WILDLIFE RESPONSE TO SPATIAL AND TEMPORAL CHANGES IN FOREST HABITAT

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by

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WILDLIFE RESPONSE TO SPATIAL AND TEMPORAL CHANGES IN FOREST HABITAT

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ABSTRACT

A common goal in land-management planning is to describe the relationship between management actions, vegetation and wildlife habitat conditions for large landscapes. Achieving this goal can be challenging because ecological processes of disturbance (natural and anthropogenic) and succession affect vegetation composition and structure, which subsequently affects current and future habitat conditions for wildlife. Habitat suitability is often used as a surrogate for demographic response by wildlife to vegetation change, yet this assumed relationship is rarely evaluated. I developed habitat suitability models for 10 wildlife species: American woodcock (*Scolopax minor*), cerulean warbler (*Dendroica cerulea*), Henslow's sparrow (*Ammodramus henslowii*), Indiana bat (*Myotis sodalis*), northern bobwhite (*Colinus virginianus*), ruffed grouse (*Bonasa umbellus*), timber rattlesnake (*Crotalus horridus*), wood thrush (*Hylocichla mustelina*), worm-eating warbler (*Helmitheros vermivorus*), and yellow-breasted chat (*Icteria virens*). I described habitat suitability by an empirical or assumed relationship between habitat quality and resource attributes on a relative scale that ranges from 0 (not suitable habitat) to 1 (highly suitable habitat). The models were spatially explicit and included habitat and landscape relationships based on the best available empirical data and expert opinion.

I validated HSI models of breeding habitat suitability for wood thrush and yellow-breasted chats, two species on opposite ends of a forest succession gradient, by evaluating the association between wildlife demographic response and HSI values. First, I evaluated the statistical significance of HSI models as a predictor of three different demographic responses, within-site territory density, site-level territory density and nest success. I demonstrated a statistically significant link between HSI values and all three types of demographic responses for the yellow-breasted chat and site-level territory density for the wood thrush. Second, I evaluated support for models based on HSI values, individual suitability values, measured habitat or landscape attributes (e.g., tree age, tree species, ecological land type), and management treatments (e.g., even-aged and uneven-aged forest regeneration treatments) for each demographic response using model selection. Models containing HSI values were, in general, more supported than models containing only landscape attributes or management treatments for all three types of wildlife response. The assumption that changes in habitat suitability represent wildlife demographic response to vegetation change is supported for these two models; however, differences in species ecology may contribute to model significance and model selection uncertainty.

I then simulated future forest conditions and evaluated habitat suitability 10, 50, and 150 years from present as part of the Hoosier National Forest (HNF) plan revision. Three important patterns emerged over time with respect to forest composition and structure: white oak increased in area of dominance under all alternatives, the proportions of red oak species and maples were affected by the intensity of forest disturbance via harvest and fire, and in the absence of anthropogenic disturbance or wildfire, the HNF was dominated by late-successional vegetation conditions. Without tree harvest or prescribed fire, early successional wildlife species were greatly reduced within 50 years. Tree harvest benefited early successional species without greatly affecting habitat suitability for late successional species. These patterns are consistent with current knowledge of vegetation and wildlife response to management. The HNF planning team used the information on vegetation conditions and habitat suitability to select Alternative 5, which utilized a focal area to concentrate harvest activities, as the preferred alternative. By incorporating ecological processes of disturbance and succession while retaining the resolution necessary for evaluating wildlife habitat suitability, this modeling approach contributed knowledge to the planning process and was a valuable tool for communicating differences among alternatives to stakeholders. As such, this approach serves as a template for successful planning on forested lands and will be of value to land managers, resource planners, and ecologists.

INTRODUCTION

A common goal in land-management planning is to describe the relationship between management actions, vegetation and wildlife habitat conditions for large landscapes. I developed an approach to evaluate and forecast wildlife habitat suitability in large landscapes and demonstrated its application to land-management planning on the Hoosier National Forest (HNF) in Indiana. In order to establish a context for the following chapters, I first provide an overview of the planning process, the modeling approach, and the selection process for determining which wildlife species were included in the HNF plan.

The planning process for the HNF occurred in 5 stages. The first stage was an analysis of the current management situation and existing conditions. During this stage the HNF planning team reviewed the existing Forest Plan and management activities, and HNF staff conducted or reviewed inventories of forest and wildlife conditions.

The second stage identified the desired conditions and developed objectives to address emerging issues, such as changes in forest species composition, wildlife population trends, or species conservation status. The HNF planning team developed various management scenarios, or alternatives, to achieve the desired conditions and objectives. Because this forest plan involved many integrated objectives and multiple wildlife species, some modeling approaches (e.g., optimization models, Usher 1966, Lu and Buongiorno 1993) would have been difficult if not impossible to implement (Thompson and Millspaugh 2008). I simulated spatial and temporal trends of vegetation change using LANDIS, a spatially explicit, landscape-level analysis tool that models vegetation growth, reproduction, and response to disturbance by timber harvest, wind, and fire (Mladenoff et al. 1996, He et al. 1999, Mladenoff and He 1999). In other words, this approach considered broad-scale landscape dynamics while retaining the fine-scale resolution needed to quantify changes in wildlife habitat (Noon et al. 2008).

Concurrent with the development of forest management alternatives was the selection of wildlife species that were evaluated in the planning process. The HNF planning team convened a Species Viability Evaluation (SVE) panel to select which species to include in the planning process. The SVE panel consisted of research specialists or scientists from the HNF and the Shawnee National Forest (SNF), Illinois, Southern Illinois University and Indiana Department of Natural Resources (Appendix 1). The SVE panel recognized the infeasibility of monitoring the status and assessing the viability of all species, and instead used a focal species approach (Committee of Scientists 1999). The criteria used to select the focal species included listing as U.S. Forest Service Region 9 sensitive species, Federally endangered, threatened, or proposed for listing; species representative of each of the habitat types within the Hoosier National Forest; and species occurrence on the HNF within the last 25 years. The SVE panel also included species for which there was high management and public interest (e.g. Neotropical migratory bird species and game species). In addition to these criteria, the HNF planning team considered expert knowledge and the availability of literature and empirical data for each species.

The third stage consisted of a scientific analysis of the expected effects of implementing each of the management alternatives on future forest conditions and wildlife habitat or populations. I included anthropogenic (i.e., tree harvest and prescribed fire) and natural (i.e., wildfire and wind damage) sources of disturbance in the analysis, as well as the effects of these sources of disturbance on the composition, structure, and configuration of vegetation and wildlife habitat.

During the fourth stage, the HNF planning team developed the proposed Forest Plan and a Draft Environmental Impact Statement and opened them to public review. The final stage occurred with the selection of the recommended alternative, development of the final Forest Plan, and approval of the final Forest Plan.

DESCRIPTION OF CHAPTERS

Chapter 2 documented the development of landscape-level habitat suitability models for 10 species selected by the SVE panel and the HNF planning team during Stage 2 of the planning process: American woodcock (*Scolopax minor*), cerulean warbler (*Dendroica cerulea*), Henslow's sparrow (*Ammodramus henslowii*), Indiana bat (*Myotis sodalis*), northern bobwhite (*Colinus virginianus*), ruffed grouse (*Bonasa umbellus*), timber rattlesnake (*Crotalus horridus*), wood thrush (*Hylocichla mustelina*), worm-eating warbler (*Helmitheros vermivorus*), and yellow-breasted chat (*Icteria virens*). The models were spatially explicit and included habitat and landscape relationships based on the best available empirical data and expert opinion. In this chapter I provided an overview of habitat characteristics for each species, discussed the habitat variables used in each model, and provided supporting reference materials for all assumed relationships between quantity of a resource and quality for each species modeled. The models were included in a stand-alone software package, Landscape HSImodels version 2.1, available from the U.S. Forest Service, Northern Research Station (www.nrs.fs.fed.us/hsi).

In Chapter 3 I evaluated whether habitat suitability actually relates to demographics. I validated HSI models of breeding habitat suitability for wood thrush and yellow-breasted chats, two species on opposite ends of a forest succession gradient, by evaluating the association between wildlife demographic response and HSI values. I evaluated the statistical significance of HSI models as a predictor of three demographic responses, within-site territory density, site-level territory density and nest success. I demonstrated a statistically significant link between HSI values and all three types of demographic responses for the yellow-breasted chat and site-level territory density for the wood thrush. I then evaluated support for models containing HSI values or individual SI values, models containing measured habitat or landscape attributes (e.g., tree age, tree species, ecological land type), and models containing management treatments (e.g., even-aged and uneven-aged forest regeneration treatments) for each demographic response using model selection. The models containing HSI values were, in general, more supported than models containing only landscape attributes or management treatments for all three types of wildlife response. These two analyses supported the assumption that changes in habitat suitability represent wildlife demographic response to vegetation change.

In Chapter 4 I presented the application of the habitat suitability models developed in Chapter 2 for land-management planning on the Hoosier National Forest. This chapter corresponded to Stage 3 of the planning process. In this chapter I evaluated habitat conditions 10, 50, and 150 years from present for 8 avian species and the Indiana bat under 5 management alternatives. I simulated future forest conditions using LANDIS and apply the habitat suitability models to the output from LANDIS. I identified important patterns of forest composition and structure, and corresponding patterns of wildlife response to changing vegetation conditions. This modeling approach incorporated ecological processes of disturbance and succession while retaining the resolution necessary for evaluating wildlife habitat suitability and thus provided knowledge and tools for communication among participants in the planning process.

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DEVELOPMENT OF LANDSCAPE-LEVEL HABITAT SUITABILITY MODELS FOR TEN WILDLIFE SPECIES IN THE CENTRAL HARDWOODS REGION

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ABSTRACT

Decades of studies on wildlife-habitat relationships have provided important insights into the habitat requisites for many game and nongame species. Many species of conservation or management importance are area or edge sensitive, or need interspersion of habitat requisites to maintain viable populations; however, most habitat suitability models do not incorporate spatial relationships or landscape attributes. Our objective was to develop landscape-level habitat suitability models for 10 species in the Central Hardwoods Region of the Midwestern United States: American woodcock (*Scolopax minor*), cerulean warbler (*Dendroica cerulea*), Henslow's sparrow (*Ammodramus henslowii*), Indiana bat (*Myotis sodalis*), northern bobwhite (*Colinus virginianus*), ruffed

grouse (*Bonasa umbellus*), timber rattlesnake (*Crotalus horridus*), wood thrush (*Hylocichla mustelina*), worm-eating warbler (*Helmitheros vermivorus*), and yellow-breasted chat (*Icteria virens*). All models included spatially explicit variables and relationships based on the best available empirical data and expert opinion. We provide an overview of habitat characteristics for each species, discuss the habitat variables used in each model, and provide supporting reference materials for all assumed relationships between quantity of a resource and quality for each species modeled. The models are included in a stand-alone software package, Landscape HSImodels version 2.1, available from the U.S. Forest Service, Northern Research Station (www.nrs.fs.fed.us/hsi). The HSI maps produced by the Landscape HSImodels software are readily displayed within GIS software (e.g., ArcView or ArcGIS). All models may be modified to address site-specific habitat conditions and then applied to other regions. For example, the models may be used to identify priority areas for conservation or management. Additionally, the models may be applied to output from forest simulation software (e.g., LANDIS) and used to evaluate the effects of forest management alternatives in a planning context. As such, these models provide a general approach for evaluating habitat suitability at large spatial scales.

INTRODUCTION

Decades of studies on wildlife-habitat relationships have provided important insights into the habitat requisites for many game and nongame species. Information gained from these studies has been used to develop wildlife habitat models (e.g., habitat suitability index [HSI] models; U.S. Fish and Wildlife Service 1980, 1981), the application of which enables assessment of current habitat conditions and predictions of how habitat suitability may change under management (e.g., habitat evaluation procedures; U.S. Fish and Wildlife Service 1980, 1981). Radio-telemetry (Rodgers 2001) and computing (e.g., geographic information systems; GIS) technology have enhanced our understanding of wildlife-habitat relationships, especially with regard to wildlife spatial ecology. We now recognize that many species of conservation or management importance are area or edge sensitive, or need interspersion of habitat requisites to maintain viable populations.

Habitat suitability index models (U.S. Fish and Wildlife Service 1980, 1981) remain a common approach for assessing wildlife habitat quality (Gustafson et al. 2001, Marzluff et al. 2002, Larson et al. 2003, Larson et al. 2004). Habitat suitability index models evaluate the resource attributes considered important to a species' abundance, survival, or reproduction. Habitat suitability is described by an empirical or assumed relationship between habitat quality and resource attributes on a relative scale that ranges from 0 (not suitable habitat) to 1 (highly suitable habitat) (U.S. Fish and Wildlife Service 1980, 1981). The HSI values can be visually presented as habitat suitability maps, which may then be used to make relative comparisons across management alternatives (Gustafson et al. 2001, Marzluff et al. 2002, Larson et al. 2004). Originally, these maps were summarized in terms of habitat units, which is the HSI value multiplied by a unit of area. In this way, habitat units became the currency for evaluating management alternatives in terms of the total amount of habitat lost or gained (U.S. Fish and Wildlife Service 1980, 1981; Klaus et al. 2005). However, habitat occupancy depends not only on the HSI values but also on the composition and configuration of habitat units. Thus, the spatial context of wildlife-habitat relationships should be incorporated in HSI models.

The use of GIS technology facilitates inclusion of spatially explicit landscape attributes in HSI models.

Our objective was to develop landscape-level, GIS-based HSI models for 10 species in the Central Hardwoods Region of the Midwestern United States (Table 1). The species selected represent a range of habitat requirements (e.g., grassland, forest, disturbance-dependent, and disturbance-sensitive) and management priorities (e.g., game species, Partners in Flight priority species, threatened and endangered species) in the Central Hardwoods Region. We developed the HSI models to evaluate breeding habitat suitability for migratory species and year-round habitat suitability for nonmigratory species. We based all models on the best available empirical data and expert opinion. All models incorporated spatially explicit variables and advances in the understanding of wildlife-habitat relationships since the original models were developed. We provided an overview of important habitat characteristics for each species and discussed the habitat variables chosen for inclusion in the model. We provided supporting reference materials for all assumed relationships between the quantity of a resource and quality for that species. All models developed were included in a stand-alone software package, Landscape HSImodels version 2.1, (Dijak et al. 2007) available from the U.S. Forest Service, Northern Research Station (www.nrs.fs.fed.us/hsi).

We purposefully developed HSI relationships for these models based on information available from GIS layers. Additionally, the HSI maps produced by the Landscape HSImodels software are readily displayed within GIS software (e.g., ArcView or ArcGIS). Thus, these models can be used for the evaluation of habitat suitability at large spatial scales. For example we used these models, coupled with appropriate GIS layers of future vegetative conditions under alternative forest management scenarios, to assist land managers and planners in the forest management planning process. Additionally, these models may be modified to address site-specific habitat conditions and then applied to other regions. As such, these models provide a general approach to evaluating habitat quality and may be used to identify priority areas for conservation or management in addition to the effects of forest management.

METHODS

Area of Applicability and Test Landscape

We developed HSI models for application to the Central Hardwoods Region in the Midwestern United States. Definitions of the Central Hardwoods Region vary; we based our definition largely on Bailey's (1996) ecoregional classification system. We defined the Central Hardwoods Region as the Hot Continental Division (220) within the Humid Temperate Domain, excluding the mountainous portions (M220), and included the eastern portion of the Prairie Division (250) (Bailey 1996). The forested areas within this region are deciduous and contain primarily oak (*Quercus* spp.) and hickory (*Carya* spp.) forests, with some maple (*Acer* spp.), beech (*Fagus* spp.), mixed upland hardwoods, bottomland hardwoods, and lesser amounts of pine (*Pinus* spp.) and cedar (*Juniperus virginiana*). We demonstrated the HSI models on a landscape defined as the Patoka district of the Hoosier National Forest (HNF, Fig. 1). The Patoka district contained approximately 26,868 ha. However, we restricted all figures presented to a smaller, 4,281 ha portion of the Patoka district (hereafter, test landscape) for optimal display resolution using a cell size of 10 m.

Primary Input Data

The HSI models required four different raster-based maps of information (Fig. 2): tree age, species of the dominant overstory trees, ecological land type, and land-cover type. Additional raster-based maps required for some of the species models will be explained within individual species account. Tree age and species information for the initial forest conditions may be obtained from forest inventories, interpreted from aerial photographs, or derived from satellite imagery (e.g., remote sensing). We used Forest Inventory Analysis (FIA) data, the HNF's inventory database, land-use and land-cover data, and Indiana GAP data to establish current forest conditions for the test landscape. We assigned tree ages (Fig. 2) for stands located on public lands by subtracting the year of stand origin from the year of analysis (2003). We identified 14 different dominant overstory tree species (or species groups) and included two additional overstory types, nonforest and grassland, for a total of 16 different dominant overstory species (Table 2, Fig. 2). We used ecological land types (ELT) derived from 10-m Digital Elevation Model (DEM) layers[1]. The ELT coding followed Van Kley et al. (1994) and grouped types by slope, aspect, and relative moisture (Table 3, Fig. 2).

We classified land-cover type for public lands using the HNF forest type codes and for private lands using the land-use land-cover data digitized by the School of Public and Environmental Affairs, Indiana University, for the HNF, cross-referenced with the Indiana GAP data. The HNF forest type codes distinguished between 12 types of closed and open canopy forests or clearcuts, as well as croplands, grasslands (i.e., grassland, pasture, or hay fields), water, urban areas, and wetlands. We collapsed the HNF forest

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[1] Created by Guafon Sho, Purdue University

type codes into six general land-cover types: 1) forest; 2) croplands; 3) grasslands; 4) water; 5) urban areas; and 6) roads (Fig. 2) for use in the HSI models.

GIS Methods and Spatial Relationships

We modeled some wildlife species considered area or edge sensitive, or that use multiple habitat types to meet life-history requirements. Because these spatial relationships were common to many of the species' models, we present the methodology for them here and address other requirements as needed within species-specific models. Area-sensitive species require a minimum area of contiguous habitat (i.e., a minimum patch size) for occupancy or breeding. We addressed minimum area requirements in two steps. First, we used a suitability index (SI) to identify cells containing suitable habitat based on tree age, tree species, ELT, or land-cover type. We used a patch-definition algorithm to aggregate cells of suitable habitat that were adjacent (i.e., horizontally, vertically or diagonally) to other cells of suitable habitat. Once aggregated, we then used a second SI to assign values to pixels based on the size of the habitat patch in which they occurred.

Edge-sensitive species may experience adverse effects due to edges, such as reduced survival, nest success, or nest density near habitat edges (Donovan et al. 1997, Winter et al. 2000, Woodward et al. 2001). In contrast, species such as the northern bobwhite (*Colinus virginianus*) use woody edges adjacent to croplands or grasslands as escape cover (Roseberry and Klimstra 1984, Williams et al. 2000). Thus, edge effects may be positive or negative, depending on the species. We defined a habitat edge as a change in land-cover type (i.e., grassland to cropland) or tree age (i.e., early successional forest to mature forest). We addressed edge sensitivity using two different approaches: a distance algorithm and a moving-window analysis. The distance algorithm assigned SI values based on the distance of a cell to a habitat or landscape feature (i.e., roads) that defined a habitat edge. Because the distance algorithm assigned an SI value to each cell within the landscape, it was often the most computationally intensive step in the HSI models. We used a moving window for edge sensitivity when the effect was limited to adjacent cells; otherwise, we used the distance algorithm. The moving-window analysis adjusted the suitability of cells adjacent to habitat edges. For example, the Henslow's sparrow (*Ammodramus henslowii*) is a grassland species that is sensitive to woody edges (Winter and Faaborg 1999, Winter et al. 2000, Bajema and Lima 2001). We applied the moving window to a previous SI that identified patches of suitable grassland habitat. If the center cell of the moving window contained suitable grassland habitat and any cell within the radius of the window contained non-grassland habitat (e.g., forest, urban areas, or roads), the SI value of the center cell was reduced. In other words, a cell containing habitat that was otherwise suitable for Henslow's sparrows had reduced suitability due to the cell's proximity to nonsuitable habitat. We also used the moving-window analysis to assign suitability based on the composition or interspersion of habitats needed for life history requisites.

Some wildlife species have different habitat needs for different activities, such as foraging habitat separate from nesting habitat or escape cover. We used a moving-window analysis to assess the proportion of different habitat requisites within a defined area, typically the average home range size for a species. For example, northern bobwhites nest in grasslands, forage in cropland, and use woody edges for escape cover (Stoddard 1931, Roseberry and Klimstra 1984, Roseberry and Sudkamp 1998, Williams et al. 2000). We applied the moving window to previous SIs that identified suitable grassland, cropland, and woody edges, respectively. We recoded each habitat type (e.g., grassland = 1, cropland = 2, and woody edges = 3) and determined the proportion of each of these three habitat requisites contained within the moving window. We assigned SI value based on the ideal proportion of these three habitat requisites. If all three habitat requisites were present within the window in the ideal proportion, the SI value of the center cell of the window was greatest (SI = 1.00). Otherwise, the SI value was reduced based on the difference between the ideal proportion and the observed proportion. If the window did not contain one of the three habitat requisites, the center cell received SI = 0.00. The final HSI value represented the composite habitat-specific SI values modified by the SI for composition.

MODEL DEVELOPMENT AND APPLICATION

Modeling Philosophy

These models were developed for the explicit purpose of assessing habitat suitability of large geographic areas (>1000 ha) at relatively high resolution (≤30 m cell size). Within the species-specific accounts, we defined suitable habitat as either breeding habitat or year-round habitat. The primary sources of information for these HSI models were extensive literature reviews and expert opinion. When available we used empirical data in the development of suitability relationships; however, the HSI approach in general is less reliant on empirical data for model application than approaches such as resource selection functions (Manly et al. 2002). In this way, HSI models may be applied to large landscapes without labor-intensive field data collection.

Wildlife species experts participated in all stages of model development including literature summaries, initial model development, model review and refinement, and final model approval (Appendix 1). A Species Viability Evaluation Panel (SVE Panel) included species experts from state and federal agencies, the scientific research community and nongovernmental organizations. The group convened in 2002 as part of the Hoosier National Forest land management planning process to summarize relevant literature on habitat requirements and population status for species of conservation concern within the Central Hardwoods Region. Following this meeting we conducted additional literature reviews and created the initial HSI models. We presented the HSI models to the SVE Panel in January 2004. The SVE Panel suggested minor revisions to the avian species models and extensive revisions to the Indiana bat (*Myotis sodalis*) and the timber rattlesnake (*Crotalus horridus*) models. We incorporated all model revisions suggested by the SVE Panel. The SVE Panel approved all models in April 2004.

American Woodcock

Overview.—The American woodcock (*Scolopax minor*) is a migratory game species confined to North America. Woodcocks breed in the eastern United States north to the boreal forest of Canada and winter in the southeastern United States (Keppie and Whiting 1994). Woodcock habitat requirements vary by gender, time of day, and season. During the breeding season, young to mid-age forests provide feeding and diurnal roosting sites for both sexes and nesting sites for females (Keppie and Whiting 1994). At night, males use open areas for display habitat and both sexes use open areas for nocturnal roosting sites. During the nonbreeding season, woodcocks use a variety of forests, including bottomland hardwoods and upland mixed pine-hardwoods (Keppie and Whiting 1994).

An existing HSI model used small-shrub cover, large-shrub cover, sapling density, and basal area to identify woodcock diurnal habitat (Straw et al. 1986). Other studies on American woodcocks indicate that forest and mixed forest, agriculture, and developed areas provide habitat for nesting and brood rearing, feeding, and displaying (Keppie and Whiting 1994). Size of openings and the interspersion of forested and open areas are also important habitat features (Klute et al. 2000).

HSI model.—We developed an American woodcock HSI model for breeding and migration habitat in the Central Hardwoods Region. The first suitability index (SI_1) identified tree species suitable for nest sites and diurnal cover. While on the wintering grounds woodcock use a variety of forests, including upland mixed pine-hardwoods and mature longleaf pine that recently has been burned (Keppie and Whiting 1994). During breeding and migration, woodcock primarily use young deciduous forests for diurnal cover. We set $SI_1 = 0.00$ if the dominant tree type was pine, cedar, nonforest, or grassland, and $SI_1 = 1.00$ otherwise. This designation zeroed out grasslands and nonforest areas that may be used for diurnal or roosting habitat. However, we assigned value to grasslands as display and roosting habitat in SI_3. Therefore, the contribution of grasslands to the overall habitat suitability was retained in the model.

In the second suitability index (SI_2), we assigned suitability based on tree age and ELT. American woodcock use deciduous forests for nesting, foraging, and diurnal roosts (Keppie and Whiting 1994). Young to mid-age forests interspersed with openings provide nest sites and young brood habitat (Keppie and Whiting 1994). Woodcock also nest and rear broods in field/forest edges (Murphy and Thompson 1993). Young hardwoods and mixed woods with shrubs adjacent to openings provide moist ground for daytime feeding and diurnal cover (Hudgins et al. 1985, Keppie and Whiting 1994). Hudgins et al. (1985) characterized diurnal sites as having lower elevation and slope than random sites, possibly due to factors affecting food availability. In upland areas, sites used by young broods had greater soil moisture than nest sites (Murphy and Thompson 1993). We grouped ELTs to account for the influence of moisture on sites used by woodcocks. Mesic ridges, north and east slopes, and bottomlands constituted the mesic ELTs, and dry ridges and south and west slopes the dry ELTs. We assigned maximum suitability ($SI_2 = 1.00$) to stands 1–10 years of age on mesic sites and $SI_2 = 0.00$ to stands >40 years of age (Fig. 3). We used linear regression to assign suitability to stands 11–40 years of age:

$$SI_2 = 1.33 - 0.033 \times age$$

where *age* is the dominant tree age for a cell. For stands on dry ELTs, we multiplied the age function by 0.5 to reduce suitability value.

In the third suitability index (SI_3), we identified open areas suitable for display, roosting, and nesting habitat. Male woodcock use open areas, including abandoned agricultural fields, forest gaps and cuts, meadows, pastures, orchards, bogs, and other natural clearings for aerial courtship displays (Keppie and Whiting 1994). Both male and female woodcock also use open areas for night roosts, but some woodcock remain in diurnal cover (e.g., forested) at dusk (Krohn 1971, Wishart and Bider 1976) and some females move to different forested cover at dusk (Sepik and Derleth 1993). Female woodcock nest in hawthorn and crabapple fields (Liscinsky 1972) and shrubby old fields (Murphy and Thompson 1993). We assigned value to all cells 0–10 years of age based on ELT. For mesic ELTs, we assigned $SI_3 = 0.30$ and for dry ELTs we assigned $SI_3 =$

0.10. All cells with trees >10 years of age received SI_3 = 0.00. Because SI_3 assigned value to all cells 0–10 years of age, including cells containing roads or urban areas, we used SI_4 to zero out these nontarget open areas. We assigned $SI_4 = SI_3$ for grassland, cropland, and forest, otherwise SI_4 = 0.00. Therefore, suitability of open areas = SI_4.

In the fifth suitability index (SI_5), we assigned value based on the interspersion of young- to mid-age forest (SI_2) and open areas (SI_4). Klute et al. (2000) compared known woodcock habitat to random areas using buffers of multiple spatial scales and found that used sites had higher interspersion of water, wetlands, and deciduous forest, with less agricultural and developed lands. Vegetative structure (e.g., tree density, basal area, edge height) and opening size also can be used to characterize breeding habitat (Gutzwiller et al. 1983). The median distance between diurnal sites and singing grounds of singing males was 364 m (range = 50–964 m) in Pennsylvania (Hudgins et al. 1985), which is comparable to studies in Maine (Dunford and Owen 1973, Sepik and Derleth 1993). The quality of singing grounds may be determined by surrounding nesting and brood-rearing cover (Dwyer et al. 1983) because females do not move young broods far from the nest (Sepik et al. 1993) and nests often are located near display sites (Murphy and Thompson 1993). We used a moving window with a 200-m radius, which corresponds to the median distance between diurnal sites and singing grounds and the average total home range size (15 ha, range 0.3–171 ha) for male woodcock in Pennsylvania (Hudgins et al. 1985). The ideal proportion of nesting, foraging, and display habitat is approximately 80 percent nest/forage (forest) to 20 percent display (open)[2].

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[2] S. Backs, Indiana Department of Natural Resources, pers. comm.

The final habitat suitability value was the geometric mean of 1) maximum of $SI_1 \times SI_2$ (nesting and foraging) and SI_4 (display); and 2) SI_5, the interspersion of these habitats:

$$HSI = \sqrt[2]{(\max((SI_1 \times SI_2), SI_4) \times SI_5)}$$

Application to test landscape.—The first suitability index identified deciduous forest with interspersion of open areas (Fig. 4). The second suitability index, which assigned value based on tree age and ELT, identified numerous forest patches with stands 1–40 years of age. The amount and type of disturbance (e.g., fire, wind, and harvest) greatly influenced the suitability of deciduous forest. Suitability index 3 assigned value to all cells <10 years of age, including roads and urban areas, for display habitat. Suitability index 4 reclassified SI_3 and retained only grasslands, croplands, and young forest as display habitat. Suitability index 5 revealed areas with high interspersion of forest and open areas. The final HSI map reflected the locations of young forest and open areas.

Cerulean Warbler

Overview.—The cerulean warbler (*Dendroica cerulea*) is a neotropical migratory bird that breeds in eastern North America and winters in northern South America. In North America, this species is found from April to September in large tracts of mature and second-growth forests with tall deciduous trees (Hamel 2000a). Because no previous HSI model existed for cerulean warblers, we developed a new model based on reported ecological relationships gathered from an extensive literature review.

HSI model.—We developed a cerulean warbler HSI model for breeding habitat in the Central Hardwoods Region. The first suitability index (SI_1) identified suitable tree species for breeding habitat. Cerulean warblers use a variety of tree species for nesting throughout their range, including maple (*Acer* spp.), American beech (*Fagus grandifolia*), ash (*Fraxinus* spp.), black walnut (*Juglans nigra*), tulip poplar (*Liriodendron tulipifera*), oak (*Quercus* spp.), and elms (*Ulmus* spp.) (Table 3b in Hamel 2000b). Hamel (2000b) noted that G. Vanderah[3] located nests in pine trees in southern Illinois. However, Robbins et al. (1989) found a negative relationship between relative abundance of cerulean warblers and coniferous canopy cover in the Middle Atlantic states. Without published information on the use of conifers for breeding habitat, we identified only deciduous trees as suitable. We believe this restriction provided a conservative estimate of breeding habitat suitability. We accomplished this by evaluating the dominant tree type for each cell and setting $SI_1 = 0.00$ if the dominant tree type was pine or cedar, and $SI_1 = 1.00$ otherwise.

In the second suitability index (SI_2), we assigned habitat quality based on forest age and ELT. Cerulean warblers breed in mature and second-growth forests with tall deciduous trees (Hamel 2000a). Habitats include wet bottomland, mesic slope, or upland (Hamel 2000b), ranging in elevation from 30–1000 m (Hamel 2000a), though cerulean warblers may occur in greater densities in floodplains or other mesic conditions (Lynch 1981, Garber et al. 1983, Kahl et al. 1985, Robbins et al. 1992). Historical accounts indicate that cerulean warblers were found in both old-growth bottomland forests (Widmann 1895a, 1895b, 1897) and upland forests (Todd 1893, Torrey 1896, Schorger 1927). Presently, cerulean warblers often are associated with bottomland or floodplain forests, but this association may be due to the current forest distribution patterns and not necessarily due to a preference for bottomland over upland forest (Hamel 2000b). Recent

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[3] Illinois Natural History Survey, pers. comm. with Hamel, May 1993

studies indicate cerulean warblers use upland habitats and ridgetops as frequently as bottomland habitats (Rosenberg et al. 2000, Weakland and Wood 2002, Bosworth and Wood 2003, Nicholson 2003).

In the U.S. Fish and Wildlife Service (USFWS) Region 3, which includes the northern edge of the Central Hardwoods Region, cerulean warblers were more numerous in riparian bottomland forest (40 percent of birds detected) than mesic uplands (28 percent) or dry upland forest (21 percent) (Rosenberg et al. 2000). Within the Central Hardwoods Region, cerulean warblers use both upland and bottomland forests. Rosenberg et al. (2000) observed cerulean warblers in mesic upland, bottomland and lake margin habitats, and dry upland forest in Indiana. In southern Indiana, Basile and Islam (2001) reported almost exclusive use of ridges, but in earlier successional forest stages. In Ohio, cerulean warblers are associated with dry oak-hickory woodlots, mixed mesophytic forests, wet beech maple woodlands, and extensive floodplain forests (Peterjohn and Rice 1991). In western Kentucky, cerulean warblers are found in mature, relatively undisturbed deciduous forests (Mengel 1965).

We used two different functions to assign suitability to trees on mesic and dry sites (Fig. 5). For trees on mesic sites, which included mesic ridges, north and east slopes, and bottomlands, we subjectively assigned a suitability value based on the equation:

$$SI_2 = \frac{1.0104}{\left(1 + e^{((-treeage - 60.1799)/8.7242)}\right)}$$

We developed this equation by fitting a sigmoid function with $SI_2 = 0.01$ at 20 years of age, $SI_2 = 0.50$ at 60 years of age, and $SI_2 = 1.00$ for ≥100 years of age. For trees on dry ridges, we subjectively assigned a suitability value based on the equation:

$$SI_2 = \frac{0.8105}{\left(1 + e^{((-treeage - 60.2385)/9.1812)}\right)}$$

We developed this equation by fitting a sigmoid function such that $SI_2 = 0.01$ at 20 years of age, $SI_2 = 0.40$ at 60 years of age, and $SI_2 = 0.80$ for ≥100 years of age. All trees <20 years of age, as well as trees on south and west slopes, received $SI_2 = 0.00$.

In the third suitability index (SI_3), we established an area requirement by assigning a suitability value based on deciduous forest area (Fig. 6). The cerulean warbler is considered an area-sensitive species. Minimum patch sizes used by individuals varies by region, ranging from 10 ha in Ontario (Hamel 2000a), 20–30 ha in Ohio (Peterjohn and Rice 1991), 700 ha in Middle Atlantic states (Robbins et al. 1989), to 1600 ha in the Mississippi Alluvial Valley in Tennessee (Robbins et al. 1992). Cerulean warbler population surveys conducted in USFWS Region 3 found 65 percent of the birds in patches >400 ha, 25 percent in patches 80–400 ha, and 10 percent in patches <40 ha in size (Rosenberg et al. 2000). Distinguishing between minimum patch size needed for occupancy and minimum patch size needed for breeding is important because the requirements may not be synonymous. In the Middle Atlantic states, 50 percent occupancy occurs at 700 ha, with the maximum probability of occurrence at 3000 ha; however, 700 ha is the minimum area required for breeding (Robbins et al. 1989). Hamel (1992) provided a minimum tract size of 1750 ha, but it is not clear whether the requirement was for occupancy or breeding.

We distinguished between area requirements for occupancy and suitability for breeding. For breeding habitat suitability, we subjectively assigned $SI_3 = 0.01$ for 100-ha forest patches, $SI_3 = 0.10$ for 700-ha patches (minimum area required for breeding) (Robbins et al. 1989), and $SI_3 = 1.00$ for patches ≥3000 ha, and fit a sigmoid function:

$$SI_3 = \frac{1.0002}{\left(1 + e^{((-patchsize - 1173.6472)/215.5805)}\right)}$$

The final habitat suitability value was the geometric mean of the three suitability indices:

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

Application to test landscape.—Suitability index 2, which assigned value based on tree age and ELT, contributed greatly to the heterogeneous pattern observed in the final habitat suitability map (Fig. 7). Stand size, homogeneity of tree age within a stand, as well as delineation of stand boundaries will influence the pattern observed when SI_2 is applied to other landscapes. Suitability index 3, which assigned value based on forest patch size, treated continuous canopy gaps (e.g., roads, power lines, and railroads) as patch boundaries. We considered the fact that the density or proportion of forested cells within a patch may affect patch value. For example, nonforested areas contained within large forested patches may reduce patch value. Conversely, predominantly forested landscapes that contain roads may be undervalued if roads create patches. Weakland and Wood (2002) found that cerulean warblers did not avoid internal edges (such as natural canopy gaps, open-canopy or partially open-canopy roads). Thus, we assumed patch size was an appropriate and conservative measure of forest value and did not include such effects in this model.

Henslow's Sparrow

Overview.—The Henslow's sparrow is a short-distance, migratory bird that breeds in east-central North America and winters in the southeastern United States. Henslow's sparrows are a ground-nesting, obligate grassland species. Throughout their range the amount of habitat has declined from historic levels due to conversion of grasslands to intensive agricultural production, woody stem invasion (especially on abandoned agricultural lands), and fragmentation of remaining grasslands (Smith 1992). Henslow's sparrows are considered both area and edge sensitive, which may intensify the effects of habitat loss and fragmentation. Although no previous HSI model existed for Henslow's sparrows, several studies have described ecological relationships, including micro- and macro-habitat characteristics. We developed an HSI model based on reported ecological relationships and an extensive literature review. Primary sources for the literature review include Burhans (2002), Herkert et al. (2002), and references contained therein (e.g., Pruitt 1996).

HSI model.—We developed a Henslow's sparrow HSI model for breeding habitat in the Central Hardwoods Region. The HSI model contained three suitability indices that addressed land-cover type, area sensitivity, and edge sensitivity. The first suitability index (SI_1) identified grasslands as breeding habitat. Henslow's sparrows nest on the ground in grasslands, but are also found in hayfields, pastures, and meadows in the northeastern United States (Smith 1992). Both habitat structure and moisture are associated with Henslow's sparrow occupancy of grassland sites. Key structural characteristics include the presence of tall, dense grass with a well developed litter layer, standing dead vegetation, and little or no woody vegetation (Herkert et al. 2002). Henslow's sparrows may breed in fields that are infrequently mowed or lightly grazed (Skinner et al. 1984, Smith and Smith 1992, Cully and Michaels 2000), but frequent disturbance, such as burning, mowing, or haying, can render areas inhospitable (Pruitt 1996, Herkert 2001). Henslow's sparrows breed principally in mesic grasslands (Hands et al. 1989), but also in dry and wet prairies (Swengel 1996). For SI_1 we assumed the disturbance interval on the Hoosier National Forest test landscape was sufficiently long for development of the necessary structural characteristics. Therefore, we evaluated only the land-cover type for each cell and set $SI_1 = 1.00$ if the land-cover type was grassland and $SI_1 = 0.00$ otherwise. The grassland cover type included warm and cool season grasslands, as well as hayfields, pastures, and prairies. Thus, the model may over-predict suitability in landscapes where Henslow's sparrows only use grasslands.

In the second suitability index (SI_2), we addressed a grassland area requirement. The minimum patch size used by Henslow's sparrows varies by region and also depends on landscape context. Samson (1980) and Harroff (1999) found Henslow's sparrows in grassland fragments as small as 10 ha, but we found no published accounts of sparrows in patches <10 ha (but see Mazur 1996). In general, Henslow's sparrow density increases with increasing area (Winter and Faaborg 1999) and amount of grassland at the landscape level (Mazur 1996, McCoy 2000). We did not find published information to quantify a suitability relationship for the percentage of grassland at the landscape level. We refrained from subjectively assigning a landscape-level relationship and instead proceeded with a patch-level relationship. Herkert (1994) provided a quantitative estimate of the probability of occurrence based on area and estimated at least 55 ha are required to detect Henslow's sparrows 50 percent of the time. We plotted $SI_2 = 0.01$ for 10-ha patches, $SI_2 = 0.50$ for 55-ha patches, and $SI_2 = 1.00$ for 100-ha patches, and fit a sigmoid function (Fig. 8):

$$SI_2 = \frac{1.0090}{\left(1 + e^{(-1*(patchsize - 55.1692)/9.5151))}\right)}$$

We applied this function to cells where $SI_1 > 0.00$ and patch size >10 ha. For grassland patches ≤10 ha, $SI_2 = 0.00$.

In the third suitability index (SI_3), we reduced the value of grassland habitat adjacent to forest and urban edges. Henlsow's sparrows nest in grasslands with little woody cover (Herkert 1994, Pruitt 1996) and do not nest within woody edges (Winter 1999). Henslow's sparrows exhibit both a demographic response (e.g., nest success) and a distributional response (e.g., density) to habitat edges. Nest success decreased with increased proximity to woody edges (Winter and Faaborg 1999, Winter et al. 2000), probably due to an increase in predator activity near woody edges (Winter et al. 2000). Adult density also decreased with increased proximity to edges (Winter et al. 2000, Bajema and Lima 2001). We found insufficient published information to develop a function describing the relationship between distance to edge and nest success or density because most studies used categorical data. Instead, we applied a moving window of 3 × 3 cells to pixels with a $SI_1 > 0.00$. The moving window assessed the land-cover type within the window and assigned $SI_3 = 0.00$ to the center pixel if the window contained non-grassland habitat. In this way, grassland immediately adjacent to edges received no suitability value. If the moving window contained only grassland habitat we assigned $SI_3 = 1.00$ to the center pixel. In other words, the center pixel retained the value assigned in SI_1 (= 1.00 for grassland).

The final habitat suitability value was the geometric mean of SI_1 and SI_2, multiplied by SI_3, to impose the edge-sensitivity penalty:

$$HSI = \left(\sqrt[2]{SI_1 \times SI_2}\right) \times SI_3$$

Application to test landscape.—The first suitability index identified numerous patches of grassland; however, few patches exceeded the minimum patch size constraint of 10 ha (Fig. 9). Habitat suitability was greatest for large patches of grassland with minimal edge habitat.

Indiana Bat

Overview.—The Indiana bat is a federally endangered, migratory species found in deciduous forests of the eastern United States. Indiana bats use different habitats for breeding and over-wintering. Indiana bats breed and raise their young in forested areas during the summer (Cope et al. 1974, Humphrey et al. 1977) and migrate to caves or abandoned mines to hibernate during the winter (Hall 1962).

HSI model.—We developed an Indiana bat breeding season (summer) HSI model for the Central Hardwoods Region. Menzel et al. (2001) provided a review of available literature on habitat requirements for the Indiana bat, Rommé et al. (1995) developed a summer habitat HSI model, and Farmer et al. (2002) developed and evaluated an Indiana bat HSI. The Farmer et al. (2002) model contained suitability indexes for number of land-cover types, roost tree density, and percentage of landscape in forest. Of these, only roost tree density differed between sites with and without Indiana bats. Our model differs from Farmer et al.'s model in two ways. First, we used Forest Inventory Analysis data and estimates of snag density by tree age class (Fan et al. 2003) to identify potential roost trees (SI_1), as recommended by Farmer et al. (2002). Second, we accounted for solar radiation of roost trees (SI_2 and SI_4). Finally, all of the SIs in our HSI model were based on reported ecological relationships for Indiana bats in the Central Hardwoods.

The first suitability index (SI_1) addressed maternity roost trees and was a function of snag suitability and density. Indiana bats form maternity roosts under the loose bark of live, dead, or dying trees (Kurta 1995) and in tree crevices (Kurta et al. 2002). Among living trees, roosts are most commonly found in shagbark hickory (Gardner et al. 1991, Callahan et al. 1997); however, the structural characteristics of snags may be more important than the tree species (Rommé et al. 1995). We derived a roost suitability function based on snag diameter at breast height (d.b.h.) and snag density as functions of tree age. Published estimates for the d.b.h. of roost trees used by maternity colonies range from 8–83 cm (Gardner et al. 1991), with an average d.b.h. of 35.0 cm (Carter et al. 2000), 36.7 cm (Gardner et al. 1991), 40.9 cm (Kurta et al. 1996), or 58.4 cm (Callahan et al. 1997). Based on published estimates and expert opinion[4], we assumed snags become suitable (SI = 0.01) at 17 cm d.b.h.; SI = 0.50 at 30 cm d.b.h.; and SI = 1.00 at 50 cm d.b.h. We fit a sigmoid function to the values with SigmaPlot (Indiana Bat "17–50" Curve, Fig. 10).

We used snag density (number of snags/ha) by size class information from Fan et al. (2003) to estimate snag density by tree age class (Fig. 11). Fan et al. (2003) used data from remnant old-growth tracts and Forest Inventory Analysis data from Missouri to predict cavity tree and snag density as a function of rotation age. After consultation with Fan, we decided that the snag density information for age class 90 may be misrepresented due to low sample size and removed age class 90 data from the following analyses. We determined the average suitability by snag size class using the Indiana Bat "17–50" Curve (Fig. 10). We multiplied snag densities for each size class by the average

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[4] S. Amelon, Northern Research Station, U.S. Forest Service; and V. Brack, Jr., Environmental Solutions and Innovations, pers. comm.

suitability from the Indiana Bat "17–50" Curve and summed across each tree age class. We scaled the results to 0–1 by dividing each tree age class value by the maximum value (age class 110) and plotted these relative values (Fig. 12). We fit a quadratic function for snag suitability by tree age class:

$$SI_1 = 0.2930 - 0.0045 \times age + 0.0001 \times age^2$$

and used this function to assign suitability value (SI_1) to trees 1–100 years of age. Suitability was maximum ($SI_1 = 1.00$) for trees ≥100 years of age.

In the second suitability index (SI_2), we identified open habitat and early successional forest. Indiana bats forage in open areas, including pastures and old fields (Brack 1983), over or near water (Jones et al. 1985, Gardner et al. 1996), and along borders of cropland (Clark et al. 1987a, 1987b) or habitat edges (Brack 1983). For SI_2 we assigned suitability value based on tree age: stands with trees 0–20 years of age, which included open areas, croplands, roads, and water as an artifact of our age-assignment process, received the highest suitability value ($SI_2 = 1.00$) and trees >20 years of age received $SI_2 = 0.00$.

In the third suitability index (SI_3), we constrained suitability of roost tree habitat by distance to water sources. Indiana bat maternity roosts are commonly located in riparian or bottomland areas (Gardner et al. 1991, Callahan et al. 1997), including wetlands (Kurta et al. 2002). In Indiana, Humphrey et al. (1977) found two roost trees located less than 200 m from a creek that was used for foraging and Brack (1983) found a roost tree on the bank of a river. In Missouri, all reported colonies were found near a stream or river (Callahan et al. 1997). We assumed that all potential roost trees located within 1000 m of permanent water sources were accessible to Indiana bats and thus had maximum suitability ($SI_3 = 1.00$). We assigned suitability for potential roost trees located 1000–4000 m from water using the function (Fig. 13):

$$SI_3 = 1.33 - \sqrt[3]{\frac{dist}{1000}}$$

which declined linearly from $SI_3 = 1.00$ at 1000 m to $SI_3 = 0.00$ at 4000 m. Potential roost trees located more than 4000 m from a water source received $SI_3 = 0.00$.

In the fourth suitability index (SI_4), we evaluated roost exposure to solar radiation. Indiana bat maternity roosts often occur in trees exposed to direct sunlight (Humphrey et al. 1977, Kurta et al. 1993a, 1993b, Callahan et al. 1997). Solar radiation may decrease time of fetal development and increase juvenile growth (Callahan et al. 1997) or reduce metabolic costs for thermal regulation. Roost exposure to sunlight may result from gaps in forest canopy or may be due to roost location near a habitat edge. We used a 3 cell × by 3 cell moving window to evaluate the interspersion of potential roost trees (SI_1) with open areas and forest gaps (SI_2). If the center cell of the moving window had $SI_1 > 0.50$ and any adjacent cell had $SI_2 > 0.50$, then we assigned $SI_4 = 1.00$; otherwise we assigned $SI_4 = 0.00$. This procedure considered solar radiation from canopy gaps due to tree fall but did not account for canopy gaps created by large snags. Thus, it likely underestimated roost exposure to solar radiation.

The final habitat suitability value was the maximum of the composite roost site suitability or the foraging suitability:

$$HSI = Maximum\left[\left(\left(\sqrt{Maximum\left(SI_1, SI_2\right) \times SI_3}\right) \times SI_4\right), \left(Maximum(SI_1, SI_2) \times SI_3 \times 0.5\right)\right]$$

Application to test landscape.—This equation identified whether an individual cell contained a potential roost tree in forest (SI_1) or in open/early successional habitat adjacent to forest (SI_2), and then considered the value of that cell based on the potential for solar radiation (SI_4) and distance to water (SI_3) (Fig. 14). If a cell did not have value as a potential roost site (SI_1) or as an open area for foraging (SI_2), it still had value as foraging habitat or alternative (secondary) roost sites. Thus, the remainder of the equation $\left(Maximum(SI_1, SI_2) \times SI_3 \times 0.5\right)$ captured the value of forests for foraging habitat and alternative roost sites (SI_1), or the value of open areas for foraging habitat (SI_2), modified by the distance to water. Distance to water was not limiting in the test landscape and therefore $SI_3 = 1.00$. The final HSI map contained large areas of forest that may be used for foraging and alternative roost sites. The greatest potential for primary roost sites was along forest edges.

