



Managed forest landscape structure and avian species richness in the southeastern US

Craig Loehle^{a,*}, T. Bently Wigley^b, Scott Rutzmoser^c, John A. Gerwin^d,
Patrick D. Keyser^e, Richard A. Lancia^f, Christopher J. Reynolds^g,
Ronald E. Thill^h, Robert Weihⁱ, Don White Jr.ⁱ,
Petra Bohall Wood^j

^aNational Council for Air and Stream Improvement, Inc., 552 S Washington Street, Suite 224, Naperville, IL 60540, USA

^bNational Council for Air and Stream Improvement, Inc., P.O. Box 340317, Clemson, SC 29634-0317, USA

^cAlabama Cooperative Fish and Wildlife Research Unit, School of Forestry and Wildlife Sciences,
108 M. White Smith Hall, Auburn University, Auburn, AL 36849, USA

^dNorth Carolina State Museum of Natural Sciences, P.O. Box 2955, Raleigh, NC 27655, USA

^eMeadWestvaco Corporation, Box 577, Rupert, WV 25984, USA

^fDepartment of Forestry, North Carolina State University, Box 8002, Raleigh, NC 27695, USA

^gWeyerhaeuser Company, P.O. Box 1060, Hot Springs, AR 71901, USA

^hUSDA Forest Service, Southern Research Station, 506 Hayter Street, Nacogdoches, TX 75965-3556, USA

ⁱSchool of Forest Resources, University of Arkansas, P.O. Box 3468, Monticello, AR 71656, USA

^jUS Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, Division of Forestry,
West Virginia University, P.O. Box 6125, Morgantown, WV 26506, USA

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Abstract

Forest structural features at the stand scale (e.g., snags, stem density, species composition) and habitat attributes at larger spatial scales (e.g., landscape pattern, road density) can influence biological diversity and have been proposed as indicators in sustainable forestry programs. This study investigated relationships between such factors and total richness of breeding birds based on data from four studies within highly forested landscapes in the southeastern United States (Arkansas, South Carolina, and West Virginia) that were managed for commercial forest products. Habitat attributes were developed from forest inventory data and other information at the stand level and in circular buffers with radii of 250, 500 m, and 1 km around each sample point. Species accumulation curves for all study sites indicated greater richness in the youngest stands, with greater landscape age heterogeneity, and with proximity of sample points to roads. However, bird richness was not related to distance to nearest water or stream density at any scale. Pine forests had the most species at two of three sites where pine forests occurred. Stand biomass and basal area were generally not predictive of avian richness. Watersheds within the Arkansas site under more

* Corresponding author. Tel.: +1 630 579 1190; fax: +1 630 579 1195.
E-mail address: cloehle@ncasi.org (C. Loehle).

intensive management showed greater bird diversity. Overall, forest management appeared to have a positive effect on total bird richness.

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1. Introduction

Forestry practices can influence forest functions, including the ability to support biological diversity (Sallabanks et al., 2001). By altering structural features at the stand scale (e.g., snags, stem density, species composition), forestry practices can enhance or reduce habitat for particular wildlife species (Duguay et al., 2000, 2001; Weakland et al., 2002). Habitat attributes at larger spatial scales (e.g., vegetation types, road density) also are related to biological diversity (Hagan et al., 1997; Brown et al., 2001; Mitchell et al., 2001; Hagan and Meehan, 2002). Because of demonstrable relationships with biological diversity, many authors have suggested that forest structural features and habitat configurations (e.g., fragmentation) at various spatial scales can serve as indicators of biological diversity (Ohlson et al., 1997; Bachmann et al., 1998; Noss, 1999; National Research Council, 2000).

Forest managers need better information about these relationships to more effectively design forest management approaches that sustain biological diversity and to identify criteria and indicators for evaluating the performance of sustainable forestry programs. However, many investigations of this topic have focused on the stand scale and short temporal periods or have used simplistic characterizations of habitat structure (e.g., forested versus non-forested). Other studies have focused on regional scales (Dove, 2000; Jones et al., 2000; Riitters et al., 1997) or have been conducted in areas where forests are fragmented by alternative land cover types such as urban or agriculture (Drolet et al., 1999; Villard et al., 1999). The results of these studies have been difficult to apply directly to commercial forestland or at scales relevant to forest managers because forest fragments surrounded by cut-over or regenerating forests do not necessarily behave like forests surrounded by non-forest uses (Brotons et al., 2003).

The objective of this study was to investigate relationships between bird species richness in the

southeastern United States and measurements related to factors that potentially affect it (e.g., forest composition/structure, disturbance regime). We were particularly interested in using relatively simple measures of forest structure that could potentially serve as metrics for use by landowners in sustainable forestry certification programs, and in evaluating these relationships in forested landscapes managed for commercial forest products. While species richness is only a single dimension of biodiversity, it is nevertheless an important metric that can be assessed with the methods we develop in this study.

2. Methods

2.1. Study sites

We used data on bird communities and forest structure that were gathered in previous or ongoing studies from four managed forest landscapes in Arkansas, South Carolina, and West Virginia.

The Arkansas study site (AR) is located near Hot Springs, Arkansas (Garland and Saline counties), in Bailey Province 231, the Ouachita Mixed Forest – Meadow Province (Bailey et al., 1994). The landscape is characterized by mountains eroded from sedimentary rock with ridges reaching a maximum elevation of about 790 m. The major soils are ultisols that are often stony. Average annual temperature is 17 °C, and average annual precipitation is 105 cm. Vegetation was dominated by oak-hickory-pine (*Quercus-Carya-Pinus*) forests and managed pine forests, including loblolly pine (*P. taeda*) 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 [*P. echinata*] in the uplands and loblolly pine on alluvial soils). Stream-side management zones were common features.

