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Regional habitat appraisals of wildlife communities: a landscape-level evaluation of a resource planning model using avian distribution data

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Abstract

A simple regional habitat model founded on the relation between vertical habitat complexity and species richness has been used to describe wildlife habitat in response to macroscale patterns in land use and land cover. While the model has a basis in ecological theory, it has not been subjected to rigorous testing. We evaluated the model's fundamental assumption on landscapes in the eastern forested region of the United States and found the model to be supported when we used a measure of avian community integrity during the breeding season. The model was improved by incorporating measures of horizontal heterogeneity, indicating that the vertical and horizontal structure of habitats should be considered in analyzing the response of wildlife to land resource policies that can affect broad land use patterns.

1. Introduction

Growing intensity of land use, increasing public interest in biological conservation, and legislated requirements for resource impact assessments demand the use of analytical tools for evaluating wildlife response to land management. Laws in the United States specify that land managing activities involving federal agencies must account for impacts to species. Much of the emphasis in developing wildlife resource planning models has been on single species. However, the number of wildlife species that can occur within a region casts doubt on whether modeling the autecological requirements of each inhabitant is feasible (Emlen and Pikitch 1989). Because it is unlikely that resource management objectives directed at maintaining biological diversity can be met solely through the analysis of single-species response models, habitat evaluation techniques that address wildlife communities need to be developed.

Extension of wildlife resource planning analyses to address species assemblages has been accompanied by a need to expand their geographic scope. Regional and national resource assessments have become a consideration as policy analysts and ecologists recognize the need to broaden the spatial and temporal scales of natural resource evaluations (Maurer 1985; Noon *et al.* 1985; Helle 1986; Hunter 1987; Knight 1987; Ricklefs 1987; Turner 1987; Swanson and Sparks 1990). While the call for a broader geographic perspective in environmental assessments (Klopatek *et al.* 1983) and resource planning (Klopatek *et al.* 1979; Sanderson *et al.* 1979) is not novel, the development of macroscale wildlife planning models has been limited by the

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availability of data to analyze large-scale resource policy questions (Hirsch *et al.* 1979; Flather and Hoekstra 1989).

Given that community-level and macroscale wildlife resource planning models are uncommon in and of themselves, their intersection is even less prevalent. Many community-level models have been developed to analyze specific plant communities that by definition examine community structure within a given locale (Schroeder 1987). Of those macroscale wildlife planning models that have been developed, most have focused solely on distribution or abundance patterns of a single species (Lennartz and McClure 1979; Sheffield 198 1; Klopatek and Kitchings 1985; Flather 1988; Walker 1990). Community or diversity properties at the scale of an entire landscape comprised of a mosaic of land types have not been the focus of much investigation (Istock and Scheiner 1987).

An exception to the above observations is a habitat structure model originally proposed by Short (1982; 1988) that associates wildlife species richness with the vertical complexity of habitats. An adapted form of the model (Streeter *et al.* 1983) was applied in a planning analysis of land use impacts on wildlife for a national appraisal of natural resources, as mandated by the Resources Conservation Act (1977; Public Law 95-192) (USDA 1989a, 1989b). While the ecological basis and the potential merits of the model have been described (Short 1988), the model has not been subjected to strict tests. Consequently, use of this model in resource planning has been limited by insufficient information on model performance and unquantified confidence in model-based evaluations of policy alternatives.

In this paper we state the fundamental assumption of the habitat structure model as a research hypothesis to be tested with both land base and wildlife data that are consistent with the scale of national policy questions. The results, in light of developing principles of landscape ecology, provide an indication of model reliability and form a basis for recommending modifications to refine its use in the decision-making process.

2. Methods

2.1. The habitat structure model and the fundamental assumption

The relationship between vegetation structure and animal community organization has received extensive empirical examination. It has been reasoned that more complex habitats offer a greater number of potential niches and therefore should support a greater variety of species (MacArthur *et al.* 1962). A common observation is a positive relation between vertical habitat complexity *(i.e.,* the number of strata within a habitat) and species diversity (MacArthur and MacArthur 1961; Recher 1969; Karr and Roth 1971; August 1983). However, vertical habitat complexity has not been found to be a general explanation for variation in animal species richness. Horizontal patchiness (Roth 1976; Wiens *et al.* 1987; Gerell 1988; Kotliar and Wiens 1990), floristics (Rotenberry 1985; MacNally 1990b), and climate (Inkley 1985; Owen 1990; Wiens 1991) also influence species richness patterns. In addition, the relative contribution of these factors has been observed to vary among habitats with basic physiognomic differences (grassland vs. forests, Wiens 1989).

