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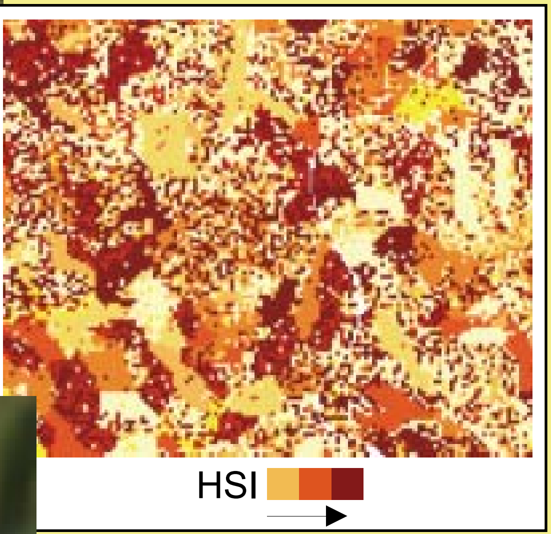
Michael A. Larson, William D. Dijak, Frank R. Thompson, III, and Joshua J. Millspaugh



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LANDSCAPE-LEVEL HABITAT SUITABILITY MODELS FOR TWELVE WILDLIFE SPECIES IN SOUTHERN MISSOURI

Michael A. Larson, William D. Dijak, Frank R. Thompson, III, and Joshua J. Millspaugh

ABSTRACT.—Geographic information systems (GIS) and abundant landscape-level data, often from remote sensing sources, provide new opportunities for biologists to model and evaluate wildlife habitat quality. Models of habitat quality have not been developed for some species, and many existing models could be improved by incorporating updated knowledge of wildlife–habitat relationships and landscape variables such as the spatial distribution of habitat components. Furthermore, landscape analyses and wildlife population priorities are common features of land management decision processes. We developed GIS-based habitat suitability index (HSI) models for 12 terrestrial vertebrate species that represent a range of potential conservation concerns and have diverse habitat requirements. We developed the models for a large, mostly forested area in southern Missouri and similar landscapes. The models are based primarily on tree species, tree age, and ecological land type—variables available in many GIS and vegetation databases. After describing and justifying the models, we applied them to maps of a study area that contained a wide range of tree ages and forest patch sizes. We believe application of the habitat models in this landscape demonstrated that they satisfactorily predict habitat suitability. Readers can download a Windows-based software program from the Internet (www.ncrs.fs.fed.us/hsi/) to use in implementing the models in other landscapes.

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Quantifying habitat quality is important for management of wildlife populations and conservation planning. Habitat suitability index (HSI) models have been used to evaluate wildlife habitat and the effects of management activities and development since the early 1980s (U.S. Fish and Wildlife Service 1980, 1981). These models are based on functional relationships between wildlife and habitat variables. Values of habitat variables (e.g., herbaceous canopy cover, tree canopy cover, tree height) are related to habitat quality on a suitability index (SI) scale from 0 = "not habitat" to 1 = "habitat of maximum suitability." Habitat suitability index scores, also on a 0–1 scale, are usually calculated using a mathematical formula representing hypothesized relationships among the individual SIs. Wildlife–habitat relationships may be supported by empirical data, expert opinion, or both (U.S. Fish and Wildlife Service 1980, 1981). Traditionally, HSI models are applied to a sample of locations within land cover types or dominant overstory vegetation types. Habitat quality in an area is typically summarized in terms of habitat units, which represent the product of the mean HSI score in each vegetation type and the area of land in that vegetation type, summed across the study area.

Now that geographic information system (GIS) software and high-speed computer hardware are widely available, their use among biologists is increasing. In addition to providing a new, powerful analytical tool, GIS technology allows land and wildlife managers to utilize novel sources of land cover, vegetation, and other habitat data, namely remote imagery from aerial photographs and satellite sensors and GIS databases of elevation, surface water, climate data, and ecological land types. Concurrent with GIS developments have been advances in our understanding of wildlife–habitat relationships, especially at landscape scales.

Using GIS for HSI-type habitat evaluations has several advantages over traditional HSI modeling. It is easier and faster to apply GIS-based habitat models to large geographic areas because time- and labor-intensive collection of field data is not necessary. Spatial structure and landscape patterns are often important aspects of habitat quality (Donovan *et al*. 1987, Rickers *et al*. 1995, Robinson *et al*. 1995) and are much easier to incorporate in GIS models. Furthermore, GIS-based habitat models can be used to evaluate landscapes simulated by spatially explicit forest landscape models [e.g., LANDIS (He *et al*. 1996, 1999; Mladenoff and He 1999)], which are useful for comparing alternative land management scenarios over time (e.g., Marzluff *et al*. 2002, Shifley *et al*. 2000).

The full use of GIS in habitat modeling, however, requires the revision of existing HSI models or the development of new ones. Whereas most existing HSI models are based on relatively small-scale habitat variables measured by biologists in the field, GIS-based HSI models have the capability to more readily focus on larger scale habitat variables that can be quantified without going afield. In addition to substituting large- for small-scale variables that may characterize similar habitat attributes (e.g., percent forest and spherical densiometer measurements both quantify canopy cover), new landscape variables (e.g., patch size and edge density) may be incorporated into the HSI model and habitat suitability may be analyzed at multiple spatial scales.

Our objective was to develop habitat suitability index models that could be used in a GIS to evaluate wildlife habitat quality in large (i.e., thousands of hectares) forested landscapes. We developed a series of single-species habitat models that satisfied three criteria: they represented a variety of terrestrial vertebrates, were applicable to landscapes in southern Missouri, and could be implemented in raster GIS using data available for large spatial extents. We described the models and demonstrated their effectiveness by applying them to landscape maps with diverse patch sizes and tree ages that were the result of forest management simulated by LANDIS. Readers can download a Windows-based software program from the Internet (www.ncrs.fs.fed.us/hsi/) to modify the models and apply them in other landscapes.

METHODS

We selected 12 species representing a variety of terrestrial vertebrates ranging from endangered species to game species, ranging from mast-dependent to disturbance-dependent species, and including three classes of vertebrates (table 1). We developed a GIS-based habitat model for each species. The models for the two bat species and salamander, which are dormant during winter, and the four neotropical migrant songbirds consider only habitat used during summer. Therefore, we did not address potential winter-habitat limitation for these species. The remaining five species are nonmigratory, and their models reflect year-round habitat requirements.

Habitat models existed for most species we selected, so we revised those models according to several needs: to reconcile conflicts among models if more than one model existed, to revise or delete variables for which field sampling would be necessary, to incorporate spatially explicit variables (i.e., interspersion of life requisites), to adapt models to our geographic and ecological context, and to incorporate advances in our understanding of wildlife–habitat relationships since the original models were developed. We developed new models for the two bat species because no previous models existed. Model revisions and newly developed models were based on published empirical data and expert opinion. These models represent our synthesis of the best information available, but potential users should recognize that the models have not been validated with independent data. While we encourage model validation efforts, our assumption is that habitat suitability models, even if not validated, are a useful method to synthesize and apply current knowledge of habitat relationships to management or conservation questions. Furthermore, because habitat suitability models can be developed from a broad base of existing knowledge, they may have more general applicability than statistical models based on single data sets that are narrow in scope. Methods that have recently been reported for setting confidence bounds on habitat suitability indices (Bender *et al*. 1996, Burgman *et al*. 2001) could potentially be applied to these models.

Mathematical and logical relationships used to calculate HSI scores varied depending upon the number and types of SI variables included in the model. We used arithmetic or geometric means (i.e., $[x_1 + x_2 + \ldots + x_n]/n$ and $[x_1 \times x_2 \times \ldots \times x_n]^{1/n}$, respectively) to combine variables representing life requisites, or tangible resources. We used a geometric mean when habitat quality was zero if the value of any single SI variable was zero, indicating that habitat characteristics were all necessary and therefore not substitutable. Otherwise, we used an arithmetic mean. Some variables (e.g., edge sensitivity), however, were used to adjust the value of a life requisite variable because they did not represent resources themselves. We incorporated such variables, which typically had two or three discrete values, using simple multiplication rather than a mean. Occasionally, life requisites for a species cannot be expected to occur in a single site or raster cell (i.e., map pixel). For example, cover and winter food requisites for ruffed grouse (see table 1 for scientific names of modeled species) are satisfied by young and mature forest, respectively. In such cases, the HSI score in a cell represented predominantly one life requisite rather than both because we used a maximum function to choose between the contrasting life requisite variables. In such cases we also included variables to account for the proximity of the life requisites and the potential for rare instances when both usually contrasting requisites were satisfied within a single cell (see Composition and Interspersion below). We used a minimum function when we wanted an HSI score to represent a single limiting factor (e.g., food or cover for gray squirrels). Exceptions to these rules were rare, simplified calculations, and resulted in HSI scores identical to those based on the methods described here.

Table 1.—*Species selected for habitat modeling in a southern Missouri landscape, their scientific names, the group or management concern they represent, and the assumed size of their smallest home range in Missouri*

Species	**Scientific name**	**Group or management concern**	**Size of high quality home range**	**Citations for home range size**
Ovenbird	*Seiurus aurocapillus*	Late-successional, area-sensitive songbird	0.8 ha	Wenny 1989, Porneluzi and Faaborg 1999
Prairie warbler	*Dendroica discolor*	Early-successional, area-sensitive songbird	0.5 ha	Nolan *et al*. 1999
Hooded warbler	*Wilsonia citrina*	Area-insensitive songbird	0.8 ha	Evans Ogden and Stutchbury 1994, Norris *et al*. 2000
Pine warbler	*Dendroica pinus*	Pine-dependent songbird	1 ha	Haney and Lydic 1999, Rodewald *et al*. 1999
Eastern wild turkey	*Meleagris gallopavo silvestris*	Mast-dependent game bird	102 ha	Speake *et al*. 1975, Wigley *et al*. 1986, Badyaev *et al*. 1996
Ruffed grouse	*Bonasa umbellus*	Disturbance-dependent game bird	5 ha	McDonald *et al*. 1998, Fearer 1999
Gray squirrel	*Sciurus carolinensis*	Mast-dependent mammal	0.6 ha	Flyger 1960, Cordes and Barkalow 1972, Schwartz and Schwartz 1981:149
Black bear	*Ursus americanus*	Wide-ranging mammal	20 km^2	Clark 1991, van Manen and Pelton 1997
Bobcat	*Lynx rufus*	Wide-ranging, disturbance-dependent mammal	9.8 km^2	Hamilton 1982, Rucker *et al*. 1989
Northern long-eared bat	*Myotis septentrionalis*	Snag-roosting bat and endangered species	~13 km^2	Foster and Kurta 1999
Red bat	*Lasiurus borealis*	Live-tree roosting bat	~13 km^2	Foster and Kurta 1999
Southern redback salamander	*Plethodon serratus*	Terrestrial amphibian	Unknown	

Geographic Area of Applicability

Our models were designed for large landscapes (thousands of hectares) in Missouri that contain mostly central hardwood forests. Users applying them to other geographic areas or landscapes, especially where the dominant land cover is not forest, should consider modifying and validating the models.

Study Area and Primary Input Data

After developing each model, we applied it to GIS maps of our study area. The study area was a 3,261-ha, nearly 100 percent forested, oak-dominated landscape in the Mark Twain National Forest in southern Missouri (fig. 1). It

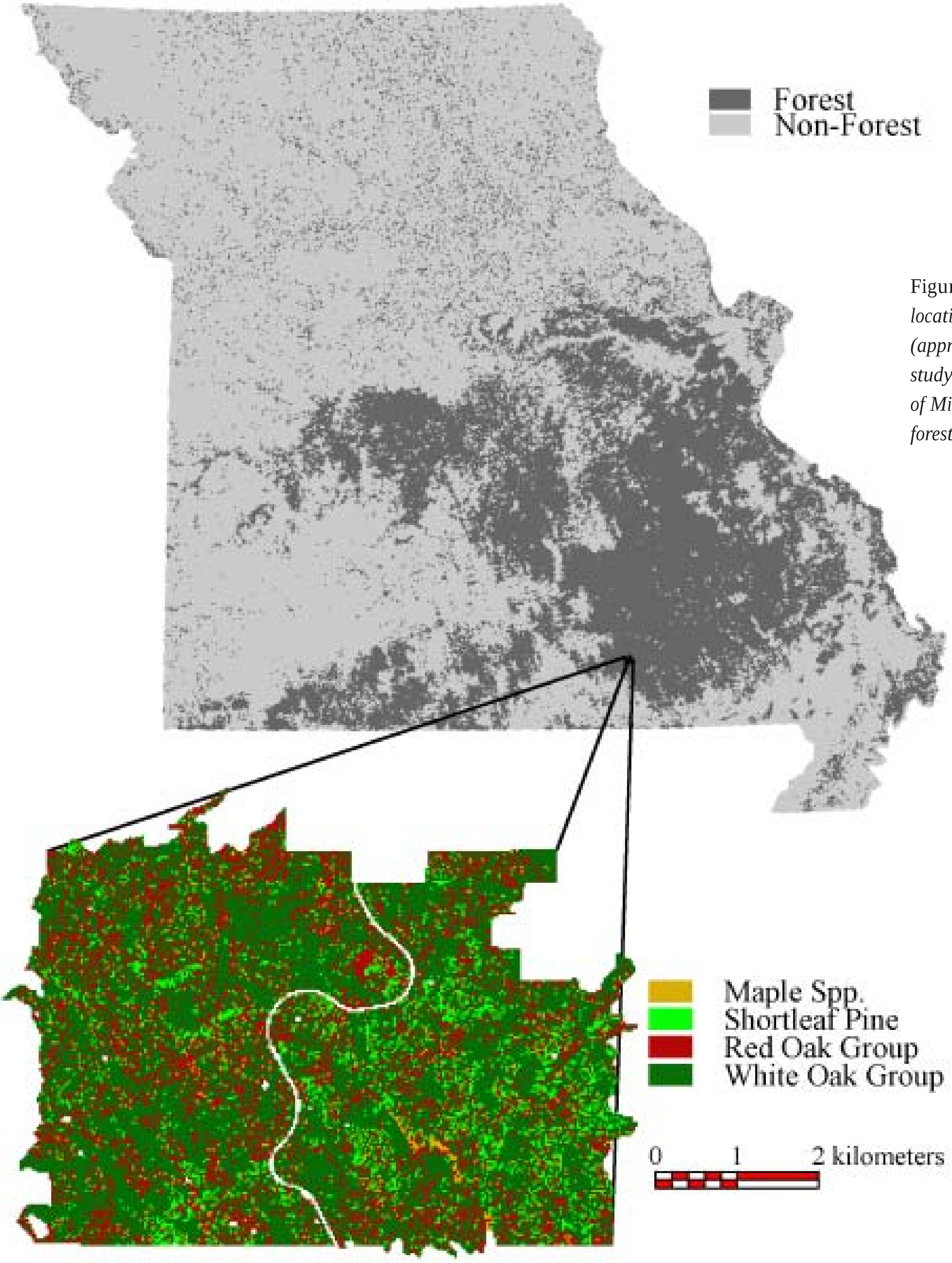


Figure 1.—*Geographic location of the 3,261-ha (approximately 5 x 7 km) study area relative to the state of Missouri and the mostly forested Ozark region.*

occurs in a 1.8-million-hectare landscape that also contains contiguous (92%) hardwood forest (Porneluzi and Faaborg 1999).

Our models utilize digital, raster-based maps of ecological land types and the age and species group of dominant overstory trees, which are available from a variety of sources such as forest inventories, interpreted aerial photos, and classified satellite imagery. For our demonstration we used output from the 100th year of simulated forest management on the study area (see appendix). The simulation resulted in a landscape with a wide range of tree ages and patch sizes (table 2, figs. 2 and 3), which is helpful for evaluation of model performance. We used a raster resolution of 30 m^2 (0.09 ha) and retained that resolution in our HSI models. Therefore, SI values were based on attributes of a single raster cell rather than a forest stand or animal home range whenever possible. A high resolution is desired because it results in the loss of less information about the real landscape than lower resolutions, and if desired, the data or associated SI values can be averaged at a coarser scale that may better represent how an animal perceives its environment.

Dominant overstory tree groups were white oak (*Quercus alba, Q. stellata*), red oak (*Q. rubra, Q. coccinea, Q. velutina, Q. marilandica*), maple (*Acer* spp.), and short leaf pine (*Pinus echinata*). We assumed that differences in the age and type of dominant trees and land type classifications (table 3, fig. 2) among pixels adequately represented variation in understory characteristics that may affect habitat quality for some species (e.g., sapling density and shrub cover) (McKenzie *et al*. 2000). The only openings in our study area were cells containing trees ≤10 years old, indicating a recent

Table 2.—*Percentage of area in the southern Missouri study area in categories of tree age and species group after 100 years of simulated forest management. The sum of reported percentages may not equal sums in the last column and row due to rounding.*

Tree age (years)	Tree species group				
	Red oak	White oak	Maple	Pine	Sum
1– 10	0.5	3.7	0.0	0.3	4.4
11– 20	0.4	3.3	0.0	0.4	4.1
21– 30	0.1	4.1	0.0	0.4	4.5
31– 40	0.1	3.5	0.0	0.3	3.9
41– 50	0.1	3.8	0.0	0.3	4.1
51– 60	0.1	3.4	0.0	0.2	3.7
61– 70	0.1	4.0	0.0	0.3	4.4
71– 80	0.1	4.8	0.0	0.1	5.0
81– 90	0.3	4.7	0.0	0.1	5.1
91–100	0.3	3.1	0.0	0.3	3.7
101–110	0.0	0.0	0.0	0.0	0.0
111–120	8.4	9.4	0.1	2.0	20.0
121–130	0.0	0.0	0.0	0.0	0.0
131–140	0.0	0.0	0.0	0.0	0.0
141–150	9.7	8.7	1.5	3.8	23.7
151–160	0.0	0.0	0.0	0.0	0.0
161–170	6.1	5.0	0.7	1.4	13.3
Sum	26.3	61.3	2.3	10.0	100.0

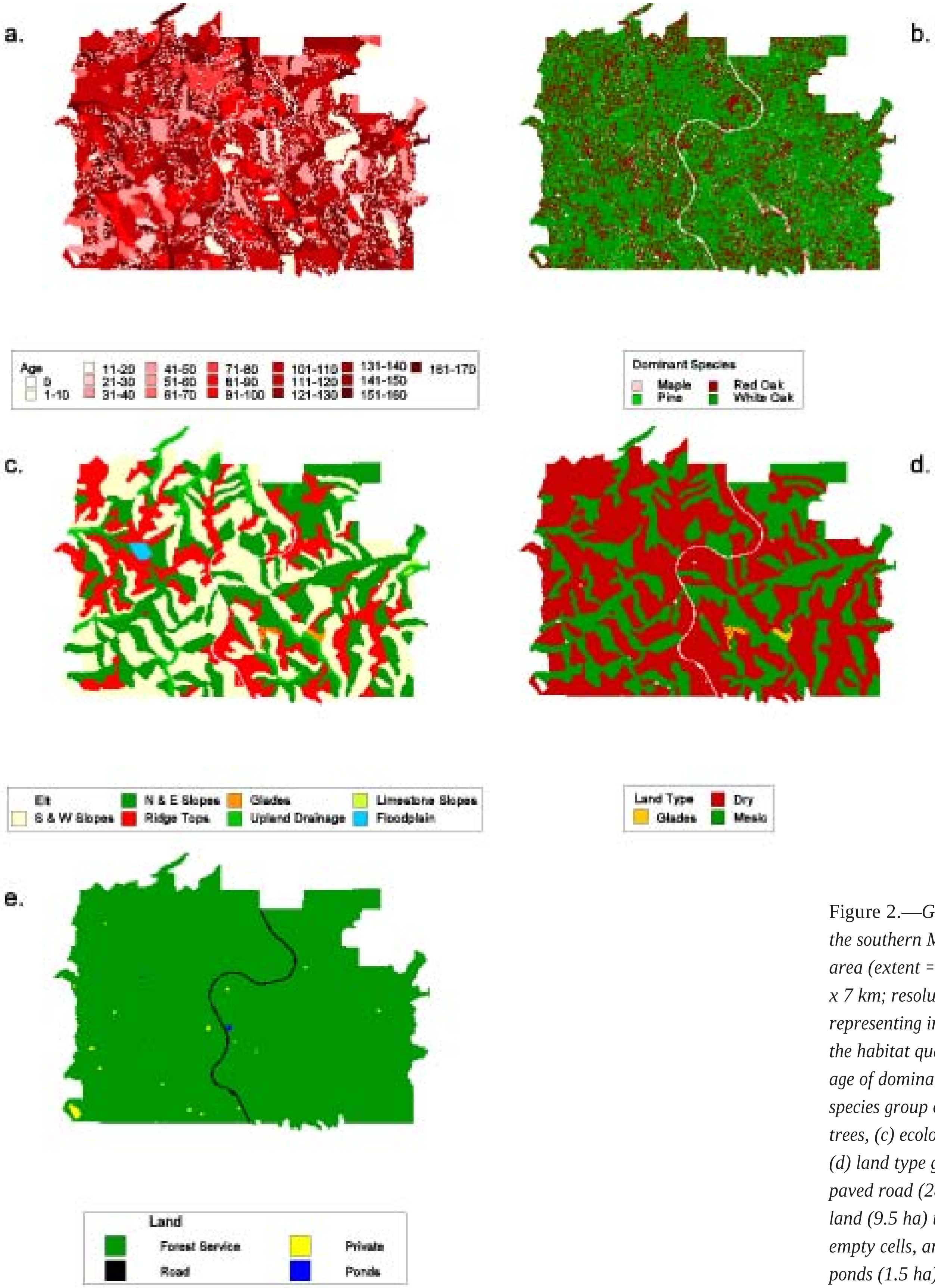
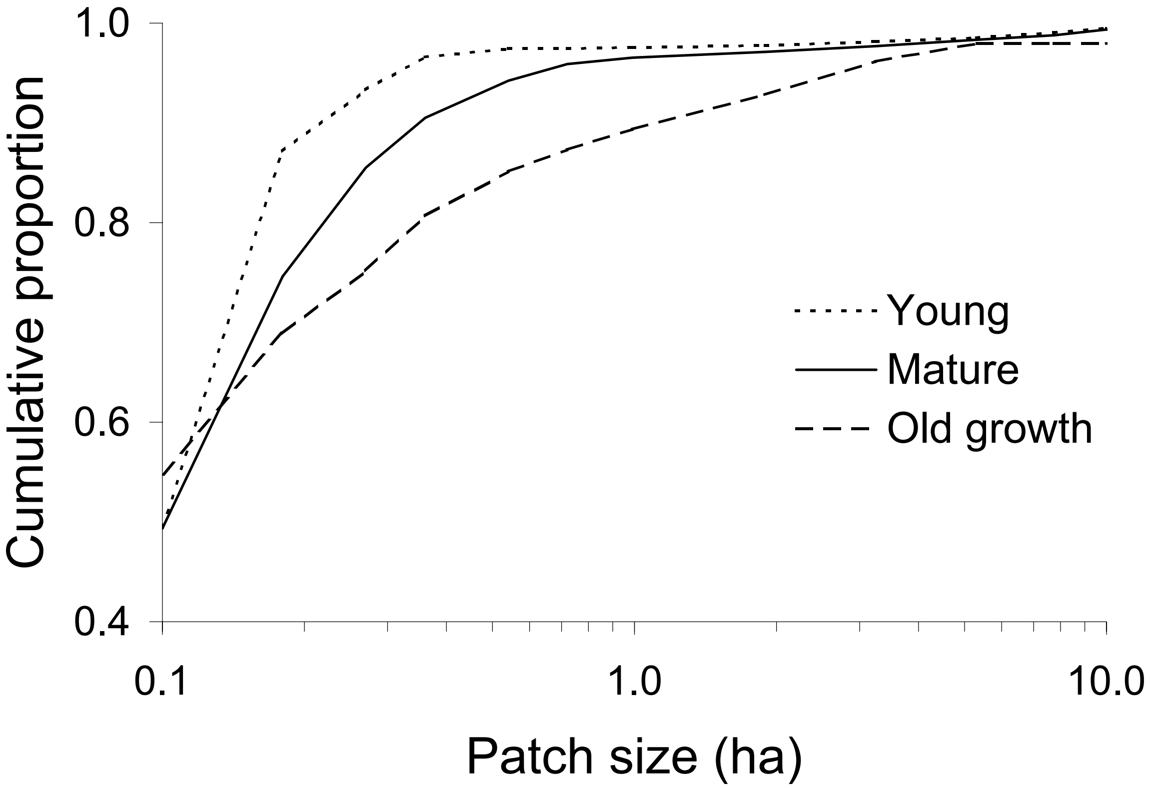


