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Relationships between avian richness and landscape structure at multiple scales using multiple landscapes

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Abstract

Little is known about factors that structure biodiversity on landscape scales, yet current land management protocols, such as forest certification programs, place an increasing emphasis on managing for sustainable biodiversity at landscape scales. We used a replicated landscape study to evaluate relationships between forest structure and avian diversity at both stand and landscape-levels. We used data on bird communities collected under comparable sampling protocols on four managed forests located across the Southeastern US to develop logistic regression models describing relationships between habitat factors and the distribution of overall richness and richness of selected guilds. Landscape models generated for eight of nine guilds showed a strong relationship between richness and both availability and configuration of landscape features. Diversity of topographic features and heterogeneity of forest structure were primary determinants of avian species richness. Forest heterogeneity, in both age and forest type, were strongly and positively associated with overall avian richness and richness for most guilds. Road density was associated positively but weakly with avian richness. Landscape variables dominated all models generated, but no consistent patterns in metrics or scale were evident. Model fit was strong for neotropical migrants and relatively weak for short-distance migrants and resident species. Our models provide a tool that will allow managers to evaluate and demonstrate quantitatively how management practices affect avian diversity on landscapes.

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Keywords: Avian communities; Forest management; Heterogeneity; Landscape; Richness; Southeastern US

Little is known about relationships between avian richness and forest structure at landscape scales. In part, this is because most field studies relating avian communities to forest structure have been performed at fine scales, generally at the level of the forest stand. Relationships established at this scale rarely extrapolate well to broader landscape scales because processes driving the distribution of individual species (e.g. habitat

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selection, foraging and mating behaviors, population dynamics) may be taking place on much broader scales than those at which they were measured (Maurer and Villard, 1994; Villard et al., 1995; Wiens, 1995). An additional challenge to understanding relationships between avian communities and forested landscapes is that few, if any, ecological mechanisms have been hypothesized for explaining why or how animal communities should respond to landscape structure (Marzluff et al., 2000; but see Rodewald and Yahner, 2001). Without a conceptual foundation for explaining patterns, most studies of relationships between animal diversity and landscape structure have been descriptive, with inductively-derived insights having unknown accuracy or generality. Further, no landscape study can avoid defining the scales at which phenomena are measured, but the absence of hypothesized mechanisms dictates that these scales must be chosen arbitrarily. Selection of ecologically appropriate scale for measuring landscapes is a concept that is broadly discussed but for which analytical solutions scarce (e.g. Wiens, 1989, Scott et al., 2002). Approaches to identifying ecologically relevant scales tend to presume underlying mechanisms, such as metapopulation dynamics (Vos et al., 2001) or dispersal (Addicott et al., 1987) that may or may not be operant or require intensive monitoring to assess cumulative movements and interactions of individuals and populations (Addicott et al., 1987). In the absence of known ecological processes, most studies select a single, arbitrary scale for evaluating relationships between animal diversity and landscape structure, but this approach is compromised if observations are a function of scale or the products of processes occurring at different or multiple scales (Mitchell et al., 2001). Finally, the rigor of landscape studies has been hampered traditionally by a lack of replication (Hargrove and Pickering, 1992), thus general patterns are indistinguishable from those idiosyncratic to the landscape being studied.

The challenges of understanding relationships between animal communities and landscape structure are of more than academic interest. Both government and commercial land management agencies are increasing their focus on maintenance of biodiversity at broad landscape scales. In recent years, sustainable forestry processes, such as the Montreal process and Helsinki process, and ownership-level sustainable forestry certification programs such as the Sustainable Forestry Initiative (SFI), Forest Stewardship Council, and Canadian Standards Association have been developed to ensure sustainable biodiversity and production of forest products on forest industry lands (Guynn et al., 2004). Criteria under some certification processes and programs are specific about the conservation of biodiversity at the landscape-level. For example, the SFI requires participants to develop and implement stand- and landscape-level measures that promote habitat diversity and the conservation of forest plants and animals (American Forest and Paper Association, 2005). However, a lack of understanding of relationships between ecological patterns and processes and the community structure of animals at landscape scales, much less how they are affected by forest management, is therefore problematic for forest product companies seeking certification.

The purpose of our study was to develop models relating richness of bird communities to stand- and landscape-level features on managed forests. We chose birds as a surrogate for biodiversity because data on avian abundance are commonly available and are generally collected under a common sampling methodology (i.e. point counts); thus, combining data collected from multiple studies is feasible. Although, more taxonomically comprehensive data sets may exist, differences in sampling methods for different taxa make combining observations into standardized estimates of biodiversity difficult. We chose richness of birds as our metric of bird community structure because it is easily derived from the presence/absence data generated by counts. Richness is a coarse measure of community structure that does not take into account abundance of species, interrelationships among them, or the identity of species counted. Given these limitations, species richness does provide a measure of the diversity of species found at a location and is practical, if incomplete, index forest managers can use to assess biodiversity. An important objective of our research was to provide forest managers with a better understanding of the effects of forest management on avian communities. Further, we designed our study to use data readily available and generally common to all forest managers; the resulting models should thus be applicable to most managed forests in the Southeastern US, providing a tool for evaluating the effects of alternate scenarios of forest management on avian richness.

Our study design was intended to address some of the research shortcomings we have outlined above. First, we synthesized predictions regarding relationships between avian species richness and forested landscapes from currently available research, and evaluated these predictions through our modeling process. Such evaluation of predictions generated from prior research does not, however, fully address the shortcomings created by the absence of a theoretical foundation relating biodiversity to landscape structure. Thus, our modeling was also exploratory, intended to generate insights that might contribute to the development of such theory. In the absence of theoretical or empirical reasons for selecting the scale at which we evaluated landscape-level relationships, we modeled these relationships across multiple spatial scales to avoid misleading insights that may come from arbitrary selection of scale. Finally, to improve the generality of our insights we used data collected independently and comparably on multiple landscapes, in essence a replicated study.

Several studies have shown landscape configuration to have important effects on the distribution of individual bird species. Bolger et al. (1997) found that bird species inhabiting coastal Southern California could be ranked on a landscape-level continuum from edge-intolerant to edge specialist. Saab (1999) found that the distributions of bird species along a riparian zone in Idaho were best explained by landscape-level habitat characteristics. Villard et al. (1999) found that both amount and configuration of forest cover in Eastern Ontario, Canada were significant predictors of presence for three of 15 bird species and configuration (but not cover) was a significant predictor for an additional six species. Mitchell et al. (2001) showed that landscape characteristics, measured at appropriate scales, strongly predicted the distribution of some bird species inhabiting managed forests in coastal South Carolina.

The extent to which such relationships extend beyond individual species to groups of species (i.e. guilds) or entire communities is unclear. Flather and Sauer (1996) showed that landscape features were strongly associated with the distribution of neotropical migrants but not resident bird species in the eastern United States. Mitchell et al. (2001) also found this pattern, as well as a strong, positive relationship between landscape configuration and degree of habitat specialization. They did not, however, find common landscape-scale relationships among any of the groups they evaluated, either in terms of landscape features or scale of habitat selection, suggesting that these relationships are likely to be unique to the natural history of each species (thus, strong relationships between landscape configuration and guilds may be unlikely).

Most landscape-scale studies of avian communities have focused on associations with the arrangement of patches, corridors, and matrix elements on landscapes and with patch area, fragmentation, and isolation (Rodewald and Yahner, 2001). Findings of such studies are often ambiguous (Debinski and Holt, 2000; Bissonette and Storch, 2003; Fahrig, 2003), in part because of simplistic assumptions about contrasts between ‘‘suitable’’ habitat patches and the ‘‘hostile’’ matrices in which they are imbedded. Thus, studies that evaluated avian diversity on highly contrasting landscapes (i.e. suburban, mixed forest and agriculture) have found important effects of landscape configuration on bird community structure (Askins and Philbrick, 1987; Robbins et al., 1989, Verboom et al., 1991; Lens and Dhondt, 1994; Villard et al., 1995). Studies that evaluated more subtly contrasting landscapes (e.g. forests consisting of different age classes and forest types) have found that availability of habitat was more important than configuration in explaining bird community structure (McGarigal and McComb, 1995; Drolet et al., 1999; Penhollow and Stauffer, 2000; Lichstein et al., 2002). Rodewald and Yahner (2001) clearly illustrated this effect by showing marked differences between avian communities on forested landscapes fragmented by agricultural versus silvicultural disturbances (but see Manolis et al., 2000). It remains unclear whether avian community structure can be described as a function of forested landscape structure, or whether such relationships might be swamped by the myriad of environmental factors that determine the distributions of individual species (McGarigal and McComb, 1995).

