluation. Fortunately, some of the sub-herds that were radio-tagged used habitats entirely within the study boundary, so the analysis could still occur; however, sample size was reduced because of a study boundary constraint. This example illustrates the significance that observational scale can have on wildlife habitat modeling results.

Measurement Scale.—Different measurement scales are inherent in either vector or raster GIS data structures. The usefulness of each data format for characterizing habitat and landscape patterns has been presented elsewhere (e.g., Johnson 1990, Haines-Young et al. 1994, Corsi et al. 2000, Wade et al. 2003). The best scenario for deciding which type of data to use in a GIS habitat modeling project is to properly frame the analysis and select the data format that best fulfills project objectives. As noted previously, that process often breaks down in that modelers are often forced into using whatever data are available to generate a product within time and budgetary constraints. Though conversions between GIS data structures are available, the processing artifacts can have significant impacts on habitat model output.

The most basic example of how measurement scale in vector and raster GIS data can influence habitat model output is in the simple calculation of patch area and edge. Consider the example in Fig. 11-4. Here, the same land cover data

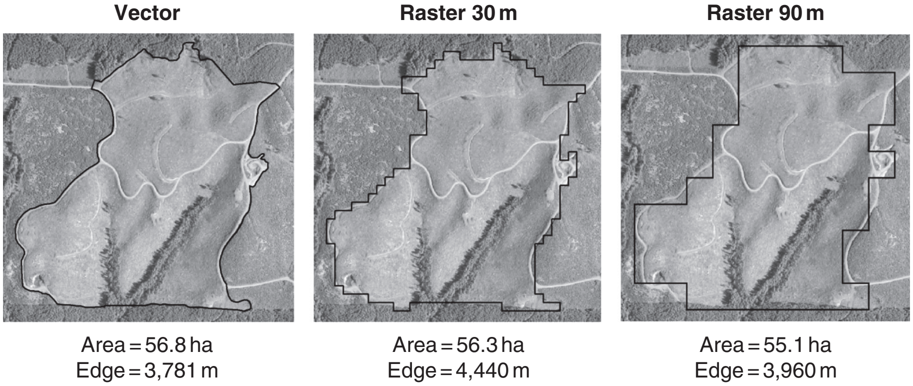


FIG. 11-4

Vector and raster representations with area and edge GIS measurements of a forested stand in Washington, USA. Background photography from the National Agriculture Imagery Program (NAIP), USDA.

for a forested stand in Washington are portrayed in vector and raster formats. These data represent typical stand boundaries used in resource management and planning. The vector data were developed using on-screen digitizing with National Agriculture Imagery Program (NAIP) as the background. The raster data represent the same vector polygon at 30 m and 90 m cell resolution. Area estimates differ depending on data structure and resolution. Edge measurements differed substantially (by almost 700 m between the extremes) depending on the data type. Which representation of the stand in Fig. 11-4 is the best? We argue that the vector-based representation is the most accurate in this case because the layer was generated directly from the air photo and because this stand had relatively hard edges (i.e., a continuous line was a good representation of the real boundary). In wildlife-habitat assessments that evaluate edge effects based on linear edge distances or boundaries between patch types, raster-based data appear to overestimate the absolute amount of edge. This data artifact is of concern only if the absolute value is important in a habitat model, i.e., relative evaluation of edge distances help alleviate this bias among data types.

An additional cautionary note on using raster data structure in wildlife habitat modeling projects warrants mention here. It is generally well accepted that square cells in rasters may not meaningfully represent space for animals (Tischendorf 1997). Tischendorf's (1997) argument is that animal movement analyses are constrained by the resolution of square cells and the fact that a diagonal movement is longer than a perpendicular movement. Thus, vector-based animal movement data can only be portrayed as a "jump" from cell to cell, and the distance of those jumps can vary. Solutions to this problem have included using a raster with cells of different sizes (Tischendorf 1997), resampling GIS data to a small resolution relative to animal movement distances, and portraying raster GIS data as hexagon-shaped cells (the idea being that a hexagon most closely resembles the least biased geometric shape, a circle, that can be portrayed in a nonoverlapping arrangement) (e.g., Schumaker 1996, Lawler and Schumaker 2004, Lawler et al. 2004, Jackson et al. 2005, Fernández et al. 2006). All these solutions have potential problems, particularly with data management, simulation times, and loss of descriptive capabilities as resolution is compromised (Gough and Rushton 2000, Hunsaker et al. 1994).

The advantages of using hexagonal shapes to describe landscapes and allocate sample plots were noted by McCollum and Cochran (2003) in their description of the previously described FIA program as (1) spatial compactness; (2) uniform spatial coverage; (3) flexibility for altering grid density; (4) reduced likelihood of correspondence to anthropogenic landscape components; and (5) reduced variance estimates in comparison to a random sample. Despite these advantages, the most common technique for characterizing landscapes in current wildlife and ecological literature is to use rasters with square cells, most likely because that geometry corresponds to how most remotely sensed GIS data are collected and made available, and the structure is amenable to common GIS software. We caution habitat modelers to at least question whether square cell biases may significantly alter their study designs or inference space prior to project implementation.

Regardless of whether raster or vector data structures are used in a habitat modeling project, one of the most important influences on habitat model interpretation is minimum mapping unit or map grain (which often corresponds to measurement scale as described previously). Minimum map unit is defined as the smallest size aerial entity to be mapped as a discrete entity (Saura 2002). It is well known that in heterogeneous landscapes between-patch variance decreases as resolution decreases (i.e., as minimum mapping unit or grain size increases, between-patch differences tend to decrease; Turner et al. 1989, Wu, F., 2004; Wu, J., 2004). In other words, coarser resolutions tend to homogenize landscapes into the dominant patch types (Saura 2002). It follows that map accuracy tends to increase as minimum map unit increases (Knight and Lunetta 2003). Sensitivity of most landscape-level data to minimum map unit further exemplifies the importance of understanding minimum map unit or measurement scale in the context of processes being modeled (i.e., operational scales) for the study area (i.e., observational scale). This same concept applies to selecting a sample plot or quadrat size. It is not uncommon for researchers to arbitrarily select a plot size without considering variation in the underlying vegetation. In some situations the natural variation in vegetation patches may provide more reliable sampling units than arbitrarily chosen plot sizes (Bowyer et al. 1996, Stohlgren et al. 1997).

Temporal Scale Considerations

Issues surrounding the effects of temporal scale on wildlife-habitat relationships modeling are equally as important as spatial scale issues but have received less attention (Morrison 2002, Chapter 14). Temporal scales can categorically be viewed similar to spatial scales, with observational temporal scale referring to the duration of the study, operational temporal scale referring to the time that certain processes operate in the environment, and measurement temporal scale referring to the smallest unit of time for which we have a measurement. With the advent of technologies for making historical map and tabular data spatially explicit, more researchers and modelers are conducting time series comparisons of habitat change.