Figure 2.—*GIS coverages of the southern Missouri study area (extent = approximately 5 x 7 km; resolution = 0.09 ha) representing input variables for the habitat quality models: (a) age of dominant trees, (b) species group of dominant trees, (c) ecological land types, (d) land type groups, and (e) a paved road (28.7 ha), private land (9.5 ha) that appeared as empty cells, and permanent ponds (1.5 ha). See the appendix for more details.*

Figure 3.—*Cumulative distribution of patch sizes by tree age category in the southern Missouri study area. Young = 1–50 years (distributions for seedling, sapling, and pole classes were very similar), mature = 51–100 years, and old growth = 101+ years. Not represented are 0.5 percent of young forest patches (n = 2,163) 10–26 ha in size, 0.6 percent of mature forest patches (n = 1,296) 10–127 ha in size, and 2 percent of old-growth forest patches (n = 544) 10–50, 627, and 798 ha in size. Note that the origin is not 0,0 and the x-axis is a* $\log_{10}$ *scale.*



stand-replacing disturbance, and some glades. The right-of-way of a State highway bisecting the study area (28.7 ha) and a few small patches of private land (<2 ha each, 9.5 ha total) appeared as empty cells (fig. 2). Depending upon the wildlife species, we also used GIS coverages for the paved road and permanent ponds in some habitat quality models (fig. 2).

Examples of GIS Methods and Common Model Components

Land Type Adjustments

Forest composition and dynamics can vary considerably by ecological land type (Host *et al.* 1987, Kupfer and Franklin 2000, Miller 1981). Land type is also a major factor that determines other forest characteristics such as density and composition of herbaceous and woody understory vegetation (Hix and Pearcy 1997, Host and Pregitzer 1992, Shifley and Brookshire 2000). Much of wildlife habitat in forest ecosystems is often characterized by successional stage and variables associated with understory or ground cover. Therefore, we used the interaction of age of dominant trees and land type as an SI variable in many of our models. Usually, we accomplished this in one step by specifying SI values in tables with tree ages in rows and land type categories in columns (e.g., table 4). Specification of such SI values was based on differences among land type categories in the rate of succession and the density of vegetation. Occasionally, an SI was dependent solely on land type, such as in the hooded warbler model, and the interaction with other variables occurred in the HSI calculation. We used similar methods to adjust SI values for tree species group (e.g., see the model for ovenbirds, which do not use areas dominated by conifers).

Table 3.—*Relationships among land type categories*

Land types used in our models	Land types used to predict oak mast production	Ecological land type[a]	
		Land form	**Soil and vegetation**
Glade	Glade	Southwest side slope	Glade savanna
		Side slope	Dolomite/limestone glade
Dry	Southwest side slope	Southwest side slope	Dry chert forest
	Flat	Ridge	Xeric chert forest
		Ridge	Dry chert forest
		Flat	Xeric chert forest
		Flat	Dry chert forest
	Limestone	Northeast side slope	Dry-mesic limestone forest
		Side slope	Xeric limestone forest
		Side slope	Dry limestone forest
Mesic	Northeast side slope	Northeast side slope	Dry-mesic chert/sand forest
	Upland drainage	Upland waterway	Gravel wash
		Upland waterway	Dry bottomland forest
		Upland waterway	Dry-mesic bottomland forest
	Mesic	Low floodplain	Wet-mesic bottomland forest
		Floodplain	Calcareous wet forest
		High floodplain	Mesic bottomland forest
		Toe slope	Mesic forest
		Sinkhole	Mesic forest
		Sinkhole	Acid seep forest

[a] Based on the classification for the Mark Twain National Forest (Miller 1981).

Table 4.—*Habitat suitability of forest by habitat requisite, land type*[a], *and age of dominant overstory trees for six bird species in southern Missouri*

Age of dominant trees (years)	Ovenbird			Prairie warbler			Hooded warbler		Pine warbler	Wild turkey				Ruffed grouse		
										Nesting and brood cover		Adult cover				
	Glade	**Dry**	**Mesic**	**Glade**	**Dry**	**Mesic**	**Nest-ing cover**	**Forag-ing**		**Glade**	**Other**	**Glade**	**Other**	**Glade**	**Dry**	**Mesic**
0[b]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00	1.0	1.0	0.0	0.00	0.0	0.0	0.0
1–10	0.0	0.0	0.1	1.0	1.0	0.5	1.0	0.0	0.00	1.0	0.5	0.0	0.00	0.0	0.8	1.0
11–20	0.0	0.1	0.2	1.0	0.5	0.1	0.0	0.0	0.00	1.0	1.0	0.0	0.00	0.0	0.8	1.0
21–30	0.0	0.3	0.4	0.8	0.1	0.0	0.0	0.0	0.00	1.0	0.0	0.0	0.25	0.0	0.5	0.3
31–40	0.0	0.6	0.7	0.5	0.0	0.0	0.0	0.0	0.25	1.0	0.0	0.0	0.50	0.0	0.0	0.0
41–50	0.0	0.9	1.0	0.3	0.0	0.0	0.0	0.0	0.50	1.0	0.1	0.0	0.75	0.0	0.0	0.0
51–60	0.0	0.9	1.0	0.3	0.0	0.0	0.0	0.0	0.75	1.0	0.2	0.0	1.00	0.0	0.0	0.0
≥61	0.0	0.9	1.0	0.3	0.0	0.0	0.0	1.0	1.00	1.0	0.3	0.0	1.00	0.0	0.0	0.0

[a] Land type categories are described in table 3.

[b] Trees not present (e.g., failed regeneration after disturbance).

Hard Mast Production

Much of the Missouri Ozarks is dominated by mast-producing hardwoods, especially oaks. Hard mast provides an important fall and winter food resource for many wildlife species. Sullivan (2001) developed a mast production model to complement other subroutines in LANDIS. The main input variables were age of dominant trees and land type, and the main output was an index of mast production. The model accounted for varying ratios and densities of red and white oaks within cells and incorporated spatial and temporal stochasticity. For the mast-dependent wildlife species we selected, we used output from Sullivan's (2001) model to develop habitat suitability relationships for mast production. We used mean mast index values from a single application of the model in our simulated study area to determine relative mast production by tree species group and age of dominant trees on a cell. Assuming no mast production on cells dominated by maples or pines, we developed separate relationships for red and white oaks only. We rescaled the raw index values to a 0–1 SI interval so that SI = 1 approximately coincided with the maximum mean production of mast on most land types for both red and white oaks (fig. 4). This resulted in SI values greater than one for 20 percent of tree age x land type x tree species group combinations. We think this is appropriate, given that the relationship is based on mean mast production and that maximum mast production could be greater than five times higher (Sullivan 2001). We fit fourth-order polynomial regression functions forced through the origin to the rescaled index values over tree age for each tree species group x land type combination (table 5, fig. 4). We used

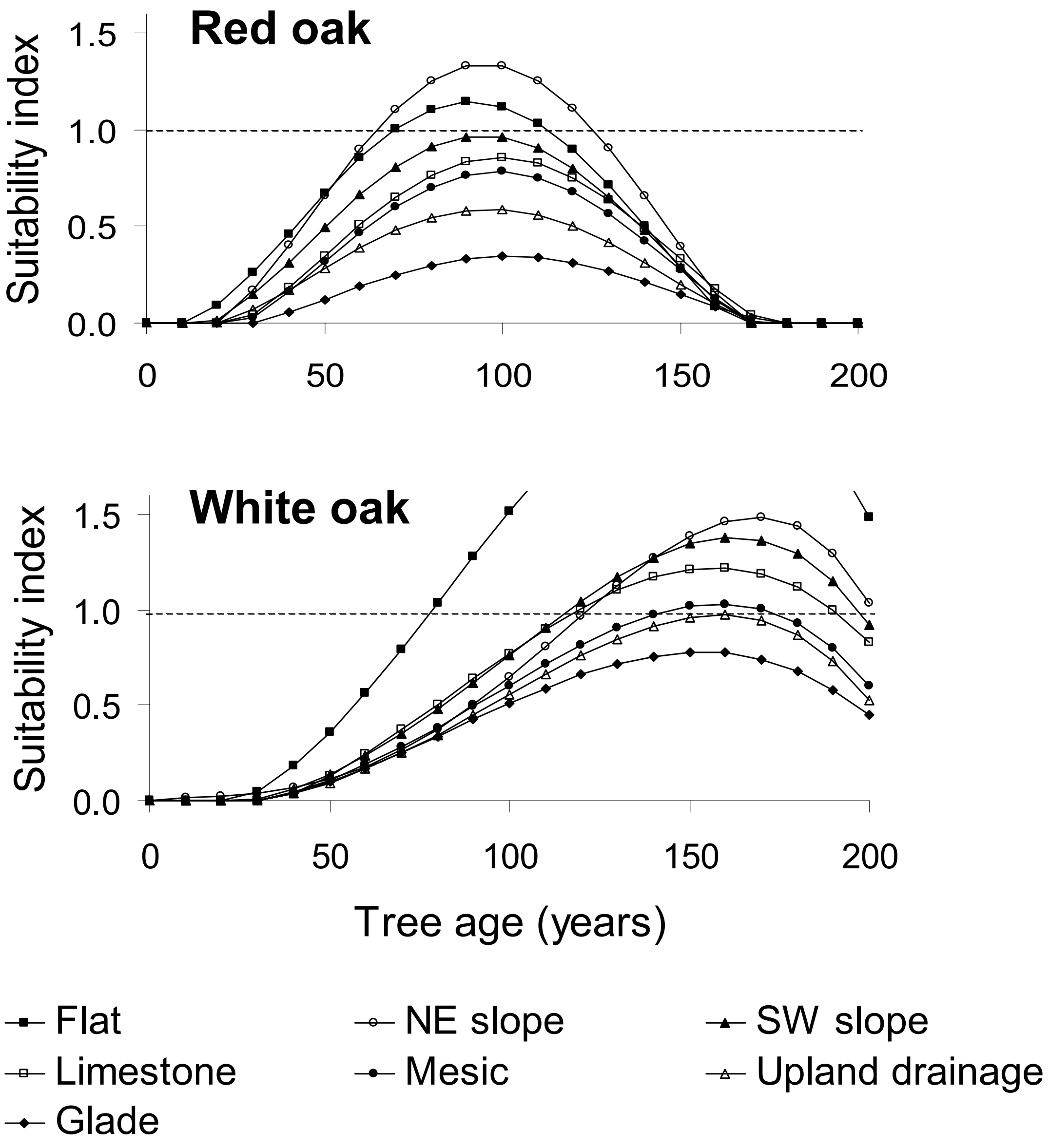


Figure 4.—*Suitability index values of cells dominated by red oaks (top) and white oaks (bottom) for hard mast production based on an index developed by Sullivan (2001) for forests in southern Missouri. Production varies by land type, and index values >1 are rounded down to 1 in the HSI models.*

the regression functions in the HSI models and assigned SI = 0 if the function resulted in values <0 and SI = 1 if the function resulted in values >1 (fig. 5). Hard mast production is a variable in models for wild turkey, ruffed grouse, gray squirrel, and black bear.

Patch and Distance Algorithms

Many species are sensitive to the size of habitat patches. In models for prairie warblers and ruffed grouse, we used a patch-definition algorithm to aggregate cells containing suitable habitat as defined earlier in the model by SI relationships with tree age and land type. A habitat cell was aggregated into a patch if it was immediately adjacent to another habitat cell, either by a shared side (i.e., horizontally or vertically) or corner (i.e., diagonally). Once habitat patches were defined, we assigned SI values based on the size of patches (fig. 6).

We used different algorithms to assign SI values based on a cell's distance from a habitat requisite or landscape features that individuals avoid. For example, our two bat species require access to surface water and black bears avoid paved roads. The distance algorithm assigned a value to each cell in the landscape; the value was equal to the distance between the cell and the nearest cell representing either water or a road. The SI value was based on that distance (fig. 7).

Moving Window Analysis

A vector-based GIS is based on lines and points, so boundaries between land units are explicit features of the landscape, and metrics such as distance from a point to a boundary can be measured easily. One limitation of vector-based GIS is that landscape characteristics are considered uniform within defined polygons. We developed our habitat models for raster-based GIS, in which landscape

Table 5.—*Polynomial regression coefficients for the mast production suitability index. The y-intercept is zero for all regression equations.*

		Regression parameter			
Oak group	**Land type[a]**	**Tree age**	**(Tree age)^2**	**(Tree age)^3**	**(Tree age)^4**
Red	Flat	-7.2535×10^{-3}	7.4473×10^{-4}	-7.6811×10^{-6}	2.0813×10^{-8}
	NE side slope	-1.7311×10^{-2}	1.0451×10^{-3}	-1.0006×10^{-5}	2.6178×10^{-8}
	SW side slope	-1.1024×10^{-2}	7.2305×10^{-4}	-7.0058×10^{-6}	1.8413×10^{-8}
	Limestone	-1.4904×10^{-2}	7.2273×10^{-4}	-6.5360×10^{-6}	1.6524×10^{-8}
	Mesic	-1.4810×10^{-2}	6.9970×10^{-4}	-6.3497×10^{-6}	1.6164×10^{-8}
	Upland drainage	-7.5360×10^{-3}	4.4903×10^{-4}	-4.2507×10^{-6}	1.1012×10^{-8}
	Glade	-6.9367×10^{-3}	3.0603×10^{-4}	-2.6928×10^{-6}	6.6967×10^{-9}
White	Flat	-9.2984×10^{-3}	4.1544×10^{-4}	-1.7617×10^{-6}	5.1103×10^{-10}
	NE side slope	2.0223×10^{-3}	-7.0890×10^{-5}	1.8744×10^{-6}	-7.2031×10^{-9}
	SW side slope	-3.5297×10^{-3}	1.2540×10^{-4}	1.5010×10^{-7}	-2.8681×10^{-9}
	Limestone	-7.5926×10^{-3}	2.5998×10^{-4}	-1.1299×10^{-6}	6.1906×10^{-10}
	Mesic	-3.3179×10^{-3}	1.1667×10^{-4}	-3.8002×10^{-8}	-1.9354×10^{-9}
	Upland drainage	-2.6792×10^{-3}	8.8265×10^{-5}	1.8711×10^{-7}	-2.4772×10^{-9}
	Glade	-4.2093×10^{-3}	1.5445×10^{-4}	-6.1443×10^{-7}	1.6130×10^{-11}

[a] Land type categories are described in table 3.

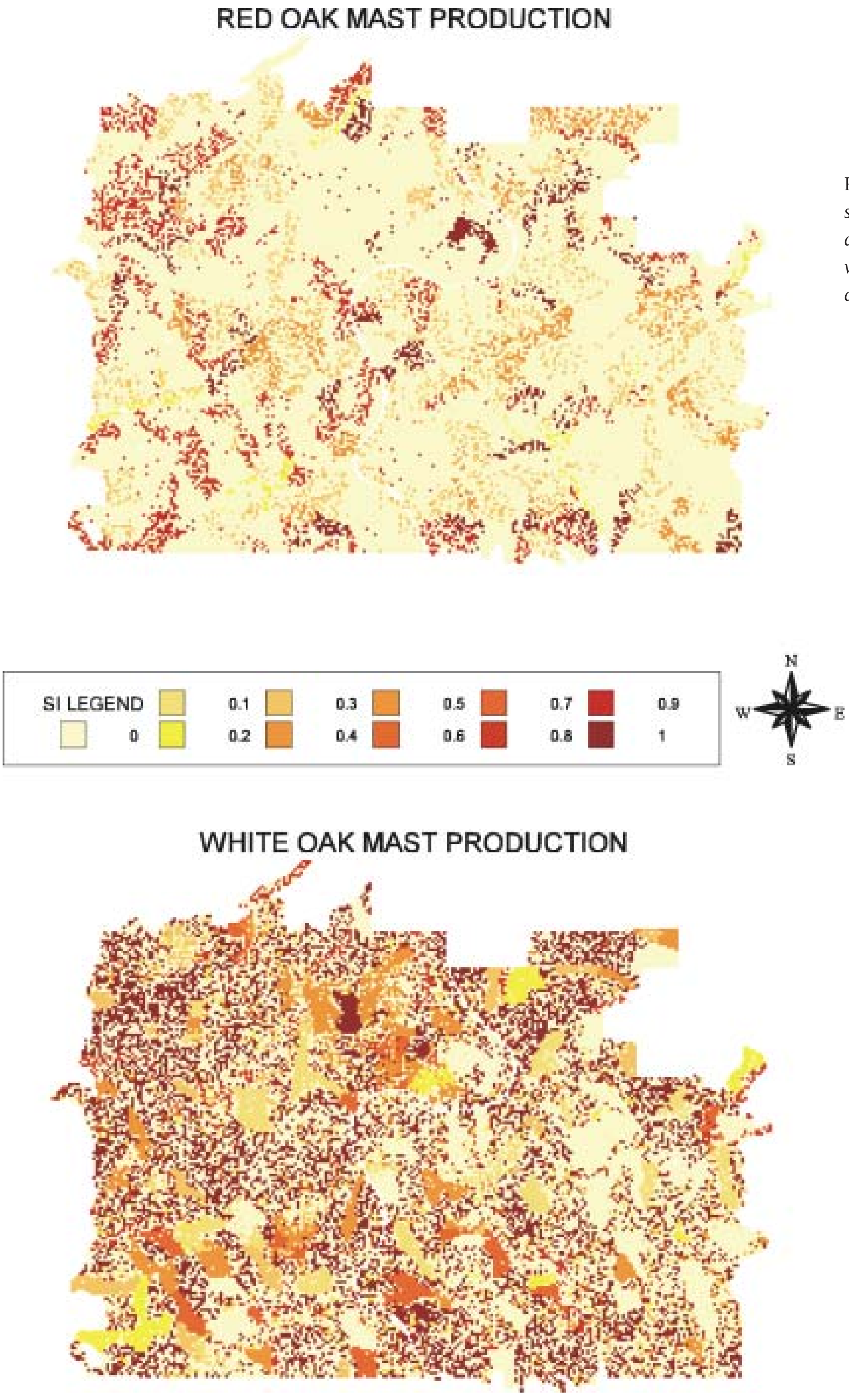


Figure 5.—*Hard mast suitability index values of cells dominated by red oaks and white oaks applied to the study area in southern Missouri.*

