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Landscape influences on breeding bird communities in hardwood fragments in South Carolina

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Abstract Results from studies on the effects of forest fragmentation on bird communities in urban-agricultural landscapes may not be applicable to forested landscapes such as the Southeastern Coastal Plain. During 1993-l 994, we measured parameters of avian communities in the Coastal Plain of South Carolina in hardwood stands surrounded by agricultural habitat (field-enclosed stands; FES) and in hardwood stands surrounded by pine (*Pinus* spp.)-forested habitat (pine-enclosed stands; PES). Total species richness was greater in FES than PES in both years ($P < 0.001$) and was associated positively with stand area in both treatments. Neotropical migrant species richness did not differ between treatments ($P > 0.05$), but was associated positively with stand area. Total bird abundance was greater in FES than in PES ($P < 0.001$). Abundance of tufted titmouse (*Parus bicolor*), Carolina wren (*Thryothorus ludovicianus*), and northern cardinal (*Cardinalis cardinalis*) was greater ($P < 0.01$) in FES than PES in ≥1 year, and abundance of red-eyed vireo (*Vireo olivaceous*) and summer tanager (*Piranga rubra*) was greater ($P < 0.02$) in PES than FES in 1 year. Ten species had greater probabilities of occurrence in FES than PES ($P < 0.05$), whereas red-eyed vireo was the only species more likely to occur in PES than in FES. Wood thrush (*Hylocichla mustelina*) and ovenbird (*Seiurus aurocapillus*) occurred in PES but not in FES. The presence of a surrounding pine forest apparently increased the suitability of PES for some area-sensitive species, but decreased suitability for several edge species.

Key words abundance, breeding birds, fragmentation, landscape management, oak-hickory forest, South Carolina, species richness

Most research on responses of avian communities to habitat fragmentation has been conducted in landscapes fragmented by agriculture or urban-suburban development. Such studies have documented a positive relationship between species richness and forest area (Forman et al. 1976, Whitcomb et al. 1981, Ambuel and Temple 1983, Blake and Karr 1987). However, information gained from fragmentation studies in urban-agricultural landscapes may be inappropriate for formulating management strategies in forest-dominated landscapes such as those of the Southeastern Coastal Plain. For example, pinelands comprise 29% of the acreage of South Carolina, whereas agricultural zones comprise only 23%, and urban-suburban zones <10% (Tansey and Hutchins 1988). Freemark and Collins (1992:451) observed that, "A better understanding of the relation between landscape structure and the distribution and survival of species is an important prerequisite for developing and implementing effective conservation plans for birds breeding in temperate forests."

Harris (1984) proposed that the functional size of a forest stand may be increased for area-sensitive species if it is surrounded by another forest type, regard-

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less of the suitability of that type as habitat, rather than by cleared or developed land. If an ecotone is not as abrupt, some negative edge effects (e.g., predation, brood parasitism, light and wind penetration) might be reduced, potentially allowing area-sensitive species to exist in relatively small stands. Some data support this "forest buffer hypothesis" indirectly, at the scale of the landscape. For example, Freemark and Collins (1992) found more area-sensitive species and a steeper slope to the species-area relationship for forest-interior species in a landscape with a greater degree of forest cover than in 1 with less cover. However, to our knowledge, the hypothesis has not been tested directly at the stand-scale. In the Southeastern Coastal Plain, hardwood stands often exist as inclusions within larger pine stands, yet the potential effects of the surrounding pine habitat on the suitability of the hardwood forest for birds has not been investigated. We compared avian communities in hardwood forests surrounded by agricultural habitat with those in hardwood forests surrounded by pine-forested habitat in the Coastal Plain of South Carolina.