The AR site consisted of four watersheds that had been managed at different levels of intensity ranging

from no timber management (W1) to intensive industry management (W4; see details in Wigley et al., 2000 and Tappe et al., 2004b). The watersheds, in order of increasing intensity of timber management, were South Alum (W1), North Alum (W2), Bread Creek (W3), and Little Glazypeau (W4). Watersheds W1 through W4 were 1499, 1535, 2275, and 3961 ha, respectively. Watershed W1 was a largely unmanaged USDA Forest Service experimental forest and watersheds W2 and W3 contained a mix of USDA Forest Service and Weyerhaeuser ownership, and W4 was under Weyerhaeuser ownership.

The two South Carolina study sites, SCA south of Summerville (Charleston, Colleton, and Dorchester counties) and SCW between the Great and Little Pee Dee Rivers (Marion county), are located in Bailey Province 232, the Outer Coastal Plain Mixed Province (Bailey et al., 1994). The province is comprised of the flat and irregular Atlantic and Gulf Coastal Plains. Local relief is <90 m, and soils are mainly ultisols, spodosols, and entisols. Mean annual temperature ranges from 16 to 21 °C, and average annual precipitation ranges from 102 to 153 cm. Regional vegetation is characterized by pine forests on upland sites, extensive coastal marshes, and interior swamps dominated by gum (*Nyssa* spp.) and cypress (*Taxodium* spp.). Many upland forests contain isolated depressional wetlands with hardwood and/or pine overstories.

The West Virginia study site (WV) was the 3413 ha Mead Westvaco Wildlife and Ecosystem Research Forest (MWERF) in Randolph County near Elkins, WV. The MWERF is in Bailey Province M221, the Central Appalachian broadleaf forest – coniferous forest – Meadow Province (Bailey et al., 1994). Elevation ranges from 734 to 1180 m and soils are acidic, well-drained inceptisols and ultisols. The landscape is characterized by a cool, humid climate with annual precipitation often >160 cm and snow common throughout the winter months. Vegetation is largely Allegheny hardwood forests at elevations above 850 m, and spruce-fir (*Picea-Abies*) forests above 1000 m. Most of the MWERF (>90%) had been only lightly managed for more than 70 years.

2.2. Bird surveys

At each study site, breeding bird communities were sampled at least once annually during the breeding

season using standard 5-min point counts on 50 m fixed-radius plots (Hutto et al., 1986; Ralph et al., 1993; Shiu and Lee, 2003). Sampling occurred during 1995–1998 in AR, 1995–1999 in SCA and SCW, and 1996–1998 and 2001–2002 in WV. Sample points were located approximately 200–400 m apart either on a grid system or allocated randomly within forest types. If the same plot was visited more than once per year, we randomly selected one of the visits, because one visit was the maximum at some study sites. We viewed the individual birds on the same plot in different years to be mostly independent of each other. The four landscapes were under active forest management, so landscape conditions changed somewhat among years due to harvests and tree growth. Therefore, we considered visits to plots on successive years to be independent observations. This introduced a small pseudoreplication, but we had far more plots than repeat measures on the same plot. In SCW and WV, the same points were used each year while in AR new plots were established each year and in SCA some new points were added each year. There were 1865 plots in AR, 1762 in SCA, 715 in SCW, and 703 in WV.

Differential detectability of species can be an issue for studies based on bird point counts (Hutto et al., 1986). We do not believe, however, that this posed a problem in our study. As long as any observer bias was relatively constant (or random) across the landscape, we believe that our methods were appropriate because we were attempting to determine effects of landscape structure on a standardized measure of species richness rather than predicting absolute richness. Observers used the same plot size and sample duration on each site. The use of different observers across sites and different plot spacing meant that sites could not be compared directly, so we tested for effects only within study areas.

2.3. Habitat data

For each sample plot, we characterized habitat at the stand, neighborhood, and buffer scales (defined below) using inventory and spatial datasets provided by landowners or compiled from public sources. We used Albers coordinates for plot locations and an Albers Equal Area projection for all data. For each habitat variable of interest, we assigned the sample points to separate categories (bins), and developed a separate

species accumulation curve for each bin (see species richness methods below). For example, several age class bins were defined. The number of categories differed among habitat variables and was selected whenever possible to achieve approximate parity in plot numbers among the bins. We also binned plots separately for Arkansas watersheds W1, W2, W3, and W4.

2.3.1. Stand scale

Data were obtained for forest age, land cover type, trees per ha (TPH), and basal area (BA; m²/ha) from stand-based landowner inventory data, where usually inventories are not done on very young stands and small trees are not sampled. Using these data, we estimated biomass following Jenkins et al. (2003). We lacked detailed estimates of TPH and BA for about 250 stands.

To facilitate creation of species accumulation curves, we created five bins for forest age (≤ 5 , >5 – ≤ 20 , >20 – ≤ 40 , >40 – ≤ 80 , >80 years), three for BA (≤ 17.2 , >17.2 – ≤ 34.4 , >34.4 m²/ha), three for biomass (≤ 50 , >50 – ≤ 100 , >100 Mg/ha). We used five bins for land cover type, including pine ($>75\%$ pine BA), hardwood ($<25\%$ pine BA), mixed pine-hardwood forest types (25–75% pine BA), harvested but unplanted stands, and non-forested habitat (e.g., agriculture, pastures, home sites). Plots in non-forested habitat and recently clearcut but unplanted stands were treated as year 0 age class, except in WV where age post-harvest is used. For the age class analysis, non-forested plots were dropped.

2.3.2. Neighborhood scale

Neighborhood parameters were extracted from USGS 1:24,000 data layers using GIS (ArcView GIS 3.3 Spatial Analyst extension), and included distances from plot center to nearest road (including non-paved forest roads) and nearest water (including small streams, ponds, and man-made canals, but not the smaller ponds or seasonal wetlands that were plentiful in the two South Carolina study areas; the exact size of the smallest water body in the database is unknown). We used three bins for distance to water (<30 , 30–100, and >100 m) and three bins for distance to roads (<100 , 100–200, and >200 m).