The effects of forest management on bird communities have been well studied, if primarily on a stand scale (summarized in Sallabanks et al., 2000). Most of these studies have been correlative, short in duration, and did not measure avian demography or mechanistic links to habitat (Sallabanks and Marzluff, 2000; Sallabanks et al., 2000). Because of these scientific shortcomings and the diversity of forested systems and management regimes studied, generalized effects of forest management on avian communities are difficult to derive. Basic habitat associations (e.g. Hamel et al., 1982; Hamel, 1992) and more elegant stand-level wildlife-habitat relationship models (e.g. Kilgo et al., 2002) allow predictions based on availability of forest types and age classes on a landscape. Indeed, several studies have suggested this is sufficient information, and fragmentation or spatial arrangement of types and age classes may be unimportant in understanding the distribution of birds on a forested landscape (McGarigal and McComb, 1995; Lichstein et al., 2002; Debinski and Holt, 2000; Bissonette and Storch, 2003). Other studies, however, have shown that spatial arrangement of forest types and age classes are important (Drolet et al., 1999; Villard et al., 1999; Mitchell et al., 2001). One possible explanation for this discrepancy is the confounding effect of scale of measurement on landscape variables, where incorrect or arbitrary choice of scale can result in misleading insights (Mitchell et al., 2001). When multiple scales are used to evaluate habitat associations, site- or system-specific differences may account for the discrepancy. A relatively consistent trend through most of the studies cited above, however, is the finding that avian diversity on landscape scales is related positively with heterogeneity of forest age classes and types. Finally, roads are an inevitable by-product of most forest management regimes. Very little is known about whether roads associated with forest management have a negative impact on bird communities, but they are widely believed to affect biodiversity adversely (Strittholt and Dellasala, 2001; DeStefano, 2002; Loucks et al., 2003).

In this study, we evaluated relationships between avian species richness and stand- and landscape-scale habitat features on four different landscapes in the Southeastern US. We evaluated these relationships for overall species richness and richness of selected bird guilds; we used guilds because landscape-scale habitat relationships are probably unique for every species of bird (Mitchell et al., 2001) but are perhaps less variable among groups of ecologically similar species. Grouping of species is also a necessary expedient in land management because it is not possible to manage for all species individually. Based on the research precedents cited above, we developed the following predictions to evaluate with our modeling:

1. Availability and configuration of forest types and age classes will both be important predictors of avian richness (Drolet et al., 1999; Villard et al., 1999; Mitchell et al., 2001).
2. Avian richness will be positively related to heterogeneity of forest types and age classes on a landscape scale (Penhollow and Stauffer, 2000; Mitchell et al., 2001).
3. Road density will be negatively related to avian richness.
4. No single spatial scale for evaluating landscape features will be appropriate for predicting avian richness overall or richness within guilds (Mitchell et al., 2001).
5. Landscape characteristics will be important predictors of richness of neotropical migrants but not of richness of short-distance migrants or residents (Flather and Sauer, 1996; Mitchell et al., 2001; Lichstein et al., 2002).

1. Study areas

We used data collected from four sites in the Southeastern US where birds were surveyed using comparable methods.

These sites were chosen because they were largely forested, were managed for commercial forestry to varying degrees, and had extensive data available.

1.1. Arkansas

The Arkansas study area (AR) is located near Hot Springs, Arkansas (Garland and Saline counties), in Bailey Province 231, the Ouachita Mixed Forest-Meadow Province. The area is characterized by mountains eroded from sedimentary rock formations with ridges reaching maximum altitudes of about 790 m. The major soils are Ultisols that are often stony, average annual temperature is about 17 °C, and average annual precipitation is about 1050 mm. Vegetation was dominated by pine-oak (*Quercus* spp.)–hickory (*Carya* spp.) forests, and managed pine forests including plantations managed on rotations of approximately 30–35 years. Even in mixed stands, pine constituted as much as 40% of the overstory cover (shortleaf pine [*Pinus echinata*] in the uplands and loblolly pine [*Pinus taeda*] on alluvial soils).

1.2. South Carolina

We used two South Carolina study areas, the Woodbury/Giles Bay landscape and Ashley/Edisto landscape, located in Bailey Province 232, the Outer Coastal Plain Mixed Province. The Province comprises the flat and irregular Atlantic and Gulf Coastal Plains down to the sea. Local relief is <90 m, and soils are mainly Ultisols, Spodosols, and Entisols. Average annual temperature is 16–21 °C, and average annual precipitation ranges from 1020–1530 mm. Regional vegetation is characterized by pine forests on upland sites, extensive coastal marshes, and interior swamps dominated by gum and cypress. Many upland forests contain isolated depressional wetlands.

The Woodbury/Giles Bay landscape (SC1), located in Marion county near Conway, South Carolina, was largely composed of sandhill ridges with interspersed bottomland hardwood forests and isolated wetlands. The sandhill ridges were dominated by planted loblolly and longleaf (*Pinus palustris*) stands that ranged from recently harvested stands to mature (>50 years old). Forested stands were managed using a variety of rotation lengths and harvesting techniques, depending upon the forest type. At the time of our study, pine plantations were on 20-yr rotations.

The Ashley/Edisto landscape (SC2), located in Charleston and Colleton counties near Charleston, South Carolina, consisted primarily of loblolly pine stands mixed with bottomland hardwood hummocks and isolated wetlands. The landscape also contained linear habitats in the form of streamside management zones (SMZs) adjacent to perennial and intermittent streams (50–100 m wide on each side) and habitat diversity zones on upland sites, which formed a network of 100 m wide corridors across the study area. At the time of our study, rotations for even-aged forests on SC2 were 20 years for pine plantations, 40–60 years for corridors, and 60 years for hardwood stands.

1.3. West Virginia

The West Virginia study area (WV) is located in Randolph County (near Elkins, West Virginia) in Bailey Province M221, the Central Appalachian Broadleaf Forest – Coniferous Forest – Meadow Province. The Province is composed of low, steep mountains with narrow valleys; elevations range from 634 to 1180 m. Soils are generally Ultisols or Inceptisols. Average annual temperatures range from below 10 °C in the north to about 18 °C at the south end of the highlands, and average precipitation varies from about 890 mm in the valleys to as much as 2040 mm on the highest peaks. Snowfall can reach almost 1 m in this Province. Vegetation changes as elevation increases, with different strata dominated by mixed oak-pine forests (at lowest elevations), mixed oak forests, northern hardwood forest (birch–beech–maple–elm–oak–basswood; *Betula–Fagus–Ulmus–Quercus.–Tilia*), and spruce–fir (*Picea–Abies*) forests (at high elevations). At the time of our study, most (>90%) of the landscape consisted of stands >80 years old.

2. Methods

2.1. Bird data

Annually on each study area, investigators sampled breeding bird communities at least once using 50 m fixed-radius plots distributed across the landscapes and standard 5 min point counts (Ralph et al., 1993). Sampling occurred May–June during 1995–1998 in Arkansas and 1995–1999 on both South Carolina landscapes. In West Virginia, sampling occurred during 1996–1998, 2001, and 2002. Sample points were located ≥200 m apart on the study landscapes either on a grid system or proportionate to forest type. If the same plot was visited more than once within a season, we randomly selected one of the visits. Because the four landscapes were under active forest management, landscape conditions changed among years and we considered visits to plots on successive years to be independent observations. The number of plots was 1865 in AR, 1762 in SC1, 715 in SC2, and 703 in WV.

We categorized all bird species on the study areas using guilds/groupings defined by Peterjohn and Sauer (1993) and computed species richness for each guild/group. The groupings divided the bird community based on breeding habitat (shrub/scrub successional, woodland), nest type (cavity, ground, canopy), and migration form (permanent resident, short-distance migrant, neotropical migrant). Observations of exotic species (European starlings [*Sturnus vulgaris*], pigeons [*Columba livia*], English sparrows [*Passer domesticus*]) were excluded from analyses.

Because relatively few species were observed at each 50 m point count plot (3.66 ± 2.01 [S.D.]), we used stands as the sample unit instead of sampling points. Because stands contained varying numbers of sampling points, aggregating all points in each stand would bias estimates of richness upward for stands that were sampled most. To identify a common number of sampling points that could be aggregated within each stand, we evaluated qualitatively the trade-off between increasing the number of points and the associated loss of sample size (from discarded sampling points and from stands with fewer than the common number of sampling points). We determined that using three sampling plots per stand increased the number of species observed (6.83 ± 3.43) and improved analytical rigor, but maintained an acceptable sample size (from $n = 5092$ to 700). Using four sampling plots per stand would have further improved the number of species observations per stand, but would have reduced sample size to what we deemed an unacceptable level ($n = 414$).

For each stand containing greater than three sampling points, we selected the three points with the smallest mean distance (i.e. those closest to each other) and averaged the neighborhood variables for these three points to represent the neighborhood of the stand. By choosing the most proximate sampling points within a stand, we minimized the likelihood of averaging across very different values of neighborhood variables, which may occur when points are sampled within stands with linear or convoluted shapes. Sampling points not selected to represent a stand and stands with greater than three sampling points were excluded from analyses.