Wildlife researchers recognize the importance of temporal variation in wildlife populations, and most try to account for this phenomenon by collecting data over multiple years or seasons. In wildlife-habitat relationships studies, less attention is given to short-term temporal variation of habitat elements, unless the wildlife response variable is explicitly linked to a habitat element known to exhibit frequent changes (e.g., Boyd 1996, Whitehead 1996, Fortin et al. 2002, McCarty et al. 2002). One standard approach used in wildlife studies is to collect population data for 2–4 years, develop a habitat GIS layer that reasonably corresponds to the time period of population data collection, and then assume that habitat remains static. Most researchers track the occurrence of major habitat altering events during their studies, but few incorporate the subtle effects of short-term fluctuations in habitat elements (e.g., vegetation reproductive status, growth, mortality, and successional processes).

We caution that habitat model components be evaluated for their sensitivity to short-term variations. For example, some of the authors (G. Roloff and D. Linden) recently completed a habitat modeling project for Canada lynx in which outputs from the model were used to influence a 5-year forest management plan. We used a standard approach for depicting habitat (see Linden 2006, Appendix D, for a description of the process used to estimate attributes for the lynx model). Because the lynx model relied on vegetation cover provided by tree branches and boles, we were concerned that 5 years of vegetation succession may have a significant influence on model results that would go undetected if we simply assumed no major vegetation changes. We tested this potential effect by simulating vegetation changes for 10 common vegetation types in the landscape using a well-established tree growth and yield model. According to the growth and yield model and Linden's (2006) method of calculating understory cover, horizontal cover differences within a stand varied from –7% to 7% over the 5-year period (Table 11-1). At first glance this change seems negligible relative to how lynx may use habitats; however, the magnitude and direction of change must be viewed in the context of how the habitat model uses the information. Our lynx project used a habitat suitability index model that was based on linear relationships with definitive thresholds. If the ±7% applied to a stand with vegetation conditions close to a critical threshold, habitat model output could be significantly affected. This example illustrates the importance of considering short-term vegetation changes in wildlife-habitat relationships modeling.

Recommendations.—Spatial scale considerations are one of the most important in characterizing and analyzing wildlife habitat for landscapes. A basic challenge faced by all wildlife-habitat modelers that use GIS is to understand how their characterization of operational processes is influenced by observational and measurement scales. We stress the importance of understanding your project objectives in the context of observational and measurement scales. Consider how GIS data formats can influence your modeling work. Make sure that data format (i.e., vector or raster) does not introduce hidden biases into your descriptions of operational processes. Minimum map unit is a critical consideration for habitat modeling projects. Modelers should ensure that operational processes are occurring at scales $\geq$ minimum map unit. If this is not the case, make sure that assumptions used to infer smaller scale habitat characteristics to map units are sound and accurately portray habitat dynamics in the landscape. Subtle temporal variations in habitat elements are often ignored in modeling projects, and we caution that these changes can influence habitat model output. We reiterate the recommendation of previous authors (Corsi et al. 2000, Maurer 2002, Morrison 2002) on the importance of evaluating research designs or habitat modeling projects in the context of influential spatial and temporal scales.

Table 11-1 Horizontal Cover Values in Three Height Strata Over a 5-Year Period as Modeled for a Canada Lynx Habitat Suitability Index Model to Demonstrate the Potential Effects of Short-Scale Temporal Changes Caused by Vegetation Succession on Habitat Model Output

	Horizontal Cover (%) Year 0			Horizontal Cover (%) Year 5			Horizontal Cover (%) Difference Between Years 0 and 5		
	Height Strata			Height Strata			Height Strata		
Stand	**0–0.99 m**	**1–1.99 m**	**2–2.99 m**	**0–0.99 m**	**1–1.99 m**	**2–2.99 m**	**0–0.99 m**	**1–1.99 m**	**2–2.99 m**
1	27	21	22	23	28	24	−4	7	2
2	26	37	31	25	38	38	−1	1	7
3	32	42	46	33	39	49	1	−3	3
4	19	23	31	19	25	29	0	2	−2
5	28	32	43	30	31	40	2	−1	−3
6	16	27	24	15	30	30	−1	3	6
7	41	71	66	39	64	69	−2	−7	3
8	19	25	28	19	25	30	0	0	2
9	45	60	69	45	56	66	0	−4	−3
10	18	23	31	20	25	29	2	2	−2

The influence of these scales on wildlife populations is inseparable, and we recommend evaluating the organization of your wildlife modeling project with this in mind (see Corsi et al. 2000; Fig. 11-3 for a useful conceptual model). Consistent with other authors, we recommend conducting habitat assessments at multiple scales (at least one scale above and below the process of interest) to ensure that the operational processes are being characterized appropriately (Orians and Wittenberger 1991, Wu and Loucks 1995, Bowyer et al. 1996, Jelinski and Wu 1996, Qi and Wu 1996, Bennetts and Kitchens 1997, Maurer 2002, Morrison 2002).

TECHNOLOGICAL CONSIDERATIONS

Another important consideration when using GIS to model wildlife habitat relates to the technology used for deriving land classification systems. Consider the common practice of automatically classifying satellite imagery to portray landscapes (e.g., Osborne et al. 2001, Betts et al. 2003, Kerr and Ostrovsky 2003, Jeganathan et al. 2004). We will focus our discussion on two principal sources of error in the process of creating a classified landscape from satellite imagery (also see O'Neil et al. 2005:433–443). The first source of error, which we will call "mixed-pixel error," is associated with image acquisition and spectral response (the range of light reflected by an object and detected by a sensor) on the Instantaneous Field of View (IFOV). The IFOV is the scan spot size or instantaneous geographic coverage of a satellite sensor. The area of the IFOV varies depending on the satellite sensor and most commonly ranges from 1 m^2 to 1 km^2. For example, the IFOV for Landsat Thematic Mapper sensor (one type of satellite sensor that produces data commonly used in characterizing landscapes) is collected at 30 m × 30 m (0.09 ha) resolution. Within that area, spectral response is integrated for all objects into a single cell value ranging from 0–255. If an IFOV is composed of a single, homogenous object on the ground (e.g., a slab of concrete), then the remote sensing analyst can be confident that the recorded cell value is associated with concrete. However, large IFOVs are rarely composed of a single, homogenous object, even in simplified ecosystems. Larger IFOVs are composed of multiple objects such as tree canopies of different species, ground cover between trees, water, or manmade structures. The ability to consistently associate a cell value with objects of interest on the ground is confounded by integration of spectral response from multiple objects over the entire area of the IFOV. In some situations mixed-pixel error may have negligible effects on habitat interpretations (e.g., Wickham and Riitters 1995). Nonetheless, it is important for the wildlife modeler to consider how habitat elements of interest relate to the size of an IFOV's integrated measure of spectral response. Habitat elements that are significantly smaller than an IFOV, and therefore "mixed" with many objects not of interest, will be much harder to accurately map from satellite imagery than those that are significantly larger than the IFOV.

