

EFFECT OF STAND WIDTH AND ADJACENT HABITAT ON BREEDING BIRD COMMUNITIES IN BOTTOMLAND HARDWOODS

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Abstract: Bottomland hardwood forests support an abundant and diverse avifauna, but area of this forest type has been reduced, and current projections indicate continued declines. We compared breeding bird abundance indices and species richness among bottomland hardwood stands ranging in width from <50 m to >1,000 m and enclosed by forested habitat. We also compared avian abundance indices and richness among stands enclosed by pine (*Pinus* spp.) forest and stands enclosed by field-scrub habitats. Total species richness and species richness of Neotropical migrants were associated positively ($P < 0.05$) with stand width in all years. Total bird counts differed among width classes in all years, with counts generally greatest in width classes <50 m and >1,000 m. Counts of Neotropical migrants differed ($P < 0.05$) among width classes in 1993 and 1995 and followed the same general trend as total bird count. Acadian flycatcher (*Empidonax vireescens*), blue-gray gnatcatcher (*Poliophtila caerulea*), and red-eyed vireo (*Vireo olivaceus*) were more abundant in smaller width classes ($P < 0.05$), whereas the opposite was true for white-eyed vireo (*Vireo griseus*) and northern parula (*Parula americana*). Probability of occurrence was associated positively ($P < 0.05$) with stand width for 12 species and negatively with stand width for 1 species. Total bird count and the counts of blue-gray gnatcatcher in 1995 and of northern cardinal (*Cardinalis cardinalis*) in both years were higher in field-enclosed stands (FES) than in pine-enclosed stands (PES). No species analyzed was more abundant in PES than in FES. We conclude that even narrow riparian zones can support an abundant and diverse avifauna, but that conservation of wide (≥ 500 m) riparian zones is necessary to maintain the complete avian community characteristic of bottomland hardwood forests in South Carolina.

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Bottomland **hardwood forests (hereafter, bottomland hardwoods) are seasonally inundated floodplain forests dominated by oak (*Quercus* spp.), gum (*Nyssa* spp.), and cypress (*Taxodium* spp.), and they support an abundant and diverse avifauna (Dickson 1978, Hamel 1989) that includes approximately 70 breeding species (Pashley and Barrow 1993). Furthermore, up to 65% of the species at any given site may be Neotropical migrants (Pashley and Barrow 1993), including many forest interior species experiencing population declines (Askins et al. 1990, Peterjohn et al. 1995). However, the pre-Columbian (15th century) extent of bottomland hardwoods has undergone considerable reduction, largely because of agricultural conversion**

and construction of hydroelectric reservoirs (Harris and Gosselink 1990). Approximately 50% of the area existing in 1940 had been lost by 1985 (Harris and Gosselink 1990).

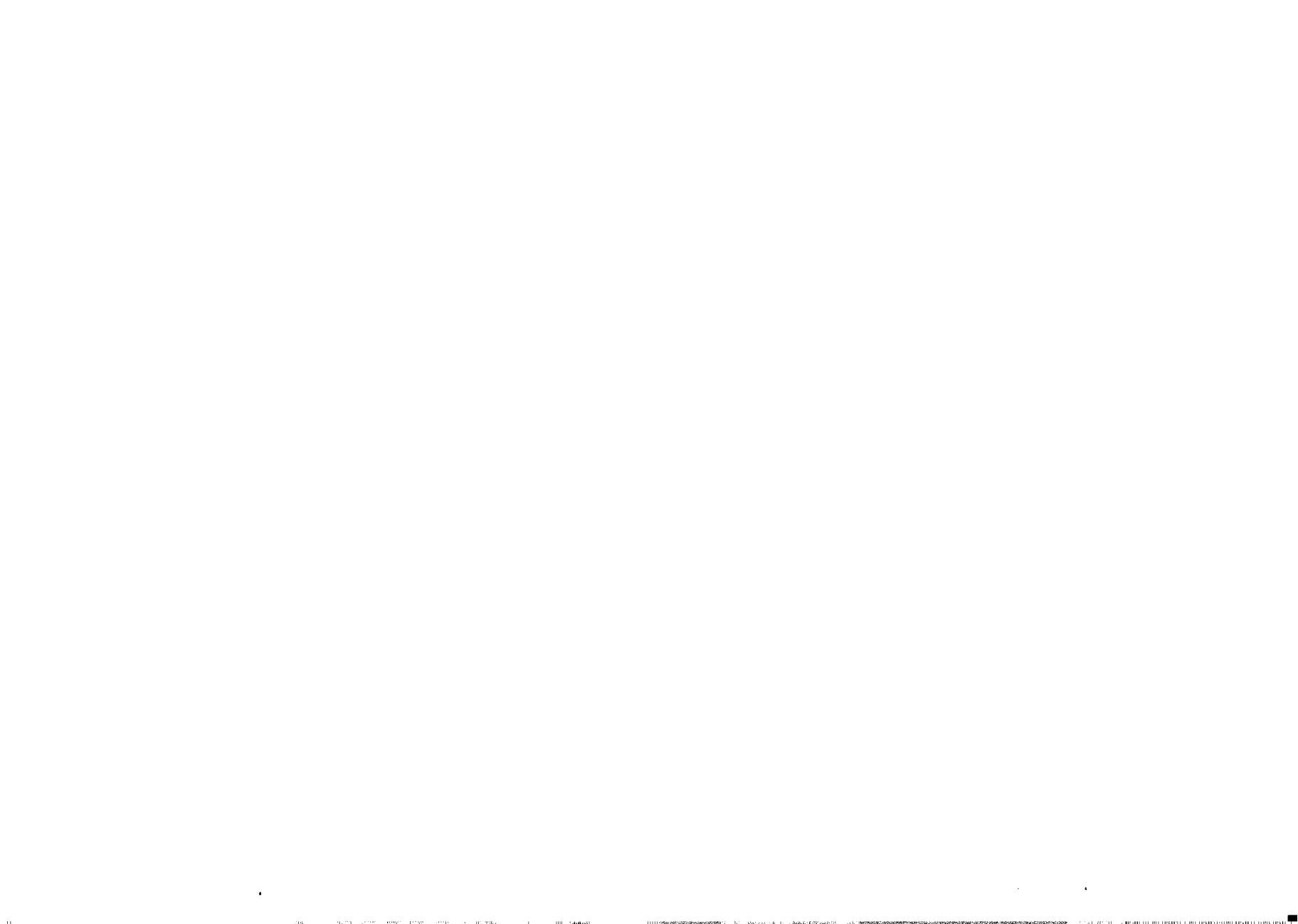
Currently, bottomland hardwoods are an important source of hardwood lumber, and demands on these forests likely will increase. Hardwood timber removals by the year 2030 are projected to have increased by 64% over 1984 levels (U.S. Forest Service 1988). During the same period, acreage of bottomland hardwoods in the Southeast is projected to decrease from about 5.5 million ha to about 4.7 million ha, a decline of 15% (U.S. Forest Service 1988). Much of the remaining bottomland hardwoods exist in narrow (<50 m) drainages and stream-side management zones. Although narrow stands may contain substantial area because of their length, their utility to forest birds may be compromised because of a lack of interior habitat conditions.