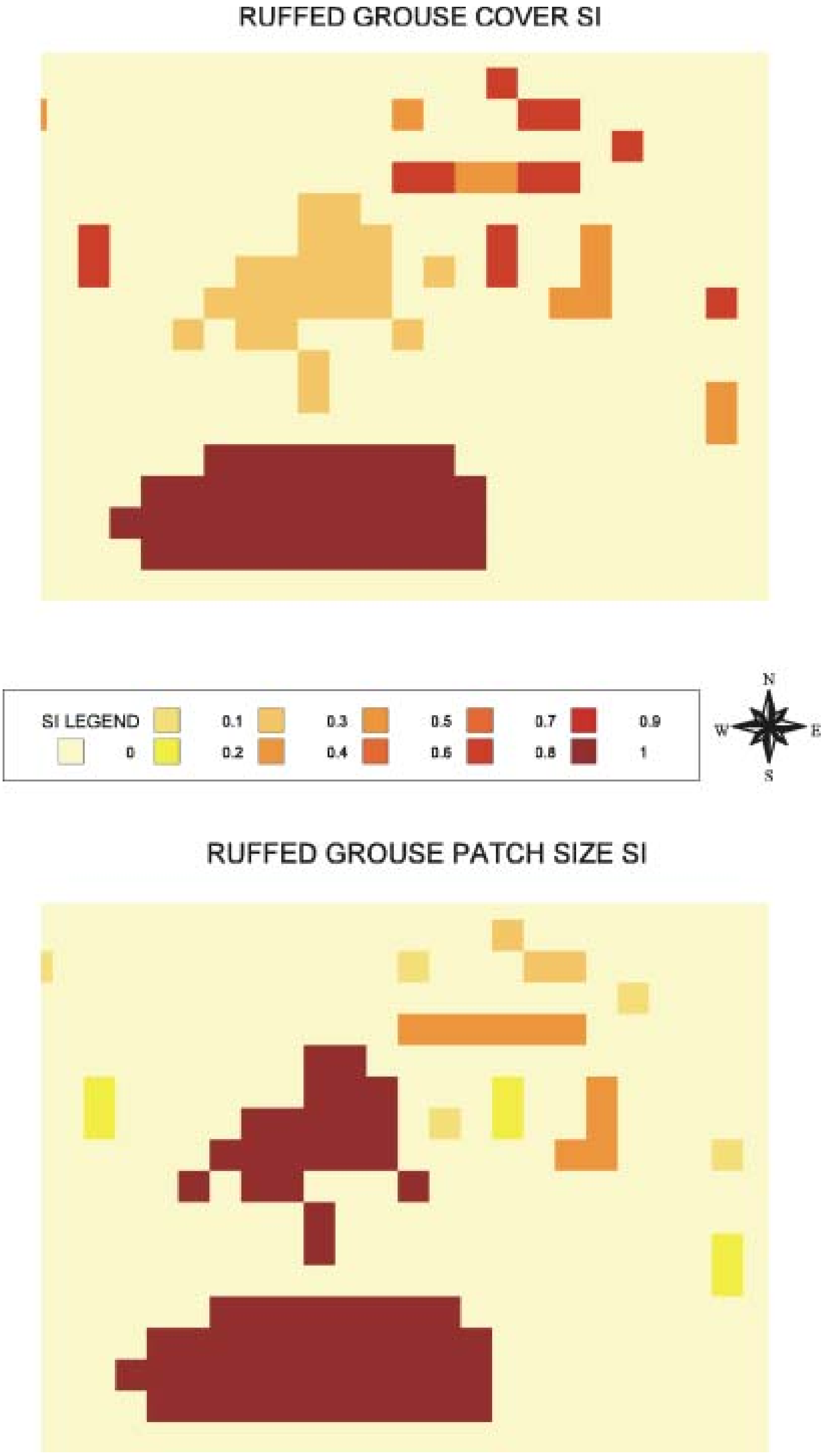


Figure 6.—*Example application of a patch definition algorithm. Cells of varying suitability (top) are aggregated into habitat patches (bottom), which vary in quality based on size. Extent = approximately 660 m wide; resolution = 0.09 ha.*

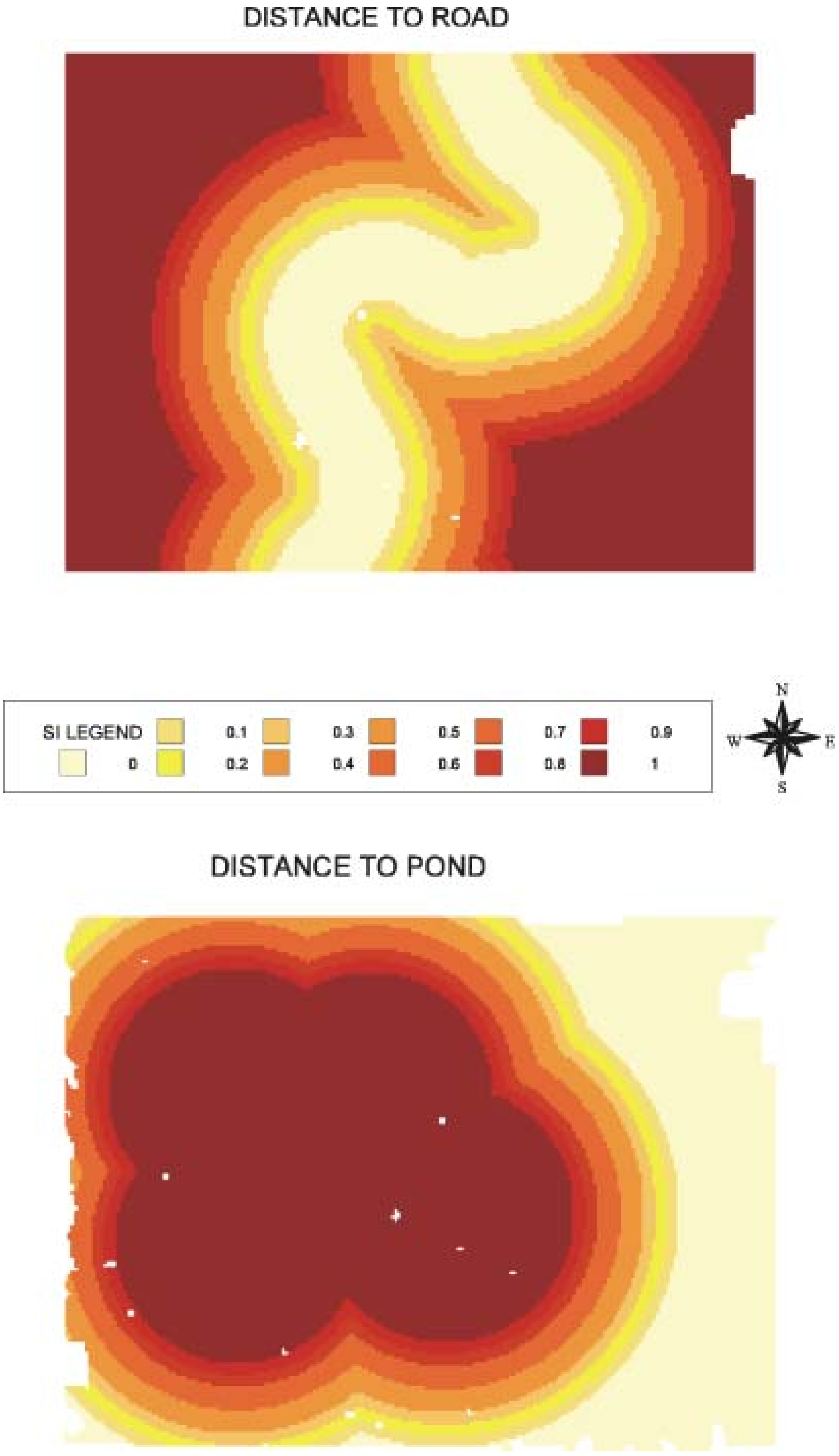


Figure 7.—*Example application of a distance algorithm. A paved road through the center of the study area (top) and four ponds (bottom) affect habitat suitability based on distance. Private lands appear as empty cells.*

characteristics occupy square grid cells. Therefore, characteristics are uniform only at the resolution of the raster cells. Another benefit is that boundaries between groups of cells representing, for example, forest stands are not fixed. A main limitation of raster-based GIS is that boundaries are not explicitly defined, so measuring distances to them is difficult. We used moving window analyses to overcome that limitation.

Edge Sensitivity.—In models for ovenbirds and prairie warblers, we used moving window analyses to evaluate habitat quality near edges between suitable habitat and non-habitat. First, we identified cells containing habitat as those containing a nonzero value for ≥1 SI relationship; all other cells were defined as non-habitat. Then, assuming habitat near an edge with non-habitat was of lower quality than habitat farther from an edge, we used a moving window approximately twice as wide as presumed edge effects to assign an SI value for edge sensitivity. The central cell of the window received an SI value ≤0.5 for edge sensitivity if the window contained non-habitat (i.e., the minimum value in the window was zero). Otherwise, the central cell of the window received an SI value of 1.0 for edge sensitivity because habitat edges would be farther from the central cell than the distance of presumed edge effects.

After the SI for edge sensitivity is multiplied by other SI values, non-habitat would appear as non-habitat (even though it was assigned SI = 1 for edge sensitivity), and habitat suitability near non-habitat edges would be half as high relative to similar cells farther than the threshold distance from edges (fig. 8). We also used this method in models for red bats and northern long-eared bats, both of which prefer foraging near edges and forest openings.

Composition and Interspersion.—In models for hooded warblers, wild turkeys, ruffed grouse, and black bears, we used moving window analyses to assign SI values based on the composition of habitat requisites. First, we recoded habitat suitability based on requisites such as nesting cover, SI_1, and foraging areas, SI_2, in the same GIS map according to the following rules: code=0 if $SI_1 < 0.5$ and $SI_2 < 0.5$, code=1 if $SI_1 \geq 0.5$, code=2 if $SI_2 \geq 0.5$, and code=3 if $SI_1 \geq 0.5$ and $SI_2 \geq 0.5$ (fig. 9). If both habitat requisites were present in ideal proportions in a moving window the approximate size of a high quality home range, suitability for composition was greatest (i.e., $SI_3 = 1$; fig. 9). The observed proportion of a habitat requisite was based on the number of cells containing the corresponding codes:

$$Proportion_{observed} = \frac{(\text{No. of 1s}) + (\text{No. of 3s})}{(\text{No. of cells in the window}) + (\text{No. of 3s})}$$

We used a similar approach to evaluate the proximity of habitat components in a moving window analysis for northern long-eared bats. Recoding of SIs using unique, generic numbers in a single GIS map was the same, but the new SI was based simply on the presence of cells of each type within the window, not on their proportions.

Software Availability

Readers can download a Windows-based software program from the Internet (www.ncrs.fs.fed.us/hsi/) to modify the models and apply them in other landscapes.

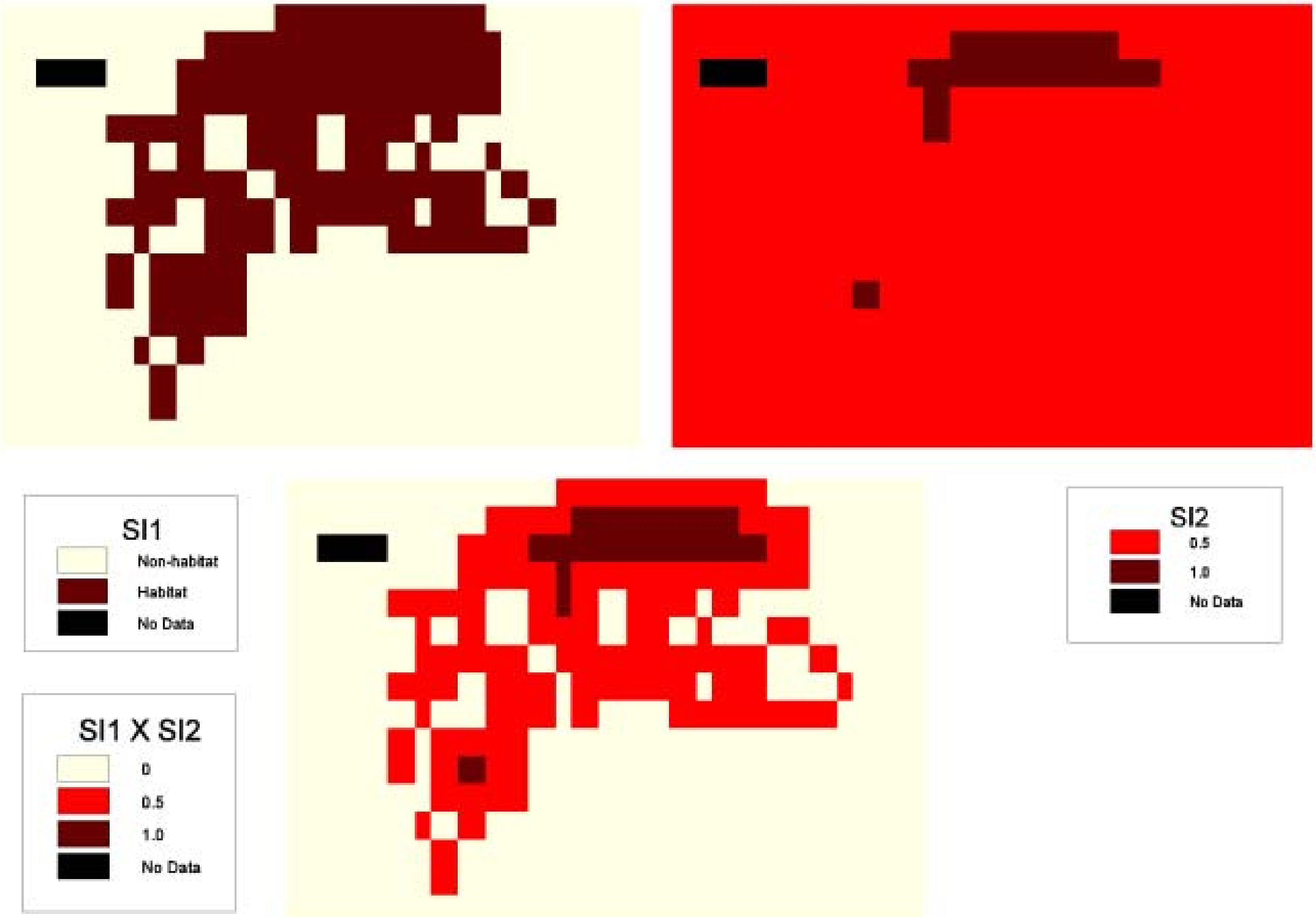


Figure 8.—*Example using a moving window to evaluate habitat suitability near edges with non-habitat.* SI_1 *defines habitat (1) and non-habitat (0).* SI_2 *based on a 3- x 3-cell moving window analysis. For the central cell of the moving window,* $SI_2 = 0.5$ *if the minimum value in the window is* $SI_1 = 0$*; otherwise* $SI_2 = 1$*. Extent = approximately 690 m wide; resolution = 0.09 ha.*

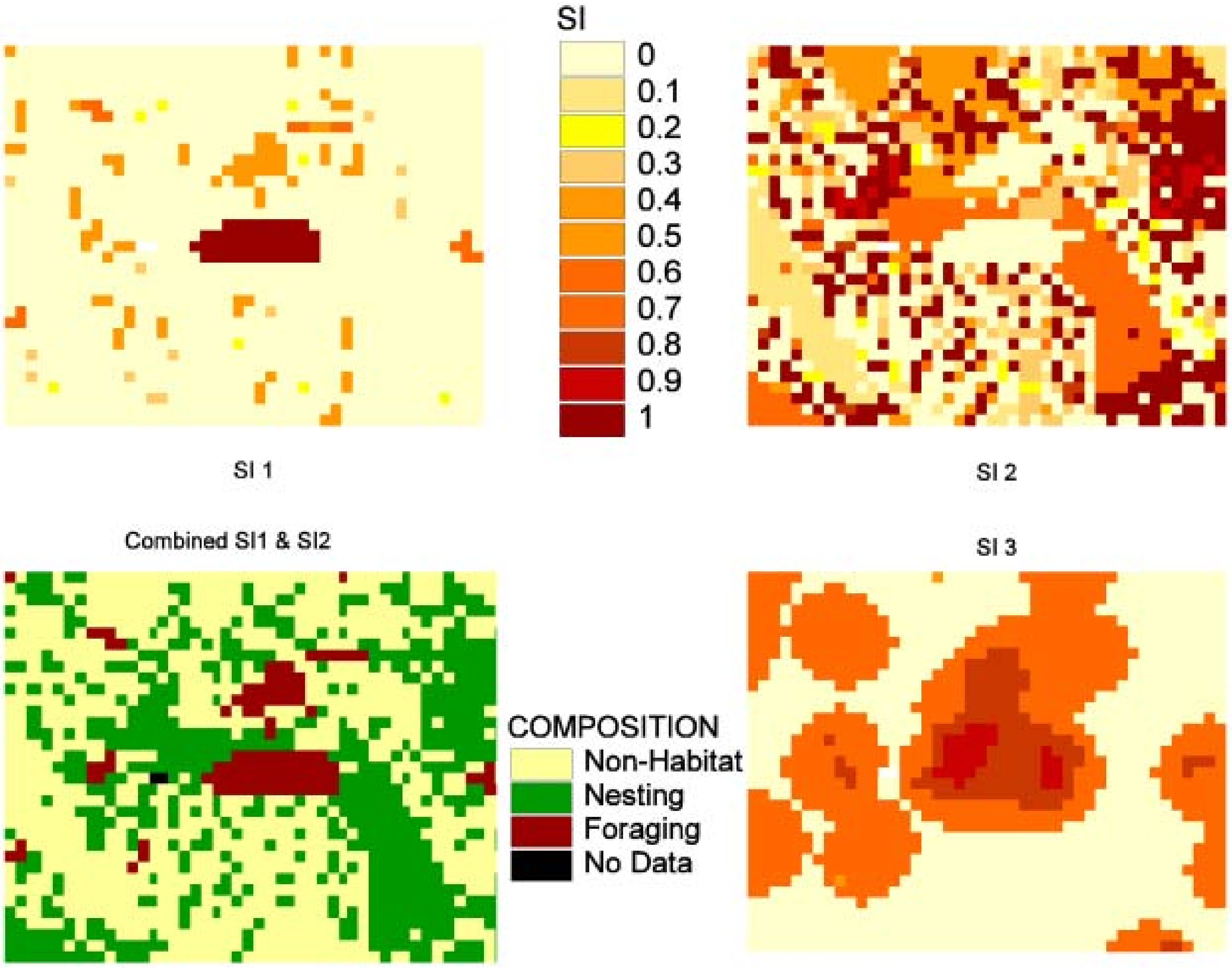


Figure 9.—*Example using a moving window to evaluate composition of habitat requisites. Nesting cover,* SI_1*, and foraging areas,* SI_2*, are recoded in the same GIS map (1 if* $SI_1 \geq 0.5$*, 2 if* $SI_2 \geq 0.5$*, 0 if* $SI_1 < 0.5$ *and* $SI_2 < 0.5$*). Suitability based on composition (*SI_3*) is 1 if half of a 4-cell-radius moving window contains high quality nesting cover and the other half contains high quality foraging habitat.* $SI_3 = 0$ *if high quality habitat for either requisite is absent from the window. Extent = 1.32 km wide; resolution = 0.09 ha.*

MODEL DESCRIPTION AND APPLICATION

Ovenbird

We chose ovenbirds because they are area-sensitive songbirds that select late-successional hardwood forests (Crawford *et al.* 1981, Stauffer and Best 1980) (table 1). Ovenbirds require a closed overstory canopy and a relatively open understory (Neimi and Hanowski 1984) because they forage and nest on the ground (Van Horn and Donovan 1994) (table 6). Although their territories are <3 ha (Porneluzi and Faaborg 1999, Van Horn and Donovan 1994, Wenny 1989), ovenbirds usually do not occur in small forest patches and can experience reduced pairing success in forest patches <500 ha in size (Hayden *et al.* 1985, Robbins *et al.* 1989, Van Horn *et al.* 1995, Villard *et al.* 1993). Furthermore, ovenbirds avoid pines (Collins 1983; c.f., Penhollow and Stauffer 2000) and the edges of even large forest tracts (Flaspohler *et al.* 2001*a*, *b*; Ortega and Capen 1999; c.f., Sabine *et al.* 1996). A pattern recognition model of ovenbird habitat in the Mark Twain National Forest indicated higher probabilities of use in forest stands associated with oak overstory, greater basal area (≥7.43 m^2/ha), intermediate crown closure (60–70%), and less ground cover (≤10%) (Sweeney and Dijak 1985).

Our ovenbird habitat model contained three suitability indices. The first SI related high habitat quality with trees >50 years old on mesic sites (Thompson *et al.* 1992, Yahner 1986) (table 4, fig. 2). Suitability of forest of a given age was lower on dry sites because succession to a relatively closed canopy and open understory occurs more slowly there (table 4). The second suitability index addressed ovenbird preference for broadleaf forest; SI_2 = 0 if the dominant trees on the cell were in the pine group, and SI_2 = 1 otherwise. Therefore, oak-pine stands would receive intermediate values for SI_2 and stands covered predominantly by pines would appear as unsuitable habitat. The third SI reduced habitat suitability by half within 30 m of an edge between mature forest and either permanent or temporary openings. Negative edge effects on nesting success may extend further into a forest (Flaspohler *et al.* 2001*b*), but we chose to be conservative because they have not been well documented in southern Missouri. We assumed that habitat patches in our landscape would be sufficiently large to preclude other spatial effects that make ovenbirds area-sensitive. We implemented SI_3 using a moving window analysis. We moved a square, 3- x 3-cell (0.81-ha) analysis window across a GIS layer containing output from SI_1. We assigned a value for SI_3 to the central cell of the window. The value was SI_3 = 0.5 if the value of SI_1 in any of the cells within the window was 0 (or “no data” due to presence of a road). Otherwise, the value of SI_3 for the central cell was 1. We moved the window systematically one cell at a time.

The HSI score for the ovenbird model was the product of the three suitability indices because tree species group and edge effects modified the suitability of appropriate-aged forest (table 6). These relationships were evident in the HSI map of the study area. The first suitability index was the main component of habitat suitability for ovenbirds, and SI_2 and SI_3 reduced suitability in small areas of pines and near openings (fig. 10).