2.2. Stand- and neighborhood-scale habitat data

Several GIS data sets were compiled and overlaid to generate habitat data. An Albers Equal Area projection was used for all data and Albers coordinates were used for plot locations. Road and water feature layers and topography were compiled from USGS 1:24,000 maps. Landowner databases included more detailed information on roads and water features than could be derived from USGS maps. Because the resolution of data needed to infer relationships with roads and water features is unknown, we elected to use both USGS data and landowner data to calculate separate metrics for roads and water features which we distinguished as "coarse" (i.e. containing only major roads

Table 1
Descriptions of stand- and landscape-level variables used to model the distribution of avian species richness on four landscapes in the Southeastern US

Variable	Description	Data Source
Stand characteristics		
Stand area	Area of stand (m^2)	Landowner forest inventory
Stand age	Age of stand (yrs)	Landowner forest inventory
Stand type	Dominant overstory type based on percent basal area in pine and hardwood trees	Landowner forest inventory
Topographic characteristics		
Elevation	m Above sea level	USGS digital elevation model
Aspect	Orientation with respect to north	USGS digital elevation model
Curvature	Net curvature of landform at plot (i.e. water-shedding vs. water-collecting)	USGS digital elevation model
Slope	Mean slope at plot (°)	USGS digital elevation model
Exposure	Extent to which plot is sheltered or exposed by surrounding terrain (measured at four different scales defined by circular neighborhoods with radii of 100, 250, 500, and 1000 m)	USGS digital elevation model
Distance to nearest road (fine)	m	Landowner data
Distance to nearest road (coarse)	m	USGS census data
Distance to nearest water (fine)	m	Landowner data
Distance to nearest water (coarse)	m	USGS census data
Neighborhood characteristics (calculated for circular neighborhoods centered on each plot at four different scales, defined by radii of 100, 250, 500, and 1000 m		
Mean forest age		Landowner forest inventory
Standard deviation of forest age		Landowner forest inventory
Shannon–Wiener diversity index of forest types, H'	Number of forest types weighted for relative representation	Landowner forest inventory
Shannon–Wiener evenness index of forest types, J	Evenness of representation among forest types	Landowner forest inventory
Fragmentation of overstory types	Extent to which area of different forest types is fragmented and represented by linear, complex stand shapes or compact, simple stand shapes	Landowner forest inventory
Fragmentation of age classes	Extent to which area of different age classes is fragmented and represented by linear, complex stand shapes or compact, simple stand shapes	Landowner forest inventory
Hardwood area	Area (m^2) classified as hardwood	Landowner forest inventory
Pine area	Area (m^2) classified as pine	Landowner forest inventory
Mixed forest area	Area (m^2) classified as mixed pine/hardwood	Landowner forest inventory
Non-forested area	Area (m^2) classified as unharvested, non-forest	Landowner forest inventory
Harvested area	Area (m^2) harvested within past year or still unplanted after harvest > 1 year ago	Landowner forest inventory
Area in stands of different age classes	Area (m^2) of stands of ages 0, 1–5, 6–20, 21–30, and >30 yrs	Landowner forest inventory
Total stream length (fine)	Length (m) of all water features	Landowner data
Total stream length (coarse)	Length (m) of major water features only	USGS census data
Total road length (fine)	Length (m) of paved and unpaved road	Landowner data
Total road length (coarse)	Length (m) of paved roads only	USGS census data

and water features, derived from USGS census data) and "fine" (i.e. containing all road types and water features, derived from landowner data). Forest stand polygons were defined from landowner inventory databases. We classified habitat types as hardwood, mixed pine-hardwood, and pine forest (defined as <25%, 25–75%, and >75% pine BA, respectively), and non-forested.

Because we used up to 1 km neighborhoods, we did not have forest inventory data for the entire neighborhood surrounding some plots located near ownership boundaries. For these cases, we used aerial photographs (USGS National Aerial Photography Program) collected during the studies to estimate forest characteristics in areas lacking forest inventory data. We estimated age and dominant forest type for these areas through visual comparisons with known locations (i.e. those with forest inventory data). In some cases, the property surrounding the managed forest was used for agriculture or low-density residential development; these areas were classified as non-forest with age zero.

Ancillary environmental data included elevation (m) taken from USGS Digital Elevation Model (DEM) databases and from which we calculated topographical metrics (aspect, curvature, and slope; Table 1). We calculated exposure (i.e. the extent to which terrain is exposed or sheltered from the elements as:

$$\text{exposure} = \frac{E_L + E_C}{S}$$

where E_L is the mean elevation of buffer around sampling point, E_C the elevation at sampling point, and S is the standard deviation of ($E_L + E_C$) across the entire landscape. Elevation was calculated for buffers 100, 200, 500 m, and 1 km in radius. Prior to analyses, we transformed aspect according to Beers et al. (1966) which yielded a value that ranged from 0 (typical of hot, sunny sites) to 2 (typical of cool, shaded sites).

We derived or calculated habitat variables from landowner-provided forest inventory data and GIS coverages and from publicly available GIS coverages. Stand-scale habitat variables (Table 1) characterized the location of the sample plots (study area identifier, aspect, elevation, landscape position, net curvature, slope) and the characteristics of the stands containing the sample points (stand age, stand area).

We computed neighborhood variables using ArcGIS[2] (Environmental Systems Research Institute, Redlands, California) built-in functions for each sample point (distance variables) and for circular buffers surrounding sample points (i.e. neighborhoods). For each sample point, we defined four different neighborhoods with radii of 100 m (fine scale), 250 m (fine/moderate scale), 500 m (moderate scale), and 1 km (broad scale). Neighborhood variables (Table 1) were related to roads (distance from sample point to nearest road, total road length within the neighborhoods), water (distance from sample point to nearest water, total stream length within the neighborhoods), neighborhood age/disturbance (mean forest age, area in different age classes of forest), neighborhood heterogeneity (fragmentation indices for forest age and type, diversity index, evenness), and neighborhood forest type (area in pine, hardwood, and mixed-pine hardwood forest, and in non-forested land).

We defined fragmentation as the breaking apart of habitat, as recommended by Fahrig (2003). We estimated fragmentation of forest type and age classes within each neighborhood using two fragmentation indices, one based on mean patch size weighted by area (F_A), the other based on a length to area ratio of patches (F_L). We calculated F_A as

$$F_A = 1 - \frac{\sum_{i=1}^{n} (\text{area of patch}_i)^2}{(\text{total neighborhood area})^2}$$

We calculated F_L as

$$F_L = \frac{\text{perimeter length of neighborhood}/\text{total neighborhood area}}{\left[\left(\sum_{i=1}^{n} \text{length of patch}_i\right) + \text{perimeter length of neighborhood}\right]/2 \times \text{total neighborhood area}}$$

Because fragmentation should represent a combination of area and shape of patches, we calculated fragmentation of overstory type and age classes as the average of F_A and F_L. Whereas calculating fragmentation of categorical variables such as forest type is straightforward, doing so for continuous variables such as stand age is not. Stands that differ in age by a small number of years are not likely to differ ecologically. Thus, fragmentation of age classes based on increments of 1 year could be meaningless. Prior to calculating fragmentation of age classes, we combined stands of approximately similar age within each neighborhood into classes relative to the age of the stand at the center of the neighborhood, A_C, as follows:

$$\text{age class 1} = (\text{stands of age} < A_C - 2\sqrt{A_C})$$

$$(\text{stands of age} < A_C - 2\sqrt{A_C}) < \text{age class 2} < (\text{stands of age} < A_C + 2\sqrt{A_C})$$

$$\text{age class 3} = (\text{stands of age} > A_C + 2\sqrt{A_C})$$

2.3. Analyses

Biological diversity is an expression of many factors simultaneously operating at multiple spatial scales. Initially, we had 79 independent variables (three stand-level variables, eight

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[2] Use of trade names does not imply endorsement by the Federal Government.

topographic variables, 16 landscape-scale variables, and one topographic variable measured at four different spatial scales each) to use in developing statistical models to explain levels of overall richness and richness within guilds. Prior to development of each model, we eliminated redundant variables. When two habitat variables or the same habitat variable at two spatial scales were highly correlated (Spearman's $\rho \geq 0.70$), we retained the variable with the largest test statistic in Kruskal–Wallis tests comparing habitat variables among classes of overall richness and richness within guilds (see Section 2).

We used stepwise ordinal logistic regression (SAS Institute, 1990) to develop statistical models for predicting classes of richness overall and for guilds across all sites. We classified overall richness and richness within guilds for each stand as low, moderate, or high by dividing observations across all sampling points into quartiles and assigning observations in each stand to the first quartile (low richness), combined second and third quartiles (moderate richness), or fourth quartile (high richness). We also included an indicator variable for study site (AR, SC1, SC2, WV) to control for possible variation among sites.