Methods

The study was conducted at the U.S. Department of Energy's Savannah River Site (SRS), a 78,000-ha tract in Aiken, Barnwell, and Allendale counties in the Upper Coastal Plain of South Carolina, and on private properties immediately east of SRS. The landscape of SRS is predominantly forested, whereas the surrounding privately-owned landscape is largely agricultural (Fig. 1). The SRS was acquired by the Department of Energy (then the Atomic Energy Commission) in 1950. Lands previously in agricultural production were planted in pine, primarily loblolly pine (*Pinus taeda*) and longleaf pine (*P. palustris*). Upland oak-hickory (*Quercus-Carya* spp.) forest existed where fire had been excluded (Whipple et al. 1981), generally in the vicinity of home sites and cemeteries and on bluffs and slopes adjacent to riparian zones. Many upland hardwood stands currently remain. The amount and composition of upland hardwood forest in the landscape generally is similar on and off SRS, and the landscapes differ primarily in the relative coverage of pine forest.

Most upland hardwood stands are <10 ha. Dominant canopy species include mockernut hickory (*Carya tomentosa*), sweetgum (*Liquidambar styraciflua*), post oak (*Quercus stellata*), white oak (*Q. alba*), southern red oak (*Q. falcata*), turkey oak (*Q. laevis*), blackjack oak (*Q. marilandica*), and water oak (*Q. nigra*). The midstory and shrub layers are dominated by flowering dogwood (*Cornus florida*) and sparkleberry (*Vaccinium arboreum*), respectively. Common ground cover species include muscadine (*Vitis rotundifolia*) and poison ivy (*Toxicodendron radicans*).

We selected 36 hardwood stands ranging in size from 0.5 to 40 ha; 21 were surrounded by closed canopy pine forest (pine-enclosed stands, PES) located on SRS, and 15 were surrounded by field-scrub habitats (field-enclosed stands, FES) adjacent to SRS. We located stands using aerial photographs and by ground searching from roads. Selection criteria included low edge-to-area ratio (i.e., non-linear in shape), upland forest with 275% hardwood canopy, and complete isolation from other hardwood forests (i.e., stands were surrounded completely by the matrix type of interest and were not adjacent to other hardwood stands). We required that 250 m of pine forest separate PES from major canopy breaks (e.g., clearcuts, roads, power line rights-of-way), and 210 m of unforested land separate FES from forested land (Lynch and Whigham 1984). However, 290% of the perimeter of each FES was separated from nearby forest by 250 m. Most hardwood stands were ≤5 ha in size. An index of isolation was calculated for each stand and was defined as the mean distance to the nearest hardwood stand >2 ha in size in each of 4 compass quadrants. The isolation index for stands on SRS was calculated with ARC/INFO Geographic Information Systems and for stands off SRS was calculated from aerial photographs.

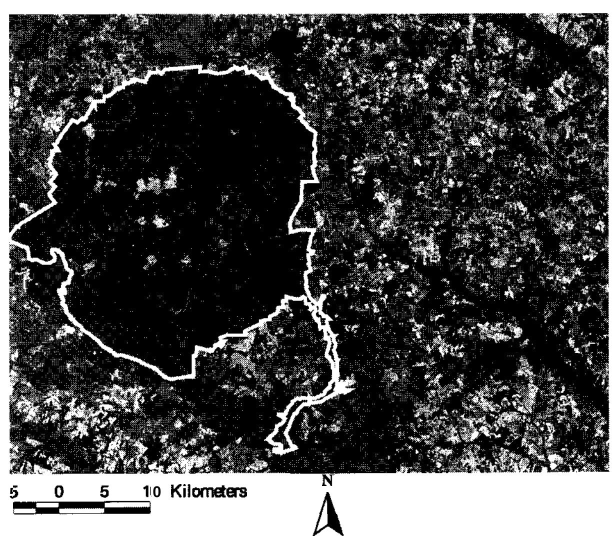

Fig. 1. SPOT Satellite image depicting contrast in landscape structure between the heavily pine-forested Savannah River Site (approx 78,000 ha, bounded by white line) and the surrounding agricultural region. Darker areas represent forest, whereas lighter areas represent open habitat.