Based on the empirical findings relating vegetation physiognomy to species richness, Short (1982; 1988) and Streeter *et al.* (1983) proposed a model that described habitat structure in terms of vertical layers. Five terrestrial strata were defined; subsurface, surface, midstory, tree bole, tree canopy. Under a niche theoretic construct, the vertebrate community was conceptualized to partition resources across habitat layers according to breeding and feeding requirements (Short and Burnham 1982; Verner 1984; Szaro 1987). An air/elsewhere 'layer' was added to account for aerial feeders and those species that do not breed in the vegetation layers defined. This resulted in a feeding/breeding matrix containing 36 'guild blocks'.

The output of the habitat structure model is an index of vertical habitat complexity calculated as the quotient of the observed number of guild blocks at an inventory sample site and the number of guild blocks that would be available under the potential natural vegetation type as defined by Küchler (1964). The index tends to vary between 0 and 1.0 depending on whether the site has been highly disturbed or is structurally similar to that expected under the natural vegetation.

Use of this model to evaluate wildlife response to land management activities assumes that vertical habitat complexity is the primary determinant of vertebrate species richness. While we agree that this index of habitat structure 'seems directly related to species richness' (Short 1988: 300), application of the model in resource planning analyses should be contingent on testing this fundamental assumption and exploring alternative relations between community structure and wildlife habitat.

We implemented the habitat structure model using the 1982 National Resources Inventory (NRI) (USDA, Soil Conservation Service 1987). The NRI is a periodic inventory of soil and water resources, including land cover, land use, and management activities, that occur on nonfederal lands. In 1982, a stratified random sample of approximately 321 thousand sample units across the U.S. were inventoried to provide statistically reliable area1 estimates of major land uses for physiographic strata termed Major Land Resource Areas (MLRA's). The MLRA's, in general, define 10,000 -km^2 regions of relatively homogeneous climate, physiography, soils, and land use (USDA, Soil Conservation Service 1981). Given the commonality between the criteria used to define MLRA's and landscapes (Forman and Godron 1986), we refer to MLRA's as landscapes, and they formed the observational unit in testing the habitat structure model (see Appendix A for identification of MLRA's used in this study).

2.2. *Wildlife community structure: an index of faunal integrity*

The availability of nationally extensive data sets on distribution and abundance patterns of most classes of wildlife is limited. Although the habitat structure model is purported to indicate the assemblage of all vertebrates, data constraints forced us to examine only avian taxa. The U.S. Fish and Wildlife Service Breeding Bird Survey (BBS) was used to provide data on the occurrence of avian species based on randomly located roadside routes. Each route is comprised of 50 stops spaced at 0.8-km (½-mile) intervals. At each stop the species and number of birds seen or heard within 402 m (¼ mile) of the route were recorded (see Droege [1990] for details). The location of the route center was used to map and assign BBS routes to MLRA-defined landscapes. Although a number of problems with the BBS have been noted (Bystrak 1981), no other geographically extensive survey exists with similar standardization and consideration for statistical design.

In order to have an avian community metric commensurate with the habitat structure model, a measure of species richness related to some standard was required. The species pool under natural conditions has been recommended as an appropriate standard for comparison when evaluating alternative management strategies (Noss and Harris 1986) and has been referenced as a method for characterizing fauna1 integrity (Karr and Dudley 198 1; Devall and Sessions 1984; Karr 1990). We compared the number of avian species observed with the number expected in each MLRA-defined landscape. This standardization helped to control for potentially confounding variation in richness among landscapes with inherently different species pool sizes unrelated to habitat structure and land use.