Prairie Warbler

Prairie warbler habitat consists of early-successional woody vegetation (Nolan *et al.* 1999). In our study area this occurred in recently disturbed forest and glades (table 4). Ideally, patches of suitable habitat are >3.5 ha, but patches as small as 0.4 ha are used (Nolan 1978:331–337, Robinson and Robinson 1999). Annand and Thompson (1997) did not detect prairie warblers in areas subject to single-tree and group-selection harvests in southeastern Missouri. Although prairie warbler habitat may be associated with edge density in some areas (Penhollow and Stauffer 2000), habitat quality may be lower near edges between suitable habitat and other land cover types than farther

Table 6.—*Relevant life and habitat requisites and their corresponding HSI model parameters from LANDIS for 12 species in southern Missouri*

Species	**Life requisite**	**Habitat requisite**	**Model parameters and implementation**	**HSI equation**
Ovenbird	Nesting cover and food	Mature hardwood forest	SI_1: Tree age by land type[a] SI_2: Tree species group	
	Nesting cover	Edge avoidance	SI_3: Moving window analysis on SI_1	$SI_1 \times SI_2 \times SI_3$
Prairie warbler	Nesting cover and food	Early-successional woody vegetation	SI_1: Tree age by land type	
		Large habitat patches	SI_2: Patch size algorithm	
	Nesting cover	Edge avoidance	SI_3: Moving window analysis on SI_1	$(SI_1 \times SI_2)^{0.5} \times SI_3$
Hooded warbler	Nesting cover	Early-successional hardwood vegetation	SI_1: Tree species group Tree age (see SI_3 below)	
	Food	Mature hardwood forest	SI_1: Tree species group Tree age (see SI_3 below)	
	Nesting cover and food	Site productivity	SI_2: Land type	
		Interspersion of nesting and foraging habitat	SI_3: Moving window analysis on tree age	$SI_1 \times (SI_2 \times SI_3)^{0.5}$
Pine warbler	Nesting cover and food	Mature coniferous forest	SI_1: Tree age SI_2: Tree species group	$SI_1 \times SI_2$
Wild turkey	Nesting and brooding cover	Forest openings	SI_1: Tree age by land type	
	Adult cover	Mature forest	SI_2: Tree age by land type	
	Fall and winter food	Hard mast	SI_3: Model of tree age, tree species group, and land type[b]	
	Cover and food	Interspersion of life requisites	SI_4: Moving window analysis on SI_1 and mean of SI_2 and SI_3	$(\max\{SI_1, [(SI_2 + SI_3) / 2]\} \times SI_4)^{0.5}$
Ruffed grouse	Fall and winter food	Hard mast	SI_1: Model of tree age, tree species group, and land type	
	Cover	Dense forest regeneration	SI_2: Tree age by land type	
		Large habitat patches	SI_3: Patch size algorithm	
	Food and cover	Interspersion of life requisites	SI_4: Moving window analysis on SI_1 and mean of SI_2 and SI_3	$\{\max[SI_1, (SI_2 \times SI_3)^{0.5}] \times SI_4\}^{0.5}$
Gray squirrel	Winter food	Hard mast	SI_1: Model of tree age, tree species group, and land type	
	Cover	Mature forest	SI_2: Tree age by land type	$\min(SI_1, SI_2)$
Black bear	Fall and winter food	Hard mast	SI_1: Model of tree age, tree species group, and land type	
	Summer and fall food	Soft mast	SI_2: Tree age by land type	
	Food	Interspersion of seasonal foods	SI_3: Moving window analysis on SI_1 and SI_2	
	Cover	Road avoidance	SI_4: Distance-to-road algorithm	$[\max(SI_1, SI_2) \times SI_3]^{0.5} \times SI_4$

(table 6 continued on next page)

(table 6 continued)

Species	Life requisite	Habitat requisite	Model parameters and implementation	HSI equation
Bobcat	Prey habitat	Proportion of early successional forest and openings in home range	SI_1: Moving window analysis on tree age by land type	
	Cover	Road avoidance	SI_2: Distance-to-road algorithm	$SI_1 \times SI_2$
Red bat	Roost sites	Crown of large, live trees	SI_1: Tree age	
		Land type preferences	SI_2: Land type	
	Water	Proximity to roost sites	SI_3: Distance-to-water algorithm	
	Food	Edge between forest canopy and openings	SI_4 and SI_5: Moving window analyses on SI_1	$\max[(SI_1 \times SI_2 \times SI_3)^{0.33}, (\{SI_1 \times [\max(SI_4, SI_5)]^2\}^{0.33})]$
Northern long-eared bat	Roost sites	Dead branches on large, live trees	SI_1: Tree age	
		Large snags	SI_2: Tree age	
	Water	Proximity to roost sites	SI_3: Distance-to-water algorithm	
	Food	Forest canopy and gaps	SI_4: Moving window analysis on SI_1	
	Roost sites and food	Interspersion of life requisites	SI_5: Moving window analysis on mean of SI_1, SI_2, and SI_3 and product of SI_1 and SI_4	$\{\max[(SI_1 \times SI_2 \times SI_3)^{0.33}, (SI_1 \times SI_4)] \times SI_5\}^{0.5}$
Southern redback salamander	Food and cover	Mature forest	SI_1: Tree age	
		Moist substrate	SI_2: Land type	$(SI_1 \times SI_2)^{0.5}$

[a] See table 3 for definitions of glade, dry, and mesic land types.

[b] The hard mast production model was developed by Sullivan (2001). See also figs. 2 and 5.

from edges. Woodward *et al*. (2001) documented that prairie warblers in southern Missouri avoided nesting ≤20 m from a forest edge.

Lancia and Adams (1985) observed a high correlation between point counts of prairie warblers and HSI values from Sheffield's (1981) HSI model, which was based on stand age and stocking densities in the shrub and overstory layers. Our HSI model for prairie warblers was similar but included two new spatial factors. Our first SI defined suitable habitat according to tree age and land type category (Robinson and Robinson 1999, Thompson *et al*. 1992) (table 4, fig. 2). The second SI scored suitable habitat patches (as defined by SI_1) based on their size using a patch-definition algorithm. Habitat patches ≤4 raster cells (0.36 ha) in size received $SI_2 = 0$, those ≥39 cells (3.51 ha) in size received $SI_2 = 1$, and those between 5 and 38 cells (0.45 and 3.42 ha) in size received $SI_2 = (0.32 \times \text{patch size in ha}) - 0.13$ (fig. 11). The third SI defined areas within 30 m of an edge between suitable and unsuitable habitat (as defined by SI_1) using a square, 3- x 3-cell moving window (Woodward *et al*. 2001). If the minimum value in the window was $SI_1 = 0$, the central window cell received $SI_3 = 0.5$ because it was near an edge; otherwise, $SI_3 = 1$.

The HSI score for a raster cell was the geometric mean of SI_1 and SI_2 multiplied by SI_3 (table 6). Habitat suitability in the study area was greatest in the interior of large patches, and most young forest patches resulting from tree mortality or group-selection cutting were too small to provide habitat for prairie warblers (fig. 12).

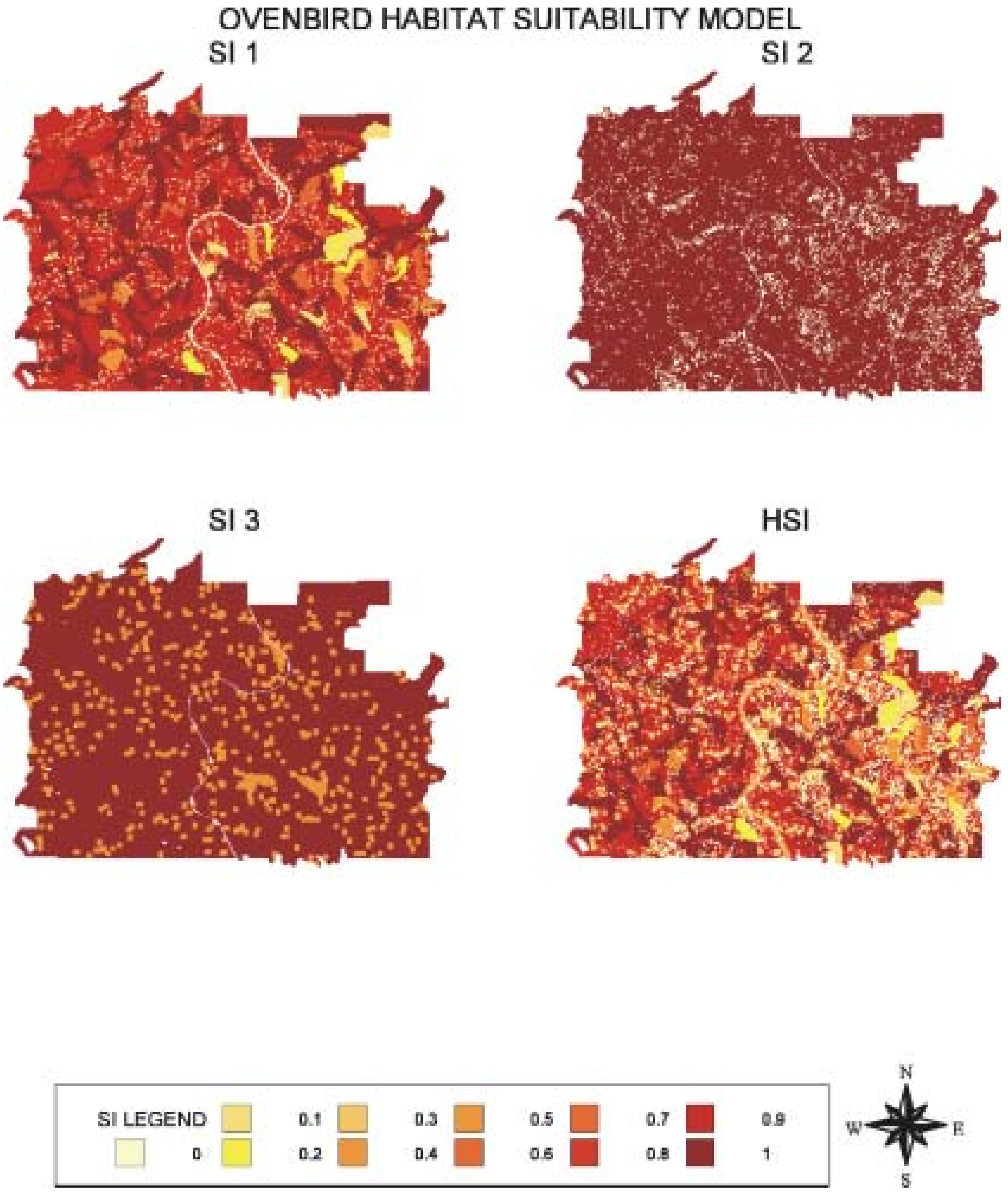


Figure 10.—*Application of the ovenbird habitat quality model to a 3,261-ha unit of the Mark Twain National Forest in southern Missouri. There are separate images for suitability as mature forest (*SI_1*), suitability as deciduous forest (*SI_2*), suitability as forest interior (*SI_3*), and HSI =* SI_1 *x* SI_2 *x* SI_3.

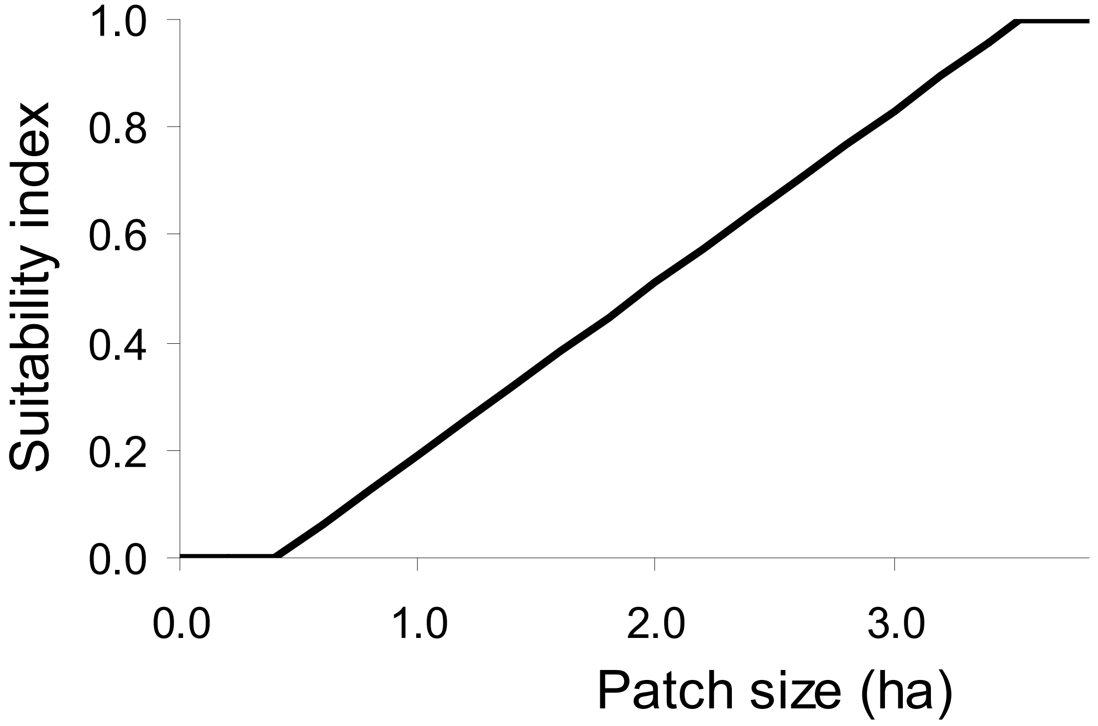


Figure 11.—*Suitability of habitat patches for prairie warblers is positively related to patch size.*

Hooded Warbler

Hooded warblers nest in openings and areas with young hardwood regeneration (Evans Ogden and Stutchbury 1994). Dense, shrubby vegetation provides good nesting cover. Hooded warblers also require mature hardwood stands for foraging (Evans Ogden and Stutchbury 1994). These two different vegetation types need to occur in proximity of each other to provide good hooded warbler habitat. The highest quality hooded warbler habitat contains both vegetation types within the size of a typical territory (0.5–1.1 ha; Evans Ogden and Stutchbury 1994, Norris *et al.* 2000). Such conditions may occur due to single-tree or group-selection forest disturbances (Annand and Thompson 1997, Baker and Lacki 1997, Robinson and Robinson 1999). The only previously published habitat model for hooded warblers was a GIS model developed and tested by Dettmers and Bart (1999). Their model predicted hooded warbler presence from topography metrics and the presence of forest. It was based on their characterization of hooded warblers in southeastern Ohio as a “hilltop species associated with the dry moisture conditions and convex land forms of ridges” (Dettmers and Bart 1999:157). That description conflicts with data indicating that in southern Missouri and northern Arkansas hooded warblers are associated with mesic sites (Smith 1977, Thompson *et al.* 1992). Evans Ogden and Stutchbury (1994:4) also noted that hooded warblers are “often associated with moist woodlands and ravines.”

Our HSI model for hooded warblers was a function of three variables. The first indicated that cells dominated by pines provided no habitat (i.e., SI_1 = 0; fig. 2). All other cells were assigned SI_1 = 1. The second SI reflected the higher densities of hooded warblers on mesic sites (SI_2 = 1) than on dry sites (SI_2 = 0.4) and glades (SI_2 = 0) in Missouri (Thompson *et al.* 1992) (table 3). The third SI specified a relationship between habitat suitability and the proportions of nesting and foraging habitat in a territory-sized moving window (3 x 3 cells = 0.8 ha; table 1). Raster cells with dominant trees 1 to 10 years old were assigned a generic code of 1 for providing nesting habitat, cells with dominant trees >60 years old were assigned a generic code of 2 for providing foraging habitat, and all other cells were assigned a generic code of 0. The ideal proportions of generic codes in the analysis window were 22 percent (2 cells) 1s and 78 percent (7 cells) 2s (Annand and Thompson 1997). When observed proportions were ideal, the central window cell received SI_3 = 1. Values of SI_3 declined as proportions

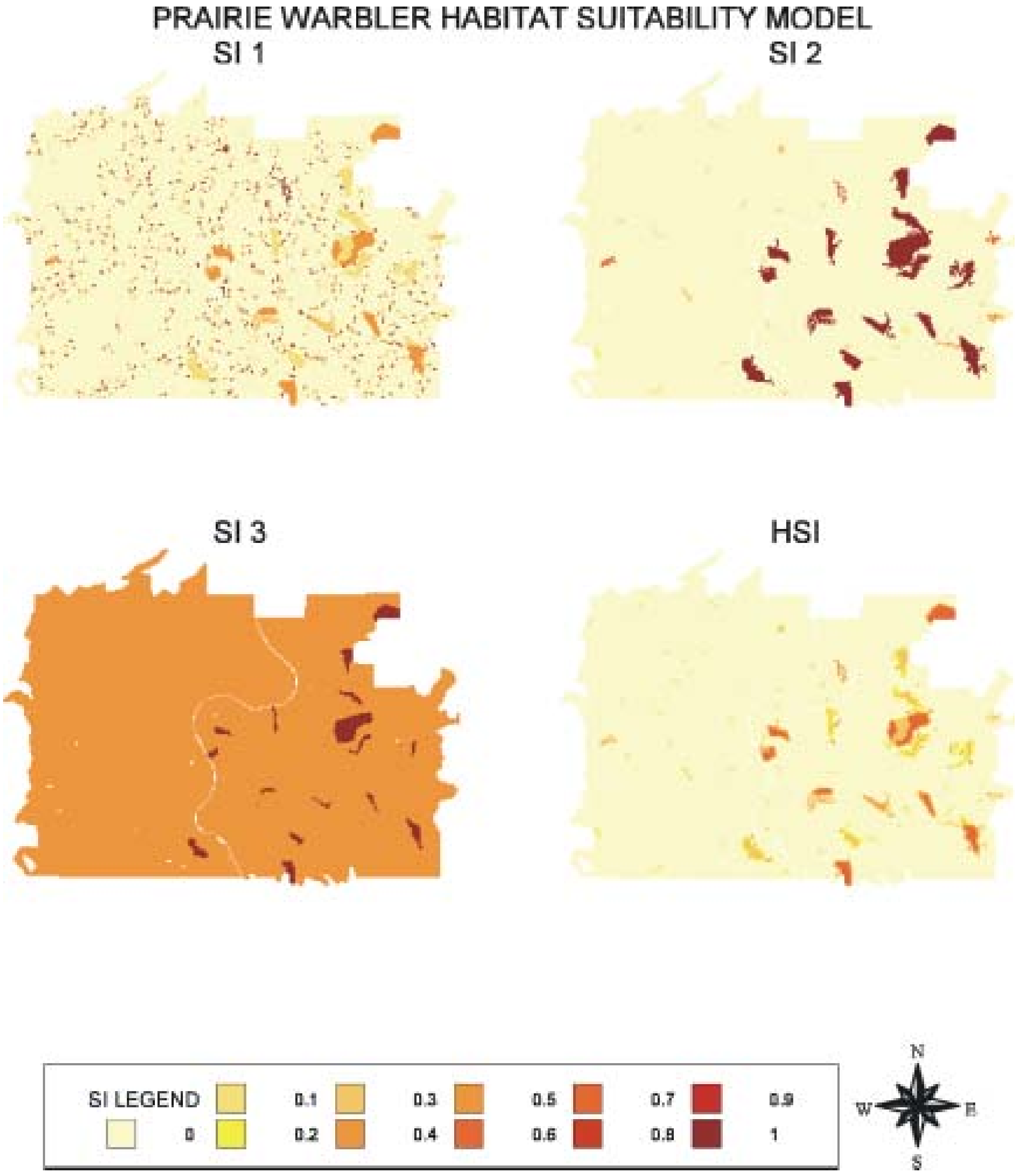


Figure 12.—*Application of the prairie warbler HSI model to a 3,261-ha unit of the Mark Twain National Forest in southern Missouri. There are separate images for suitability as early-successional forest (SI_1), suitability as large habitat patches (SI_2), suitability as habitat interior (SI_3), and HSI = $(SI_1 \times SI_2)^{0.5} \times SI_3$.*

deviated from the ideal according to the following equation:

$$SI_3 = (1 - |\text{proportion of } 1s_{\text{observed}} - 0.22|) \text{ x } (1 - |\text{proportion of } 2s_{\text{observed}} - 0.78|).$$

If either habitat requisite was absent in the window, $SI_3 = 0$ (table 7).

The HSI score was the product of SI_1 and the geometric mean of SI_2 and SI_3 (table 6). Large amounts of optimal nesting cover and food existed in the study area, but juxtaposition of those life requisites, as identified by SI_3, drastically limited overall habitat suitability for hooded warblers (fig. 13). As expected, suitable habitat appeared at the interface between nesting and foraging habitats, along the edges of large openings, and near recent group-selection cuts and gaps created by wind.

Table 7.—*Values of SI_3 based on the proportion of cells providing good nesting cover (hardwoods 1–10 years old) and foraging habitat (hardwoods >60 years old) for hooded warblers in a home range-sized moving window (0.8 ha = 9 cells) in a southern Missouri landscape. Optimal proportions are 0.22 and 0.78, respectively*[a].

Proportion in nesting cover	**Proportion in foraging habitat**									
	0.00	**0.11**	**0.22**	**0.33**	**0.44**	**0.56**	**0.67**	**0.78**	**0.89**	**1.00**
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.11	0.00	0.29	0.39	0.49	0.59	0.69	0.79	0.89	0.79	
0.22	0.00	0.33	0.44	0.55	0.66	0.78	0.89	1.00		
0.33	0.00	0.29	0.39	0.49	0.59	0.69	0.79			
0.44	0.00	0.26	0.34	0.43	0.51	0.61				
0.56	0.00	0.22	0.29	0.36	0.44					
0.67	0.00	0.18	0.24	0.30						
0.78	0.00	0.15	0.19							
0.89	0.00	0.11								
1.00	0.00									

[a] SI_3 = (1 – |[proportion of cells with dominant trees 1–10 years old] – 0.22|) x (1 – |[proportion of cells with dominant trees >60 years old] – 0.78|).

Pine Warbler

Pine warblers were the only pine-dependent species we selected (table 1), and they do not occur in areas of pure hardwood forest (Johnston and Odum 1956, Neimi *et al*. 1997, Rodewald *et al*. 1999). Densities of pine warblers generally increase with stand age (Conner *et al*. 1979, Evans 1978, Haney and Lydic 1999, Thompson *et al*. 1992) and may also be positively correlated with distance from streams (Murray and Stauffer 1995). Lancia and Adams (1985) observed a high correlation between point counts of pine warblers and values from HSI models (Sheffield 1981, Schroeder 1982). Schroeder's (1982) HSI scores were the geometric mean of three variables. Suitability was positively related to canopy closure of pines and seral stage of the stand but was negatively related to presence of a tall deciduous understory. Sheffield's (1981) model described stands <15 years old and not predominantly pine or oak-pine as unsuitable and reserved the highest suitability for stands with high basal area of pines, high stocking density of pines >6 m tall, and low stocking density in the understory.

We developed a model similar to the two previous ones (Schroeder 1982, Sheffield 1981). Our first SI_1 was based on tree age, with trees >60 years old being of the highest quality (table 4, fig. 2). We assumed that in pine stands tree age was highly correlated with canopy closure and basal area of pines. Our second variable was SI_2 = 1 if the dominant tree species group was pine or SI_2 = 0 if it was not. The HSI score was the product of SI_1 and SI_2 (table 6). Pine forest limited the location of pine warbler habitat in the study area, but the tree age variable (SI_1) identified less suitable and unsuitable pine forests in the HSI map as well (fig. 14).