We measured habitat characteristics in randomly located 0.04-ha circular plots (James and Shugart 1970) in 1993: 5 plots in stands 22.0 ha, 3 in stands 0.6-1.9 ha, and 1 in stands 10.5 ha. We measured canopy coverage using a densiometer at the 4 cardinal points on the plot perimeter. Vegetation profile was measured using a 3-m high density board standing upright on the ground (Noon 1981). Percent cover was recorded for each 0.5-m increment of the density board, as viewed from plot center to plot edge in each of the cardinal directions. We recorded species and size class of all trees >3 cm in diameter at breast height in the plot using a Biltmore stick (James and Shugart 1970).

We used 5-minute fixed-radius (50 m) point counts (Hutto et al. 1986, Ralph et al. 1995) to evaluate the avian communities in each stand. Within each stand, we spaced 2 points, centered width-wise, evenly along the long axis of the stand. We sampled only 1 point in stands <3.0 ha. We placed flagging tape at trees on the perimeter of each plot to aid in estimating distances. Counts were conducted from sunrise to 3.5 hours post-sunrise, except during periods of high wind or ram (Ralph et al. 1995). We visited each stand at approximately equal intervals 3 times per year between mid-May and late June 1993-1994, once each during early (0630-0740), middle (0740-0850), and late (0850-1000) morning (approx times). We attempted to record birds only once that were detectable from both points in a stand (Ralph et al. 1995). Birds flying over the stand were not recorded. Species detected within the stand, but beyond the 50-m radius or within ±3 minutes of the count period while en route to points, were included in species richness estimates (Hutto et al. 1986). For stands with radii <50 m ($n = 5$), abundance counts were adjusted according to the fraction of a 50-m radius plot that each stand comprised (i.e., abundance is reported as birds/O.79 ha, the area of a 50-m radius plot). We averaged the high count for each species per point over both points to get an index of relative abundance for each stand (Blonde1 et al. 1981, Blake and Karr 1987). We assumed any bias in bird detection among points was minimal because vegetation characteristics did not differ between treatments, only 2 observers were used, weather conditions were standardized, and timing of counts within day and season was stratified.

The habitat variables we included in principal components analysis (PCA; PROC PRINCOMP; SAS Inst., Inc. 1990) were: vegetation profile (PROFILE; the mean percent coverage from the density board, a measure of understory structure), basal area of hardwood pole timber (POLE; hardwood stems 8-23 cm dbh, a measure of midstory structure), canopy coverage (CANOPY), and basal area of hardwood sawtimber (SAW; hardwood stems >23 cm dbh). This approach was taken because it minimized the number of vegetation variables; thus, it simplified interpretation, yet provided measures of structure for 3 primary habitat layers and included 2 variables commonly invento ried by forest managers. For inclusion in analyses of bird-habitat relations, we selected only those principal components (PC) with eigenvalues 21.0. The original variables (PROFILE, POLE, CANOPY, SAW) and the principal components scores (PC1 and PC2) were compared between treatments with analysis of covariance (ANCOVA; PROC GLM; SAS Inst., Inc. 1990), using stand area as a covariate.

We tested the null hypotheses that bird species richness, total abundance, and abundance indices of each species did not differ between treatments (i.e., surrounding habitat type). Because of current concern over population declines of neotropical migrants, we tested species richness and abundance of neotropical migrants (forest interior and interior-edge species only; Whitcomb et al. 1981) using the same procedures. We analyzed individually only those species for which we recorded 220 observations. Comparisons between treatments were made using repeated measures analysis of covariance (2 years; RM-ANCOVA; PROC GLM; SAS Inst., Inc. 1990) with stand area, isolation index, and PC1 and PC2 as covariates, and site-nested-within-treatment and the year-x-treatment interaction as additional terms. We converted covariates to deviations from the mean before analysis. We tested all variables except year and year-x-treatment with site-within-treatment as the error term. When year-x-treatment was significant ($P < 0.05$), we analyzed years separately. When covariate effects were not significant ($P > 0.05$), they were eliminated.