2.3.3. Buffer scale

We used ArcGIS functions to estimate measures of habitat structure in circular buffers with radii of 250,

500 m, and 1 km surrounding each sample point (Pearson, 1993). Buffer-scale variables included area-weighted standard deviation of forest age (SDA), which is a measure of heterogeneity, and road density. Bins for SDA were ≤ 10 , >10 – ≤ 20 , and >20 years for 250 m and 500 m buffers and ≤ 20 , >20 – ≤ 30 , and >30 years for 1 km buffers. Bins for road density were ≤ 2 , >2 – ≤ 5 , and >5 km/km² for all buffers. Many of the 1 km neighborhoods included stands off our study sites for which we did not have forest inventory data. For these cases we used aerial photographs to estimate forest characteristics for the surrounding areas (USGS National Aerial Photography Program, at <http://edc.usgs.gov/products/aerial/napp.html>). It was assumed that land use type was stable enough that classification of land off the study area (mostly agricultural and urban) did not change for the years being evaluated. For WV some offsite areas were unmanaged forest. Agricultural and urban areas around these study areas are relatively stable, justifying our assumption. Although we were unable to extract measurements such as BA or TPH from the aerial photographs, we were able to estimate forest age grouping and forest type. We measured the amount of each forest age grouping and SDA in each buffer using Fragstats (<http://www.umass.edu/landeco/research/fragstats/fragstats.html>) and Patch Analyst 3.1 extension for ArcView GIS (Elkie et al., 1999).

2.4. Species accumulation curves

Our particular interest in this study was the assessment of relationships between landscape structure and measures of bird species richness. In contrast to parameters such as basal area, which can be measured with some precision on any given piece of ground, richness is a function of scale of measurement and number of samples. For example, it is possible to evaluate landscape effects on richness at the plot scale, but these results may not represent responses at the landscape scale, particularly when there are few species per plot. Plot-level species counts do not allow consideration of the extent to which species are different from plot to plot, even on a uniform habitat. Thus, it is necessary to take into account the sampling properties of species on a landscape.

The consequence of sampling a larger area or more plots is typically to include more habitats, hence more

species. This leads to the well-known species-area relationship, $S = cA^z$, where c and z are parameters, S is number of species, and A is area. Typically this relationship is used with complete (or nearly complete) floral or faunal lists for areas (e.g., islands) of different size (for examples, see Rosenzweig, 1995). In this study, we instead used the related species accumulation function $S = cN^z$, where N is number of sample plots because all plots were sampled using a standard method and were the same size. This approach has been used previously (Loehle et al., 2005).

We used the sample-based rarefaction method (Gotelli and Colwell, 2001; Koellner et al., 2004) to obtain the expected value for S for different-sized sets of plots (e.g., sets of 10, 12, etc., plots up to the total available for each bin). For example, for the 10-plots group, we selected 30 samples of 10 plots at random (without replacement) from the entire universe of available plots and computed the mean number of species over these 30 replicates. This was repeated at each N . This approach smoothed the data, resulting in an excellent fit to the species accumulation model (Colwell and Coddington, 1994). The goal was not to estimate true S per se, but to develop species accumulation curves that could be overlaid for comparison. This approach allowed us to evaluate how species numbers changed as more area was sampled within each bin. Potential abundance effects (i.e., more species because there are more individual animals per plot) did not affect our results. Thus, when two species accumulation curves were overlaid, we interpreted the higher curve to be more species rich. Curves for bins or watersheds that had a larger area, and subsequently more plots, extended further; however, we compared the curves only at the highest point of the shortest curve. Our null hypotheses were that species accumulation curves for each habitat variable bin would be coincident, with larger bins with more plots simply having a longer but not higher curve.

After rarefaction, we fitted the data and estimated asymptotic 95% confidence limits using non-linear least squares with optimization software available in Mathematica (<http://www.wolfram.com>). This has been shown to be superior to using a linearized fitting method (Rosenzweig, 1995). Because of the large number of plots, the fit to the rarefaction curves

usually was excellent ($R^2 > 0.97$) and even very small differences in c and z (and therefore, in S) were statistically significant. However, if one habitat type had an accumulation curve predicting eight species and another had a curve predicting 8.1 species, we would not consider this difference to be biologically meaningful. This is, of course, the common problem of distinguishing between statistical and biological significance. Therefore, we did not declare a difference between two habitats or classes of plots unless the critical distance between the curves (at the highest point of the shortest curve) was ≥ 2 species. This is a fairly conservative minimum distance for testing.

We also used the species accumulation curves to decipher the contribution of various habitat components to diversity (Olszewski, 2004). If each habitat type has a unique set of species, then plots for the individual types will fall below the plot utilizing samples from all the types. This represents additive diversity (Veech et al., 2002; Olszewski, 2004), which suggests that more habitat types will yield higher overall richness. In contrast, if some habitat types contain a subset of species found in another type, a combined sample or mixed landscape will be less diverse on a per unit area basis than the richest type alone and the combined sample curve will fall between the two individual curves. This is a dilution effect which suggests that more habitat types will not produce more diversity.

3. Results

3.1. Stand scale

We developed species accumulation curves for each land cover type on each landscape. No pine type (which was intensively managed on landscapes where it existed) occurred on WV; thus, no forest type curves were developed for WV. There also were too few non-forested plots on any site to analyze this type. Recently harvested, unplanted stands were only sampled on SCA and SCW. Best-fit models were determined for the remaining sites and land cover types, and all but one curve (SCA pine $R^2 = 0.93$) fit with $R^2 > 0.96$ (Fig. 1).