Stepwise logistic regression builds models by selecting subsets of explanatory variables that best explain a categorical response variable, classes of species richness in our case (SAS Institute, 1990). Explanatory variables were selected for initial inclusion and subsequent retention in all models at the $\alpha = 0.05$ level. For both dependent and independent categorical variables, logistic regression evaluates variation among the categories by setting the intercept of the logistic function (dependent variables) or the parameter estimate (independent variables) for 1 category to 0 and allowing those of remaining categories to vary. Statistically significant differences (Wald's-χ^2; SAS Institute, 1990) between these estimates indicate important variation between categories. For all our analyses, the intercept for richness class 1 (low richness) and the parameter estimate for the West Virginia site were set to 0. We assessed the fit of logistic models to the data used to generate them using the receiver operating characteristic (ROC) statistic (Hosmer and Lemeshow, 2000). An ROC = 0.5 indicates the model does not discriminate among the data. An ROC between 0.7 and 0.8 indicates acceptable discrimination, between 0.8 and 0.9 indicates excellent discrimination, and >0.9 indicates outstanding discrimination (Hosmer and Lemeshow, 2000). We assessed the relative contribution of each variable included in models using global odds ratios, i.e. the likelihood of richness observations being assigned to richness class 1 versus classes 2 and 3 combined based on the contribution of a single variable to the overall model. We calculated 95% Wald's confidence limits (SAS Institute, 1990) for each odds ratio. Confidence limits that include 1 indicate that the odds of a richness observation being assigned to class 1 or to classes 2 and 3 based on that variable are even. In this case, the variable may add information to the overall model but does not itself make a strong contribution to distinguishing classes of richness.

3. Results

Using logistic regression analysis, we generated models that explained classes of species richness overall and among the selected guilds. Model discrimination ranged from acceptable to excellent (Tables 2–5).

The model for overall species richness distinguished among all three richness classes (Table 2). Overall species richness did not differ among the study sites, but had a strong (i.e. an odds ratio that differed strongly from 1) positive relationship with net curvature of the terrain, a weak (i.e. an odds ratio that differed slightly from 1) positive relationship with standard deviation of age on a fine/moderate scale and total road length (coarse) at a fine scale. Overall species richness also had a strong negative relationship with exposure at a broad scale. Positive relationships existed with stand area, total road length (coarse) and total stream length (coarse) at broad scales, and a negative relationship existed with area in mixed forest at the broad scale; although these variables contributed information to the overall model, they did not distinguish among richness classes. Model fit was acceptable to excellent (Table 2).

Table 2
Models for predicting probability of belonging to classes of overall avian richness calculated using stand- and landscape-level data on four managed forest landscapes in the Southeastern US

Intercepts		Slope	Variable	Scale[a]	Effect size[b]			ROC[c]
Richness class (n)	Value[d]				Odds ratio	LCL	UCL	
1 (150)	0.0000A	0.9620	Curvature		2.617	1.086	6.307	0.77
2 (357)	0.4849B	3.116×10^{-7}	Stand area		1.000	1.000	1.000	
3 (193)	−2.4282C	−0.4618	Exposure	1000	0.630	0.489	0.812	
		0.0456	Standard deviation of age	200	1.047	1.029	1.065	
		0.0065	Total road length (coarse)	100	1.007	1.003	1.010	
		0.0001	Total road length (coarse)	1000	1.000	1.000	1.000	
		0.0002	Total stream length (coarse)	1000	1.000	1.000	1.000	
		-1.210×10^{-6}	Mixed forest area	1000	1.000	1.000	1.000	

Richness classes represent low (class 1), medium (class 2), and high richness (class 3).

[a] Radius (m) of circular neighborhood centered on sampling point.

[b] Odds of being in class 1 vs. classes 1 and 2 combined, with lower and upper 95% Wald confidence limits.

[c] Receiver operating characteristic, indicates goodness of fit for the model. 0.7–0.8 = acceptable, 0.8–0.9 = excellent, >0.9 = outstanding.

[d] Intercepts with the same letter do not differ.

Table 3
Models for predicting probability of belonging to classes of richness for migratory guilds calculated using stand- and landscape-level data on four managed forest landscapes in the Southeastern US

Guild	Intercepts		Slope	Variable	Scale[a]	Effect size[b]			ROC[c]
	Richness class (n)	Value[d]				Odds ratio	LCL	UCL	
Neotropical migrants	1 (139)	0.0000A	1.4997	Curvature		4.480	1.801	11.142	0.79
	2 (303)	−0.7315B	2.519×10^{-7}	Stand area		1.000	1.000	1.000	
	3 (258)	−3.3153C	−0.5926	Exposure	1000	0.553	0.429	0.713	
			−3.4312	Evenness of forest types	1000	0.032	0.007	0.142	
			3.6023	Fragmentation of forest type	1000	36.684	3.722	361.519	
			0.0551	Standard deviation of age	200	1.057	1.038	1.076	
			−0.0052	Total road length (fine)	100	0.995	0.992	0.997	
			0.0001	Total road length (fine)	1000	1.000	1.000	1.000	
			0.0098	Total road length (coarse)	100	1.010	1.007	1.013	
			0.0003	Total stream length (coarse)	1000	1.000	1.000	1.000	
			-1.000×10^{-5}	Mixed forest area	200	1.000	1.000	1.000	
			-2.000×10^{-5}	Pine forest area	100	1.000	1.000	1.000	
Short-distance migrants	1 (77)	0.0000A	0.0000A[e]	Site: West Virginia		–	–	–	0.67
	2 (426)	−0.4262A	−0.4193B	Site: Arkansas		0.116	0.056	0.240	
	3 (197)	−3.6971B	−0.4432B	Site: South Carolina 1		0.114	0.053	0.245	
			−0.8693C	Site: South Carolina 2		0.074	0.033	1.69	
			1.3308	Fragmentation of forest age	100	3.784	1.036	13.821	
			2.2334	Fragmentation of forest age	1000	9.332	1.710	50.927	
			0.0010	Total road length (coarse)	200	1.001	1.000	1.002	
			-3.000×10^{-5}	Hardwood forest area	100	1.000	1.000	1.000	
			1.500×10^{-5}	Pine forest area	100	1.000	1.000	1.000	
Residents	1 (104)	0.0000A	0.0000A	Site: West Virginia		–	–	–	0.74
	2 (360)	−0.2971B	−0.6155B	Site: Arkansas		2.394	1.142	5.020	
	3 (236)	−3.2716C	1.2428C	Site: South Carolina 1		15.353	6.730	35.024	
			0.8612D	Site: South Carolina 2		10.482	4.624	23.764	
			0.0190	Standard deviation of age	200	1.019	1.002	1.037	
			-5.000×10^{-5}	Area in 1–5-yr-old stands	100	1.000	1.000	1.000	
			0.0001	Total road length (coarse)	1000	1.000	1.000	1.000	
			0.0003	Total stream length (fine)	500	1.000	1.000	1.000	
			5.065×10^{-6}	Hardwood forest area	200	1.000	1.000	1.000	

Richness classes represent low (class 1), medium (class 2), and high richness (class 3).

[a] Radius (m) of circular neighborhood centered on sampling point.

[b] Odds of being in class 1 vs. classes 1 and 2 combined, with lower and upper 95% Wald confidence limits.

[c] Receiver operating characteristic, indicates goodness of fit for the model. 0.7–0.8 = acceptable, 0.8–0.9 = excellent, >0.9 = outstanding.

[d] Intercepts with the same letter do not differ.

[e] Richness among sites with the same letter did not differ.

3.1. Migratory status guilds

Among the guilds based on migratory status (Table 3), the model for neotropical migrants distinguished among all three richness classes (Table 3). Richness of neotropical migrants did not differ among study areas, but had a strong positive relationship with terrain curvature and fragmentation of forest type at a broad scale, and a weak positive relationship with standard deviation of age on a fine/moderate scale and total road length (coarse) on a fine scale. Richness of neotropical migrants also had a strong negative relationship with evenness of forest types at a broad spatial scale and terrain exposure, and a weak negative relationship with total road length (fine) on a fine scale. Positive relationships existed with stand area, total road length (fine) and total stream length (coarse) on broad scales, and negative relationships existed with area in mixed forest on a fine/moderate scale and area in pine forest on a fine scale; although these variables contributed information to the overall model, they did not distinguish among richness classes. Model fit was acceptable to excellent.

The model for short-distance migrants distinguished high from low and medium richness, but could not distinguish between low and medium richness (Table 3). WV had the highest richness of short-distance migrants, SC2 had the lowest, and AR and SC1 had moderate richness. Richness of short-distance migrants had a strong positive relationship with fragmentation of age classes on fine and broad scales. Positive relationships existed with total road length (coarse) on a fine/moderate scale and area in pine forest on a fine scale, and a negative relationship existed with area in hardwood forest on a fine scale; these variables contributed information to the overall model but did not distinguish among richness classes. Model fit was marginal.