Species richness and abundance of forest bird communities are associated positively with

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stand area (Galli et al. 1976, Whitcomb et al. 1981, Blake and Karr 1987). However, recent research attention has focused on width of riparian zones rather than area (Keller et al. 1993, Darveau et al. 1995, Dickson et al. 1995, Thurmond et al. 1995, Hodges and Kremenetz 1996) because of difficulties associated with defining area when riparian zones are interconnected. Further, species richness of some avian guilds is correlated positively with riparian zone width (Keller et al. 1993). However, most research on the effect of width on bird communities in Southeastern bottomland hardwoods has been restricted to narrow stands surrounded by young pine plantations. Although these studies are applicable in most forest management contexts, research addressing the range of stand widths encompassed in bottomland hardwood systems is necessary to assess the habitat requirements of area-sensitive species. We compared avian abundance indices and species richness among bottomland hardwood stands of various widths (<50 to >1,000 m) that were surrounded by closed-canopy pine (*Pinus taeda*, *P. palustris*) forest. We also compared abundance indices and species richness among stands enclosed by pine forest and stands enclosed by field-scrub habitats.

STUDY AREA

The study was conducted on the U.S. Department of Energy's Savannah River Site, a 78,000-ha tract in Aiken, Bamwell, and Allendale counties, and on private property in Allendale County. This region lies in the Upper Coastal Plain of westcentral South Carolina and is bounded on the west by the Savannah River. Topography is characterized by gently rolling ridges, broad flat regions, and interspersed stream courses (Soil Survey Staff 1977). Elevation ranges from <25 m at the Savannah River to 80 m at first-order streams. Bottomland hardwoods are found along stream courses and may be flooded seasonally, usually during late winter-early spring. Dominant canopy species of bottomland hardwoods include sweetgum (*Liquidambar styraciflua*), swamp tupelo (*Nyssa sylvatica* var. *biflora*), red maple (*Acer rubrum*), water oak (*Quercus nigra*), laurel oak (*Q. laurifolia*), overcup oak (*Q. lyrata*), and cherrybark oak (*Q. falcata* var. *paegodifolia*). The midstory is composed of American holly (*Ilex opaca*), sweet bay (*Magnolia virginiana*), and red bay (*Persea borbonia*). Switchcane (*Arundinaria gi-*

gantea) and dog hobble (*Leucothoe axillaris*) dominate the shrub layer, and Christmas fern (*Polystichum acrostychoides*) and netted-chain fern (*Woodwardia areolata*) are the dominant ground cover (Workman and McLeod 1990).

METHODS

We used a completely randomized design with repeated measures across years. We selected 4 replicates of bottomland hardwood stands in each of 5 width classes: <50 m, 50–150 m, 150–300 m, 300–1,000 m, and >1,000 m. We used width classes rather than size classes because the forested watershed in which we worked was nearly continuous throughout the study area. Thus, first-order streams (narrow floodplains) were continuous with second- and third-order streams (wider floodplains), which made delineation of stand boundaries (and therefore determination of area) impossible. We believe that width was a good index to area because wider stands contained more area; hence, width was more useful in a forest management context. We used aerial photographs to locate sites from which we measured width of the entire floodplain, including both sides of a creek or drainage. The 2 largest sites were located on the Savannah River floodplain; width of these sites refers to 1 side only because the Savannah River constituted a significant break in the canopy (≥ 100 m) and likely served as an effective barrier to cross-stream movement of birds (Hodges and Kremenetz 1996). All sites were on different creeks, except those on the Savannah River, which were separated by >1 km to ensure independence of replicates. We selected sites characterized by Zone III, IV, and V vegetation types (Wharton et al. 1982) in an attempt to control for differences in vegetation among sites. Larger sites encompassed a greater diversity of habitat types, and a few plots slightly overlapped communities of baldcypress (*Taxodium distichum*)-water tupelo (*Nyssa aquatica*).

We measured habitat characteristics in 5 circular 0.04-ha plots (James and Shugart 1970) per stand in 1994. We measured canopy coverage with a densiometer and vegetation profile with a 3-m density board (Noon 1981); each measurement was from the cardinal points on the perimeter of each plot. We recorded species and size class of all trees in the plot (James and Shugart 1970). For analysis, we selected vegetation profile (PROFILE) as a measure of un-

derstory structure, basal area of hardwood pole timber (POLE), which we defined as hardwood stems 8-23 cm dbh and which provided a measure of midstory structure, canopy coverage (CANOPY), and basal area of hardwood sawtimber (SAW), which we defined as hardwood stems >23 cm diameter at breast height (dbh). This approach minimized the number of vegetation variables, yet provided measures of structure for 3 primary habitat layers and also included 2 variables commonly inventoried by forest managers. We subjected these data to principle components analysis (PCA; PROC PRINCOMP; SAS Institute 1990) to reduce the number of habitat variables included in the bird-habitat analyses (Hodges and Kremetz 1996). We selected for inclusion in analyses of bird-habitat relations only those principal components (PC) that had eigenvectors ≥ 1.0 . We used 1-way analysis of variance (ANOVA; PROC GLM; SAS Institute 1990) to compare PC scores among width classes.