We experienced the effect of IFOV in working with the data for Michigan's Gap Analysis Program (GAP; Donovan et al. 2004). Michigan's GAP project relied on a cover type map derived from 30 m Landsat Thematic Mapper imagery. For those wildlife species that required specialized habitat elements (e.g., snags, rock outcroppings, vernal ponds), "mixed-pixel error" was accounted for by assuming that these features are consistently associated with specific cover types (Donovan et al. 2004). This adjustment, along with other error accumulated in the GAP process (Dean et al. 1997, Laba et al. 2002), results in commission (i.e., erroneously designating an entity something it is not) and omission errors (i.e., erroneously not designating something it truly is), with a tendency for higher commission errors. These sources of error tend to diminish at larger scales consistent with the intended use of GAP products for regional-level conservation assessments (Edwards et al. 1996). The importance of accounting for these errors in conservation decision making cannot be lost because those wildlife species with specialized habitat requirements frequently are those in greatest conservation need (Short and Hestbeck 1995).

Another source of error in classifying a landscape from satellite data that affects wildlife habitat modeling in GIS relates to "mixed-pixel error" and the level of detail (or number of classes) desired in the final classification system. We will refer to this error as "spectral-distance error." A remote sensing analyst generally embarks on a mapping project with a predefined classification system or some idea as to what constitutes a class in the final map. In satellite image interpretation, the only information available to the analyst is the measure of spectral response in the IFOV over multiple wavelength bands provided by the sensor. For example, Landsat Thematic Mapper has seven wavelength bands available for transformation into map classes. The process for classifying imagery usually involves plotting the spectral response of different vegetation classes in multidimensional spectral space with the hope that identifiable and clearly separable clusters are present. This is rarely the case; usually there are multiple classes of interest that intersect or cluster very near each other (Fig. 11-5). The closer classes are in spectral space, the more they will be confused with each other in the classification process (Fig. 11-5). This level of confusion constitutes "spectral-distance error."

Both "mixed-pixel error" and "spectral-distance error" can have substantial effects on the inference drawn from landscape-level wildlife habitat models. For those classification processes that include accuracy assessments, these sources of error are typically portrayed in classification error matrices, though these matrices also contain other error sources (Congalton and Green 1993, Stehman 1997, Congalton and Green 1999, McGwire and Fisher 2001). Nonetheless, classification error matrices should be consulted prior to using GIS layers for habitat modeling to ensure that data classes required by the habitat model can be portrayed with acceptable accuracy levels. Also, habitat modelers should ensure that the classification error matrix contains data from all ecologically significant portions of their assessment landscape. Without well-dispersed classification

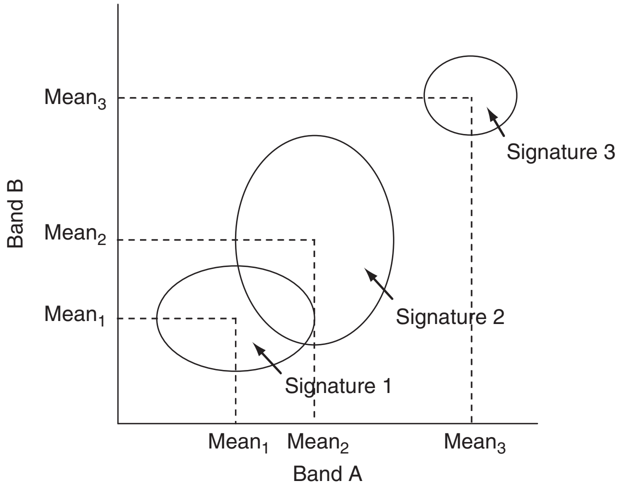


FIG. 11-5

Spectral-distance error and its effect on classification accuracy (based on ERDAS 1982). Means correspond to multidimensional means in spectral space and correspond to average classification values (i.e., the values used to map classes).

test data, important nuances in the classification process or the classification system may be overlooked. For example, one of the co-authors (M. Donovan) recently completed a project that used a wildlife-habitat relationships model to estimate statewide sharp-tailed grouse (*Tympanuchus phasianellus*) habitat potential in Michigan (Fig. 11-6). Landsat derived cover types were used in the model, and a good understanding of classification error was based on dispersed training plots throughout the state (Space Imaging Solutions 2001). The model identified several potential areas for sharp-tailed grouse habitat management and restoration. In the Upper Peninsula the predicted habitats corresponded well to known grouse locations. However, the model also predicted substantial habitat potential in the thumb of the Lower Peninsula. This area was visited by field biologists, and they concluded that although the vegetation was typed correctly, habitat potential for sharp-tailed grouse was low because of current land management practices. In this example, classification accuracy for cover types important to sharp-tailed grouse was high, but the classification scheme lacked an important component of habitat: current land management status. Without field visits by biologists to Michigan's thumb area, potential sharp-tailed grouse habitat would have been significantly overpredicted. This example also points to the utility of using predictive models even if classification data or schemes are less than perfect. Here, the model helped direct field biologists to a specific area in a large landscape.

There is a common misconception among wildlife-habitat modelers that high resolution is always better. This is not always the case. Often, modelers focus on