We used data from a continent-wide range map study conducted by Inkley (1985) to define the expected avian species pool for each landscape unit. Inkley overlaid a stratified random sample of points on bird species distribution maps generated from range descriptions in *The Checklist of North American Birds* (American Ornithologists' Union 1983). Casual or accidental sightings were omitted in the construction of the species ranges as were all nonnative avian species. The number of species ranges that each sample point intersected defined the expected avian community composition at each point. We associated each sample point with an MLRA-defined landscape based on its mapped location. The proportion of the expected community composition that was observed by the BBS was used as an index to avian community integrity for each landscape.

2.3. Analysis and model testing

We limited our test of the model to the eastern United States because the NRI inventories only nonfederal lands and the western U.S. is characterized by large blocks of federal ownership. Forest is the predominant natural vegetation in the East, and we included only those landscape units that had the potential to support forest ecosystems (n = 66) (USDA, Soil Conservation Service 1981). We view our evaluation of the model as a conservative test because vertical complexity was expected to be a more important factor explaining avian richness patterns in forest ecosystems than more simply structured habitats (e.g., grassland and shrubland systems) (Wiens 1989).

A mean habitat structure index, weighted by the area expansion factor associated with each NRI sample point, was calculated for each landscape. Two measures reflective of the spatial pattern of habitat within landscapes were also calculated from the NRI. The sample variance of the habitat structure index was used as an indirect measure of horizontal habitat heterogeneity. A second, and direct measure of land type diversity was the number of major land uses *(i.e.,* cropland, grassland, forest, urban, water, wetland) within 402 m of an inventory point. The measurement scale of 402 m was chosen to be commensurate with that used by the BBS to record bird species occurrence.

The observed avian community composition for each landscape was based on a sampling frame comprised of all BBS routes that were run during a 5-year window centered on 1982 (the year of the NRI inventory). Any route that was run at least once during this 5-year window was included, and each route-year defined an observation. Only those landscapes that had a frame size of at least 30 route-years were considered in the analysis. A simple resampling plan (Efron 1982) was implemented which involved: 1) selecting a random sample, with replacement, of 30 route-years to compile avian species lists for each landscape; 2) calculating the proportion of the expected avian community (as determined from 62 of Inkley's range map. sample points) that was observed by the BBS for each landscape; and 3) repeating the previous steps 30 times and calculating a mean index of avian community integrity. This resampling procedure was implemented to control for noted sampling effort effects on diversity values (Sanders 1968; Fager 1972; James and Rathbun 1981; Wilson and Shmida 1984). The resampling plan also permitted a variance estimate of avian community integrity – the inverse of which was used to weight the observations in regression analysis to control for violation of the homogeneous variance assumption under least-squares estimation (Kleinbaum *et al.* 1988)

We tested the habitat structure model by restating the fundamental assumption as the following null hypothesis: vertical habitat structure (VHS) shows no positive relation with avian community integrity (ACI). A significant (α = 0.05) Spearman's rank correlation between these indices was interpreted as evidence for rejecting the null hypothesis. Simple linear regression analysis was used to examine the amount of variation in ACI that was explained by VHS. Multiple linear regression analysis was used to determine if the explanatory power of the simple linear model could be improved when measures of horizontal heterogeneity in land types were also included.

Finally, we explored alternative measures of landscape spatial pattern that may be useful in explaining variation in avian community structure by incorporating digitized land cover data from the U.S. Geological Survey (USGS) (USDI, Geological Survey 1987). High-altitude aerial photographs, usually at scales smaller than 1:60,000, were used to digitize and transfer data to 1:250,000 base maps. Raster format data with grids of 200 m^2 provided information on 9 broad land cover types, including urban or built-up land, agricultural land, rangeland, forest, water, wetlands, barren land, tundra, and perennial snow or ice. We extracted circular (radius = 19.7 km, ½ the length of a BBS route) land cover scenes centered on each BBS route. The landscape pattern indices used, their description, and the source of the index are provided in Table 1. Land cover scenes within each MLRA-defined landscape were pooled to provide landscape-wide measures of spatial pattern.

We let NRI and USGS-based measures of landscape pattern 'compete' in a stepwise variable selec-

Table 1. NRI and USGS landscape variables used in analysis of relations with the index of avian community integrity.