We used 5-min, fixed-radius (50 m) point counts (Hutto et al. 1986, Ralph et al. 1995, Smith et al. 1995) to sample the bird population for each stand. Within each stand, 2 points were spaced 200 m apart along a transect centered within each corridor and oriented parallel to the general bearing of the drainage. To aid in estimation of distance, we placed high-visibility flagging tape on trees at the perimeter of each plot in each of the cardinal directions. We visited each stand at approximately equal intervals 3 times per year between mid-May and late June 1993-95, once each during early, middle, and late morning. This design yielded 72 point counts in each width class during the study (4 stands X 2 points X 3 visits X 3 years). Smith et al. (1995) suggested 50 counts per factor level were sufficient to detect most biologically meaningful variation.

We conducted counts from sunrise to 3.5 hr after sunrise, except during periods of high wind or rain (Ralph et al. 1995). We only recorded birds once, if they were detectable from both points in a stand (Ralph et al. 1995). Birds flying over the stand were not recorded (Ralph et al. 1995). Species detected within the stand but beyond the 50-m radius or within ± 3 min of the count period while en route to points were recorded for evaluation of species richness. We took the high count for each species per point and averaged values from both points to obtain an index of relative abundance for

each site (Blonde1 1981, Blake and Karr 1987). For stands with widths <100 m (i.e., too narrow for a plot of 50-m radius, $n = 4$), counts were adjusted by extrapolation based on the fraction of a 50-m-radius plot that each plot comprised. We assumed any bias in bird detection among points was minimal because vegetation characteristics did not differ among sites (see below), only 2 observers were used, weather conditions were standardized, and timing of counts within day and season was stratified.

We evaluated the effect of stand width (log-transformed), habitat variables (i.e., PC), and year on species richness via a generalized linear model (PROC GLM; SAS Institute 1990). We used the same procedure to evaluate the effect of corridor width on species richness of Neotropical migrants (forest interior and interior-edge species only; Whitcomb et al. 1981). We compared the slopes of our regressions of species richness by stand width to slopes from species-area relations of other studies to test the null hypothesis that the species-width slopes did not differ from species-area slopes. Because we were aware of no published species-area relations from bottomland hardwood habitats, we used slopes from studies in upland hardwood forests in South Carolina (Kilgo 1996) and Illinois (Blake and Karr 1987).

We tested the null hypotheses that total bird count, total Neotropical migrant count, and counts of each species did not differ among width classes. We analyzed only those species for which we recorded an average of ≥ 20 observations/year. We made comparisons among width classes with repeated-measures (3 yr) analysis of covariance (RM-ANCOVA; PROC GLM; SAS Institute 1990). The linear model included the following terms: width class, site (width class), year, year x width class, PC1, PC2, and PC3, where PC1-PC3 were PC scores. Before analysis, we converted covariates to deviations from the mean. We tested covariates and width class with the site-within-width class as the error term. When the year x width class interaction was significant ($P < 0.05$), we analyzed years separately. When covariate effects were nonsignificant, they were eliminated. When RM-ANCOVA revealed significance ($P < 0.05$), we separated covariate-adjusted means via the least significant difference, calculated with site-within-width class as the error term.

We used logistic regression (PROC LOGISTIC; SAS Institute 1990) to model the effect of

year and width on the probability of occurrence for each species. We analyzed only species recorded in $\geq 5\%$ of the 60 stand-years (20 stands sampled 3 yr). The year effect was nonsignificant for all species, so we pooled data among years. Significance of the model was assessed with the score statistic (SAS Institute 1990). When the linear model was not significant, we added a quadratic term, $B_2x_i^2$, (Robbins et al. 1989), and accepted the model with the greatest significance.

To examine the effect of adjacent habitat type, we added 4 stands in 1994 with field-scrub habitat adjacent on both sides: 2 in the width class of 50-150 m and 2 in the width class of 150-300 m. Vegetation was sampled in 1994, and birds were sampled in 1994-95. We compared data from these FES with those from the 8 PES in the same width classes. Habitat data from the 12 stands were subjected to PCA, and PC scores were compared between treatments with incomplete block design ANOVA, blocking on width class. We compared total species richness, species richness of Neotropical migrants, total bird count, Neotropical migrant count, and species counts between treatments (i.e., surrounding habitat type) with RM-ANCOVA as described above, but with the addition of the treatment term and associated interactions.

RESULTS

Each of the first 3 PC from the analysis of vegetation in the 20 PES had eigenvectors >1.0 , and they accounted for 91% of the variation in vegetation measured among sites: PC1 = 35.3%, PC2 = 30.3%, and PC3 = 25.2%. High scores on PC1, which was correlated positively with PROFILE and SAW and negatively with POLE and CANOPY (Table 1), represented stands with an open midstory and canopy, dense understory, and high basal area of hardwood sawtimber. High scores on PC2, which was correlated positively with PROFILE and POLE and negatively with SAW (Table 1), represented stands with well-developed understories and midstories, but low basal area of hardwood sawtimber. Finally, high scores on PC3, which was correlated positively with SAW and CANOPY (Table 1), reflected stands with large trees and a closed canopy. The PC scores did not differ among width classes ($P > 0.05$).

We detected 56 species of birds in the 20 PES of which 23 (41%) were forest-dwelling Neotropical migrants. No edge-scrub or field-

Table 1. Eigenvectors for variables included in principal components (PC) analysis of 20 bottomland hardwood stands enclosed by pine forest in South Carolina, 1993-95. The PC1-PC3 (only components with eigenvalues >1.00) accounted for 91% of the variation in the variables measured among sites.

| Variable | PC1 | PC2 | PC3 |
|-----------------------------------|-------|-------|------|
| Vegetation profile | 0.58 | 0.57 | 0.09 |
| canopy coverage | -0.63 | 0.03 | 0.59 |
| Basal area: | | | |
| hardwood pole timber ^a | -0.29 | 0.80 | 0.10 |
| Basal area: | | | |
| hardwood sawtimber ^b | 0.43 | -0.18 | 0.80 |

^a Defined as all hardwood stems 8-23 cm dbh

^b Defined as all hardwood stems >23 cm dbh.

edge Neotropical migrants (Whitcomb et al. 1981) were detected because we sampled at the centers of forested stands. We analyzed species richness data by year because both total and Neotropical migrant species richness differed among years ($P < 0.001$), with highest values ($P < 0.05$) in 1993. Total species richness and species richness of Neotropical migrants were associated positively ($P < 0.05$) with the natural log of stand width in all years (Fig. 1). The slope of the species-width relation did not differ in any year from that of species-area relations in upland hardwoods of South Carolina (slope = 3.5, Kilgo 1996; 1993: $F_{1,1} = 1.20$, $P = 0.471$; 1994: $F_{1,1} = 1.79$, $P = 0.409$; 1995: $F_{1,1} = 3.02$, $P = 0.332$) and Illinois (slope = 5.2, Blake and Karr 1987; 1993: $F_{1,1} = 0.05$, $P = 0.862$; 1994: $F_{1,1} = 0.24$, $P = 0.709$; 1995: $F_{1,1} = 0.50$, $P = 0.609$).