We used logistic regression (PROC LOGISTIC; SAS Inst., Inc. 1990) to test the null hypotheses that probability of occurrence for each species did not differ by year, between treatments, or by stand area. When the year effect was significant ($P < 0.05$), years were analyzed separately. When the effect of stand area was nonsignificant ($P > 0.05$), we added a quadratic term, $B_2x_i^2$, where x = stand area (Robbins et al. 1989). The best model was determined by significance of the Score statistic (SAS Inst., Inc. 1990). Only species recorded in 25% of the stand-years were included in logistic regression analysis.

Results

The first 2 components produced by PCA (PC1 and PC2) had eigenvalues >1.0 and, together, accounted for 70% of the variation among stands (PC1, 43.2%; PC2, 26.9%). High scores on PC1 (which was positively correlated with CANCOV and SAW and negatively correlated with PROFILE; Table 1) represented stands with a closed canopy of larger trees but poorly developed under- and midstories. High scores on PC2 (which was positively correlated with POLE and negatively correlated with PROFILE and SAW; Table 1) represented stands with few large trees, many small trees, and a poorly developed understory. We found no difference between treatments in PROFILE, POLE, CANOPY, SAW, PC1, or PC2 ($P > 0.10$), but PC1 was inversely related to stand size ($F_{1,36} = 11.67$, $P = 0.002$) indicating that larger stands had smaller trees, a more open canopy, and better developed under- and midstories. The lack of differences in vegetation between treatments probably was due to our site-selection criteria; we selected sites as vegetatively similar as possible. Because neither habitat structure nor area ($t = 1.29$, df = 23, $P = 0.21$) differed between treatments, we believe that the primary factor affecting bird abundance and distribution in our study was the surrounding habitat type.

Because total species richness differed between years ($P < 0.001$), and the year-x-treatment interaction for neotropical migrant species richness was significant ($P = 0.029$) we analyzed years separately for both groups. Neither habitat covariates nor isolation contributed significantly to the RM-ANCOVA model for either group. Richness of total species as well as richness of neotropical migrant species were associated positively with the natural logarithm of stand area, and total species richness was greater in FES than PES in both years (Fig. 2). Stand areas were log-transformed because the resulting model accounted for a greater amount of variation in the number of species and a better fit than the model based on the untransformed data.