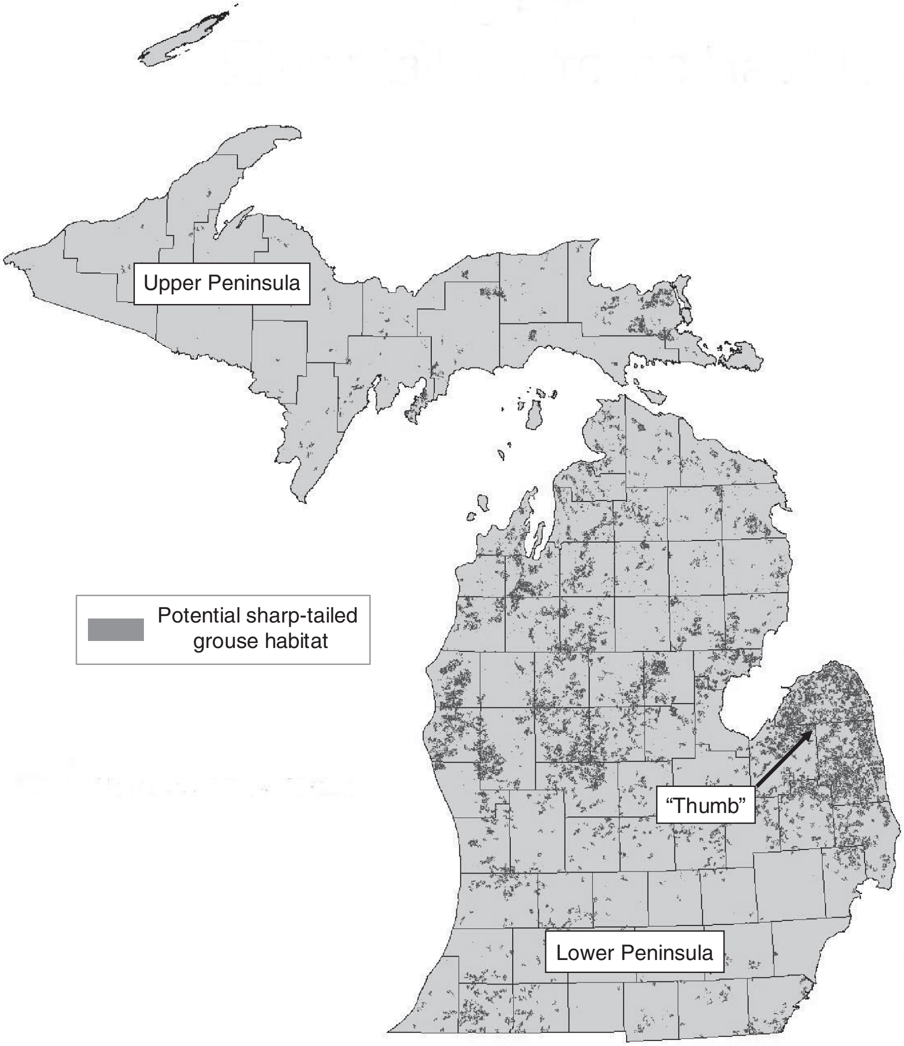


FIG. 11-6

Potential sharp-tailed grouse habitat in Michigan, USA, as estimated by a wildlife-habitat relationships model.

spatial resolution as the primary determinant of data utility, but spectral contrast of habitats in relation to their surroundings is also an important consideration. Trade-offs between spatial and spectral resolutions of data should be evaluated in the context of importance to the modeling effort. This decision depends on habitat element size, with higher spatial resolution not necessary for coarser habitat elements (e.g., mature tree canopies). For coarse habitat elements, it may prove more advantageous to favor higher spectral resolution. Most modelers have a limited choice in available imagery and thus may not spend much time in evaluating spatial and spectral resolution trade-offs.

Recommendations

We cannot overstress the importance of evaluating the classification error matrix as a means to understand how "mixed-pixel" and "spectral-distance" errors can potentially influence habitat model results (see Foody 2002). Conducting error simulations (e.g., Fleming et al. 2004, Hines et al. 2005) holds great promise for understanding not only class errors but also spatial location errors when using satellite imagery. Remember that classification accuracy errors compound as data layers are overlaid in a GIS, and care should be exercised when conducting operations that modify polygons or combine raster cells. Always incorporate known errors into metadata descriptions and in caveats on how habitat model results should be used. Avoid the misconception that higher resolution data are always better. There is a trade-off between spatial and spectral resolution, and the best approach is to align data resolution with the project objectives.

SUMMARY

Habitat maps generated by a GIS are often viewed by decision makers and the general public as absolute truth regardless of accuracy assessments, summaries of data use limitations, or spatial and temporal scale considerations. We caution wildlife-habitat relationships modelers to consider how the inherent properties of data sets and uncertainty from all these sources should be included and portrayed in their analyses. Texts have been devoted specifically to some of these topics such as accuracy assessments (Goodchild and Gopal 1989, Congalton and Green 1999, Lowell and Jaton 1999), spatial and temporal scale considerations (Bissonette 1997, Waring and Running 1998), and integrating uncertainty into GIS analyses (Chiles and Delfiner 1999, Mowrer and Congalton 2000, Hunsaker et al. 2001), and our intention was not to repeat that information. Rather, we offered some of our experiences in using GIS to model habitats at landscape levels as a means of drawing attention to commonly overlooked issues with data analysis and interpretation.

Successful development and implementation of wildlife models over large landscapes is a complex endeavor. The process often involves using landscape-level data derived from a variety of technologies and by analysts not necessarily associated with the wildlife modeling project. GIS software has empowered analysts and modelers to rapidly manipulate data, sometimes at the expense of evaluating data and processing limitations. During our experience in diverse GIS applications and projects, we have repeatedly witnessed poor planning or processing methodologies resulting in extra work to correct problems found in the results. In our opinion, a small amount of time spent understanding the data, the planned analysis, the limitations of both, and project needs will facilitate completion of project goals. We echo the sentiments of O'Neil et al. (2005) who noted that spatial technologies are only as accurate and reliable as the underlying data. Spatial tools alone cannot improve accuracy, precision, and bias of information. It is our hope that by sharing our experiences using GIS for landscape-level wildlife habitat modeling, we encouraged critical thinking about establishing project objectives, data limitations and structures, and issues of temporal and spatial scale.

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LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.

Anderson, S. H., and K. J. Gutzwiller. 2005. Wildlife habitat evaluation. Pages 489–502 *in* C. E. Braun, editor. *Techniques for wildlife investigations and management.* The Wildlife Society, Bethesda, Maryland, USA.

Barbour, M. G., J. H. Burk, W. D. Pitts, F. S. Gilliam, and M. W. Schwartz. 1999. *Terrestrial plant ecology.* Third edition. Addison Wesley Longman, Menlo Park, California, USA.

Barry, S., and J. Elith. 2006. Error and uncertainty in habitat models. *Journal of Applied Ecology* 43:413–423.

Bender, L. C., G. J. Roloff, and J. B. Haufler. 1996. Evaluating confidence intervals for habitat suitability models. *Wildlife Society Bulletin* 24:347–352.

Bennetts, R. E., and W. M. Kitchens. 1997. Population dynamics and conservation of snail kites in Florida: The importance of spatial and temporal scale. *Colonial Waterbirds* 20:324–329.

Betts, M. G., S. E. Franklin, and R. G. Taylor. 2003. Interpretation of landscape pattern and habitat change for local indicator species using satellite imagery and geographic information system data in New Brunswick, Canada. *Canadian Journal of Forest Research* 33:1821–1831.

Beutel, T. S., R. J. S. Beeton, and G. S. Baxter. 1999. Building better wildlife-habitat models. *Ecography* 22:219–223.

Bian, L., and E. West. 1997. GIS modeling of elk calving habitat in a prairie environment with statistics. *Photogrammetric Engineering and Remote Sensing* 63:161–167.

Bissonette, J. A. 1997. *Wildlife and landscape ecology: Effects of pattern and scale*. Springer-Verlag, New York, New York, USA.

Bissonette, J. A., and I. Storch. 2003. *Landscape ecology and resource management: Linking theory with practice*. Island Press, Washington, D.C., USA.