Northern Bobwhite

Overview.—The northern bobwhite is a nonmigratory game species that breeds throughout the eastern United States. In the northern part of their range, bobwhite are associated with heterogeneous, patchy landscapes that contain early successional woody cover, grasslands, and row crops (Roseberry and Sudkamp 1998). Due to their importance as a game species, northern bobwhite are a popular research species, perhaps the most intensively studied bird in the world (Guthery 1997). Several HSI (or HSI-type) models exist for northern bobwhite, including an early quantitative method for evaluating habitat from aerial photos (Backs 1981), the original HSI developed by Schroeder (1985), and several recent models that incorporate landscape-level attributes (e.g., Brady et al. 1993, Roseberry 1993, Roseberry and Sudkamp 1998, Burger et al. 2004).

HSI model.—We developed a northern bobwhite HSI model for the Central Hardwoods Region. The first suitability index (SI_1) identified grasslands used for nest sites, cover, and food. Northern bobwhite nest in fields where plant succession has progressed at least 1 year following disturbance (Dimmick 1972). Prescribed fire or mechanical disturbance conducted every 1–5 years maintains habitat conditions for bobwhite populations (Stoddard 1931, Landers and Mueller 1986). We evaluated the land-cover type for each cell and set $SI_1 = 0.50$ if the land-cover type was grassland and $SI_1 = 0.00$ otherwise.

In the second suitability index (SI_2), we identified food sources. Bobwhite eat seeds of agricultural crops and weeds, as well as forest, agricultural, and rangeland vegetation, especially understory plants and plants along field margins (Brennan 1999). Common foods include beggarweeds (*Bidens* spp.), ragweeds (*Ambrosia* spp.), *Lespedezas* spp., corn (*Zea* spp.), partridge peas (*Chamaecrista* spp.), acorns (*Quercus* spp.), sumacs (*Rhus* spp.), pine seeds (*Pinus* spp.), soybeans (*Glycine* spp.), and rowpeas (*Pisum* spp.) (Landers and Johnson 1976). Seeds from agricultural crops, such as corn, soybeans, and wheat (*Triticum* spp.), predominate fall and winter diets (Larimer 1960, Roseberry and Klimstra 1984). We assumed grasslands identified in SI_1 provided food in addition to nesting habitat and that woody edges identified in SI_3 provided food in addition to escape cover. Therefore, we used SI_2 to identify agricultural food sources. We evaluated the land-cover type for each cell and set $SI_2 = 0.40$ if the land-cover type was cropland and $SI_2 = 0.00$ otherwise.

In the third suitability index (SI_3), we identified woody edge cover. Bobwhite prefer areas where approximately 50 percent of the ground is exposed and 50 percent contains upright growth of herbaceous and woody vegetation (Schroeder 1985). Brushy or woody edges along crop fields and grasslands often meet these requirements. In addition to grasslands and croplands, bobwhite will also use open canopy (<50 percent) pinelands and mixed pine-hardwood forests (DeVos and Mueller 1993, Brennan 1999). A landscape-level assessment of bobwhite habitat suitability in Illinois associated bobwhite abundance with high woody edge density (≥30 m/ha) (Roseberry and Sudkamp 1998). Woody edge often is used for escape cover (Williams et al. 2000), thus the first 30 m of woody cover from a field edge appears the most important, with use declining with distance from the field edge. We used a 60-m moving window to identify forest within 30 m of grassland or cropland. If the center pixel contained forest ≥1 year of age and the remaining cells contained either grassland or cropland, we set $SI_3 = 0.30$ for the center pixel. Otherwise, we set $SI_3 = 0.00$.

In the fourth suitability index (SI_4), we used a moving window to evaluate interspersion of habitat types. In agricultural regions, the interspersion of nesting (grassland), food (grassland and cropland), and cover (woody edge) provide optimum habitat for bobwhite (Roseberry and Sudkamp 1998). The proportion of each habitat type varies somewhat by study: 30–65 percent row crops and 15–30 percent grassland in Illinois (Roseberry and Sudkamp 1998); 75–90 percent open land consisting of 50–60 percent cropland and 20–30 percent grassland in Missouri (Dailey 1989); and 30–40 percent grassland, 40–60 percent cropland, 5–20 percent brushy cover, and 5–40 percent woodland cover (Johnsgard 1973). We evaluated the proportion of grassland, cropland, and woody edge using a moving window with a 360-m radius. The area within the moving window equaled 40.7 ha, which approximated the maximum average northern bobwhite home range of 38 ha[5] reported within the Central Hardwoods. Estimates of

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[5] Burger, L. W., Jr., J. D. Taylor, II, T. V. Dailey, E. W. Kurzejeski, and M. R. Ryan. Unpublished report. Habitat model to predict landscape use of northern bobwhite in Missouri.

bobwhite home range size vary by season and location. Home ranges averaged 38 ha in winter in northeast Missouri[5], 9 ha (range 6–11 ha) during a late-winter period with prolonged snow cover in southern Illinois (Roseberry 1964), and 15 ha (range 12–19 ha) for late winter in a different year in Illinois (Bartholomew 1967). We based the ideal proportion on the midpoints of Roseberry and Sudkamp (1998): grassland = 0.22, cropland = 0.47, and woody cover = 0.31, and set $SI_4 = 0.50$ if the window contained the ideal proportion. The suitability value declined toward zero as a function of the difference between the observed proportion within the moving window and the ideal proportion:

$$SI_4 = 0.5 * ((1 - PROP1) * (1 - PROP2) * (1 - PROP3))$$

where $PROP1$, $PROP2$, and $PROP3$ equaled the absolute value of the observed proportion minus the ideal proportion of grassland, cropland, and woody cover, respectively. In other words, SI_4 was maximized when the observed proportions equaled the ideal proportions.

We used the fifth suitability index (SI_5) to zero out roads and urban areas that received suitability value from SI_4 because we assigned value to all cells based on the composition of habitat within the moving window. We assigned $SI_5 = 1.00$ for forest, cropland, and grassland, otherwise $SI_5 = 0.00$.

The final habitat suitability value was the sum of 1) the maximum value of SI_1, SI_2, and SI_3; and 2) the product of SI_4 and SI_5 (Fig. 15):

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

We used an additive HSI equation as opposed to a multiplicative equation because we recognized that grassland, cropland, or woody cover provided bobwhite habitat; however, the highest suitability value occurred when at least two of the three habitat types were present within the moving window.

Application to test landscape.—The first, second, and third suitability indices identified grasslands, croplands, and woody edges within the landscape. The fourth suitability index identified several areas where the interspersion of these three habitat requirements occurred. After excluding nonusable open areas (i.e., roads and urban areas), the final HSI map reflected the cumulative value of each habitat type and its interspersion. In general, grasslands adjacent to woody edges provided the greatest area of suitable habitat on the landscape.

Ruffed Grouse

Overview.—The ruffed grouse (*Bonasa umbellus*) is a nonmigratory game species that breeds throughout the boreal forests of North America and in portions of deciduous forest in the eastern United States. Ruffed grouse are associated with early successional forests in all parts of their range, including aspen and poplar forests in the north and oak-hickory or mixed deciduous-coniferous forests in the south and east (Rusch et al. 2000). Cade and Sousa (1985) developed the first HSI model for grouse; however, the model relied on aspen buds for winter food and thus has limited application within the Central Hardwoods due to the low abundance of aspen.

HSI model.—We developed a ruffed grouse HSI model for the Central Hardwoods Region. The first suitability index (SI_1) identified potential food sources for ruffed grouse. Ruffed grouse diets vary seasonally but usually contain leaves, buds, and fruits of deciduous forest plants (Rusch et al. 2000). During brood rearing, adults and chicks eat invertebrates (Bump et al. 1947) in addition to the leaves of herbaceous plants

(Norman and Kirkpatrick 1984). In late autumn and winter, hard mast, consisting primarily of white oak, red oak, chinkapin oak, and black oak acorns, are an important food source (Thompson and Fritzell 1986). We assumed hard mast was the most limiting of these food sources given its predominance in fall and winter diets and used SI_1 to estimate suitability based on acorn mast production. Sullivan (2001) developed models for acorn production based on tree age, species (white oak or red oak) and ELT, which he subsequently modified[6] for application to the Hoosier National Forest.

In the second suitability index (SI_2), we identified early successional forest used for nesting, feeding, and roosting. While ruffed grouse in the northern portion of their range are associated with aspen-dominated forests (Gullion et al. 1962, Kubisiak et al. 1980, DeStefano and Rusch 1984, Kubisiak 1984), grouse in the southern portion of their range use early successional forests containing oaks, hickories, and pines (Rodgers 1980, Gudlin and Dimmick 1984, Hunyadi 1984, Wiggers et al. 1992). Grouse also will use young cedar stands for winter roosts (Thompson and Fritzell 1988). For SI_2 we assigned suitability value based on tree age and ELT. Stands with trees 1–20 years of age on mesic ridges, slopes, and bottomlands received the highest suitability value ($SI_2 = 1.00$). Stands with trees 1–20 years of age located on dry ridges and slopes had $SI_2 = 0.80$. For both mesic and dry sites, suitability value declined to zero with increasing stand age.

In the third suitability index (SI_3), we addressed known early successional forest area requirements. Grouse home ranges vary in size depending on region and forest type. In central Pennsylvania, male home ranges averaged 5.0–9.4 ha in the breeding season and 11.0–14.0 ha in the summer (McDonald et al. 1998). Home ranges of male grouse in

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[6] N. Sullivan, Northern Research Station, U.S. Forest Service, pers. comm.

Missouri ranged from 45–68 ha in spring and summer to 84–109 ha in fall and winter (Thompson and Fritzell 1989). In southern Illinois, grouse home ranges were 26.9–226.2 ha (Woolf et al. 1984). We assumed the minimum year-round early successional forest area requirement was 4 ha; however, patches smaller than 4 ha may be used or defended during the spring (Archibald 1975, Maxson 1989). Therefore, we developed a suitability function to assign value to patches 0.01–4 ha:

$$SI_3 = patchsize / 4$$

where $patchsize$ was the area of early successional forest. Patches of early successional forest >4 ha received maximum suitability value ($SI_3 = 1.00$).

In the fourth suitability index (SI_4), we used a moving window with a 180-m radius to evaluate the interspersion of early successional forest and acorn production. The 10-ha area of the moving window corresponded to the average home range size of ruffed grouse (McDonald et al. 1998). We calculated SI_4 in three steps. First we assigned a value (M_4) based on the proportion of acorn mast within the moving window. We plotted $M_4 = 0.01$ for proportion of mast = 0.00, $M_4 = 0.50$ at 0.05, and $M_4 = 1.00$ at 0.10, and fit a sigmoid function to these values:

$$M_4 = \frac{0.999478}{\left(1 + e^{((-ppnMast - 0.0499892)/0.00288211)}\right)}$$

If the proportion of mast exceeded 0.10, the mast value was $M_4 = 1.00$. Second, we assigned a value (ES_4) based on the proportion of early successional forest that met the minimum area requirement within the moving window. We plotted $ES_4 = 0.01$ for proportion of early succesional forest = 0.00, $ES_4 = 0.50$ at 0.20, and $ES_4 = 1.00$ at 0.40, and fit a sigmoid function to these values:

$$ES_4 = \frac{1.00329}{\left(1+e^{((-ppnES-0.200233)/0.0398903)}\right)}$$

If the proportion of early successional forest exceeded 0.40, $ES_4 = 1.00$. Last, we calculated the suitability value as the product of the mast value and the early successional forest value (Fig. 16):

$$SI_4 = M_4 \times ES_4$$

In SI_1 we assumed that acorn mast was an important food source for grouse during late fall and winter (Thompson and Fritzell 1986). When applied to SI_4, this assumption will produce $SI_4 = 0.00$ when $M_4 = 0.00$. The proportion of mast within the moving window may equal zero when the proportion of early successional forest within the moving window is 1.00 (e.g., the size of an early successional forest patch exceeds the size of the moving window). Future users may want to adjust the function for M_4 such that M_4 receives a nonzero value (i.e., ≥ 0.01) to retain early successional patches in the SI_4 equation.

In the fifth suitability value (SI_5), we addressed a minimum forest area requirement. Although grouse use relatively small patches of early successional forest, these patches must be imbedded within a larger, contiguous forested area. In Missouri, grouse were released in early successional patches located within forests of 109, 259, and 1090 ha (Hunyadi 1984). Backs (1984) recommended that release locations in Indiana have a minimum of 400 ha of relatively contiguous forested area surrounded by 5–8 km^2 of primarily forested cover types. We plotted $SI_5 = 0.01$ for forested area = 100 ha, $SI_5 = 0.25$ at 200 ha, and $SI_5 = 1.00$ at 400 ha, and fit a sigmoid function to these values (Fig. 17):

$$SI_5 = \frac{1.0009}{\left(1 + e^{((-patchsize - 277.118)/24.6569)}\right)}$$

The suitability value increased to a maximum of $SI_5 = 1.00$ for patches ≥400 ha.

The final habitat suitability value was the geometric mean of 1) the maximum value of SI_1 or the geometric mean of SI_2 and SI_3; and 2) SI_4; multiplied by SI_5 (Fig. 18):

$$HSI = \left(\sqrt{Maximum\left(SI_1, \sqrt{SI_2 \times SI_3}\right) \times SI_4}\right) \times SI_5$$

Application to test landscape.—We used the maximum of either acorn mast production (SI_1) or early successional forest patches $\left(\sqrt{SI_2 \times SI_3}\right)$ because a single cell cannot provide both habitat requirements. The fourth suitability index identified several areas where the interspersion of acorn mast production and early successional forest patches occurred. After imposing the minimum forested area constraint (SI_5), the final HSI map consisted of several small patches of suitable grouse habitat (e.g., early successional forest embedded within mast-producing forest) surrounded by predominantly unsuitable habitat.

Timber Rattlesnake

Overview.—The timber rattlesnake is the only woodland rattlesnake in the eastern United States. During the active season (May – September) typical habitat includes rocky, open sites in deciduous hardwood forest (Klauber 1997) and lightly wooded clearings and oak-hickory knolls containing boulders, rock slabs, and outcrop fissures (Brown 1992). Reinert (1984a) found timber rattlesnakes in forested areas with greater surface vegetation and less rock density than in other portions of their range. Because rattlesnakes hibernate for up to 7 months of the year in southern Indiana (Walker 2000), over-wintering sites (hibernacula) are critical habitat features. We developed our HSI model based on the reported ecological relationships from studies conducted in Indiana (Walker 2000), Pennsylvania (Reinert 1984a, 1984b), New York (Brown et al. 1982, Brown 1991), New Jersey (Reinert and Zappalorti 1988), South Carolina (Andrews and Gibbons 2005), and West Virginia (Adams 2005).

HSI model.—We developed a timber rattlesnake HSI model for breeding habitat in the Central Hardwoods Region. The first suitability index (SI_1) identified early successional forested habitat used for foraging and basking. Rattlesnakes eat a variety of animals but the primary prey species are small mammals. Early successional habitat, such as canopy gaps and forest edges, affects small mammal abundance (Osbourne et al. 2005), diversity, and richness (Sekgororoane and Dilworth 1995). Additionally, canopy gaps may provide rattlesnake rookery (i.e., birthing) and basking opportunities (Adams 2005). While rattlesnakes are typically found in forests with large coarse woody debris (e.g., fallen logs) and high canopy closure, most rattlesnake relocations in southern Indiana were associated with small canopy breaks where sunlight reached the ground (Walker 2000). Gravid females were particularly associated with forest clearings in Indiana (Gibson and Kingsbury 2002) and with road edges, log landings, and regenerating hardwood stands in West Virginia (Adams 2005).

We grouped ELTs to account for the influence of moisture on vegetation growth. Mesic ridges, north and east slopes, and bottomlands constituted the mesic ELTs, and dry ridges and south and west slopes the dry ELTs. We assigned $SI_1 = 1.00$ to stands 1–10 years of age on both mesic and dry ELTs. Mesic sites with stands >10 years of age had $SI_1 = 0.00$, but stands on dry sites retained higher suitability value due to delayed canopy closure. We assigned $SI_1 = 0.50$ for stands 11–20 years of age, $SI_1 = 0.30$ for stands 21–

30 years of age, and $SI_1 = 0.10$ for stands 31–40 years of age. Dry ELTs with trees >40 years of age had $SI_1 = 0.00$.

In the second suitability index (SI_2), we identified woody debris habitat used for cover and foraging. Rattlesnakes use mid- to late-successional second growth deciduous forest with 62 percent mean canopy closure and 19.3 cm mean d.b.h. (Reinert 1984a). Males use predominantly forest sites (69 percent canopy cover) with moderate to dense forest floor vegetation (Reinert 1984b). Nongravid females used forested sites with 67 percent mean canopy cover but with less surface vegetation than male sites (Reinert 1984b). We assumed stands containing trees >100 years of age contained coarse woody debris suitable for rattlesnake use, and that suitability declined with decreasing stand age. We evaluated tree age for each cell and set $SI_2 = 0.00$ for trees 1–30 years of age. For trees 31–100 years of age, we assigned suitability using the function (Fig. 19):

$$SI_2 = \frac{treeage}{70} - 0.42857$$

We developed this equation by fitting a linear regression equation such that $SI_2 = 0.00$ at 30 years of age and $SI_2 = 1.00$ for trees ≥100 years of age.

In the third suitability index (SI_3), we evaluated the proportion of woody debris and foraging habitat using a moving window with an 850-m radius. The area within the moving window equaled 227 ha, which approximated the maximum average male rattlesnake home range size of 207 ha (Reinert and Zappalorti 1988). Home range sizes in southern Indiana averaged 174 ha (range 112–382 ha) for males and 72 ha (range 15–181 ha) for females (Walker 2000). We based the ideal proportion for foraging and woody debris cover on the average percentage canopy cover of rattlesnake locations reported by Walker (2000): foraging, basking, and rookery (open canopy) = 0.15, and woody debris cover and foraging (closed canopy) = 0.85. We set $SI_3 = 1.00$ if the window contained the ideal proportion. The suitability value declined toward zero with increasing difference between the actual proportion within the moving window and the ideal proportion.

In the fourth suitability index (SI_4), we assigned value based on proximity to den sites or hibernacula. Rattlesnake habitat requirements vary by sex and reproductive status. Gravid female rattlesnakes often bask on rocks near den sites (Reinert 1984b). The mean dispersal distance for female rattlesnakes (gravid and nongravid) in New York averaged 280 m and ranged from 191–425 m (Brown et al. 1982). In West Virginia the mean dispersal distance was 584 m (range 328–832 m) for gravid females and 872 m (range 618–1121 m) for nongravid females (Adams 2005). The spatial requirements for male rattlesnakes greatly exceed the requirements for nongravid females. Male rattlesnakes dispersed up to 1.4 km from hibernacula in New York (Brown et al. 1982) and up to 3.6 km in West Virginia (Adams 2005). Male rattlesnakes also make movements during the breeding season of 2 km (Walker 2000). Based on the large spatial requirements of rattlesnakes in New York, Brown (1993) estimated a population with 50 adults would require a 2.4 km radius of protected land around a den site. We calculated the distance from each cell to the nearest den site and assigned $SI_4 = 1.00$ to cells within 500 m of den sites. For cells located 500–2500 m from den sites, we assigned suitability using the function (Fig. 20):

$$SI_4 = 1.25 - 0.0005 \times distden$$

where *distden* is the distance from a cell to the nearest den site. Suitability declined with increasing distance from a den site. Cells located >2500 m from a den site received $SI_4 =$

0.00. This suitability index will underestimate the suitability of habitat in situations where not all den site locations are known. Therefore, comprehensive knowledge of den site locations is needed. We recommend consulting with local experts to identify den sites.

In the fifth suitability index (SI_5), we reduced the suitability value of habitat near roads. Roads may present barriers to rattlesnake movements (Fitch 1999, Sealy 2002) or reduce rattlesnake survival (Seigel and Pilgrim 2002). An experimental study on the Savannah River Site in South Carolina revealed that large rattlesnakes had a greater tendency to avoid roads than smaller rattlesnakes (Andrews and Gibbons 2005). Male rattlesnakes had higher road mortality during the breeding season than females, presumably due to increased movements associated with mate searching (Aldridge and Brown 1995). We calculated the distance from each cell to the nearest road and assigned $SI_5 = 1.00$ to cells greater than 100 m from roads. For cells <100 m from roads we assigned suitability using the function (Fig. 21):

$$SI_5 = \frac{distroad}{100}$$

where *distroad* is the distance from a cell to the nearest road. Suitability increased with increasing distance from a road.

The final habitat suitability value was the geometric mean of the maximum value of SI_1 or SI_2 multiplied by SI_3, and reduced by the product of SI_4 and SI_5 (Fig. 22):

$$HSI = \left(\sqrt{Maximum(SI_1, SI_2) \times SI_3}\right) \times SI_4 \times SI_5$$

Application to test landscape.—We used the maximum of either the first or the second suitability indices because a single cell could not contain both early successional and mid- to late-successional habitat. We reduced the value of each cell based on its distance from den sites and roads. These two requirements greatly reduced the amount of suitable habitat; the final HSI map reflects the importance of conserving near-den habitat for rattlesnakes. We used pseudo-den locations in the test landscape to demonstrate the full capability of the model without revealing actual den locations.

Wood Thrush

Overview.—The wood thrush (*Hylocichla mustelina*) is a neotropical migratory bird that breeds in eastern North America and winters in Central America. Wood thrushes nest in shrubs and small trees of deciduous, mixed-deciduous coniferous, bottomland hardwood, and pine forests with deciduous understory (Roth et al. 1996). Existing habitat studies for wood thrush indicate forest area (Robbins et al. 1989), harvest type and age (Thompson et al. 1992, Robinson and Robinson 1999, Pagen et al. 2000, Gram et al. 2003), as well as canopy height, tree density, and type of canopy cover (e.g., deciduous vs. coniferous) (Robbins et al. 1989), are important habitat features. A breeding habitat suitability index model for the Gulf of Maine watershed used vegetative cover, forest patch size, distance from edge, and moisture regime as suitability indices (Banner and Schaller 2001).

HSI model.—We developed a wood thrush HSI model for breeding habitat in the Central Hardwoods Region. The first suitability index (SI_1) identified suitable tree species for nesting habitat. Wood thrush nest in a variety of deciduous trees, and conifer stands are used if a deciduous subcanopy is present (Roth et al. 1996). We accomplished this by evaluating the dominant tree type for each cell and setting $SI_1 = 0.20$ if the dominant tree type was pine or cedar, and $SI_1 = 1.00$ otherwise.

In the second suitability index (SI_2), we assigned suitability value based on tree age and ELT. Wood thrush abundance varies by forest age with a peak in early to mid-successional forest, a decline, and then an increase in mature deciduous or mixed forest (Kahl et al. 1985). In Missouri, the density of breeding birds did not vary in regeneration (0–10 years of age), sapling (11–20 years of age), and pole and sawtimber (>20 years of age) within clearcutting sites, but was higher than uncut sites (Thompson et al. 1992). Also in Missouri, wood thrush density was greater in even-aged treatments compared to control sites 2–3 years after harvest, suggesting wood thrush use mature forest that includes some disturbance (Gram et al. 2003). Wood thrush abundance and density also varied with respect to slope. In southern Illinois, the number of wood thrush detected in ravines was greater than on ridges (Table 1 in Robinson and Robinson 1999), possibly due to differences in moisture conditions and subsequent effects on forage availability and understory development.

We ranked ELTs based on slope and moisture and multiplied that ranking by an age function to determine the suitability value. We ranked ELTs as follows: north and east slopes and bottomlands = 1.00, mesic ridges = 0.75, and dry ridges and south and west slopes = 0.50 based on Robinson and Robinson (1999). All forested stands 11–40 years of age received a suitability value corresponding to the ELT rank described above (Fig. 23). For stands 41–90 years of age, we multiplied the ELT ranking by an age function:

$$SI_2 = 4 - 0.012 \times treeage + 0.001 \times treeage^2$$

to reduce suitability value of mid-successional forests. Forest stands >91 years of age received a suitability value corresponding to the ELT rank described above.

In the third suitability index (SI_3), we addressed known forest area requirements. Wood thrushes have been detected in forest fragments as small as 0.2 ha (Robbins et al. 1989) and have successfully nested in 3-ha fragments (Friesen et al. 1999), but nest success is typically higher in larger fragments and contiguous forests. In rural Pennsylvania, nesting success in forest fragments less than 80 ha in size was usually below a sustainable level (Hoover et al. 1995). Robbins et al. (1989) suggested that the minimum area required for breeding was 1.0 ha, with a maximum probability of occurrence at 500 ha. Mueller et al. (1999) estimated forest patch size requirement for 500 breeding pairs was 2800 ha. We developed a suitability function based on the 1-ha minimum area required for occupancy in the Middle Atlantic States (Robbins et al. 1989) (Fig. 24). Although percentage forest in the landscape may be a better metric of habitat suitability than patch size, we lacked data on 1) breeding as a function of percentage forest; and 2) effective landscape size (e.g., size of moving window) in which to evaluate percentage forest. Instead, we fit a power function such that $SI_3 = 0.01$ for forest patch size = 1 ha, $SI_3 = 0.50$ for forest patch size = 100 ha, and $SI_3 = 1.00$ for forest patches ≥500 ha:

$$SI_3 = 0.0568 \times patchsize^{(0.4626)}$$

In the fourth (SI_4) and fifth suitability indexes (SI_5), we addressed the interspersion of post-fledging habitat and breeding habitat. Recent studies indicate juvenile (Anders et al. 1998, Vega Rivera et al. 1998) and adult wood thrush (Thompson et al. 1992, Pagen et al. 2000, Gram et al. 2003) used early successional and mature forest during breeding and post-breeding. Juvenile wood thrush used early successional forest (<30 years of age), including abandoned farms, roadsides, and forest openings, and use shifted to mature deciduous forest late in the post-fledging period (Vega Rivera et al. 1998). Survival of post-fledging juvenile wood thrush increased with an increase in shrub density associated with mid-successional or edge habitats within forest fragments in Missouri (Fink 2003). For juveniles, the distance between natal area and first dispersal sites varied, but averaged 1.5 ± 0.3 km in Virginia (Vega Rivera et al. 1998) and 2.2 ± 0.3 km in Georgia (Lang et al. 2002). In Missouri, the mean distance for first dispersal was 824.5 m, and total average dispersal distance was 1067 m (Fink 2003). We used SI_4 to assign suitability value to cells with stands 11–40 years of age. We applied a moving window (SI_5) with a 1-km radius to SI_4 and determined the proportion of 11–40 year old habitat in the window. We assumed the minimum suitability value was 0.10 irregardless of the proportion of post-fledging habitat within the moving window. We also assumed that the maximum suitability value was reached when the proportion of post-fledging habitat = 0.20. If the proportion of post-fledging habitat ranged from 0.0–0.40, we assigned suitability value using the function (Fig. 25):

$$SI_5 = e^{-0.5\times\left(\frac{(ppnPFhab-0.200)}{0.0932}\right)^2}$$

We developed this equation using a Guassman function such that $SI_5 = 0.10$ if the proportion of post-fledging habitat = 0.00 or 0.40, and $SI_5 = 1.00$ if the proportion of post-fledging habitat = 0.20. If the proportion of post-fledging habitat exceeded 0.40, then $SI_5 = 0.10$. The 1-km moving window was computationally intensive and may be prohibitive when multiple model runs are conducted. In forested landscapes that have diverse and juxtaposed stand ages, SI_5 might be omitted without compromising the general utility of the HSI model. However, knowledge of site-specific conditions and known dispersal distances by wood thrush should be considered before omitting SI_5. We recommend comparison of HSI results with and without SI_5 to aid in the decision process.

The final habitat suitability value was the geometric mean of SI_2, SI_3, and SI_5, multiplied by SI_1 to account for reduced suitability of pines (Fig. 26):

$$HSI = SI_1 \times \left(\sqrt[3]{SI_2 \times SI_3 \times SI_5} \right)$$

Application to test landscape.—Suitability index 2, which assigned value based on tree age and ELT, contributed greatly to the heterogeneous pattern observed in the final habitat suitability map. Stand size, homogeneity of tree age within a stand, as well as delineation of stand boundaries will influence the pattern observed when SI_2 is applied to other landscapes. Suitability index 3, which assigned value based on forest patch size, treated continuous canopy gaps (e.g., roads, power lines, and railroads) and nonforested areas as patch boundaries. Natural disturbance from wind and fire, combined with moderate tree harvest, created post-fledging habitat. While the moving-window analysis was computationally intensive due to the large size of the window, it identified several large areas with low interspersion of breeding and post-fledging habitat. When applied to other landscapes, consideration of the known dispersal distances and the level of disturbance should be made before committing computer resources to calculation of SI_5. The final HSI map reflected the diversity of stand ages, sizes, and fire histories.

Worm-eating Warbler

Overview.—The worm-eating warbler (*Helmitheros vermivorus*) is a neotropical migratory bird that breeds in eastern North America and winters in Central America and the Greater Antilles. Worm-eating warblers nest on the ground in large tracts of mature deciduous and mixed-deciduous-coniferous forests with moderate to steep slopes and patches of dense understory shrubs (Hanners and Patton 1998). Existing habitat studies for worm-eating warblers indicate forest area (Robbins et al. 1989, Wenny et al. 1993, Gale et al. 1997), forest edge (Wenny et al. 1993), slope (Robbins et al. 1989, Wenny et al. 1993), prescribed fire (Artman et al. 2001), harvest type and age (Thompson et al. 1992, Robinson and Robinson 1999, Pagen et al. 2000, Gram et al. 2003), as well as canopy height, tree density, moisture gradient, and foliage density up to 1 m (Robbins et al. 1989), are important habitat features.

HSI model.—We developed a worm-eating warbler HSI model for breeding habitat in the Central Hardwoods Region. The first suitability index (SI_1) identified suitable tree species for nesting habitat. Worm-eating warblers rarely occur in pine forest (James and Neal 1986, McNair and Post 1993). Without published information on the use of conifers for nest sites, we identified only deciduous trees as suitable for nesting habitat. We accomplished this by evaluating the dominant tree type for each cell and setting $SI_1 = 0.00$ if the dominant tree type was pine or cedar, and $SI_1 = 1.00$ otherwise.

In the second suitability index (SI_2), we assigned suitability value based on tree age and ELT. Worm-eating warblers inhabit large tracts of mature forest. In addition to mature forest, worm-eating warblers use early successional forest during the breeding (Robinson and Robinson 1999, Pagen et al. 2000) and post-breeding periods (Pagen et al. 2000). Several studies associate worm-eating warblers with moderate to steep slopes (Mengel 1965, Wenny et al. 1993, Gale et al. 1997, Faaborg et al. 1998), but they also use ridges (Dunn and Garrett 1997, Robinson and Robinson 1999). The distribution of worm-eating warblers also is associated with a moisture gradient, with increased abundance associated with increased moisture (Robbins et al. 1989). Artman et al. (2001) had a higher proportion of territories in mesic than intermediate and xeric sites.

We ranked ELTs based on slope and moisture and multiplied that ranking by an age function to determine the suitability value. We ranked ELTs as follows: ravines (slopes) = 1.00 and ridges = 0.859 (from Table 1 in Robinson and Robinson 1999); mesic sites = 1.00, intermediate sites = 0.660, and xeric sites = 0.226 (from Table 5 in Artman et al. 2001). All forested stands <39 years of age received a suitability value corresponding to the ELT rank described above (Fig. 27). For stands 40–89 years of age, we multiplied the ELT ranking by an age function:

$$SI_2 = 17.125 - 0.7698 \times treeage + 0.01125 \times treeage^2 - 0.000052083 \times treeage^3$$

to reduce suitability value of mid-successional forests (Fig. 27). Forest stands ≥90 years of age received a suitability value corresponding to the ELT rank described above.

In the third suitability index (SI_3), we addressed known forest area requirements. The worm-eating warbler is considered an area-sensitive species. Robbins et al. (1989) found worm-eating warblers in isolated forest fragments as small as 21 ha in the Middle Atlantic States, but they suggested that the minimum area required for breeding was 150 ha with a maximum probability of occurrence at 3000 ha. Nesting success in small forest fragments (21–56 ha) located within a 70 percent forested landscape (10-km radius) in southern New England was similar to nesting success in a large, unfragmented forest exceeding 750 ha in size (Gale et al. 1997), suggesting that landscape context may ameliorate nesting success in small forest fragments. Worm-eating warblers may also be an edge-sensitive species, but determining whether edge sensitivity occurs in addition to area sensitivity or is an artifact of the distribution of forest remnants (e.g., along moderate to steep slopes unsuitable for agriculture or development) is an area for further research. In the oak-hickory forests of central Missouri, worm-eating warblers did not occupy a 300-ha isolated forest with over 40 percent forest edge, but occupied an isolated forest of 340 ha with less than 10 percent forest edge (Wenny et al. 1993). Worm-eating warblers bred in an 800-ha forest with less than 10 percent forest edge that was connected to forest along the Missouri River (Wenny et al. 1993).

We developed a suitability function based on the minimum area (150 ha) required for occupancy in the Middle Atlantic States (Robbins et al. 1989) and in Missouri (340 ha) (Wenny et al. 1993) (Fig. 28). For forest patches 0–1000 ha, we assigned suitability using the following function:

$$SI_3 = \frac{1.0032}{\left(1 + e^{((-patchsize - 530.1425)/81.8617)}\right)}$$

We developed this equation by fitting a sigmoid function such that $SI_3 = 0.01$ for 150-ha patches, $SI_3 = 0.10$ for 340-ha patches, and $SI_3 = 1.00$ for patches ≥1000 ha.

In the fourth suitability index (SI_4), we reduced suitability value based on fire history for the previous decade. Worm-eating warblers nest on the ground in depressions along steep slopes (Gale 1995) and thus are susceptible to the effects of fire on nest habitat. Site moisture levels may mitigate the initial effects of fire, but the proportion of breeding territories and the density of adults declines in the first breeding season post-burn (Artman et al. 2001). Over time, additional fires result in a continued decline in density with no recovery to preburn conditions observed 1 year post fire (Artman et al. 2001). Aquilani et al. (2003) reported no difference in worm-eating warbler abundance in unburned and burned areas 1–4 years post-burn, suggesting that the effects of fire may be relatively short-lived. We accounted for the effects of fire that extend several years post-burn but did not completely devalue the habitat for the entire decade because our model input consisted of a fire history for the previous decade. We assigned a suitability value of 0.50 to a cell where fire occurred during the previous decade and 1.00 to unburned cells. In applications with shorter time steps (e.g., annual instead of decade), SI_4 should be adjusted to increase the fire penalty. Additionally, we assumed fires of different intensities affected worm-eating warblers similarly and assigned a single suitability value based on the presence of fire regardless of intensity. However, SI_4 may be adjusted to assign suitability value based on fire intensity.

The final habitat suitability value was the geometric mean of SI_1, SI_2, and SI_3, multiplied by SI_4, to account for reduced suitability due to fire (Fig. 29):

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

Application to test landscape.—Suitability index 2, which assigned value based on tree age and ELT, contributed greatly to the heterogeneous pattern observed in the final habitat suitability map. Stand size, homogeneity of tree age within a stand, as well as delineation of stand boundaries will influence the pattern observed when SI_2 is applied to other landscapes. Suitability index 3, which assigned value based on forest patch size, treated continuous canopy gaps (e.g., roads, power lines, and railroads) and nonforested areas as patch boundaries. Prescribed burning (SI_4) reduced suitability for approximately 5 percent of the landscape. The final HSI map reflects the diversity of stand ages, sizes, and fire histories.

Yellow-breasted Chat

Overview.—The yellow-breasted chat (*Icteria virens*) is a migratory bird that breeds in North America and winters in Central America. Chats are considered a disturbance-dependent shrubland species (Eckerle and Thompson 2001). In the eastern and Midwestern United States, chats are found in early second-growth forest and shrubs in abandoned agricultural fields, clear-cuts, power-line corridors, fencerows, forest edges and openings (Eckerle and Thompson 2001). Like other shrubland bird species, the yellow-breasted chat is both area and edge sensitive (Annand and Thompson 1997, Woodward et al. 2001, Rodewald and Vitz 2005). Because no previous HSI model existed for yellow-breasted chats, we developed a new model based on reported ecological relationships gathered from extensive literature review.

HSI model.—We developed a yellow-breasted chat HSI model for breeding habitat in the Central Hardwoods Region. The first suitability index (SI_1) identified early successional forest habitat and old fields for nesting habitat. Yellow-breasted chats nest in low, dense, deciduous and coniferous vegetation (Eckerle and Thompson 2001), and use old fields when woody plants invade and reach peak densities in dense shrub thickets (Shugart and James 1973). Chats also colonize clearcuts and power-line corridors (Kroodsma 1982). Use of old fields in Indiana declined when saplings shaded 50 percent of the ground (Kahl et al. 1985). In Virginia, chats were present in mixed-oak stands 3–12 years of age (Connor and Adkisson 1975). In southeast Missouri, chat numbers were higher in clearcut areas than shelterwood, group selection, or single-tree selection forest regeneration methods (Annand and Thompson 1997).

We assigned a suitability value to each cell based on tree age and ELT (Table 4). All forested stands <10 years of age received $SI_1 = 1.00$ for both mesic and dry ELTs. On the two driest ELTs, suitability value declined as tree age increased to 40 years.

Trees ≥41 years of age on dry ELTs and trees ≥11 years of age on mesic ELTs had SI_1 = 0.00.

In the second suitability index (SI_2), we addressed an early successional forest area requirement. The minimum patch size used by yellow-breasted chats varies by region and type of opening, but chats are rarely detected in patches <0.40 ha (Robinson and Robinson 1999). The minimum patch size for breeding may be larger than 0.40 ha observed by (Robinson and Robinson 1999). For example, chats nested in uneven-aged openings of 0.14–0.58 ha in Missouri, but nested in higher densities in even-aged openings of 3–13 ha (Gram et al. 2003). Patch size in old fields surrounded by oak-hickory forest ranged from 2.4–16.3 ha in Missouri (Burhans and Thompson 1999). We developed a breeding suitability function for patches of contiguous cells where SI_1 >0.00 and applied the function to patches 0.01–5 ha in size (Fig. 30):

$$SI_2 = \frac{1.0442}{\left(1 + e^{((-patchsize - 3.3389)/0.5965)}\right)}$$

We developed this equation by fitting a sigmoid function such that SI_2 = 0.01 for 0.4 ha patches, SI_2 = 0.10 for 2.0 ha patches, and SI_3 = 1.00 for patches ≥5 ha. Patches ≤0.01 ha had SI_2 = 0.00.

In the third suitability index (SI_3), we reduced the value of early successional habitat adjacent to mid- to late-succesional forest and urban edges. Yellow-breasted chats are considered edge sensitive, with reduced captures of both hatch-year and after-hatch-year chats near mature-forest edges (Rodewald and Vitz 2005). Edge avoidance likely occurs for a variety of reasons, including reduction in nest predation rates; yellow-breasted chat nests located within 20 m of a forested edge had higher daily predation rates than nests located ≥20 m from a forested edge (Woodward et al. 2001). We applied a moving window with a 20-m radius to cells with $SI_1 > 0.00$. The moving window reduced the value of cells located <20 m from a nonsuitable edge ($SI_3 = 0.00$), but retained the value assigned in SI_1 for cells located >20 m from a nonsuitable edge ($SI_3 = SI_1$).

The final habitat suitability value was the geometric mean of SI_1 and SI_2, multiplied by SI_3, to impose the edge-sensitivity penalty (Fig. 31):

$$HSI = \left(\sqrt[2]{SI_1 \times SI_2}\right) \times SI_3$$

Application to test landscape.—The first suitability index identified numerous patches of early successional forest ranging in size from 0.10–7.52 ha (Fig. 31). Imposing the minimum patch size constraint removed only patches created by small-scale disturbance (e.g., treefall gaps) and identified 10 patches greater than 5 ha ($SI_2 = 1.00$). The edge penalty had a large effect on the amount of suitable habitat. Small patches and irregularly shaped patches (e.g., linear) had a higher proportion of habitat lost to the edge penalty than large, regularly shaped patches (e.g., round). In addition to patch size and shape, harvest type also will influence the amount of habitat lost to the edge penalty. Harvest techniques that retain trees in older size classes (e.g., from selective harvest, shelterwood) will lose a greater amount of habitat to the edge penalty than even-aged techniques.

CONCLUSIONS

The landscape-level, GIS-based habitat suitability models we developed represent the state of our knowledge, given tradeoffs between model complexity and model utility. We quantified the suitability relationships using information gained from empirical studies and expert opinion. Some models had detailed functions describing suitability relationships because existing data supported the complexity of those relationships, whereas other models had sigmoid or linear functions that described the same relationship. For example, both the wood thrush and the worm-eating models had age × ELT-specific functions (Fig. 23, Fig. 27) supported by point count, nesting, mist-netting, and radio-telemetry data, for both nesting and post-fledging habitat use. Contrast this with the American woodcock age × ELT functions (Fig. 3), which were developed from a more limited database. The resulting suitability relationship clearly lacks the specificity of the wood thrush or worm-eating warbler functions. The importance of data collection during different parts of the breeding season cannot be overemphasized. Additional research may reveal whether the functions used in other models are equally complex or as simple as we portrayed them. In this way, the HSI models reveal the limitations of existing data and suggest areas where additional research efforts may be focused.

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Table 1. Wildlife species selected for habitat suitability modeling in the Central Hardwoods Region and their management or conservation status.

Species	Scientific name	Management or conservation description
American woodcock	*Scolopax minor*	Disturbance-dependent, migratory game bird
Cerulean warbler	*Dendroica cerulean*	Late-successional, area-sensitive songbird
Henslow's sparrow	*Ammodramus henslowii*	Grassland-dependent, area- and edge-sensitive songbird
Indiana bat	*Myotis sodalis*	Snag- and cave-roosting bat, endangered species
Northern bobwhite	*Colinus virginianus*	Disturbance-dependent game bird
Ruffed grouse	*Bonasa umbellus*	Early successional forest-dependent game bird
Timber rattlesnake	*Crotalus horridus*	Threatened species
Wood thrush	*Hylocichla mustelina*	Forest-dependent songbird
Worm-eating warbler	*Helmitheros vermivorus*	Late-successional, fire-sensitive songbird
Yellow-breasted chat	*Icteria virens*	Disturbance-dependent songbird

Table 2. Dominant overstory tree species (or species group) classifications for the Central Hardwoods Region.

Species Code	Name	Species / Description
1	Nonforest	cropland, urban areas, roads, or water
2	n/a	species code not used
3	Eastern red cedar	*Juniperus virginiana*
4	Pine	*Pinus echinata* and *P. strobus*
5	Sugar maple	*Acer saccharum*
6	Red maple	*Acer rubrum*
7	Hickories	*Carya* spp.
8	American beech	*Fagus grandifolia*
9	White and green ash	*Fraxinus americana* and *F. pennsylvanica*
10	Yellow poplar	*Liriodendron tulipifera*
11	Black cherry	*Prunus serotina*
12	White oak	*Quercus alba*
13	Chestnut oak	*Q. prinus*
14	Red oaks	*Q. rubra*, *Q. falcata*, *Q. velutina*, and *Q. coccinea*
15	Shingle and pin oak	*Q. imbricaria* and *Q. palustris*
16	American elm	*Ulmus americana*
17	Grassland	cool or warm season grassland, pasture, or hay fields

Table 3. Ecological land type codes and descriptions for the Central Hardwoods Region.

Code	ELT	Description
1	Dry ridges	Summit or upper shoulder slope positions with ridgetops generally narrower than 75 m and slope gradient <15%.
2	South and west slopes	Backslope positions with generally south aspect and slope gradient >15%.
4	Mesic ridges	Summit or upper shoulder slope positions with broad, flat ridgetops generally wider than 75 m and slope gradient <15%.
5	North and east slopes	Backslope positions with generally north aspect and slope gradient >15%.
6	Bottomlands	Bottomland positions along minor stream valleys and floodplains of minor streams
7	Water	Water

Table 4. Nesting habitat suitability by tree age and ecological land type (ELT) for yellow-breasted chats. We assigned maximum suitability ($SI_1 = 1.00$) to stands 1–10 years of age on all ELTs. Suitability declined to zero for stands 11–40 years of age on the two driest ELTs. Stands >11 years of age on mesic ELTs and stands >41 years of age on all ELTs had no suitability ($SI_1 = 0.00$).

	SI_1				
Stand Age	Dry Ridges	S and W Slopes	Mesic Ridges	N and E Slopes	Bottomlands
1 – 10	1.00	1.00	1.00	1.00	1.00
11 – 20	0.50	0.50	0.00	0.00	0.00
21 – 30	0.30	0.30	0.00	0.00	0.00
31 – 40	0.10	0.10	0.00	0.00	0.00
≥41	0.00	0.00	0.00	0.00	0.00

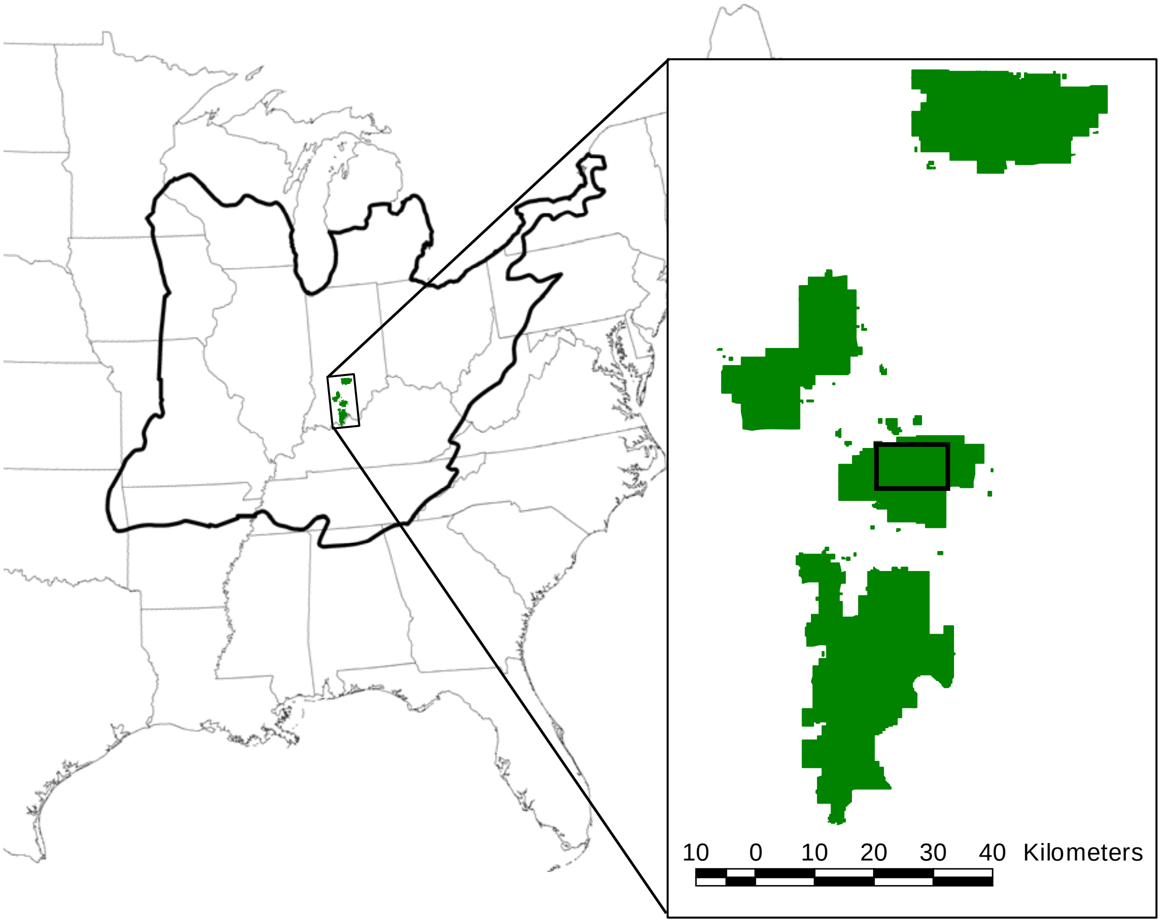

Figure 1. The Central Hardwoods Region of the Midwestern United States includes the Hoosier National Forest in Indiana. The 4,281 ha display area within the Patoka district is outlined.