Although it would have been feasible to determine the presence and approximate dominance status of a deciduous understory in cells dominated by pines (Schroeder's V_3), we chose not to include it as a variable in our model because it would be difficult or impossible to incorporate in applications of our model that are not based on LANDIS. Therefore, we had to assume that a high density or tall deciduous understory was absent in all areas dominated by

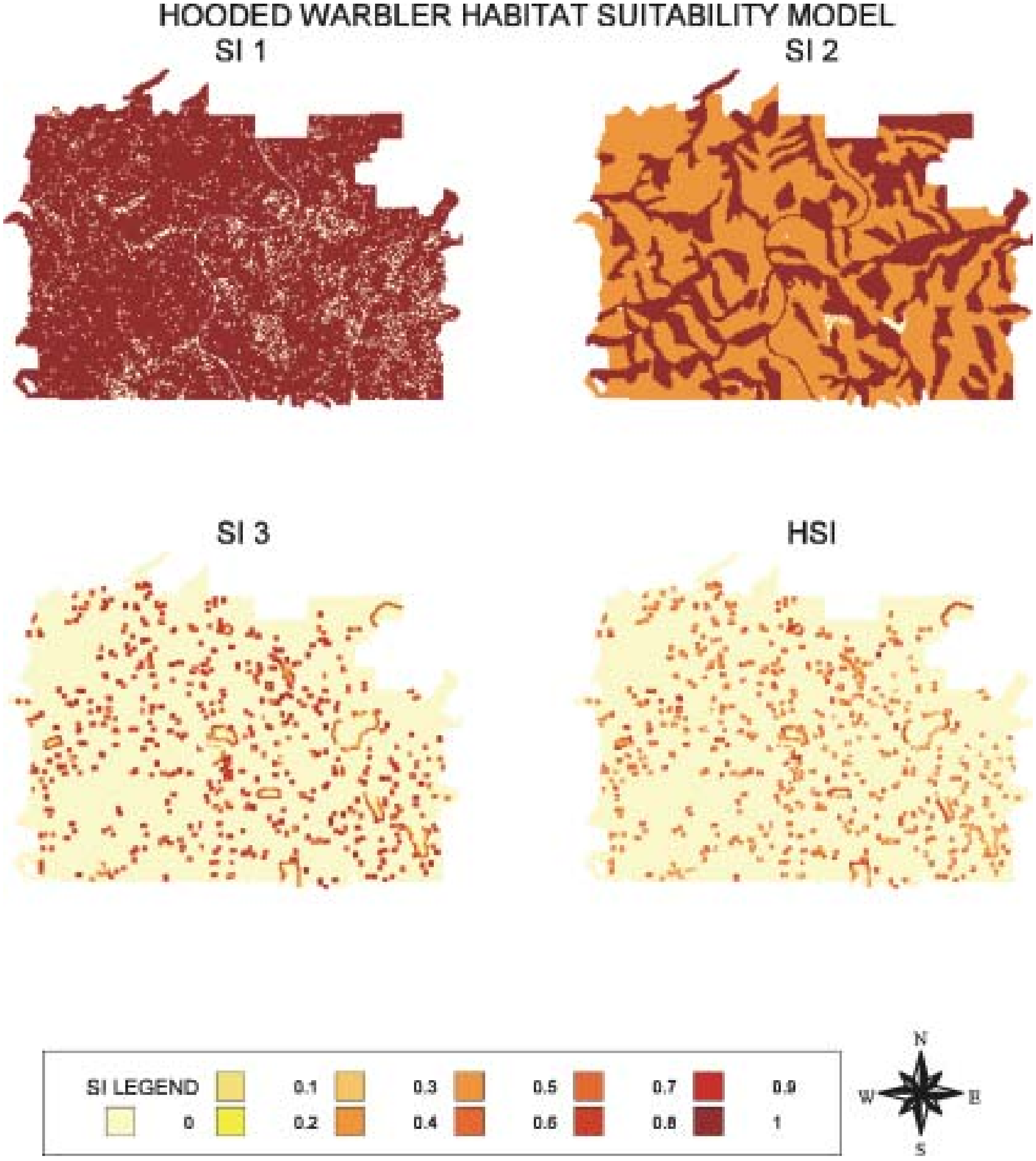


Figure 13.—*Application of the hooded warbler HSI model to a 3,261-ha unit of the Mark Twain National Forest in southern Missouri. There are separate images for suitability as deciduous forest* (SI_1)*, suitability of land types* (SI_2)*, suitability of composition of young and mature forest in adjacent cells* (SI_3)*, and* $HSI = SI_1 \times (SI_2 \times SI_3)^{0.5}$.

pines >30 years old. Violation of that assumption would result in our model overestimating the quantity and quality of pine warbler habitat.

Wild Turkey

The wild turkey is a popular game bird throughout its range. Schroeder (1985) developed an HSI model for wild turkeys as a function of summer–brood habitat and seasonal foods. Winter home ranges of turkeys in Arkansas were smaller when acorns, a significant food source, were more abundant (Badyaev *et al*. 1996). Relative abundance of wild turkeys in a predominantly forested area of southwestern New York was related positively with proportion of open land, edge density, and interspersion determined using satellite imagery of landscape cover types (Glennon and Porter 1999). Badyaev (1995) and Thogmartin (1999), however, found that nesting females in Arkansas selected large patches of habitat and avoided areas with high edge density. They selected nest sites in clearcuts and other forest openings and in pine stands with a hardwood understory (Badyaev 1995). The age of forests also affects their use by wild turkeys. Roost sites were associated with older pine and pine–hardwood stands in

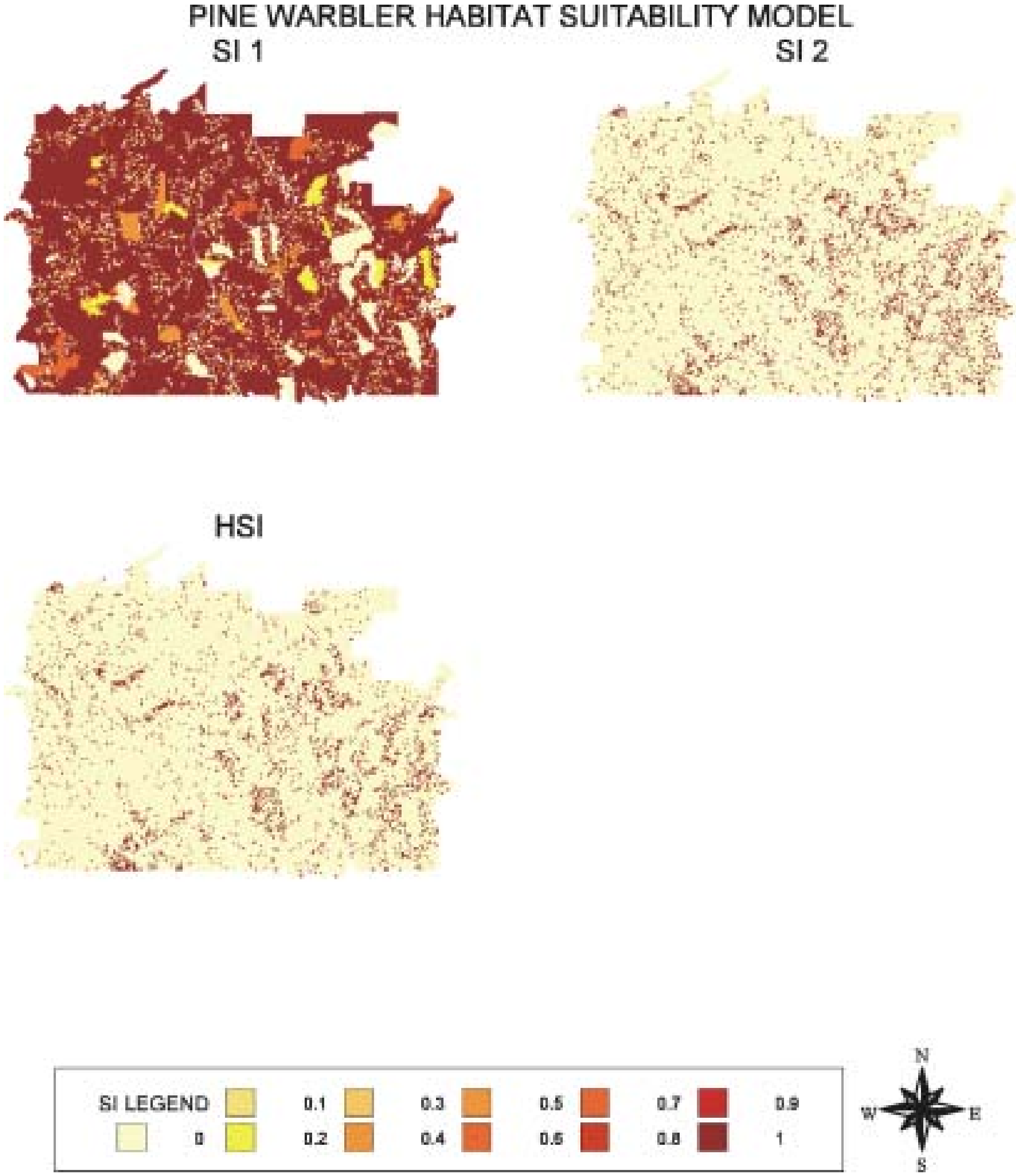


Figure 14.—*Application of the pine warbler HSI model to a 3,261-ha unit of the Mark Twain National Forest in southern Missouri. There are separate images for suitability as mature forest (SI_1), suitability as coniferous forest (SI_2), and HSI = SI_1 x SI_2.*

Mississippi (Chamberlain *et al.* 2000). Adult males in the Ouachita Mountains of Arkansas selected forest stands >40 years old during spring, and adult females selected them during all seasons (Wigley *et al.* 1986). In central Mississippi, turkeys of both sexes selected pines ≥30 years old and hardwoods >40 years old (Miller *et al.* 1999). Radio-tracking locations also indicated an avoidance of stands approximately 15 to 35 years old. Miller *et al.* (2000) built statistical models of sex- and season-specific habitat selection from much of the same radio-tracking data.

Our HSI model was based largely on the interspersion of habitat for nesting and brood-rearing and habitat for adults. We defined glades and areas with young trees as being the highest quality nesting and brooding habitat (SI_1; table 4, fig. 2). More mature forest also provided nesting and brooding habitat, but its quality was less than young forest. In our model, adult habitat was the arithmetic mean of variables for cover provided by mature trees (SI_2; table 4) and hard mast production for fall and winter food (SI_3; fig. 5). The fourth SI was a composition index to account for the interspersion of high quality nesting and brood-rearing habitat and adult habitat within a home range-sized moving window (102 ha [19-cell radius circle]; table 1). Presence of the requisites was designated as code=1 if $SI_1 \geq 0.5$, code=2 if $[(SI_2 + SI_3) / 2] \geq 0.25$, code=3 if inequalities for both requisites were satisfied, and code=0 otherwise. The suitability threshold for adult cover was 0.25 because in terms of interspersion, a cell was considered good adult habitat if either $SI_2 \geq 0.5$ or $SI_3 \geq 0.5$. Values of SI_4 declined as proportions of window area deviated from an ideal of 15 percent nesting and brood cover and 85 percent adult food and cover (i.e., $SI_4 = \{[1 - |(\text{proportion of cells with } SI_1 \geq 0.5) - 0.15|] \times [1 - |(\text{proportion of cells with } [SI_2 + SI_3] / 2 \geq 0.25) - 0.85|]\}^2$) (Schroeder 1985). If values of $SI_1 \geq 0.5$ or $[SI_2 + SI_3] / 2 \geq 0.25$ were absent in the window, $SI_4 = 0$ (table 8).

The HSI score was the geometric mean of composition (SI_4) and the maximum of nesting and brood cover (SI_1) and adult habitat ($[SI_2 + SI_3] / 2$) (table 6). The presence of large patches of high quality nesting and brood cover in the eastern half of the study area resulted in relatively higher interspersion–composition values (SI_4), whereas high quality nesting and brood rearing patches in the west were too small to constitute a sufficient proportion of ideal home range areas (fig. 15). The map of HSI scores revealed high quality habitat in areas with high interspersion–composition values, especially in the northeast and south-central portions of the study area, and the influence of the individual life requisites elsewhere in the landscape.

Ruffed Grouse

The ruffed grouse is another popular game bird. Descriptions of its habitat differ between northern and southern portions of its range. In the north where aspens (*Populus* spp.) are a common component of forests, ruffed grouse rely on them as a primary winter food source. In the south where winters are less severe, ruffed grouse use a variety of winter foods, including acorns, multiflora rose (*Rosa multiflora*), and hophornbeam (*Ostrya virginiana*) (Korschgen 1966, Thompson and Fritzell 1986). The U.S. Fish and Wildlife Service HSI model for ruffed grouse, as originally developed, was heavily dependent on aspen as a winter food source, so it is not directly applicable to our

Table 8.—*Values of SI_4 based on the proportion of cells providing good nesting and brood-rearing habitat and adult habitat for wild turkeys in a home range-sized moving window (102 ha) in a southern Missouri landscape. Optimal proportions are 0.15 and 0.85, respectively*[a].

Proportion in nesting and brood habitat	Proportion in adult habitat										
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
0.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.1	0.00	0.06	0.11	0.18	0.27	0.38	0.51	0.65	0.81	0.81	
0.2	0.00	0.06	0.11	0.18	0.27	0.38	0.51	0.65	0.81		
0.3	0.00	0.05	0.09	0.15	0.22	0.31	0.41	0.52			
0.4	0.00	0.04	0.07	0.11	0.17	0.24	0.32				
0.5	0.00	0.03	0.05	0.09	0.13	0.18					
0.6	0.00	0.02	0.04	0.06	0.09						
0.7	0.00	0.01	0.02	0.04							
0.8	0.00	0.01	0.02								
0.9	0.00	0.00									
1.0	0.00										

[a] $SI_4 = \{[1 - |(\text{proportion of cells with } SI_1 \geq 0.5) - 0.15|] \times [1 - |(\text{proportion of cells with } (SI_2 + SI_3 / 2) \geq 0.25) - 0.85|]\}^2$.

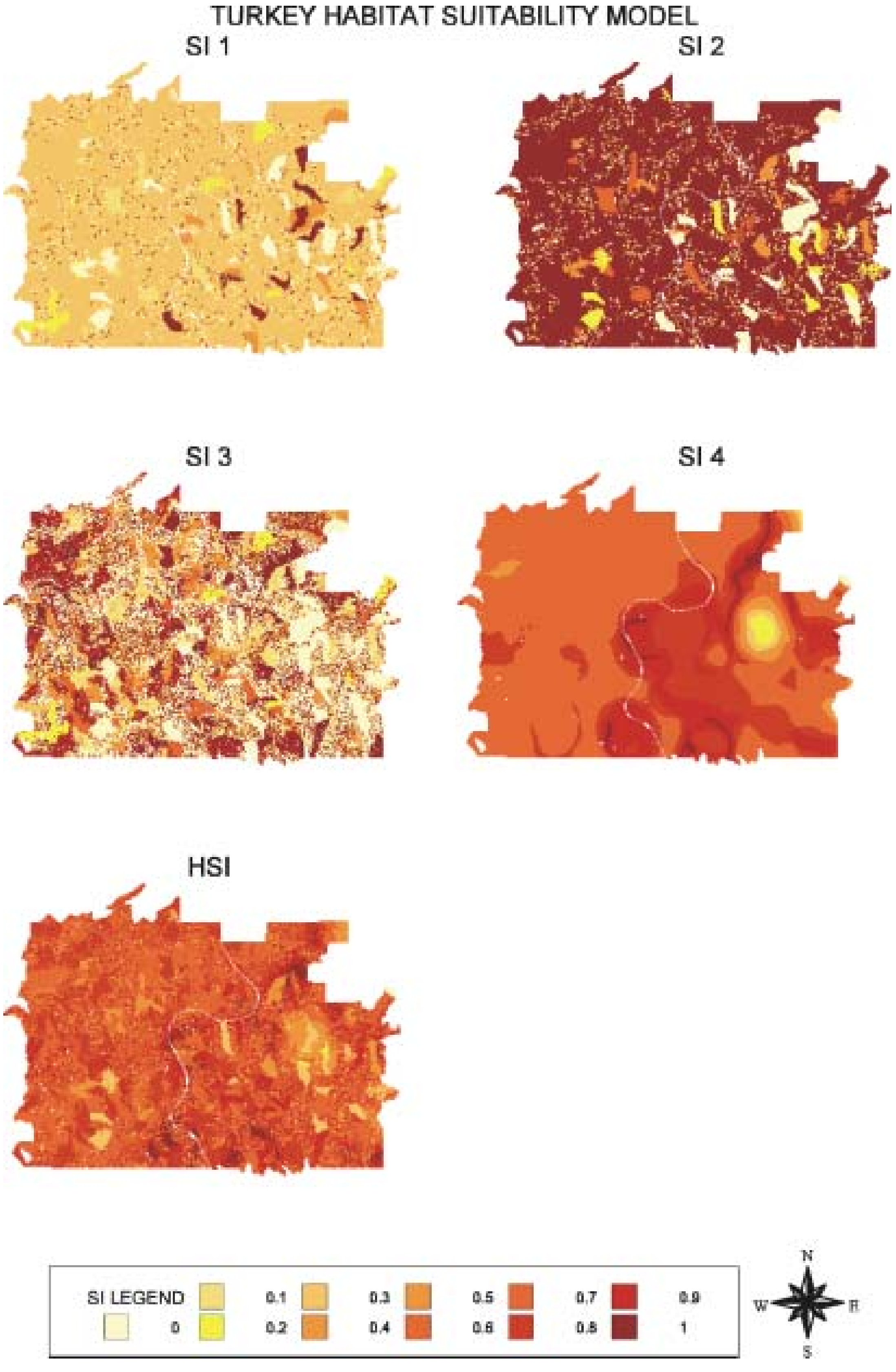


Figure 15.—*Application of the wild turkey HSI model to a 3,261-ha unit of the Mark Twain National Forest in southern Missouri. There are separate images for suitability as nesting and brood-rearing cover (SI_1), suitability as mature forest for adult cover (SI_2), suitability of hard mast production (SI_3), suitability of composition of previous SIs (SI_4), and* $HSI = (\max\{SI_1, [(SI_2 + SI_3) / 2]\} \times SI_4)^{0.5}$.

study area (Cade and Sousa 1985). Habitat quality for the other component of the model, fall-to-spring cover, was based on high stem densities. Hammill and Moran (1986) revised the model by Cade and Sousa (1985), and despite assuming winter food requirements would be met in the study area, they included a variable for interspersion of fall-to-spring cover and winter food. The high stem densities that provide cover for ruffed grouse are found in recently disturbed sites. Wiggers *et al*. (1992) found that 7- to 15-year-old hardwood regeneration was correlated with ruffed grouse density in Missouri. McDonald *et al*. (1998) found that ruffed grouse in central Pennsylvania used mixed oak sapling stands (i.e., trees <12.6 cm d.b.h.) more than expected and avoided mixed oak sawtimber stands (i.e., trees >28 cm d.b.h.). Gullion (1977, 1990) and Gullion and Svoboda (1972) recommended that both mature forest for winter foods and young forest for cover occur in a 4-ha area. Thompson and Dessecker (1997), however, indicated that habitat quality in the central hardwood region is also related to the size of cover patches, with larger being better. McDonald *et al*. (1998) observed seasonal grouse home ranges of 5.0–9.4 ha and suggested that 1-ha clearcuts in southern mixed oak forests could provide good grouse habitat. Observations in Missouri indicated home ranges of 16–100 ha (Thompson and Fritzell 1989, Wiggers *et al*. 1992), but presumably habitat of high quality would result in substantially smaller home ranges.

Our habitat model for ruffed grouse was similar to other models for this species in that winter food, provided by hard mast (SI_1; fig. 5), and cover, provided by forest <31 years old (SI_2; table 4, fig. 2), were main variables. Two additional variables defined spatial aspects of the model. Following the recommendation of Thompson and Dessecker (1997), we included a variable whose value was positively associated with the size of cover patches. We defined contiguous patches of cover (i.e., $SI_2 > 0$), and assigned a value of $SI_3 = 1$ for patches >1 ha in size and a value equal to the fraction of a hectare for patches <1 ha in size (fig. 16). The cover component of the model was a combination of tree age, land type, and patch size ($[SI_2 \times SI_3]^{0.5}$). The second spatial variable (SI_4) was a composition index to account for the interspersion of high quality food and cover in a moving window analysis. The window was the size of an ideal home range (17.7 ha = an 8-cell radius circle; table 1), and we assumed the ideal composition was 50 percent food and 50 percent cover (i.e., [proportion of cells with $SI_1 \geq 0.5$] x [proportion of cells with $(SI_2 \times SI_3)^{0.5} \geq 0.5$] x 4; table 9).

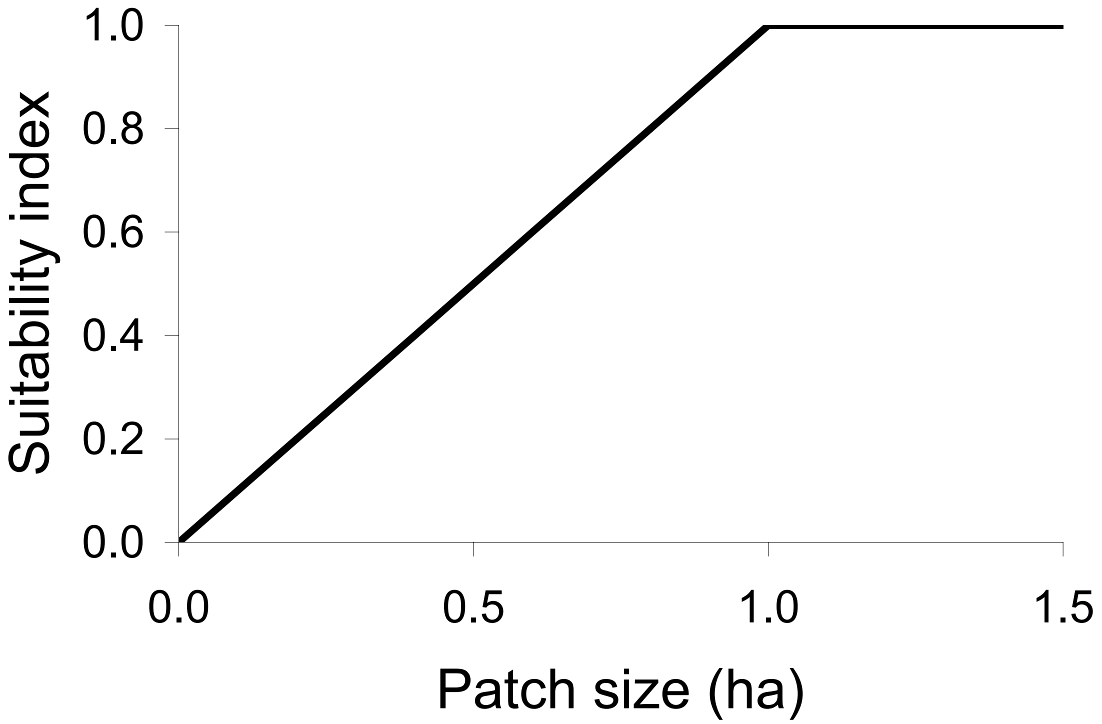


Figure 16.—*Suitability of habitat patches for ruffed grouse is positively related to patch size.*

Table 9.—*Values of* SI_4 *based on the proportion of cells providing hard mast and cover for ruffed grouse in a home range-sized moving window (4.4 ha) in a southern Missouri landscape. Optimal proportions are 0.5 for each requisite*[a].