Variable	Description	Source (if proposed elsewhere)
NRI-based		
VHS	Index of vertical habitat structure.	Streeter *et al.* (1983)
VAR-VHS	Sample variance of vertical habitat structure.	
No-LT	Number of land types within 402 m of an inventory point.	
URBAN	Proportion of urban or built-up land.	
USGS-based		
H'	Shannon diversity index $H' = \sum_{i=1}^{n} P_i \ln P_i$ where P_i is the proportion of land type i and n is the number of land types in the landscape.	O'Neill *et al.* (1988)
D	Measures land type dominance, or the tendency for one or a few land types to comprise the majority of the landscape. $D = \ln n + \sum_{i=1}^{n} P_i \ln P_i$	O'Neill et al. (1988)
c	Measure of land type contagion, or the extent to which land types are aggregated in contiguous patches. $C = n \ln n + \sum_{i=1}^{n} \sum_{j=1}^{n} P_{ij} \ln P_{ij}$ where P_{ij} is the probability that land type i is adjacent to land type j.	O'Neill et al. (1988)
FD-PA	Fractal dimension based on the perimeter-area method. Measures the complexity of forest patch shape.	Krummel *et al.* (1987)
FD-GR	Fractal dimension based on the grid method. Measures the dispersion of forest patches.	Milne (1991)
PAT-No	Average number of forest patches.	
PAT-SZ	Average size of forest patches.	

tion procedure under multiple linear regression. The USGS data, which was collected primarily during the early and mid-1970's, was not temporally congruent with the NRI data. Consequently, we emphasize that our purpose here was to explore potentially useful relations rather than propose a model for predictive use in resourse decision-making.

3. Results and Discussion

3.1. Relations between habitat structure and avian community integrity

We implemented the habitat structure model in a fashion consistent with the Soil Conservation Service's national planning application (USDA 1989b). Prior to applying the model, we eliminated from the land, base NRI inventory points that fell within land types that were assumed to be unsuitable for wildlife habitat *(i.e.,* urban and built-up