In AR, bird richness in hardwood forests was greater than in mixed pine-hardwood forests (Fig. 1a). Other-

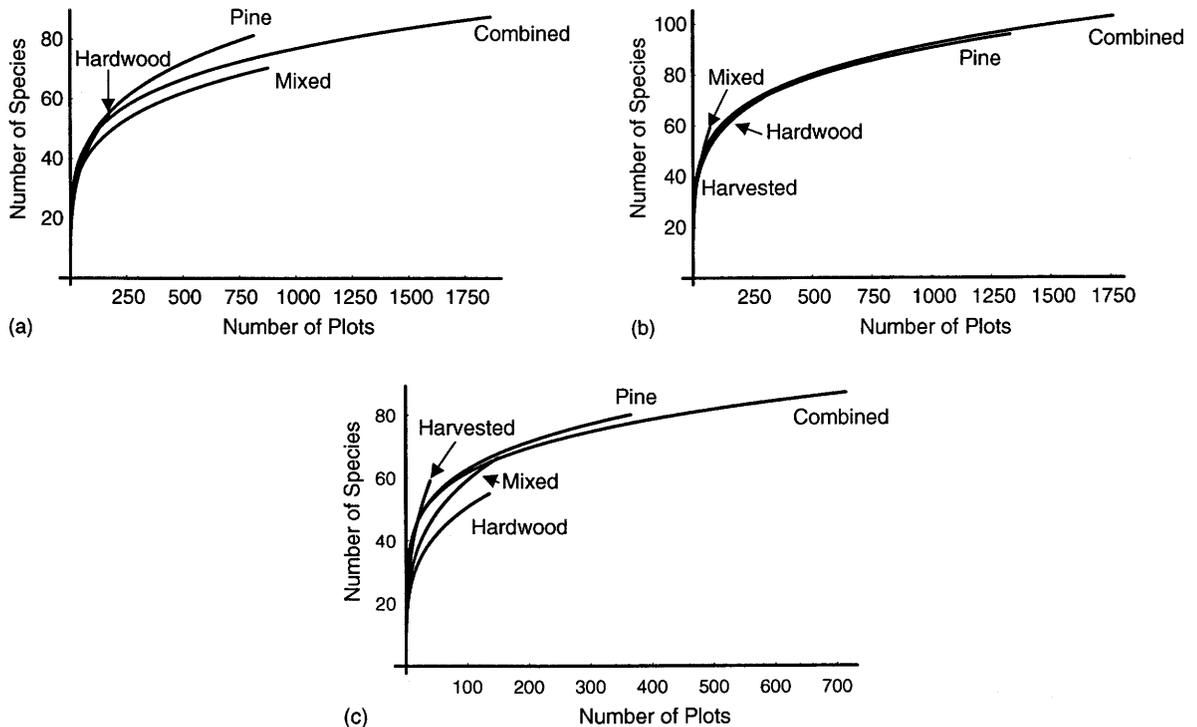


Fig. 1. Species accumulation curves for bird communities on the (a) Arkansas (AR), (b) Ashley-Edisto (SCA), and (c) Woodbury (SCW) study areas in pine, hardwood, and mixed pine-hardwood forest, and for all forest types combined.

wise, diversity in hardwood forests was always less than or equal to diversity in other forest types, although this result is somewhat ambiguous due to the limited sample size for hardwood forests. Hardwood stands did not have a unique species composition. In AR, 52 of 53 species in hardwood plots were also found in pine plots, with 65 of 69 in SCA and 50 of 54 in SCW. In AR, richness in the mixed pine-hardwood type was lowest, while in SCW it was intermediate. In SCA, richness in mixed pine-hardwood forests was possibly greatest, but we had few stands in mixed pine-hardwood forests on this landscape (Fig. 1b). Where pine stands occurred (AR, SCA, SCW), bird communities generally were most diverse in that type. The harvested stands appeared to have higher richness in SCW (Fig. 1c), but had the fewest plots. Hardwood stands in SCW had much lower richness than all other types. We observed only a modest additive effect for land cover types in SCA and a dilution effect in AR and SCW (Fig. 1).

Mean age of plots by type was computed to determine if types differed in age. The hardwood, mixed, and pine plots mean ages were, respectively,

57.4, 65.4, and 45.4 years for AR, 49.2, 45.1, and 21.4 years for SCA, 39.0, 45.6, and 15.9 years for SCW, and 69 years for hardwood in WV. In AR and SCW, the pine type differed from the other two, and in SCA all three differed from each other (Table 1), with pine always being significantly younger.

Species accumulation curves for the forest age bins at all four study sites (Fig. 2) fit with $R^2 \geq 0.97$ except for the WV >80 year age class ($R^2 = 0.95$). On AR no ≤ 5 year plots were sampled. However, the youngest two age classes in AR, $>5-\leq 20$ years and $>20-\leq 40$ years, had the highest richness, followed by the oldest stands (>80 years) (Fig. 2a). On SCA, the ≤ 5 year age class was the richest, followed by a progression of oldest to youngest, although no >80 year classes were sampled (Fig. 2b). In SCW, the ≤ 5 year and $>20-\leq 40$ year age classes were richest, with both lines overlapping (Fig. 2c). The oldest class at this site had the fewest species, perhaps due to the absence of understory in older cypress stands. In WV, only three age class groups were sampled. The WV ≤ 5 year age class result is ambiguous because its curve rose steeply

Table 1
Plot age test for categories

Type	Hardwood	Mixed	Pine
AR	57.4 ^a	65.4 ^a	45.4 ^b
SCA	49.2 ^a	45.1 ^b	21.4 ^c
SCW	39.0 ^a	45.6 ^a	15.9 ^b
Distance to roads	≤100 m	100–200 m	>200 m
AR	50.6 ^a	52.1 ^a	60.0 ^b
SCA	24.0 ^a	31.0 ^b	39.0 ^c
SCW	51.4 ^a	18.3 ^b	52.2 ^a
WV	49.9 ^a	68.8 ^b	70.5 ^b
Distance to water	<30 m	30–100 m	>100 m
AR	49.6 ^a	47.6 ^a	57.0 ^b
SCA	30.8 ^a	28.8 ^a	26.4 ^a
SCW	52.4 ^a	33.4 ^b	23.6 ^c
WV	53.1 ^a	67.0 ^b	66.8 ^b

Mean age by category is shown with superscript showing which means differ at 0.05 level. Since data were not normal and variances differed, pairwise Mann–Whitney tests were done at 0.017 level (=0.05/3) using SAS (SAS Institute, 1990).

but had only 23 plots (Fig. 2d). Otherwise, the oldest age class had the fewest species. Thus at all four sites the richest grouping was one or more of the youngest age classes.