Proportion providing hard mast	**Proportion providing cover**										
	0.0	**0.1**	**0.2**	**0.3**	**0.4**	**0.5**	**0.6**	**0.7**	**0.8**	**0.9**	**1.0**
0.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.1	0.00	0.04	0.08	0.12	0.16	0.20	0.24	0.28	0.32	0.36	
0.2	0.00	0.08	0.16	0.24	0.32	0.40	0.48	0.56	0.64		
0.3	0.00	0.12	0.24	0.36	0.48	0.60	0.72	0.84			
0.4	0.00	0.16	0.32	0.48	0.64	0.80	0.96				
0.5	0.00	0.20	0.40	0.60	0.80	1.00					
0.6	0.00	0.24	0.48	0.72	0.96						
0.7	0.00	0.28	0.56	0.84							
0.8	0.00	0.32	0.64								
0.9	0.00	0.36									
1.0	0.00										

[a] SI_4 = [proportion of cells with $SI_1 \geq 0.5$] x [proportion of cells with $(SI_2 \times SI_3)^{0.5} \geq 0.5$] x 4.

The HSI score was the geometric mean of composition and the maximum of either the hard mast or cover component (table 6). Locations providing interspersion of both life requisites in home range-sized areas limited overall habitat suitability in the study area (fig. 17). Furthermore, SI_3 appeared to adequately discount the quality of small patches of cover, reserving the highest HSI scores for areas near the edges of large cover patches that were adjacent to mature oak forest.

Gray Squirrel

Gray squirrels are dependent on hard mast for food more than any other species in our study (table 1). The link between hard mast availability and habitat quality for gray squirrels is well established (Gorman and Roth 1989, Gurnell 1983, McShea 2000, Nixon *et al*. 1975). Allen (1987) developed an HSI model for gray squirrels, and the main components were hard mast production and mature trees, which provide cavities for cover and reproductive habitat. Our HSI model for gray squirrels had the same structure. Rather than predict potential mast production from canopy cover of mast producing trees and number of hard mast species, we used our hard mast index (SI_1; fig. 5). We used the age of dominant trees in a cell as a surrogate variable for canopy cover and tree cavity availability (SI_2). The minimum age of trees that provided cover with suitability > 0 was 30 years (table 10, fig. 2). That was the approximate age at which trees in our study area achieved the cover-tree criteria explained in the U.S. Fish and Wildlife Service HSI model (i.e., ≥6 m in height and ≥12.7 cm d.b.h., Allen 1987). The minimum age of trees that provided cover with suitability = 1 was 101 years, and the tree age function between ages 30 and 100 was $SI_2 = 0.011 \times \text{age} - 0.222$ (table 10). Glades never provided cover or appropriate cavities, regardless of tree age, because we assumed trees would always be too sparse on glades.

The HSI score for gray squirrels was the minimum of the food and cover components (table 6). Hard mast production limited habitat quality throughout much of the study area (fig. 18). However, cover suitability was lower than food suitability in a few places on the flat and northeast slope land types containing white oaks ≤100 years old.

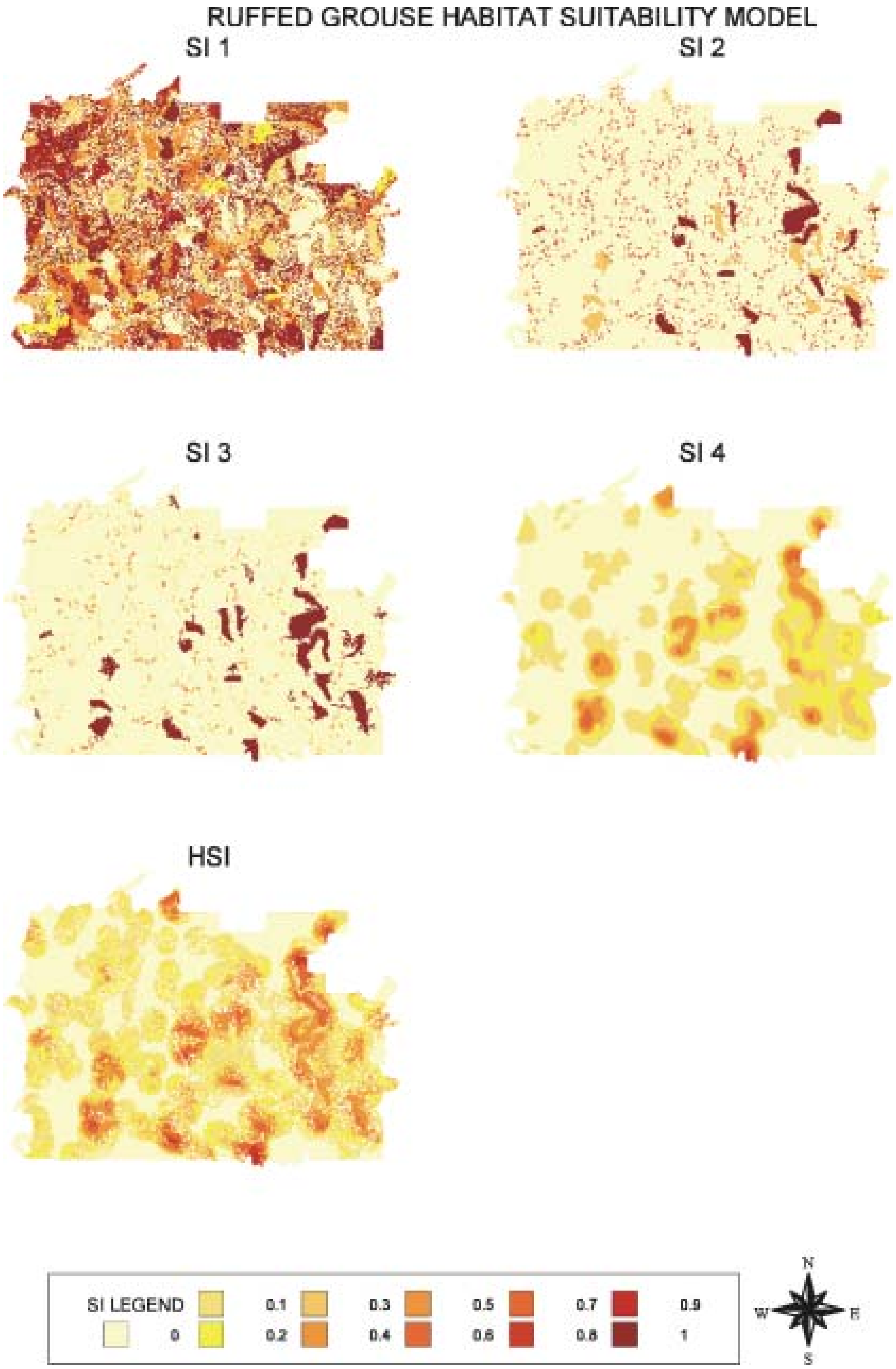


Figure 17.—*Application of the ruffed grouse HSI model to a 3,261-ha unit of the Mark Twain National Forest in southern Missouri. There are separate images for suitability of hard mast production (SI_1), suitability as early-successional forest (SI_2), suitability as large habitat patches (SI_3), suitability of composition of previous SIs (SI_4), and HSI = $\{max[SI_1, (SI_2 \times SI_3)^{0.5}] \times SI_4\}^{0.5}$.*

Table 10.—*Habitat suitability of forest by habitat requisite, land type*[a]*, and age of dominant overstory trees for five mammal and one amphibian species in southern Missouri*

Age of dominant trees (yr)	Gray squirrel		Black bear		Bobcat			Red bat	Northern long-eared bat		Southern redback salamander
	Glade	**Other**	**Glade**	**Other**	**Glade**	**Dry**	**Mesic**		**Foraging and roosting**	**Snags for roosting**	
0[b]	0.0	0.00	1.0	1.0	1.0	1.0	1.0	0.00	0.00	0.00	0.00
1–10	0.0	0.00	1.0	1.0	1.0	1.0	0.5	0.00	0.00	0.80	0.00
11–20	0.0	0.00	0.2	0.1	1.0	0.5	0.1	0.00	0.00	0.40	0.00
21–30	0.0	0.11	0.1	0.0	0.8	0.1	0.0	0.00	0.00	0.00	0.00
31–40	0.0	0.22	0.0	0.0	0.5	0.0	0.0	0.14	0.14	0.00	0.00
41–50	0.0	0.33	0.0	0.0	0.3	0.0	0.0	0.29	0.29	0.14	0.05
51–60	0.0	0.44	0.0	0.0	0.3	0.0	0.0	0.43	0.43	0.29	0.10
61–70	0.0	0.56	0.0	0.0	0.3	0.0	0.0	0.57	0.57	0.43	0.15
71–80	0.0	0.67	0.0	0.0	0.3	0.0	0.0	0.71	0.71	0.57	0.20
81–90	0.0	0.78	0.0	0.0	0.3	0.0	0.0	0.86	0.86	0.71	0.40
91–100	0.0	0.89	0.0	0.0	0.3	0.0	0.0	1.00	1.00	0.86	0.60
101–110	0.0	1.00	0.0	0.0	0.3	0.0	0.0	1.00	1.00	1.00	0.80
111–120	0.0	1.00	0.0	0.0	0.3	0.0	0.0	1.00	1.00	1.00	1.00
121–130	0.0	1.00	0.0	0.0	0.3	0.0	0.0	1.00	1.00	1.00	1.00
≥131	0.0	1.00	0.0	0.0	0.3	0.0	0.0	1.00	1.00	1.00	1.00

[a] Land type categories are described in table 3.

[b] Trees not present (e.g., failed regeneration after disturbance).

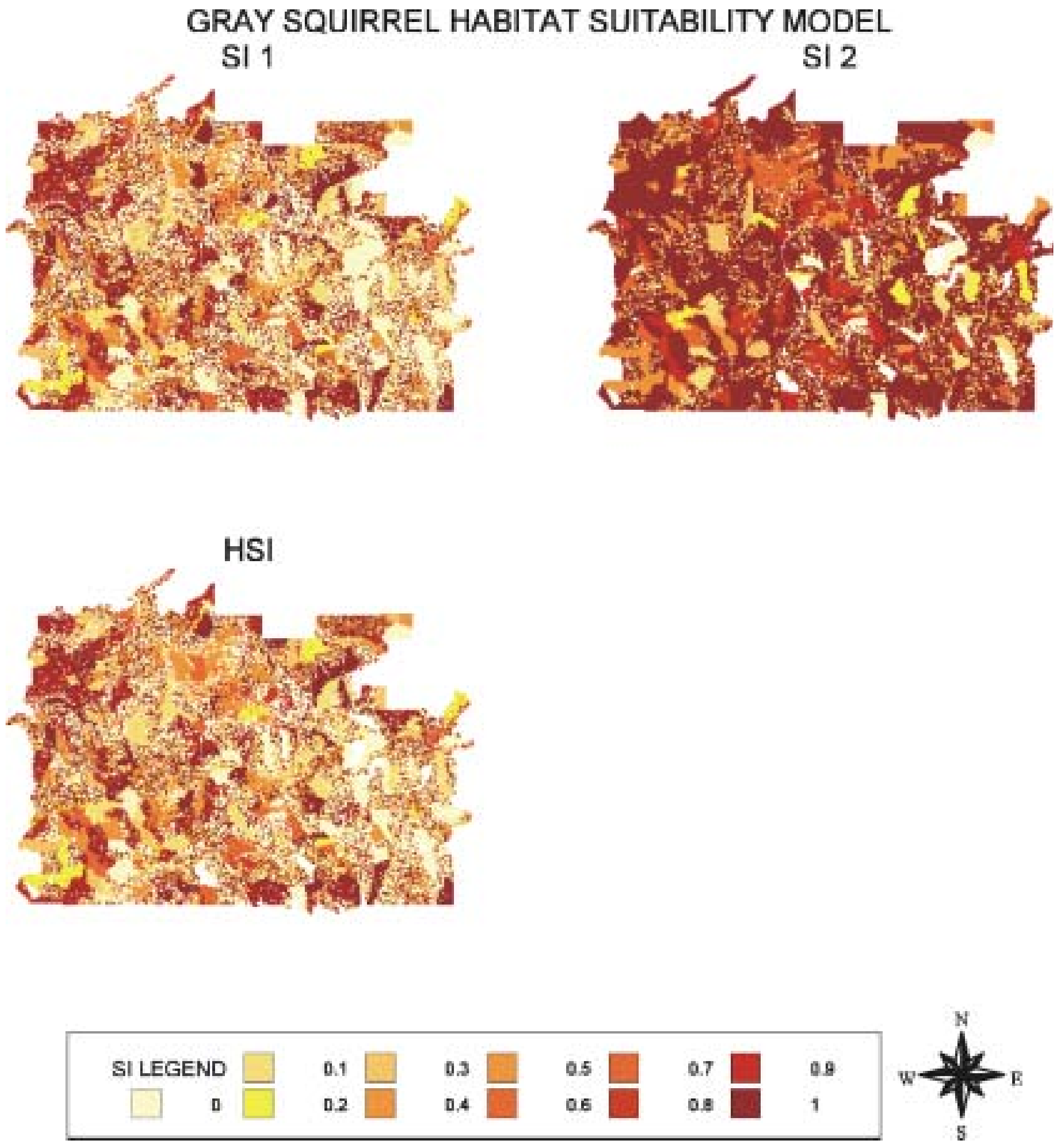


Figure 18.—*Application of the gray squirrel HSI model to a 3,261-ha unit of the Mark Twain National Forest in southern Missouri. There are separate images for suitability of hard mast production (SI_1), suitability as mature forest for cover (SI_2), and HSI = min(SI_1, SI_2).*

Black Bear

We selected black bears because they are the largest, widest ranging mammals in southern Missouri (table 1). Rogers and Allen (1987) developed an HSI model for black bears in the upper Great Lakes region. Their model incorporated wetland cover types for spring food, soft mast for summer food, hard mast for fall food, and avoidance of human influence. Although Rogers and Allen (1987) acknowledged that interspersion of food and cover resources contributed to habitat quality for bears, they did not include it in the model because data to establish a relationship were lacking and bears are highly mobile. Van Manen and Pelton (1997) developed logistic regression models of habitat use from radio-tracking locations of bears in Tennessee and randomly selected points. Models for males and females had the following GIS-based variables in common: overstory vegetation type, proximity to streams, aspect, proximity to improved roads, and proximity to human activity sites. Avoidance of pines (*Pinus* spp.) in favor of oak and oak-pine forests and avoidance of human influence appeared to have the strongest influence on habitat use of bears (Van Manen and Pelton 1997). Clark *et al*. (1993) also developed statistical models of black bear habitat use from GIS-based habitat variables.

Their radio-tracking data from Arkansas indicated that bears used poletimber classes of hardwood and hardwood-pine more than expected and northeastern aspects, flat terrain, and areas <240 m from roads and >600 m from streams less than expected.

We chose to use hard and soft mast foods, interspersion of areas producing them, and avoidance of roads as variables in our HSI model. Perennial streams were absent from our study site, and we considered slope aspect much less important to habitat quality than resource needs (Rogers 1987) and intolerance of human activity (Beringer 1986, Kerley *et al*. 2002, Linnell *et al*. 2000). Hard mast production based on tree species group, tree age, and land type was SI_1 (fig. 5). Our variable for soft mast production was based mainly on tree age (SI_2; table 10, fig. 2). Fantz and Hamilton (1997) documented high soft mast production in young clearcuts in southern Missouri, substantially lower production in stands 7 to 10 years old, and minimal production in stands without disturbance for >40 years. Others have found similar relationships (Perry *et al*. 1999, Stransky and Roese 1984). The third SI was a composition index that accounted for the presence of potential hard and soft mast production within a home range-sized area (20 km^2 = 84-cell radius circle; table 1). The values of SI_1 and SI_2 had to be ≥0.5 to be included in the moving window analysis. The ideal proportions were 70 percent hard mast and 30 percent soft mast because fall foods are more critical to reproductive success (Elowe and Dodge 1990) and more alternative foods are available during summer. Values of SI_3 declined as proportions deviated from that ideal according to the following equation:

$$SI_3 = ([1 - |(\text{proportion of cells with } SI_1 \geq 0.5) - 0.7|] \text{ x } [1 - |(\text{proportion of cells with } SI_2 \geq 0.5) - 0.3|])^2.$$

If values of $SI_1 \geq 0.5$ or $SI_2 \geq 0.5$ were absent in the window, $SI_3 = 0$ (table 8). Research on black bear dens indicated that they are ≥0.3 – 0.8 km from roads and ≥1.0 – 3.4 km from human activity (Linnell *et al*. 2000, Tietje and Ruff 1983). Therefore, the value of SI_4 increased linearly from 0 when a cell was ≤0.2 km from a road to 1 when a cell was ≥1 km from a road (fig. 19).

The HSI value for a cell was the geometric mean of the greater of summer or fall food and interspersion multiplied by the road avoidance variable (table 6). Large patches conducive to soft mast production resulted in slightly greater

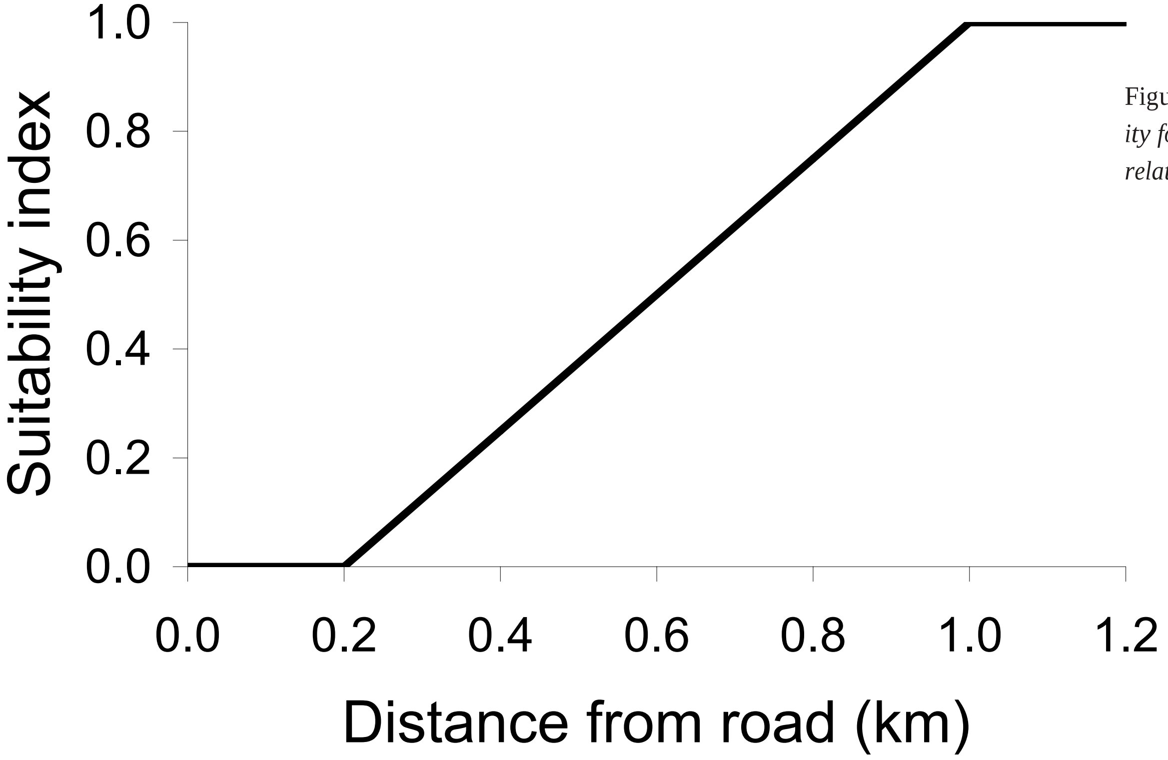


Figure 19.—*Habitat suitability for black bears is positively related to distance from roads.*

values for interspersion in the eastern quarter of the study area (fig. 20). The HSI scores, however, were slightly greater in the western part of the study area where more forest patches had high mast production.