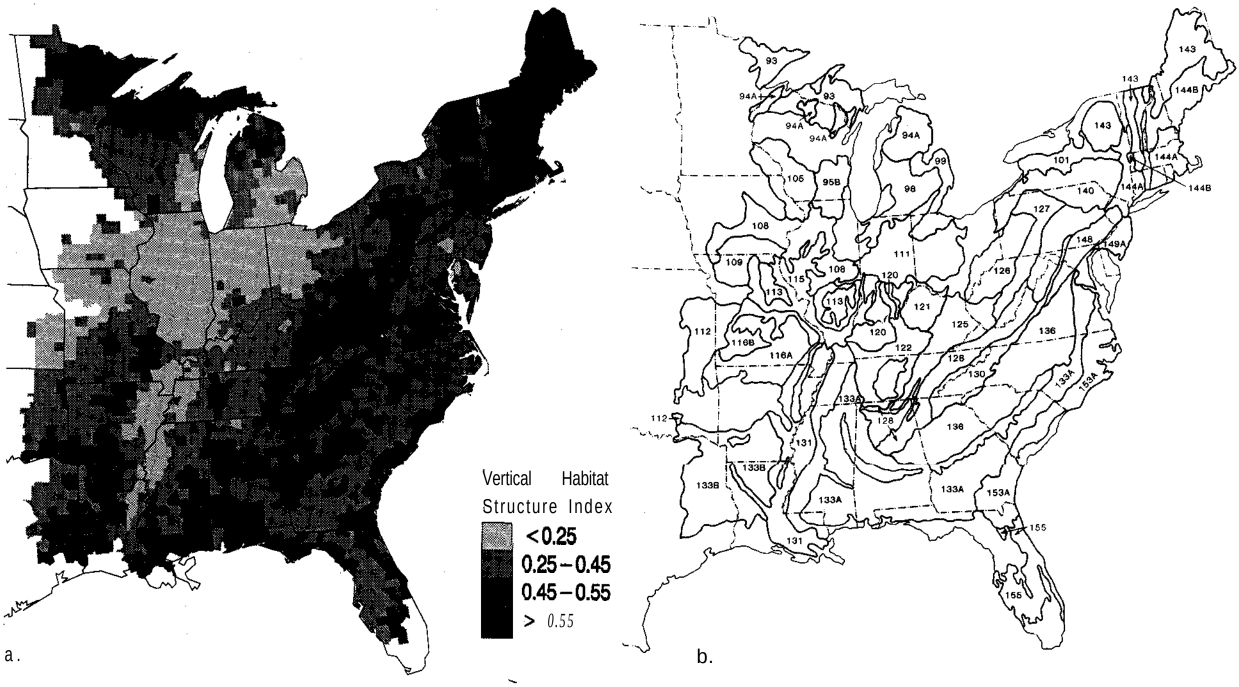

Fig. I. a) Weighted mean vertical habitat structure index for each county in those MLRA-defined landscapes that could support forest ecosystems based on the 1982 NRI, and b) the 35 landscapes that were used to test the habitat structure model (numeric codes defined in Appendix A).

land, transportation routes, and farmsteads) (Streeter *et al.* 1983). The geographic distribution of VHS (Fig. la) was consistent with our *a priori* expectations, namely that intensive land use in the corn belt region (*i.e.,* western Ohio, Indiana, Illinois, and Iowa) and the lower Mississippi River Valley has greatly simplified vertical habitat complexity. Conversely, New England, the Southern Appalachians, and northern portions of Michigan and Wisconsin have retained a greater proportion of the vertical habitat complexity expected under natural vegetation. Thirty-five of the 66 MLRA-defined landscapes that could support forest vegetation had sufficient avian data to be included in the test of the habitat structure model's fundamental assumption (Fig. lb).

While the habitat structure model was consistent with our perceptions of the regional patterns of land use intensity, evidence that avian communities exhibit simplification in extensively disturbed landscapes would eliminate reliance on conventional wisdom for model verification. Spearman's rank correlation between the VHS and ACI resulted in rejection of the null hypothesis of no positive relation between these indices ($r_s = 0.46$; $P = 0.0054$; $n = 35$). Noted spurious correlation among ratio variables (Atchley *et al.* 1976; Jackson *et al.* 1990) was not a concern as our ratios did not share common variables (Kenney 1982). While the correlation is significant, it is weak and indicated that substantial variability in ACI remains unaccounted for by VHS. Weighted linear regression with the habitat structure index as the sole predictor accounted for approximately ⅓ of the total variation in the index of avian community integrity (Fig. 2). Examination of the residuals in normal probability plots (Kleinbaum *et al.* 1988: 191) did not reveal departures from normality, suggesting that data transformations were unnecessary.

It was not surprising that a model characterizing only vertical habitat complexity failed to account for much of the observed variation in avian community integrity. A cornerstone of landscape ecology is its focus on spatial patterns of land type mosaics, how those mosaics were formed, and how they effect the distribution and movement of eco-

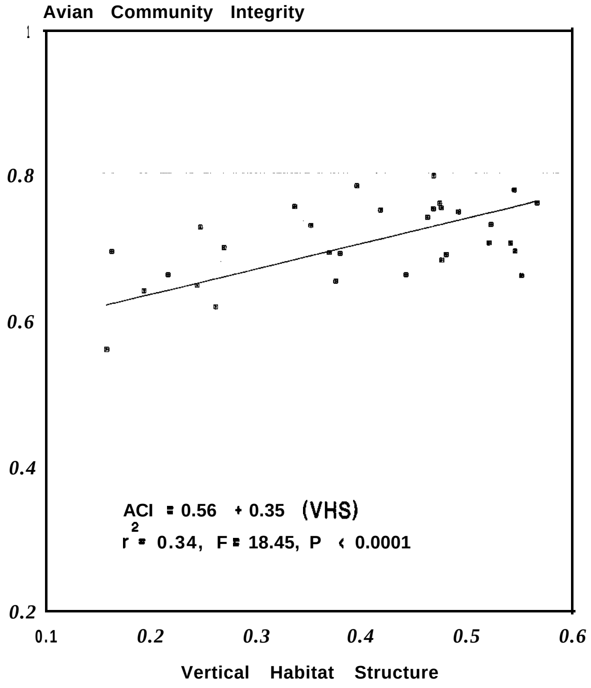

Fig. 2. Simple linear regression of avian community integrity as a function of vertical habitat structure.

system components (e.g., species) within the landscape (Forman and Godron 1981; Urban et *al.* 1987; Swanson et *al.* 1988). With this broader perspective, there is a growing appreciation that patterns observed at a local scale are influenced by processes that operate at larger scales (Brown and Roughgarden 1990; Helle 1986; MacNally 1990a; Askins and Philbrick 1987).