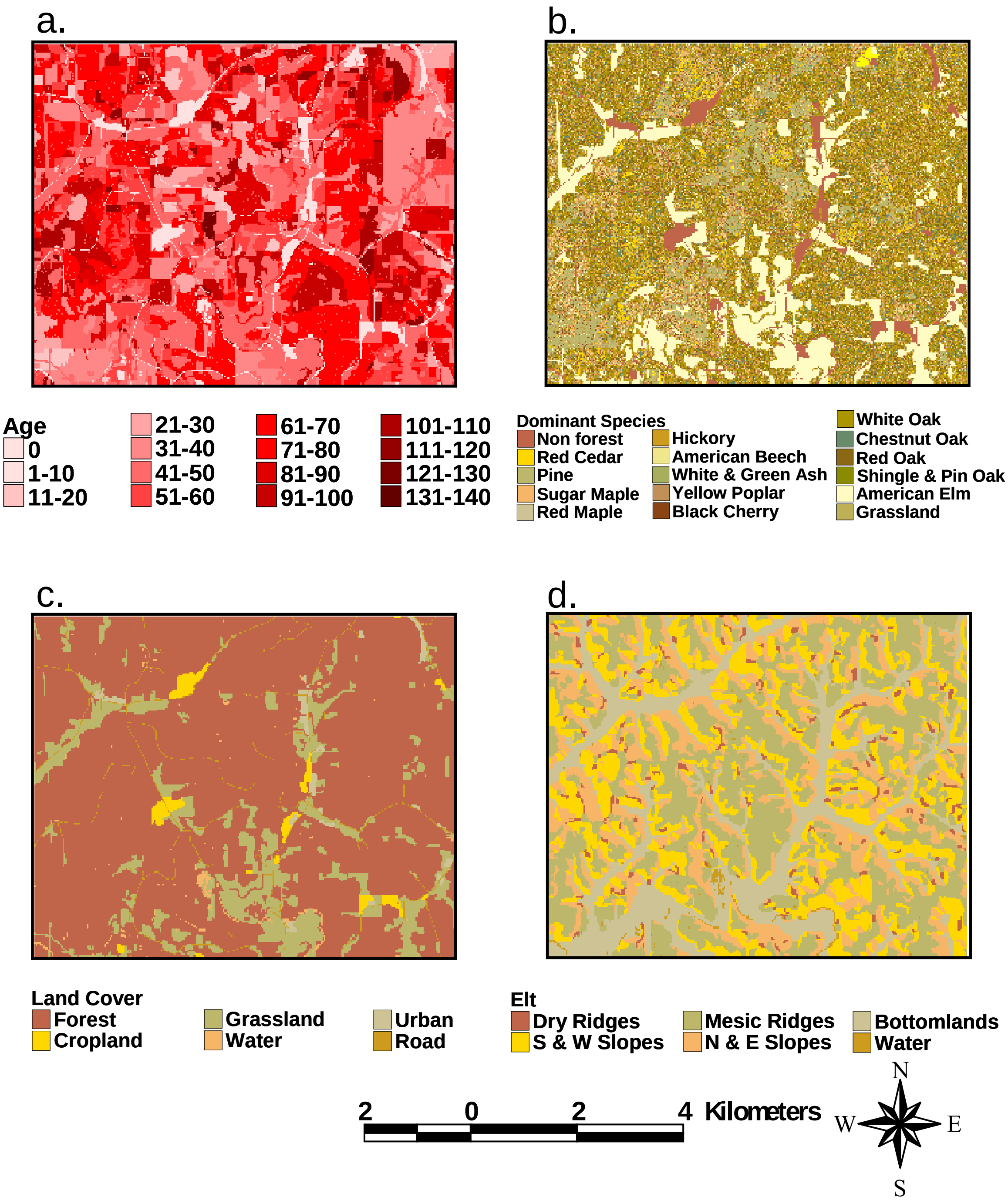

Figure 2. Primary input data for landscape-level HSI models developed for the Central Hardwoods Region. Information included tree age (a), dominant overstory species (b), land-cover type (c), and ecological land type (d).

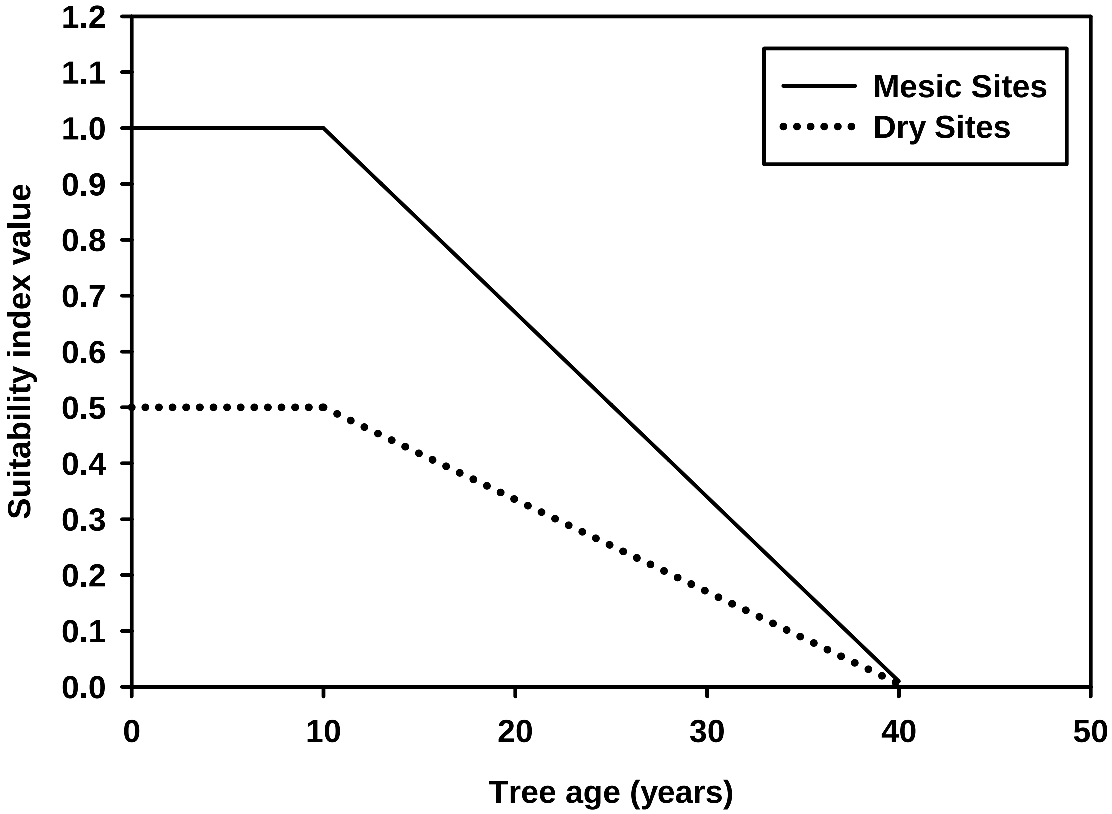

Figure 3. American woodcock habitat suitability as a function of stand age and ecological land type. Suitability value (SI2) on mesic sites (mesic ridges, north and east slopes, and bottomlands) = 1.00 at maximum (solid line). Suitability value (SI2) on dry sites (dry ridges and south and west slopes) = 0.50 at maximum (dashed line).

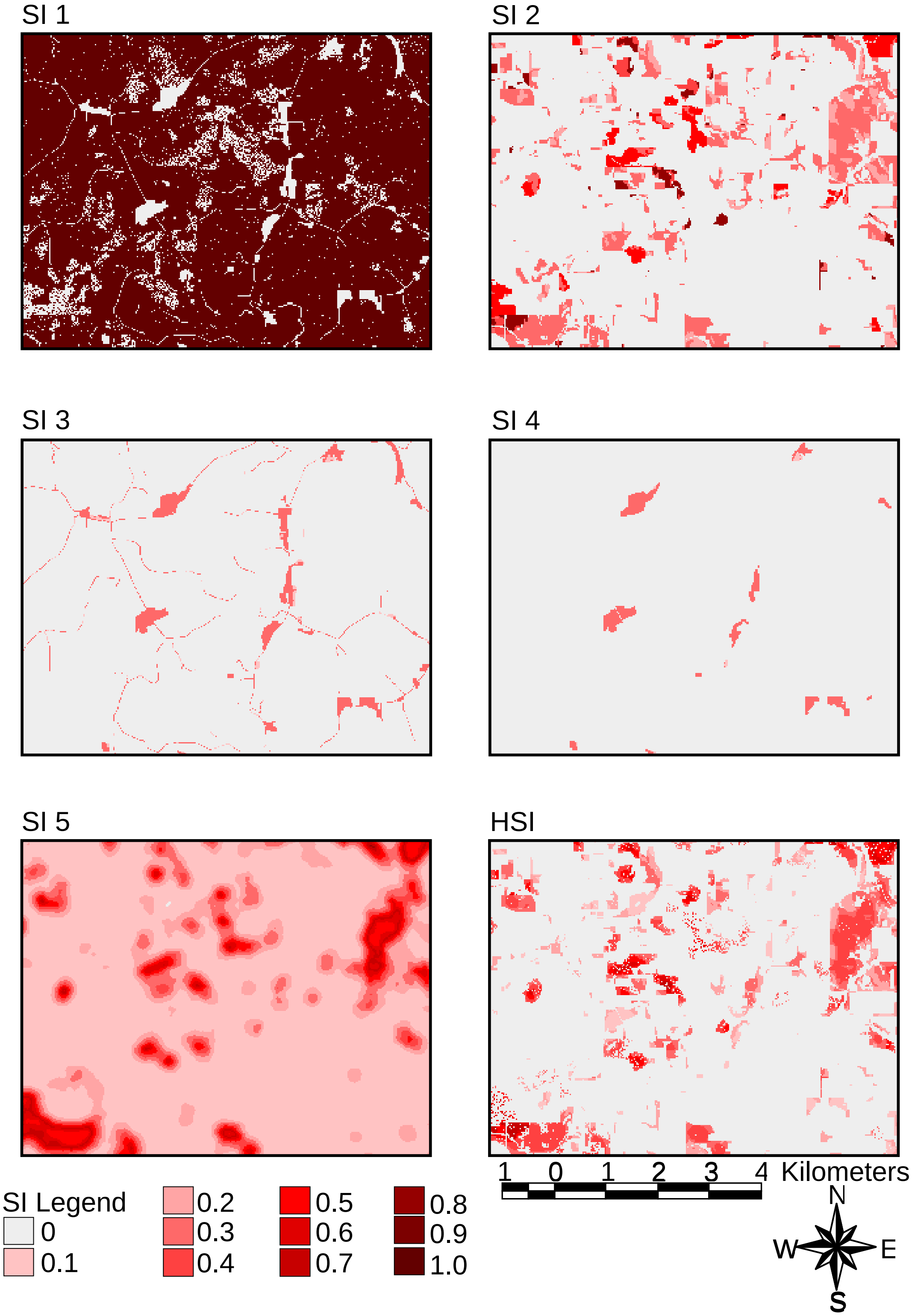

Figure 4. American woodcock habitat suitability for a 4,281-ha portion of the Hoosier National Forest, Indiana.

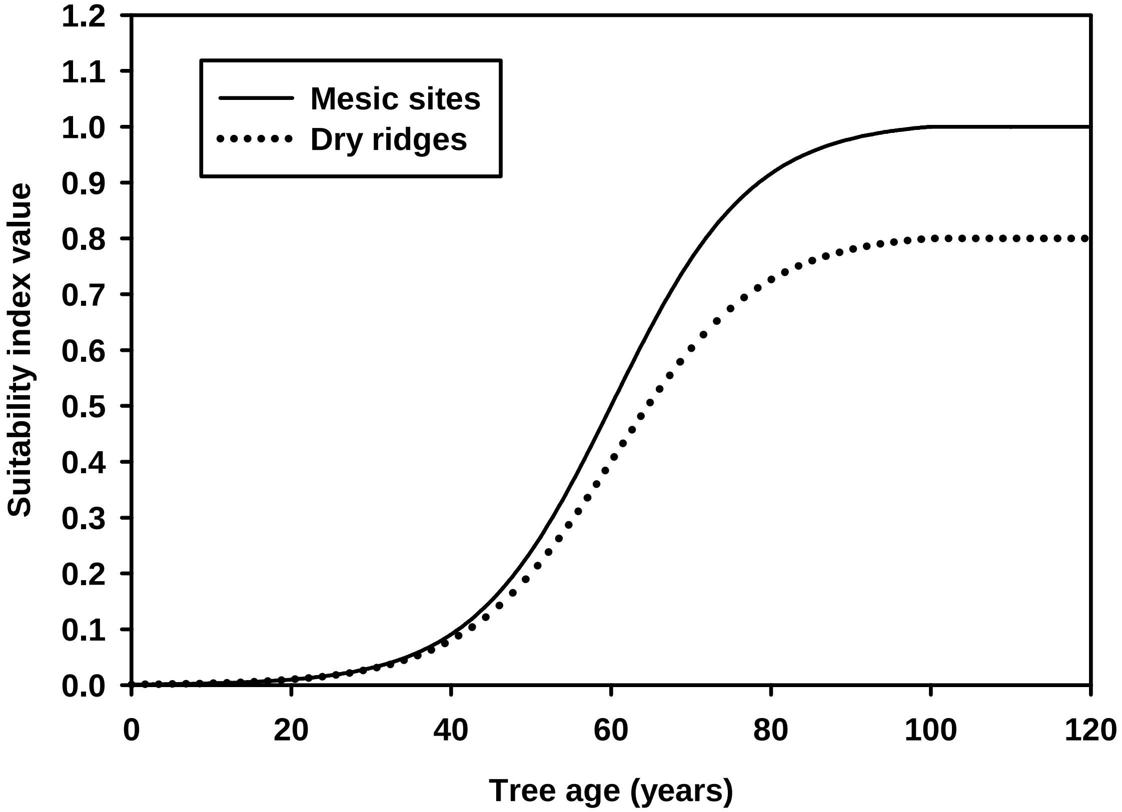

Figure 5. Cerulean warbler habitat suitability for breeding as a function of stand age and ecological land type. Suitability value (SI_2) on mesic sites (mesic ridges, north and east slopes, and bottomlands) = 1.00 at maximum (solid line). Suitability value (SI_2) on dry ridges = 0.80 at maximum (dashed line).

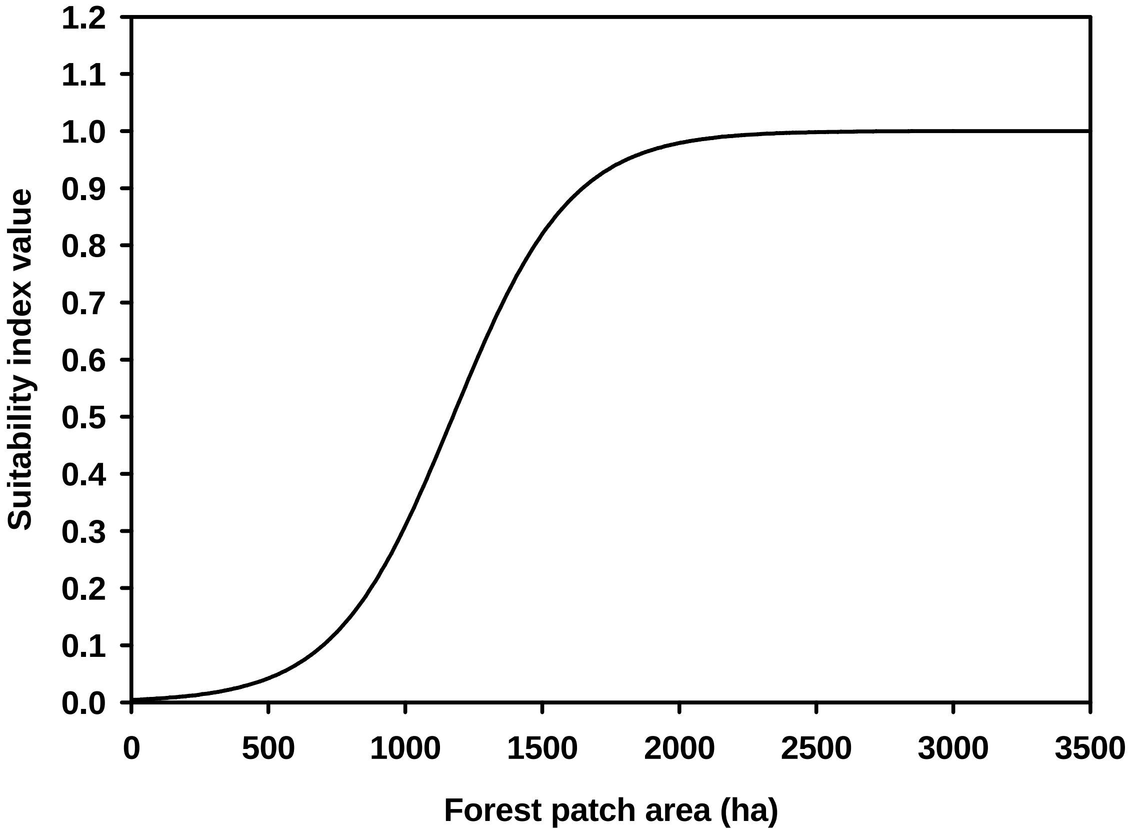

Figure 6. Cerulean warbler habitat suitability for breeding as a function of deciduous forest area. Suitability value (SI_3) = 0.10 at 700 ha (min. area required for breeding, Robbins et al. 1989). Suitability value is maximum (= 1.00) for 3000 ha patches.

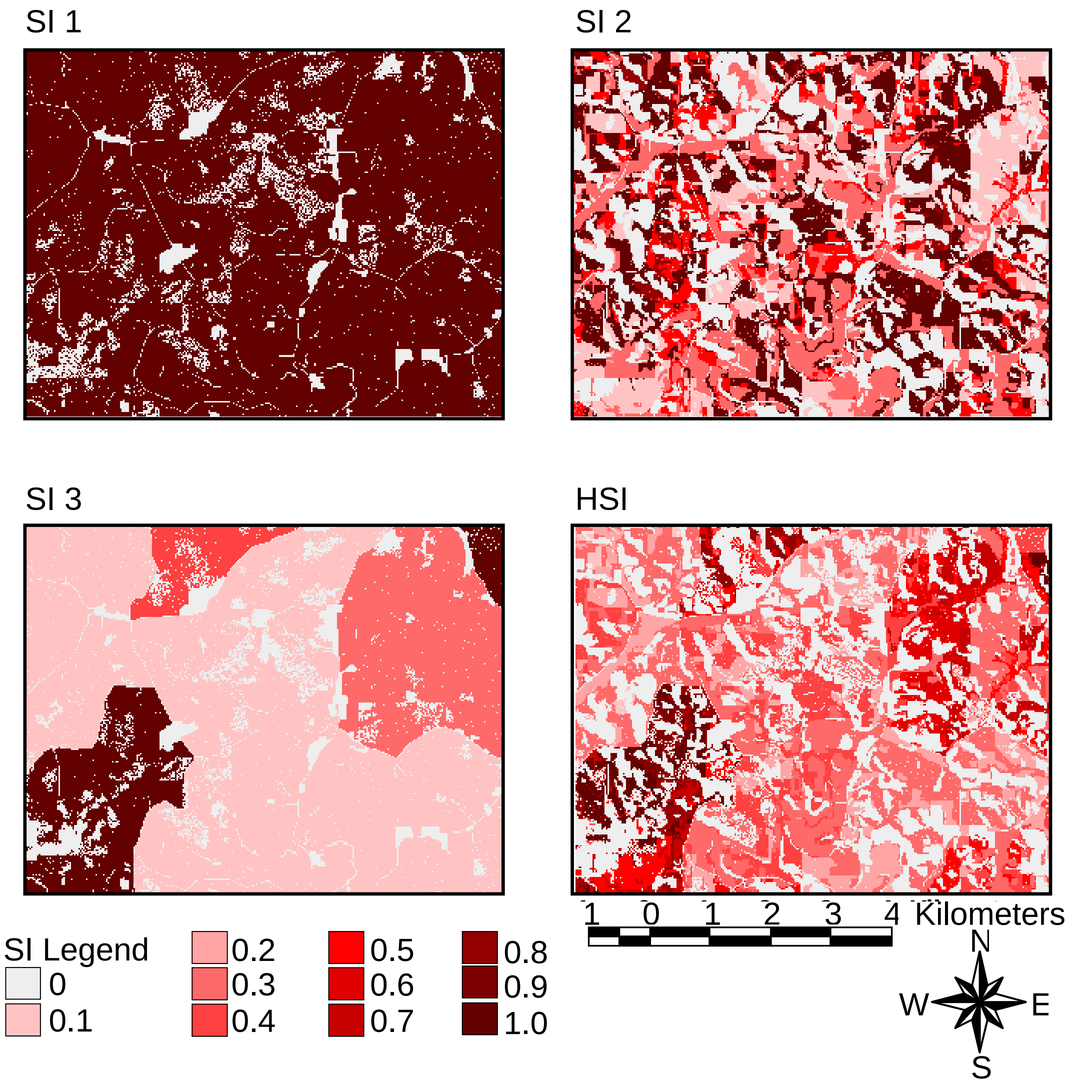

Figure 7. Cerulean warbler habitat suitability for breeding on a 4,281-ha portion of the Hoosier National Forest, Indiana. The final habitat suitability value was the geometric mean of three suitability indices.

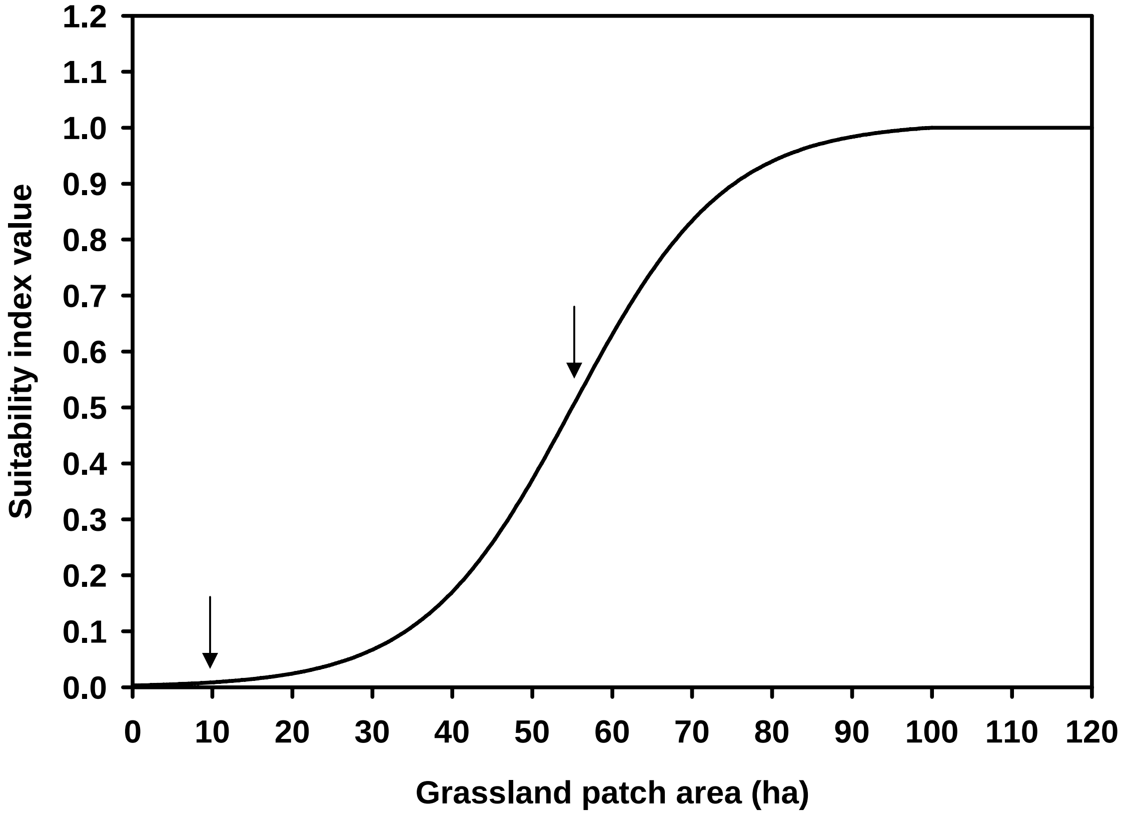

Figure 8. Henslow's sparrow habitat suitability for breeding as a function of grassland area. Left arrow indicates 10 ha (minimum area requirement, Samson 1980, Harroff 1999) and right arrow indicates 55 ha (50 percent occurrence, Herkert 1994). Suitability value (SI_2) = 0.00 for patches ≤10 ha and SI_2 = 1.00 for patches >100 ha.

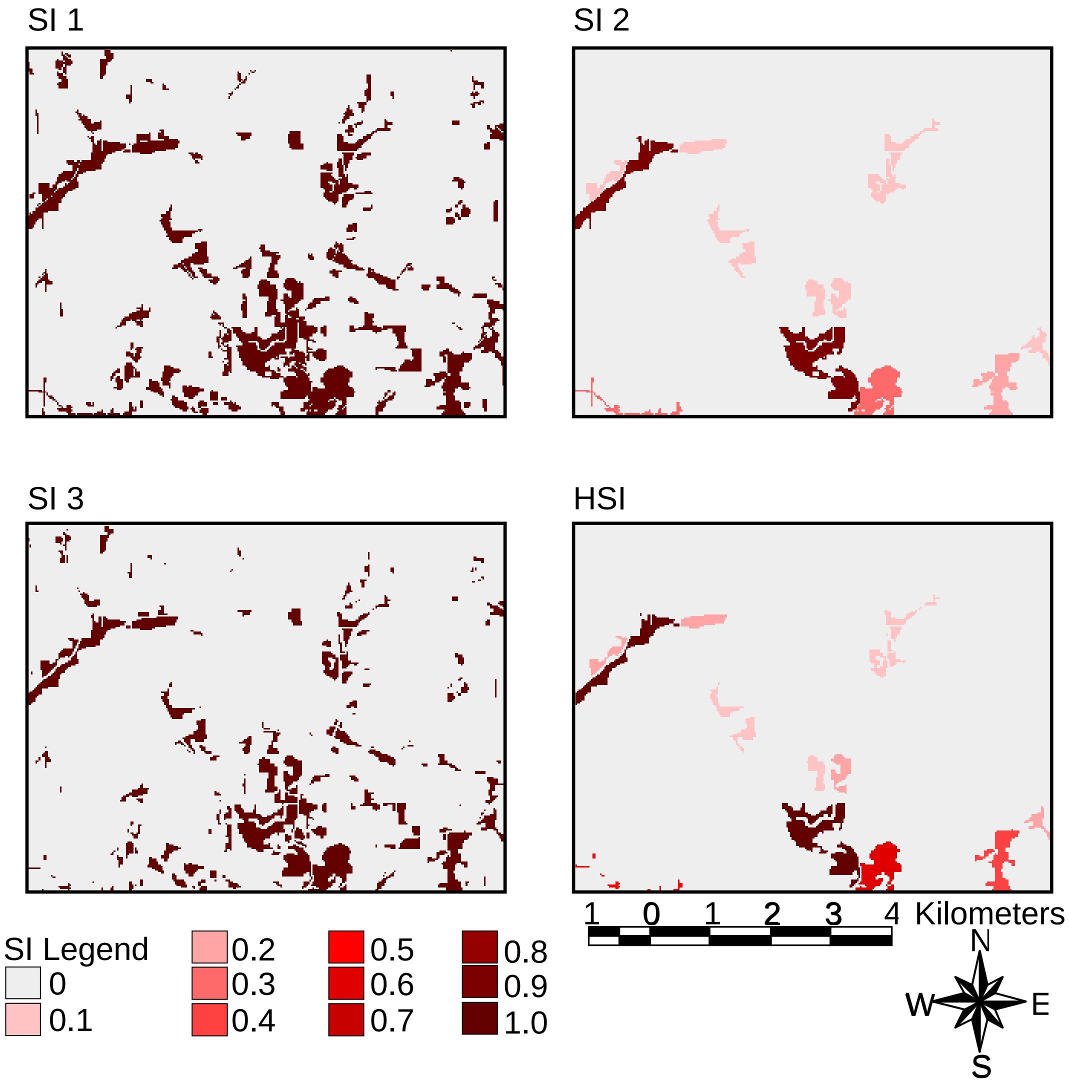

Figure 9. Henslow’s sparrow habitat suitability for breeding on a 4,281-ha portion of the Hoosier National Forest, Indiana.

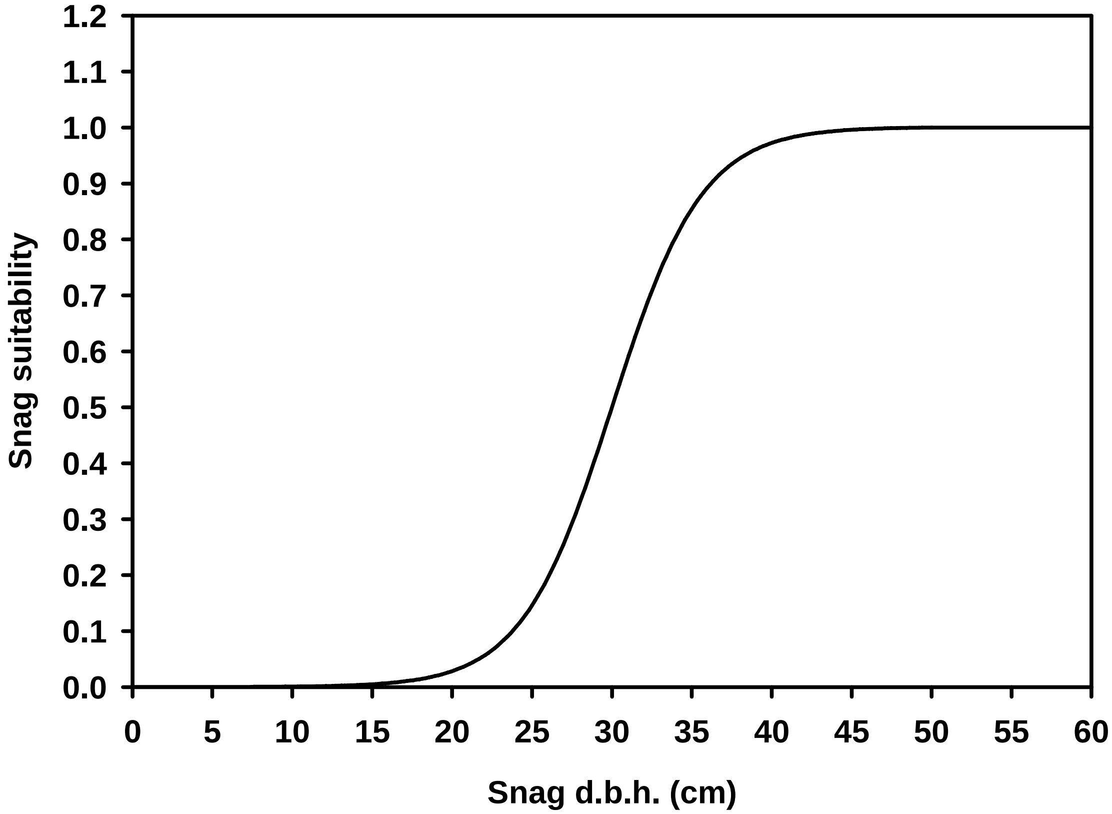

Figure 10. Indiana bat “17–50” curve describing snag suitability as a function of diameter at breast height (cm).

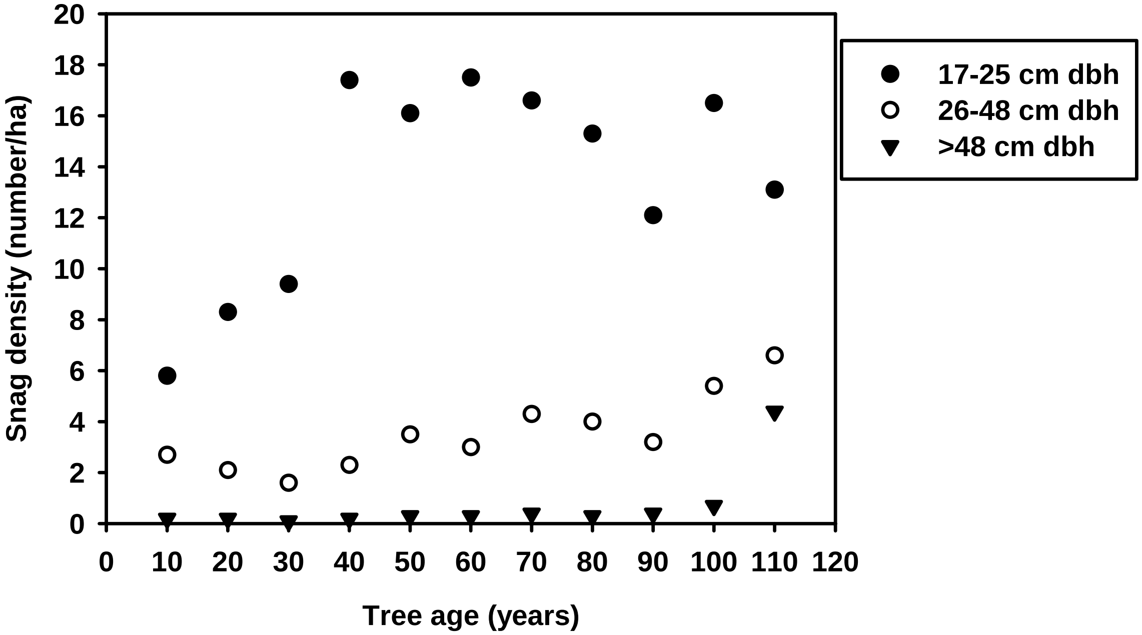

Figure 11. Snag density by tree age class for three snag size classes. Age class 90 data was not included in analyses because of small sample size.

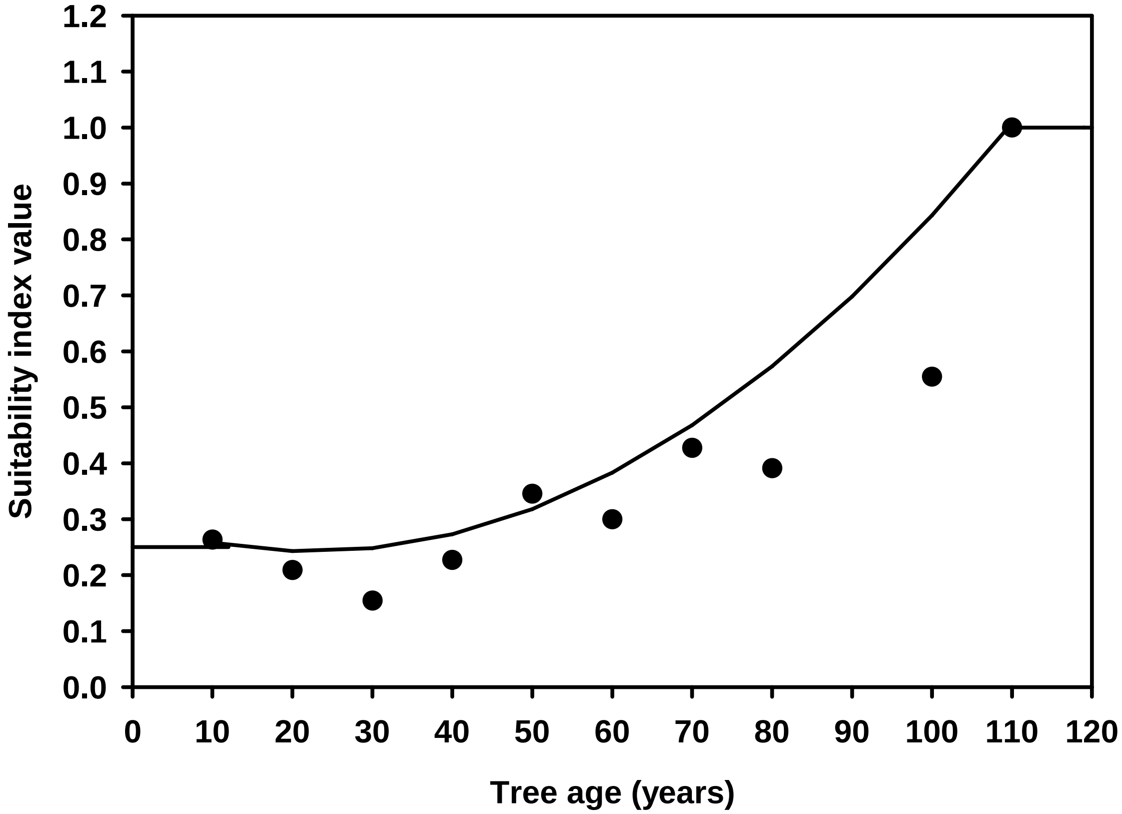

Figure 12. Indiana bat habitat suitability for roost sites as a function of tree age, snag density, and size class.

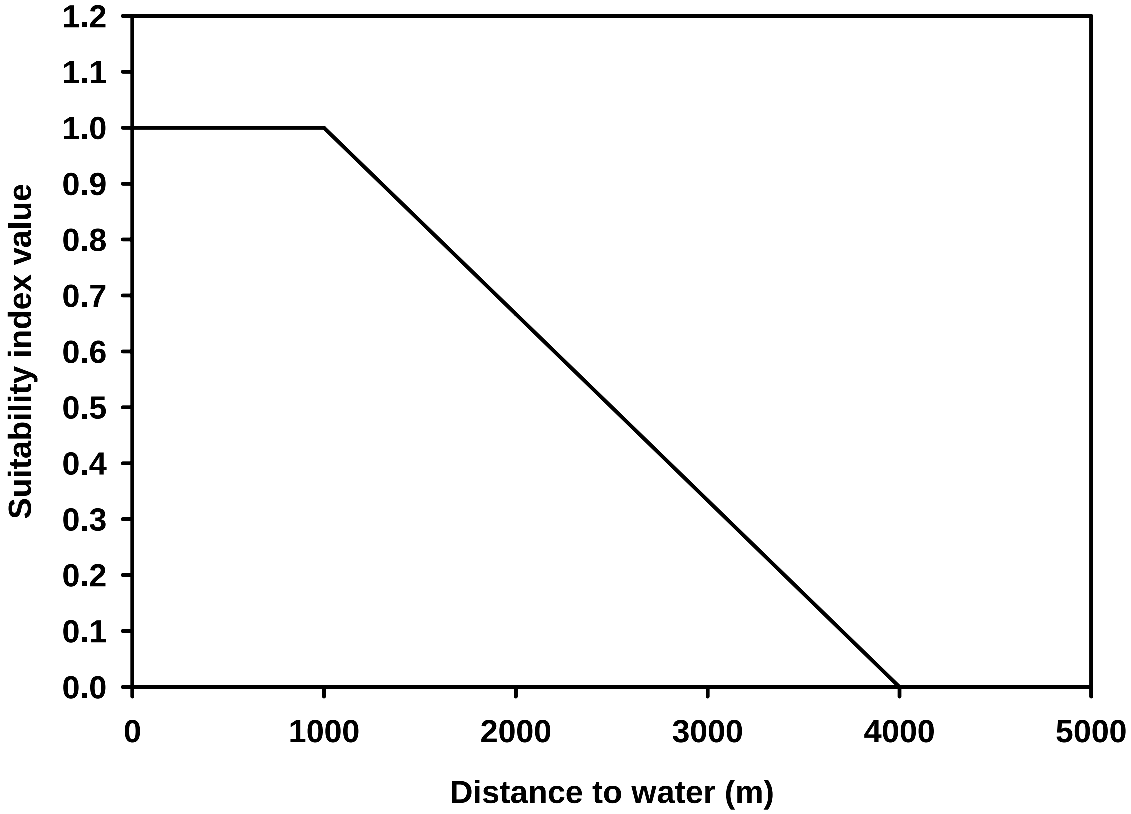

Figure 13. Indiana bat habitat suitability for roost sites as a function of distance from roost tree to water. Suitability value (SI3) = 1.00 for roost trees <1000 m from water and SI3 = 0.00 for roost trees >4000 m from water.

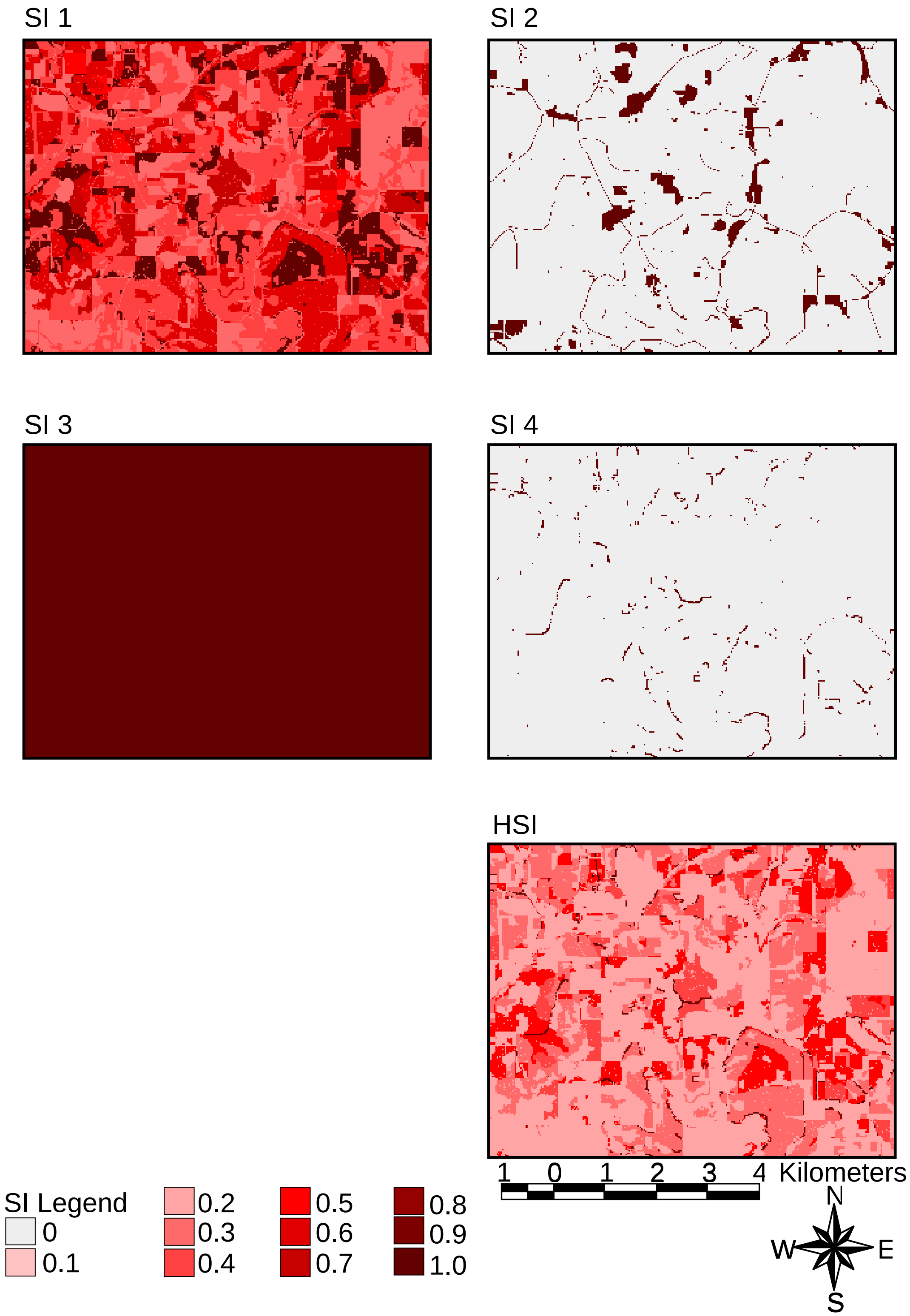

Figure 14. Indiana bat habitat suitability for a 4,281-ha portion of the Hoosier National Forest, Indiana.

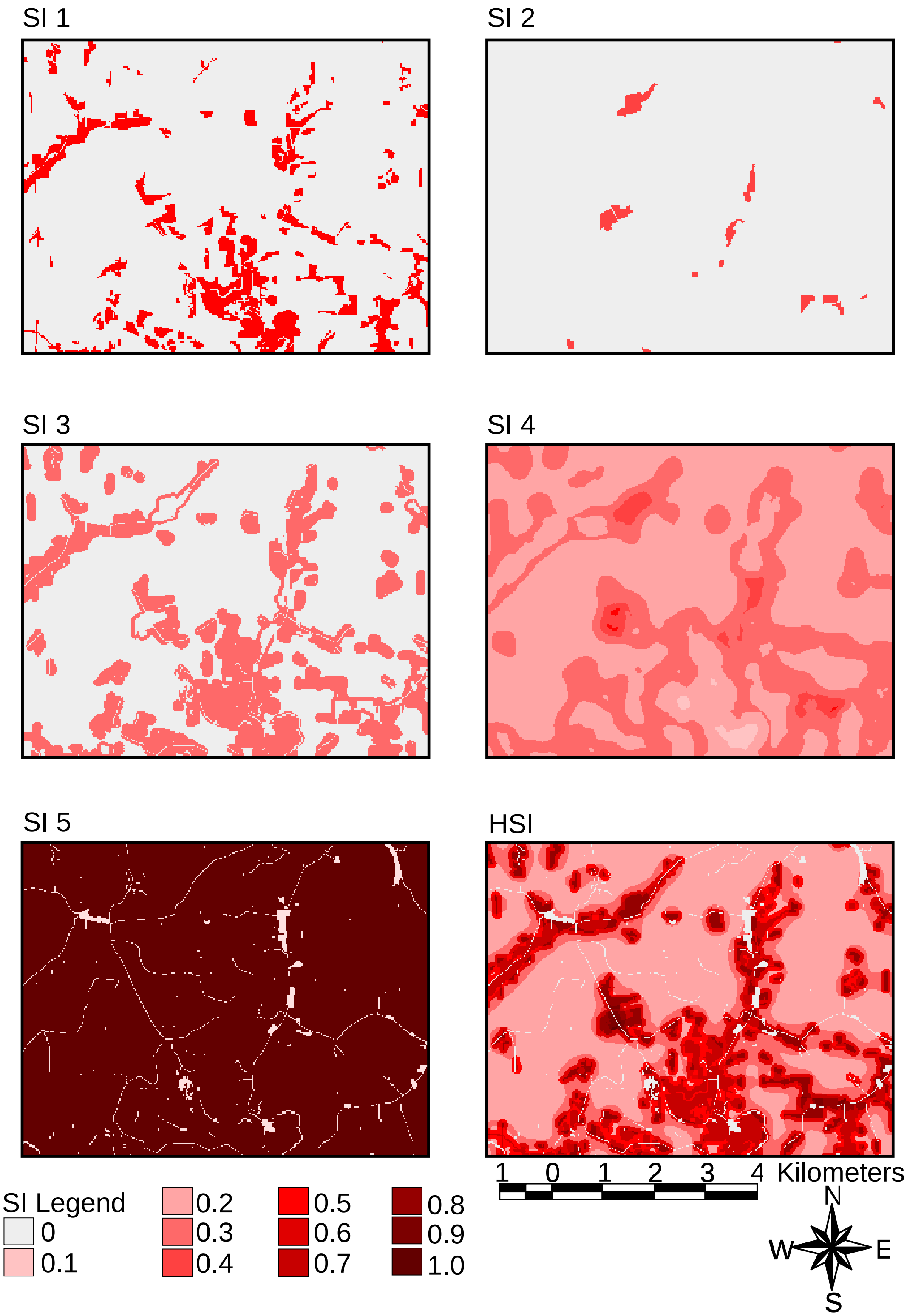

Figure 15. Northern bobwhite habitat suitability for a 4,281-ha portion of the Hoosier National Forest, Indiana.

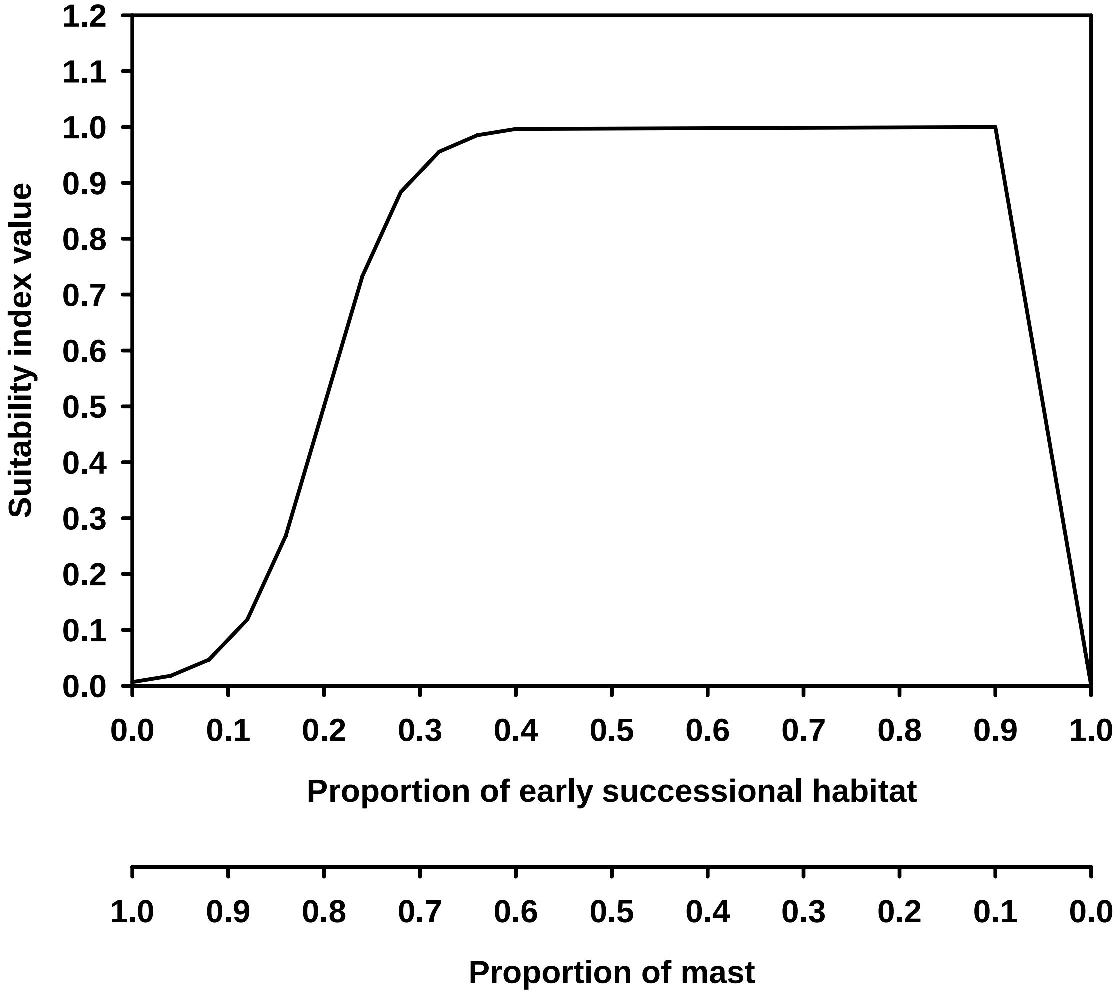

Figure 16. Ruffed grouse habitat suitability as a function of early successional habitat and proportion of mast within a 10-ha moving window.