Total species richness was associated positively with PC2 in 1993 ($P = 0.018$), indicating that number of species increased with increasing understory and midstory development. Similarly, species richness of Neotropical migrants was associated positively with PC2 in 1993 ($P = 0.021$) and 1995 ($P = 0.051$) but was associated negatively with PC1 in 1993 ($P = 0.032$) and 1995 ($P = 0.019$), indicating a positive association with canopy coverage.

Because the year \times width class interaction was significant for both total bird count ($F_{8,59} = 3.02$, $P = 0.014$) and Neotropical migrant count ($F_{8,59} = 3.08$, $P = 0.012$), we analyzed years separately. Total bird count was not associated with PC in any year ($P > 0.05$) but differed among width classes in each year (1993: $F_{4,19} = 26.18$, $P < 0.001$; 1994: $F_{4,19} = 4.54$, $P = 0.013$; 1995: $F_{4,15} = 3.62$, $P = 0.030$; Fig. 2); counts generally were greatest in width classes <50 m and $>1,000$ m (Fig. 2). Neotropical migrant

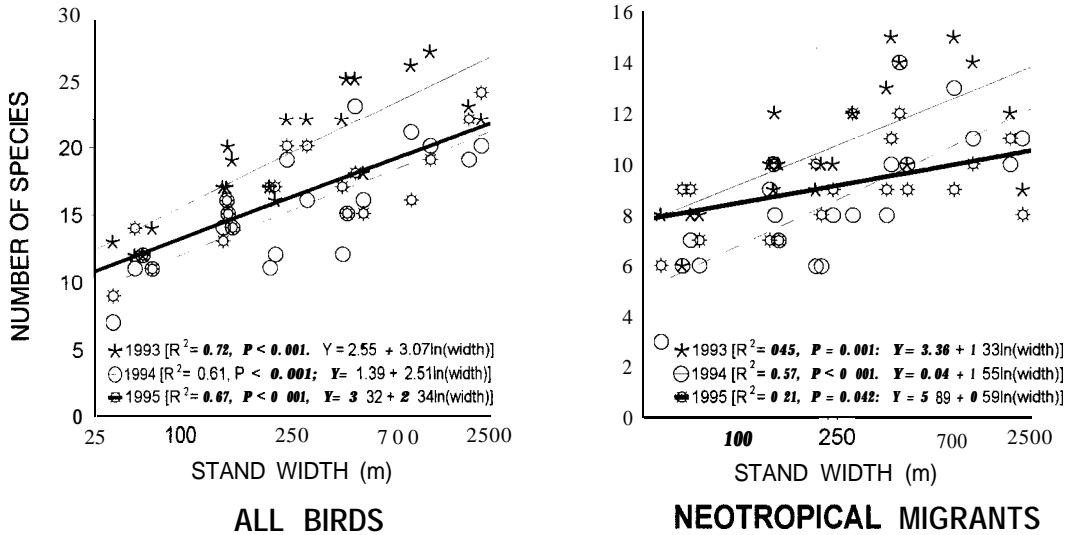


Fig. 1. Relation between breeding bird species richness and width of bottomland hardwood stands in South Carolina, 1993–95.

count differed among width classes in 1993 ($F_{4,19} = 28.41$, $P < 0.001$) and 1995 ($F_{4,15} = 3.43$, $P = 0.035$) and followed the same general trend as total bird count (Fig. 2). Neotropical migrant count also was associated negatively with PC3 in 1993 ($F_{1,12} = 6.91$, $P = 0.022$).

Eight species had sufficient data for individual analysis: Acadian flycatcher, Carolina wren (*Thryothorus ludovicianus*), blue-gray gnatcatcher, white-eyed vireo, red-eyed vireo, northern parula, hooded warbler (*Wilsonia citrina*), and northern cardinal. Only blue-gray gnatcatcher count was associated with a habitat covariate (positively with PC3; $F_{1,12} = 7.20$, $P = 0.020$). The year \times width class interaction was significant for northern cardinal ($F_{8,59} = 3.21$, $P = 0.009$), so years were analyzed separately; northern cardinal counts generally were greatest in width classes < 50 m and $> 1,000$ m (Fig. 2). Counts differed among width classes for the following species: Acadian flycatcher ($F_{4,15} = 9.53$, $P = 0.001$), blue-gray gnatcatcher ($F_{4,12} = 10.51$, $P = 0.001$), white-eyed vireo ($F_{4,15} = 5.54$, $P = 0.006$), red-eyed vireo ($F_{4,15} = 11.99$, $P < 0.001$), and northern parula ($F_{4,15} = 4.11$, $P = 0.019$). Counts of Acadian flycatcher, blue-gray gnatcatcher, and red-eyed vireo were greatest in smaller width classes (Fig. 3), whereas counts of white-eyed vireo and northern parula were greatest in wider width classes (Fig. 3).

Probability of occurrence was associated pos-

itively with stand width for 12 species and negatively with stand width for 1 species (Table 2). The best model for 6 species contained a quadratic term, but only 3 of these models were significant ($P < 0.05$; Table 2). Acadian flycatcher was detected in every site in every year, and we failed to detect blue-gray gnatcatcher in only 1 site in 1 year.

The PC analysis of the vegetation characteristics in the 12 stands used to evaluate the effect of adjacent habitat type on the bird community revealed that PC1 and PC2 had eigenvectors > 1.0 and together accounted for 70% of the variation among stands (PC1 = 40.4%, PC2 = 29.2%). High scores on PC1 represented stands with a closed canopy and high basal area of sawtimber but a poorly developed understory, and high scores on PC2 represented stands with a high basal area of sawtimber and a well-developed understory but poorly developed midstory (Table 3). We found no difference between width class or treatment scores along either PC1 or PC2 ($P > 0.05$).