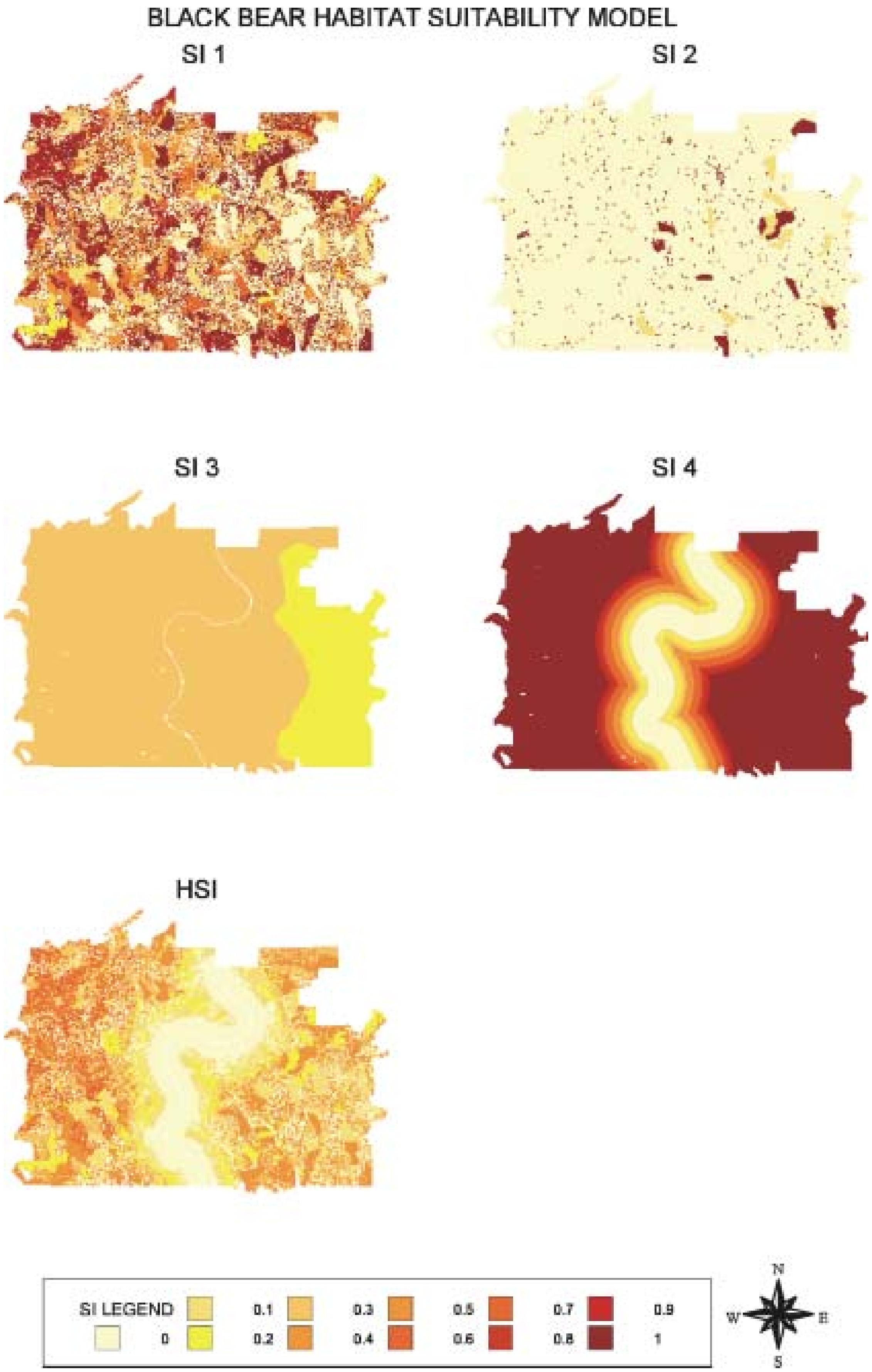


Figure 20.—*Application of the black bear HSI model to a 3,261-ha unit of the Mark Twain National Forest in southern Missouri. There are separate images for suitability of hard mast production (*SI_1*), suitability of soft mast production (*SI_2*), suitability of composition of hard and soft mast production (*SI_3*), suitability as distance from roads (*SI_4*), and* $HSI = [\max(SI_1, SI_2) \times SI_3]^{0.5} \times SI_4$.

Table 11.—*Values of SI_3 based on the proportion of cells providing good hard mast and soft mast foods for black bears in a home range-sized moving window (20 km^2) in a southern Missouri landscape. Optimal proportions are 0.7 and 0.3, respectively*[a].

Proportion providing fall and winter food	Proportion providing soft mast										
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
0.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.1	0.00	0.10	0.13	0.16	0.13	0.10	0.08	0.06	0.04	0.03	
0.2	0.00	0.16	0.20	0.25	0.20	0.16	0.12	0.09	0.06		
0.3	0.00	0.23	0.29	0.36	0.29	0.23	0.18	0.13			
0.4	0.00	0.31	0.40	0.49	0.40	0.31	0.24				
0.5	0.00	0.41	0.52	0.64	0.52	0.41					
0.6	0.00	0.52	0.66	0.81	0.66						
0.7	0.00	0.64	0.81	1.00							
0.8	0.00	0.52	0.66								
0.9	0.00	0.41									
1.0	0.00										

[a] $SI_3 = ([1 - |(\text{proportion of cells with } SI_1 \geq 0.5) - 0.7|] \times [1 - |(\text{proportion of cells with } SI_2 \geq 0.5) - 0.3|])^2$.

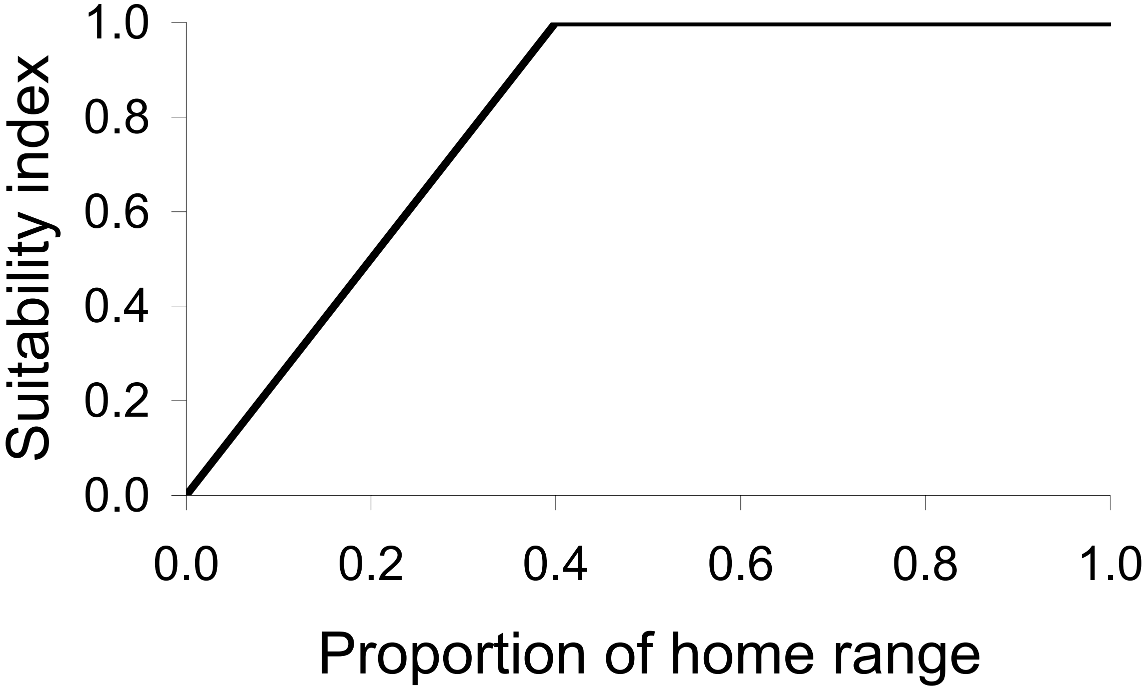
Bobcat

The bobcat is a furbearer whose distribution and abundance are stable or increasing in Missouri (D. Hamilton, Missouri Department of Conservation, personal communication). The most important aspect of bobcat habitat is prey availability (Boyle and Fendley 1987). Primary prey are small mammals, such as lagomorphs (e.g., *Sylvilagus* spp.) and rodents (e.g., *Sciurus* spp., *Sigmodon hispidus*, *Microtus* spp.) (Erickson 1981, Fritts and Sealander 1978, Korschgen 1957). Boyle and Fendley (1987) provided many citations indicating that grassy and shrubby openings, including forest clearcuts, are the best prey producing areas in the Southeastern United States. Bobcats in southeastern Missouri preferred brushy fields and forest regeneration most and agricultural crops, cool season grasslands, and oak–pine forest least (Hamilton 1982). Bobcats in southeastern Oklahoma also preferred grassy and brushy cover types (Rolley and Warde 1985). Preferred forest ages in Arkansas were 0- to 20-year-old regeneration and mature hardwood stands (Rucker *et al*. 1989). Bobcats in Illinois (Nielsen and Woolf 2002, Woolf *et al*. 2002) and Wisconsin (Lovallo and Anderson 1996a, b) either showed no preference for or avoided unforested areas and selected forested areas with low road densities.

The U.S. Fish and Wildlife Service HSI model for bobcats in the Southeastern United States was simply a function of equivalent food value, calculated as the weighted mean of an SI based on grass and forb-shrub vegetation across land cover types in a home range-sized area (Boyle and Fendley 1987). Another habitat quality model for bobcats in the Southeast was based on food, cover, and reproductive requirements within a land cover type and the distance between land cover types (Lancia *et al*. 1982). Burch and Nichols (1997) developed a GIS-based HSI model for bobcats in a unit of the Wayne National Forest in Ohio. Their model was a function of SIs for food, using specific habitat preferences of prey species, and cover/reproduction based on the presence of forest and brush.

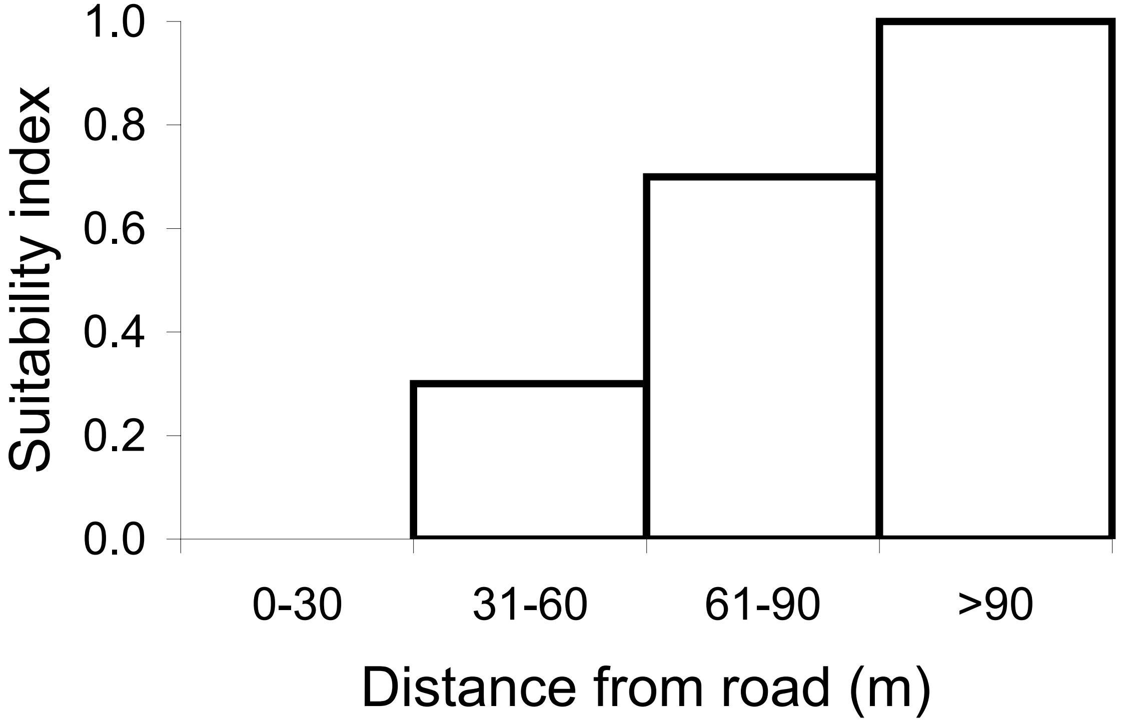
Our HSI model for bobcats included a food variable similar to the one used by Boyle and Fendley (1987) and a road disturbance variable. We assumed that escape, thermal, and reproductive cover requirements would be met throughout our study area. SI_1 was calculated in two

Figure 21.—*Habitat suitability for bobcats is positively related to proportion of home range area consisting of prey-producing habitat.*



steps. First, we assigned cells a value between 0 and 1 based on tree age and land type (table 10, fig. 2) to indicate high prey production in forests <20 years old and glades. Then we conducted a moving window analysis to assign an SI_1 value to the central window cell based on the mean within the window of cell values from the previous step. The window was a 59-cell radius circle (9.8 km^2; table 1) based on observed home ranges of 1–60 km^2 (Conner *et al*. 1999, Hamilton 1982, Kitchings and Story 1979, Miller 1980, Rucker *et al*. 1989). Ideally, 40 percent of an area should be in optimal prey habitat (Boyle and Fendley 1987), so our SI_1 relationship increased linearly from the origin to a value of 1 when the mean in the window was 0.4 (fig. 21). Lovallo and Anderson (1996b:71) suggested that "in general, areas ≤100 m from roads contained less preferred bobcat habitat than roadless areas," so SI_2 increased from 0 at a road edge to 1 at distances >90 m (fig. 22).

Figure 22.—*Habitat suitability for bobcats is positively related to distance from roads.*



The HSI score was a product of the two SIs (table 6), rather than a geometric mean, because road disturbance reduced habitat quality, but roads did not constitute a resource needed by bobcats. Large patches of young forest (fig. 2) resulted in slightly greater prey habitat quality in the eastern part of the study area (fig. 23). Even there, however, optimal prey habitat constituted <10 percent of home range-sized areas, which severely limited overall habitat suitability for bobcats.

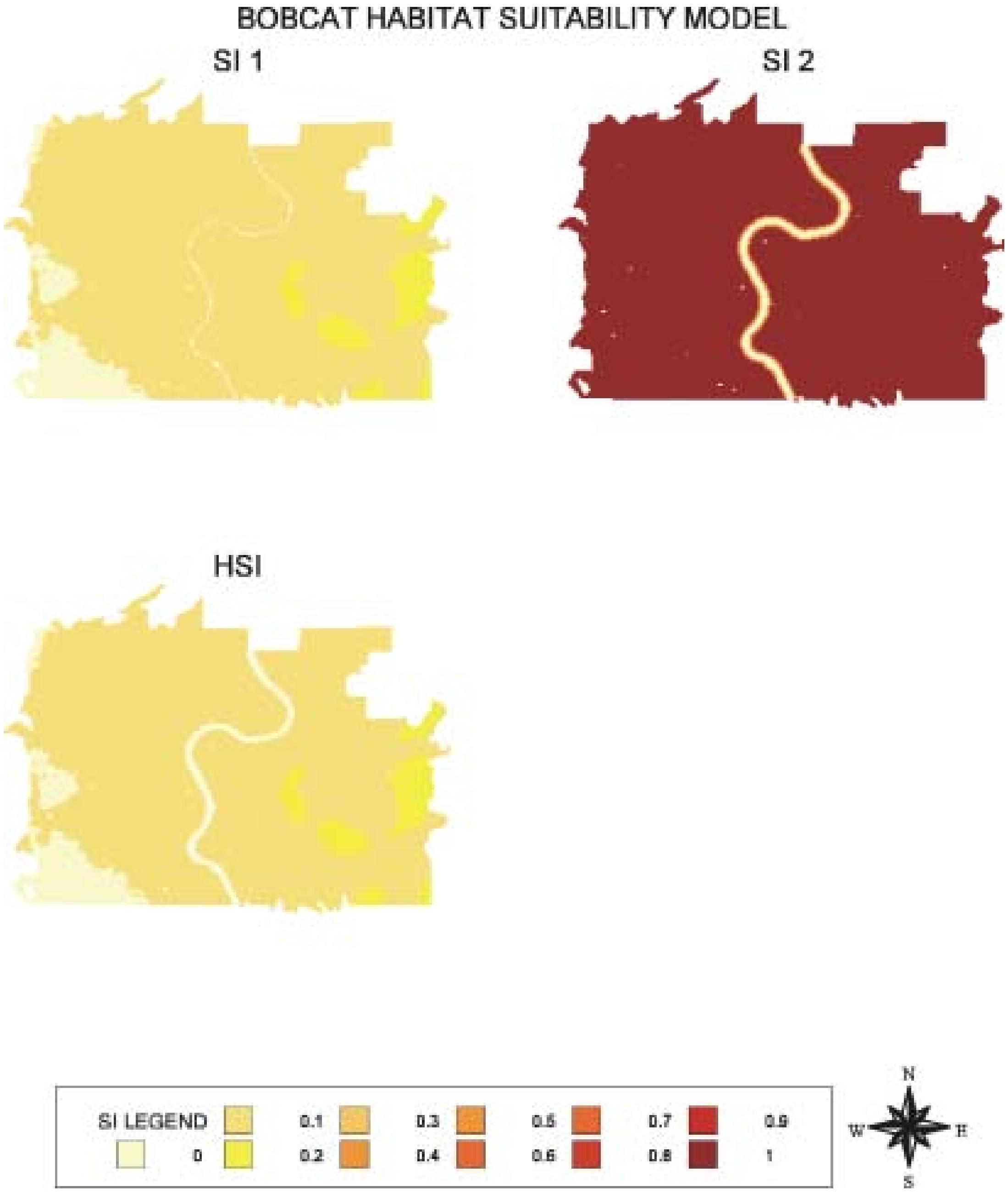


Figure 23.—*Application of the bobcat HSI model to a 3,261-ha unit of the Mark Twain National Forest in southern Missouri. There are separate images for suitability as high proportion of early-successional forest or openings (SI_1), suitability as distance from roads (SI_2), and HSI = SI_1 x SI_2.*

Red Bat

The red bat is a solitary, foliage-dwelling bat that is common in Missouri (LaVal and LaVal 1979). It is migratory and therefore rare in Missouri during winter (Schwartz and Schwartz 1981, Shump and Shump 1982). Primary non-winter habitat components are roosting sites, foraging areas, and water (Kurta 2001). Red bat day roosts in eastern Kentucky and two sites in South Carolina occurred in trees that averaged 18.5–25 m tall and 38–41 cm d.b.h. in stands with relatively low tree densities (Hutchinson and Lacki 2000, Menzel *et al*. 1998), which are characteristics consistent with mature forests. Roost trees in Kentucky were on upper slopes <500 m from water (Hutchinson and Lacki 2000). Red bats forage for a variety of insects around and above the canopy of trees (LaVal and LaVal 1979, Shump and Shump 1982). Much is still unknown about the habitat needs of red bats.

Our model of non-winter habitat quality for red bats consisted of a roosting component and a foraging component. The roosting component was a geometric mean of three variables. The quality of roost trees increases with age (SI_1; table 10, fig. 2). It is highest on sloping terrain ($SI_2 = 1$ on southwest and northeast side slopes), and red bats are almost never observed roosting on ridge tops ($SI_2 = 0$ on flats, and $SI_2 = 0.5$ otherwise). Roost quality declines >0.75 km from surface water (SI_3, figs. 2 and 24) because red bats often travel directly from their roosts to drink (S.K. Amelon, USDA Forest Service, personal communication). The foraging component of the model consists of trees of an appropriate age (SI_1; table 10), presumably near an opening, where the forest edge provides a travel lane and flight around the canopies of trees is less restricted than in contiguous forest. We defined high quality foraging areas using moving windows of two different sizes—0.8 ha (3 x 3 cells) and 13.8 ha (7-cell radius circle)—representing preferred distance to edge (30 m) and the size of the largest clearcut used for foraging, respectively (S. K. Amelon, USDA Forest Service, personal communication). Using the smaller window, we assigned the central cell $SI_4 = 1$ if the minimum value in the window was $SI_1 = 0$ and the maximum value was $SI_1 \geq 0.5$, indicating an edge between an opening and trees >60 years old; the central cell was $SI_4 = 0$ otherwise. Using the larger window, we assigned the central cell $SI_5 = 0.7$ if the minimum value in the window was $SI_1 = 0$ and the maximum value was $SI_1 \geq 0.5$; the central cell was $SI_5 = 0$ otherwise. The geometric mean for the foraging component weighted edge quality (i.e., maximum of SI_4 and SI_5) twice as much as tree age (table 6).

The HSI score was the maximum of the roosting and foraging components (table 6). We did not include a variable for interspersion between roost sites and foraging areas because we assumed

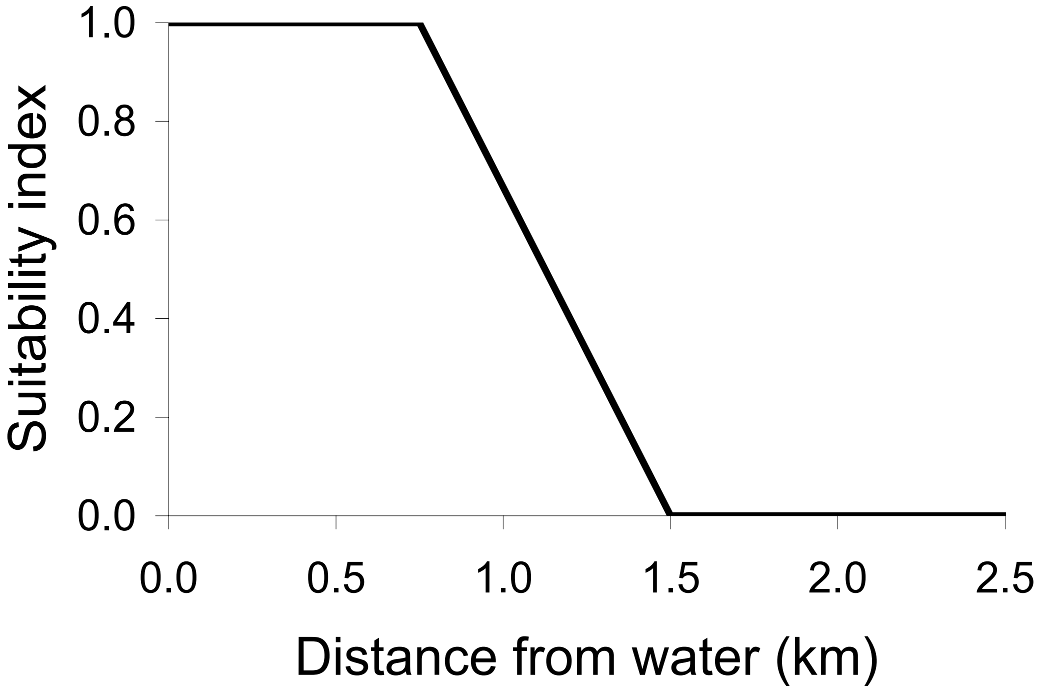


Figure 24.—*Habitat suitability for red bats is negatively related to distance from water.*

suitable roosts were available ≤8 km from all foraging areas. The highest quality roost sites near ponds on the west side of the study area were evident in the HSI map (fig. 25). The quality of foraging habitat, however, was generally higher than the quality of roosting habitat throughout the study area, especially around the edges of both small and large forest openings.