Black, B. A., and M. D. Abrams. 2001. Analysis of temporal variation and species-site relationships of witness tree data in southeastern Pennsylvania. *Canadian Journal of Forest Research* 31:419–429.

Bojórquez-Tapia, L. A., L. Juárez, and G. Cruz-Bello. 2002. Integrating fuzzy logic, optimization, and GIS for ecological impact assessments. *Environmental Management* 30:418–433.

Bolger, D. T., T. A. Scott, and J. T. Rotenberry. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. *Conservation Biology* 11:406–421.

Bowyer, R. T., J. G. Kie, and V. Van Ballenberghe. 1996. Sexual segregation in black-tailed deer: Effects of scale. *Journal of Wildlife Management* 60:10–17.

Boyd, I. L. 1996. Temporal scales of foraging in a marine predator. *Ecology* 77:426–434.

Brennan, J. M., D. J. Bender, T. A. Conteras, and L. Fahrig. 2002. Focal patch landscape studies for wildlife management: Optimizing sampling effort across scales. Pages 68–91 *in* J. Liu and W. W. Taylor, editors. *Integrating landscape ecology into natural resource management.* Cambridge University Press, Cambridge, United Kingdom.

Brotons, L., W. Thuiller, M. B. Araújo, and A. H. Hirzel. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* 27:437–448.

Brown, D.G 1998*a*. Classification and boundary vagueness in mapping presettlement forest types. *International Journal of Geographical Information Science* 12:105–129.

Brown, D.G 1998*b*. Mapping historical forest types in Baraga County Michigan, USA as fuzzy sets. *Plant Ecology* 134:97–111.

Burnham, K. P., and D. R. Anderson. 1998. *Model selection and inference: A practical information-theoretic approach*. Springer-Verlag, New York, New York, USA.

Cao, C., and N. S.-N. Lam. 1997. Understanding the scale and resolution effects in remote sensing and GIS. Pages 57–72 *in* D. A. Quattrochi and M. F. Goodchild, editors. *Scale in remote sensing and GIS.* CRC Press, Boca Raton, Florida, USA.

Cheung, W. W. L., T. J. Pitcher, and D. Pauly. 2005. A fuzzy logic expert system to estimate intrinsic vulnerabilities of marine fishes to fishing. *Biological Conservation* 124:97–111.

Chiles, J.-P., and P. Delfiner. 1999. *Geostatistics: Modeling spatial uncertainty.* Wiley, New York, New York, USA.

Comer, P. J., D. A. Albert, H. A. Wells, B. L. Hart, J. B. Raab, D. L. Price, D. M. Kashian, R. A. Corner, and D. W. Schuen. 1995. *Michigan's native landscape, as interpreted from the General Land Office Surveys 1816–1856*. Report to the U. S. Environmental Protection Agency Water Division and Michigan Department of Natural Resources Wildlife Division, Michigan Natural Features Inventory, Lansing, Michigan, USA.

Congalton, R. G., and K. Green. 1993. A practical look at the sources of confusion in error matrix generation. *Photogrammetric Engineering and Remote Sensing* 59:641–644.

Congalton, R. G., and K. Green. 1999. *Assessing the accuracy of remotely sensed data: Principles and practices*. Lewis Publishers, Boca Raton, Florida, USA.

Conner, L. M., M. D. Smith, and L. W. Burger. 2003. A comparison of distance-based and classification-based analyses of habitat use. *Ecology* 84:526–531.

Corsi, F., J. de Leeuw, and A. Skidmore. 2000. Modeling species distribution with GIS. Pages 389–434 *in* L. Boitani and T. K. Fuller, editors. *Research techniques in animal ecology: Controversies and consequences.* Columbia University Press, New York, New York, USA.

Cowell, C. M. 1995. Presettlement piedmont forests: Patterns of composition and disturbance in central Georgia. *Annals of the Association of American Geographers* 85:65–83.

Cowell, C. M. 1998. Historical change in vegetation and disturbance on the Georgia Piedmont. *American Midland Naturalist* 140:78–89.

Daubenmire, R. 1952. Forest vegetation of Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. *Ecological Monographs* 22:301–330.

Dean, D. J., K. R. Wilson, and C. H. Flather. 1997. Spatial error analysis of species richness for a gap analysis map. *Photogrammetric Engineering and Remote Sensing* 63:1211–1217.

Delcourt, H. R., and P. A. Delcourt. 2006. Presettlement landscape heterogeneity: Evaluating grain of resolution using General Land Office survey data. *Landscape Ecology* 11:363–381.

Donovan, M. L., G. M. Nesslage, J. J. Skillen, and B. A. Maurer. 2004. *The Michigan gap analysis project final report*. Michigan Department of Natural Resources, Wildlife Division, Lansing, Michigan, USA.

Dunning, J. B., Jr., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: Current forms and future uses. *Ecological Applications* 5:3–11.

Dussault, C., J.-P. Ouellet, and R. Courtois. 2005. A comparison of distance-based and classification-based analyses of habitat use: Comment. *Ecology* 86:3119–3125.

Edwards, T. C., Jr., E. T. Deshler, D. Foster, and G.G Moisen. 1996. Adequacy of wildlife habitat relation models for estimating spatial distributions of terrestrial vertebrates. *Conservation Biology* 10:263–270.

Edwards, T. C., Jr., G.G Moisen, T. S. Frescino, and J. J. Lawler. 2003. Modeling multiple ecological scales to link landscape theory to wildlife conservation. Pages 153–176 *in* J. A. Bissonette and I. Storch, editors. *Landscape ecology and resource management: Linking theory with practice.* Island Press, Washington, D.C., USA.

Engler, R., A. Guisan, and L. Rechsteiner. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology* 41:263–274.

ERDAS. 1982. *ERDAS field guide*. Fourth edition. ERDAS, Atlanta, Georgia, USA.

Erickson, W. P., T. L. McDonald, K. G. Gerow, S. Howlin, and J. W. Kern. 2001. Statistical issues in resource selection studies with radio-marked animals. Pages 209–242 *in* J. J. Millspaugh and J. M. Marzluff, editors. *Radio tracking and animal populations.* Academic Press, San Diego, California, USA.

Estes, J. E., and D. W. Mooneyhan. 1994. Of maps and myths. *Photographic Engineering and Remote Sensing* 60:517–524.

Eyre, F. H. 1980. *Forest cover types of the United States and Canada*. Society of American Foresters, Washington, D.C., USA.

Farley, S. C., R. E. Masters, and D. M. Engle. 2002. Riparian landscape change in central Oklahoma 1872–1991. *Proceedings of the Oklahoma Academy of Sciences* 82:57–71.

Fernández, N., M. Delibes, and F. Palomares. 2006. Landscape evaluation in conservation: Molecular sampling and habitat modeling for the Iberian lynx. *Ecological Applications* 16:1037–1049.