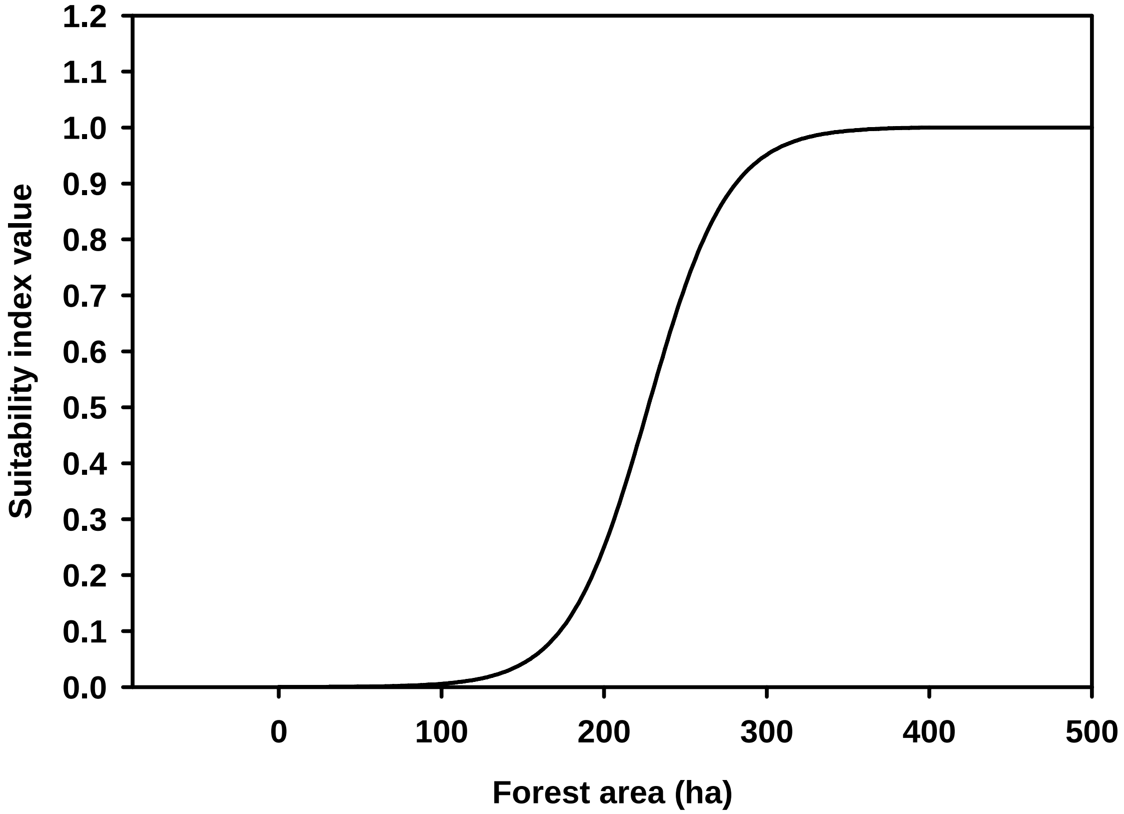

Figure 17. Ruffed grouse habitat suitability as a function of forest area. Suitability value (SI_5) = 0.00 for patches ≤100 ha and SI_5 = 1.00 for patches >400 ha.

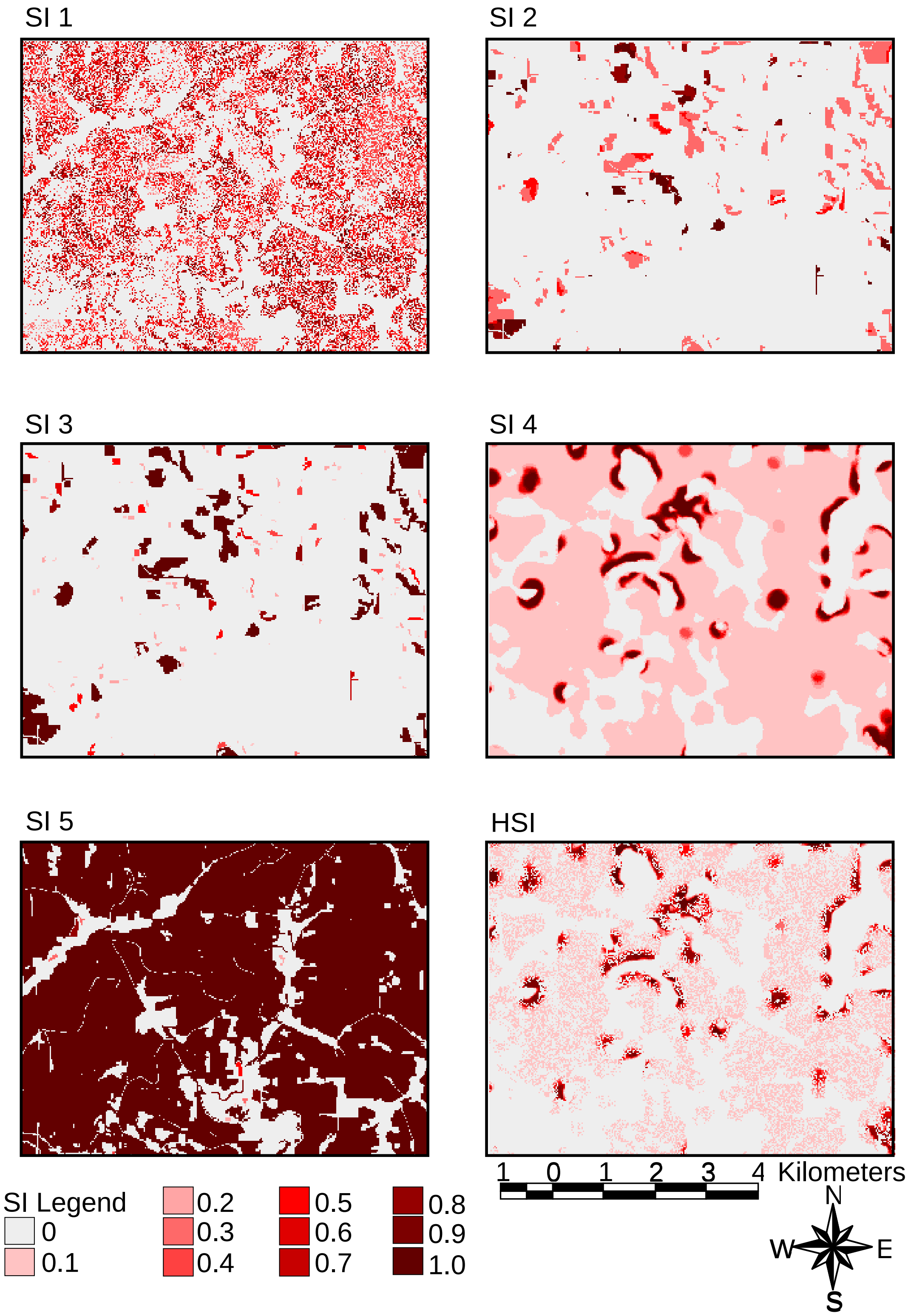

Figure 18. Ruffed grouse habitat suitability for a 4,281-ha portion of the Hoosier National Forest, Indiana.

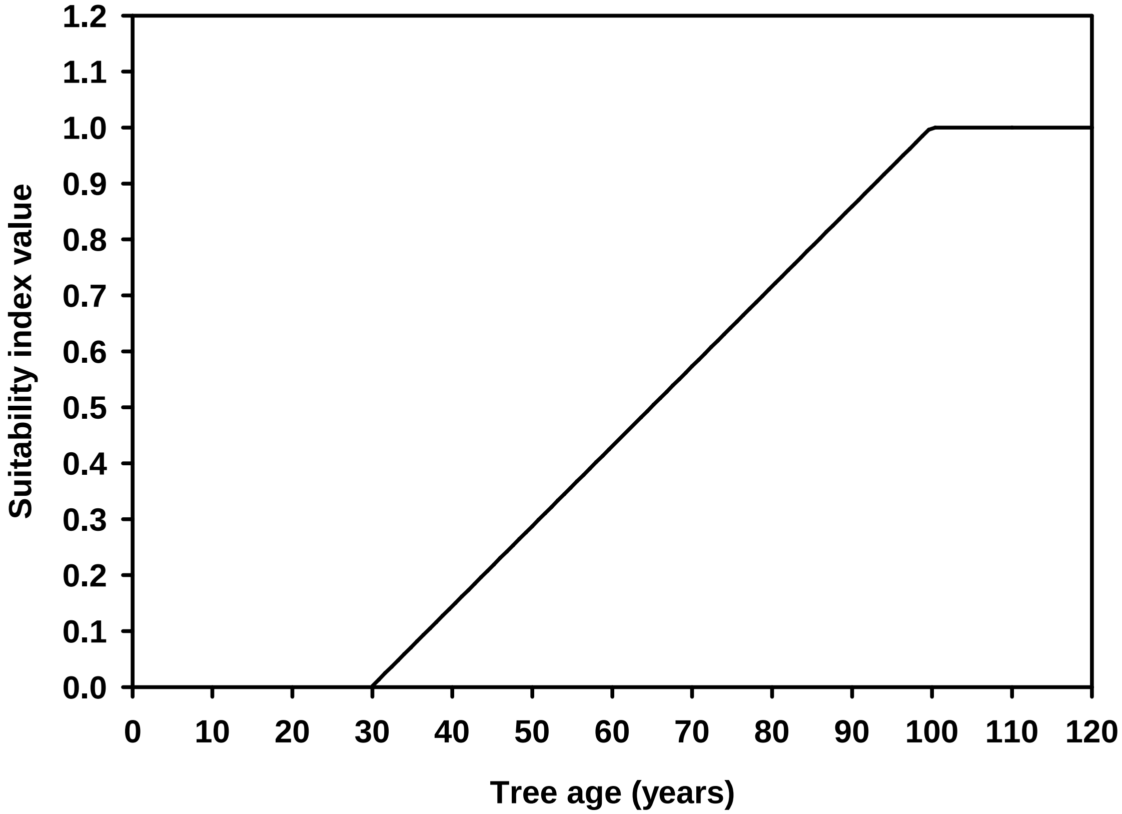

Figure 19. Timber rattlesnake habitat suitability as a function of stand age. Suitability value (SI_2) = 0.00 for stands ≤30 years and SI_2 = 1.00 for stands >100 years.

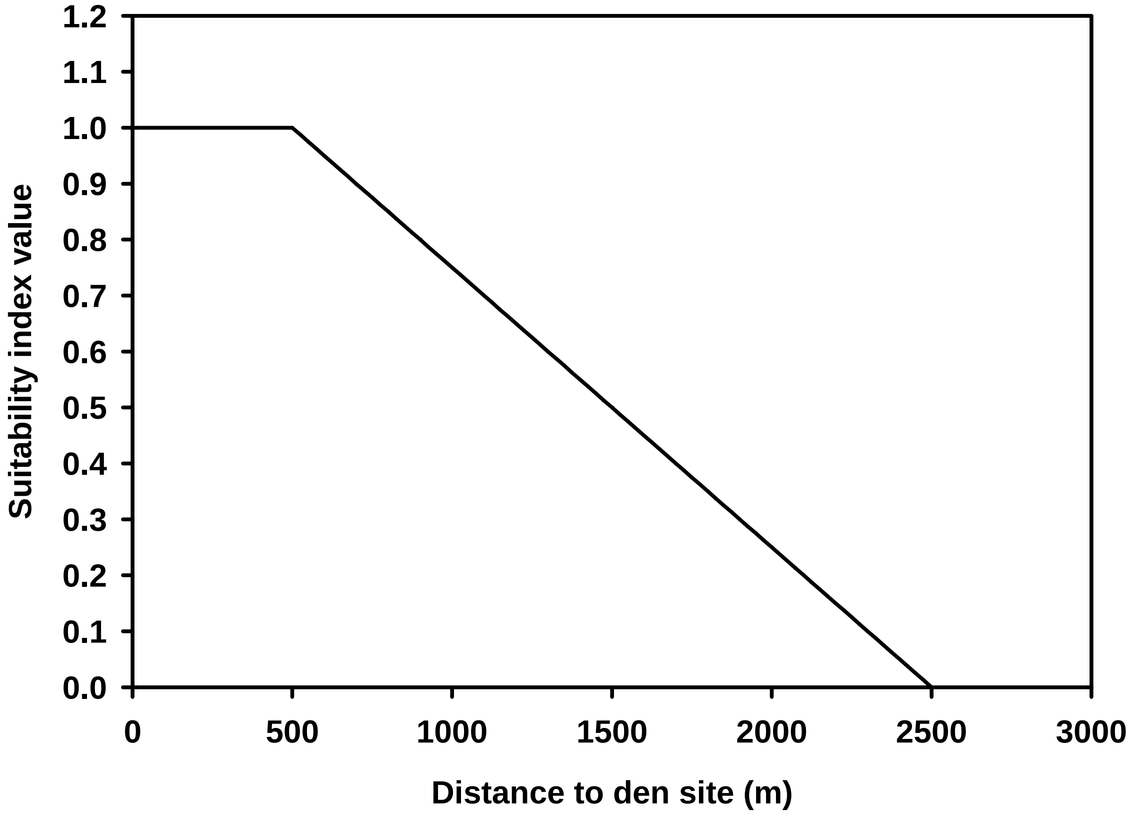

Figure 20. Timber rattlesnake habitat suitability as a function of distance from den sites. Suitability value (SI_4) = 1.00 for habitat ≤500m from den sites and SI_4 = 0.00 for habitat >2500m from den sites.

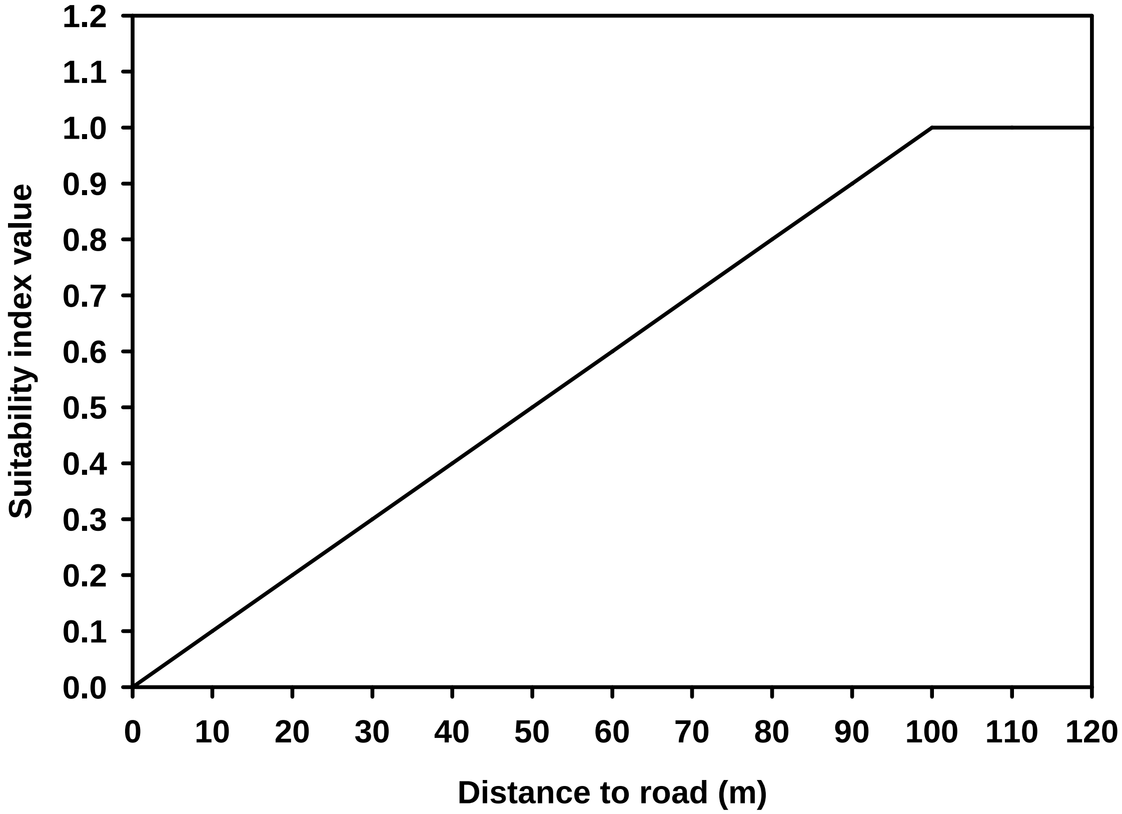

Figure 21. Timber rattlesnake habitat suitability as a function of distance from roads.

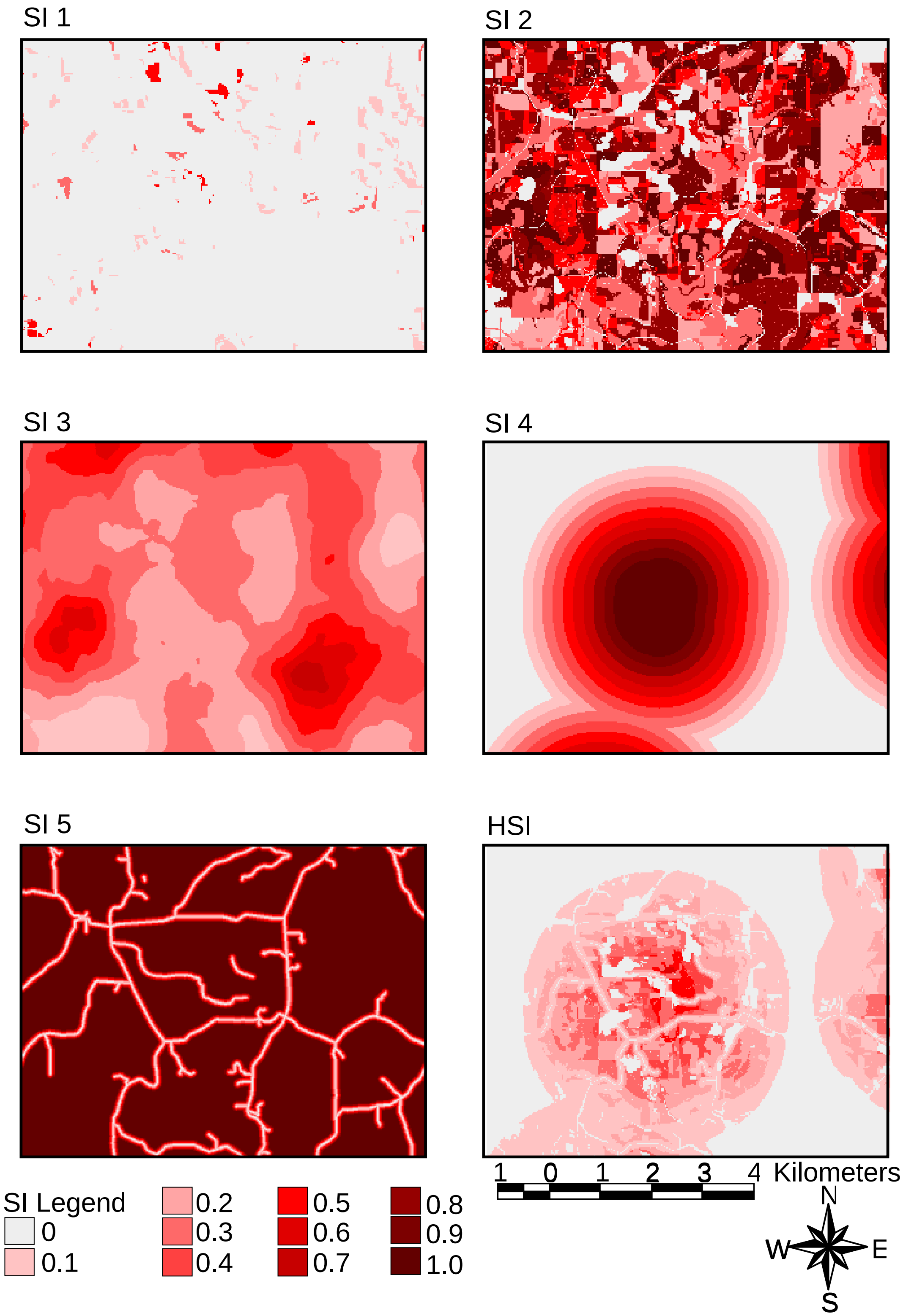

Figure 22. Timber rattlesnake habitat suitability for a 4,281-ha portion of the Hoosier National Forest, Indiana.

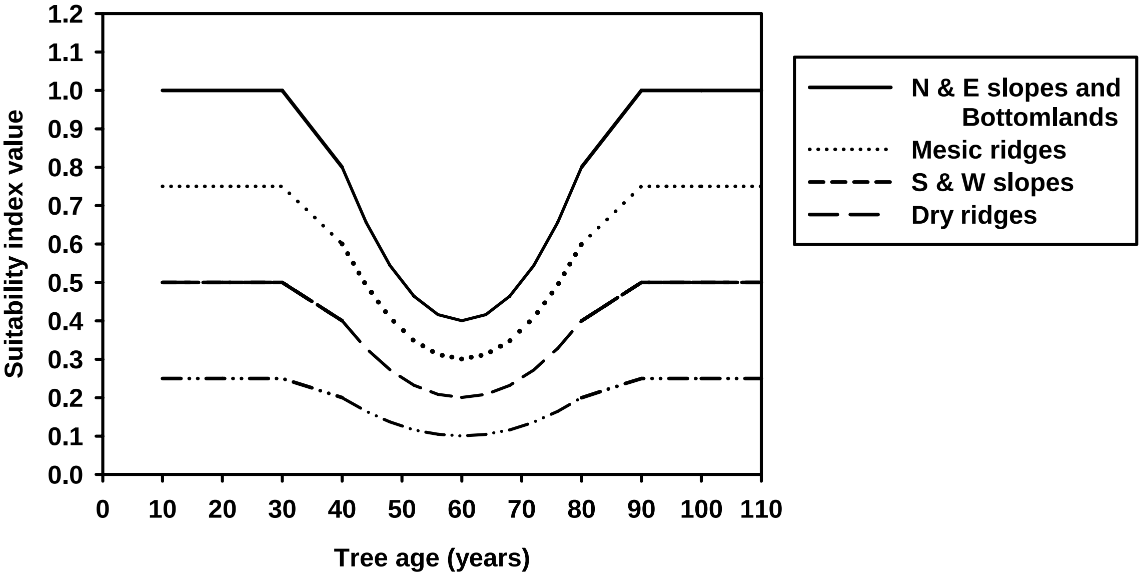

Figure 23. Wood thrush habitat suitability as a function of tree age and ecological land type.

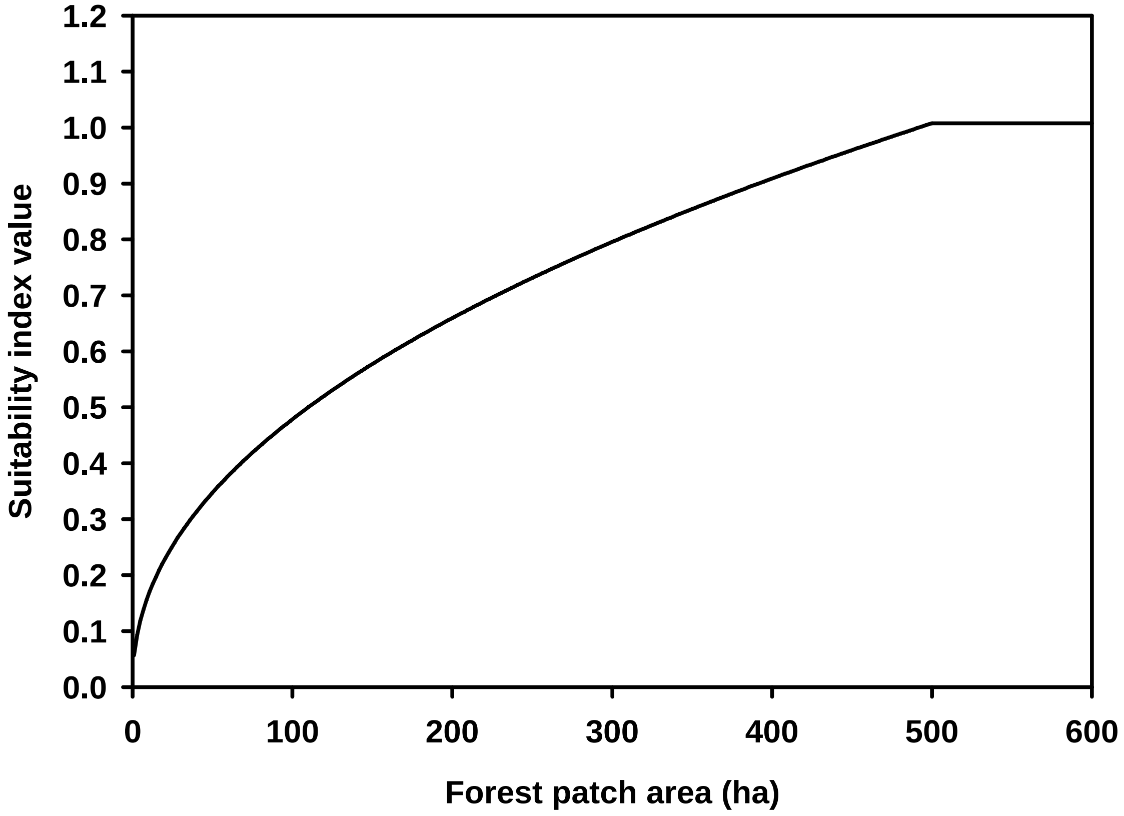

Figure 24. Wood thrush habitat suitability as a function of deciduous forest area. Suitability value (SI_3) = 0.00 at 1.0 ha and SI_3 = 1.00 for patches >500 ha (from Table 5, Robbins et al. 1989).

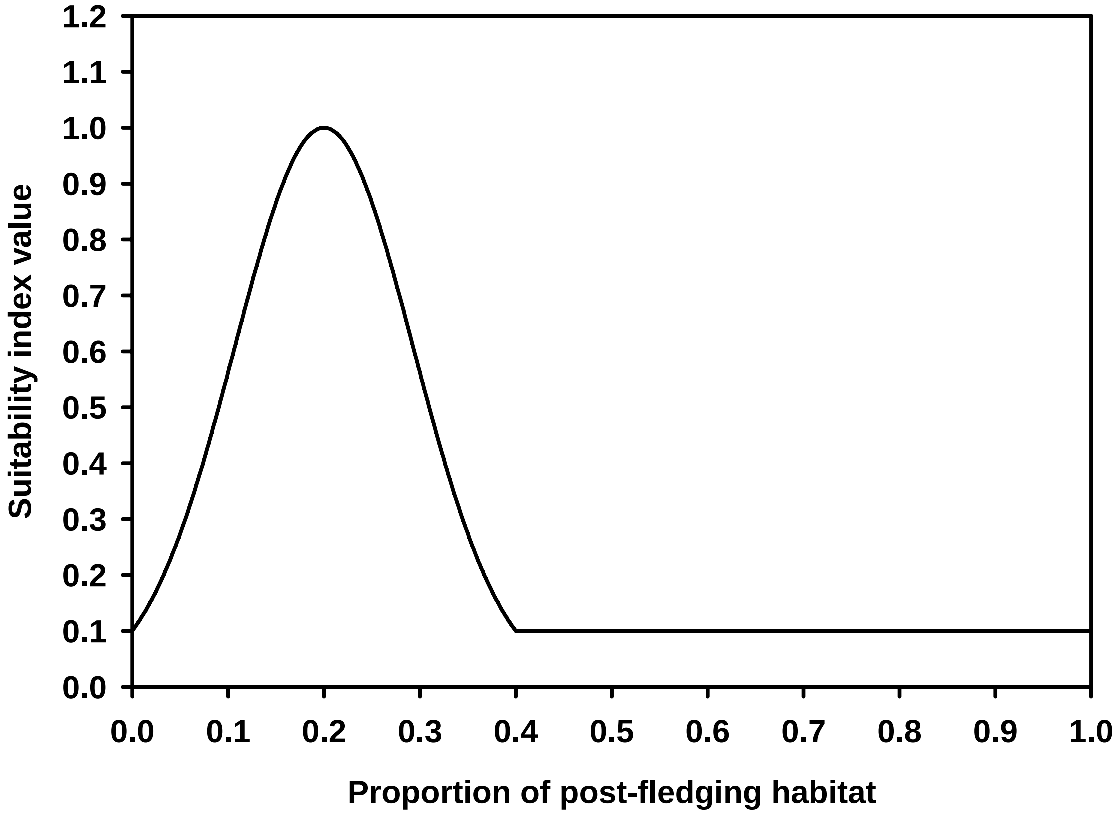

Figure 25. Wood thrush habitat suitability based on the proportion of post-fledging habitat within 1 km of natal site. Suitability value (SI_5) = 1.00 for landscapes with 20 percent post-fledging habitat. Suitability value (SI_5) = 0.10 for landscapes with >40 percent of post-fledging habitat.

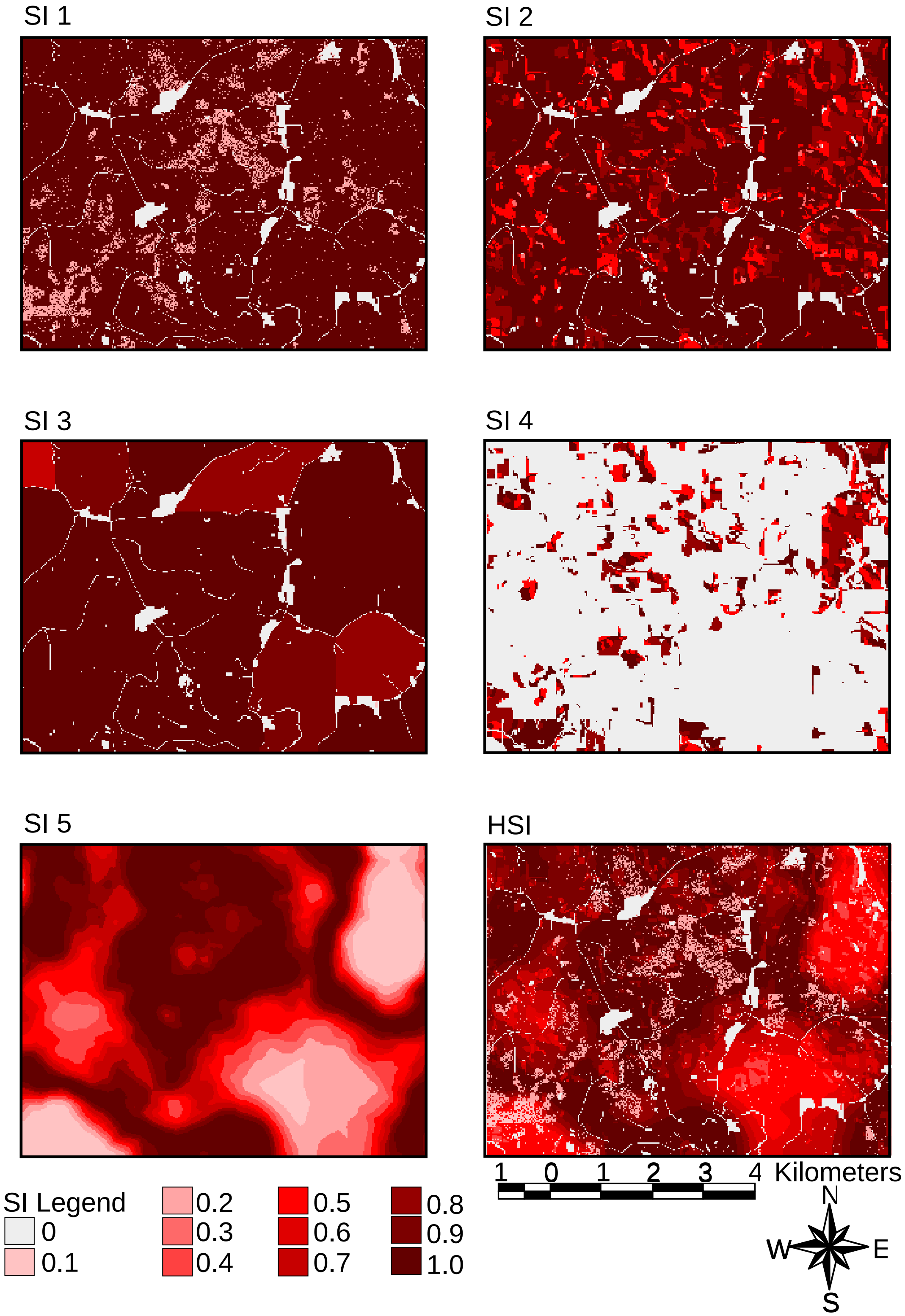

Figure 26. Wood thrush habitat suitability for a 4,281-ha portion of the Hoosier National Forest, Indiana.

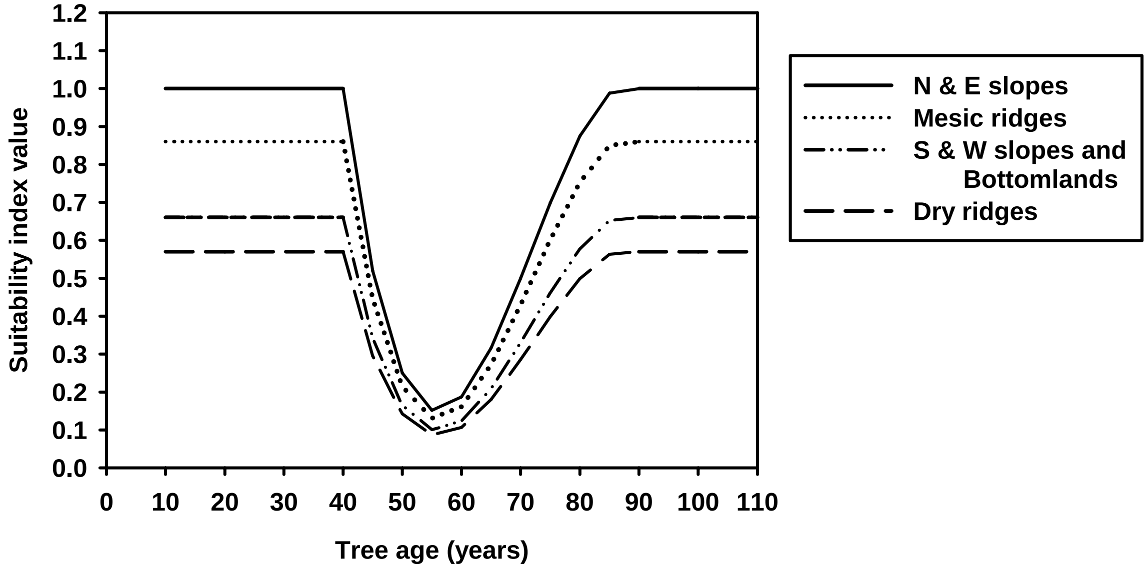

Figure 27. Worm-eating warbler habitat suitability as a function of tree age and ecological land type.

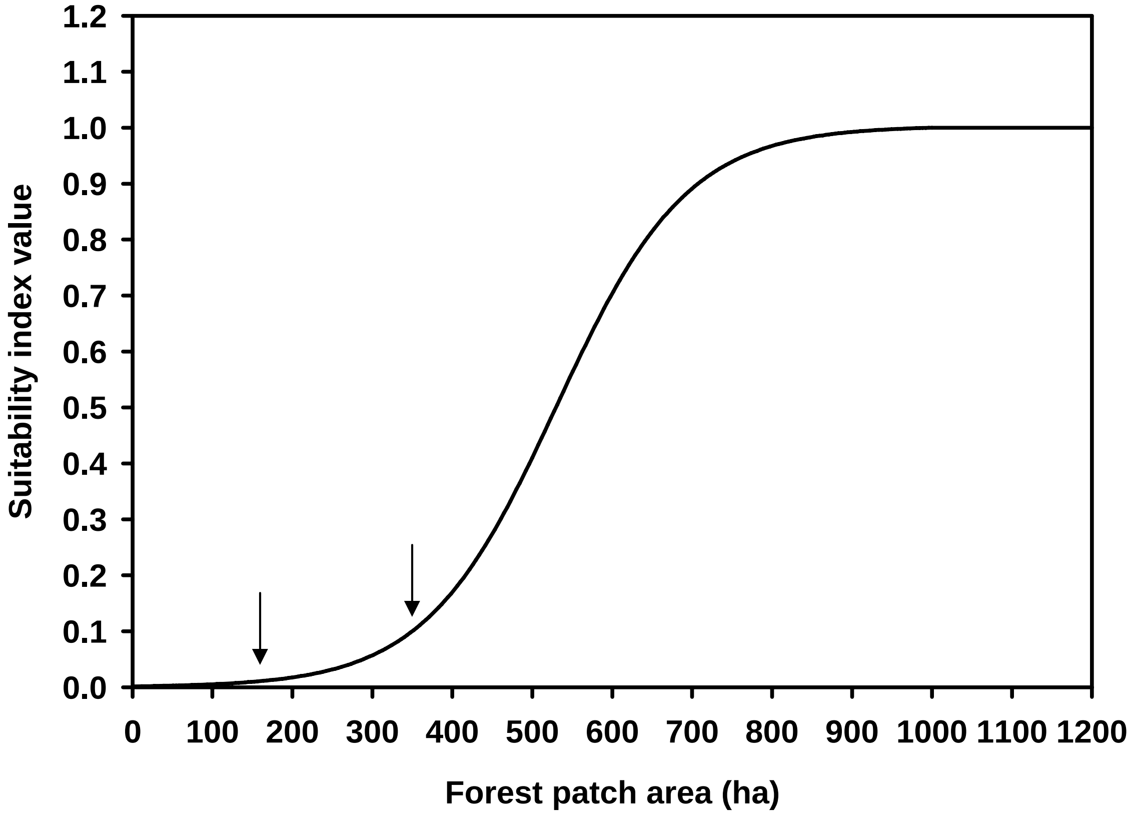

Figure 28. Worm-eating warbler habitat suitability for breeding as a function of deciduous forest area. Suitability value (SI_3) = 1.00 for patches >1000 ha. Left arrow indicates 150 ha (minimum area requirement, Robbins et al. 1989) and right arrow indicates 340 ha (minimum area requirement, Hayden et al. 1985, Wenny et al. 1993).

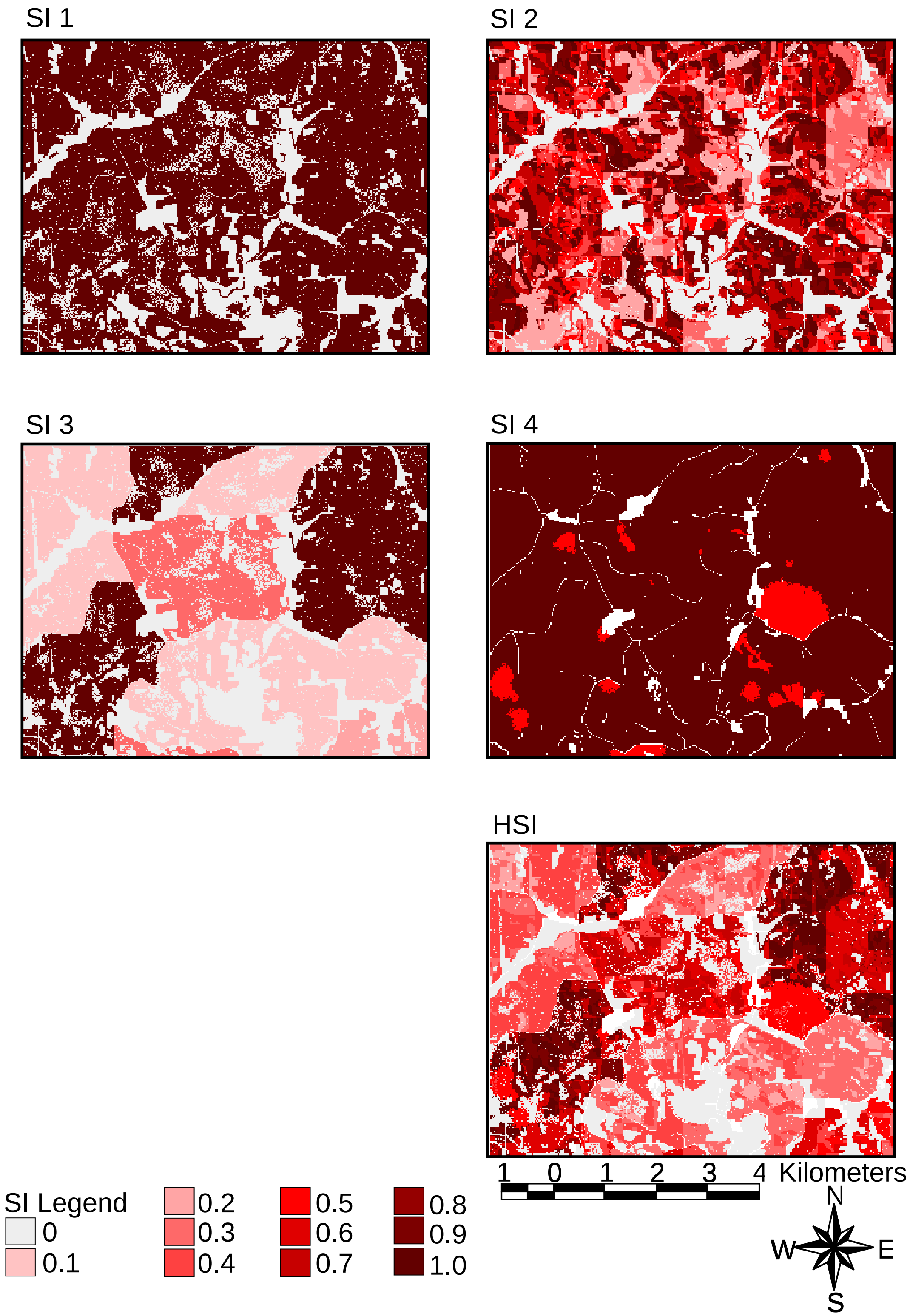

Figure 29. Worm-eating warbler habitat suitability for breeding on a 4,281-ha portion of the Hoosier National Forest, Indiana.

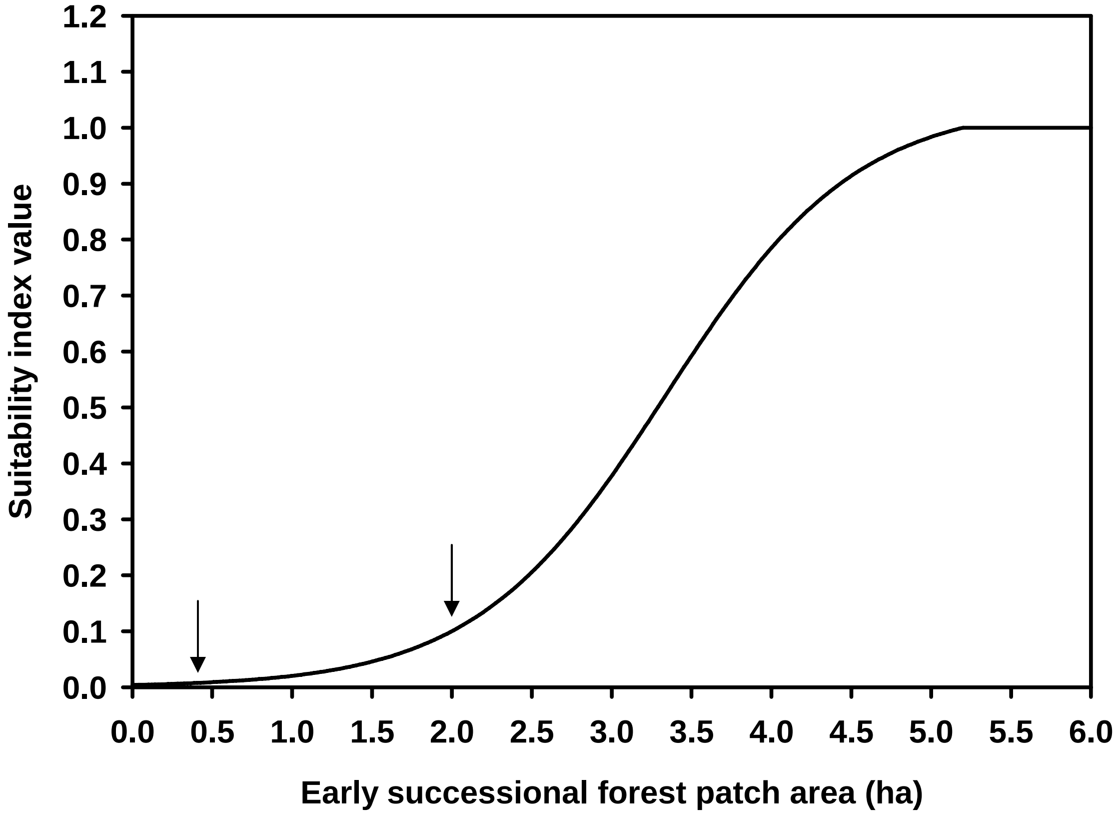

Figure 30. Yellow-breasted chat habitat suitability for breeding as a function of early successional forest area. Suitability value (SI_2) = 0.00 for patches ≤0.01 ha and SI_3 = 1.00 for patches ≥5 ha. Left arrow indicates 0.4 ha (minimum area requirement, Robinson and Robinson 1999) and right arrow indicates 2.0 ha (minimum area requirement; SVE Panel 2002).

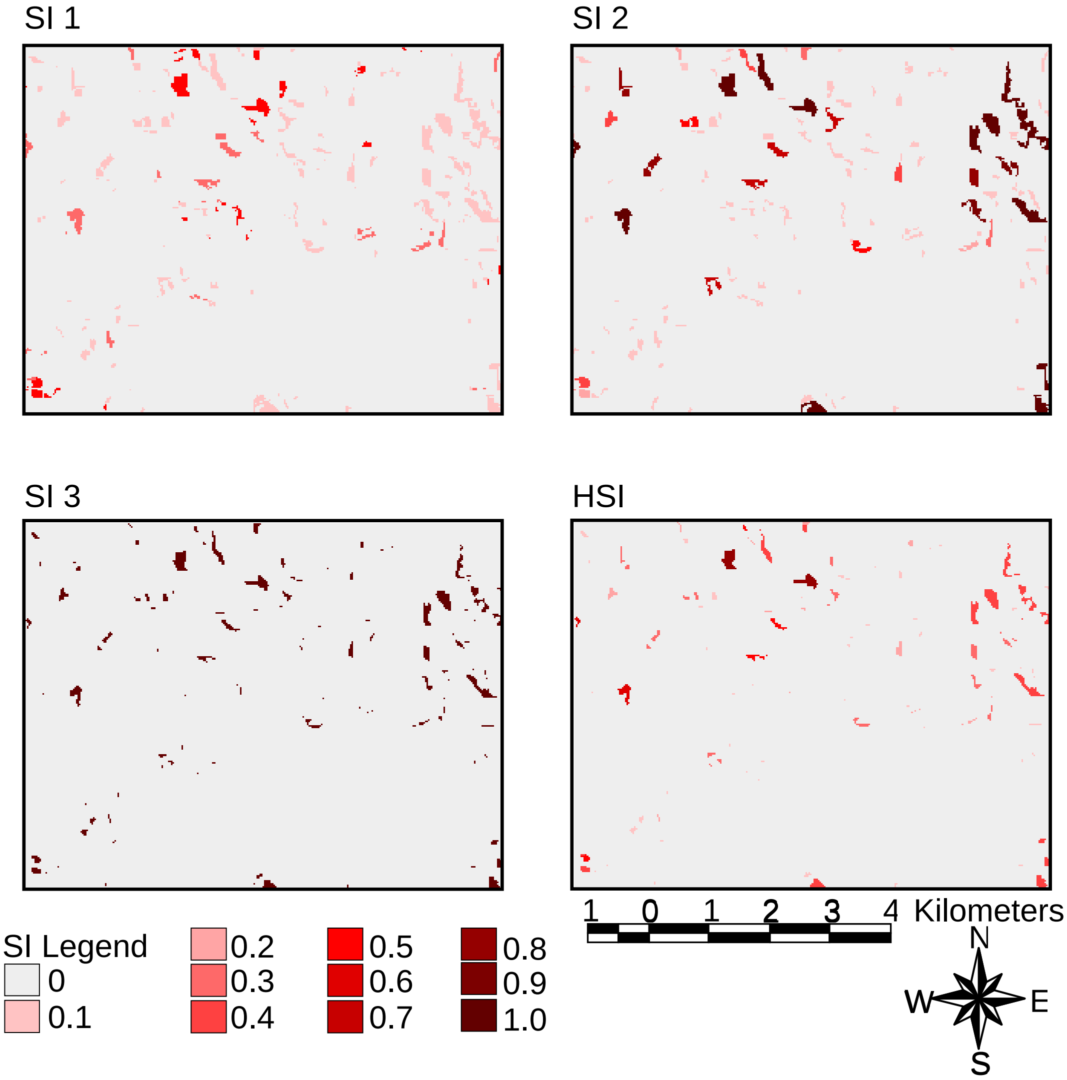

Figure 31. Yellow-breasted chat habitat suitability for breeding on a 4,281-ha portion of the Hoosier National Forest, Indiana.