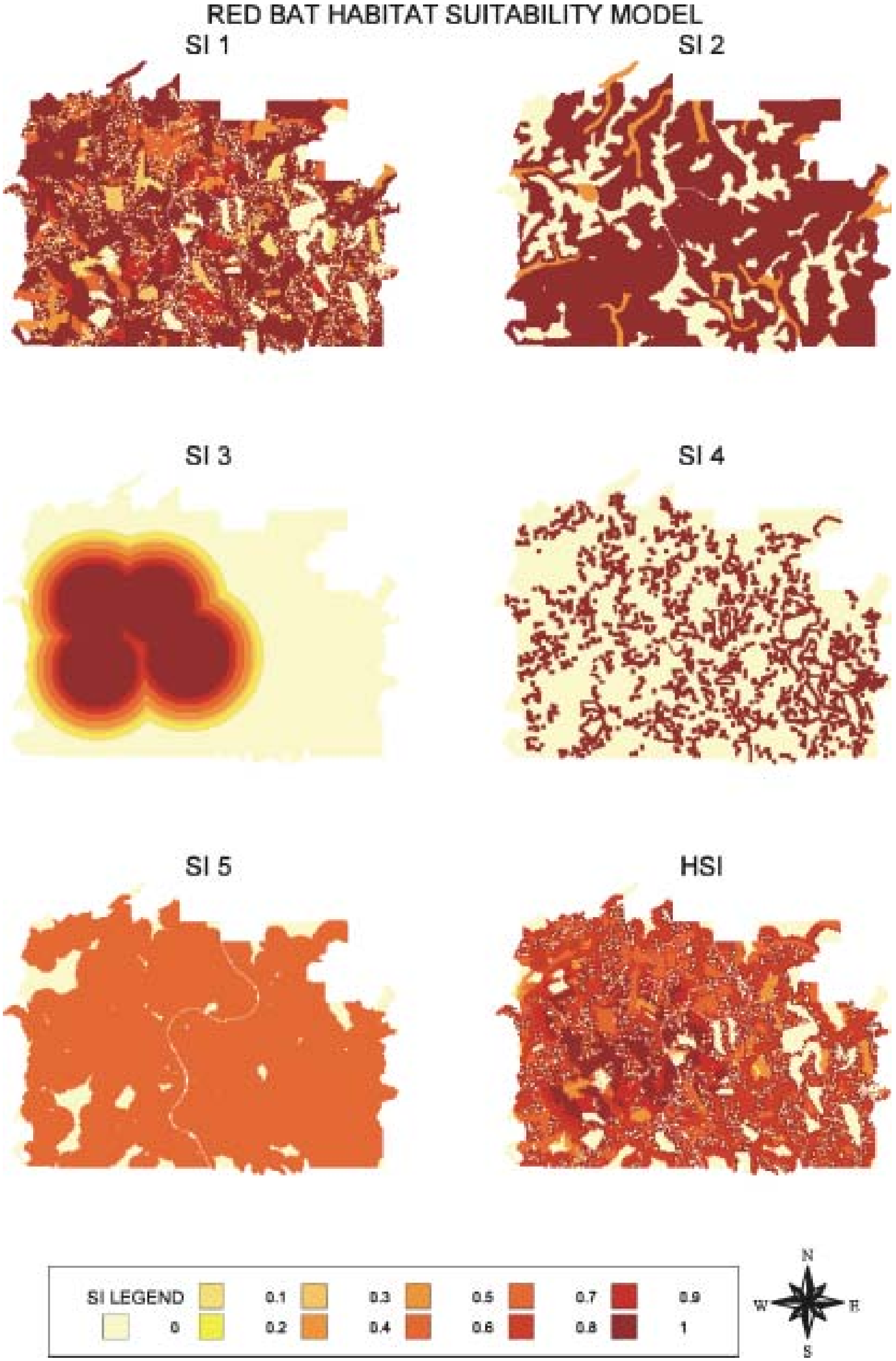


Figure 25.—*Application of the red bat HSI model to a 3,261-ha unit of the Mark Twain National Forest in southern Missouri. There are separate images for suitability as mature forest (SI_1), suitability of land types (SI_2), suitability as distance from water (SI_3), suitability as forest edge ($\max[SI_4, SI_5]$), and HSI = $\max[(SI_1 \times SI_2 \times SI_3)^{0.33}, (\{SI_1 \times [\max(SI_4, SI_5)]^2\}^{0.33})]$.*

Northern Long-Eared Bat

The northern long-eared bat, also called the northern bat and formerly considered an eastern subspecies of Keen's bat (Schwartz and Schwartz 1981), is a year-round resident of Missouri but hibernates in caves during winter. It is relatively rare and of conservation concern in Missouri (ranked S3 on The Nature Conservancy's [1992] 5-point endangerment scale [Missouri Natural Heritage Program 2001]), and it is considered to have some habitat requirements in common with the endangered Indiana bat (*Myotis sodalis*) (Callahan *et al.* 1997, Foster and Kurta 1999, Kurta *et al.* 1993). Primary non-winter habitat components are roosting sites, foraging areas, and water (Kurta 2001). Roost sites in Michigan were predominantly in large trees, approximately half of which were dead (Foster and Kurta 1999). Also, half of the roosts were under exfoliating bark, whereas the other half were inside hollows or crevices. Day roosts in Kentucky were in cavities and under bark of live and dead trees in forest stands with a higher mean d.b.h. than randomly selected stands (Lacki and Schwierjohann 2001). Northern bats forage in mature deciduous forest with small gaps (Cowan and Guiguet 1965 cited by Barbour and Davis 1969). Much is still unknown about the habitat needs of northern bats.

Our model of non-winter habitat quality for northern long-eared bats consisted of roosting, foraging, and interspersion components. The roosting component was a geometric mean of three variables. We modeled cavity availability in live trees as a function of tree age (SI_1, table 10, fig. 2). Snag availability, the second variable, increased with stand age (SI_2; table 10), but data from the USDA Forest Service Forest Inventory and Analysis program collected in Missouri in 1989 (Hansen *et al*. 1992, Miles *et al*. 2001) indicated that large snags are also available during the first two decades after stand-replacing disturbance. Third, we assumed that roosts needed to be within 2 km of water to be suitable because that was the longest distance observed between two roost trees used by the same bat (Foster and Kurta 1999) (SI_3, figs. 2 and 26). The foraging component was defined by tree age (SI_1) adjusted downward if the forest canopy was not near an edge (S.K. Amelon, USDA Forest Service, personal communication). We identified edges of mature forest using a moving window analysis on a GIS theme containing SI_1 values. The window was a 0.8-ha square (3 x 3 cells), assuming the bats prefer to forage within 30 m of a forest edge, and the central cell was assigned $SI_4 = 1$ if the minimum value in the window was 0; the value was $SI_4 = 0.8$ otherwise. We considered areas in which roost sites and foraging areas did

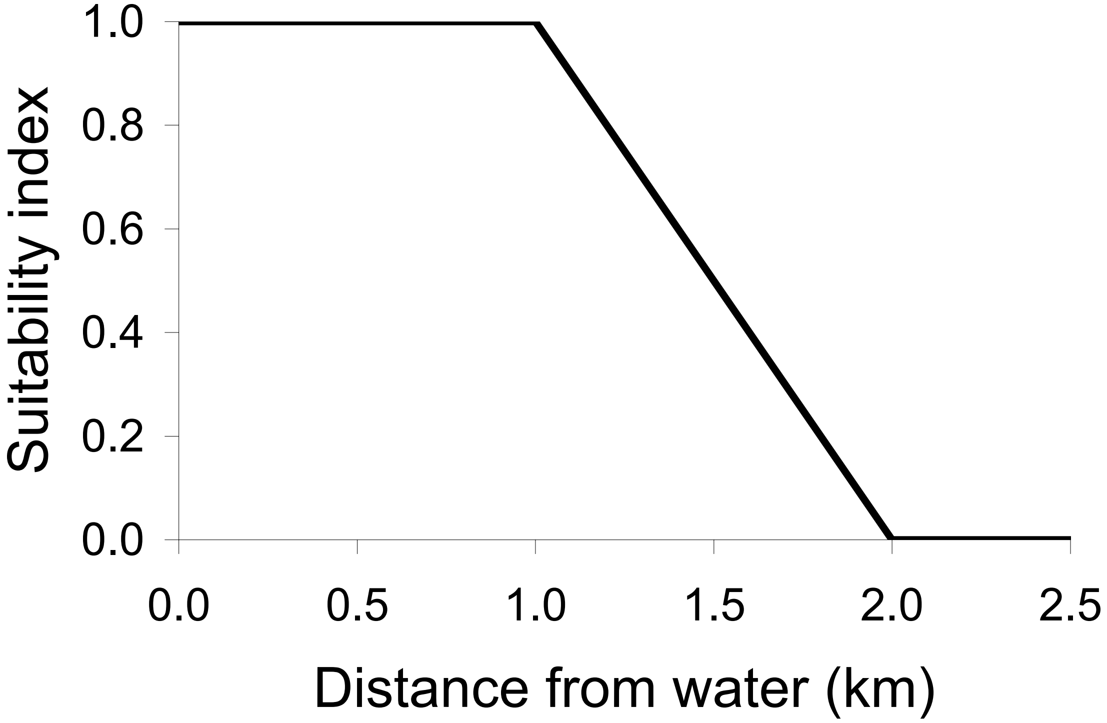


Figure 26.—*Habitat suitability for northern long-eared bats is negatively related to distance from water.*

not occur within a distance typically traveled by a bat during 1 night to be of low habitat quality. Our interspersion component was calculated using a moving window 2 km (67 cells) in radius (12.7 km^2; table 1) in which cells were coded 0 for the roosting component (i.e., if $[SI_1 \times SI_2 \times SI_3]^{0.33} > 0$), 3 for the foraging component (i.e., $SI_1 \times SI_4 > 0$), 2 if the inequalities for both requisites were satisfied, and 1 otherwise. The central cell of the moving window was $SI_5 = 1$ if both roosting and foraging components were present within the window (i.e., if the minimum coded value in the window was 0 and the maximum coded value was 3 or if any coded value in the window was 2). Otherwise, the central cell of the moving window was $SI_5 = 0$.

The HSI score was the geometric mean of the interspersion component and the maximum of the roosting and foraging components (table 6). The interspersion of roosting and foraging habitats was limited only on the extreme eastern edge of the study area by a lack of a nearby water source (fig. 27). Overall habitat quality was most influenced by foraging habitat except in the west where the quality of roosting habitat was high due to proximity of water.

Southern Redback Salamander

Species richness and abundance of salamanders vary with microhabitat characteristics that often correlate with forest age (Petranka *et al.* 1994). A literature review by deMaynadier and Hunter (1995) indicated that Plethodontid salamanders are more sensitive to clearcutting than other groups of amphibians. Characteristics such as their sensitivity to disturbance, longevity, and site fidelity make them good candidates for indicators of biodiversity and ecosystem integrity (Welsh and Droege 2001).

Gustafson *et al.* (2001) developed a GIS model to predict salamander abundance from terrestrial habitat information. Their model was based on site moisture (as a function of slope position and aspect) and stand age. We modified their model by simplifying the calculations and calibrating our tree age variable to salamander abundance data from southern Missouri (Herbeck and Larsen 1999). Habitat quality defined by tree age increased slowly from $SI_1 = 0$ between 40 and 80 years and then increased more rapidly to $SI_1 = 1$ by 111 years (table 10, fig. 2). We incorporated site moisture using land type categories (table 3), where mesic sites were $SI_2 = 1$, dry sites were $SI_2 = 0.5$, and glade sites were $SI_2 = 0$.

The HSI score was the geometric mean of the two variables because they interacted to describe combined food and cover requirements (table 6). Habitat suitability maps of the study area indicated broad patterns based on land types and patterns at a higher resolution based on tree age (fig. 28).

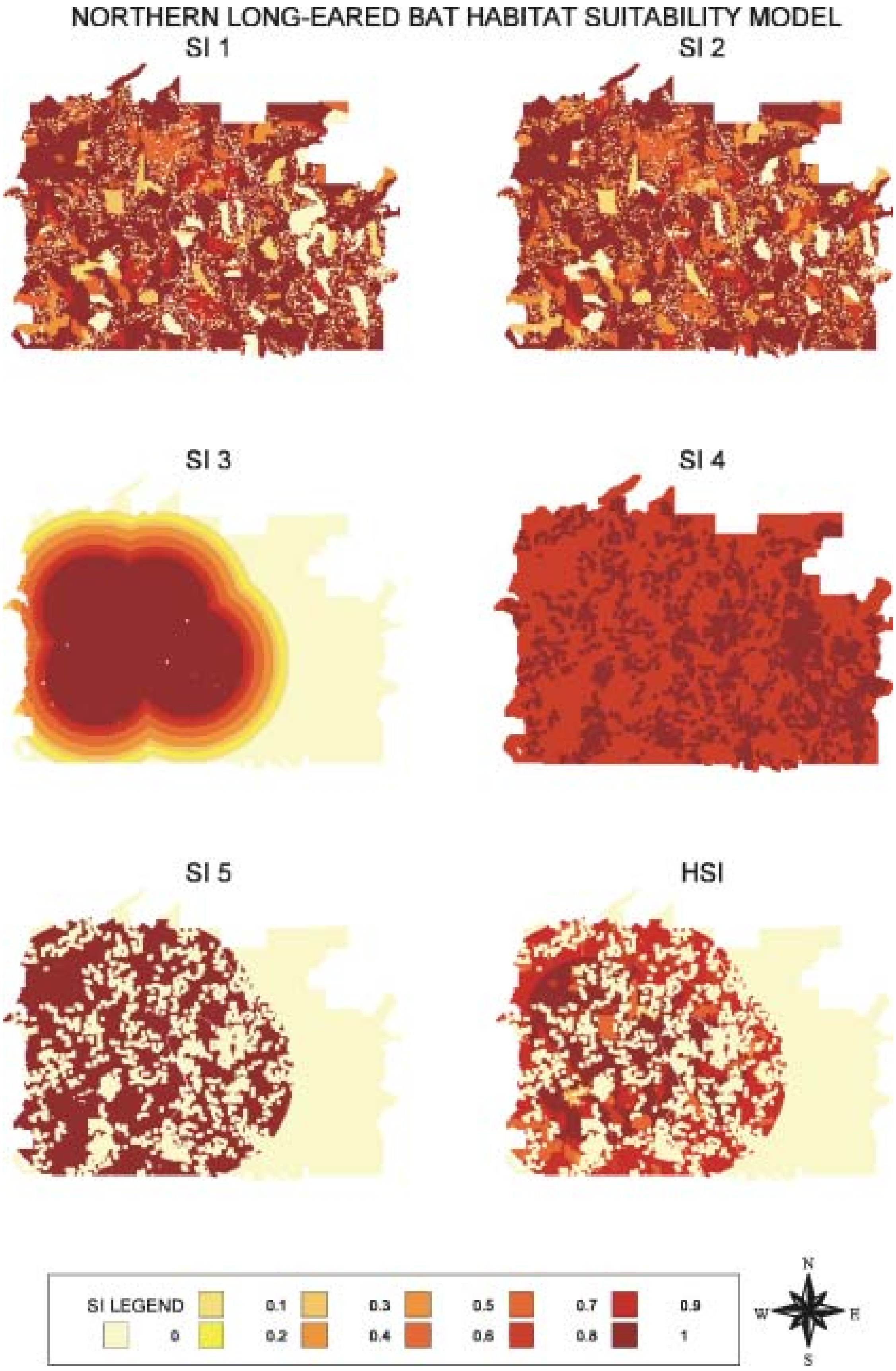


Figure 27.—*Application of the northern long-eared bat HSI model to a 3,261-ha unit of the Mark Twain National Forest in southern Missouri. There are separate images for suitability as mature forest for roosting and foraging* (SI_1)*, suitability of density of large snags for roosting* (SI_2)*, suitability as distance from water* (SI_3)*, suitability as forest gaps* (SI_4)*, suitability of interspersion of roost sites and foraging habitat* (SI_5)*, and* $HSI = \{\max[(SI_1 \times SI_2 \times SI_3)^{0.33}, (SI_1 \times SI_4)] \times SI_5\}^{0.5}$.

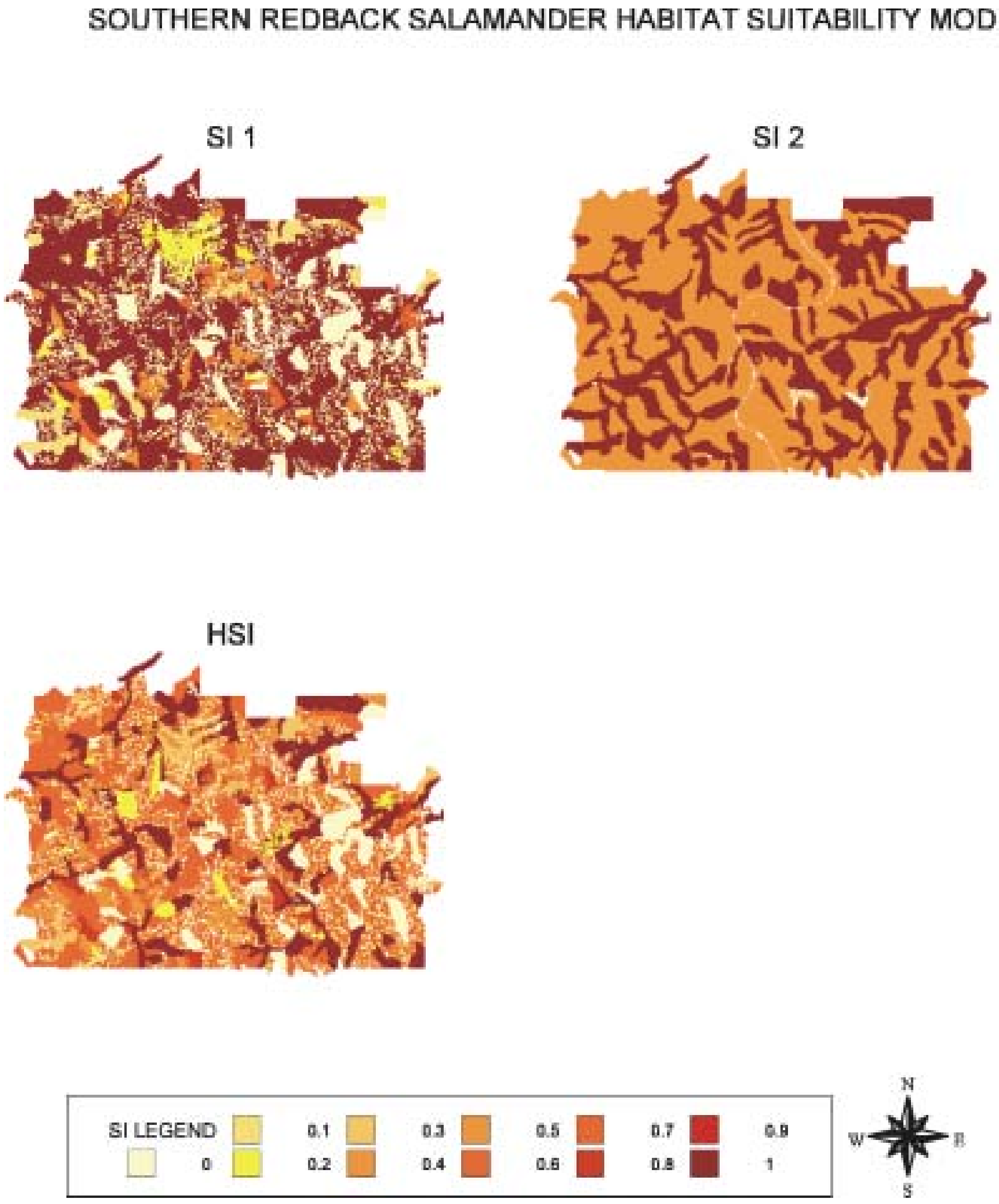


Figure 28.—*Application of the southern redback salamander HSI model to a 3,261-ha unit of the Mark Twain National Forest in southern Missouri. There are separate images for suitability as mature forest (SI_1), suitability of land types (SI_2), and HSI = $(SI_1 \times SI_2)^{0.5}$.*

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APPENDIX—Landscape Simulation

Program LANDIS

For demonstration purposes, we applied our HSI models to output from a LANDIS simulation of our study area. We simulated forest growth and disturbance for 100 years under a sustained long rotation harvest scenario (5 percent of land area affected each decade) with an equal mixture of even-aged and uneven-aged management. This resulted in a diverse landscape with large clearcuts, small forest gaps (~0.2 ha), and contiguous old growth.

LANDIS is a spatially explicit model of forest growth, succession, and disturbance in potentially large landscapes with a range of potential spatial resolutions (e.g., 300,000 map pixels, each of which is 0.01–100 ha in size) (He *et al*. 2000). We used a raster resolution of 30 m^2 (0.09 ha). LANDIS requires user specification of many parameters, including rates of tree establishment, growth, and mortality and sources, frequency, and intensity of disturbances. This provides flexibility in its application to different forest types in different geographic areas. We used the same model specifications that Shifley *et al*. (2000) used.

The presence of four tree species groups (i.e., white oak, red oak, maple, and pine) in decade-wide age classes was determined by several dynamic processes. LANDIS simulated tree establishment, growth, senescence, and disturbance due to wind, fire (He and Mladenoff 1999), and harvest. All simulated processes were at least partially dependent upon seven land type classifications (glade = glade; southwest side slope, flat, and limestone = dry; northeast side slope, upland drainage, and mesic = mesic; table 3). Initial conditions for the LANDIS simulations were specified based on forest inventory data from the Mark Twain National Forest.

Although >1 age class of >1 tree type could occur on a raster cell at any given time, we assumed forest characteristics were best represented by the oldest age class of the dominant tree type. Dominance was calculated as the age of the oldest trees present within a tree type divided by the longevity of that tree type. For example, 50-year-old pines with a longevity of 250 years were dominant to 60-year-old white oaks with a longevity of 400 years.

Larson Michael A.; Dijak, William D.; Thompson, Frank R., III; Millspaugh, Joshua J.
2003. **Landscape-level habitat suitability models for twelve species in southern Missouri**. Gen. Tech. Rep. NC-233. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station. 51 p.

Describes GIS-based habitat suitability index models for twelve terrestrial vertebrate species in southern Missouri. Demonstrates model application to a simulated forest landscape.

KEY WORDS: Landscape, habitat suitability index model, GIS, vertebrates, Missouri.

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