Fleming, K. K., K. A. Didier, B. R. Miranda, and W. F. Porter. 2004. Sensitivity of a white-tailed deer habitat-suitability index model to error in satellite land-cover data: Implications for wildlife habitat-suitability studies. *Wildlife Society Bulletin* 32:158–168.

Foody, G. M. 2002. Status of land cover classification accuracy assessment. *Remote Sensing of Environment* 80:185–201.

Forman, R. T. T., and M. Godron. 1981. Patches and structural components for a landscape ecology. *BioScience* 31:733–740.

Forman, R. T. T., and M. Godron. 1986. *Landscape ecology.* John Wiley and Sons, New York, New York, USA.

Fortin, D., J. M. Fryxell, and R. Pilote. 2002. The temporal scale of foraging decisions in bison. *Ecology* 83:970–982.

Frescino, T. S., T. C. Edwards, Jr., and G. G. Moisen. 2001. Modeling spatially explicit forest structural attributes using generalized additive models. *Journal of Vegetation Science* 12:15–26.

Garbrecht, J., F. L. Ogden, P. A. DeBarry, and D. R. Maidment. 2001. GIS and distributed watershed models. I: Data, coverages, and sources. *Journal of Hydrologic Engineering* 6:506–514.

Goodchild, M. F., and S. Gopal, editors. 1989. *The accuracy of spatial databases.* Taylor & Francis, Bristol, Pennsylvania, USA.

Gough, M. C., and S. P. Rushton. 2000. The application of GIS-modelling to mustelid landscape ecology. *Mammal Review* 30:197–216.

Grossman, D. H., P. Bourgeron, W.-D. Busch, D. Cleland, W. Platts, G. C. Ray, C. R. Robins, and G. Roloff. 1999. Principles for ecological classification. Pages 353–393 *in* R. C. Szaro, N. C. Johnson,

W. T. Sexton, and A. J. Malk, editors. *Ecological stewardship: A common reference for ecosystem management*. Volume 2, Elsevier Science, Oxford, United Kingdom.

Grossman, D. H., D. Faber-Langendoen, A. S. Weakley, M. Anderson, P. Bourgeron, R. Crawford, K. Goodin, S. Landaal, K. Metzler, K. Patterson, M. Pyne, M. Reid, and L. Sneddon. 1998. *International classification of ecological classification: Terrestrial vegetation of the United States*. Volume I. The National Vegetation Classification System: Development, status, and applications, The Nature Conservancy, Arlington, Virginia, USA.

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

Haines, D. A., and R. W. Sando. 1969. *Climatic conditions preceding historically great fires in the north central region*. U.S. Forest Service, North Central Forest Experiment Station, Research Paper NC-34, St. Paul, Minnesota, USA.

Haines-Young, R., D. R. Green, and S. H. Cousins, editors. 1994. *Landscape ecology and GIS*. Taylor & Francis, Philadelphia, Pennsylvania, USA.

Hammond, J. S., R. L. Keeney, and H. Raiffa. 1999. *Smart choices: A practical guide to making better decisions*. Harvard Business School Press, Boston, Massachusetts, USA.

Haufler, J. B., C. A. Mehl, and G. J. Roloff. 1996. Using a coarse-filter approach with species assessment for ecosystem management. *Wildlife Society Bulletin* 24:200–208.

Hess, G. R., and J. M. Bay. 2004. Generating confidence intervals for composition-based landscape indexes. *Landscape Ecology* 12:309–320.

Hines, E. M., J. Franklin, and J. R. Stephenson. 2005. Estimating the effects of map error on habitat delineation for the California spotted owl in southern California. *Transactions in GIS* 9:541–559.

Hirzel, A. H., J. Hausser, D. Chessel, and N. Perrin. 2002. Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data. *Ecology* 83:2027–2036.

Holmström, H., and J. E. S. Fransson. 2003. Combining remotely sensed optical and radar data in kNN-estimation of forest variables. *Forest Science* 49:409–418.

Hunsaker, C. T., M. F. Goodchild, M. A. Friedl, and T. J. Case, editors. 2001. *Spatial uncertainty in ecology: Implications for remote sensing and GIS applications.* Springer-Verlag, New York, New York, USA.

Hunsaker, C. T., R. V. O'Neill, B. L. Jackson, S. P. Timmins, D. A. Levine, and D. J. Norton. 1994. Sampling to characterize landscape pattern. *Landscape Ecology* 9:207–226.

Jackson, V. L., L. L. Laack, and E. G. Zimmerman. 2005. Landscape metrics associated with habitat use by ocelots in south Texas. *Journal of Wildlife Management* 69:733–738.

Jeganathan, P., R. E. Green, K. Norris, I. N. Vogiatzakis, A. Bartsch, S. R. Wotton, C. G. R. Bowden, G. H. Griffiths, D. Pain, and A. R. Rahmani. 2004. Modelling habitat selection and distribution of the critically endangered Jerdon's courser *Rhinoptilus bitorquatus* in scrub jungle: An application of a new tracking method. *Journal of Applied Ecology* 41:224–237.

Jelinski, D. E., and J. Wu. 1996. The modifiable areal unit problem and implications for landscape ecology. *Landscape Ecology* 11:129–140.

Johnson, C. G., Jr., R. R. Clausnitzer, P. J. Mehringer, and C. D. Oliver. 1994. *Biotic and abiotic processes of eastside ecosystems: The effects of management on plant and community ecology, and on stand and landscape vegetation dynamics*. U.S. Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-322, Portland, Oregon, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.

Johnson, L. B. 1990. Analyzing spatial and temporal phenomena using geographical information systems: A review of ecological applications. *Landscape Ecology* 4:31–43.

Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* 373:299–302.

Karl, J. W., P. J. Heglund, E. O. Garton, J. M. Scott, N. M. Wright, and R. L. Hutto. 2000. Sensitivity of species habitat-relationship model performance to factors of scale. *Ecological Applications* 10:1690–1705.

Kerr, J. T., and M. Ostrovsky. 2003. From space to species: Ecological applications for remote sensing. *Trends in Ecology and Evolution* 18:299–305.

Knight, J. F., and R. S. Lunetta. 2003. An experimental assessment of minimum mapping unit size. *IEEE Transactions on GeoScience and Remote Sensing* 41:2132–2134.

Laba, M., S. K. Gregory, J. Braden, D. Ogurcak, E. Hill, E. Fegraus, J. Fiore, and S. D. DeGloria. 2002. Conventional and fuzzy accuracy assessment of the New York gap analysis project land cover map. *Remote Sensing of Environment* 81:443–455.

Lawler, J. J., R. J. O'Connor, C. T. Hunsaker, K. B. Jones, T. R. Loveland, and D. White. 2004. The effects of habitat resolution on models of avian diversity and distributions: A comparison of two land-cover classifications. *Landscape Ecology* 19:515–530.