The model for residents distinguished among all three richness classes (Table 3). SC2 had the highest richness, followed by SC1, AR, and WV. Richness of residents had a

Table 4
Models for predicting probability of belonging to classes of richness for habitat guilds calculated using stand- and landscape-level data on four managed forest landscapes in the Southeastern US

Guild	Intercepts		Slope	Variable	Scale[a]	Effect size[b]			ROC[c]
	Richness class (n)	Value[d]				Odds ratio	LCL	UCL	
Scrub/shrub nesters	1 (157)	0.0000A	0.0214	Stand age		1.022	1.001	1.043	0.84
	2 (306)	2.1217B	−0.0060	Distance to nearest road (fine)		0.994	0.992	0.996	
	3 (237)	−0.9000C	0.0007	Distance to nearest water (coarse)		1.001	1.000	1.001	
			−2.9867	Fragmentation of forest age	1000	0.050	0.009	0.292	
			0.0545	Standard deviation of age	1000	1.056	1.033	1.080	
			−0.0526	Mean forest age	100	0.949	0.926	0.972	
			−0.0005	Total road length (fine)	500	1.000	0.999	1.000	
			0.0002	Total road length (coarse)	1000	1.000	1.000	1.000	
			0.0003	Total stream length (coarse)	1000	1.000	1.000	1.000	
			1.607×10^{-6}	Non-forested area	1000	1.000	1.000	1.000	
			3.000×10^{-5}	Hardwood forest area	100	1.000	1.000	1.000	
			6.636×10^{-5}	Pine forest area	200	1.000	1.000	1.000	
Woodland nesters	1 (171)	0.0000A	0.0000A[e]	Site: West Virginia		–	–	–	0.80
	2 (351)	2.0017B	−0.7908B	Site: Arkansas		0.159	0.087	0.290	
	3 (178)	−0.6884C	0.2814C	Site: South Carolina 1		0.465	0.190	1.140	
			−0.5372D	Site: South Carolina 2		0.205	0.079	0.536	
			−0.0438	Slope		0.957	0.927	0.988	
			−0.3005	Aspect		0.740	0.584	0.939	
			1.4056	Curvature		4.078	1.717	9.689	
			−0.5720	Exposure	1000	0.564	0.436	0.731	
			0.0466	Standard deviation of age	1000	1.048	1.030	1.066	
			−0.0001	Area in 1–5-yr-old stands	100	1.000	1.000	1.000	
			-6.690×10^{-6}	Area in 21–30-yr-old stands	200	1.000	1.000	1.000	

Richness classes represent low (class 1), medium (class 2), and high richness (class 3).

[a] Radius (m) of circular neighborhood centered on sampling point.

[b] Odds of being in class 1 vs. classes 1 and 2 combined, with lower and upper 95% Wald confidence limits.

[c] Receiver operating characteristic, indicates goodness of fit for the model. 0.7–0.8 = acceptable, 0.8–0.9 = excellent, >0.9 = outstanding.

[d] Intercepts with the same letter do not differ.

[e] Richness among sites with the same letter did not differ.

weak positive relationship with standard deviation of age at a fine/moderate scale. Positive relationships existed with total road length (coarse) on a broad scale, total stream length (fine) on a moderate scale, and area in hardwood forest on a fine/moderate scale, and a negative relationship existed with area in 1–5-yr-old stands on a fine scale; these variables contributed information to the overall model but did not distinguish among richness classes. Model fit was acceptable.

3.2. Breeding habitat guilds

The model for scrub/shrub nesters distinguished among all three richness classes (Table 4). Richness of shrub/scrub nesters did not differ among study areas but had a weak positive relationship with stand age and standard deviation of age on a broad scale. Richness of shrub/scrub nesters also had a strong negative relationship with fragmentation of forest age classes and weak negative relationships with distance to nearest road (fine) and mean forest age on a fine scale. Positive relationships existed for distance to nearest water (coarse), area in hardwood forest on a fine scale, area in pine forest on a fine/moderate scale, and broad-scale measures for area in non-forest, total road length (coarse), total stream length (coarse),whereas a negative relationships existed for total road length (fine) on a moderate scale; these variables contributed information to the overall model but did not distinguish among richness classes. Model fit was excellent.

The model for woodland nesters distinguished among all three richness classes (Table 4). Richness of woodland nesters was highest on SC1, followed by WV, SC2, and AR. Richness had a strong positive relationship with terrain curvature a weak positive relationship with standard deviation of age at a broad scale, a strong negative relationship with aspect and terrain exposure on a broad scale, and a weak negative relationship with slope. Negative relationships with area in 1–5-yr-old stands on a fine scale and area in 21–30-yr-old stands on a fine/moderate scale contributed information to the overall model but did not distinguish among richness classes. Model fit was acceptable to excellent.

3.3. Nest type guilds

The model for richness of cavity nesters distinguished among all three richness classes (Table 5). SC1 had the highest richness, followed by SC2, WV, and AR. Richness of cavity nesters had weak positive relationships with stand age and standard deviation of age at a fine/moderate scale. Positive relationships existed with area in 1–5-yr-old stands on a broad scale and area in hardwood forest on a fine scale, whereas a negative relationship existed with area in 1–5-yr-old stands on a fine scale; these variables

Table 5
Models for predicting probability of belonging to classes of richness for nest type guilds calculated using stand- and landscape-level data on four managed forest landscapes in the Southeastern US

Guild	Intercepts		Slope	Variable	Scale[a]	Effect size[b]			ROC[c]
	Richness class (*n*)	Value[d]				Odds ratio	LCL	UCL	
Cavity nesters	1 (80)	0.0000A	0.0000A[e]	Site: West Virginia		–	–	–	0.71
	2 (333)	−0.5870B	−0.5554B	Site: Arkansas		2.197	1.118	4.319	
	3 (287)	−3.4479C	1.2251C	Site: South Carolina 1		13.034	6.234	27.253	
			0.6727D	Site: South Carolina 2		7.502	3.520	15.989	
			0.0080	Stand age		1.008	1.002	1.014	
			0.0260	Standard deviation of age	200	1.026	1.009	1.044	
			-5.000×10^{-5}	Area in 1–5-yr-old stands	100	1.000	1.000	1.000	
			6.269×10^{-7}	Area in 1–5-yr-old stands	1000	1.000	1.000	1.000	
			2.400×10^{-5}	Hardwood area	100	1.000	1.000	1.000	
Ground nesters	1 (106)	0.0000A	−0.0017	Distance to nearest road (fine)		0.998	0.997	1.000	0.78
	2 (371)	1.0460B	−0.3946	Exposure	1000	0.674	0.526	0.864	
	3 (223)	−2.1780C	−1.6968	Evenness of forest types	1000	0.183	0.081	0.414	
			0.0248	Standard deviation of age	200	1.025	1.003	1.048	
			0.0488	Standard deviation of age	1000	1.050	1.023	1.078	
			−0.0129	Mean forest age	100	0.987	0.978	0.997	
			-4.590×10^{-5}	Area in 1–5-yr-old stands	100	1.000	1.000	1.000	
			5.870×10^{-6}	Area in 21–30-yr-old stands	200	1.000	1.000	1.000	
			0.0042	Total road length (coarse)	100	1.004	1.001	1.007	
			-4.0×10^{-5}	Area in mixed forest	100	1.000	1.000	1.000	
Canopy nesters	1 (136)	0.0000A	0.0000A[e]	Site: West Virginia		–	–	–	0.75
	2 (280)	−0.3654B	−0.8108B	Site: Arkansas		1.002	0.506	1.984	
	3 (284)	−2.6882C	1.1979C	Site: South Carolina 1		7.468	3.524	15.826	
			0.4256D	Site: South Carolina 2		3.450	1.584	7.515	
			−0.3564	Aspect		0.770	0.550	0.892	
			1.3349	Curvature		3.800	1.651	8.743	
			0.0359	Standard deviation of age	100	1.037	1.107	1.056	
			0.0112	Mean forest age	100	1.011	1.002	1.021	
			−0.0001	Area in 1–5-yr-old stands	100	1.000	1.000	1.000	
			9.693×10^{-7}	Area in 1–5-yr-old stands	1000	1.000	1.000	1.000	
			-5.470×10^{-6}	Area in 21–30-yr-old stands	200	1.000	1.000	1.000	

Richness classes represent low (class 1), medium (class 2), and high richness (class 3).

[a] Radius (m) of circular neighborhood centered on sampling point.

[b] Odds of being in class 1 vs. classes 1 and 2 combined, with lower and upper 95% Wald confidence limits.

[c] Receiver operating characteristic, indicates goodness of fit for the model. 0.7–0.8 = acceptable, 0.8–0.9 = excellent, >0.9 = outstanding.

[d] Intercepts with the same letter do not differ.

[e] Richness among sites with the same letter did not differ.

contributed information to the overall model but did not distinguish among richness classes. Model fit was acceptable.

The model for richness of ground nesters distinguished between all three richness classes (Table 5). Richness of ground nesters did not differ among study areas, but had a weak positive relationship with standard deviation of age at fine/moderate and broad scales and total road length (coarse) at a fine scale. Richness also had strong negative relationships with exposure of terrain and evenness of forest types at broad scales; a weak negative relationship existed with mean forest age on a fine scale. A positive relationship existed for area in 21–30-yr-old stands on a fine/moderate scale, and a negative relationship existed for distance to nearest road (fine), area in 1–5-yr-old stands at fine scales, and area in mixed forest at fine scales; although these variables contributed information to the overall model, they did not distinguish among richness classes. Model fit was acceptable to excellent.