We developed species accumulation curves for the bins of total BA and total biomass, with $R^2 > 0.96$ for all curves (>0.98 in most cases). Overall, 16 pairwise comparisons could be made between bins for total BA and biomass (Table 2). In two of the comparisons species richness was equivalent, in six cases the higher BA or biomass class had greater species richness, and in eight comparisons the lower BA or biomass class had greater species richness. Thus, we observed no consistent relationship between species richness and BA or total biomass over the four study sites.

3.2. Neighborhood and buffer scales

Based on the species accumulation curves (all fit with $R^2 > 0.98$), relationships between distance to

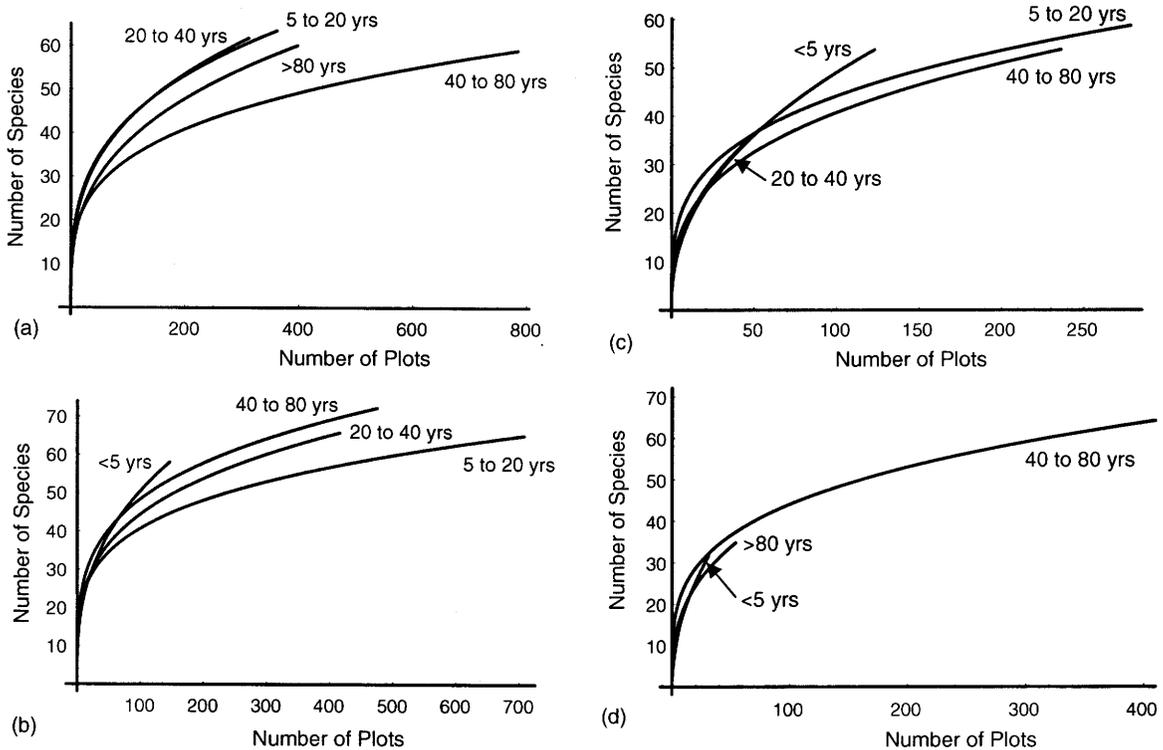


Fig. 2. Species accumulation curves for bird communities in stands on the (a) Arkansas (AR), (b) Ashley-Edisto (SCA), (c) Woodbury (SCW), and (d) West Virginia (WV) study areas that were <5, 5–20, 20–40, 40–80, and >80-years-old. Not all age classes occurred on all study areas. For SCW, the 20–40 year age class curve with 83 plots lies on top of the <5 year age class.

Table 2

Comparisons of species accumulation curves for sample points located in stands with different amounts of total basal area and biomass

Site	Comparisons of basal area or biomass		
	Low vs. moderate	Low vs. high	Moderate vs. high
Basal area^a			
AR	Moderate	ND ^b	ND
SCA	Low	Low	Moderate
SCW	ND	ND	ND
WV	Equivalent	High	High
Biomass^c			
AR	Moderate	High	High
SCA	Low	Low	Moderate
SCW	ND	ND	ND
WV	Equivalent	Low	Moderate

The bin with greatest richness in each pairwise comparison is listed.

^a For basal area, low was ≤ 17.2 m²/ha, moderate was < 17.2 – ≤ 34.4 m²/ha, and high was > 34.4 m²/ha.

^b ND = no data.

^c For biomass, low was ≤ 50 Mg/ha, moderate was > 50 – ≤ 100 Mg/ha, and high was > 100 Mg/ha.

water and bird species richness differed among study sites. In AR, the > 100 m zone was much less diverse than zones closer to water, and the intermediate (30–100 m) zone was marginally richer than the zone < 30 m from water (the riparian zone). In SCA, the riparian zone was marginally richer than the other two zones, but only after more than 100 plots were sampled (i.e., where the curves crossed), and the > 100 m zone was richer than the 30–100 m zone. In SCW, the riparian zone had lower richness than the other two zones, with the intermediate zone being richest. In WV, the riparian zone had lower richness than the other two zones, and the intermediate zone was richest. Thus, our results did not indicate a consistent relationship between bird species richness and distance to water. It is possible, however, that water bodies too small to be recorded in the database created ambiguity in these results, particularly for the two South Carolina sites where small and seasonal wetlands are common. These results were not related to age of plots in the bins (Table 1). Types of the plots were tallied as a function of distance from water (Table 3). Notable trends were more hardwood in the farthest zone in AR, pine replacing hardwood with distance from water in SCA, the highest hardwood composition in the intermediate zone in SCW, and