EVALUATION OF LANDSCAPE-LEVEL HABITAT SUITABILITY MODELS USING DEMOGRAPHIC DATA

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ABSTRACT

Habitat suitability is often used as a surrogate for demographic response (i.e., abundance, survival, fecundity, or population viability) in the application of habitat suitability (HSI) models. Whether habitat suitability actually relates to demographics, however, has rarely been evaluated. We validated HSI models of breeding habitat suitability for wood thrush (*Hylocichla mustelina*) and yellow-breasted chats (*Icteria virens*), two species on opposite ends of a forest succession gradient, by evaluating the

association between wildlife demographic responses and HSI values. First, we evaluated the statistical significance of HSI models as a predictor of three demographic responses, within-site territory density, site-level territory density and nest success. We used a mixed-effects model for repeated measures, with year as the repeated effect for our multi-year data set, within-site territory density or site-level territory density as the dependent variable and HSI values as the independent variable. We used the logistic-exposure method to estimate nest success with HSI values as the independent variable. We demonstrated a statistically significant link between HSI values and all three types of demographic responses for the yellow-breasted chat and site-level territory density for the wood thrush. Second, we evaluated support for models containing HSI values or individual SI values, models containing measured habitat or landscape attributes (e.g., tree age, tree species, ecological land type), and models containing management treatments (e.g., even-aged and uneven-aged forest regeneration treatments) for each demographic response using model selection. Models containing HSI values were, in general, more supported than models containing only landscape attributes or management treatments for all three types of wildlife response. The assumption that changes in habitat suitability represent wildlife demographic response to vegetation change is supported for our models. However, differences in species ecology may contribute to model significance and model selection uncertainty. Knowledge of the absolute and relative ability of HSI models to quantify species-specific demographic responses to habitat change provides an invaluable basis for making management decisions. Given the differences among species in life history traits and ecologies, a blanket assumption that suitability represents demographic response without specifying which demographic response is inappropriate.

INTRODUCTION

Land-management planning, such as national forest plans, often involves the simulation of vegetation change and evaluation of associated wildlife response using habitat-relationship models (Kliskey et al. 1999, Klaus et al. 2005). Planning approaches that use habitat suitability index (HSI) models provide a means to quantify and rank differences in habitat suitability among sites or alternative management strategies (Gustafson et al. 2001, Marzluff et al. 2002, Larson et al. 2004). When choosing among management alternatives, planners and managers often assume that habitat suitability is a surrogate for animal response, either in terms of occupancy (i.e., probability of finding an animal at a location) or demography (i.e., density, survival, fecundity, or population viability), and that changes in habitat suitability correspond to numerical changes in wildlife populations. Model validation is necessary to assess whether there is a link between predicted habitat suitability and demographic response (Rykiel 1996). Determining what constitutes adequate model validation can be difficult because the reliability of the link may vary depending on species ecology (Van Horne 1983) and spatial scale (Orians and Wittenberger 1991, Chalfoun and Martin 2007). In addition, the type of habitat suitability model and wildlife demographic data used for model validation might affect the ability to validate the relationship. An assessment of these issues may reduce the uncertainty of planning decisions based on HSI models and thereby improve the reliability of the planning process.

Rykiel (1996) defined model validation as demonstration that a model possesses the accuracy required for intended applications. Accuracy may be assessed in different ways depending on the type of modeling approach and the validation criteria specified prior to validation. Because HSI models are conceptual, not statistical models, rigorous statistical methods for model validation, including significance testing, data partitioning methods (e.g., *k*-fold cross validation) and threshold-independent measures of classification error (e.g., receiver operating characteristic plots) used for regression models are not applicable (Fielding and Bell 1997, Pearce and Ferrier 2000, Boyce et al. 2002). Instead, most HSI model validation efforts consist of simple correlations of HSI values and animal abundance, density, or nest success (Duncan et al. 1995, Breininger et al. 1998, Kroll and Haufler 2006). A rarely addressed question during the model validation process is whether or not the type of model used (i.e., traditional HSI model vs. a regression model) is appropriate. We suggest HSI values could be used as independent variables in a regression analysis for model validation to determine their statistical significance as a predictor, be compared to other candidate models in a model selection framework, and be used to estimate density or nest success.

An additional consideration for model validation is the type of wildlife data used. Previous HSI model validation efforts have used wildlife data on abundance or density (Cook and Irwin 1985, Breininger et al. 1998), demographic rates such as survival, fecundity, or nest success (Breininger et al. 1998, Kroll and Haufler 2006), or the product of density, juvenile production and survival of breeding adults (Duncan et al. 1995), and found some variation in HSI model performance depending on which type of data was used for validation. For example, Breininger et al. (1998) examined density, yearling production, and demographic performance (potential-breeder production minus breeder mortality) of Florida Scrub Jays (*Aphelocoma coerulescens*). All measures were correlated with HSI values but density was the weakest correlation among the three measures. Similarly, Kroll and Haufler (2006) found lower correlation of site-specific HSI values with density than with nesting success of Dusky Flycatchers (*Empidonax oberholseri*). These results corroborate Van Horne's (1983) suggestion that density alone may be an insufficient indicator of habitat quality and indicate that HSI models may represent some wildlife responses, but not all. The results also illustrate the importance of defining *a priori* the purpose of the habitat suitability model, such as habitat suitability for breeding as opposed to a year-round habitat suitability model. While most validation efforts continue to use wildlife location or density information for model validation, at present there is no consensus as to which demographic response is best for HSI model validation. The lack of consensus may be due, in part, to the use of multiple data sources (e.g., point counts, spotmapping data, and nest success information) that correspond to different demographic responses (i.e., abundance, density, and nest success) in the development of HSI models and the purpose of the model. Validation of HSI models for breeding using different demographic responses would help determine which response is appropriate for a given HSI model.

There may also be species-specific differences in the strength of the link between demographic responses and habitat suitability. The two species mentioned above, Florida Scrub Jay and Dusky Flycatcher, are habitat specialists. We might expect a stronger relationship between suitability and demographic response when a specific habitat feature affects suitability for a habitat specialist. For example, nest success and territory density for Yellow-breasted Chats (*Icteria virens*) is higher in young than mature forest stands (Thompson et al. 1992, Annand and Thompson 1997, Gram et al. 2003). In contrast wood thrush (*Hylocichla mustelina*), a habitat generalist, use a range of forest habitats and age classes resulting from forest regeneration techniques (Thompson et al. 1992, Annand and Thompson 1997, Anders et al. 1998, Vega Rivera et al. 1998, Pagen et al. 2000, Gram et al. 2003). Thus, we might expect a weaker relationship between suitability and nest success for habitat generalists.

Our objective was to validate HSI models by evaluating the association between wildlife demographic response and HSI values. First, we evaluated the significance of HSI models of breeding habitat suitability for wood thrush and yellow-breasted chats (developed by Rittenhouse et al. 2007) as a predictor of three different demographic responses: within-site territory density, site-level territory density, and vital rates (i.e., nest success). We chose these two species because they represent opposite ends of a habitat-generalist to habitat-specialist gradient. Wood thrushes nest in mid- to late-successional forest, but both adults and juveniles may occupy early successional forest during the post-breeding and post-fledging periods (Kahl et al. 1985, Thompson et al. 1992, Roth et al. 1996, Anders et al. 1998). In contrast, yellow-breasted chats are associated with early successional forest and rarely use mid- to late-successional forest (Annand and Thompson 1997, Eckerle and Thompson 2001).

Second, we evaluated support for HSI models versus other candidate models using model selection based on AIC (Akaike's Information Criterion; Burnham and Anderson 2002). We considered models containing HSI values or individual SI values, models containing measured habitat or landscape attributes, and models containing management treatments as predictors of territory density or nest success. We anticipated two possible outcomes when comparing HSI models to measured habitat, landscape, or management treatments as predictors. Variation in expert opinion, uncertainty in habitat suitability relationships, and model complexity may influence HSI model performance (Johnson and Gillingham 2004), particularly when applied to a specific study site and validated with site-specific data. Previous studies comparing HSI models to quantitative models (e.g., resource selection models, ecological niche models) found that HSI models performed the worst among models examined when applied to specific sites or regions (Johnson and Gillingham 2005). Alternatively, we might expect the HSI models to perform better than landscape attribute or management effects models because the HSI models were developed to evaluate breeding habitat suitability and they inherently consider demography (Rittenhouse et al. 2007). Thus, our validation approach considers whether each HSI model was a significant predictor of demographic response or not, and how well each HSI model performs relative to other types of models.

METHODS

Study Area and Demographic Data

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a large-scale, long-term experiment conducted by the Missouri Department of Conservation and collaborators to determine the effects of even-aged and uneven-aged management on biotic and abiotic ecosystem attributes (Brookshire et al. 1997). The experimental design consists of 9 sites, 3 each of control, even-aged management (EAM), and uneven-aged management (UAM). The sites range in size from 312 – 514 ha and are located in the Ozark hills of south-central Missouri. Treatments occurred May – November 1996. The

EAM treatments included clearcutting applied to stands 3 – 13 ha in size and intermediate cutting (i.e., thinning) applied to 5 – 24% of each EAM site (Kabrick et al. 2002). The UAM included small group and single-tree selection cuts applied to 41 – 69% of each UAM site. The small group cuts, applied to 5% of the harvested area per UAM site, ranged in size from 21 – 43 m in diameter. Approximately 10% of the total forest area within EAM and UAM treatment sites was designated old growth preserve and remained uncut. No tree harvest occurred on control sites.

We used nest success and territory density information from MOFEP for HSI model validation. Territory density was determined for each of the 9 MOFEP sites by spotmapping. Observers visited each site 10 times at 2 – 3 day intervals from mid-May to the end of July each year from 1991 – 1995 and from 1997 – 2000. During each visit, observers marked all detections of birds on an enlarged topographic map of each site. A composite map containing detections from all visits was compiled by year and used to determine the number of territories (Clawson et al. 1997). A territory consisted of a cluster of ≥3 observations across all visits within a year. The MOFEP data set contained 1,297 wood thrush territories and 357 yellow-breasted chat territories from 1991 – 2000. Concurrent with spotmapping, observers located and monitored nests for target species. Nests were monitored every 3 – 5 days until nest fate was determined. Due to insufficient sample sizes for yellow-breasted chats pretreatment, we limited the analysis of nest success to 1997 – 2002 and territory density to 1997 – 2000. We analyzed the fates of 109 wood thrush nests and 66 yellow-breasted chat nests from 1991 – 2002, resulting in effective sample sizes (number of observation days × number of nests; Rotella et al. 2000) of 2556 for wood thrush and 618 for yellow-breasted chats. The median interval length between nest visits was 3 days for both species with 99% of all intervals less than 8 days for wood thrush and less than 7 days for yellow-breasted chats.

Habitat Suitability Index Models

We determined breeding habitat suitability for wood thrush and yellow-breasted chat using LandscapeHSI models version 2.1 (Dijak et al. 2007). Details for wood thrush and yellow-breasted chat HSI model development, including citations supporting the suitability relationships for each species are provided by Rittenhouse et al. (2007). Both models assigned suitability for breeding based on tree species groups (forest types), tree age class, landform type, and patch size. The wood thrush HSI model contained five suitability indexes

$$HSI = SI_1 \times \left(\sqrt[3]{SI_2 \times SI_3 \times SI_5} \right) \qquad \text{(eq 1)}$$

where SI_1 was a function of tree species groups suitable for nesting, SI_2 was a function of tree age and landform, SI_3 was a function of forest area requirements, and SI_5 was a function of the proportion of post-fledging habitat within 1 km of natal sites. SI_4 was used to identify early successional forest as part of the calculation for SI_5 and was not included in HSI equation. The yellow-breasted chat HSI model contained three suitability indexes

$$HSI = \left(\sqrt[2]{SI_1 \times SI_2} \right) \times SI_3 . \qquad \text{(eq 2)}$$

where SI_1 was a function of early successional forest based on tree age and landform, SI_2 was a function of patch area requirements, and SI_3 represented a negative edge effect and was a function of early successional habitat adjacent to mid- to late-successional forest.

The HSI models used information on landform type, tree species groups, and tree age to assign suitability. We developed a landform map using a digital elevation model

(DEM) and the Topographic Position Index (TPI) extension (Jenness 2006) for ArcView 3.x (Environmental Systems Research Institute, Redlands, California, USA). We defined 5 landform classes based on different combinations of slope, aspect, and TPI: 1) ridges, 2) south and west slopes, 3) upland drainages, 4) north and east slopes, and 5) bottomlands.

We used the woody vegetation inventory from 1994 – 1995 to populate the initial landscape conditions for the MOFEP sites and create the GIS layers required for the HSI models. Shifley et al. (2000) and Brookshire and Dey (2000) presented details of the sampling procedure and vegetation information, which we used to obtain tree species composition and size class distribution by ecological land type. The inventory contained approximately 55,000 trees greater than 11 cm dbh and totaled 48 tree species. To facilitate the landscape population process and remain compatible with the habitat suitability models (Rittenhouse et al. 2007), we collapsed the tree species into the following tree species groups: white oaks (*Quercus alba* L., *Q. stellata* Wangenh., *Q. muehlenbergii* Engelm.), black oaks (*Q. velutina* Lam., *Q. rubra* L., *Q. coccinea* Muenchh.), conifers (*Pinus echinata* Mill., *Juniperus virginiana* L.), and other hardwoods (*Acer rubrum* L., *A. saccharum* Marsh, *Carya* spp.). Additionally, we considered only the dominant overstory trees within each plot. We defined the dominant overstory trees as the top 9 trees ranked by dbh for each plot. We determined the proportion of each tree species group within the top 9 trees and assigned tree species based on those proportions. Because age data were not collected for all trees, we assigned an approximate age based on species (group)-specific equations (S. R. Shifley, unpublished data). We applied EAM by resetting tree age to 4 years on harvested cells.

For UAM group selection we reset tree age to 4 years. Because UAM single-tree harvest removes only the dominant tree from a cell, we assigned a new tree species and tree age by sampling from the top 10 – 18 tree ranked by dbh. These trees averaged 10 – 25 years younger than the harvested tree.

We applied the HSI models to the MOFEP landscape and used the resulting habitat suitability maps to summarize habitat suitability at the territory and site scales. For the territory scale, we used a moving-window analysis to calculate the mean (HTm) and standard deviation of mean HSI value (HTsd) within an area equivalent to the average territory size for each species, as well as the mean (SIm) and standard deviation of the mean (SIsd) for individual suitability indexes. We used a 120-m radius moving window for wood thrush, which resulted in a moving window size of 4.52 ha and approximated the mean natal territory size of 4.5 ha (Anders et al. 1998). For the yellow-breasted chat, we used a 60-m radius moving window, which resulted in a moving window size of 1.13 ha and approximated a mean territory size of 1.2 ha (Thompson and Nolan 1973). For the site scale, we calculated the mean (HSm) and standard deviation (HSsd) of HSI value of each of the 9 sites. We used HTm, HTsd, SIm, SIsd, HSm, and HSsd as independent variables in subsequent analyses.

Validation of HSI Models

We evaluated the statistical significance of the HSI models as a predictor of three different demographic responses, within-site territory density, site-level territory density, and nest success, by fitting generalized linear mixed models with the appropriate HSI term. We conducted likelihood ratio tests (LRT) to determine whether the model containing the HSI variable had a greater likelihood than an intercept-only model. We defined the LRT statistic as $2(\ln(L_{model}) - \ln(L_{null}))$, where $\ln(L_{model})$ is the maximum log likelihood of the model containing the HSI term and $\ln(L_{null})$ is the log likelihood of the null model. We also examined the statistical significance of the estimated coefficient for the HSI effect using a Type III test of fixed effects. Finally, we plotted the predicted density or nest success as a function of the HSI variable for all statistically significant models.

Within-site and site-level territory density.—We created the within-site territory density response variable by applying a weighted distance function to the composite map of territories for each year. We calculated the distance (d_i) from a focal cell to each territory centroid within a 3-km radius of the focal cell. The weighted density estimate W for each cell was

$$W = \sum_{i=1}^{n} \left(\frac{1}{d_i} \right). \qquad \text{(eq 3)}$$

where d_i was the distance (in m) from the cell to the territory i. In other words, if 10 territories occurred within the focal pixel and no other territories occurred within a 3-km radius, the density was 10 territories per 28.3 km^2. The weighted density estimate declined towards zero as the distance between territories increased. To address spatial correlation, we used a semivariogram to estimate the range (distance) at which correlation was insignificant for each species (200 m for wood thrush and 350 m for yellow-breasted chat). We then sampled the 10-m grid at either the 200- or 350-m interval and used those cells for the analysis. We defined site-level territory density as the count of all territories within a site by year, divided by the site's area.

We used a mixed-effects model for repeated measures, with year as the repeated effect and within-site territory density or site-level territory density as the dependent variable. Repeated measures analyses account for multiple observations of the same subject (i.e., cell) over time (i.e., year) through specification of the covariance structure. We used restricted maximum likelihood estimation to examine four different covariance structures: simple, compound symmetry, autoregressive, and unstructured. We used AIC to determine which covariance structure was appropriate for the model that included the most fixed effects (i.e., global model) (Wolfinger 1993, 1996; Diggle et al. 1994). The unstructured covariance model, which estimated a unique correlation for within-subject errors for each pair of years, received the most support for both species and was used for all within-site territory density models. For the site-level territory density analysis, the compound symmetry covariance structure received the most support for the wood thrush and the autoregressive covariance structure received the most support for the yellow-breasted chat. We conducted the analyses using the MIXED procedure of SAS software version 9.1 (SAS Institute 2002, Cary, North Carolina, USA).

We determined the effect of the continuous HSI covariate, HTm on within-site territory density and HSm on site-level territory density, for specific HSI values. Because the estimated HSI values for each species ranged from 0 – 1.0, we predicted within-site territory density and site-level territory density for the entire range of HSI values.

Nest Success.—We conducted the nest success analysis in two stages to control for temporal factors known to influence nest success and minimize the number of models examined in the second stage (Shaffer 2004, Grant et al. 2005, Grant et al. 2006). In the first stage we developed a set of models that contained only temporal effects (i.e., nest stage, Julian date, Julian^2, Julian^3, and year) as univariate models and combinations of the five temporal variables. We fit all models using the logistic-exposure method to estimate nest success (Shaffer 2004, Shaffer and Thompson 2007), and ranked them using ΔAIC_c to determine the most supported temporal model (Burnham and Anderson 2002). The most supported temporal model for each species contained nest stage. In the second stage, we used the most supported temporal model as the base model and added the HSI variable HTm to the base model. In this way, temporal factors were included as nuisance parameters in the analysis (Link and Sauer 2002, Thogmartin et al. 2004, Thogmartin and Knutson 2007). We fit logistic-exposure models using the GENMOD procedure of SAS software version 9.1 (SAS Institute 2002, Cary, North Carolina, USA).

We determined the effect of the continuous HSI covariate HTm on nest survival by estimating average daily survival rate (DSR) for specific HSI values while holding the effects of other covariates in the model (e.g., nest stage) constant at their mean value. Because the estimated HSI values for each species ranged from 0 – 1.0, we predicted DSR for the entire range of HSI values.

Comparison of Competing Models

We evaluated the relative significance of HSI models versus other models using model selection (Burnham and Anderson 2002). We conducted a separate model selection analysis for each demographic response. The candidate model set for both species included the relevant HSI variable (HTm or HTsd for within-site territory density, HS for site-level territory density) or SI variable (SIm, SIsd) singly or in combination with other HSI (or SI) variables, each landscape attribute (tree age, tree species group, and landform type) singly or in combination with other landscape attributes, and management effects of period (pretreatment or posttreatment), treatment type (EAM, UAM, or control), and a period × treatment interaction. Because no yellow-breasted chats occurred in sufficient sample sizes pretreatment, we omitted period and the period × treatment interaction from all yellow-breasted chat analyses.

We fit the mixed-effects models, with the appropriate covariance structure as described above, using full maximum likelihood instead of restricted maximum likelihood to enable comparison of models with different fixed effects (Wolfinger 1993, 1996). We fit the logistic-exposure models in the same manner described above. We used likelihood ratio tests to quantitatively assess significance of the global model against a null model. We ranked models using ΔAIC_c, calculated the relative likelihood of a model given the data and set of models for each species using Akaike weights (ω), and reported the inverse of the evidence ratios (i.e., model likelihood) (Burnham and Anderson 2002).

RESULTS

The MOFEP landscape was largely homogenous with respect to tree age and distance to edge prior to management treatments. Following tree harvest, the mean tree age declined to 82 years and the standard deviation of tree age increased due to differences among sites in harvest treatments (Table 1). Correspondingly, the distance to edge (open habitat) decreased 4-fold posttreatment. The mean habitat suitability value for wood thrush increased from 0.35 pretreatment to 0.41 posttreatment (Table 1). The mean habitat suitability value for yellow-breasted chat was 0.02 with a maximum HSI = 1.00 posttreatment. No yellow-breasted chat habitat occurred pretreatment.

Validation of HSI Models

Within-site territory density.—The wood thrush model containing HTm did not have greater likelihood than the intercept-only model (χ^2 = 0.12, *df* = 1, *P* = 0.7518). While the β_{HTm} was positive, the 95% confidence interval included zero (Table 2) and there was no significant effect on density ($F_{1,1187}$ = 0.13, *P* = 0.7143). Therefore we did not develop a plot of effect of HTm on within-site territory density. A post-hoc addition of distance to edge to the HTm model produced a model with greater likelihood than the intercept only model (χ^2 = 138.2, *df* = 2, *P* < 0.0001).

The yellow-breasted chat model containing HTm had a greater likelihood than the intercept-only model (χ^2 = 124.39, *df* = 1, *P* < 0.0001). Within-site territory density increased with increasing mean HSI value ($F_{1,223}$ = 189.6, *P* < 0.0001; Table 2). Within-site territory density increased 8.5 times from HSI = 0.0 to HSI = 1.0 (Figure 1).

Site-level territory density.—The wood thrush model containing HSm did not have a greater likelihood than the intercept-only model when using both the pretreatment and posttreatment data (χ^2 = 0.2, *df* = 1, *P* = 0.6547). The effect of HSm on site-level territory density was negative but not significant ($F_{1,71}$ = 0.17, *P* = 0.6856). When considering only the posttreatment data, the wood thrush model containing HSm had a greater likelihood than the intercept-only model (χ^2 = 6.6, *df* = 1, *P* = 0.0102). The effect of HSm on site-level territory density posttreatment was positive and significant ($F_{1,7}$ = 9.74, *P* = 0.0168) (Table 2). Site-level territory density for wood thrush posttreatment ranged from 0.01 territories/ha at HSI = 0.30 to 0.15 territories/ha at HSI = 1.0 (Figure 2).

The yellow-breasted chat model containing HSm had a greater likelihood than the intercept-only model (χ^2 = 4.75, *df* = 1, *P* = 0.0293). The effect of HSm on site-level territory density was positive and significant ($F_{1,7}$ = 6.81, *P* = 0.0349) (Table 2). Site-level territory density for yellow-breasted chat ranged from 0.01 territories/ha at HSI = 0.00 to 0.46 territories/ha at HSI = 1.0 (Figure 2).

Nest success.—The wood thrush nest survival model containing HTm and nest stage did not have a greater likelihood than the nest stage-only model ($\chi^2 = 1.34$, *df* = 1, *P* = 0.2470). The effect of HTm on nest success was positive but not significant ($\chi^2 = 2.46$, *df* = 1, *P* = 0.1167) (Table 3).

The yellow-breasted chat nest survival model containing HTm and nest stage had a greater likelihood than the nest stage-only model ($\chi^2 = 3.14$, *df* = 1, *P* = 0.0764). The effect of HTm on yellow-breasted chat nest success was positive and significant ($\chi^2 = 4.43$, *df* = 2, *P* = 0.0353) (Table 3). Yellow-breasted chat DSR increased from 0.93 at HSI = 0.0 to 0.99 at HSI = 1.0 (Figure 3).

Comparison of Competing Models

Within-site territory density.—The global model for wood thrush did not adequately fit the data ($\chi^2 = 8533.95$, *df* = 8479, *P* < 0.0001). The global model was the most supported model, followed by the management effects model and then distance to edge (Table 4). The model containing HTm had $\Delta\mathrm{AIC_c} = 328.15$ and $\omega_i = 0.00$, indicating no support (Table 4). All models containing distance to edge received more support than models containing HTm or HTsd (Table 4).

For yellow-breasted chat, the global model adequately fit the data ($\chi^2 = 895$, *df* = 869, *P* = 0.2632). The most supported model contained HTm ($\omega_i = 0.65$), followed by the model that contained HTm and HTsd (Table 4). The data did not support models containing landscape attributes or management effects (Table 4).

Site-level territory density.—The global model for wood thrush adequately fit the data (χ^2 = 0.02, *df* = 67, *P* = 1.000). The most supported model for the complete data set (1991–2000) was the model containing management effects (ω_i = 0.67), followed by the model containing age and distance to edge (ΔAIC_c = 2.34) (Table 5). The model containing HSm had ΔAIC_c = 10.07 and ω_i = 0.00, indicating no support for the habitat suitability variable (Table 5). When we fit models for just the posttreatment period, the most supported model for the posttreatment period was the model containing HSm (ω_i = 0.56), followed by the model containing HSm and HSsd (ΔAIC_c = 2.60) (Table 5).

For yellow-breasted chat, the global model for site-level territory density adequately fit the data (χ^2 = 0.02, *df* = 26, *P* = 1.000). The most supported model for the posttreatment period contained tree age (ω_i = 0.38), followed by distance to forest (ΔAIC_c = 1.33) and the model containing HSm (ΔAIC_c = 1.60) (Table 5).

Nest success.—The global model for wood thrush nest success adequately fit the data (χ^2 = 847.9, *df* = 804, *P* = 0.1374). The most supported model contained the effects of nest stage and HTm (Table 6). The nest stage model had ΔAIC_c = 0.67 and the nest stage and tree age model had ΔAIC_c = 1.82, indicating some competition among the top temporal, landscape attribute, and HSI models (Table 6). We found no support for landscape attribute models that included landform type ($\Delta AIC_c \geq 3.4$).

For yellow-breasted chat, the global model for nest success adequately fit the data (χ^2 = 169.8, *df* = 196, *P* = 0.912). The most supported model contained the effects of nest stage and distance to forest edge (Table 6). The nest stage and HTm model had ΔAIC_c =1.73 and evidence ratio = 2.38, indicating some competition with the top model (Table 6).

DISCUSSION

The ultimate goal of HSI model validation is identify the level of risk associated with using a model to influence management decisions (Brooks 1997). Confidence intervals (Bender et al. 1996) and reliability bounds (Burgman et al. 2001) quantify uncertainty associated with estimating HSI values, but they do not address uncertainty regarding the relationship of HSI values to demographic rates. Our validation approach provides a general framework for evaluating the absolute (statistical significance) and relative (comparison to other models using model selection) measures of HSI model performance for three types of avian demographic responses, within-site territory density, site-level territory density, and nesting success. We demonstrated a statistically significant link between HSI values and all three demographic responses for the yellow-breasted chat and posttreatment site-level territory density for the wood thrush. We also found support for the HSI model when competing against models of landscape attributes and management effects. Based on our validation results, our HSI models represented wildlife demographic response to vegetation change.

We developed large-scale HSI models to assess habitat suitability for breeding. Defining habitat suitability for breeding presented a challenge because HSI model development involved expert opinion and empirical data from multiple data sources (Rittenhouse et al. 2007). While models should be developed with a specific objective in mind, factors affecting abundance, territory density, and nest success are not mutually exclusive. Thus, we were not surprised that our HSI models represented multiple forms of demographic response to habitat conditions. The yellow-breasted chat HSI model was a significant predictor of within-site territory density, site-level territory density, and nest success. Our estimate of territory density in high quality habitat (0.46 territories/ha at HSI = 1.00) was comparable to estimates of territory density in glade habitat (0.533 ± 0.281 SE territories/ha) but below that of regenerating forest (0.968 ± 0.072 SE territories/ha) for the MOFEP sites (Fink et al. 2006). Similarly, our estimated daily nest survival rate was 0.990 at HSI=1.00, which is higher than the daily survival rate at MOFEP sites (Fink et al. 2006) but comparable to the range of daily survival rates (0.96 ± 0.009 to 0.97 ± 0.011) observed by Ricketts and Ritchison (2000) in Kentucky. These results suggest that our estimates of yellow-breasted chat territory density and nest success from HSI values are reasonable.

In contrast, the wood thrush HSI model was not a significant predictor of within-site territory density, site-level territory density, or nest success. However, we obtained statistically significant models when we included distance to edge with HTm as a predictor of within-site territory density and when we repeated the site-level territory density analysis using only the posttreatment data. Taken together, these results suggest that the wood thrush HSI model may fail to capture important suitability relationships in homogenous (with respect to forest cover and tree age) forest landscapes. Wood thrushes are considered area sensitive (Robbins et al. 1989, Hoover et al. 1995, Mueller et al. 2000), but the effects depend on landscape context (Driscoll and Donovan 2004). In general, fragmented landscapes have lower fledging success than contiguous forests (Donovan et al. 1995). Adding a suitability relationship for edge sensitivity may improve the predictive ability of the wood thrush HSI model when applying it to homogenous forest landscapes.

Alternatively, the wood thrush HSI model may not be a significant predictor of within-site territory density, site-level territory density or nest success if factors experienced during the non-breeding season decouple the link between breeding habitat suitability and wood thrush demographics. For example, the North American Breeding Bird Survey estimated a survey-wide population trend of -1.6 % for wood thrush for the period 1966 – 2006 (Sauer et al. 2007) yet over this same period the amount of forest cover in the eastern United States increased (Trani et al. 2001). If non-breeding season habitat conditions limit wood thrush, then we might expect some suitable breeding habitat to remain unoccupied. In this situation, the wood thrush HSI model still predicts suitable habitat.

The comparison of models containing HSI values to models containing landscape attributes or management effects revealed differences in model support for all three response variables and by species. As with statistical significance, the differences in HSI model support may be related to each species' ecology. Factors influencing nest success include predation and brood parasitism (Martin 1988, Paton 1994, Robinson et al. 1995), in addition to landscape attributes such as micro- and macro-habitat features. While some studies found that the strength of the relationship between nest success and fragmentation changed with increasing spatial scale (Chalfoun et al. 2002, Stephens et al. 2003, Lloyd et al. 2005), some bird species adjusted breeding habitat selection or nest site selection based on local nest predator abundance or space use (Marzluff et al. 2007).

For yellow-breasted chats, nest predation risk can be strongly related to a specific landscape attribute; nests close to forest edges have higher predation rates than nests further from forest edges (Woodward et al. 2001). When we defined habitat suitability for breeding in terms of nest success only, the yellow-breasted chat HSI model performed adequately (i.e., competed with the distance to forest edge model), but was not the most supported model. In contrast, when we defined suitability for breeding in terms of within-site territory density the HSI model was the most supported model and no other model received support. From a planning perspective, it may be impractical to develop a new model for every metric of avian fitness (i.e., clutch size, clutch mass, nestling mass, nest success, seasonal reproductive success, seasonal productivity). Thus, it may be desirable to use the yellow-breasted chat HSI model for planning because it captured a general demographic response as well as specific ones, whereas the opposite was true for models based on a specific landscape attribute.

Given the differences among species in life history traits and ecologies, a blanket assumption that suitability represents demographic response without specifying which demographic response is inappropriate. Some demographic responses may be decoupled from habitat conditions when species exist below carrying capacity or there is spatial or temporal variation in predation or brood parasitism (Wiens and Rotenberry 1981, Van Horne 1983, Orians and Wittenberger 1991, Chalfoun et al. 2002, Chalfoun and Martin 2007, Marzluff et al. 2007). Besides these ecological issues, model validation may also be affected by the data used for validation (Shifley et al. 2008). The volume or amount of data and its availability, how representative the data is of site-specific habitat conditions and the temporal context of the data may have a profound impact on evaluations of HSI model performance (Bender et al. 1996, Roloff and Kernohan 1999).

We offer two suggestions regarding the model validation process in hopes of strengthening the relationship between wildlife demography and HSI values. First, we encourage modification of vegetation inventory and monitoring protocols to acquire spatially explicit information for a subset of sites within the study area. This will improve the ability to develop and test suitability relationships for specific habitat features, such as forest canopy gaps that are used by adult and juvenile birds for foraging, as opposed to using simple habitat type associations. Second, we suggest including sufficient resources to monitor wildlife response to management as part of the planning process. Collection of long-term demographic data is invaluable for detecting and quantifying wildlife response to habitat changes, especially in managed landscapes.

MANAGEMENT IMPLICATIONS

We validated HSI models of breeding habitat suitability for wood thrush and yellow-breasted chat using demographic data. Knowledge of the absolute and relative ability of HSI models to quantify species-specific demographic responses to habitat change provides an invaluable basis for making management decisions. The yellow-breasted chat HSI model was a significant predictor of territory density and nest success; therefore it indicates breeding habitat suitability. If the wood thrush is included in the planning process and habitat is not limiting posttreatment, then the HSI model may not be indicative of demographic response to habitat management.

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Table 1. Summary statistics for habitat suitability and landscape attributes on the Missouri Ozark Forest Ecosystem Project. Even-aged and uneven-aged harvest treatments were each applied to 3 sites in 1996, with 3 sites serving as non-harvest controls.

Period	Variable	Mean	Std. Dev.	Median	Min	Max
1991 – 1995	Woth_HSI	0.35	0.04	0.35	0.10	0.43
	Tree age	87.86	7.18	88.41	0	109.10
	Distance to edge	477.44	327.16	412.31	0	1745.22
1997 – 2002	Woth_HSI	0.41	0.11	0.39	0	0.84
	Ybch_HSI	0.02	0.11	0	0	1.00
	Tree age	82.19	16.17	86.24	0	109.10
	Distance to open	118.06	103.76	90.00	0	586.69
	Distance to forest	1.64	8.44	0	0	130.38

Table 2. Mixed-effects model estimates for wood thrush (WOTH) and yellow-breasted chat (YBCH) within-site territory density (HTm) and site-level territory density (HSm). Parameter estimates, standard errors, and lower and upper 95% confidence limits are reported.

Species	Parameter	β	SE	L95cl	U95cl
		Within-site territory density			
WOTH	Intercept	0.03341	0.002574	0.028262	0.038559
	HTm	0.002490	0.006630	-0.010770	0.015750
YBCH	Intercept	0.01058	0.000767	0.009050	0.012117
	HTm	0.08006	0.005723	0.068610	0.091504
		Site-level territory density			
WOTH	Intercept	-0.06882	0.03180	-0.13183	-0.00462
	HTm	0.2376	0.07611	0.08536	0.38978
YBCH	Intercept	0.01258	0.007141	-0.00170	0.02687
	HTm	0.4485	0.17184	0.10485	0.79221

Table 3. Logistic-exposure model estimates of regression coefficients relating daily survival rate of wood thrush (WOTH) and yellow-breasted chat (YBCH) nests to nest stage and mean HSI value within a moving window size equivalent to average territory size (HTm). Parameter estimates, standard errors, lower and upper 95% confidence limits, odds ratios, and lower and upper confidence limits of odds ratio are reported.

Species	Parameter	β	SE	L95cl	U95cl	OR	ORl	ORu	χ^2	Pr > χ^2
WOTH	Intercept	2.61	0.41	1.78	3.44	13.59	5.93	31.17	39.56	<.0001
	HTm	1.54	0.98	-0.42	3.50	4.66	0.66	33.17	2.46	0.1167
	Stage-egg	-0.39	0.19	-0.77	-0.02	0.68	0.46	0.98	4.38	0.0365
	Stage-nstl	0.0	0.0	0.0	0.0	1.0	1.0	1.0		
YBCH	Intercept	3.17	0.32	2.53	3.81	23.79	12.55	45.08	98.32	<.0001
	HTm	1.97	0.94	0.10	3.84	7.17	1.10	46.63	4.43	0.0353
	Stage-egg	-0.82	0.38	-1.59	-0.05	0.44	0.20	0.95	4.56	0.0327
	Stage-nstl	0.0	0.0	0.0	0.0	1.0	1.0	1.0		

Table 4. Model selection criteria for analysis of within-site territory density of wood thrush (WOTH) and yellow-breasted chats (YBCH) in the Missouri Ozark Forest Ecosystem Project, south-central Missouri, 1991 – 2002. The MOFEP data set contained 1,297 wood thrush territories and 357 yellow-breasted chat territories. K is the number of parameters in the model, $-2^* \ln(L_{model})$ is twice the negative value of the maximized log-likelihood function, $\mathrm{AIC_c}$ is Akaike's Information Criterion adjusted for small-sample bias, $\Delta\mathrm{AIC_c}$ is the scaled value of $\mathrm{AIC_c}$, ω_i is the Akaike weight, and ω_i/ω_{max} is the inverse of the evidence ratio. The wood thrush models contain 45 parameters and the yellow-breasted chat model contains 10 parameters for estimating the covariance structure.

Species	Model[a]	K	$-2^*\ln(L_{model})$	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	ω_i	ω_i/ω_{max}
WOTH	D_{Global}	71	-30925.7	-30772.0	0.00	1.00	1.00
	$D_{\mathrm{P+T+P\times T}}$	60	-30832.6	-30704.4	67.65	0.00	0.00
	D_{DE}	47	-30637.4	-30574.4	197.68	0.00	0.00
	$D_{\mathrm{TA+DE}}$	48	-30674.2	-30573.0	199.10	0.00	0.00
	$D_{\mathrm{LT+DE}}$	52	-30681.1	-30570.9	201.13	0.00	0.00
	$D_{\mathrm{TA+DE+LT}}$	53	-30682.0	-30569.6	202.48	0.00	0.00
	$D_{\mathrm{SI2m+SI2sd}}$	48	-30564.8	-30463.6	308.42	0.00	0.00
	D_{SI2m}	47	-30562.1	-30463.1	308.93	0.00	0.00
	$D_{\mathrm{HTm+HTsd}}$	48	-30551.4	-30450.2	321.87	0.00	0.00
	D_{TA}	47	-30546.8	-30447.8	324.28	0.00	0.00
	$D_{\mathrm{TA+LT}}$	52	-30556.1	-30446.0	326.05	0.00	0.00
	D_{Int}	46	-30542.8	-30446.0	326.06	0.00	0.00

	D_{LT}	51	-30552.3	-30444.4	327.66	0.00	0.00
	D_{HTm}	47	-30542.9	-30443.9	328.15	0.00	0.00
YBCH	D_{HTm}	12	-3461.91	-3437.56	0.00	0.65	1.00
	$D_{\mathrm{HTm + HTsd}}$	13	-3462.65	-3436.24	1.32	0.34	0.52
	D_{DF}	12	-3452.79	-3428.43	9.13	0.01	0.01
	$D_{\mathrm{TA + DF}}$	13	-3453.75	-3427.33	10.23	0.00	0.01
	$D_{\mathrm{SI1m + SI1sd}}$	13	-3453.58	-3427.17	10.39	0.00	0.01
	D_{Global}	26	-3478.58	-3424.96	12.60	0.00	0.00
	$D_{\mathrm{LT + DF}}$	17	-3454.23	-3419.54	18.02	0.00	0.00
	$D_{\mathrm{TA + DF + LT}}$	18	-3455.20	-3418.42	19.14	0.00	0.00
	D_{SI1}	12	-3435.12	-3410.77	26.79	0.00	0.00
	D_{T}	15	-3441.27	-3410.72	26.84	0.00	0.00
	D_{TA}	12	-3407.20	-3382.84	54.72	0.00	0.00
	$D_{\mathrm{TA + LT}}$	17	-3411.07	-3376.37	61.19	0.00	0.00
	D_{Int}	11	-3337.52	-3315.22	122.34	0.00	0.00
	D_{LT}	16	-3340.13	-3307.51	130.05	0.00	0.00

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[a] P: period; T: treatment; PT: period-by-treatment interaction; TA: tree age (yrs); DE: distance to edge (m); DF: distance to forest (m); LT: landform type; SI1m: mean SI1 value; SI1sd: standard deviation of SI1m; SI2m: mean SI2 value; SI2sd: standard deviation of SI2m; HTm: mean HSI value of territory; HTsd: standard deviation of HTm

Table 5. Model selection criteria for analysis of site-level territory density of wood thrush (WOTH) and yellow-breasted chats (YBCH) in the Missouri Ozark Forest Ecosystem Project, south-central Missouri. The MOFEP data set contained 1,297 wood thrush territories and 357 yellow-breasted chat territories. *K* is the number of parameters in the model, -2*ln(L_{model}) is twice the negative value of the maximized log-likelihood function, AIC_c is Akaike's Information Criterion adjusted for small-sample bias, ΔAIC_c is the scaled value of AIC_c, ω_i is the Akaike weight, and ω_i/ω_{max} is the inverse of the evidence ratio. Both models contain 2 parameters for estimating the covariance structure.

Species (Years)	Model[a]	*K*	-2*ln(L_{model})	AIC_c	ΔAIC_c	ω_i	ω_1/ω_i
WOTH (1991–2000)	$D_{P + T + P\times T}$	14	-417.9	-383.5	0.00	0.67	1.00
	$D_{TA + DE}$	5	-392.0	-381.2	2.34	0.21	0.31
	D_{DE}	4	-388.0	-379.4	4.08	0.09	0.13
	D_{Int}	3	-381.8	-375.5	8.02	0.01	0.02
	D_{Global}	18	-421.6	-374.5	8.98	0.01	0.01
	D_{HSm}	4	-382.0	-373.4	10.07	0.00	0.01
	D_{TA}	4	-381.8	-373.3	10.18	0.00	0.01
	$D_{HSm + HSsd}$	5	-383.9	-373.1	10.36	0.00	0.01
WOTH (1997–	D_{HSm}	4	-180.7	-171.5	0.00	0.56	1.00

2000)							
	$D_{\mathrm{HSm + HSsd}}$	5	-180.9	-168.9	2.60	0.15	0.27
	D_{TA}	4	-177.1	-167.8	3.62	0.09	0.16
	D_{Int}	3	-174.1	-167.4	4.06	0.07	0.13
	$D_{\mathrm{TA + DE}}$	5	-179.2	-167.2	4.27	0.07	0.12
	D_{T}	6	-180.4	-165.5	5.97	0.03	0.05
	D_{DE}	4	-174.4	-165.1	6.38	0.02	0.04
	D_{Global}	10	-182.3	-153.5	18.00	0.00	0.00
YBCH	D_{TA}	4	-179.5	-170.2	0.00	0.38	1.00
	D_{DF}	4	-178.2	-168.9	1.33	0.20	0.51
	D_{HSm}	4	-177.9	-168.6	1.60	0.17	0.45
	$D_{\mathrm{TA + DF}}$	5	-179.6	-167.6	2.65	0.10	0.27
	D_{Int}	3	-173.2	-166.4	3.80	0.06	0.15
	$D_{\mathrm{HSm + HSsd}}$	5	-178.0	-166.0	4.25	0.05	0.12
	D_{T}	6	-180.6	-165.7	4.48	0.04	0.11
	D_{Global}	10	-184.6	-155.8	14.46	0.00	0.00

[a] P: period; T: treatment; PT: period-by-treatment interaction; TA: tree age (yrs); DE: distance to edge (m); DF: distance to forest (m); LT: landform type; HSm: mean HSI value of site; HSsd: standard deviation of HSm

Table 6. Model selection criteria for analysis of daily survival rates of wood thrush (WOTH) and yellow-breasted chats (YBCH) in the Missouri Ozark Forest Ecosystem Project, south-central Missouri, 1991 – 2002. The effective sample size was 2556 for wood thrush and 618 for yellow-breasted chats. *K* is the number of parameters in the model, -2*ln(L_{model}) is the twice the negative value of the maximized log-likelihood function, AIC$_c$ is Akaike's Information Criterion adjusted for small-sample bias, ΔAIC$_c$ is the scaled value of AIC$_c$, ω_i is the Akaike weight, and ω_1/ω_i is the evidence ratio.

Species	Model^a	*K*	-2*ln(L_{model})	AIC$_c$	ΔAIC$_c$	ω_i	ω_1/ω_i
WOTH	$S_{\mathrm{S + HTm}}$	3	-332.23	670.47	0.00	0.231	1.00
	S_{S}	2	-333.57	671.13	0.67	0.165	1.40
	$S_{\mathrm{S + SI2m}}$	3	-332.89	671.79	1.32	0.119	1.94
	$S_{\mathrm{S + TA}}$	3	-333.14	672.29	1.82	0.093	2.48
	$S_{\mathrm{HTm + HTsd}}$	4	-332.23	672.47	2.00	0.085	2.72
	$S_{\mathrm{S + DE}}$	3	-333.53	673.07	2.60	0.063	3.67
	$S_{\mathrm{SI2m + SI2sd}}$	4	-332.80	673.62	3.15	0.048	4.81
	Intercept	1	-335.87	673.74	3.27	0.045	5.13
	$S_{\mathrm{S + LT}}$	6	-330.92	673.88	3.41	0.042	5.50
	$S_{\mathrm{S + TA + DE}}$	4	-333.00	674.02	3.55	0.039	5.92
	$S_{\mathrm{S + TA + LT}}$	7	-329.99	674.03	3.56	0.039	5.92
	$S_{\mathrm{S + LT + DE}}$	7	-330.92	675.89	5.44	0.015	15.40
	$S_{\mathrm{S + TA + LT + DE}}$	8	-329.93	675.92	5.45	0.015	15.40
	$S_{\mathrm{S + TA + LT + DE}}$ + HTm + HTsd +	12	-328.08	680.28	9.81	0.002	115.50

	SI2m + SI2sd						
YBCH	$S_{\mathrm{S + DF}}$	3	-78.77	163.58	0.00	0.324	1.00
	$S_{\mathrm{S + TA + DF}}$	4	-78.59	165.25	1.67	0.140	2.31
	$S_{\mathrm{S + HTm}}$	3	-79.64	165.31	1.73	0.136	2.38
	$S_{\mathrm{S + LT + DF}}$	7	-76.10	166.38	2.80	0.080	4.05
	$S_{\mathrm{S + SI1m}}$	3	-80.42	166.87	3.29	0.062	5.23
	$S_{\mathrm{S + HTm + HTsd}}$	4	-79.54	167.15	3.57	0.054	6.00
	$S_{\mathrm{S + TA}}$	3	-80.56	167.16	3.58	0.054	6.00
	$S_{\mathrm{S + HTsd}}$	3	-80.99	168.03	4.45	0.035	9.26
	$S_{\mathrm{S + SI1m + SI1sd}}$	4	-80.04	168.15	4.57	0.033	9.82
	$S_{\mathrm{S + TA + LT + DF}}$	8	-75.98	168.19	4.61	0.032	10.13
	$S_{\mathrm{S + TA + LT}}$	7	-77.68	169.54	5.96	0.016	20.25
	S_{S}	2	-82.78	169.57	6.00	0.016	20.25
	$S_{\mathrm{S + SI1sd}}$	3	-82.73	171.51	7.93	0.006	54.00
	$S_{\mathrm{S + LT}}$	6	-79.70	171.53	7.95	0.006	54.00
	Intercept	1	-85.76	173.52	9.94	0.002	162.00
	$S_{\mathrm{S + TA + LT + DF}}$ + HTm + HTsd + SI1m + SI1sd	12	-74.91	174.34	10.76	0.001	324.00

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[a] NS: nest stage, included as a nuisance variable in all models; TA: tree age (yrs); DE: distance to edge (m); DF: distance to forest (m); LT: landform type; SI2m: mean SI2

value; SI2sd: standard deviation of SI2m; HTm: mean HSI value; HTsd: standard deviation of HTm.