The NRI contains numerous variables that could improve the simple linear relation between ACI and VHS. However, our approach to exploring model improvement was to specify, *apriori,* a model to explain avian community integrity based on: 1) factors thought to affect avian communities that were ignored in the Soil Conservation Service's national planning application *(i.e.,* urban land), and 2) spatial pattern factors suggested from principles of landscape ecology.

Elimination of data about urban land likely underestimated the impacts of anthropogenic disturbance on avian communities. Therefore, we added the proportion of urban and built-up land within a landscape as a predictor of ACI in an attempt to capture the simplification of avian community composition that has accompanied urbanization (DeGraaf 1986).

Based on principles of landscape ecology, the variance of the habitat structure index (VAR-VHS) and the mean number of land types (No-LT) within 402 m of an inventory point were chosen to indicate the spatial pattern of land types. Scatter plots of these data indicated that the variance of the habitat index was related to ACI as a quadratic, suggesting that landscapes of intermediate levels of heterogeneity support a greater number of the expected species pool. Attainment of maximum species richness at intermediate levels of habitat variation has been an observed landscape-level pattern (Pickett 1976; Fuentes 1988) that was formalized as the intermediate disturbance hypothesis (Connell 1978).

Our fully specified model to explain variation in avian community integrity was as follows: ACI = f(VHS, VAR-VHS, $VAR\text{-}VHS^2$, No-LT, URBAN). The model (F = 7.88, P < 0.0001) explained an additional 15% of the variation in avian community integrity (adj R^2 = 0.503) over the simple linear model. All parameter estimates were significant at the 90% confidence level (Table 2).

3.2. USGS-derived measures of landscape pattern

Because the NRI was originally conceived to provide periodic estimates of land area, the spatial pattern metrics we derived were opportunistic. In order to explore the premise that an inventory designed to provide spatial pattern metrics would offer improved explanation of avian community structure, we used the USGS digital land use and land cover data to contribute a more comprehensive set of landscape structure variables. The median year for the landscape scenes in our study area was 1974 – nearly a decade earlier than the NRI. Because of the temporal discrepancy between these data sets, the results of incorporating detailed landscape pattern statistics from the USGS are only suggestive of the improvement that may be realized.

The spatial pattern variables from the USGS were allowed to compete with NRI-derived variables. The stepwise-selected model (F = 12.73; $P <$ 0.0001) retained the proportion of urban land and

Table 2. Regression model coefficients for the fully specified model of avian community integrity as a function of vertical habitat structure and land use variables based on the NRI data.

Variable	Coefficient	*F*	*P > F*
VHS	0.315	16.44	0.0003
URBAN	0.470	3.66	0.0656
VAR-VHS	0.374	5.00	0.0332
$VAR\text{-}VHS^2$	-0.186	3.95	0.0564
No-LT	0.069	7.34	0.0112

Table 3. Regression model coefficients for stepwise-selected model of avian community integrity as a function of NRI and USGS digitized land use and land cover data.

Variable	Coefficient	*F*	*P > F*
VHS	0.260	13.68	0.0009
URBAN	0.912	16.59	0.0003
No-LT	0.085	11.73	0.0019
D	- 0.264	16.09	0.0004
FD-PA	-0.510	4.16	0.0510

the number of land types within 402 m, but replaced the variance of the habitat structure index with measures of land type dominance and the perimeter/area fractal measure of forest edge complexity (Table 3). Both USGS-derived measures of landscape structure were negatively correlated with avian community integrity, and their inclusion has the potential to improve the model's predictive capability (adj R^2 = 0.633).