Table 3

Plot land cover type as a function of distance from water

Type	Distance from Water		
	< 30 m	30–100 m	> 100 m
AR			
Non-forested	0	0	0
Mixed	45.5%	41.4%	45.9%
Hardwood	3.7%	5.3%	10.6%
Pine	50.7%	53.3%	43.5%
Harvested	0	0	0
SCA			
Non-forested	0.9%	0	1.0%
Mixed	3.5%	3.1%	4.3%
Hardwood	30.1%	24.1%	14.8%
Pine	64.6%	70.8%	77.1%
Harvested	0.8%	2.1%	2.9%
SCW			
Non-forested	4.7%	2.3%	3.3%
Mixed	15.6%	19.8%	22.2%
Hardwood	28.1%	36.0%	11.7%
Pine	51.6%	39.0%	55.6%
Harvested	0	2.9%	7.1%
WV			
Non-forested	11.6%	3.8%	4.0%
Mixed	4.7%	1.9%	1.5%
Hardwood	83.7%	93.3%	92.5%
Pine	0	0	0
Harvested	0	0.9%	2.0%

non-forested being replaced by hardwood with distance from water in WV.

Species accumulation curves for each bin for distance from roads fit with $R^2 > 0.96$ for all curves. In AR, the two zones closer to roads were equivalent and were richer than the zone farthest from roads. In SCA, the closest and farthest zones had the most species, compared to the intermediate zone. In SCW, the intermediate zone was richest, followed by the closest zone, then the farthest zone. In WV, the intermediate zone was richer than the closest and farthest zones, which were equivalent. Thus, in two of four landscapes (AR, SCW) the zone farthest from roads had the lowest species richness. The zone closest to roads never had the lowest richness and in two cases was richest. At all four sites, the farthest zone was oldest, and at all sites except SCW the closest sites were youngest (Table 1). This suggests that younger age classes near roads may contribute to the road effect, but the relationship is not strong.

Table 4
Comparisons of species accumulation curves for sample points located in buffers with different radii and road densities

Site	Comparisons of road density ^{a,b,c}		
	Low vs. moderate	Low vs. high	Moderate vs. high
250 m radius buffer			
AR	Low	Equivalent	Equivalent
SCA	Equivalent	Equivalent	High
SCW	AM ^a	AM	High
WV	Low	Equivalent	Equivalent
500 m radius buffer			
AR	Equivalent	Equivalent	Equivalent
SCA	Low	AM	AM
SCW	Moderate	ND	ND
WV	Equivalent	ND	ND
1 km radius buffer			
AR	Moderate	ND	ND
SCA	ND	ND	ND
SCW	Moderate	ND	ND
WV	Moderate	ND	ND

The bin with greatest richness in each pairwise comparison is listed.

^a For all buffers, low road density was ≤ 2 km/km², moderate was >2 – ≤ 5 km/km², and high was >5 km/km².

^b AM = ambiguous result due to small sample size or crossing lines.

^c ND = no data.

We made 19 pairwise comparisons of species accumulation curves for buffers (250, 500 m, and 1 km radii) with low, moderate, and high road densities (Table 4). In two of the comparisons, stands surrounded by buffers with lower road density had the most species, in ten cases the species accumulation curves were equivalent, and in six cases stands surrounded by buffers with higher road density had the most species. These results do not support a negative relationship between road density and bird species richness, and suggest a possible modest positive effect.

We had sufficient data to make 31 pairwise comparisons of species accumulation curves (Table 5) among the three levels of standard deviation of age (SDA) in the 250, 500 m, and 1 km buffers. All curves fit with $R^2 > 0.96$. Overall, across the three scales more age-diverse buffers were more species rich than less age-diverse buffers. In eight pairwise comparisons, the less age-diverse buffer had more species, in five cases they were equivalent, and in eighteen cases the more age-diverse buffers had more species. In 14 of 21 pairwise comparisons involving

Table 5
Comparisons of species accumulation curves for sample points located in buffers with different radii and standard deviations of forest age

Site	Comparisons of S.D. forest age		
	Low vs. moderate	Low vs. high	Moderate vs. high
250 m radius buffer ^a			
AR	Low	High	High
SCA	Moderate	High	High
SCW	Moderate	High	Equivalent
WV	Low	Low	High
500 m radius buffer ^a			
AR	Equivalent	High	High
SCA	Moderate	High	Moderate
SCW	Equivalent	High	High
WV	Low	Low	Equivalent
1 km radius buffer ^b			
AR	Equivalent	High	High
SCA	Moderate	ND ^c	ND
SCW	ND	ND	Moderate
WV	Low	Equivalent	High

The bin with greatest richness in each pairwise comparison is listed.

^a For 250 and 500 m radius buffers, low S.D. forest age was ≤ 10 years, moderate was >10 – ≤ 20 years, and high was >20 years.

^b For 1 km radius buffers, low S.D. forest age was ≤ 20 years, moderate was >20 – ≤ 30 years, and high was >30 years.

^c ND = no data.

buffers with high SDA, richness was greater for high-SDA buffers than for low- or moderate-SDA buffers. This shows a strong positive effect of age class heterogeneity on diversity for birds. The effect is strong at smaller spatial scales (250, and 500 m), and weak to absent at the 1 km scale based on the number of paired comparisons showing an effect at each scale.

3.3. Watershed scale

Species accumulation curves for the four Arkansas watersheds fit with $R^2 > 0.98$ for all curves. The order of species richness (low–high) was the same as the order of management intensity: $W1 < W2 < W3 < W4$.