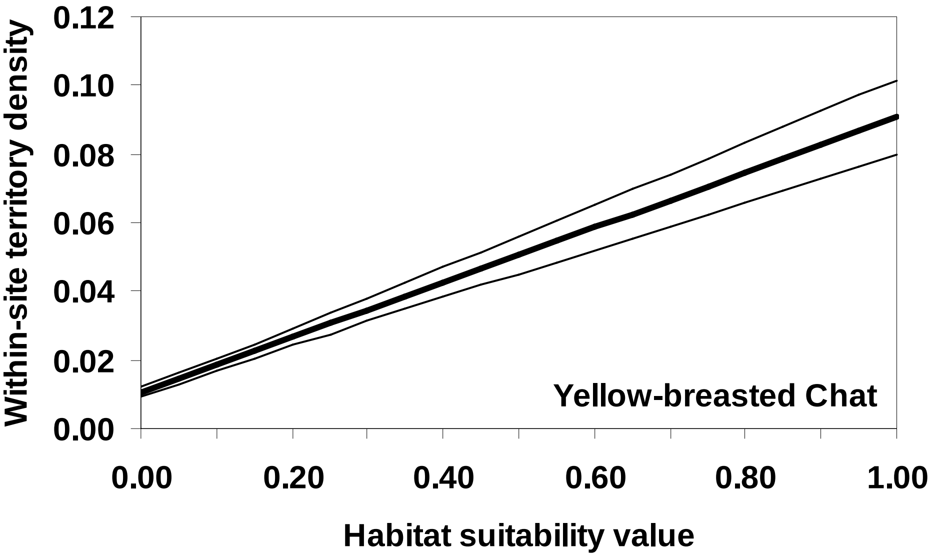

Figure 1. Predicted within-site territory density of yellow-breasted chats based on habitat suitability value for Missouri Ozark Forest Ecosystem Project, south-central Missouri, 1997 – 2000. The wood thrush model was not significant and therefore not included in this figure. Thin lines represent 95% confidence limits.

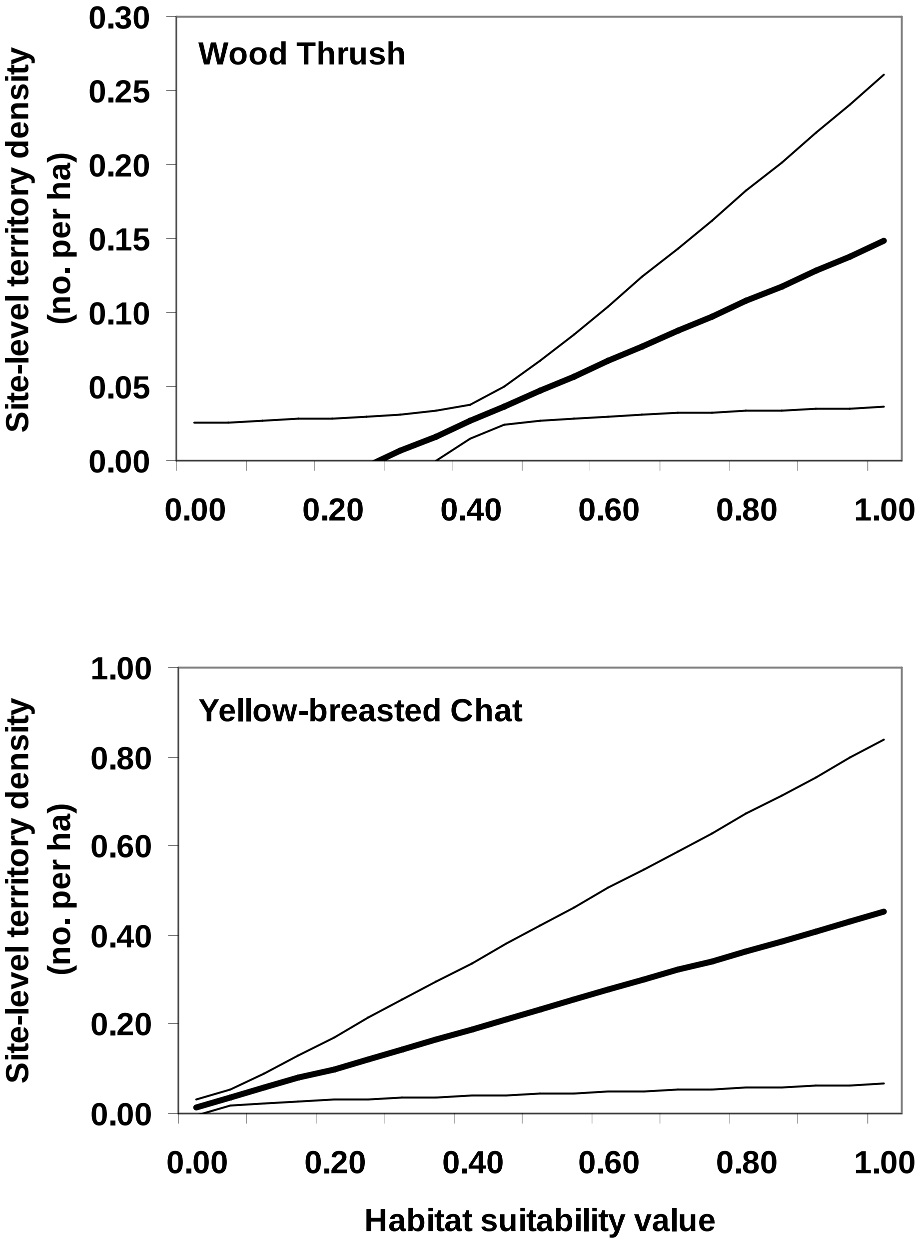

Figure 2. Site-level density of wood thrush and yellow-breasted chat territories in relation to mean habitat suitability value for 9 sites in Missouri Ozark Forest Ecosystem Project, south-central Missouri, 1997 – 2000. Thin lines represent 95% confidence limits.

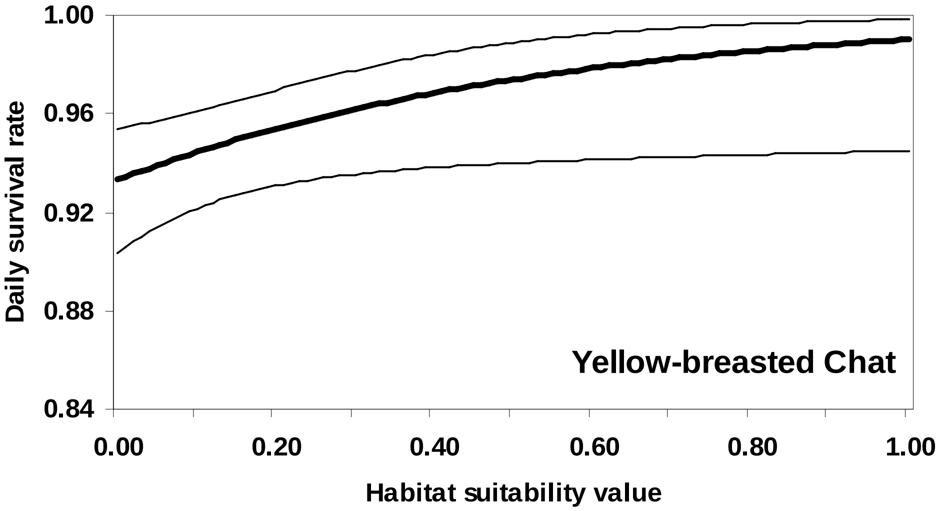

Figure 3. Daily survival rates of yellow-breasted chats in relation to habitat suitability values in Missouri Ozark Forest Ecosystem Project, south-central Missouri, 1997 – 2002. Thin lines represent Wald 95% confidence limits for the logistic-exposure model.

APPLICATION OF LANDSCAPE AND HABITAT SUITABILITY MODELS TO CONSERVATION: THE HOOSIER NATIONAL FOREST LAND-MANAGEMENT PLAN

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ABSTRACT

Traditional forest and wildlife management planning efforts focus on quantifying the tradeoffs among timber production and wildlife benefits. Increasingly, land managers and planners are asked to incorporate a broader range of interests, including aesthetic, economic, social, political, recreational, and ethical or moral interests. We used an approach for forest planning that addresses ecological and biological issues associated with forest and wildlife habitat management as part of large-scale conservation plans. We evaluated habitat conditions 10, 50, and 150 years from present for 8 avian and 1 mammalian species under 5 management alternatives on the Hoosier National Forest, Indiana (HNF) as part of the HNF plan revision. We simulated future forest conditions with LANDIS, developed GIS-based habitat suitability models, and applied the models to the forest output. Three important patterns emerged over time with respect to forest composition and structure: white oak increased in area of dominance under all alternatives, the proportions of red oak species and maples were affected by the intensity of forest disturbance via tree harvest and fire, and in the absence of anthropogenic disturbance or wildfire, the HNF was dominated by late-successional vegetation conditions. Without tree harvest or prescribed fire, early successional wildlife species were greatly reduced within 50 years. Tree harvest benefited early successional species without greatly affecting habitat suitability for late successional species. These patterns are consistent with current knowledge of vegetation and wildlife response to management. The HNF planning team used the information on vegetation conditions and habitat suitability to select Alternative 5, which utilized a focal area to concentrate tree harvest activities, as the preferred alternative. The Forest Plan was appealed but upheld

and the HNF is moving forward with plan implementation. By incorporating ecological processes of disturbance and succession while retaining the resolution necessary for evaluating wildlife habitat suitability, our modeling approach contributed knowledge to the planning process and was a valuable tool for communicating differences among alternatives to stakeholders. As such, this approach serves as a template for successful planning on forested lands and will be of value to land managers, resource planners, and ecologists.

INTRODUCTION

Science, policy, and the public interact in complex and sometimes contentious ways. The controversy surrounding management of the Northern Spotted Owl (*Strix occidentalis*), Red-cockaded Woodpecker (*Picoides borealis*), Marbeled Murrelet (*Brachyramphus marmoratus*), and the Northern Goshawk (*Accipiter gentilis*) are examples. Collectively, management of these species resulted in volumes of scientific research, scores of management plans, and public debate regarding the management and conservation of forest resources amid competing interests. The discussions regarding these and other wildlife species can be a challenge to forest and wildlife planning.

Whereas traditional forest and wildlife management efforts focused on quantifying the tradeoffs among timber production and wildlife benefits (Kuusipalo and Kangas 1994), increasingly managers and planners are asked to incorporate a broader range of interests, including ecological (i.e., ecosystem structure, function, and processes), aesthetic, economic, social, political, recreational, and ethical. Much debate has focused on “old growth” forests of the western United States where the sharpest tradeoffs between timber production and wildlife habitat occur. The Midwestern United

States is not immune from the “old growth” issue; however, there is increasing concern regarding grassland, shrubland, and early successional forest habitat (Thompson and DeGraaf 2001). Decades of fire suppression and changes in tree harvest (Trani et al. 2001), as well as conversion to other land uses (e.g., low-density residential development) have reduced the amount of these habitats in the Midwestern and Eastern United States (Brown et al. 2005, Pocewicz et al. 2008). Concomitant with these activities are the declines of many avian species dependent on forest, shrubland, and grassland habitats. Since large-scale monitoring via the North American Breeding Bird Survey (BBS) began in 1966, many species of neotropical migratory birds have exhibited population declines (Sauer et al. 2007). Current land-use trends point to continued changes in the distribution and quality of avian habitat (Brown et al. 2005, Huston 2005). By addressing these issues in the forest planning process, National Forests can contribute greatly to avian conservation.

The U.S. National Forest Management Act, passed in 1976 (36 CFR 219) and most recently amended in 2005 (U.S. Department of Agricultural Forest Service 2005), requires that National Forests “provide for ecological conditions to support a diversity of native plant and animal species in the plan area” (Section 219.10(b)). The 2005 regulations shifted the focus from maintaining population viability to species diversity, and further assumed that sustaining ecosystem diversity is sufficient to sustain species diversity (Noon et al. 2005). Problem definition and priority setting are critical elements of planning, especially when multiple management objectives are desired, competition or tradeoffs among management objectives exists, or when not all objectives are considered equal (Lindenmayer et al. 2008). Because forest planning often involves many integrated objectives and multiple wildlife species, some modeling approaches (e.g., optimization models, Usher 1966, Lu and Buongiorno 1993) may be difficult if not impossible to implement (Thompson and Millspaugh 2008). When multiple, integrated, or adaptive objectives exist the conceptual model used to characterize and simulate landscape change should provide the spatial and temporal information needed for management decisions (Lindenmayer et al. 2008). Thus, for planning purposes an ideal modeling approach might consider broad-scale landscape dynamics while retaining the fine-scale resolution needed to quantify changes in wildlife habitat (Noon et al. 2008).

A common goal in National Forest planning is to describe the relationship between management actions, vegetation and wildlife habitat conditions for large landscapes. Inherent in the 2005 regulation change are concepts of landscape ecology, such as ecological processes of disturbance and succession, as well as the implications of those processes on the composition, structure, and configuration of vegetation and wildlife habitat. While many approaches exist for modeling vegetation change in forests (Vanclay 1995, Murray and Snyder 2000, Kurttila 2001, Baskent and Keles 2005), forest landscape disturbance and succession models are increasingly applied to large-scale analyses of forest management because they retain the spatial and temporal contexts to inform management decisions (Shifley et al. 2000, Larson et al. 2004, Shifley et al. 2006, Shifley et al. 2008). For example, raster-based landscape simulation models such as HARVEST (Gustafson and Crow 1996) and LANDIS (Mladenoff et al. 1996, He et al. 1999, Mladenoff and He 1999) can provide vegetation information at the scale and resolution needed to model species-specific changes in habitat suitability (Larson et al. 2003, Larson et al. 2004, Rittenhouse et al. 2007).

We used a landscape simulation model and habitat suitability models to forecast the effects of alternative land-management plans on forest vegetation and wildlife as part of the Hoosier National Forest planning process. We developed large-scale, GIS-based habitat suitability models for 9 wildlife species: American Woodcock (*Scolopax minor*), Cerulean Warbler (*Dendroica cerulea*), Henslow's Sparrow (*Ammodramus henslowii*), Northern Bobwhite (*Colinus virgnianus*), Ruffed Grouse (*Bonasa umbellus*), Wood Thrush (*Hylocichla mustelina*), Worm-eating Warbler (*Helmitheros vermivorus*), Yellow-breasted Chat (*Icteria virens*), and Indiana bat (*Myotis sodalis*) (Rittenhouse et al. 2007). We simulated ecological processes of disturbance (e.g., tree harvest, prescribed fire, wildfire, windthrows) and succession using LANDIS, and applied the habitat suitability models to the output from LANDIS. In this way, we linked large-scale wildlife habitat suitability models to spatially explicit vegetation change models that include ecological processes affecting vegetation composition, structure, and configuration.

Our objectives were to demonstrate an approach to integrated land-management planning and to quantify differences in vegetation and wildlife habitat conditions among management alternatives on the HNF. The alternatives differed in terms of the type, extent, magnitude, frequency, and location of management activities. We were interested in the differences in vegetation and habitat conditions due to anthropogenic disturbance, defined as tree harvest and prescribed fire, as well as natural disturbance (e.g., wind or wildfire). In some situations complex interactions may make the distinction between anthropogenic or natural disturbance difficult, such as when multiple disturbance types operate in succession or concurrently. To facilitate this comparison, we used the same extent, magnitude, and frequency of wildfire for each alternative. In other words, we standardized wildfire across all alternatives so that the alternatives differed only with respect to anthropogenic disturbance and tree age-dependent wind mortality.

METHODS

Study Area

The Hoosier National Forest is located in southern Indiana and consists of four purchase units totaling approximately 261,000 ha. This region was subject to intensive forest harvest from 1870 to 1910, followed by a period of settlement and conversion to agricultural land uses that persisted into the early 1930s. Concurrent with the Great Depression, the region experienced large-scale abandonment of farms. The HNF was established by proclamation in 1935 to reduce vacant tax rolls and became a national forest in 1954. In the absence of continued anthropogenic disturbance most of the abandoned farms became forested again. At present, the HNF is characterized as second-growth forest with approximately 75% of the total forest area exceeding 50 years of age (Woodall et al. 2007).

Although the HNF is more than 70 years old, landownership within the purchase units is predominantly private. Approximately 81,000 ha of the land within the purchase units is owned by the HNF and 96 percent of this is forested (Figure 1). The predominance of private lands within the HNF purchase units resulted from the acquisition of lands over time. The fragmented nature of the HNF, coupled with public opposition to tree harvest over the past 20 years and the HNF's proximity to metropolitan cities of Indianapolis, Indiana and Louisville, Kentucky, are important features that largely define current land-management issues (Welch et al. 2001).

Overview of the Planning Process

Forest Plans provide strategic guidance for all natural resource management activities that take place on National Forest System lands for a period of 10 – 15 years, at which time they are reviewed and revised as needed. All Forest Plans must be accompanied by a scientific analysis for the expected effects of implementing management alternatives. The 1982 version of 36 CFR 219 requires Forest Plans to include: establishment of forest-wide multiple use goals and objectives; establishment of forest-wide management requirements; establishment of management area direction applying to future management activities; establishment of allowable timber sales, including the quantity and designation of suitable timber lands; monitoring and evaluation requirements; and recommendations to Congress regarding designation of additional Wilderness Areas or Wild, Scenic and Recreational Rivers.

The planning process for the HNF occurred in 5 stages, which began with an analysis of the current management situation and existing conditions. During this stage the existing Forest Plan and management activities were reviewed, and inventories of forest and wildlife conditions were conducted. The existing Forest Plan, amended in 1991, provided the starting point for discussion on the HNF. Setting the direction of the Forest Plan (or revision in this case) began with identifying the major issues, concerns, and opportunities affecting management. The HNF planning team solicited public participation early in the planning process using a variety of means and continued the identification and refinement of public issues throughout the planning process.

The public involvement goals for the Hoosier Forest Plan were to develop a revised Forest Plan that could be implemented, and to develop, maintain, and enhance

Forest-public relationships. The HNF planning team identified the following objectives for public involvement in the planning process: build informed consent for what would be considered in plan revision; provide multiple ways for the public to be involved; establish and maintain two-way communication with interested publics; ensure employees have the opportunity to become and stay well informed about revision issues and revision processed; communicate information in a timely manner; and establish and maintain credibility and understanding of the agency and planning process. In this way, the HNF planning team broadened the information base upon which decisions were made.

The second stage identified the desired conditions and developed objectives to address emerging issues, such as changes in forest species composition, wildlife population trends, or species conservation status. Various management scenarios, or alternatives, were developed in the second stage to achieve the desired conditions and objectives. Simultaneous with the development of forest management alternatives was the selection of wildlife species that were evaluated in the planning process. The third stage consisted of a scientific analysis of the expected effects of implementing each of the management alternatives on future forest conditions and wildlife habitat or populations. During the fourth stage, the proposed Forest Plan and a Draft Environmental Impact Statement were developed and opened to public review. The final stage occurred with the selection of the recommended alternative, development of the final Forest Plan, and approval of the final Forest Plan.

The Hoosier Forest Plan revision process included several key time periods for public notification and involvement at each stage of the planning process to ensure public involvement goals were met. These included: validating the need for change and proposing the scope of the revised plan; commenting on the Notice of Intent to review the plan and refine the scope of the issues to be addressed; development of management alternatives; reviewing and commenting on the proposed Forest Plan and Draft Environmental Impact Statement, as well as identifying additional information needs and options to be considered; and participating in implementation of the selected alternative.

The final products of the models and analysis were presented to the public in the Environmental Impact Statement. Along with the release of the EIS, Forest Planners held public meetings to explain the results, methodology, and gain input from the public. Interactive maps were also utilized that allowed the public to turn off and on various layers depicting results of the modeling process. This allowed the public and HNF planning team to gain insight into the modeling process and visualize the effects on species composition and habitat suitability indices. This, in turn, allowed the planning team to rethink the proposed plan and make adjustments to increase habitat suitability for some species.

Description of the Forest Management Alternatives

The HNF Planning Team originally drafted 5 forest management alternatives, each of which contained different tree harvest procedures (e.g., even-aged and uneven-aged techniques, including shelter-wood and group selection), amounts of tree harvest and prescribed burning, and types of recreation opportunities (Table 1). After reviewing the LANDIS and LandscapeHSI model output from initial model runs, the HNF Planning team created a 5260-ha focal area to concentrate even-aged management within the Tell

City District. Alternatives 3, 4, and 5 were amended to include the focal area; Alternatives 1 and 2 remained the same.

Alternative 1.—The first management alternative, referred to in the Draft EIS (Hoosier National Forest 2005) as the No Action alternative, represented the 1985 forest plan as amended and continued the current forest management plan. This alternative emphasized ecosystem sustainability by creating a diversity of habitat types and forest seral stages. Alternative 1 provided areas with continuous canopy mature forest, maintained current forest openings, wilderness and recreation areas, and used tree harvest and prescribed fire to maintain biological diversity within specified management units. Vegetation management, including timber production, occurred on approximately 41% of the HNF. Tree harvest methods included both uneven-aged and even-aged management techniques. Uneven-aged management techniques, including shelterwood, single-tree, and group selection, were applied, on average, to 1,940 ha (2.4% of HNF) per decade. Even-aged regeneration methods (clearcuts), were applied, on average, to 820 ha (1.0% of HNF) per decade and the size of even-aged management treatments was limited to a maximum of 4.05 ha in pine conversion areas and 2.02 ha in hardwood management areas. Minimum rotation length for management areas subject to even-aged harvest was 100 years. Prescribed fire was used to restore fire-dependent ecosystem processes (e.g., oak regeneration) and to reduce fuel build up. Prescribed fire occurred on approximately 8,095 ha (10.0% of HNF) per decade.

Alternative 2.—The second management alternative emphasized natural processes and limited vegetation management. Alternative 2 encouraged development of large areas of continuous forest canopy, which over time would allow the HNF to progress towards old growth. Under Alternative 2 no areas of the HNF were managed for timber production and no prescribed fire was implemented. Existing wildlife openings were allowed to convert to forest over time, reducing the amount of early successional wildlife habitat.

Alternative 3.—The third management alternative provided a diversity of forest size and age classes, areas with continuous forest canopy, and increased recreational opportunities. This alternative allowed construction of additional recreation trails and development of an ATV trail system. Additionally, this alternative provided wildlife habitat for both interior forest and early successional species. Current wildlife openings were maintained and new wildlife openings were created with a goal of creating larger openings or complexes of openings. Tree harvest and prescribed fire promoted oak-hickory regeneration. Under Alternative 3 vegetation management including timber production occurred on approximately 56% of the HNF, primarily within a 5260-ha focal area to concentrate tree harvest activities. Uneven-aged management was applied, on average, to 3,290 ha (4.1% of HNF) per decade, even-aged management was applied, on average, to 650 ha (0.8% of HNF) per decade, and prescribed fire occurred on approximately 20,235 ha (25.0% of HNF) per decade. Minimum rotation length for management areas subject to even-aged harvest was 100 years.

Alternative 4.—The fourth management alternative emphasized fire-dependent and early successional habitat while maintaining habitat for late-successional forest species. Alternative 4 focused on biological diversity with increased recreational opportunities and economic return. This alternative promoted restoration of native hardwoods and provide habitat for early successional species using tree harvest and prescribed fire. Current wildlife openings were maintained and new wildlife openings were created with a goal of creating larger openings or complexes of openings. Under Alternative 4, vegetation management including timber production occurred on approximately 56% of the HNF, primarily within a 5260-ha focal area to concentrate tree harvest activities. Tree harvest methods included both uneven-aged and even-aged management techniques; however, the emphasis was on even-aged techniques. Even-aged management was applied, on average, to 2,435 ha (3.0% of HNF) per decade, with a maximum treatment size of 16.2 ha. Minimum rotation length for management areas subject to even-aged harvest was 100 years. Uneven-aged management was applied, on average, to 3,545 ha (4.4% of HNF) per decade and prescribed fire occurred on approximately 40,470 (50.0% of HNF) per decade.

Alternative 5.—The fifth management alternative was similar to Alternative 1 in that it provided areas with continuous canopy mature forest, maintained current forest openings, wilderness and recreational areas, and used tree harvest and prescribed fire to maintain biological diversity within specified management units. However, Alternative 5 added a 5260-ha focal area to concentrate tree harvest activities and provide early successional habitat. Under Alternative 5, vegetation management including timber production occurred on approximately 41% of the HNF. Tree harvest methods included both uneven-aged and even-aged management techniques; however, the emphasis was on even-aged techniques and even-aged management occurred primarily within the 5260-ha focal area. Even-aged management was applied, on average, to 820 ha (1.0% of HNF) per decade, with a maximum treatment size of 16.2 ha within the focal area, 4.05 ha in pine conversion areas, and 2.02 ha in hardwoods management areas. Minimum rotation length for management areas subject to even-aged harvest was 100 years. Uneven-aged management was applied, on average, to 1,940 ha (2.4% of HNF) per decade and prescribed fire occurred on approximately 8,095 ha (10.0% of HNF) per decade.

Simulation of Vegetation Change Using LANDIS

We simulated spatial and temporal trends of vegetation change using LANDIS (version 3.6), a spatially-explicit, landscape-level analysis tool that models vegetation growth, reproduction, and response to disturbance by tree harvest, wind, and fire (Mladenoff et al. 1996, He et al. 1999, Mladenoff and He 1999). In LANDIS, a landscape is organized as a (raster) grid of cells. Each cell contains a matrix of vegetation information such as the tree species (or species groups) present or absent in the cell and the age class of each tree in the cell by 10-year age classes. Cell size in LANDIS is user defined. We used a 10m by 10m cell size because it approximated the size of a canopy gap created by the death or harvest of a mature tree.

We simulated four spatial processes (fire, windthrow, harvesting, seed dispersal) and four temporal processes (succession, regeneration, age-dependent mortality, sequential patterning of disturbance events) that affect the projected species composition and age structure of individual cells and, in aggregate, of the landscape as a whole. We began calibrating the model to the study area, establishing initial vegetation conditions (e.g., cell contents for all cells in the landscape), and defining the natural disturbance regime. LANDIS output included maps of tree species composition and dominance, tree age classes, fire history, wind history, and tree harvest history in 10-year increments for each cell in the landscape.

Model calibration.—We followed the general approach of Shifley et al. (2006) who simulated forest landscape change on a 71,000 ha Ozark landscape, but we recalibrated the LANDIS regeneration and succession algorithms for 14 tree species (or groups of similar species) common to Southern Indiana (Table 2). Silvical characteristics for each species, including shade tolerance, fire tolerance, and sprouting probabilities were derived from Burns and Honkala (1990) and Johnson et al. (2002).

Initial estimates of LANDIS regeneration coefficients for each species or species group (i.e., relative rates of species establishment following disturbance) were derived from Forest Inventory and Analysis (FIA) data for southern Indiana (Schmidt et al. 2000, Alerich et al. 2004, Woodall et al. 2006). We summarized data by tree species group, tree diameter at breast height (dbh) and ecological land type. For each species group by ecological land type, the ratio of the relative frequency of trees in the 2.5 – 7.5 cm dbh class to that of the 7.6 – 12.5 cm dbh class was used as an indicator of species persistence on that ecological land type. We used this value as an initial estimate of the relative species regeneration coefficient required by LANDIS for each ecological land type. We then graphically analyzed the predicted century-long shifts in tree species composition in the absence of disturbance that resulted from the application of those coefficients. We focused on relative changes in the red oak (*Quercus* section *Lobatae*), white oak (*Q.* section *Quercus*), and sugar maple (*Acer saccharum* Marsh.), red maple (*A. rubrum* L.) and yellow-poplar (*Liriodendron tulipifera* L.) species groups. We made small adjustments to coefficients to remain consistent with expected changes in species composition from other sources, including expert opinion from regional managers.

Initial forest conditions.—We established the initial forest conditions (tree age and species) for public and private lands within the Hoosier National Forest purchase unit boundary from Forest Inventory Analysis (FIA) data, the HNF’s inventory database, land-use and land-cover data, and Indiana GAP data. For forest stands on public lands, the HNF vegetation inventory included a forest type classification and year of origin for mapped forest stands. We computed stand age from the date of stand origin and categorized stands by age class: seedling or sapling, age 1 – 40 years; pole, age 41 – 60 years; sawtimber, age 61 – 80 years; and mature, age ≥ 81 years. We used the stand age class to set corresponding age classes for tree cohorts in each stand on the initial landscape condition map. We used FIA data for southern Indiana (Schmidt et al. 2000, Alerich et al. 2004, Woodall et al. 2006) to estimate the expected number of trees by age class for each 0.01 ha cell in a given stand and to develop observed species frequency distributions by forest cover type and age class. We assigned tree species to each cell in each stand by random draw from those frequency distributions. The total number of tree records (i.e., species by age class combinations) mapped on a given 10m by 10m cell decreased with increasing tree age to explicitly account for the number of trees of various size or age classes that typically occur on 0.01ha of a well-stocked forest (i.e., more small trees vs. fewer large trees).

We lacked spatially explicit maps of forest cover type and age class data for forest stands on private lands within the HNF purchase units. Instead, we utilized the land use and land cover data created by Pangea Information Technologies (2003), the Indiana GAP data (http://gapanalysis.nbii.gov), and by the National Agricultural Statistics Service (2008) to map locations of nonforest, coniferous forest, upland deciduous forest, mixed forest and bottomland forest types for private lands. In some instances where the land cover data indicated the location of early successional forest stands, we assigned these an age class of 10. For the remainder of the private forest land within the HNF purchase units we used the intersection of ELT and land cover boundaries to identify homogenous units (analogous to forest stands), and we assigned an age class and forest cover type for each unit based on the frequency distribution of forest age classes (10, 30, 50, 70, 90, and 110 years old) and forest cover types from FIA data for southern Indiana. In the absence of spatially exact data on ownership boundaries and forest stand condition for private lands, this provided a reasonable approximation of the spatial pattern of forest conditions on private lands. We combined the tree age maps for private lands with corresponding maps for the HNF and used them as initial conditions for LANDIS scenario analyses. We identified 16 different dominant overstory species, including 14 different dominant overstory tree species (or species groups), and 2 additional overstory types, nonforest and grassland (Table 2, Figure 2).

We used ecological land types (ELT) derived from 10 m Digital Elevation Model (DEM) layers by Guafon Sho (Purdue University). The ELT coding followed Van Kley et al. (1994) and grouped types by slope, aspect, and relative moisture. ELT classes generally correspond to north and east (cool and mesic) slopes, south and west (warm and dry) slopes, wide ridges or upland flats, narrow ridges, and mesic bottoms.

We classified land-cover type using the HNF forest type codes (for public lands) and the land-use and land-cover data described above for private lands. The HNF forest type codes distinguished between 12 types of closed and open canopy forests or clear cuts, grasslands, and water. We collapsed the HNF forest type map and the public land-cover map into 6 general land-cover types: 1) forest, 2) croplands, 3) grasslands, 4) water, 5) urban areas, and 6) roads for use in the HSI models.

Simulating natural disturbance.—The only regional source of information for small wind disturbances estimated that wind damage affected approximately 0.142% of the landscape annually by creating openings from 0.05 to 20 ha in size (Rebertus and Meier 2001). Rebertus and Meier (2001) did not record wind events smaller than 0.05 ha, but by extrapolating their reported trends for gaps in the 0.3, 0.2 and 0.1 ha size classes (Figure 1 in Rebertus and Meier 2001), we estimated the additional landscape area in smaller gaps was approximately 0.008 percent, and, thus, the combined wind disturbance rate for patches from 0.02 to 20 ha is approximately 0.15 percent annually. This equates to a mean wind disturbance interval of 670 years. For simulation we rounded the wind return interval to 700 years. Under this assumption approximately 120 ha of the Hoosier National Forest would be disturbed by small wind events annually (1,200 ha per decade of simulation).

Historical records indicate that about 650 ha of the HNF area is damaged by tornados per decade (Tom Thake, Hoosier National Forest, personal communication). Thus, the mean tornado-free interval is approximately 1300 years. After a series of trials, we determined that the current algorithms in LANDIS 3.6 are incapable of simultaneously simulating small scale wind events (typically less than 4 ha in size) and catastrophic wind events such as tornadoes (typically greater than 40 ha in size and linear in shape). The spatial scales of the events are so disparate that a composite mean wind disturbance size is representative of neither the frequent small-scale events nor the rare but large tornado events. Thus, for the simulation on the Hoosier National Forest we excluded tornado events and simulated wind damage events that could range up to approximately 20 ha in size.

We derived probability of wildfire from 27 years of fire incident data recorded for the Hoosier National Forest and for other private and public lands in southern Indiana. Based on summaries of those data we modeled wildfire with a mean fire return interval of approximately 700 years, with a mean fire size of 39 ha and fire locations determined randomly. Management using prescribed fire on the Hoosier National Forest was modeled by increasing the incidence of wildfire within a given management area and ecological land type to cause the total burned area to approach the level called for in the proposed management alternative (Table 1). The version of LANDIS we used (version 3.6) does not include detailed provisions for simulating prescribed fire, but recent work has greatly expanded fire simulation detail and capability in LANDIS (He et al. 2004).

Simulating tree harvest.—We simulated tree harvests to mimic the proposed harvest actions for each Forest Plan alternative (Table 1) (United States Department of Agriculture Forest Service, 2006) using the methodology described by Gustafson et al (2000). The Hoosier National Forest has designated Management Areas that divide the forest into thematic zones based on suitable management activities (e.g., riparian buffers vs. wilderness vs. timber management vs. habitat for a designated wildlife species). Management Areas are typically thousands of ha in extent and can be spatially discontinuous. We used a feature of LANDIS that allows tree harvest activity to be varied by Management Area and tailored the simulated management activities to follow the HNF Forest Plan (Table 1) as closely as possible.

Summarizing vegetation change.—We expected the forest plan alternatives would differentially affect the spatial and temporal distribution of forest based on the *a priori* differences in the type, frequency, and extent of disturbances due to tree harvest and prescribed fire. To capture those differences, we summarized forest and landscape attributes for spatially defined groups of cells at different spatial scales (e.g., purchase units, management areas, or the entire HNF). Attributes included tree age class distribution, tree species composition, contiguous core forest area, length of edge habitat, tree harvest volume, and disturbance history.

We modeled 14 tree species groups (Table 2) and tracked the presence or absence of species by age class over time and/or by location. Of particular interest was the proportion of oaks relative to maples and other mesic species that are successionally replacing oaks across much of the southern Indiana landscape (Shifley and Woodall 2007). We report summaries by forest area for the dominant species (i.e., highest canopy position) on each 0.01 ha cell. However, cells within the model may contain multiple tree species.

The total area of core forest habitat and cumulative length of forest edge are metrics that can be used to summarize habitat conditions important to some species of wildlife. We defined edge as the total length of the boundary between any two mutually exclusive categories of land (e.g., forest vs. open land, young forest vs. mature forest, hardwood forest vs. pine forest, etc.). We defined core area for a given land category as the total area that is a specified distance from an edge with another category. Core area can be computed for any land cover type, but it is frequently computed for the area of mature or old-growth forest that is buffered from edge habitat, which we defined as area of mature forest that is at least 60m from an edge with young forest or open land. In most situations core area and edge area are inversely related. We computed the length of edge for each of following land classes vs. any other land class: (a) permanent openings,

(b) forest land without trees, (c) the combined seedling and sapling forest age classes, and (d) the combined pole, sawtimber and mature forest age classes. We used the same land classes to compute core area at least 60 m from the nearest edge with another land class (i.e., with a 60 m edge buffer).

Although it is possible to compute edge and core area for each land cover type and for multiple edge buffer widths, some combinations are difficult to interpret in a biologically meaningful way. Consequently we illustrated only the quantity of edge and core area for the combined pole, sawtimber and mature forest age classes (representative of mature, closed canopy forest) vs. all other younger forest or open land categories combined. This is an index of core area available to species that prefer blocks of mature, closed canopy forest and an index of the amount of edge between young and mature forest. Other specific core and edge metrics used in the evaluation of habitat suitability indices were computed by the habitat suitability algorithms as they were implemented (discussed later).

The total tree harvest per decade is one indicator of anthropogenic disturbance for each management alternative. Since harvested areas naturally regenerate in this ecosystem, it is also an index of the intensity of forest regeneration. We used Indiana FIA data on wood volume by forest age class to calibrate a nonlinear, asymptotic equation to estimate tree volume as a function of stand age:

$$\text{volume} = 173.90\,(1 - \exp(-0.0038886\,\mathit{age}^{1.4986}))$$

where volume is cubic meters per hectare for trees 13 cm dbh and larger, and *age* is forest age class in years. We applied the model to tabular summaries of harvested sites by harvest type, forest age class, decade and management alternative to arrive at estimates of available harvest volume for growing stock trees 13 cm dbh and larger.

Wildlife Species Selection

The HNF planning team convened a Species Viability Evaluation (SVE) panel to select which species to include in the planning process. The SVE panel consisted of research specialists or scientists from the HNF and the Shawnee National Forest (SNF), Illinois, Southern Illinois University and Indiana Department of Natural Resources. The SVE panel recognized the infeasibility of monitoring the status and assessing the viability of all species, and instead used a focal species approach (Committee of Scientists 1999). The criteria used to select the focal species included listing as U.S. Forest Service Region 9 sensitive species; Federally endangered, threatened, or proposed for listing; species representative of each of the habitat types within the Hoosier National Forest; the availability of literature and empirical data on a species; and species occurrence on the HNF within the last 25 years. The SVE panel also included species for which there was high management and public interest (e.g. Neotropical migratory bird species and game species). Forest Service resource specialists decided that only species potentially affected, either positively or negatively by forest management, would be carried forward through the planning process. Wildlife experts recognized by their peers as having expertise (research, education, study, or experience) in one or more of the species reviewed the species list and validated the SVE process. The recommendations of the wildlife experts and final review completed by resource specialists resulted in a list of 9 SVE species, including 8 bird species and one mammal species (Table 3). The selected species varied in life history traits, habitat associations, and conservation status.

Assessment of Wildlife Habitat Suitability using Landscape HSImodels

We used Landscape HSImodels version 2.0 (Dijak et al. 2007) to evaluate breeding habitat suitability or year-long habitat suitability for the 9 wildlife species selected by the HNF Planning Team. Landscape HSImodels is a Microsoft Windows-based software program that uses suitability indices (SI) to assign habitat quality across large landscapes for individual species (Larson et al. 2003, Dijak et al. 2007, Dijak and Rittenhouse 2008). Habitat suitability is described by an empirical or assumed relationship between habitat quality and resource attributes on a relative scale that ranges from 0 (not suitable habitat) to 1 (highly suitable habitat) (U.S. Fish and Wildlife Service 1980, 1981). Similar to McComb et al. (2002), we developed the SIs with specific objectives in mind. First, the SIs addressed habitat requirements for reproduction or survival and were supported by empirical data, published literature, or expert opinion. Second, all SIs were estimated from existing GIS layers of vegetation (and landscape) structure and composition. Third, all vegetation information was amenable to projection into the future using LANDIS. Thus, we could apply the HSI models to simulated vegetation output and compare future landscapes in terms of demographic response to habitat conditions.

The primary input data (i.e., resource attributes) for the SIs included raster maps of tree species, tree age, ecological land type, land-cover type, and fire history. Landscape HSImodels contained functions for patch size, edge effects, distance to resource, and composition of habitat. Thus, the suitability value of a cell considered attributes of a cell as well as the landscape surrounding the cell. Landscape HSImodels combined the suitability indices using an HSI equation so that a single composite value represented the overall habitat suitability for each species.

Rittenhouse et al. (2007) provided a thorough discussion of habitat variables used in the development of the habitat suitability models, including literature citations supporting suitability relationships for each species. We summarized the Landscape HSImodel for each species by life requisite, habitat requisite, model parameters and implementation, and provided the HSI equation in Table 4. We verified that each HSI model operated correctly by hand-calculating HSI values for a sample of approximately 20 pixels from a test landscape (Chapter 1). We identified several instances where the function used to calculate suitability values or the HSI equation performed incorrectly. Most of these errors were due to the order of operations for the function. We fixed all errors and repeated the verification procedure to ensure that each HSI model was correct.

Application of models to LANDIS output.—We applied the species-specific habitat suitability models to raster maps from LANDIS output at four time periods: initial conditions, year 10, year 50, and year 150 of the simulation. The extent of the Hoosier National Forest (~81,000 ha) and the resolution (10 m pixels) necessitated modeling each forest district separately. We partitioned the largest forest district (Tell City) into a northern and a southern section.

Summarizing HSI output.—We summarized habitat quality in terms of the amount of suitable habitat and the distribution of habitat suitability values for years 0, 10, 50 and 150 of the simulation for each forest management alternative. We followed traditional habitat evaluation procedures and used the habitat unit as our metric for the amount of suitable habitat. We defined a habitat unit as the HSI value of an individual pixel multiplied by the pixel's area (100 m^2, or 0.01 ha). We summarized habitat units in terms of the distribution of habitat units by HSI value categories (0, 0.01-0.24, 0.25-0.49, 0.50-0.74, and 0.75-1.00) and summed across all pixels to determine the total number of habitat units (Rickers et al. 1995, Marzluff et al. 2002). For convenience, we refer to habitat units with HSI value of 0.75 – 1.00 as high quality habitat.

RESULTS

Vegetation Conditions

The five management alternatives differed in the type and frequency of disturbance due to tree harvest and prescribed fire. Disturbance affected the spatial and temporal distribution of forest, including stand structure and composition. We summarized landscape attributes of length of edge habitat, contiguous core forest area, and harvested volume from maps of forest age class (Figure 2), species composition (Figure 3), fire disturbance history (Figure 4) and wind disturbance history (Figure 5). Modeling each management alternative by decade over the 150-yr project horizon at a cell resolution of 0.01 ha for 81,000 ha created an enormous amount of data. Where appropriate, we present data for landscape attributes by decade. However, the primary emphasis for planning purposes was to summarize effects at short, intermediate, and long periods of plan implementation. Therefore, we present results at simulation year 0, 10, 50, and 150 years for each plan alternative.

Forest age class distribution.—The initial forest age class distribution was the same for all management alternatives. At year 0 of the simulation, less than 1 percent of the initial HNF landscape was classified in the seedling age class (0 – 10 years old), 18 percent was in the sapling age class (11 – 29 years old), 15 percent was in the pole age class (30 – 59 years old), and two-thirds of the HNF was in the sawtimber age class (60+ years old) (Figure 6). The relative proportions of each age class shifted over time in response to disturbance by tree harvest, fire, and wind (Table 1, Figure 6). On a forest-wide basis, Alternative 2 provided the least structural diversity, and the least forest in seedling and sapling age classes. The proportion of the forest area in the seedling plus sapling age classes (i.e., trees ≤ 30 years old) increased with increasing disturbance level by alternative as follows: Alternative 2 (7%) < Alternative 1 (18%) = Alternative 5 (18%) < Alternative 3 (21%) < Alternative 4 (26%) (Figure 1). The corresponding forest-wide rotation length (i.e., number of years to regenerate the equivalent of the total forest area one time, based on the proportion of forest area ≤ 60 years of age at the end of the projection period) was highest for Alternative 2 at 870 years, and decreased sequentially for Alternative 1 (240 years), Alternative 5 (220 years), Alternative 3 (200 years), and Alternative 4 (170 years). Even the most intensive tree harvest regime, Alternative 4, provided relatively little early successional forest compared to a typical management regime designed for timber production (e.g., rotation age ≤100 years).

Three patterns stand out in the comparison of forest age class proportions over time for each alternative (Figures 2, 6). The first pattern, a "V" in the age class distribution, appears in the seedling age class at year 10, the sapling class at years 20 – 40, and the pole age class at years 40 – 60 (Figure 6). The "V" shape is partially an artifact of the way we developed the initial landscape conditions and the way LANDIS implemented disturbance. The initial landscape consisted primarily of the sawtimber age class with few young trees embedded within the older stands. As LANDIS implemented age-dependent mortality and wind disturbance (i.e., blowdowns), many small patches of seedlings appeared even for alternatives with no tree harvest (Alternative 2). These disturbance agents occurred in addition to tree harvest and fire-related seedling regeneration. Also, Dutch elm disease is endemic throughout the HNF. We eliminated elms in the first few decades of simulation as they reached the pole age class, which resulted in a small, proportional increase in seedling regeneration as elms were systematically replaced. In actuality, not all age-dependent mortality would be likely to occur in the first time step. It may be more realistic to see a gradual shift in the age class distribution over a 10 – 30 year period. In other words, shift happens just not as quickly as the simulation suggests.

The second pattern occurred 90 – 100 years from plan implementation when equilibrium in age class distribution as a proportion of area was reached (Figure 6). From years 100 to 150 of the simulation the proportion of the landscape in the 4 age classes was similar across alternatives implementing tree harvest and prescribed fire. By year 150, the combined total of the seedling and sapling age classes as a proportion of area declined for the Alternative 1 (1 percent decline), Alternative 2 (14 percent decline), and Alternative 5 (1 percent decline), whereas the same proportion increased for Alternative 3 (2 percent increase) and Alternative 4 (7 percent increase) compared to initial conditions.

The third pattern was evident in the spatial arrangement of forest age classes beginning in year 10 and continuing to year 150 of the simulation (Figure 2). Even-aged harvest in the Alternatives 1, 3, 4, and 5, produced even-aged patches ranging in size from 2 ha to 16.2 ha. The largest even-aged patches occurred in Alternative 4, which had the largest maximum cut size of 16.2 ha. Uneven-aged harvest produced many small, similar age patches on the landscape (group selection) and stippled areas of intermixed age classes (single-tree selection). Alternative 2 resulted in a homogenous landscape dominated by the oldest age class, although younger age classes were maintained by a combination of fire disturbance, wind disturbance, and gap-scale replacement of senescent trees. As a result of these random disturbance agents, no clear spatial pattern was evident in the Alternative 2.

Core area and edge.—Core area (Figure 7) and length of edge (Figure 8) also illustrate the effect of forest regeneration in the first decade of the modeled scenario. When projected core and edge values equilibrated approximately 100 years into the projection, Alternative 2 created about three times as much core area and about half the edge length of the other alternatives. The other 4 alternatives were clustered in their estimated edge and core area. Considering both core area and length of edge together, Alternative 1 was nominally closer to Alternative 2 than were Alternatives 3-5, but Alternatives 1, 3, 4, and 5 are most notable for the similarity in values for core area and edge length.

Tree species composition.—The initial tree species composition was the same for all management alternatives. At year 0, oaks were dominant (i.e., highest canopy position) on 42 percent of the HNF forested landscape (white and post oak comprised 19 percent; red, black and scarlet oak 18 percent; and chestnut oak 5 percent). Sugar and red maples were dominant on 10 and 2 percent of the HNF, respectively. Other dominant species included hickories (14 percent), yellow-poplar (7 percent), and pine species (10 percent, primarily non-native pine plantations). Each of the remaining species groups was dominant on less than 5 percent of the initial landscape. Following implementation of each alternative, the proportion of pine decreased to approximately 0 percent of the forest either due to targeted harvest or mortality due to longevity constraints. All pine was replaced by natural hardwood regeneration. Dominant elms declined from 3 percent of the initial landscape to less than 0.5 percent due to anticipated mortality from Dutch elm disease. Dominance by hickory species also declined under each alternative with the greatest decreases in Alternatives 3 and 4, which had the greatest level of disturbance and greatest increase in oak dominance.

The HNF planning team was particularly interested in the proportion of oaks relative to maples and other mesic species; therefore, we summarized tree species composition for each alternative beyond year 0 in terms of white oak, maple, and red oak groups (Figure 3, Figure 9). Over the 150-year simulation of vegetation change, the proportion of oak- and maple-dominated forest varied greatly among the five management alternatives (Figure 3, 9). Alternative 2 realized the greatest increase in maple dominance, from 12 to 39 percent of the forest in 150 years (Figure 9). White oaks increased to 26 percent while red oaks decreased to 8 percent of forest area in 150 years under Alternative 2 (Figure 9). Under Alternative 4, the area of forest dominated by the maple group remained nearly constant over the 150-yr simulation while the area dominated by the red oak group increased to 25 percent and the area dominated by the white oak group increased to 52 percent (Figure 9). Alternatives 3 and 4 reached the highest dominance by white oaks at 50 and 52 percent of forest area, respectively and were the only alternatives that maintained dominance by the red oak group over the maple group (Figure 9). Alternative 5, which added the focal area for tree harvest activities but retained the same levels of tree harvest and prescribed fire, had the same species composition as Alternative 1 (Figure 9).

Tree harvest.—Mean harvest volume per decade varied from a low of zero under Alternative 2 to a high of 560,000 cubic meters under Alternative 4. Within each alternative the harvested volume differed by decade and tree harvest method (Figure 10).

Wildlife Habitat Suitability

American Woodcock.—Alternative 4 had the largest even-aged cut size (16.2 ha), highest tree harvest levels, and highest prescribed fire levels among all alternatives. The high levels of disturbance created early successional (regeneration) habitat used by woodcock for display and nesting, and the interspersion of young and old forest. Compared to Alternative 1, the amount of high quality habitat (HSI > 0.75) in Alternative 4 would increase 2.46 times by year 10 and 109.35 times by year 150 (Figure 11). Alternative 5, which added the focal area to Alternative 1, increased the amount of high quality habitat 2.74 times by year 50 and 9.26 times by year 150. Under Alternative 2, the amount of high quality habitat increased 1.32 times by year 10, largely due to succession of open areas and gap-level dynamics associated with tree mortality from senescence, windthrow, or disease. However, the continued absence of tree harvest or prescribed fire agents led to the elimination of high quality habitat by year 50 (Figure 11). When ranked by the total amount of suitable habitat, the rank of each alternative was constant over time (Figure 11). The highest mean HSI values were achieved in Alternative 4 and the lowest mean HSI values in Alternative 2 (Table 5).