The year \times treatment interaction was significant for total species richness ($P < 0.001$); richness was greater in PES in 1994 and greater in FES in 1995 (Table 4). Total species richness was not related ($P > 0.05$) to habitat covariates in either year. Species richness of Neotropical migrants did not differ between treatments (Table 4) but was positively associated with PC1 ($F_{1,6} = 6.09$, $P = 0.049$). Total bird count,

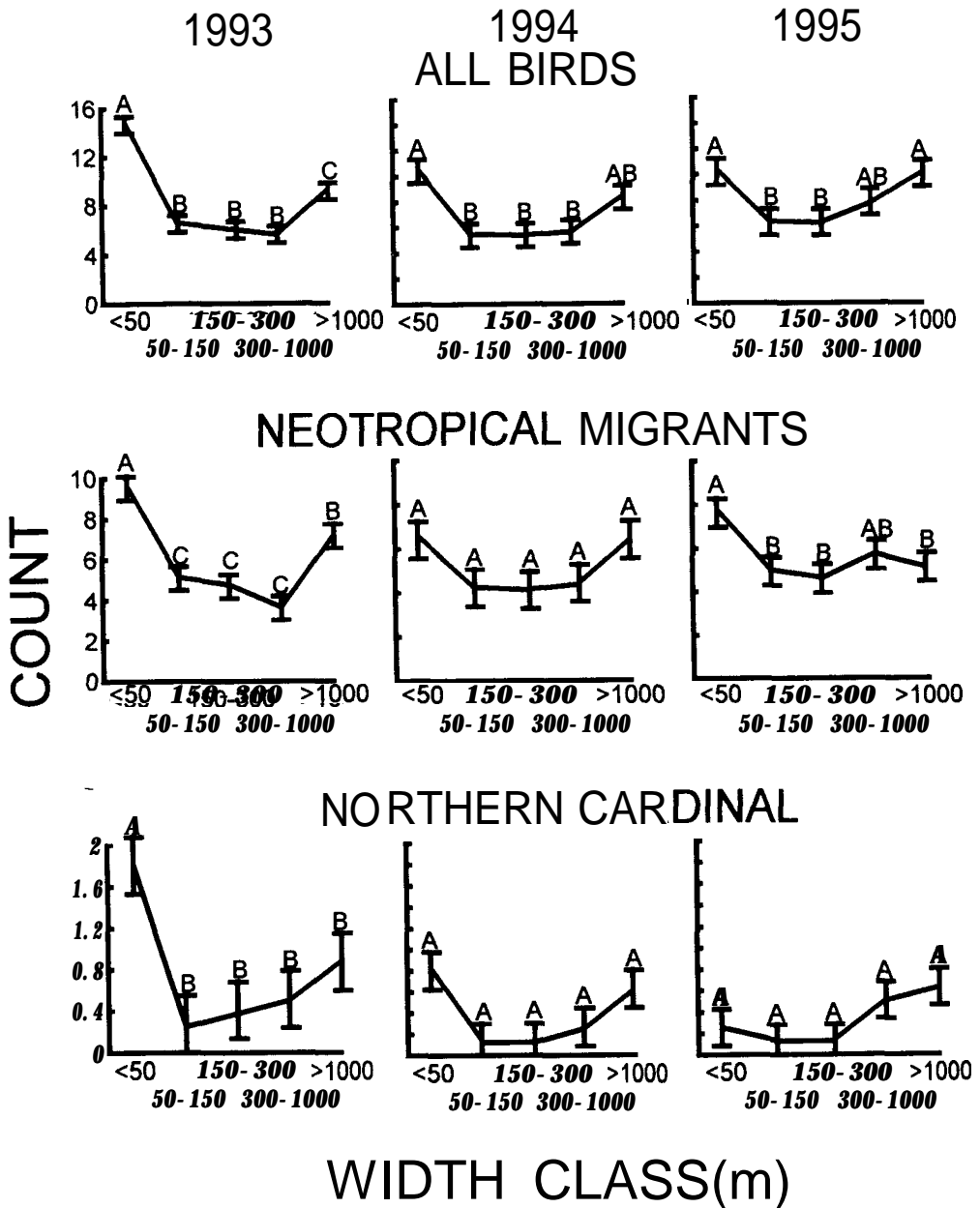


Fig. 2. Counts (mean ± SE) of breeding birds in 5 width classes of bottomland hardwood forests in South Carolina, 1993-95, analyzed by year because the year × width class interaction was significant ($P < 0.05$). Means with the same letter above them are not different ($P > 0.05$).

counts of blue-gray gnatcatcher in 1995, and counts of northern cardinal were greater in FES than in PES (Table 4). No species analyzed was significantly more abundant in PES than FES (Table 4), and no species' count was associated with PC1 or PC2 ($P > 0.05$).

DISCUSSION

Species richness exhibited a strong positive relation with bottomland forest width (Fig. 1). This relation existed although the adjacent habitat also was forested. Hence, there was a less abrupt ecotone in our study than in previous