4. Discussion

The analyses we performed enabled us to evaluate relationships between breeding bird richness and a

number of spatial and habitat factors such as distance to roads and water, stand-level forest structure, and forest heterogeneity at larger scales.

4.1. Stand scale

The pine-hardwood dichotomy is the most obvious difference between plantations and native forest in the southeastern United States; i.e., most plantations are pine dominated. Many previous studies have documented fewer bird species in pine forests than in hardwood (Anderson, 1975; Guilfoyle, 1993; Shackelford and Conner, 1996; Daniel and Fleet, 1999) or pine-hardwood forests (Kerpez and Stauffer, 1989).

We found, however, that, where they occurred, pine forests (composed mostly of plantations) had the highest bird species richness. Although these analyses do not address differences in bird species composition or habitat associations for individual species, they do indicate that pine plantations in our study areas provided habitat for a significant portion of the overall bird community. Other studies also have documented high levels of bird diversity in pine forests. Turner et al. (2002) reported that in our SCA study area species richness of breeding birds was greatest (40 species) within the matrix of pine stands of all ages, intermediate (32 species) in hardwood stands (aged 20–60 years), and least (27 species) in rotation-age pine stands (approximately 20-years-old), though these results did not adjust for number of plots in each type which correlated with number of species in that type. Our finding of high bird species richness in pine forests also may reflect a higher level of stand age class and structural diversity in this type than in hardwood or pine-hardwood forests. The pine type was on average considerably younger than other forest types and the youngest classes within the pine type had the highest species richness in AR, SCA, and SCW (Table 1). Finally, the pine stands in both South Carolina sites had abundant small trees, shrubs, and vines, which could also increase bird richness. While different forest types often support different bird communities (Shackelford and Conner, 1996), in our study the hardwood type supported largely a subset of species found in the pine type, rather than having a distinct community composition. The difference between relative richness in hardwood stands in the two South Carolina sites may be due to the larger hardwood stand size in SCW, which

might cause lower diversity because of lower neighborhood age heterogeneity.

Relative richness in pine-hardwood forests differed among the three study landscapes where that type was present and was lowest in AR, intermediate in SCW, and possibly greatest in SCA. Kerpez and Stauffer (1989) indicated that pine-hardwood forests provide optimal or suitable habitat for more breeding bird species than loblolly-shortleaf pine forests. In Virginia, however, Childers et al. (1986) found that species richness of breeding birds in second-growth pine-hardwood forests was comparable to that in the 7–24-year-old loblolly pine plantations.

Because of fire suppression, many pine-hardwood forests in the South occupy sites that once were maintained in pine-grassland ecosystems by frequent fire (Ware et al., 1993). Although bird richness can be high in pine-hardwood forests, several authors (Wilson et al., 1995; Gordon et al., 2001; Conner et al., 2002; Provencher et al., 2002) have reported benefits to bird communities from restoring these sites to pine-grassland systems. In plantations, fire applied alone or following herbicide or mechanical treatments can promote more diverse and abundant bird populations (Conner et al., 2002), including breeding birds of high conservation priority (Gordon et al., 2001).

While we might assume that a landscape with more land cover types should be more diverse, we found no evidence for this. It is possible that our definitions of forest type were not particularly relevant to birds. However, these are the basic types used by forest managers in the southeastern United States. One consideration is that many of the pine stands we studied, particularly those in South Carolina, had some midstory consisting of shrubs and small-diameter hardwoods. Although these hardwoods did not contribute significantly to total BA, they probably provided nesting and foraging substrates for many bird species. Dickson et al. (1993) found that structure of the bird community in pine plantations following canopy closure was directly related to the presence of hardwoods and shrubs. On the SCA study area, nest survival for Acadian flycatchers (*Empidonax vireescens*) was positively related to the height of the deciduous subcanopy and to the density of shrub cover (Hazler et al., in press).

Our results for stand age indicated that younger stands had more bird species at all four sites. The pine

type was youngest on average on all three study areas where pine occurred (AR, SCA, and SCW), so these results could reflect the effect of higher richness in pine forest except in WV. However, reported relationships between forest age and bird richness are complex and variable. Some researchers have reported little difference in richness among forests of different ages (Conner et al., 1979; Conner and Dickson, 1997), some have reported increasing richness with increasing age or successional stage (Zimmerman and Tatschl, 1975; Meyers and Odum, 1991; Buffington et al., 1997), and others have reported a complex pattern. For example, Dickson et al. (1993) found that in a Texas loblolly pine plantation bird species diversity increased with age, peaking at age 10 and 11 years, then decreased. During ages 12–17 years early successional avian species were virtually absent, a few shrub-associated species persisted, and some species associated with older stands occupied the plantation. In Virginia, Childers et al. (1986) found that species richness and species diversity were higher in the 2–5-year-old loblolly pine plantations than in the older, 7–24-year-old plantations. Kremenetz and Christie (1999) found that older longleaf pine stands had 18–24 fewer scrub-successional bird species than recently clearcut and regenerating stands, and all species that occurred in mature stands also occurred in regenerating stands. Mitchell et al. (1991) found that species richness and diversity in naturally regenerated bald cypress-tupelo stands were high initially, declined at the sapling and poletimber stages, then increased again as these stands matured. Marshall et al. (2003) found typical forest birds to commonly use regenerating clearcuts in Virginia and West Virginia.

We hypothesized that measures such as BA and biomass would be positively associated with bird species richness because we expected stands with more biomass to provide more resources such as insect prey, nest sites, and roost sites. Some researchers have documented a positive relationship between bird richness, diversity, or abundance and measures related to biomass (Verner and Larson, 1989; Mills et al., 1991), while others have found an inverse relationship. For example, Gates and Giffen (1991) found high richness of neotropical migrant species at forest-stream ecotones where short shrub cover was highest and deciduous and total canopy cover and deciduous basal area were lowest. Our species accumulation curves revealed no consistent relationship between

bird diversity and BA/biomass. Note that BA and biomass were only available for pole size and larger stands. Although our analysis encompassed a range of biomass commonly found in commercial forests in the southeastern United States, it did not extend to levels of biomass (e.g., deserts, arctic, old-growth forest) where relationships with diversity may be more demonstrable. Measures of site quality (e.g., site index) might show a relationship, but such data were not available in our study.