Lawler, J. J., and N. H. Schumaker. 2004. Evaluating habitat as a surrogate for population viability using a spatially explicit population model. *Environmental Monitoring and Assessment* 94:85–100.

Lehmann, A. 2004. GIS modeling of submerged macrophyte distribution using generalized additive models. *Plant Ecology* 139:113–124.

Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.

Liegel, C. 1982. The pre-European settlement vegetation of the Aldo Leopold Memorial Reserve. *Transactions of the Wisconsin Academy of Science, Arts and Letters* 70:13–26.

Linden, D. W. 2006. *Modeling current and historic habitat for Canada lynx (*Lynx canadensis*) in the upper peninsula of Michigan*. Thesis, Michigan State University, East Lansing, USA.

Lowell, K., and A. Jaton, editors. 1999. *Spatial accuracy assessment: Land information uncertainty in natural resources.* Ann Arbor Press, Chelsea, Michigan, USA.

Lu, D. S., P. Mausel, E. Brondízio, and E. Moran. 2004. Relationships between forest stand parameters and Landsat TM spectral responses in the Brazilian Amazon Basin. *Forest Ecology and Management* 198:149–167.

Luoto, M., and M. Seppälä. 2002. Modelling the distribution of palsas in Finnish Lapland with logistic regression and GIS. *Permafrost and Periglacial Processes* 13:17–28.

MacQueen, J. 1967. Some methods for classification and analysis of multivariate observations. Pages 281–297 *in* L. M. L. Cam and J. Neyman, editors. *Proceedings of the Fifth Berkeley symposium on mathematical statistics and probability.* Volume 1, University of California Press, Berkeley, USA.

Manies, K. L., and D. J. Mladenoff. 2000. Testing methods to produce landscape-scale presettlement vegetation maps from the U.S. General Land Office survey records. *Landscape Ecology* 15:741–754.

Manly, B. F. J. 1997. *Randomization, bootstrap and Monte Carlo methodology in biology.* Second edition. CRC Press, Boca Raton, Florida, USA.

Maurer, B. A. 2002. Predicting distribution and abundance: Thinking within and between scales. Pages 125–139 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. W. Wall, and F. B. Samson, editors. *Predicting species occurrences: Issues of accuracy and scale.* Island Press, Washington, D.C., USA.

McCarty, J. P., D. J. Levey, C. H. Greenberg, and S. Sargent. 2002. Spatial and temporal variation in fruit use by wildlife in a forested landscape. *Forest Ecology and Management* 164:277–291.

McCollum, J. M., and J. K. Cochran. 2003. Forest inventory and analysis and forest health monitoring: Piecing the quilt. Pages 175–182 *in* R. E. McRoberts, G. A. Reams, P. C. Van Deusen, and W. H. McWilliams, editors. *Proceedings of the Fifth Annual Forest Inventory and Analysis Symposium.* U.S. Forest Service, General Technical Report WO-69, Washington, D.C., USA.

McGwire, K. C., and P. Fisher. 2001. Spatially variable thematic accuracy: Beyond the confusion matrix. Pages 308–329 *in* C. T. Hunsaker, M. F. Goodchild, M. A. Friedl, and T. J. Case, editors. *Spatial uncertainty in ecology: Implication for remote sensing and GIS applications.* Springer-Verlag, New York, New York, USA.

Michigan Department of Natural Resources. 2001. *Current use inventory classification system definitions*. MDNR, Michigan Resource Information System, Land Resource Programs Division, Lansing, Michigan, USA.

Mladenoff, D. J., T. A. Sickley, and A. P. Wydeven. 1999. Predicting gray wolf landscape recolonization: Logistic regression models vs. new field data. *Ecological Applications* 9:37–44.

Moellering, H., H. J. G. L. Aalders, and A. Crane, editors. 2005. *World spatial metadata standards.* Elsevier Press, San Diego, California, USA.

Morris, D. W. 1987. Ecological scale and habitat use. *Ecology* 68:362–369.

Morrison, M. L. 2002. Role of temporal and spatial scale. Pages 123–124 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. W. Wall, and F. B. Samson, editors. *Predicting species occurrences: Issues of accuracy and scale.* Island Press, Washington, D.C., 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.

Mowrer, H. T., and R. G. Congalton. 2000. *Quantifying spatial uncertainty in natural resources: Theory and applications for GIS and remote sensing*. Ann Arbor Press, Chelsea, Michigan, USA.

O'Neil, T. A., P. Bettinger, B. G. Marcot, B. W. Luscombe, G. T. Koeln, H. J. Bruner, C. Barrett, J. A. Pollock, and S. Bernatas. 2005. Application of spatial technologies in wildlife biology. Pages 418–447 *in* C. E. Braun, editor. *Techniques for wildlife investigations and management.* The Wildlife Society, Bethesda, Maryland, USA.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137:S29–S49.

Osborne, P. E., J. C. Alonso, and R. G. Bryant. 2001. Modelling landscape-scale habitat use using GIS and remote sensing: A case study with great bustards. *Journal of Applied Ecology* 38:458–471.

Pearlstine, L. G., S. E. Smith, L. A. Brandt, C. R. Allen, W. M. Kitchens, and J. Stenberg. 2002. Assessing state-wide biodiversity in the Florida Gap analysis project. *Journal of Environmental Management* 66:127–144.

Pereira, J. M. C., and R. M. Itami. 1991. GIS-based habitat modeling using logistic multiple regression: A study of the Mt Graham red squirrel. *Photogrammetric Engineering and Remote Sensing* 57:1475–1486.

Pidgeon, A. M., L. A. Schulte, and D. J. Mladenoff. 2005. *Pre-Euroamerican distribution of pine warblers* (Dendroica pinus) *in Wisconsin: A tool for setting regional conservation priorities*. U.S. Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-191, Berkeley, California, USA.

Porter, W. F., and K. E. Church. 1987. Effects of environmental pattern on habitat preference analysis. *Journal of Wildlife Management* 51:681–685.

Qi, Y., and J. Wu. 1996. Effects of changing spatial resolution on the results of landscape pattern analysis using spatial autocorrelation indices. *Landscape Ecology* 11:39–49.

Radeloff, V. C., D. J. Mladenoff, H. S. He, and M. S. Boyce. 1999. Forest landscape change in the northwestern Wisconsin pine barrens from pre-European settlement to the present. *Canadian Journal of Forest Research* 29:1649–1659.

Ramsey, E. W., III, and M. L. Strong. 2000. Conveying multiple, complex themes and classes for natural resource assessments. *Geocarto International* 15:29–35.

Raphael, M. G., and B. G. Marcot. 1986. Validation of a wildlife-habitat-relationships model: Vertebrates in a Douglas-fir sere. Pages 129–138 *in* J. Verner, M. Morrison, and C. J. Ralph, editors. *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates.* University of Wisconsin Press, Madison, USA.