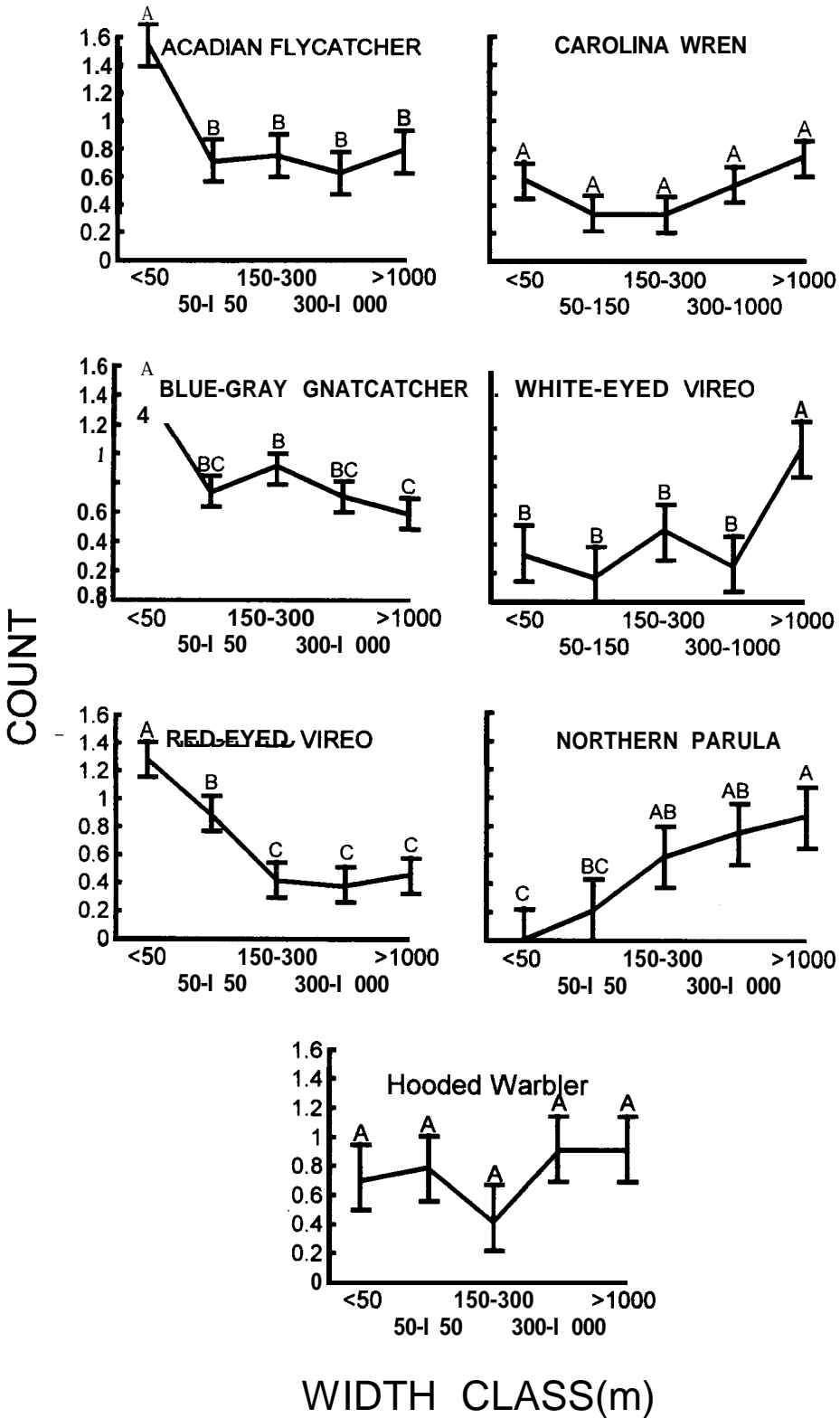


Table 2. Probabilities of detecting species in bottomland hardwood forests of various widths, as estimated by logistic regression analysis of data from 20 stands measured from 1993 to 1995, in South Carolina. Species are ordered from those with the strongest positive relation with forest width to those with the most negative relation. Only species detected in $\geq 5\%$ of the sites over all years are included.

| Species ^a | Bottomland forest width (m) | | | | | | | Wald X ² | P |
|--------------------------------------|-----------------------------|------|------|------|------|-------|-------|---------------------|--------------|
| | 25 | 50 | 100 | 200 | 500 | 1,000 | 2,500 | | |
| Swainson's warbler | 0.05 | 0.05 | 0.06 | 0.07 | 0.14 | 0.36 | 0.95 | 23.86 | 0.000 |
| American crow | 0.13 | 0.14 | 0.15 | 0.19 | 0.30 | 0.56 | 0.97 | 17.08 | 0.000 |
| Prothonotary warbler | 0.13 | 0.14 | 0.15 | 0.18 | 0.28 | 0.51 | 0.95 | 16.02 | 0.000 |
| Northern parula | 0.07 | 0.12 | 0.28 | 0.78 | 1.00 | 1.00 | 1.00 | 13.60 | 0.000 |
| Barred owl | 0.05 | 0.06 | 0.06 | 0.07 | 0.11 | 0.22 | 0.76 | 13.38 | 0.000 |
| Pileated woodpecker | 0.40 | 0.41 | 0.43 | 0.47 | 0.60 | 0.78 | 0.98 | 7.40 | 0.01 |
| Red-bellied woodpecker | 0.32 | 0.36 | 0.44 | 0.60 | 0.92 | 1.00 | 1.00 | 6.33 | 0.01 |
| White-eyed vireo | 0.52 | 0.55 | 0.60 | 0.69 | 0.88 | 0.98 | 1.00 | 6.26 | 0.01 |
| Summer tanager ^b | 0.27 | 0.29 | 0.33 | 0.42 | 0.65 | 0.82 | 0.24 | 7.61 | 0.02 |
| Kentucky warbler ^b | 0.56 | 0.59 | 0.65 | 0.75 | 0.90 | 0.95 | 0.09 | 7.52 | 0.02 |
| Yellow-billed cuckoo | 0.54 | 0.55 | 0.57 | 0.61 | 0.73 | 0.86 | 0.99 | 4.97 | 0.03 |
| Red-shouldered hawk | 0.19 | 0.19 | 0.20 | 0.21 | 0.25 | 0.34 | 0.66 | 4.25 | 0.04 |
| American redstart ^c | 0.10 | 0.11 | 0.14 | 0.20 | 0.39 | 0.46 | 0.00 | 5.65 | 0.06 |
| Downy woodpecker | 0.28 | 0.29 | 0.29 | 0.31 | 0.36 | 0.45 | 0.73 | 3.39 | 0.07 |
| Northern cardinal | 0.71 | 0.72 | 0.75 | 0.79 | 0.89 | 0.97 | 1.00 | 3.22 | 0.07 |
| Black-and-white warbler ^b | 0.12 | 0.13 | 0.16 | 0.21 | 0.37 | 0.09 | 0.01 | 4.88 | 0.09 |
| Hooded warbler | 0.65 | 0.74 | 0.86 | 0.97 | 1.00 | 1.00 | 1.00 | 2.67 | 0.10 |
| Yellow-throated vireo ^b | 0.23 | 0.24 | 0.27 | 0.33 | 0.50 | 0.63 | 0.09 | 4.25 | 0.12 |
| Tufted titmouse | 0.86 | 0.90 | 0.95 | 0.99 | 1.00 | 1.00 | 1.00 | 1.00 | 0.32 |
| Red-eyed vireo | 0.83 | 0.95 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.57 | 0.45 |
| Great-crested flycatcher | 0.45 | 0.45 | 0.45 | 0.46 | 0.48 | 0.52 | 0.62 | 0.47 | 0.49 |
| Carolina wren | 0.83 | 0.95 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.40 | 0.53 |
| Yellow-throated warbler | 0.11 | 0.11 | 0.11 | 0.11 | 0.12 | 0.13 | 0.17 | 0.14 | 0.71 |
| Ruby-throated hummingbird | 0.04 | 0.04 | 0.04 | 0.05 | 0.07 | 0.10 | 0.35 | 0.07 | 0.78 |
| Carolina chickadee | 0.29 | 0.29 | 0.29 | 0.29 | 0.30 | 0.31 | 0.35 | 0.06 | 0.80 |
| Common yellowthroat | 0.14 | 0.14 | 0.15 | 0.15 | 0.15 | 0.16 | 0.17 | 0.03 | 0.87 |
| Acadian flycatcher | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.00 | 1.00 |
| Blue-gray gnatcatcher ^c | 0.98 | 0.98 | 0.98 | 0.98 | 0.98 | 0.98 | 0.98 | N/A | N/A |
| Blue jay | 0.23 | 0.23 | 0.22 | 0.21 | 0.18 | 0.13 | 0.05 | 1.00 | 0.32 |
| Pine warbler | 0.14 | 0.13 | 0.11 | 0.07 | 0.02 | 0.00 | 0.00 | 1.00 | 0.32 |
| Mourning dove ^b | 0.02 | 0.02 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 2.32 | 0.31 |
| Louisiana waterthrush | 0.44 | 0.43 | 0.42 | 0.39 | 0.31 | 0.21 | 0.05 | 3.36 | 0.07 |
| wood thrush | 0.70 | 0.70 | 0.69 | 0.67 | 0.60 | 0.49 | 0.19 | 4.75 | 0.03 |