4.2. Neighborhood scale

In our study, we found generally increased bird richness for plots closer to roads and with higher road densities, though the effect was not strong. We are unable to separate management intensity (which necessarily involves creation of roads) from road effects per se. The fact that stands closer to roads are younger and such young stands had more species in our study suggests that the road effect may reflect management more than road impacts. We were able to reject a net negative effect of road proximity. Roads, however, are widely perceived to adversely affect forest wildlife communities through direct mortality, increased predation at edges, and reduced habitat quality (Strittholt and Dellasala, 2001; Bissonette, 2002). For example, Ortega and Capen (1999) concluded that habitat quality for ovenbirds (*Seiurus aurocapillus*) may be lower within 150 m of unpaved roads in extensive forested landscapes, affecting territory density and possibly reproductive success. Other studies have found forest roads to have little effect on richness of some bird guilds. Using Breeding Bird Survey data and measures of surrounding landscape pattern, Jones et al. (2000) found that road density in the mid-Atlantic region was unrelated to richness for ten of sixteen bird guilds, inversely related to richness of five guilds (nest predators/brood parasites, exotic species, temperate migrants, upper canopy foragers, canopy nesters), and positively related to richness of one guild (lower canopy nesters). Road density, however, explained no more than 5% of variation in richness of any guild. Our study, of course, did not consider predation, productivity, or shifts in bird species composition near roads.

Riparian zones are widely viewed as critical for protection of biological diversity. Our study, however,

found no consistent differences in bird richness between plots close to and far from water. In AR, we found zones closer to water to be higher in bird species richness. Results at the other three sites indicated the closer zone to either be no higher (SCA) or lower (SCW, WV) in richness. At the two South Carolina sites, this result could be complicated by the presence of small water bodies across the landscape that are not recorded in the database. An evaluation of confounding factors (Tables 1 and 3) gave a conflicting result. In AR the zone with fewest species (>100 m) was oldest and had the most hardwoods, which was similar to SCW where the lowest richness zone (<30 m) was oldest and had the second highest hardwood percentage. In contrast, in SCA the <30 m zone was richest and also had the oldest stands and the most hardwoods. In WV, richness increased with decreasing non-forest percentage, which is easily understood. Likewise, results of previous studies on this topic are disparate. In central Pennsylvania, Croonquist and Brooks (1993) found that bird species richness and abundance generally decreased with distance from the stream in a watershed disturbed by agriculture and residential development, but remained relatively constant through an undisturbed reference watershed. Murray and Stauffer (1995) found that total bird density and species richness in Virginia showed no riparian influence and distance from stream was important to only two species (Acadian flycatcher [*Empidonax vireescens*] and Louisiana waterthrush [*Seiurus motacilla*]). Hooper (1991) observed a riparian effect in Maine for bird species richness, but only for floodplain forests, and noted that the increases near streams were primarily generalist species responding to the presence of open, shrubby vegetation (rather than to distance to water per se). A large-scale study (Sabo et al., 2005) found that riparian zones did not harbor more species of multiple taxa, but did tend to have some unique species. Our results do not directly extrapolate to the value of riparian buffer strips left during timber harvest, because our riparian zones generally were part of contiguous forest rather than being surrounded by clearings.

We found a positive effect of buffer age class diversity (SDA) on bird richness. We also found that the strength of this effect differed with scale. Bird communities often differ among forest types and structural classes (Kendeigh and Fawver, 1981; White et al., 1996; Buffington et al., 1997). Thus, it is not

unexpected that bird diversity would be positively associated with landscape heterogeneity. A study of the effects of an ice storm in New England (Faccio, 2003) showed that the resulting heterogeneity increased bird richness. Several researchers who have documented different bird assemblages associated with different structural classes and forest types have noted that managers can encourage the presence of all species assemblages by maintaining a mixture of forest age classes (Thompson and Capen, 1988; Daniel and Fleet, 1999). We believe this strategy would be appropriate in the landscapes we studied. Further study of the scale dependence of bird responses to heterogeneity is needed because very little data exist on this effect.

4.3. Watershed and landscape comparisons

At the watershed scale, we were only able to contrast species accumulation curves for the four Arkansas watersheds. The ordering of bird richness was the same as the ordering of habitat heterogeneity and management intensity, suggesting a positive influence of these factors on richness. This same conclusion has been reached for these watersheds in a prior study using different methods (Tappe et al., 2004a). However, comparisons of more watersheds would be useful.

5. Conclusions

In this study, we evaluated multiple aspects of landscape configuration at different scales, including proximity to water and roads, stand condition, neighborhood condition, and management aspects. Our results suggest that effects of forest management cannot be understood by conducting studies only at the stand scale. Birds, as well as other vertebrates, often respond to spatial context at multiple scales (Mazerolle and Villard, 1999; Mitchell et al., 2001). We found significant relationships for birds extending out to 1 km. This complicates efforts to manage forests for the conservation of biological diversity, because forest planning tools do not easily incorporate wildlife habitat effects beyond the stand scale.

In general, our results suggest a potentially positive role for management in enhancing biological diversity

for birds through enhanced heterogeneity of forest age structure. We recognize that results for winter or fall could also be important (Laiolo et al., 2004) and may differ from those we observed during the breeding season. Results for particular high-priority species or guilds also can, of course, differ from responses of overall richness and should be given consideration by landowners in biological diversity-related planning. Special consideration may also need to be given to factors that discourage exotics or nest parasites. It is particularly noteworthy that responses to some habitat factors (e.g., forest age, forest type) differed among the four study areas. Thus, forest management prescriptions to address bird communities probably should not be “one-size-fits-all” and should account for site-specific conditions.

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