The model for richness of canopy nesters distinguished between all three classes of richness (Table 5). SC1 had the highest richness, followed by SC2, WV, and AR. Richness of canopy nesters had a strong positive relationship with terrain curvature, a weak positive relationship with standard deviation of age and mean forest age at fine scales, and a strong negative relationship with aspect. Positive relationships existed with total road (fine) on a fine/moderate scale, total stream (coarse) length on a broad scale, area in 1–5-yr-old stands on a broad scale, and area in hardwood forest on a fine scale, and negative relationships existed with area in 1–5-yr-old stands on a fine scale, and area in 21–30-yr-old stands on fine/moderate scale; although these variables contributed information to the overall model, they did not distinguish among richness classes. Model fit was acceptable to excellent.

4. Discussion

Our analyses resulted in models with acceptable to excellent fit that explained much of the distribution of avian richness across the four landscapes used in our study. The only model with relatively poor fit was that for short-distance migrants. Overall richness and richness of neotropical migrants, shrub/scrub nesters, and ground nesters did not vary among study sites. Among the guilds showing a site effect, SC1 had the highest richness of residents, cavity nesters, canopy nesters, and woodland nesters. Odds ratios suggested that differences in richness for these guilds between SC1 and the other sites were pronounced (i.e. richness of cavity nesters was 13 times more likely to be moderate to high in SC1 than in WV; Tables 2–5). WV had the highest richness of short-distance migrants (Tables 2–5). AR consistently had the lowest richness among study sites, with the exception of short-distance migrants (lowest at SC2; Tables 2–5).

Topography was important in six of the 10 models. Terrain curvature was strongly and positively associated with overall richness, and richness of neotropical migrants, woodland nesters, and canopy nesters. Richness of neotropical migrants, woodland nesters, and ground nesters was negatively associated with terrain exposure (i.e. richness was lower in more exposed locations). Richness of woodland nesters and canopy nesters was negatively associated with aspect (i.e. richness was higher on hot, sunny sites than on cool, shaded sites). Richness of woodland nesters was negatively related to slope; site and topographic variables appeared to be nearly the sole predictors of richness for this guild. When site and topography were included in models, they tended to be the variables with the strongest relationships to richness. We therefore hypothesize that the habitat heterogeneity caused by geographic and topographic variability on broad scales are likely to be more important determinants of avian richness than heterogeneity in forest age and type created by forest management on fine scales.

Whereas all 10 models included landscape-scale variables, only five included stand-scale variables. Stand area made very weak but positive contributions to overall richness, and richness of neotropical migrants. Stand age was weakly but positively associated with richness of scrub/shrub nesters and cavity nesters. Stand type (i.e. pine, hardwood, mixed pine/hardwood, non-forest) was not included in any models. Although associations clearly exist between the presence/abundance of bird species and structural features (e.g. snags, number of canopy layers; Kilgo et al., 2002), stand-scale variables appeared to contribute little to our models for predicting avian richness (i.e. few stand-scale variables were selected for models and those that were generally had odds ratios near 1; Tables 2–5). The small number of stand-scale variables included in our analyses and their relatively general nature as habitat variables probably does not represent a fair evaluation of the relative importance of stand-scale versus landscape-scale variables in predicting avian richness. A more complete comparison, including stand-scale variables that go beyond those typically maintained by forest managers, would likely support stronger conclusions. Nonetheless, our results are consistent with previous work showing that landscape variables are at least as predictive of avian distributions as more detailed stand-scale variables (Mitchell et al., 2001).

Consistent with our first prediction, landscape variables included in models comprised both measures of availability and configuration of forest habitats on the landscape, although measures of availability predominated (Tables 2–5). This suggests that landscape configuration may be important to some bird communities. Evidence for effects of configuration was substantial for neotropical migrants, short-distances migrants, and scrub/shrub nesters. By contrast, measures of availability were included in all models, with effects ranging from strong to weak. The ubiquity of associations we observed with availability, along with high variability in the strength of associations with both availability and configuration, may explain some of the disparities in the importance of landscape configuration observed by different studies. Further, most landscape studies have focused on presence-absence or demography of individual species (e.g. McGarigal and McComb, 1995; Drolet et al., 1999; Villard et al., 1999; Mitchell et al., 2001; Lichstein et al., 2002) and inferred community-level patterns through synthesis of patterns among individual species. If landscape-level habitat associations are unique to the life histories of individual species (Mitchell et al., 2001), it may be that landscape-level patterns cannot be detected until a sufficient number of ecologically similar species are considered together, such as the guilds we used. Studies that have examined landscape associations at the community level directly (e.g. Penhollow and Stauffer, 2000; Rodewald and Yahner, 2001) have found more consistent evidence for effects of landscape configuration on avian communities than have studies based on individual species.

The strongest landscape-scale relationships between avian diversity were those with measures of heterogeneity, consistent with our second prediction. A positive relationship with variability in forest age classes was included in all models except for short-distance migrants. Evenness of forest types was negatively related to richness of neotropical migrants and ground nesters. Richness for neotropical migrants was strongly and positively associated with fragmentation (i.e. a breaking up of habitat; Fahrig, 2003) of forest type. Fragmentation of age classes was positively associated with richness of short-distance migrants (at two spatial scales), but negatively associated with richness of shrub-scrub nesters. From these results we hypothesize that a diversity of forest types and forest ages on a landscape is generally beneficial to avian richness, although overly fragmented age classes undoubtedly affect avian richness adversely.

Relatively weak landscape-scale relationships between richness and road length and stream length were included in nearly all models. Contrary to our third prediction, road length was positively, but weakly, related to overall richness, and richness for canopy nesters, residents, short-distance migrants, and woodland nesters. Apparently contradictory effects of roads are evident in models for richness of neotropical migrants and shrub/scrub nesters, where the sign of the relationship depended on whether the road data were coarse (positive) or fine (negative; with the exception of richness of neotropical migrants on a broad scale). These results suggest that choice of data can influence modeling results; whereas large, primary roads such as those depicted on USGS census maps may have no ill effect on avian richness within large forested landscapes, the addition of smaller roads in the analysis may indicate otherwise. Additionally, effects of roads appeared to vary with scale in some models. For overall richness, roads had positive effects on both fine and broad scales. For richness of neotropical migrants and scrub/shrub nesters, roads had a positive effect on broad scales, but a negative effect on fine-moderate scales. Richness of ground nesters, and canopy nesters was positively associated with total road length at a fine scale. Distance to nearest road was negatively associated with richness of ground nesters only. Establishing (or hypothesizing) a cause-effect relationship between avian communities and roads is difficult because mechanisms by which roads interact with bird richness are unclear, beyond the possibility that roads fragment bird habitat and promote edge effects (e.g. increased predation and brood parasitism). In the case of logging roads, which made up most of the roads on our study areas, the likelihood that narrow, little-used gravel roads would adversely impact avian communities seems small (King and DeGraaf, 2002, but see Ortega and Capen, 2002). On the other hand, a reason why they should benefit avian communities is equally unclear. We hypothesize that: (1) on industrial forests, apparent positive effects of roads may be a by-product of management practices that contribute to forest heterogeneity, thus increasing avian richness, and (2) the roads themselves may contribute to heterogeneity because of the shrub/scrub habitat associated with roadsides. At each of the four neighborhood scales, we found significant positive correlations ($P < 0.05$) between road density and habitat measures that likely were associated with recent forest management activities (i.e. area in forest <4 years old, area in forest 5–30 years old, fragmentation index). We note, however, that no variables we used to evaluate effects of roads were strongly associated with any measure avian richness; all had odds ratios equal or near 1. Thus, any insights our analyses provide into the effects of roads on avian richness are tenuous and require further testing.

Total stream length measured on a coarse grain and a broad scale was positively, but very weakly (i.e. odds ratio = 1), associated with overall richness, and richness of neotropical migrants, scrub/shrub nesters, and canopy nesters. Total stream length measured on a fine grain and a moderate scale was positively associated only with richness of residents. Because the merits of the model for residents are somewhat questionable (see below) and stream length measured on a coarse grain was common among other models, it is uncertain whether water features measured on a fine grain are important to explaining richness of birds on a landscape scale.

Landscape-scale associations between richness and area in different forest types were very weak (i.e. odds ratio = 1) across all models. Area in mixed forest was associated negatively with overall richness, and richness of neotropical migrants and ground nesters. Area in hardwood forest was positively associated with richness of residents, scrub/shrub nesters, cavity nesters, and canopy nesters, but negatively associated with richness of short-distance migrants. Area in pine forest was positively associated richness of short-distance migrants and scrub/shrub nesters and negatively associated with richness of neotropical migrants. Because effects of forest type were relatively very weak when present, we hypothesize that avian richness is less strongly linked to particular forest types (e.g. pine, hardwood) than to forest structure and successional stages.