Robinson, V. B. 2003. A perspective on the fundamentals of fuzzy sets and their use in geographic information systems. *Transactions in GIS* 7:3–30.

Rodgers, C. S., and R. C. Anderson. 1979. Presettlement vegetation of two prairie peninsula counties. *Botanical Gazette* 140:232–240.

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

Roloff, G. J., J. J. Millspaugh, R. A. Gitzen, and G. C. Brundige. 2001. Validation tests of a spatially explicit habitat effectiveness model for Rocky Mountain elk. *Journal of Wildlife Management* 65:899–914.

Roloff, G. J., M. C. Reynolds, and J. B. Haufler. 1994. Variability in the structure and composition of regenerating aspen with implications for ruffed grouse management. *Michigan Academician* 26:75–82.

Saura, S. 2002. Effects of minimum mapping unit on land cover data spatial configuration and composition. *International Journal of Remote Sensing* 23:4853–4880.

Schulte, L. A., and D. J. Mladenoff. 2001. The original U.S. public land survey records: Their use and limitations in reconstructing pre-European settlement vegetation. *Journal of Forestry* 99:5–10.

Schulte, L. A., A. M. Pidgeon, and D. J. Mladenoff. 2005. One hundred fifty years of change in forest bird breeding habitat: Estimates of species distributions. *Conservation Biology* 19:1944–1956.

Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. *Ecology* 77:1210–1225.

Segurado, P, and M. B. Araújo. 2004. An evaluation of methods for modelling species distributions. *Journal of Biogeography* 31:1555–1568.

Short, H. L., and J. B. Hestbeck. 1995. National biotic resource inventories and GAP analysis: Problems of scale and unproven assumptions limit a national program. *BioScience* 45:535–539.

Silvert, W. 1997. Ecological impact classification with fuzzy sets. *Ecological Modelling* 96:1–10.

Simon, J. L. 1997. *Resampling: The "new statistics."* Resampling Statistics, Arlington, Virginia, USA.

Space Imaging Solutions. 2001. *Integrated forest monitoring assessment and prescription, IFMAP. Review of remote sensing technologies for the IFMAP project*. Report prepared for the Michigan Department of Natural Resources, Space Imaging Solutions, Ann Arbor, Michigan, USA.

Starfield, A. M. 1997. A pragmatic approach to modeling for wildlife management. *Journal of Wildlife Management* 61:261–270.

Stehman, S. V. 1997. Selecting and interpreting measures of thematic classification accuracy. *Remote Sensing of Environment* 62:77–89.

Stohlgren, T. J., G. W. Chong, M. A. Kalkhan, and L. D. Schell. 1997. Multiscale sampling of plant diversity: Effects of minimum mapping unit size. *Ecological Applications* 7:1064–1074.

Stoms, D. M. 1994. Scale dependence of species richness maps. *The Professional Geographer* 46:346–358.

Stoms, D. M., F. W. Davis, and C. B. Cogan. 1992. Sensitivity of wildlife habitat models to uncertainties in GIS data. *Photogrammetric Engineering and Remote Sensing* 58:843–850.

Théau, J., D. R. Peddle, and C. R. Duguay. 2005. Mapping lichen in a caribou habitat of northern Quebec, Canada, using an enhancement-classification method and spectral mixture analysis. *Remote Sensing of Environment* 94:232–243.

Tischendorf, L. 1997. Modelling individual movements in heterogeneous landscapes: Potentials of a new approach. *Ecological Modelling* 103:33–42.

Tuominen, S., S. Fish, and S. Poso. 2003. Combining remote sensing, data from earlier inventories, and geostatistical interpolation in multisource forest inventory. *Canadian Journal of Forest Research* 33:624–634.

Tuominen, S., and A. Pekkarinen. 2005. Performance of different spectral and textural aerial photograph features in multi-source forest inventory. *Remote Sensing of Environment* 94:256–268.

Turner, M. G., R. V. O'Neill, R. H. Gardner, and B. T. Milne. 1989. Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology* 3:153–162.

U.S. Forest Service. 1996. *Status of the interior Columbia basin: Summary of scientific findings*. U.S. Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-385, Portland, Oregon, USA.

U.S. Forest Service. Forest inventory and analysis program. <http://fia.fs.fed.us/>. Accessed 5 January 2007.

Van Deelen, T. R., K. S. Pregitzer, and J. B. Haufler. 1996. A comparison of presettlement and present-day forests in two northern Michigan deer yards. *American Midland Naturalist* 135:181–194.

Verbyla, D. L., and J. A. Litvaitis. 1989. Resampling methods for evaluating classification accuracy of wildlife habitat models. *Environmental Management* 13:783–787.

Wade, T. G., J. D. Wickham, M. S. Nash, A. C. Neale, K. H. Riitters, and K. B. Jones. 2003. A comparison of vector and raster GIS methods for calculating landscape metrics used in environmental assessments. *Photogrammetric Engineering and Remote Sensing* 69:1399–1405.

Wang, Y.-C. 2005. Presettlement land survey records of vegetation: Geographic characteristics, quality and modes of analysis. *Progress in Physical Geography* 29:568–598.

Waring, R. H., and S. W. Running. 1998. *Forest ecosystems: Analysis at multiple scales*. Second edition. Academic Press, San Diego, California, USA.

Whitehead, H. 1996. Variation in the feeding success of sperm whales: Temporal scale, spatial scale and relationship to migrations. *Journal of Animal Ecology* 65:429–438.

Wickham, J. D., and K. H. Riitters. 1995. Sensitivity of landscape metrics to pixel size. *International Journal of Remote Sensing* 16:3585–3594.

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

Wolock, D. M., and C. V. Price. 1994. Effects of digital elevation model map scale and data resolution on a topography-based watershed model. *Water Resources Research* 30:3041–3052.

Wu, F. 2004. GIS-based simulation as an exploratory analysis for space-time processes. *Journal of Geographical Systems* 1:199–218.

Wu, J. 2004. Effects of changing scale on landscape pattern analysis: Scaling relations. *Landscape Ecology* 19:125–138.

Wu, J., and O. L. Loucks. 1995. From balance-of-nature to hierarchical patch dynamics: A paradigm shift in ecology. *Quarterly Review of Biology* 70:439–466.

Zaniewski, A. E., A. Lehmann, and J. M. Overton. 2002. Predicting species spatial distributions using presence-only data: A case study of native New Zealand ferns. *Ecological Modelling* 157:261–280.

Zhang, L., C. Liu, C. J. Davis, D. S. Solomon, T. B. Brann, and L. W. Caldwell. 2004. Fuzzy classification of ecological habitats from FIA data. *Forest Science* 50:117–127.

Zhu, A. X., B. Hudson, J. Burt, K. Lubich, and D. Simonson. 2001. Soil mapping using GIS, expert knowledge, and fuzzy logic. *Soil Science Society of America Journal* 65:1463–1472.