Cerulean Warbler.—Alternative 2 had no tree harvest or prescribed fire, while Alternative 4 had the highest levels of tree harvest and prescribed fire. Compared to Alternative 1 at year 10, the percent change in the amount of habitat ranged from an 8 percent decrease in Alternative 3 to no difference in Alternative 5 (Figure 11). The greatest separation of management alternatives occurred around year 50, with Alternative 3 producing a 53 percent decrease and Alternative 2 producing a 15 percent increase in the amount of high quality habitat compared to Alternative 1 at year 50 (Figure 11). It is unclear whether the percent change at year 50 was an artifact of the initial landscape conditions and concomitant change in forest age class distribution, or a result of the tree harvest and prescribed fire levels. By year 150, all management alternatives had greater amounts of high quality habitat and greater total amount of suitable habitat than initial conditions. Alternative 2 produced 1.21 times more high quality habitat than Alternative 1 (Figure 11). The relative rank of each alternative was not constant over time; Alternative 4 provided a greater amount of suitable habitat in year 50 than all other alternatives except Alternative 2. By year 150, though, Alternative 4 had the least amount of suitable habitat among all alternatives (Figure 11). The highest mean HSI values were achieved in Alternative 2 and the lowest mean HSI values in Alternative 4 (Table 5).

Henslow's Sparrow.—The HSI model for Henslow's sparrow was only sensitive to changes in land cover type; tree harvest did not affect HSI values. Because grasslands on the HNF were maintained using prescribed fire, the absence of fire under Alternative 2 eliminated Henslow's sparrow habitat by year 10 of the simulation (Table 5). Alternatives 1, 3, 4, and 5 had only 27 – 34 ha of high quality habitat over the 150-yr simulation period, representing a 7.5 – 34.0 percent increase over current conditions (Figure 11). Only the American woodcock ranked lower than the Henslow's sparrow in terms of the amount of high quality habitat for all alternatives (Figure 11).

Northern Bobwhite.—Similar to Henslow's sparrow, the HSI model for bobwhite was most sensitive to changes in land cover type. Alternative 2 had the lowest amount of high quality habitat, the lowest total amount of habitat due to loss of open areas to succession, and the lowest mean HSI value (Figure 11, Table 5). Compared to the Alternative 1, Alternative 2 had only 7 percent of the high quality habitat in year 10 and only 1 percent remained by year 50. Alternatives 1, 3, 4, and 5 had similar mean HSI values and similar amounts of high quality habitat (Table 5, Figure 11).

Ruffed Grouse.—All four of the alternatives that implemented tree harvest had a greater amount of high quality habitat and higher mean HSI values than Alternative 2 (Figure 11, Table 5). Alternatives 3 and 4 consistently produced more high quality habitat than Alternatives 1 and 5 due to the higher tree harvest levels and increase in prescribed fire (Figure 11). Alternative 5, which added the focal area to Alternative 1, increased the amount of high quality habitat 1.11 times by year 150 (Figure 11). However, the greatest increase in total amount of suitable habitat and high quality habitat was achieved through a combination of the focal area and higher tree harvest and prescribed fire levels: Alternative 3 increased the amount of high quality habitat 2.40 and Alternative 4 increased the amount of high quality habitat 2.43 times from that under the Current Plan by year 10 (Figure 11). The large increase in high quality habitat was maintained for the plan duration such that by year 150, Alternative 3 had 1.61 times more high quality habitat and Alternative 4 had 2.44 times more high quality habitat than Alternative 1 at year 150 (Figure 11). The relative rank of each alternative was constant over time (Figure 11).

Wood Thrush.—The change in the amount of high quality habitat compared to Alternative 1 was greatest for Alternative 3 (9 percent decrease) and Alternative 4 (8 percent decrease) in year 10 (Figure 11). At year 50, Alternative 3 had 1.05 times and Alternative 4 had 1.06 times the amount of high quality habitat as Alternative 1. The change from a decrease to an increase in the amount of high quality habitat from year 0 to year 50 was an artifact of the HSI model and the 10-year time step of the simulation. In year 10, all cells subject to tree harvest during the first time step had a tree age of 0 because the initial landscape contained only dominant trees. The wood thrush HSI model assigned SI = 0 for all cells with tree age = 0. As a result, the alternatives that implemented the highest levels of tree harvest (Alternative 3 and 4) had the largest decrease in the amount of high quality habitat. By year 50, cells subject to tree harvest in the previous time steps were 10 – 40 years old. Of those, any cells 20 – 40 years post-harvest were retained by the wood thrush HSI model as post-fledging habitat. Addition of the focal area in Alternative 5 produced less than 1 % difference in the amount of high quality habitat for wood thrush compared to Alternative 1 (Figure 11). The relative rank of each alternative was constant over time (Figure 11). The highest mean HSI values were achieved under Alternative 2 (Table 5).

Worm-eating Warbler.—Alternative 1 had the greatest total amount of suitable habitat, the greatest amount of high quality habitat, and the highest mean HSI value in year 10 (Figure 11, Table 5). Alternative 2 had only 61 percent of the high quality habitat as Alternative 1 in year 10 but provided 1.10 times more high quality habitat than Alternative 1 in year 50 and 1.16 times more high quality habitat in year 150 (Figure 11). Alternatives 3 and 4, which had the highest levels of prescribed fire (25 and 50 percent, respectively), provided 10 to 20 percent less high quality habitat than Alternative 1 at each time step (Figure 11). Addition of the focal area to Alternative 1 resulted in small changes in the mean HSI values for each time step and a 5 percent reduction in the amount of high quality habitat at year 150 (Table 5, Figure 11). With the exception of year 10, Alternative 2 had the highest mean HSI values among all Alternatives (Table 5).

Yellow-breasted Chat.—Without tree harvest or prescribed fire, Alternative 2 contained only 82 percent of the high quality habitat as Alternative 1 in year 10 and had no high quality habitat by year 50 (Figure 11). Alternative 5 increased the amount of high quality habitat 1.16 times in year 10 of the simulation, 1.55 times in year 50, and 2.56 times in year 150 compared to Alternative 1 (Figure 11). However, the greatest amounts of high quality habitat were produced under Alternatives 3 and 4, which had higher tree harvest and prescribed fire levels than Alternatives 1 and 5, in addition to the focal area. Alternative 4, which had the largest even-aged cut size (16.19 ha), the highest level of even-aged management (3.0 percent per decade) and the highest level of prescribed fire (50 percent per decade), produced 4.03 times more high quality habitat than Alternative 1 in year 10, 5.79 times more in year 50, and 12.58 times more high quality habitat in year 150 (Figure 11). The relative rank of each alternative was constant over time (Figure 11). The highest mean HSI values were achieved under Alternative 4 for all time steps (Table 5).

Indiana Bat.—At year 10 Alternative 4 provided 1.21 times more high quality habitat than Alternative 1, at year 50 Alternative 1 provided the most high quality habitat, but at year 150 Alternative 3 provided 1.26 times more high quality habitat than Alternative 1 (Figure 11). The large increases in the amount of high quality habitat by year 10 was due to the gap-level disturbances of age-related senescence, mortality due to disease (i.e., Dutch elm disease), and windthrow events. These disturbance agents provided foraging opportunities for bats and solar radiation of maternity roosts, resulting in a 10.15- to 15.71-fold increase in the amount of high quality habitat at year 10 from the 1457 ha present at initial conditions (Figure 11). Among the alternatives that implemented tree harvest, Alternative 3 had the lowest percentage of forest in even-aged management (0.8 percent) and the second highest percentage of forest in uneven-aged management (4.0 percent) (Table 1). The uneven-aged harvest techniques were similar to gap-level disturbances and likely contributed to the greater amount of habitat provided by Alternative 3 in year 150. Even-aged harvest may also increase solar radiation and foraging opportunities, but not at the same level as uneven-aged techniques. Alternative 5, which added a focal area to concentrate even-aged harvest but had the same tree harvest and prescribed fire levels as Alternative 1, had only 90 percent of the amount of high quality habitat by year 50 and 88 percent by year 150 (Figure 11). The highest mean HSI values, with the exception of year 10, were achieved under Alternative 2, but all alternatives had higher mean HSI values than at the beginning of the simulation (Table 5).

DISCUSSION

Our approach to land-management planning on the Hoosier National Forest contains desirable features from a large-scale, landscape perspective while retaining the fine-scale information useful for evaluating wildlife habitat suitability. We simulated spatially explicit changes in landscape structure, composition, and configuration due to anthropogenic and natural agents of disturbance and succession. Our comprehensive treatment of these processes differs from previous National Forest planning efforts (e.g., Klaus et al. 2005) by utilizing spatially explicit vegetation and wildlife habitat suitability models. By retaining the spatial context, we revealed important differences among alternatives in terms of the cumulative effects of management actions. First, tree harvest and prescribed fire influenced not only the species composition of vegetation communities, but also the species composition of wildlife communities. In the absence of tree harvest and prescribed fire, the HNF will likely be dominated by sugar maple within 125 years, and Henslow's Sparrow, Yellow-breasted Chat, and Ruffed Grouse may face extirpation within 50 years. Second, the spatial context of tree harvest affected habitat suitability for early successional wildlife species. By concentrating even-aged timber harvest within a focal area, a given level of tree harvest provided more suitable habitat for Yellow-breasted Chat and Ruffed Grouse than applying the same tree harvest level across the entire HNF, without greatly affecting habitat suitability for late-successional species. Thus, linking vegetation simulation and wildlife habitat models provided a straightforward, intuitive, and scientific basis to support subsequent management decisions.

This approach was also beneficial because it provided a comprehensive yet communicable perspective of landscape change. One of the goals of the HNF planning team was to engage the public and instill ownership of the HNF plan. The vegetation and wildlife habitat suitability maps were important tools for visualizing changes in landscape configuration, such as the spatial patterns that emerged from the different tree harvest techniques, despite similar composition with respect to tree age classes (Figures 2, 6). The maps also facilitated discussion of the HNF management goals and the methodology for achieving those goals, including the type and location of tree harvest activities. The consensus among the HNF planning team members was that using LANDIS and Landscape HSImodels made the science aspect of the planning process largely immune from appeals or litigation, but the plan was still challenged on other grounds.

Most of the appeals and litigation challenged the management goals and methods for achieving those goals but not the scientific basis of the plan. For example, appellants questioned the need for anthropogenic disturbance (i.e. tree harvest and prescribed fire) as opposed to natural disturbance (i.e. windfall and storms). However, our results demonstrate that suppression of wildfire and reliance upon windfall and storms is insufficient for retaining early successional wildlife species on the HNF. Appellants also questioned the need for oak-hickory restoration within an area that historically had a higher maple-beech component than at present. The oak-dominated forests in southern Indiana today are the product of land use practices in the late 19th and 20th centuries. Since the middle of the 20th century, the lower frequency and intensity of disturbance has favored recruitment of maple, beech, and yellow popular, but not oaks (Shifley and Woodall 2007). From some appellants' perspective, succession to maple was viewed as achieving half of the original predominant vegetation type. However, a shift in species composition that favors maples was considered undesirable by the planning team. Oaks provide mast, a durable and staple food for many species of wildlife, and they are declining in abundance in southern Indiana (Shifley and Woodall 2007) and elsewhere in the Central Hardwood Region (Johnson et al. 2002).

A clear explanation of the basis for management goals in a land-management plan may reduce challenges or appeals of the plan. In general, objectives in National Forest planning are broadly defined and often get refined during the planning process based on public comments or opposition. While the traditional basis for developing objectives include management for desired vegetation conditions, timber production, fuels management, and wildlife habitat; emerging management issues include increasing demand for sustainable forestry practices, human recreation opportunities, and conservation of all wildlife species. Addressing these emerging issues will require acknowledgement of constraints that limit management in National Forests. First, only a small portion of any National Forest may be devoted to a primary objective whereas the majority of the forest will be subject to multiple and sometimes competing objectives. Second, the amount of resources allocated to any given objective will likely compete with the amount of resources available for other objectives. Third, the amount of land is finite; increasing human use may exclude some wildlife species (Noon et al. 2008). Thus, important questions to ask include: What should our National Forests look like? From a regional or national perspective, should they all look the same? And, what level of responsibility are we willing to accept for domestic forest resource production to meet our national demand for forest products (Shifley 2006)? Public responses to proposed management actions on the Hoosier National Forest typically identified tree harvest as a controversial activity. The type and intensity of tree harvest affected forest species composition (Figure 9) and ultimately affected wildlife habitat suitability through impacts on forest structure and mast production. Thus, it is important to clearly understand the simultaneous tradeoffs and potential conflicts among wildlife habitat quality for multiple species, levels of tree harvest, and by extension the availability of products, services and amenities that improve people's lives.

Tradeoffs Among Management Alternatives

We tracked tree age class, tree species, core area, length of edge, and wildlife habitat suitability information for 5 different management alternatives over a 150-yr planning horizon. No single management alternative maximized vegetation and habitat conditions for all features and species of interest. Rather, tradeoffs existing among all management alternatives. The sharpest tradeoffs occurred among Alternative 2, which contained no tree harvest or prescribed fire, and the remaining alternatives in terms of early vs. late-successional forest conditions and species composition.

The LANDIS projections of dominant forest vegetation (Figure 3, 9) illustrate three important points with respect to management decisions. First, white oak will increase in area of dominance under all alternatives. White oaks are generally longer lived and marginally more shade tolerant than species in the red oak group. Over the next century, white oaks currently in the forest canopy are expected to survive in greater proportion than the red oaks. Second, the proportions of red oak species and maples are affected by the intensity of forest disturbance via tree harvest and fire. Red oak species are relatively fast growing and aggressive sprouters when top-killed (Johnson et al. 2002). Red oaks are favored more than white oaks and much more than maples in the face of intense and/or repeated disturbances such as tree harvest or fire. This dynamic is visible in the pattern of tree species composition change over time (Figure 3, 9). The relative ranking of red oak to maple changes over time in response to increasing levels of disturbance. Third, in the absence of anthropogenic disturbance or wildfire, the HNF will be dominated by late-successional vegetation conditions. The differences in future forest conditions resulting from the management alternatives illustrate the cumulative effects of management decisions.

Estimates of tree harvest by decade provided a numeric way to compare the relative intensity of tree harvest among alternatives. The harvest volume rankings and magnitudes (Figure 10) from the modeled output were identical in rank and similar in numeric magnitude to values published in the Hoosier National Forest Land and Resource Management Plan (U.S. Department of Agriculture Forest Service, 2006). The alternatives differed greatly in terms of the area subject to even-aged versus uneven-aged harvest techniques. Alternative 4 contained 2–3.5 times more even-aged harvest than Alternatives 1, 3, and 5 (Table 1, Figure 10), producing a forest with a larger proportion of seedling and saplings than all other alternatives. Importantly, the relatively large increase in early successional vegetation due to even-aged management under Alternative 4 did not correspond to a large reduction in the amount of suitable habitat for late-successional wildlife species. Several recent studies support our simulation results that small, single-tree, group selection or clearcuts have minimal impacts on late-successional birds while improving habitat conditions for early successional species (Annand and Thompson 1997, Robinson and Robinson 1999, Gram et al. 2003, Campbell et al. 2007).

We implemented a focal area for tree harvest to investigate the biological effects of this management option on wildlife habitat suitability. The effect of the focal area was most apparent when comparing Alternatives 1 and Alternative 5, which had the same tree harvest and prescribed fire levels but Alternative 5 contained the focal area. Alternative 5 provided a greater amount of suitable habitat for Ruffed Grouse and Yellow-breasted Chat than Alternative 1 by increasing the effective size of early successional forest patches. For Ruffed Grouse, the focal area also increased interspersion of early successional forest patches with mature, mast-producing forest. Besides the biological benefits of the focal area, it also served an aesthetic and practical purpose by reducing the amount of tree harvest occurring forest-wide. We also manipulated cut size, but evaluating this factor was difficult because different tree harvest levels were used in conjunction with the different cut sizes.

In terms of core area and edge values, Alternative 2 created about three times as much core area and about half the edge length of any of the other alternatives. The other 4 alternatives were clustered in their estimated edge and core area. It is important to note that the core and edge statistics were influenced by how we defined core and edge zones. A larger cell size (e.g., 30 m, or 0.09 ha) rather than 10 m (0.01 ha) would result in substantially different numeric estimates of core and edge area because (a) a vast number of regenerated sites smaller than 0.09 ha would drop out of the analysis and (b) the ratio of edge to site area and the ratio of excluded core area to site area decreases with increasing site size. The rank order of sites with respect to core area and edge length would generally remain the same with changing site size, but the absolute values and numeric differences among alternatives would differ (Riitters et al. 2007). In the absence of a stated management goal it is hard to interpret absolute values of core and edge statistics; these metrics were best interpreted in the context of wildlife habitat suitability.

Application to Other Landscapes

Our approach to land-management planning was designed to take advantage of several features of LANDIS, namely the ability to simulate changes in forest vegetation over time under different management scenarios, obtain GIS layers of LANDIS outputs (e.g., tree age, tree species, wind damage, and fire history) in 10-year time steps, and use those GIS layers as inputs for the HSI models. This approach worked well within the predominantly forested landscape of the HNF; however, it had less value when applied to the non-forested parts of the HNF and surrounding private lands. Time since disturbance and type of disturbance (e.g., grazing, haying, and prescribed fire) are important factors in determining what bird species will be present within grasslands (Madden et al. 1999, Walk and Warner 2000). For example, the Henslow's Sparrow breeds in grasslands 1-3 years postdisturbance and will continue breeding there until woody vegetation develops 5-8 years postdisturbance (Herkert et al. 2002). We were able to track the age of grasslands in LANDIS by using a pseudo-tree species for grass, but the 10-yr time step prevented us from obtaining the temporal resolution necessary to fully parameterize the Henslow's Sparrow HSI model. Thus, it is likely that we overestimated the amount of suitable habitat for Henslow's Sparrow in frequently disturbed grasslands (Pruitt 1996, Herkert 2001). One way to overcome this limitation would be to simulate vegetation change on a shorter time scale (e.g., annual or every 5 years) within LANDIS, but this may be impractical for planning horizons exceeding 50 years as in this study. Another alternative is to simulate changes in grasslands on a shorter time scale, but separate from changes in forest vegetation. When combined with information on grassland management (e.g., disturbance agents and disturbance regimes), this would provide the temporal resolution necessary to identify grasslands available to Henslow's Sparrows as breeding habitat.

An important consideration of our approach was the treatment of private lands adjacent to the HNF. Private lands play a vital role in the conservation and management of habitat for many avian species, particularly when public lands are embedded within a predominantly private land matrix as in southern Indiana. Private lands may provide adjacent, contiguous habitat thereby increasing the effective size of public lands and providing the landscape context amenable to breeding. For example, as the amount of grassland at the landscape level increases Henslow's Sparrow density increases as well, even within grassland patches that in isolation may be too small for breeding (Walk and Warner 1999, McCoy 2000).

While we did account for different tree harvest scenarios on private lands (e.g., high grading and selective harvest), we made three assumptions with respect to trends in private land management that simplified our modeling process but also may affect the applicability of our results beyond the first few 10-year time steps. First, we assumed private land-management trends were static over time. In other words, we did not increase or decrease the amount of area on private lands subject to tree harvest. However, tree harvest constraints on public lands may increase tree harvest on private lands (Haynes 2002). Second, we assumed future land-ownership patterns would be static with respect to conversion of agricultural and forested areas to residential development, although conversion to residential development is likely to increase in some regions of the United States (Brown et al. 2005, Pocewicz et al. 2008). Third, we assumed private land parcel size would be stable over time. However, private land parcel size is decreasing over time (Mehmood and Zhang 2001). If these trends extend to private lands adjacent to the HNF, then wildlife habitat suitability may decline over time despite management efforts on the HNF. Coordination of site-specific management efforts among private and public ownerships may be necessary to achieve regional avian habitat and conservation goals (Thompson and DeGraaf 2001).

Comparisons to Other Planning Approaches

Many different approaches exist for determining the effects of management on vegetation and wildlife in a planning context. The choice of which approach to use is often constrained by time, available data, and management priorities. For example, expert opinion matrices and panel assessments use the proportion of landscape by habitat type, forest type, age class, or management technique as a proxy for suitable habitat of a single or multiple species. Common assumptions of these approaches are that suitability is synonymous with population viability and that maintenance of the same or similar amounts of suitable habitat will maintain population viability. An advantage of these approaches is that species can be incorporated in the planning process for which little empirical data exists. A disadvantage of these approaches is that spatial context may not be directly incorporated in the assessment of suitable habitat. Omitting spatial context may result in overestimation of habitat suitability for species with area or edge sensitivity or for species where local colonization is needed to maintain population viability (Harper et al. *In press*).

Loehle et al. (2006) applied spatially explicit logistic regression models of avian species response to output from the Habplan harvest scheduler under different forest management scenarios. Their models included spatial features of the landscape such as stand area, measures of landscape pattern, and distance to roads (Mitchell et al. 2006). Although the Habplan harvest scheduler optimized tree harvest, it also treated forest stands as homogeneuous with respect to age. Considering all trees within a stand to be the same age may be advantageous from a silviculture perspective, but may limit the ability to identify fine-scale, within-stand features (i.e., microhabitat) such as canopy gaps that create foraging opportunities for birds or solar radiation of roosts for bats. Additionally, the Loehle et al. (2006) approach did not consider the succesional trajectory of vegetation. In other words, the stand composition was fixed over time. This may limit the utility of this approach in forests undergoing stand conversion treatments or where tree harvest or prescribed fire alters tree species regeneration patterns over time.

Our approach includes ecological processes of disturbance and succession, retains the spatial context, and incorporates both empirical data and expert opinion in the wildlife habitat suitability models, which may be seen as advantageous over the previously described approaches. However, developing a land-management plan with this level of detail takes time. We estimate 1.5 years of full time effort for the modeling effort only (i.e., Stage 3, Overview of Planning Process). The greatest amount of time, approximately 1 year, was spent 1) developing initial landscape conditions and calibrating the LANDIS model, and 2) developing the wildlife habitat suitability models in Landscape HSImodels. We spent approximately 3 months running the scenarios, and an additional 3 months post-processing and summarizing results.

Modeling Issues and Future Directions

Will et al. (2005) described the Five Elements Process, a general framework for conservation of avian populations using spatially explicit landscape-level habitat objectives. As guiding principles, Will et al. (2005) suggested that the modeling process and products should be as transparent as possible with clearly defined objectives and all assumptions stated, and that the appropriate spatial scale(s) should be used.

Throughout the forest planning process the HNF planning team assumed that changes in habitat suitability were synonymous with numerical changes in avian populations. Rittenhouse et al. (Chapter 2) validated the Wood Thrush and Yellow-Breasted Chat HSI models using 10 years of territory density and nest success data from the Missouri Ozark Forest Ecosystem Project. They found support for HSI models as predictors of demographic response to vegetation change, but the strength of support varied by demographic response (e.g., territory density, nest success) and species. Other modeling approaches link population viability modeling to LANDIS using a habitat model as an intermediate step between vegetation simulation and viability analysis (e.g., Akcakaya et al. 2004, Wintle et al. 2005). These modeling approaches may be considered an advancement over HSI models because of the link to population viability. Yet, at a minimum population viability analysis requires estimates of adult survival and fecundity. Demographic data is lacking for many avian species despite being the critical link needed to translate population goals into habitat objectives. Demographic data from similar species may be used (Wintle et al. 2005) but doing so adds additional assumptions to the modeling process, namely that species share common life history traits and respond to changes in habitat conditions similarly. Further, when multiple species are included in the planning process it is convenient to have one metric for comparison among species. Thus while HSI models may not represent a demographic response for all species, they remain a common basis for evaluating wildlife habitat for many species.

Choosing the appropriate spatial scale(s) for vegetation and wildlife habitat suitability models represents tradeoffs among resolution (cell size) and spatial extent (landscape size). Computing capabilities such as processing speed and RAM are typically listed as limiting factors that dictate either a coarse resolution for large spatial extents or a fine resolution for small spatial extents. Based on our experience with this project and others (Shifley et al. 2000, Larson et al. 2003, Shifley et al. 2006, Rittenhouse et al. 2007), we are confident that computing power is no longer limiting. Rather, the limiting factor is empirical data of spatial wildlife habitat relationships at the landscape scale to parameterize suitability relationships. An obvious solution is to conduct more studies at multiple sites over time.

SUMMARY AND MANAGEMENT IMPLICATIONS

We simulated future vegetation conditions and assessed wildlife habitat suitability under 5 different forest management alternatives as part of the HNF planning process. Each management alternative differed in the amount, type, or location of tree harvest techniques and prescribed fire, and subsequently the effects on wildlife habitat suitability varied by species. Three important patterns emerged over time with respect to forest composition and structure. First, white oak will increase in area of dominance under all alternatives. Second, the proportions of red oak species and maples are affected by the intensity of forest disturbance via tree harvest and fire. Third, in the absence of anthropogenic disturbance or wildfire, the HNF will be dominated by late-successional vegetation conditions. Correspondingly, we identified several patterns of wildlife response to changing vegetation conditions. First, without tree harvest or prescribed fire, early successional wildlife species will be extirpated from the HNF within 50 years. Second, tree harvest benefited early successional species without greatly affecting habitat suitability for late successional species. These patterns are consistent with current knowledge of vegetation and wildlife response to management.

The planning process offers the opportunity to discuss management for each National Forest every 10 – 15 years. We offer the following recommendations to help the discussion proceed as smoothly as possible:

1) Well-defined management objectives are crucial to the planning process because they establish focal points for discussion and comparisons among management alternatives.
2) Utilize broad scale, fine resolution modeling approaches. Select a resolution that is small enough to simulate disturbance, succession, and wildlife habitat suitability at species-specific spatial scales while not being to burdensome on computing resources and data management.
3) Model outputs, and even the modeling process, can be a valuable tool for fostering communication and discussion with stakeholders. Understanding the differences among management alternatives is critical for making informed management decisions. Presentation of future vegetation conditions and wildlife habitat suitability as interactive maps provides scientific information in a format amenable to comprehension by the diversity of stakeholders involved in the planning process.
4) Develop methods for evaluating and comparing multidimensional outcomes of management alternatives. The task of summarizing and interpreting vegetation and habitat conditions increases geometrically for every wildlife species and management alternative under consideration. We used simple tabular and graphical comparisons of

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Table 1. Area (ha) treated by management practices for the 150-year planning horizon for 5 management alternatives on the Hoosier National Forest, Indiana. Alternative 5 differs from Alternative 1 only in concentrating most of the clearcutting in a 2500 ha block designated for improved habitat for early successional wildlife species.

Treatment	Alternative 1	Alternative 2	Alternative 3	Alternative 4	Alternative 5
Site preparation	8,749	0	15,202	29,428	8,749
Plant	0	0	0	0	0
Release	1,995	0	3,579	6,709	1,995
Prescribed burn w/ harvest	25,474	0	44,721	85,689	25,474
Clearcut	7,413	0	10,389	24,311	7,413
Prep cut	1,336	0	4,813	5,117	1,336
Overstory removal	1,336	0	4,776	5,087	1,336
Group selection	25,090	0	25,639	4,174	25,090
Single tree selection (20-yr reentry cycle)	17,984	0	0	3,232	17,984
Single tree selection (30-yr reentry cycle)	13,478	0	2,005	10,317	13,478
Diameter limit	0	0	0	0	0
Financial maturity	0	0	0	0	0
Total mechanical harvest	66,637	0	47,622	52,239	66,637
Prescribed burn only	63,595	0	0	359,655	63,595

Table 2. Tree species groups and life history information used to simulate plant succession and regeneration on the Hoosier National Forest, Indiana.

Species group	Species included	Longevity (years)	Age of sexual maturity (years)	Shade tolerance (rank)	Fire tolerance (rank)	Effective seeding distance (m)	Maximum seeding distance (m)	Sprouting probability	Minimum sprouting age ^{a} (years)
Red cedar	Eastern redcedar *Juniperus virginiana* L.	190	10	1	1	20	3000	0	0
Pine	Shortleaf pine *Pinus echinata* Mill. Virginia pine *Pinus virginiana* Mill. White pine *Pinus strobes* L.	130	20	1	1	45	120	0	0
Sugar maple	Sugar maple *Acer saccharum* Marsh.	300	50	5	1	100	250	0.3	10
Red maple	Red maple *Acer rubrum* L.	160	20	4	1	100	250	0.8	10
Hickory	*Carya* spp.	250	30	3	2	30	3000	0.5	10
Beech	American beech *Fagus grandifolia* Ehrh.	300	40	5	1	30	200	0.2	10
Ash	White ash *Fraxinus americana* L. Green ash *Fraxinus pennsylvanica* Marsh.	200	20	2	2	75	140	0.6	10
Yellow poplar	Yellow poplar *Liriodendron tulipifera* L	200	15	2	2	45	3000	0.5	10
Black cherry	Black cherry *Prunus serotina* Ehrh.	200	10	1	1	15	3000	0.6	10
White oak	*Quercus alba* L.	300	50	3	4	20	3000	0.7	10
Chestnut oak	*Quercus prinus* L.	250	20	3	4	20	3000	0.7	10
Red oaks	Northern red oak *Quercus rubr*a L. Black oak *Q. velutina* Lam. Scarlet oak *Q. coccinea* Muenchh.	150	25	3	3	20	3000	0.9	10
Pin oak	Northern pin oak *Quercus ellipsoidalis* E. J. Hill Shingle oak *Quercus imbricaria* Michx.	160	20	2	2	20	3000	0.8	10

Elm	*Ulmus* spp	50	15	3	2	90	400	0.4	10
Understory-species	Generic understory vegetation capable of spreading a ground fire	20	10	--	--	1000	10000	1	10

Table 3. Wildlife species selected for habitat suitability modeling in the Hoosier National Forest, Indiana, and their habitat association. The population trend for American woodcock in Indiana is for the time period 1995–2004 (Kelley 2004). All other population trends are for the time period 1980–2006 (Sauer et al. 2007).

Species	Scientific name	Habitat association	Population trend	
			FWS Region 3	Indiana
American woodcock	*Scolopax minor*	Disturbance-dependent, migratory game bird[1]	-14.4%	-3.9%
Cerulean warbler	*Dendroica cerulean*	Late-successional forest, area-sensitive songbird[2]	-8.0%	-12.8%
Henslow's sparrow	*Ammodramus henslowii*	Grassland-dependent, area- and edge-sensitive songbird[3]	-6.1%	7.1%
Northern bobwhite	*Colinus virginianus*	Disturbance-dependent game bird[4]	-2.2%	-2.7%
Ruffed grouse	*Bonasa umbellus*	Early successional forest-dependent game bird[5]	-0.2%	Unknown
Wood thrush	*Hylocichla mustelina*	Forest-dependent songbird[6]	0.7%	-0.3%
Worm-eating warbler	*Helmitheros vermivorus*	Late-successional forest, fire-sensitive songbird[7]	1.9%	0.7%

Yellow-breasted chat	*Icteria virens*	Disturbance-dependent songbird[8]	0.2%	1.1%
Indiana bat	*Myotis sodalis*	Snag- and cave-roosting bat, Federal endangered species[9]	Unknown	Unknown

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[1] (Keppie and Whiting 1994)

[2] (Hamel 2000a)

[3] (Herkert et al. 2002)

[4] (Brennan 1999)

[5] (Rusch et al. 2000)

[6] (Roth et al. 1996)

[7] (Hanners and Patton 1998)

[8] (Eckerle and Thompson 2001)

[9] (Hall 1962, Cope et al. 1974, Humphrey et al. 1977)

Table 4. Description of habitat suitability index models for wildlife species used to evaluate proposed management alternatives on the Hoosier National Forest, Indiana.

Species	Life requisite	Habitat requisite	Model parameters and implementation	HSI equation
American woodcock	Nest sites, roost sites, and food.	Early- and mid-succesional forest.	SI_1: Tree species SI_2: Tree age by ELT	$HSI = \sqrt[2]{\left(\max\left(\left(SI_1 \times SI_2\right), SI_4\right) \times SI_5\right)}$
	Display sites, roost sites, and food.	Open habitat.	SI_3: Land cover type SI_4: Land cover type	
		Interspersion of life requisites.	SI_5: Moving window analysis on SI_2 and SI_4	
Cerulean warbler	Nest sites and food.	Mature deciduous forest.	SI_1: Tree species SI_2: Tree age by ELT	$HSI = \sqrt[3]{SI_1 \times SI_2 \times SI_3}$
		Large forest patches.	SI_3: Patch size algorithm	
Henslow's sparrow	Nest sites and food.	Large grassland patches.	SI_1: Land cover type SI_2: Patch size algorithm	$HSI = \left(\sqrt[2]{SI_1 \times SI_2}\right) \times SI_3$
		Edge sensitive.	SI_3: Moving window analysis on SI_2	
Northern	Nest sites.	Grasslands.	SI_1: Land cover type	$HSI = \max\left(\max\left(SI_1, SI_2\right), SI_3\right) + \left(SI_4 \times SI_5\right)$

bobwhite	Food.	Croplands.	SI_2: Land cover type	
	Cover.	Woody cover.	SI_3: Tree age	
		Interspersion of life requisites.	SI_4: Moving window analysis on SI_1, SI_2, and SI_3	
			SI_5: Land cover type	
Ruffed grouse	Food.	Hard mast.	SI_1: Model of tree age, tree species, and land type	$HSI = \left(\sqrt{\max\left(SI_1, \sqrt{SI_2 \times SI_3}\right) \times SI_4} \right) \times SI_5$
	Nest sites, food, and cover.	Dense forest regeneration.	SI_2: Tree age by ELT	
		Large habitat patches.	SI_3: Patch size algorithm	
		Interspersion of life requisites.	SI_4: Moving window analysis of SI_1, SI_2, and SI_3	
		Large forested area.	SI_5: Patch size algorithm	
Wood thrush	Nest sites and food.	Deciduous forest.	SI_1: Tree species	$HSI = SI_1 \times \left(\sqrt[3]{SI_2 \times SI_3 \times SI_4} \right)$
			SI_2: Tree age by ELT	
		Large forest patch.	SI_3: Patch size algorithm	

	Post-fledging habitat.	Early successional forest.	SI$_4$: Tree age by ELT	
		Interspersion of life requisites.	SI$_5$: Moving window analysis of SI$_4$	
Worm-eating warbler	Nest sites and food.	Deciduous forest.	SI$_1$: Tree species	$HSI = \left(\sqrt[3]{SI_1 \times SI_2 \times SI_3}\right) \times SI_4$ $HSI = \left(\sqrt[3]{SI_1}\right)$
			SI$_2$: Tree age by ELT	
		Large forest patch.	SI$_3$: Patch size algorithm	
		Fire avoidance.	SI$_4$: Fire history	
Yellow-breasted chat	Nest sites and food.	Early successional forest and old fields.	SI$_1$: Tree age by ELT	$HSI = \left(\sqrt[2]{SI_1 \times SI_2}\right) \times SI_3$
		Large habitat patch.	SI$_2$: Patch size algorithm	
		Edge sensitivity.	SI$_3$: Moving window analysis on SI$_2$	
Indiana bat	Roost sites.	Large snags.	SI$_1$: Tree age	$HSI = Maximum\left[\left(\sqrt{Maximum\left(SI_1, SI_2\right) \times SI_4 \times SI_3}\right), \left(SI_1 \times SI_3 \times 0.5\right)\right]$
	Solar radiation and food.	Open habitat, forest edges and openings.	SI$_2$: Tree age	
	Water.	Proximity to roost sites.	SI$_3$: Distance-to-water	

	Interspersion of life requisites.	SI_4: Moving window analysis on SI_1 and SI_2

Table 5. Mean and standard error of the habitat suitability values for American Woodcock, Cerulean Warbler, Henslow's Sparrow, Northern Bobwhite, Ruffed Grouse, Wood Thrush, Worm-eating Warbler, Yellow-breasted Chat, and Indiana Bat, by management alternative and year.

		Year 0		Year 10		Year 50		Year 150	
Species	Alternative	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
American Woodcock	1	0.053	0.044	0.065	0.046	0.085	0.049	0.056	0.040
	2			0.047	0.039	0.025	0.024	0.010	0.016
	3			0.095	0.056	0.126	0.062	0.075	0.049
	4			0.100	0.057	0.143	0.064	0.100	0.058
	5			0.066	0.046	0.088	0.050	0.063	0.043
Cerulean Warbler	1	0.283	0.111	0.274	0.113	0.278	0.110	0.360	0.120
	2			0.285	0.112	0.313	0.113	0.419	0.123
	3			0.256	0.111	0.190	0.092	0.335	0.117
	4			0.255	0.111	0.259	0.103	0.320	0.116
	5			0.274	0.113	0.282	0.110	0.357	0.120

Henslow’s Sparrow	1	0.002	0.009	0.002	0.009	0.002	0.009	0.002	0.009
	2			0	0	0	0	0	0
	3			0.002	0.010	0.002	0.010	0.002	0.010
	4			0.002	0.010	0.002	0.010	0.002	0.010
	5			0.002	0.010	0.002	0.010	0.002	0.010
Northern Bobwhite	1	0.254	0.044	0.256	0.045	0.257	0.045	0.233	0.049
	2			0.230	0.033	0.215	0.025	0.513	0.026
	3			0.257	0.045	0.257	0.045	0.257	0.045
	4			0.257	0.045	0.257	0.045	0.257	0.045
	5			0.257	0.045	0.257	0.045	0.258	0.045
Ruffed Grouse	1	0.112	0.074	0.126	0.078	0.158	0.090	0.120	0.071
	2			0.091	0.063	0.057	0.044	0.048	0.036
	3			0.178	0.097	0.233	0.107	0.184	0.085
	4			0.181	0.098	0.226	0.105	0.224	0.086
	5			0.124	0.077	0.154	0.089	0.125	0.074

Wood Thrush	1	0.773	0.100	0.694	0.118	0.750	0.106	0.814	0.090
	2			0.730	0.109	0.771	0.096	0.844	0.070
	3			0.642	0.127	0.758	0.108	0.802	0.094
	4			0.636	0.128	0.762	0.108	0.798	0.097
	5			0.690	0.119	0.756	0.105	0.815	0.090
Worm-eating Warbler	1	0.592	0.118	0.572	0.118	0.601	0.112	0.695	0.099
	2			0.366	0.126	0.619	0.115	0.751	0.092
	3			0.549	0.113	0.595	0.105	0.628	0.100
	4			0.550	0.112	0.593	0.104	0.606	0.099
	5			0.569	0.118	0.604	0.112	0.684	0.099
Yellow-breasted Chat	1	0.012	0.028	0.016	0.034	0.005	0.019	0.002	0.013
	2			0.014	0.032	0.001	0.005	0	0
	3			0.038	0.057	0.011	0.030	0.010	0.027
	4			0.042	0.061	0.017	0.037	0.018	0.038
	5			0.017	0.036	0.006	0.021	0.005	0.019

Indiana Bat	1	0.365	0.050	0.509	0.095	0.423	0.076	0.456	0.071
	2			0.485	0.087	0.466	0.068	0.527	0.058
	3			0.522	0.099	0.388	0.078	0.455	0.078
	4			0.533	0.101	0.357	0.073	0.430	0.079
	5			0.511	0.095	0.415	0.074	0.442	0.070

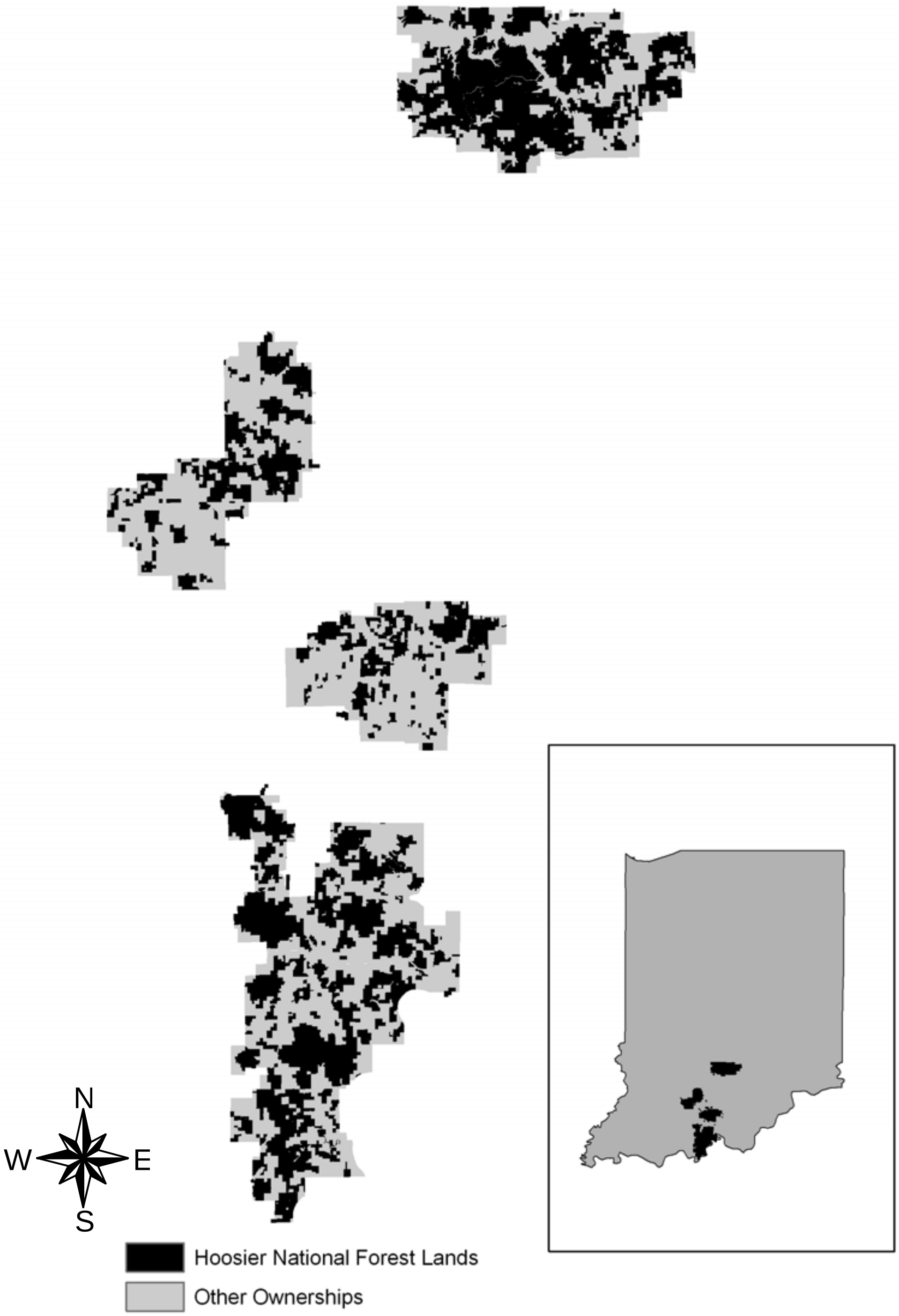


Figure 1. The four Hoosier National Forest purchase units (proclamation boundaries) in southern Indiana. National Forest ownership is approximately 81,000 ha, or 31% of the total 261,000 ha within the purchase units. The majority of the remaining area within the purchase unit boundaries is privately owned.

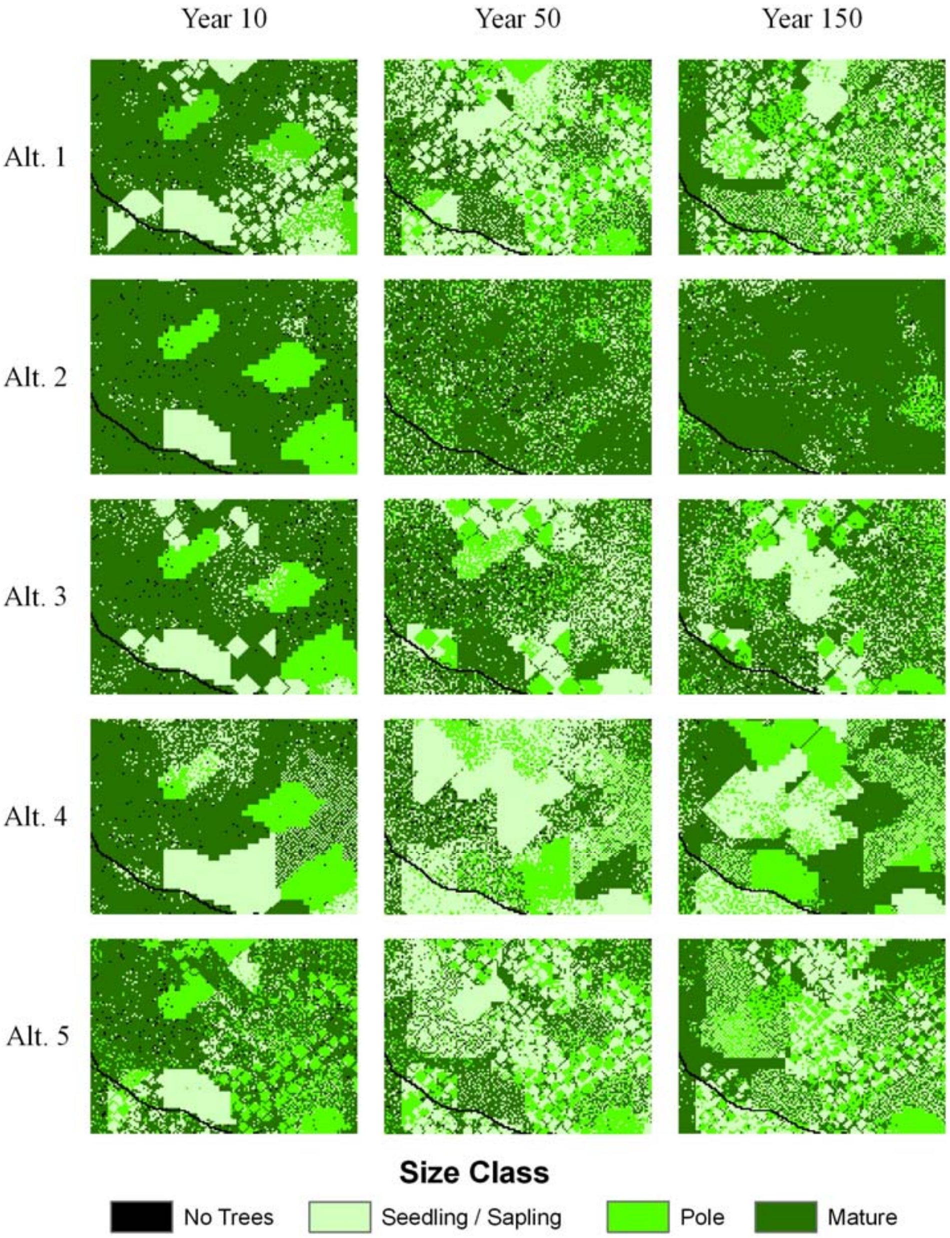


Figure 2. Forest age class maps for 5 management alternative at years 10, 50, and 150 on a 150-ha portion of the Hoosier National Forest, Indiana.

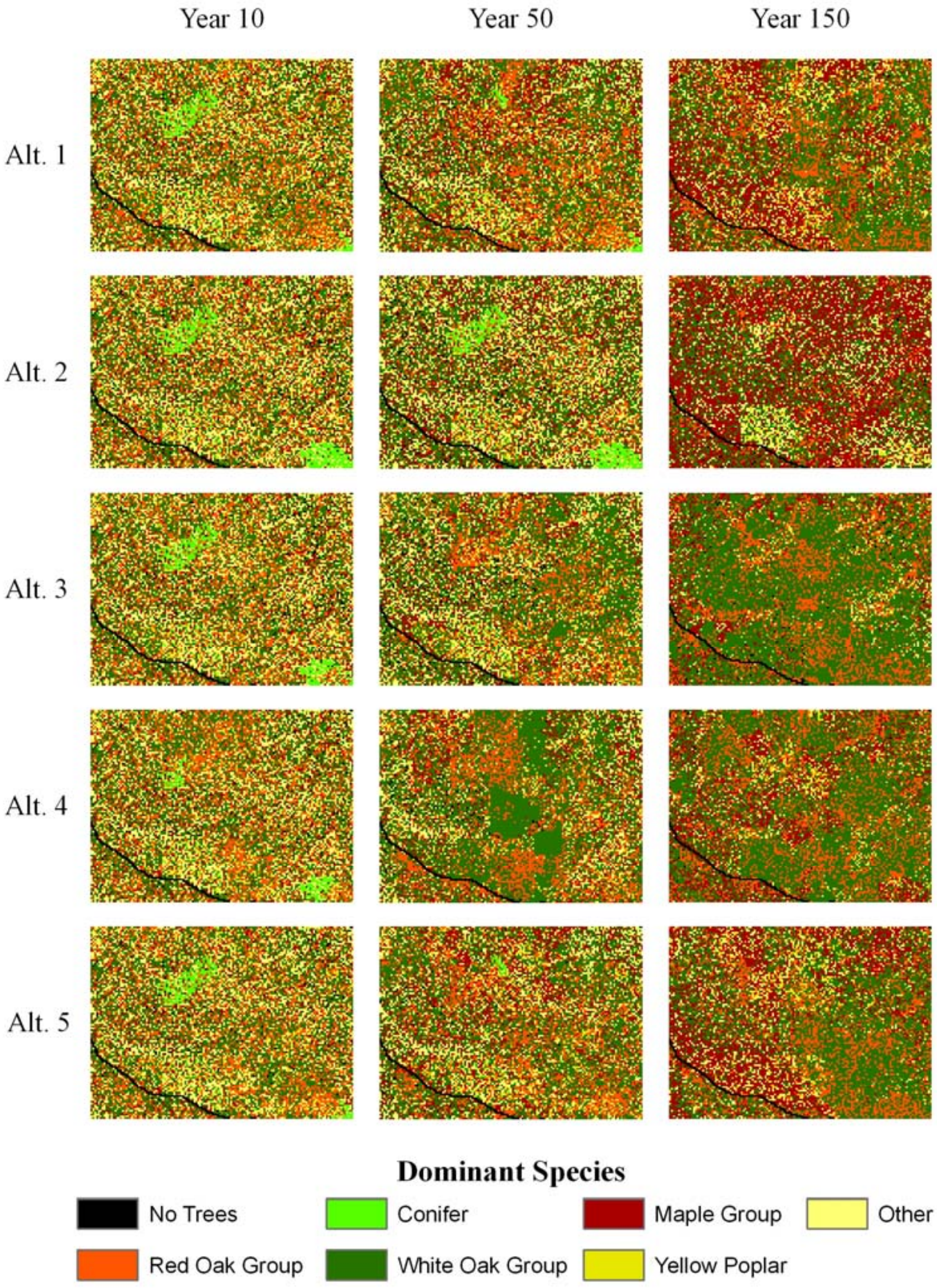


Figure 3. Dominant tree species composition maps for 5 management alternative at years 10, 50, and 150 on a 150-ha portion of the Hoosier National Forest, Indiana.