In agreement with our fourth prediction, the scales at which landscape variables proved significant were not consistent across any measure of avian richness or across any metric. The absence of a single scale where landscape-level variables are predictive of avian distributions is consistent with the findings of Mitchell et al. (2001) and Lichstein et al. (2002). Mitchell et al. (2001) concluded that scales at which landscape configuration is predictive is likely unique to the natural histories of individual species. For ecologically similar species such as those in the guilds we modeled, it is possible that life histories are sufficiently similar to allow the use of common scales of measurement. Across the myriad life histories included in overall richness, however, the possibility of common scales would seem much less likely. Further work is needed to discern whether the scales selected for the overall richness model are simply the best-fitting averages of the many scales associated with each of the included species, whether they represent causal linkages between landscape configuration and community structure, or whether they are no more than spurious correlations. Our insights into scale are correlative and do not shed light on the ecological processes that could underlie the patterns we observed. They may, however, suggest appropriate spatial scales for investigating causal mechanisms. Given the multitude of candidate mechanisms (e.g. dispersal, structured population dynamics, predator–prey interactions, foraging, fitness-based habitat selection (Johns, 1980), territoriality, etc.), the identification of scales at which patterns are manifested may be an important first step for developing mechanistic hypotheses, rather than arbitrarily presuming a mechanism (e.g. metapopulation dynamics) and choosing a scale of investigation accordingly.

The landscape factors most consistently associated with avian richness across all models were positive relationships with topographic complexity and variability of forest age across multiple scales and negative relationships with terrain exposure on a broad scale. These relationships suggest broadly rolling terrain with a diversity of forest types and age classes should maximize avian richness. Our results accord with other studies that found topography to be strongly associated with avian richness on landscape scales (Rahbek and Graves, 2001; Luoto et al., 2004). Intuitively and over sufficiently broad spatial scales (e.g. the Southeastern US), variation in topography, with its associated variation in hydrology and exposure to the elements, should contribute considerably to the heterogeneity of habitats available to birds. The absence of site indicator variables in the model for overall avian richness suggests that, for all the differences among the sites (e.g. unmanaged hardwood forests in the mountains of West Virginia, intensively managed pine forests on the coastal plain of South Carolina), avian species richness, but not necessarily constituent species, was relatively consistent across all study sites. Our results suggest that, within the Southeastern US, relationships between richness of avian species and landscape structure do not vary with latitude, longitude, or predominant overstory type. We hypothesize that the primary factors governing richness of avian species across the Southeastern US is the diversity of habitats associated with variable terrain and the diversity of forest ages and types.

Because landscape-level models could be fitted to the short-distance migrant, resident, and neotropical migrant guilds, we refuted our fifth prediction that landscape-variables would be important predictors for neotropical migrants but not for short-distance migrants and residents. We do not believe grounds for doing so are firm, however. Although the model for richness of neotropical migrants showed good fit and contained several strong, landscape-level relationships, the model for short-distance migrants fit the data only weakly and the model for residents contained no strong landscape-level relationships. Thus, we conclude that our results support the finding from previous studies (Mitchell et al., 2001, Lichstein et al., 2002) that residents and short-distance migrants are less sensitive to landscape characteristics than neotropical migrants.

The models for shrub/scrub and woodland nesters suggest important relationships between these two guilds and availability of young forests and topography, respectively. Richness of shrub/scrub nesters had strong negative associations with fragmentation of forest age on a broad scale and mean forest age on a fine scale; a positive association existed with variability in forest age on a broad scale. This model had the strongest fit of any that we generated (ROC = 0.84) and is consistent with previous research (Mitchell et al., 2001) that suggests early-successional shrub/scrub species can be area-sensitive, requiring relatively broad, homogeneous expanses of young forested stands. The strongest habitat relationships for woodland nesters were with topography only, with richness positively associated with terrain curvature and negatively associated with slope, aspect, and terrain exposure on a broad scale. These results suggest strong regional variability in the richness of woodland nesters, with variability within sites driven more by topographic diversity than forest characteristics.

Cavity nesters had their strongest relationship (positive) with variability in forest age on a fine/moderate scale. Model fit for cavity nesters was relatively modest (ROC = 0.71), possibly because we included woodpeckers in this guild. Because woodpeckers are relatively large among the species we sampled and their movements can take them well beyond the sizes of neighborhoods we evaluated, our landscape variables may have been insufficient for fully assessing richness of a guild including woodpeckers. The negative relationship between richness of cavity nesters and area in 1–5-yr-old forest on a fine scale suggests a potential negative effect, possibly due to the removal of cavity trees. The positive association with the same variable on a broad scale however indicates that availability of early successional habitat on a landscape remains important to species within this guild.

For canopy nesters, odds ratios suggested that topographical variables (i.e. terrain curvature, variability in age on a broad scale, aspect) were much more important in explaining richness of canopy nesters than variability in forest age (Table 5). The importance of topography over forest characteristics seems surprising given that relatively mature trees are required to provide nesting habitat for this guild. The positive relationship with variability of age on broad scales is consistent with findings of Mitchell et al. (2001) that heterogeneity of forest age was an important factor for several species typically considered residents of mature forests.

The primary landscape features associated with avian diversity appear to have been geographic location, topography, and heterogeneity of habitat. These findings have important implications for forest management. Diversity of forest structures produced by silvicultural practices in managed forests of the Southeastern US appear to affect diversity of avian species positively by diversifying the habitats available on a landscape beyond those already provided by variation in terrain and hydrology. Whereas high levels of disturbance and heterogeneity (e.g. high fragmentation of age classes) are likely to affect avian diversity adversely, those levels do not appear to have been reached generally on the landscapes we studied.

Caution should be exercised, however, to avoid over-interpretation of our findings. Species richness is, at best, a very coarse index of community structure. Because it incorporates no information on species turnover or changes in relative abundance among species, it is insensitive to dynamics important to community structure and function. Our approach assumes that species richness is a positive indicator of community health, and that correlations between richness and landscape features represent cause–effect relationships that define community function. Further, we used presence–absence data to estimate species richness, a very coarse standard in ecological terms. Lacking demographic data (i.e. survival, reproduction, population growth rate), we assumed that the presence of a bird represented a healthy breeding population with strong prospects for persistence. Good reasons exist to question each of these assumptions (Sallabanks et al., 2000; Thompson et al., 2000), and our findings must be viewed as conditional upon more biologically rigorous investigation. Nonetheless, the statistical rigor of our research is unusually high for a landscape-level study because we used data from four landscapes. Thus, our findings have generality that extends well beyond what might have been found for any one of our landscapes alone and should be relatively robust for avian communities of the Southeastern US. Further research should investigate the cause/effect relationships that might underlie the patterns we observe, preferably using a manipulative, long-term, and hypothetico-deductive study design (Sallabanks et al., 2000, Thompson et al., 2000).

5. Application

Few practical tools for managing biodiversity are available to forest managers (Sallabanks and Marzluff, 2000). In addition to providing insights into how forest management affects avian richness, our models provide a valuable tool to forest managers seeking to address biodiversity criteria for forest certification.

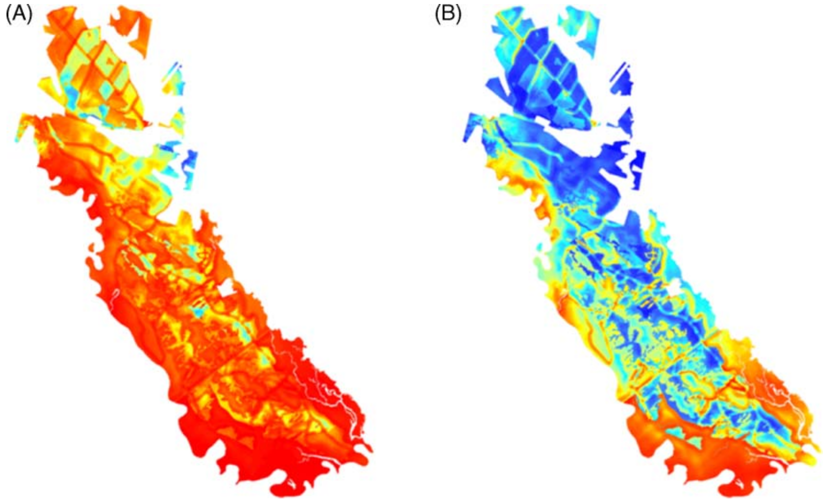

Fig. 1. Map representing probability of overall avian richness being low to moderate (A) and high (B) on the SC1 study site (South Carolina, Woodbury and Giles Bay tracts) used to model relationships between avian richness and stand- and landscape-level characteristics on four study sites in the Southeastern US. Blue indicates low probability, red indicates high probability. Classes of richness estimated by logistic regression are nested; e.g. if sites are assigned to a high richness class because they contain greater than nine species, then by definition they would also contain the number of species required for classification in medium (between four and eight species) and low richness (greater than four species) classes. This is reflected in figure, where A shows the probability that sites qualify for the low/medium richness class, which would include the sites shown to qualify for the high richness class in B.