^a Scientific names of species not mentioned in text: American crow (*Corvus brachyrhynchos*); prothonotary warbler (*Protonotaria citrea*); barred owl (*Strix varia*); pileated woodpecker (*Dryocopus pileatus*); summer tanager (*Piranga rubra*); red-bellied woodpecker (*Melanerpes carolinus*); yellow-billed cuckoo (*Coccyzus americanus*); red-shouldered hawk (*Buteo lineatus*); American redstart (*Setophaga ruticilla*); downy woodpecker (*Picoides pubescens*); black-and-white warbler (*Mniotilta varia*); yellow-throated vireo (*Vireo flavifrons*); tufted titmouse (*Parus bicolor*); great-crested flycatcher (*Myiarchus crinitus*); yellow-throated warbler (*Dendroica dominica*); ruby-throated hummingbird (*Archilochus colubris*); Carolina chickadee (*Parus carolinensis*); common yellowthroat (*Geothlypis trichas*); blue jay (*Cyanocitta cristata*); pine warbler (*Dendroica pinus*); mourning dove (*Zenaidura macroura*).

^b The best-fit logistic regression equation included a quadratic term (width²)

^c Because we failed to detect blue-gray gnatcatcher in only 1 site in 1 year, convergence could not be attained in logistic regression analysis. Therefore, the probability of detection reported is the proportion of all stands, by year, in which the species was detected. This represents the maximum-likelihood estimate appropriate when probability of detection is not related to width (Robbins et al. 1989).

studies relating species richness to area (Blake and Karr 1987, Robbins et al. 1989) or width (Keller et al. 1993). However, the slope of this relation did not differ from slopes of species-area relations, indicating that our wider stands did not exhibit a greater increase in species richness than was expected from simple species-

area regressions. The general lack of associations between the bird community and habitat features is likely attributable to the general similarity of vegetation among the study sites; stands were selected because of their apparent similarity of vegetation. Thus, the observed relation of species richness to stand width is due

Fig. 3. Counts (mean \pm SE) of 7 breeding bird species in 5 width classes of bottomland hardwood stands in South Carolina, 1993-95. Means with the same letter are not different ($P > 0.05$).

Table 3. Eigenvectors for variables included in principal components (PC) analysis of 12 bottomland hardwood stands, 8 enclosed by pine forest and 4 enclosed by fields, in South Carolina, 1994-95. The PC1 and PC2 (only components with eigenvalues >1.00) accounted for 70% of the variation in the variables measured among sites.

| Variable | PC1 | PC2 |
|--|-------|-------|
| Vegetation profile | -0.44 | 0.52 |
| Canopy coverage | 0.72 | -0.12 |
| Basal area: hardwood poletimber ^a | -0.04 | -0.64 |
| Basal area: hardwood sawtimber ^b | 0.53 | 0.55 |

^a Defined as all hardwood stems 8-23 cm dhh

^b Defined as all hardwood stems >23 cm dhh.

either to a response to width per se or to unmeasured features of the habitat. Pashley and Barrow (1993) described several aspects of bottomland hardwood habitats important to birds. These included scour channels, Spanish moss (*Tilandsia usneoides*), canebrakes (i.e., switch-cane thickets), vine tangles, and thickets of palmetto (*Sabal minor*). The wider a stand, the more likely it is to contain each of these features, yet all are difficult to quantify with the conventional techniques we used to sample avian habitat.

Both total and species-specific counts generally were greatest in the narrowest and widest width classes. This U-shaped pattern in total bird count was inconsistent with our expectation that fewer species in narrow stands would mean fewer birds. We suggest that the observed

pattern might better be understood by examining the 2 segments of this relation separately (i.e., the portion of the abundance-width curve for which the relation is negative vs. that for which the curve is positive). Three factors may have contributed to the negative relation that characterized the narrow stands. First, the relation potentially resulted from the combined effects of species positively associated with width (e.g., northern parula, white-eyed vireo), and of species negatively associated with width (e.g., Acadian flycatcher, blue-gray gnatcatcher, red-eyed vireo). Second, a greater amount of edge habitat was censused in the narrow stands because census plots in these stands overlapped both stand edges. Consequently, edge species such as northern cardinal and Carolina wren were more abundant in the narrowest width classes than in the medium width classes (this trend was nonsignificant for Carolina wren). Finally, densities in our narrowest stands potentially were high simply because birds were confined within a smaller area, whereas territories were not as packed in medium width stands, because space was not limited. Previous studies reported that bird density decreased with increased width of the riparian zone, whereas species richness increased with width (Darveau et al 1995, Thurmond et al. 1995). Such a pattern is consistent with our results for the narrow width classes, which encompassed the widths