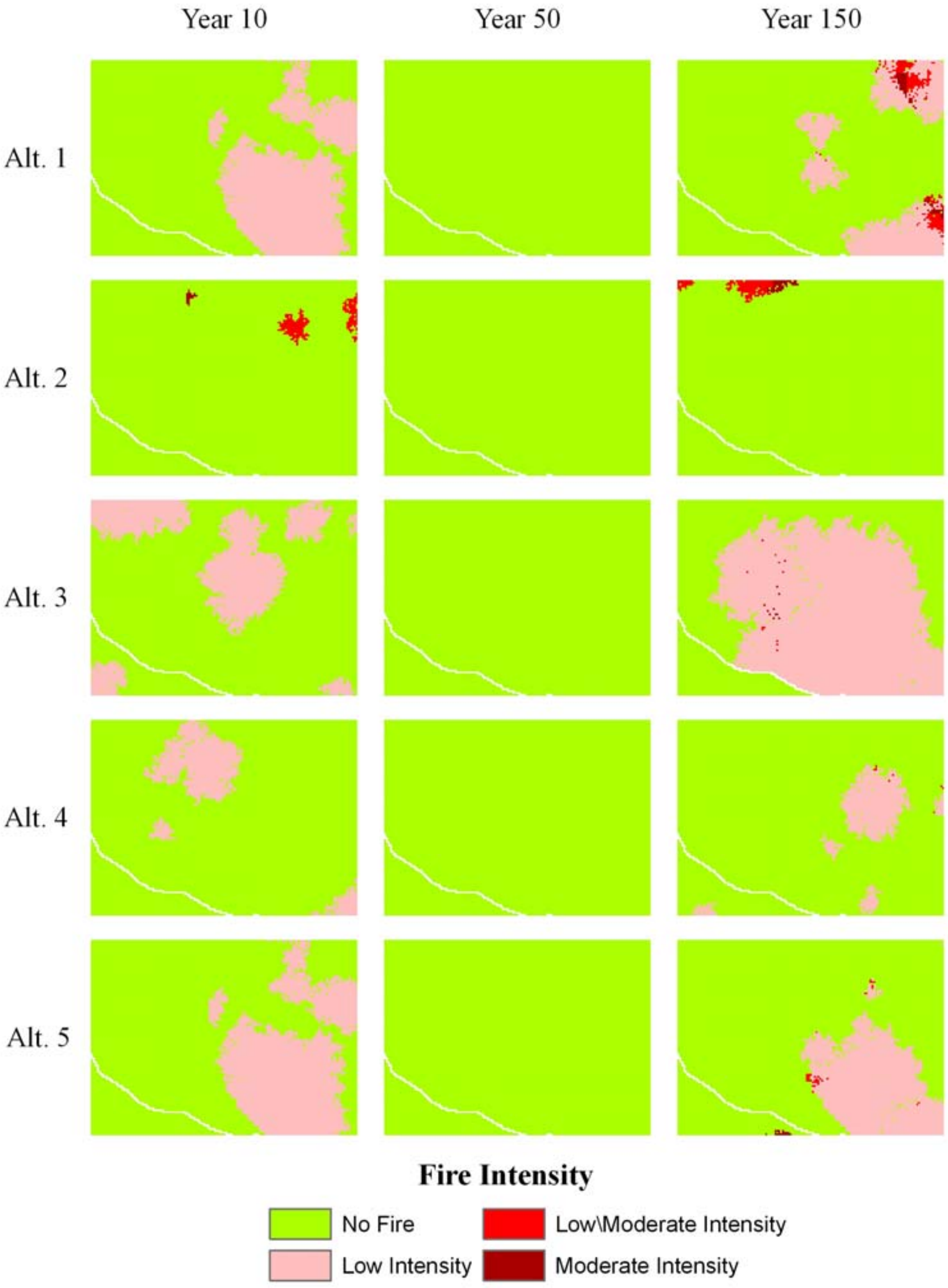


Figure 4. Fire disturbance maps for 5 management alternative at years 10, 50, and 150 on a 150-ha portion of the Hoosier National Forest, Indiana.

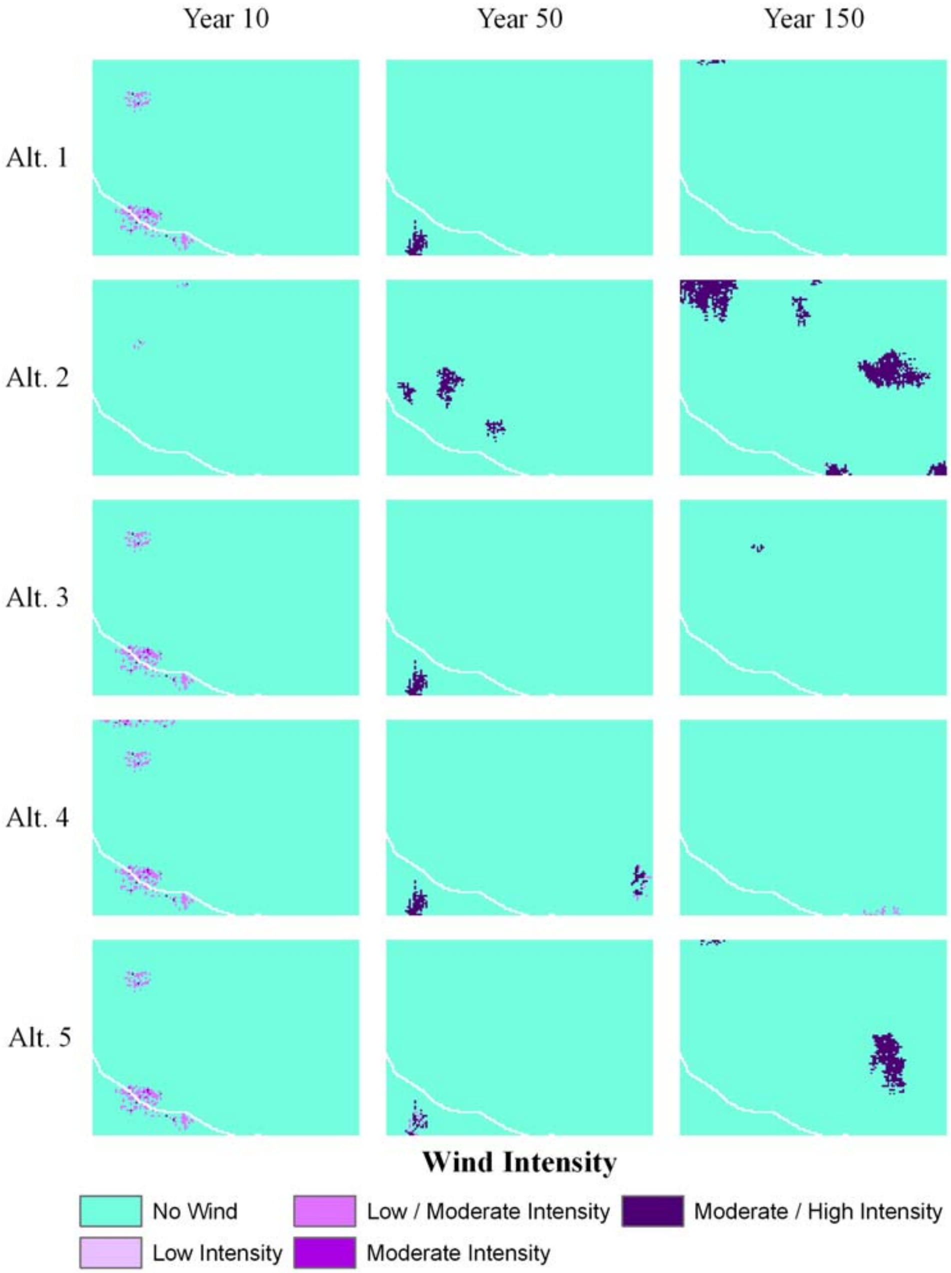
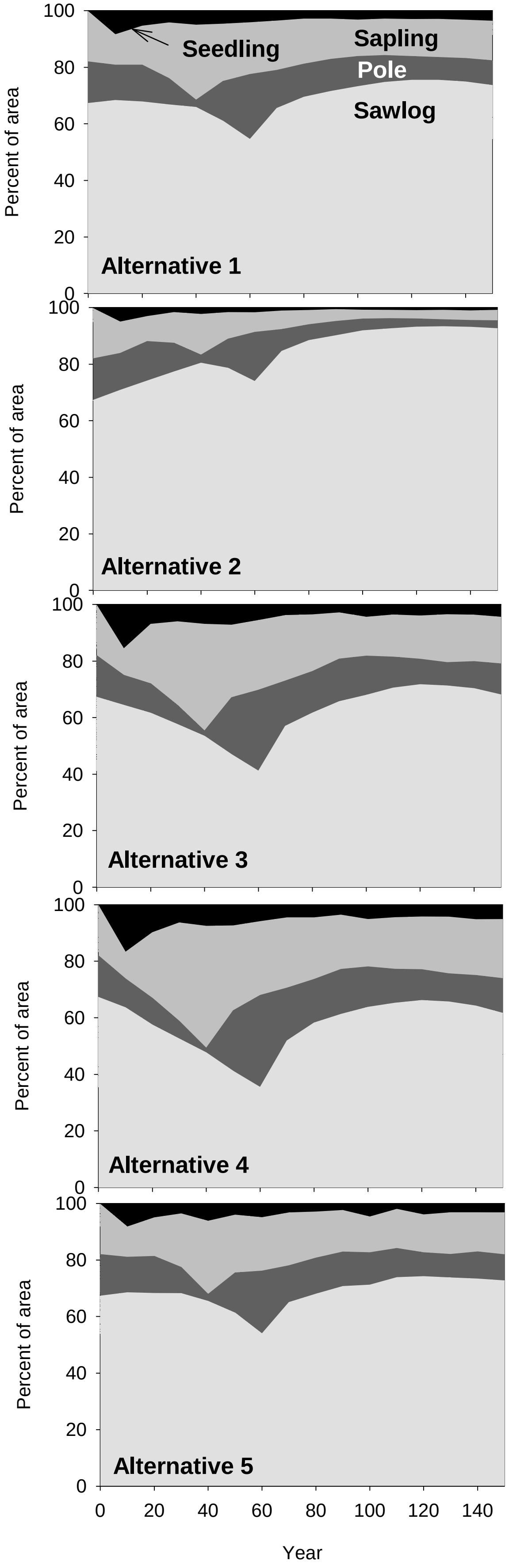


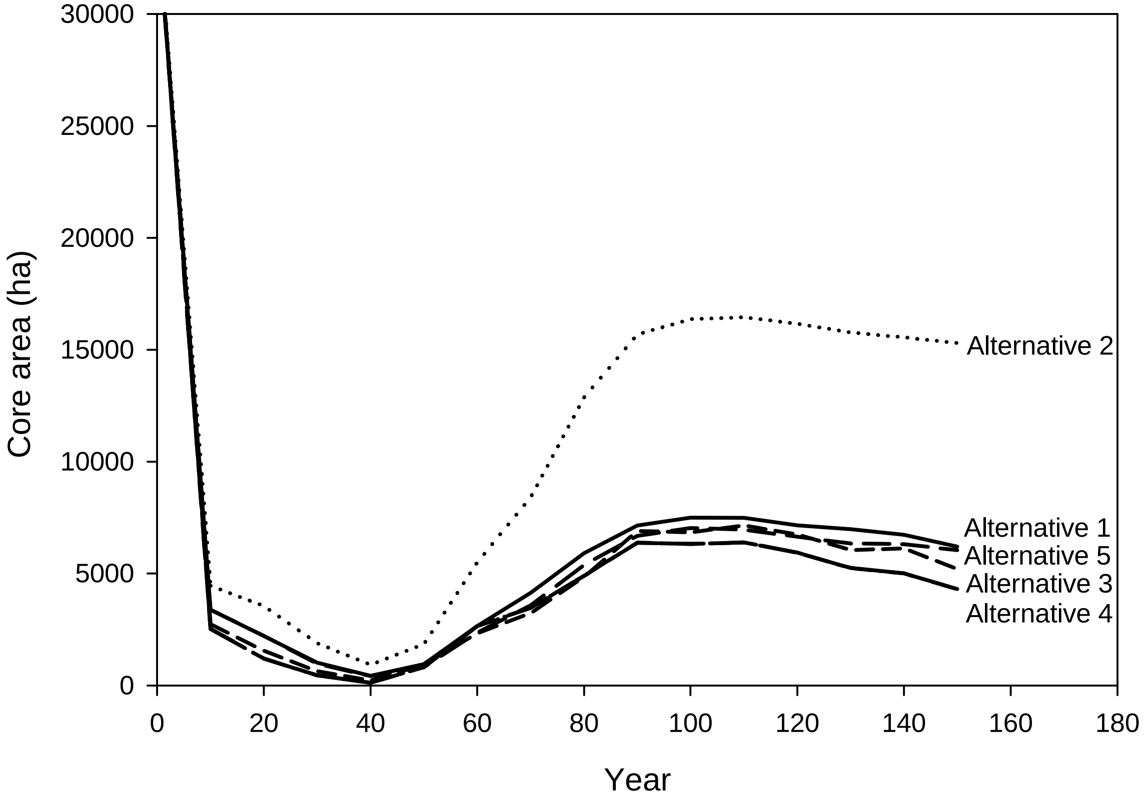
Figure 5. Wind disturbance maps for 5 management alternative at years 10, 50, and 150 on a 150-ha portion of the Hoosier National Forest, Indiana.

Figure 6. Forest area by age class for 5 management alternatives on the Hoosier National Forest, Indiana. See Table 1 for details of the management practices associated with each alternative.



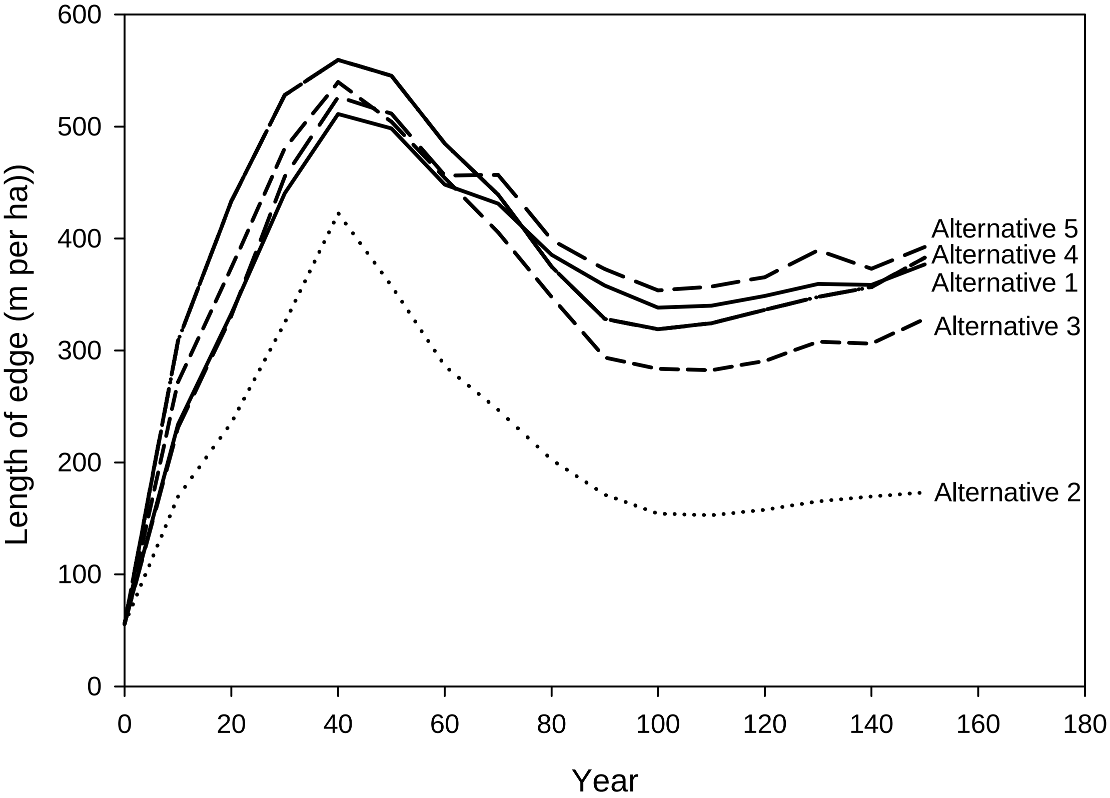
Seedling
Sapling
Pole
Sawlog
Alternative 1
Alternative 2
Alternative 3
Alternative 4
Alternative 5
Percent of area
0
20
40
60
80
100
0
20
40
60
80
100
120
140
Year

Figure 7. Core area of forest in the pole and sawtimber age classes that was at least 60 m from an edge with a younger age class or nonforest on the Hoosier National Forest, Indiana. Pole and sawtimber age classes correspond to forest ages of 30-59 years and $\geq$ 60 years, respectively. Computations were based on a 0.01 ha pixel size, so any 0.01 ha or larger opening created by mortality or tree harvest was a breach in the core area. The minimum size opening that is ecologically relevant as a breach of core area can differ with wildlife habitat preferences and can be recomputed for other minimum opening sizes.



Core area (ha)
30000
25000
20000
15000
10000
5000
0
0
20
40
60
80
100
120
140
160
180
Year
Alternative 2
Alternative 1
Alternative 5
Alternative 3
Alternative 4

Figure 8. Length of edge (m per ha) between forest in the pole and sawtimber age classes (i.e. > 30 years of age) with a younger forest and nonforest on the Hoosier National Forest, Indiana. Computations were based on 0.01-ha pixel size.



Length of edge (m per ha))
600
500
400
300
200
100
0
0
20
40
60
80
100
120
140
160
180
Year
Alternative 5
Alternative 4
Alternative 1
Alternative 3
Alternative 2

Figure 9. Percent of area dominated by 3 tree species composition by decade for 5 management alternatives on the Hoosier National Forest, Indiana. Species groups were: red oaks (northern red, black and scarlet oaks), white oaks (white and chestnut oak), and maple (sugar and red maple).

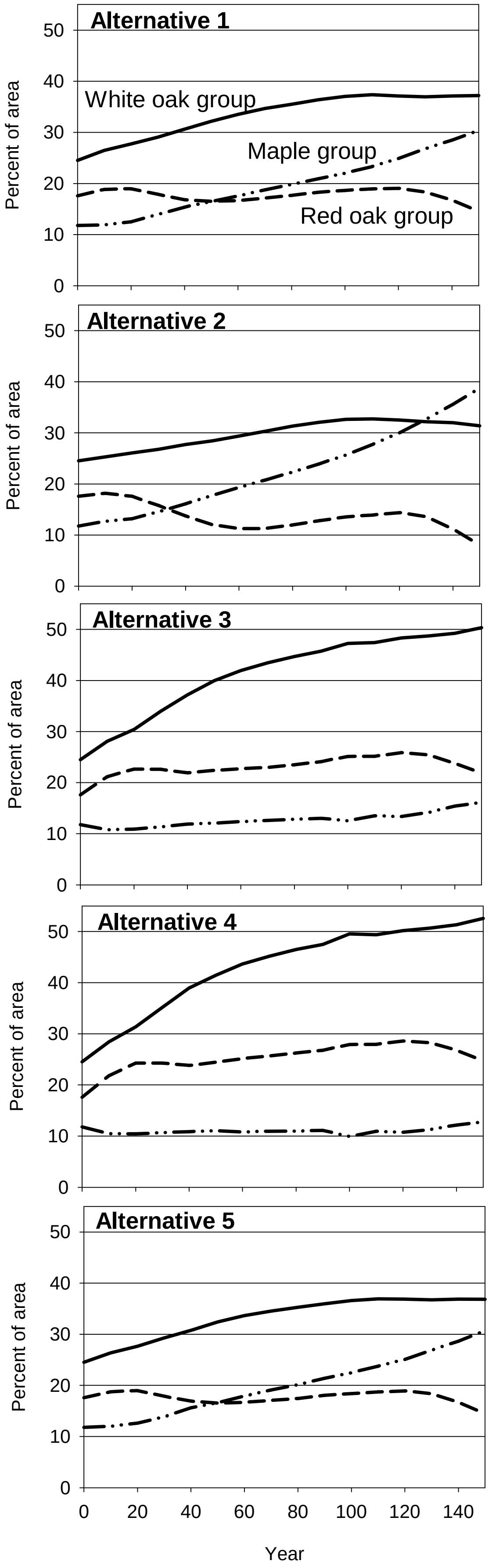
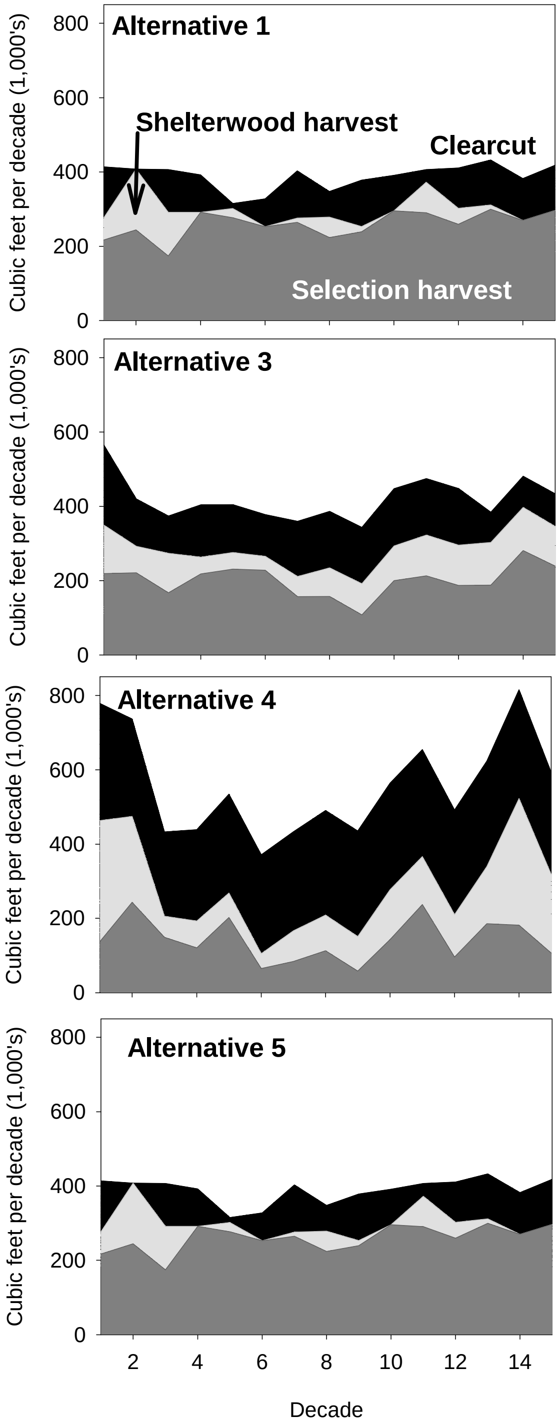
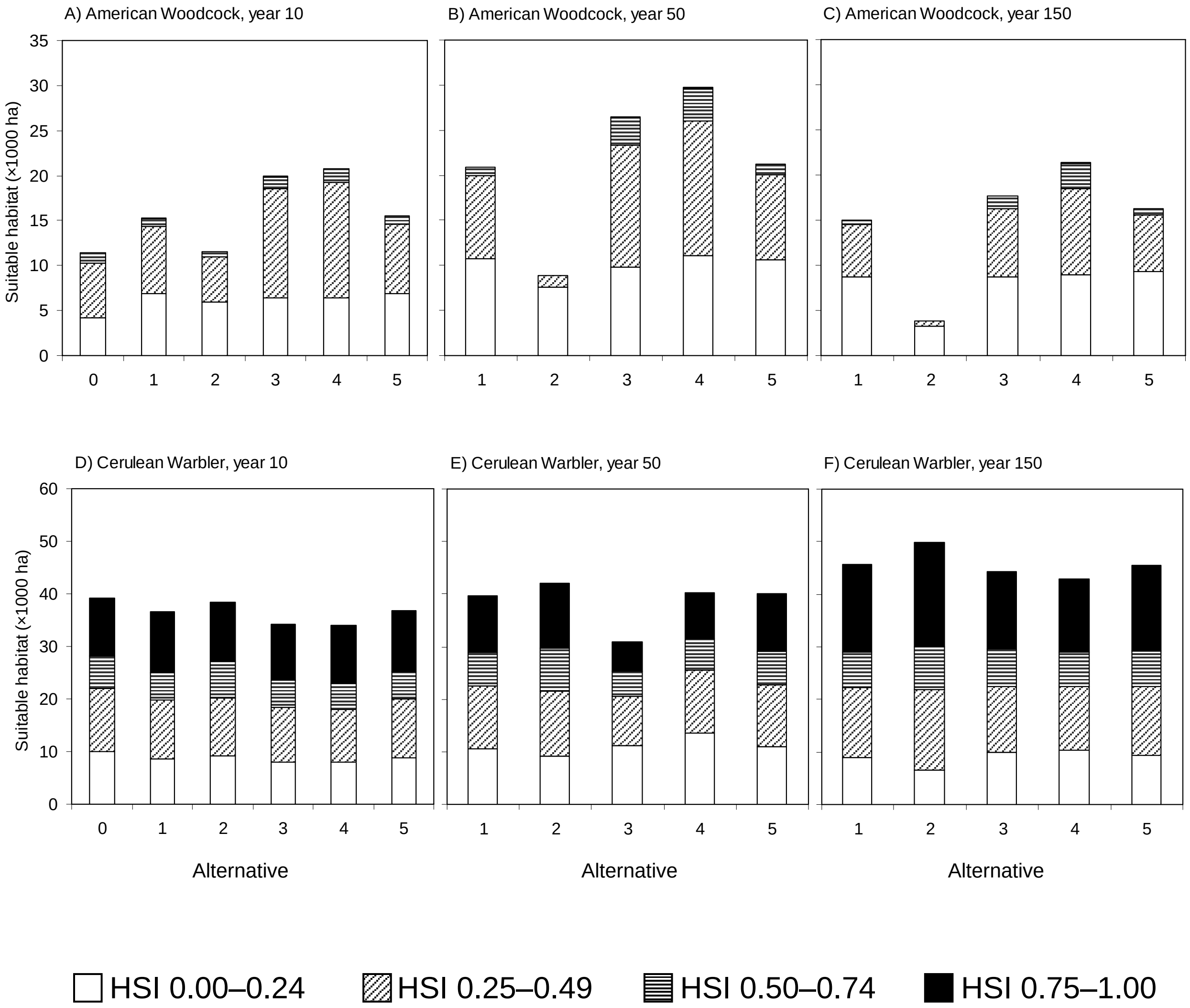
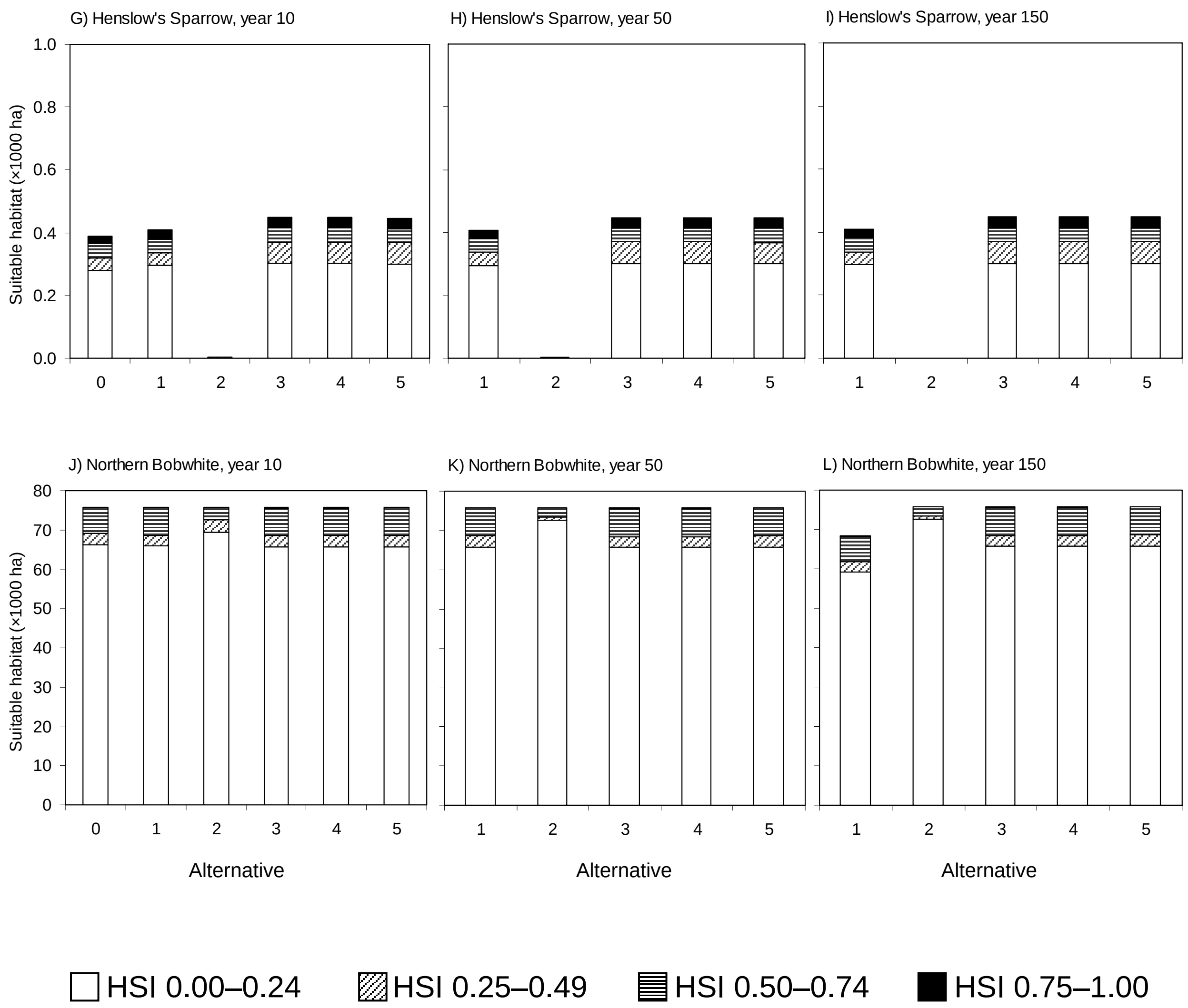
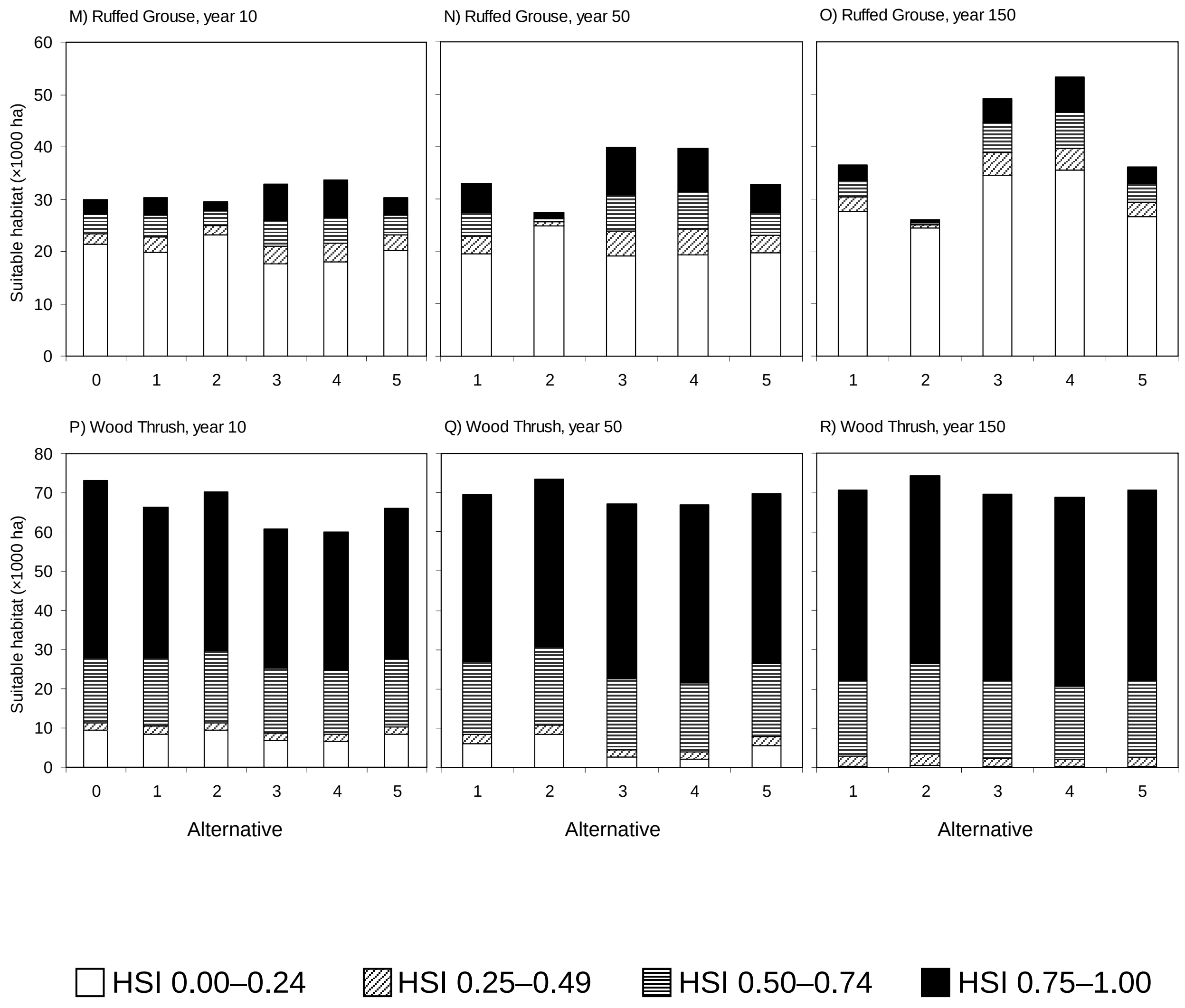

Alternative 1
White oak group
Maple group
Red oak group
Alternative 2
Alternative 3
Alternative 4
Alternative 5
Percent of area
0
10
20
30
40
50
0
20
40
60
80
100
120
140
Year

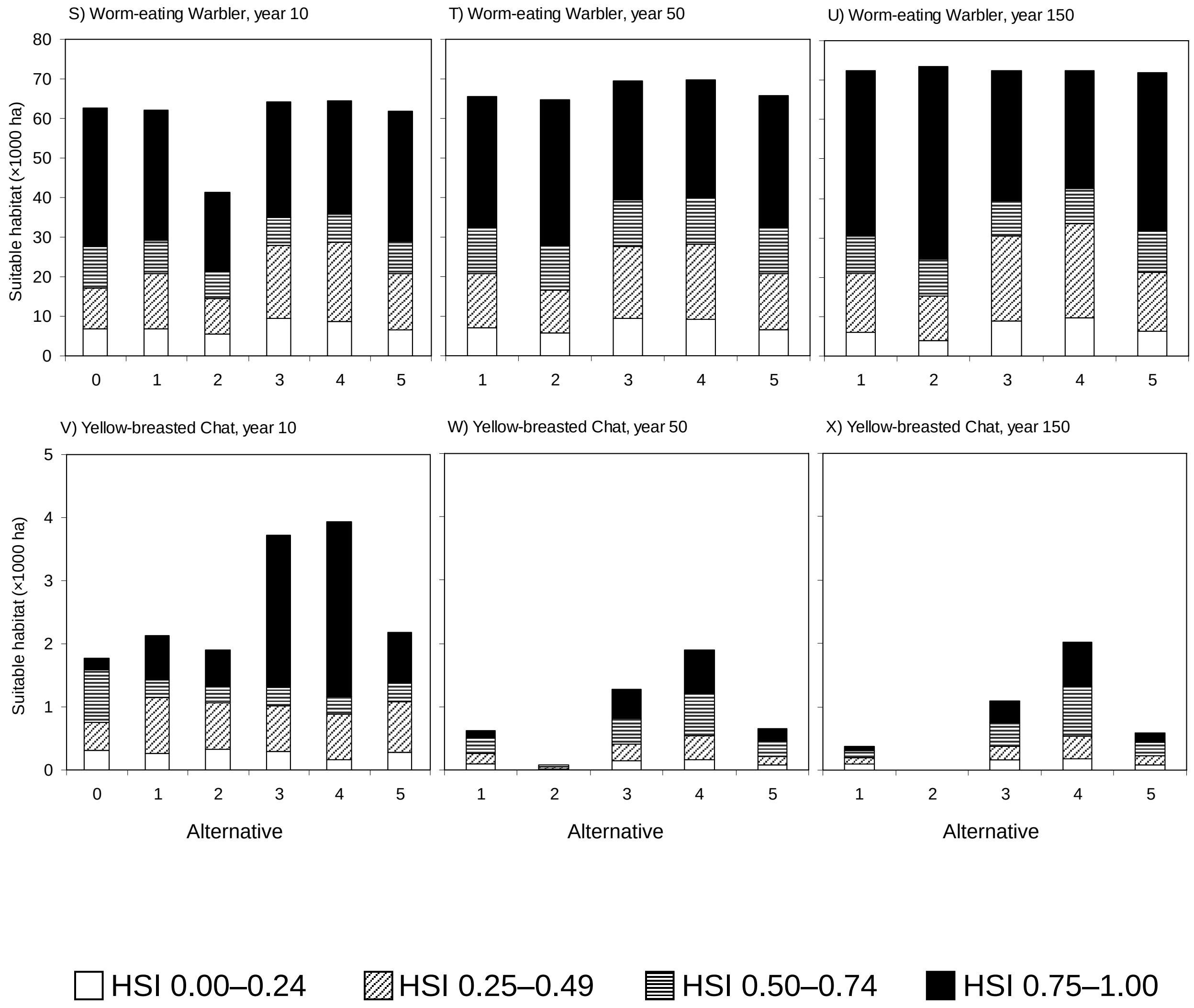
Figure 10. Tree harvest volume by management alternative and harvest type, Hoosier National Forest. There was no tree harvest under Alternative 2. Estimated volumes are in 1,000's of cubic meters per hectare per decade for trees at least 13 cm dbh.


Alternative 1
Shelterwood harvest
Clearcut
Selection harvest
Alternative 3
Alternative 4
Alternative 5
Cubic feet per decade (1,000's)
0
200
400
600
800
2
4
6
8
10
12
14
Decade


A) American Woodcock, year 10
B) American Woodcock, year 50
C) American Woodcock, year 150
D) Cerulean Warbler, year 10
E) Cerulean Warbler, year 50
F) Cerulean Warbler, year 150
Suitable habitat (×1000 ha)
0
5
10
15
20
25
30
35
40
50
60
0
1
2
3
4
5
Alternative
HSI 0.00–0.24
HSI 0.25–0.49
HSI 0.50–0.74
HSI 0.75–1.00


G) Henslow's Sparrow, year 10
H) Henslow's Sparrow, year 50
I) Henslow's Sparrow, year 150
Suitable habitat (×1000 ha)
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
5
J) Northern Bobwhite, year 10
K) Northern Bobwhite, year 50
L) Northern Bobwhite, year 150
Suitable habitat (×1000 ha)
80
70
60
50
40
30
20
10
0
Alternative
Alternative
Alternative
☐ HSI 0.00–0.24
▨ HSI 0.25–0.49
▤ HSI 0.50–0.74
■ HSI 0.75–1.00


M) Ruffed Grouse, year 10
N) Ruffed Grouse, year 50
O) Ruffed Grouse, year 150
P) Wood Thrush, year 10
Q) Wood Thrush, year 50
R) Wood Thrush, year 150
Suitable habitat (×1000 ha)
0
10
20
30
40
50
60
70
80
0
1
2
3
4
5
Alternative
HSI 0.00–0.24
HSI 0.25–0.49
HSI 0.50–0.74
HSI 0.75–1.00


S) Worm-eating Warbler, year 10
T) Worm-eating Warbler, year 50
U) Worm-eating Warbler, year 150
V) Yellow-breasted Chat, year 10
W) Yellow-breasted Chat, year 50
X) Yellow-breasted Chat, year 150
Suitable habitat (×1000 ha)
0
10
20
30
40
50
60
70
80
0
1
2
3
4
5
Alternative
☐ HSI 0.00–0.24
▨ HSI 0.25–0.49
☰ HSI 0.50–0.74
■ HSI 0.75–1.00

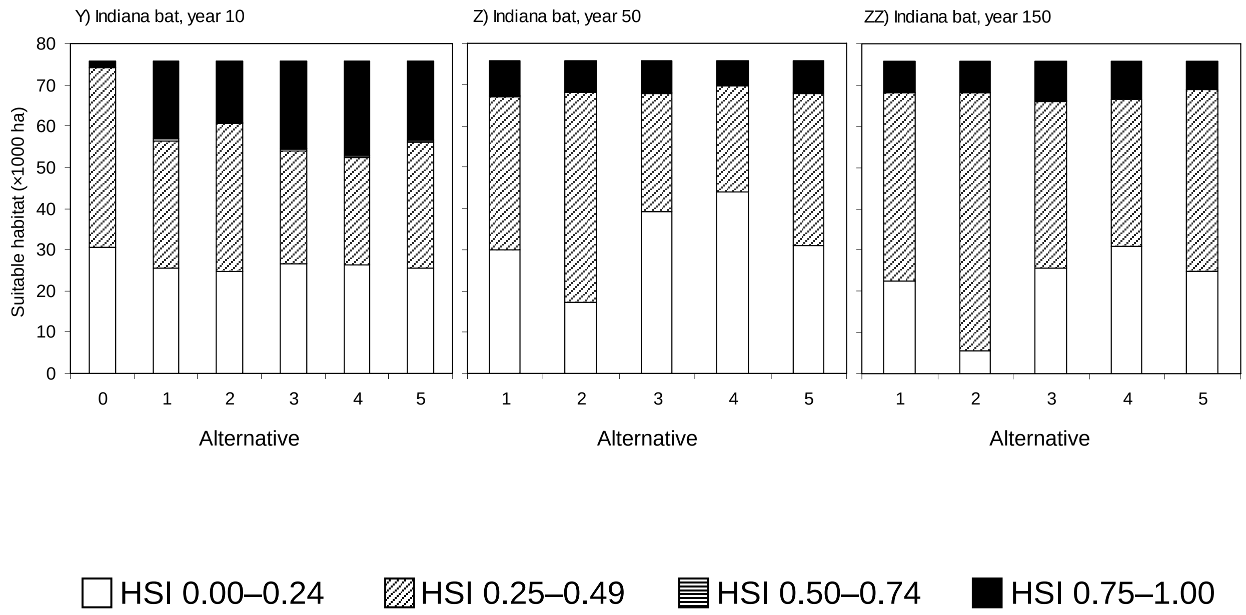


Figure 11. Amount of suitable habitat (in ha) by alternative at year 10, 50 and 150 on the Hoosier National Forest, Indiana. Current conditions presented as Alternative 0 in year 10 column.

APPENDIX 1: SPECIES VIABILITY EVALUATION PANEL MEMBERS

The following people are recognized by their peers as experts in the biology, ecology, or management of the plant or animal species included in the Hoosier National Forest planning process. All experts attended at least one SVE panel meeting. A minimum of 3 species experts reviewed each wildlife habitat suitability model.

Person	Organization
Dr. Rebecca Dolan	Butler University
Dr. Virgil Brack	Environmental Solutions/Innovations
Alice Heikens	Franklin College
Cynthia Basile	Hoosier National Forest
Kirk Larson	Hoosier National Forest
Clark McCreedy	Hoosier National Forest
Steve Olson	Hoosier National Forest
Kelle Reynolds	Hoosier National Forest
Tom Thake	Hoosier National Forest
Scott Ballard	Illinois Department of Natural Resources
Bob Bluett	Illinois Department of Natural Resources
Larry David	Illinois Department of Natural Resources
Joe Kath	Illinois Department of Natural Resources
Jody Shimp	Illinois Department of Natural Resources
Steve Bailey	Illinois Natural History Survey
Dr. Steven Hill	Illinois Natural History Survey
Dr. Joyce Hoffman	Illinois Natural History Survey

Dr. Jeff Hoover	Illinois Natural History Survey
Dr. L. Rick Phillippe	Illinois Natural History Survey
Dr. Christopher Phillips	Illinois Natural History Survey
Scott Robinson	Illinois Natural History Survey
Dr. Chris Taylor	Illinois Natural History Survey
Steve Backs	Indiana Department of Natural Resources
John Castrale	Indiana Department of Natural Resources
Brant Fisher	Indiana Department of Natural Resources
Mike Homoya	Indiana Department of Natural Resources
Scott Johnson	Indiana Department of Natural Resources
Bruce Plowman	Indiana Department of Natural Resources
Katie Gremillion-Smith	Indiana Department of Natural Resources
Zach Walker	Indiana Department of Natural Resources
Bruce Kingsbury	Indiana-Purdue University
Marion Jackson	Indiana State University
Dr. John Whitaker, Jr.	Indiana State University
Dr. Michael Ewert	Indiana University
George Yatskievych	Missouri Botanical Garden
Kay Yatskievych	Missouri Botanical Garden
Bob DeStafano	Missouri Department of Conservation
Jeff Ehman	Pangaea Information Technologies, Inc.
Dr. John Dunning	Purdue University
Dr. Harmon Weeks	Purdue University

Sybill Amelon	North Central Research Station
Dr. Dirk Burhans	North Central Research Station
Bill Dijak	North Central Research Station
Dr. Frank Thompson	North Central Research Station
Adam Bump	Ruffed Grouse Society
Becky Banker	Shawnee National Forest
Michael Spanel	Shawnee National Forest
Beth Shimp	Shawnee National Forest
Chad Stinson	Shawnee National Forest
Steve Widowski	Shawnee National Forest
Ginny Adams	Southern Illinois University
Reed Adams	Southern Illinois University
Dr. Ronald Brandon	Southern Illinois University
Dr. Brooks Burr	Southern Illinois University
Tim Carter	Southern Illinois University
Dr. George Feldhamer	Southern Illinois University
Dr. James Garvey	Southern Illinois University
Dr. John Roseberry	Southern Illinois University
Dr. Alan Woolf	Southern Illinois University
Dr. Jim Herkert	The Nature Conservancy
Andy King	U.S. Fish and Wildlife Service
Mike Thomas	U.S. Fish and Wildlife Service
Chris Frisbee	U.S.D.A. Forest Service

Ted Schenck	U.S.D.A. Forest Service
Norm Weiland	U.S.D.A. Forest Service
Bill Pearson	University of Louisville
Chadwick Rittenhouse	University of Missouri-Columbia

VITA

Chadwick Damson Rittenhouse was born in Madison, Wisconsin and graduated from Oregon Senior High School in Oregon, Wisconsin in 1996. He obtained a Bachelor of Science in Wildlife Ecology with a Degree Certificate in Environmental Studies from the University of Wisconsin-Madison in 2000 and a Master of Science in Wildlife Science from the University of Missouri-Columbia in 2003. He began his PhD research at the University of Missouri in 2003.

Chad met his wife Tracy Ann Green in Zoology 151, held in Birge Hall on the University of Wisconsin campus. Chad is now a post-doctoral fellow in the Department of Forest and Wildlife Ecology at the University of Wisconsin and Tracy is a post-doctoral fellow in the Department of Botany, located in Birge Hall. They are astonished and delighted to be back in Madison where it all started.