Monitoring all biodiversity on a landscape is unfeasible, but data on avian presence–absence is relatively inexpensive and easy to collect and birds clearly are an important component of overall biodiversity. Using forest inventory and topographical data that are readily available to most forest managers, our models can portray graphically the distribution of avian richness on a forest, either real or hypothetical, based on the distribution of forest structure on a landscape scale (Fig. 1). The maps will allow managers the unprecedented ability to estimate quantitatively the contribution of their management practices to the maintenance of an important component of biodiversity on their landscapes. By applying our models to future landscape conditions, managers can explore the effects of alternative management plans on avian richness. Statistical analysis of a series of probability surfaces representing management alternatives would allow managers to quantify the relative effects of each alternative on biodiversity. Partial satisfaction of biodiversity criteria required for sustainable forestry certification programs can thus be demonstrable rather than subjective.

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References

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S., Soluk, D.A., 1987. Ecological neighborhoods: scaling environmental patterns. OIKOS 49, 340–346.

American Forest and Paper Association, 2005. Sustainable Forestry Initiative® (SFI) Standard 2005–2009 Edition. The Sustainable Forestry Initiative® Program, Sustainable Forestry Board, and American Forest & Paper Association®, Washington, DC.

Askins, R.A., Philbrick, M.J., 1987. Effect of changes in regional forest abundance of forest and the composition of a forest bird community. Wilson Bull. 99, 7–21.

Beers, T.W., Dress, P.E., Wensel, L.C., 1966. Aspect transformation in site productivity research. J. Forest. 64, 691–692.

Bissonette, J., Storch, I., 2003. Understanding fragmentation: getting closer to 42. Conserv. Ecol. 7(2):r5. Online URL: http://www.consecol.org/vol7/iss2/resp5.

Bolger, D.T., Scott, T.A., Rotenberry, J.T., 1997. Breeding bird abundance in an urbanizing landscape in coastal Southern California. Conserv. Biol. 11, 406–421.

Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. Conserv. Biol. 14, 342–355.

DeStefano, S., 2002. Regional and national issues for forest wildlife research and management. Forest Sci. 48, 181–189.

Drolet, B., Desrochers, A., Fortin, M., 1999. Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. CONDOR 101, 699–704.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Ann. Rev. Ecol. Evol. Syst. 34, 487–515.

Flather, C.H., Sauer, J.R., 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. Ecology 77, 28–35.

Guynn Jr., D.C., Guynn, S.T., Layton, P.A., Wigley, T.B., 2004. Biodiversity metrics in sustainable forestry programs. J. Forest. 102, 46–52.

Hamel, P.B., 1992. The land manager's guide to the birds of the South. In: The Nature Conservancy, Chapel Hill, NC, 367 pp. + appendices.

Hamel, P.B., LeGrand Jr., H.E., Lennartz, M.R., Gauthreaux Jr., S.A., 1982. Bird-habitat relationships on Southeastern forest lands. General Technical Report SE-22, US Department of Agriculture, Southeastern Forest Experiment Station.

Hargrove, W.W., Pickering, J., 1992. Pseudoreplication: a sine qua non for regional ecology. Landscape Ecol. 6, 251–258.

Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression, 2nd ed. Wiley, New York, NY, USA.

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

Kilgo, J.C., Gartner, D.L., Chapman, B.R., Dunning Jr., J.B., Franzreb, K.E., Gauthreaux, S.A., Greenberg, C.H., Levey, D.J., Miller, K.V., Pearson, S.F., 2002. A test of an expert-based bird-habitat relationship model in South Carolina. Wildlife Soc. Bull. 30, 783–793.

King, D.I., DeGraaf, R.M., 2002. The effect of forest roads on the reproductive success of forest-dwelling passerine birds. Forest Sci. 48, 391–396.

Lens, L., Dhondt, A.A., 1994. Effects of habitat fragmentation on the timing of crested tit Parus cristatus natal dispersal. IBIS 136, 147–152.

Lichstein, J.W., Simons, T.R., Franzreb, K.E., 2002. Landscape effects on breeding songbird abundance in managed forests. Ecol. Appl. 12, 836–857.

Loucks, C., Brown, N., Loucks, A., Cesareo, K., 2003. USDA forest service roadless areas: potential biodiversity conservation reserves. Conserv. Ecol. 7:5. Online URL: http://www.consecol.org/vol7/iss2/art5.

Luoto, M., Virkkala, R., Heikkinen, R.K., Rainio, K., 2004. Predicting bird richness using remote sensing in boreal agricultural-forest mosaics. Ecol. Appl. 14, 1946–1962.

Marzluff, J.M., Raphael, M.G., Sallabanks, R., 2000. Understanding the effects of forest management on avian species. Wildlife Soc. Bull. 28, 1132–1143.

Maurer, B.A., Villard, M., 1994. Population density: geographic variation in abundance of North American birds. Natl. Geogr. Res. Expl. 10, 306–317.

Manolis, J.C., Anderson, D.E., Cuthbert, F.J., 2000. Patterns in clearcut edge and fragmentation effect studies in northern hardwood-conifer landscapes: retrospective power analysis and Minnesota results. Wildlife Soc. Bull. 28, 1088–1101.

McGarigal, K., McComb, W.C., 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecol. Monogr. 65, 235–260.

Mitchell, M.S., Lancia, R.A., Gerwin, J.A., 2001. Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. Ecol. Appl. 11, 1692–1708.

Ortega, Y.K., Capen, D.E., 2002. Roads as edges: effects on birds in forested landscapes. Forest Sci. 48, 381–390.

Penhollow, M.E., Stauffer, D.F., 2000. Large-scale habitat relationships of neotropical migratory birds in Virginia. J. Wildlife Manage. 64, 362–373.

Peterjohn, B.G., Sauer, J.R., 1993. North American breeding bird survey annual summary 1990–1991. Bird Popul. 1, 1–24.

Rahbek, C., Graves, G.R., 2001. Multiscale assessment of patterns of avian richness. Proc. Natl. Acad. Sci. 98, 4534–4539.

Ralph, C.J., Geupel, G.R., Tyle, P., Martin, T.E., Sante, D.F., 1993. Handbook of Field Methods for Monitoring Landbirds. USDA Forest Service General Technical Report PSW-GTR-144.

Robbins, C.S., Dawson, D.K., Dowell, B.A., 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic States. Wildlife Monogr. 103.

Rodewald, A.D., Yahner, R.H., 2001. Influence of landscape composition on avian community structure and associated mechanisms. Ecology 82, 3493–3504.

Saab, V., 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecol. Appl. 9, 135–151.

Sallabanks, R., Arnett, E.A., Marzluff, J.M., 2000. An evaluation of research on the effects of timber harvest on bird populations. Wildlife Soc. Bull. 28, 1144–1155.

Sallabanks, R., Marzluff, J.M., 2000. Forest management and bird populations: an introduction. Wildlife Soc. Bull. 28, 1086–1087.

SAS Institute, 1990. SAS/STAT User's Guide, Version 6. SAS Institute, Cary, North Carolina, USA.

Scott, J.M., Heglund, P.J., Morrison, M.L., haufler, J.B., Raphael, M.G., Wall, W.A., Samson, F.B., 2002. Predicting Species Occurrences: Issues of Accuracy and Scale. Island Press, Washington, DC, USA.

Strittholt, J.R., Dellasala, D.A., 2001. Importance of roadless areas in biodiversity conservation in forested ecosystems: case study of the Klamath-Siskiyou ecoregion of the United States. Conserv. Biol. 15, 1742–1754.

Thompson III, F.R., Brawn, J.D., Robinson, S., Faaborg, J., Clawson, R.L., 2000. Approaches to investigate effects of forest management on birds in eastern deciduous forests: how reliable is our knowledge? Wildlife Soc. Bull. 28, 1111–1122.

Verboom, J., Schotman, A., Opdam, P., Metz, J.A.J., 1991. European nuthatch metapopulations in a fragmented agricultural landscape. OIKOS 61, 149–156.

Villard, M., Merriam, G., Maurer, B.A., 1995. Dynamics in subdivided populations of neotropical migratory birds in a fragmented temperate forest. Ecology 76, 27–40.

Villard, M., Trzcinski, M.K., Merriam, G., 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conserv. Biol. 13, 774–783.

Vos, C.C., Verboom, J., Opdam, P.F.M., Ter, C.J.F., 2001. Braak toward ecologically scaled landscape indices. Am. Nat. 183, 24–41.

Wiens, J.A., 1989. Spatial scaling in ecology. Funct. Ecol. 3, 385–397.

Wiens, J.A., 1995. Habitat fragmentation: island versus landscape perspectives on bird conservation. IBIS 137, S97–S104.