Table 4. Comparison of breeding birds in bottomland hardwood stands enclosed by pine forest (PES; $n = 8$) and enclosed by fields (FES; $n = 4$) in South Carolina, 1994-95.

| Variable | PES | | FES | | P |
|------------------------------------|-----------|------|-----------|------|-------|
| | \bar{x} | SE | \bar{x} | SE | |
| Species richness | | | | | |
| All birds ^a | | | | | |
| 1994 | 18.75 | 0.73 | 14.50 | 1.03 | 0.007 |
| 1995 | 14.63 | 0.82 | 19.00 | 1.16 | 0.012 |
| Neotropical migrants ^b | 8.42 | 0.54 | 8.02 | 0.76 | 0.530 |
| Count | | | | | |
| All birds | 5.88 | 0.45 | 9.03 | 0.63 | 0.015 |
| Neotropical migrants | 4.50 | 0.29 | 5.20 | 0.41 | 0.356 |
| Acadian flycatcher | 0.81 | 0.45 | 0.78 | 0.10 | 0.879 |
| Carolina wren | 0.34 | 0.07 | 0.59 | 0.10 | 0.301 |
| Blue-gray gnatcatcher ^a | | | | | |
| 1994 | 0.69 | 0.09 | 0.90 | 0.13 | 0.216 |
| 1995 | 0.56 | 0.07 | 1.15 | 0.10 | 0.001 |
| White-eyed vireo | 0.25 | 0.05 | 0.25 | 0.07 | 1.000 |
| Red-eyed vireo | 0.69 | 0.11 | 0.64 | 0.15 | 0.801 |
| Northern parula | 0.47 | 0.08 | 0.71 | 0.11 | 0.426 |
| Hooded warbler | 0.59 | 0.08 | 0.25 | 0.11 | 0.237 |
| Northern cardinal | 0.13 | 0.03 | 0.84 | 0.04 | 0.001 |

^a Year \times treatment interaction was significant ($P < 0.05$), so years were analyzed separately.

^b Species richness was positively correlated with PC1 ($P = 0.049$).

reported in these studies. For example, Thurmond et al. (1995) reported higher bird densities but fewer species in narrow (16-20 m) versus wide (53-58 m) streamside management zones in Georgia. Similarly, Darveau et al. (1995) reported that 20-m-wide riparian strips in Quebec contained greater bird densities but fewer species than 40- and 60-m-wide strips, although the wider strips supported a greater number of territories because they contained greater areas. Thus, the negative relation between count and width for narrow stands may be related to area and sampling effects, whereas counts from wider stands, for which no comparison from the literature is available, actually may reflect superior habitat conditions that support higher densities of birds.

Some species generally considered to be area sensitive (Robbins et al. 1989) exhibited unexpected patterns of occurrence and abundance. The probabilities of occurrence for wood thrush (*Hylocichla mustelina*) and Louisiana waterthrush (*Seiurus motacilla*) were negatively related to width. Capture rates of wood thrush in a concurrent mistnetting study (R. A. Sargent et al., unpublished data) also were negatively related to width. Keller et al. (1993) found these species positively associated with riparian zone width in the mid-Atlantic states. Counts of red-eyed vireo, also considered an area-sensitive species (Robbins et al. 1989, Keller et al. 1993), declined as width increased, although this species' probability of occurrence increased (nonsignificantly) with width. Similarly, Acadian flycatcher was detected even in our narrowest stands, and their counts declined in wider stands. Conversely, counts of white-eyed vireo, an edge species, were positively related to width. Our results for Acadian flycatcher and white-eyed vireo are corroborated by those of Hodges and Kremetz (1996) from the Altamaha River basin, a tributary of the Savannah River. Reasons for lower densities in sites where a species is more likely to occur are unclear but may be related to the species' sociobiology. Density also is not necessarily an accurate reflection of habitat quality (Wiens 1989:306).

We failed to detect a consistent effect of adjacent habitat on species richness. We hypothesized that more species would be found in PES than in FES because the presence of an adjacent, closed canopy forest might serve as a buffer against negative edge effects (Harris 1984, Kilgo et al. In press), and thereby increase the

functional width of the stand. Such an effect was evident in 1994, but the pattern was reversed in 1995. Similarly, we failed to detect an effect of adjacent habitat on the counts of area-sensitive species. The northern cardinal, an edge species, was more abundant in FES, but counts of the area-sensitive northern parula and white-eyed vireo (this study) were not affected negatively by the presence of field habitat adjacent to the stand. The expected pattern may have been evident had we sampled narrower FES (i.e., some species may be sensitive to external fragmentation below the range of widths we sampled).

MANAGEMENT IMPLICATIONS

We concur with the conclusion of Thurmond et al. (1995) that even retention of narrow streamside buffer zones can benefit local bird assemblages. Several area-sensitive species (e.g., Acadian flycatcher, wood thrush, red-eyed vireo, Louisiana waterthrush, Kentucky warbler [*Oporornis formosus*], hooded warbler) were common in our narrowest stands. However, because we sampled a broad range of widths, we detected several species that were highly area-sensitive and apparently would benefit only from conservation of very wide stands. For example, the narrowest stand in which we detected Swainson's warbler (*Limothlypis swainsonii*) was 475 m wide. Although we could not include them in our analysis, Mississippi kite (*Ictinia mississippiensis*) was recorded only in stands 21,000 m wide, and swallow-tailed kite (*Elanoides forficatus*) was recorded only in stands 21,900 m wide. Keller et al. (1993) and Hodges and Kremetz (1996) recommended that a minimum forested buffer zone of ≥ 100 m be maintained adjacent to drainages to provide habitat for forest interior species. In our study, the width at which probability of occurrence was 50% of its maximum (i.e., a conservative estimate of the minimum amount of habitat required by a species for breeding; Robbins et al. 1989) exceeded 100 m for 8 species (pileated, red-bellied, and downy woodpeckers, yellow-throated vireo, northern parula, American redstart, black-and-white warbler, summer tanager) and exceeded 500 m for 6 additional species (barred owl, red-shouldered hawk, ruby-throated hummingbird, American crow, prothonotary warbler, Swainson's warbler). Thus, although narrow riparian stands are extremely valuable avian habitat, we feel that the complete avian

community characteristic of bottomland hardwoods in South Carolina can be maintained only in the few remaining riparian zones that are extremely wide (>500m).

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