3.3. Implications to resource planning

The development of large-scale wildlife planning models has proceeded along a path of first generating models and then demonstrating feasible application. Because compatible large-scale data sets are rare, relatively little effort has been devoted to rigorously testing model assumptions and predictions. As noted by Salazar and Lee (1990), a consequence of such an approach is policy proposals with weak empirical foundations. Subjecting resource planning models to falsification is required if decision-makers are to have a basis for evaluating the information content of resource models, if analysts are to improve the performance of planning models, and if resource inventory specialists are to improve the data bases that are the foundation of resource policy analysis.

Our test of the habitat structure model supported the model's fundamental assumption. However, it also showed that considerable uncertainty regarding the factors affecting.avian community integrity at a landscape scale remained even after spatial pattern metrics were incorporated into a multiple regression model. Half the variation in avian community integrity remained unaccounted for by the fully specified model using the NRI. However, with the magnitude of the uncertainty quantified, resource policy analysts now have a basis for weighting the information content of this model relative to other resource models used in the resource decision-making process. In addition, a benchmark against which to gauge improvements in model performance has been established.

While the focus of the habitat structure model is on species richness, we are not suggesting that richness be the sole criterion for analyzing land policy impacts. Indeed our measure of avian community integrity appears to offer an approach to identify: ing species that should receive disproportionate conservation consideration. Patterns in life history attributes (e.g., habitat requirements, migratory strategy, and body size) that are shared among the unobserved portion of the expected species pool within and among landscapes may provide further insights into regional conservation needs that could be incorporated into resource policy decisions.

4. Conclusion

Natural resource planning and management is becoming increasingly complex as expanding human populations place competing demands on a finite resource base. Understanding and anticipating the consequences of alternative land management strategies is critical if informed and tenable policy regarding natural resource management is to be developed.

Our landscape-level test and analysis of the habitat structure model using the NRI, USGS digitized land cover data, and avian community composition data during the breeding season has established two points. First, the fundamental assumption that avian community integrity is related to vertical habitat complexity was supported in eastern forested ecosystems. Second, reliance on vertical habitat structure as the sole indicator of avian community response at the landscape scale was inadequate. More complex models that incorporate spatial patterns of land types are required if the capability to anticipate avian community response to alternative land management policy is to be realized.

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Appendix A. Major Land Resource Areas, and their approximate area, that were used to test the habitat structure model (USDA, Soil Conservation Service 1981).

MLRA code	MLRA name	Area (km²)
93	Superior Stony and Rocky Loamy Plains and Hills	56,080
94A	Northern Michigan and Wisconsin Sandy Drift	39,920
95B	Southern Wisconsin and Northern Illinois Drift Plain	28,530
98	Southern Michigan and Northern Indiana Drift Plain	60,050
99	Erie-Huron Lake Plain	35,780.
101	Ontario Plain and Finger Lakes Region	32,790
105	Northern Mississippi Valley Loess Hills	57,520
108	Illinois and Iowa Deep Loess and Drift	79,790
109	Iowa and Missouri Heavy Till Plain	37,110
111	Indiana and Ohio Till Plain	84,980
112	Cherokee Prairies	57,520
113	Central Claypan Areas	28,570
115	Central Mississippi Valley Wooded Slopes	60,860
116A	Ozark Highland	69,810
116B	Ozark Border	35,470
120	Kentucky and Indiana Sandstone and Shale Hills and Valleys	30,990
121	Kentucky Bluegrass	29,490
122	Highland Rim and Pennyroyal	52,640
125	Cumberland Plateau and Mountains	63,840
126	Central Allegheny Plateau	50,770
127	Eastern Allegheny Plateau and Mountains	43,680
128	Southern Appalachian Ridges and Valleys	69,430
130	Blue Ridge	47,030
131	Southern Mississippi Valley Alluvium	93,600
133A	Southern Coastal Plain	285,050
133B	Western Coastal Plain	140,640
136	Southern Piedmont	161,430
140	Glaciated Allegheny Plateau and Catskill Mountains	70,540
143	Northeastern Mountains	101,760
144A	New England and Eastern New York Upland, Southern Part	52,040
144B	New England and Eastern New York Upland, Northern Part	48,570
148	Northern Piedmont	29,870
149A	Northern Coastal Plain	20,870
153A	Atlantic Coast Flatwoods	73,760
155	Southern Florida Flatwoods	54,570