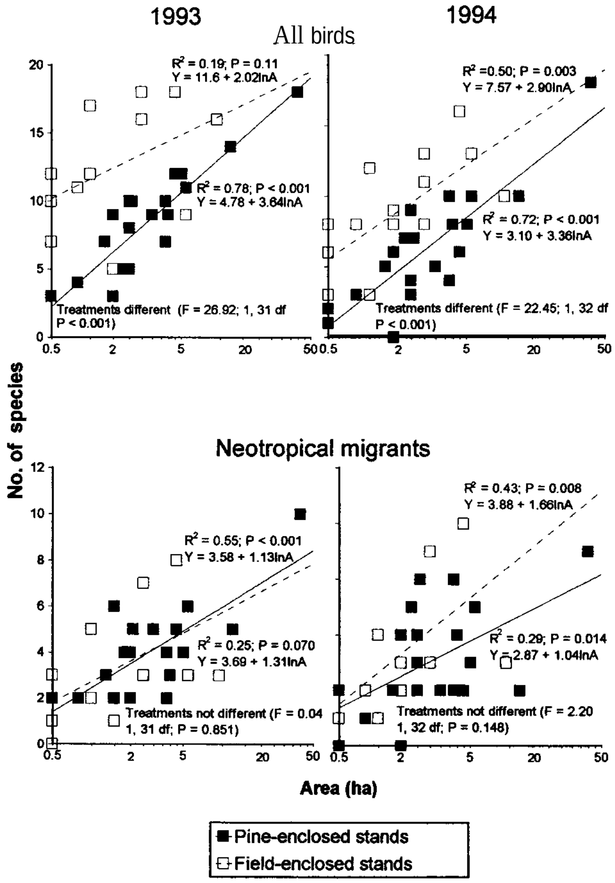

Fig. 2. Relationship between the natural logarithm of stand area (lnA) and species richness (Y) for: (A) breeding birds in pine-enclosed stands (PES; $Y = 4.78 + 3.64\ln A$; $R^2 = 0.78$; $P < 0.001$) and field-enclosed stands (FES; $Y = 11.6 + 2.02\ln A$; $R^2 = 0.19$; $P = 0.110$) in 1993 (treatments differed: $F_{1,31} = 26.92$; $P < 0.001$); (B) breeding birds in PES ($Y = 3.10 + 3.36\ln A$; $R^2 = 0.72$; $P < 0.001$) and FES ($Y = 7.57 + 2.90\ln A$; $R^2 = 0.50$; $P = 0.003$) in 1994 (treatments differed: $F_{1,32} = 22.45$; $P < 0.001$); (C) neotropical migrants in PES ($Y = 3.58 + 1.13\ln A$; $R^2 = 0.55$; $P < 0.001$) and FES ($Y = 3.69 + 1.31\ln A$; $R^2 = 0.25$; $P = 0.070$) in 1993 (treatments did not differ: $F_{1,31} = 0.04$; $P = 0.851$); and (D) neotropical migrants in PES ($Y = 2.87 + 1.04\ln A$; $R^2 = 0.29$; $P = 0.014$) and FES ($Y = 3.88 + 1.66\ln A$; $R^2 = 0.43$; $P = 0.008$) in 1994 (treatments did not differ: $F_{1,31} = 2.20$; $P = 0.148$).

Table 1. Eigenvectors for variables included in principal components analysis of 36 hardwood stands, 21 enclosed by pine forest, and 15 enclosed by field-scrub habitats, in South Carolina. PC1 and PC2 (only components with eigenvalues >1.00) accounted for 70% of the variation in the measured variables among sites.

Variable	PC1	PC2
Vegetation profile	− 0.54	− 0.33
Canopy coverage	0.59	0.06
Basal area: hardwood poletimber[a]	− 0.08	0.91
Basal area: hardwood sawtimber[b]	0.60	− 0.24

[a] Defined as all hardwood stems 8-23 cm in dbh.
[b] Defined as all hardwood stems >23 cm in dbh.

Total bird abundance was more than twice as high in FES as in PES (Table 2). However, neotropical migrant abundance did not differ between treatments. Abundance was not related in either group to stand area, isolation, PC1, or PC2 ($P > 0.05$). We recorded sufficient data on 6 species for individual analysis: tufted titmouse (*Parus bicolor*), Carolina wren (*Thryothorus ludovicianus*), blue-gray gnatcatcher (*Polioptila caerulea*), red-eyed vireo (*Vireo olivaceous*), northern cardinal (*Cardinalis cardinalis*), and summer tanager (*Piranga rubra*). The year-x-treatment interaction was significant for red-eyed vireo, northern cardinal, and summer tanager, so data

Table 2. Relative abundance of breeding birds in hardwood stands enclosed by pine forest (PES; n = 21) and by field-scrub habitat (FES; n = 14 [1993], 15 [1994]) in South Carolina, 1993-1994.

Species	PES		FES			
	$\bar{x}$	SE	$\bar{x}$	SE	F	P
All birds	3.34	0.44	7.44	0.53	30.28	0.000
Neotropical migrants	2.13	0.17	2.25	0.20	0.05	0.820
Tufted titmouse	0.28	0.09	0.56	0.10	7.82	0.009
Carolina wren	0.08	0.07	0.51	0.08	17.52	0.000
Blue-gray gnatcatcher	0.61	0.07	0.69	0.09	0.19	0.662
Red-eyed vireo[a]						
1993	0.58	0.08	0.00	0.10	24.55	0.000
1994	0.35	0.10	0.27	0.11	0.29	0.594
Northern cardinal[a]						
1993	0.31	0.13	0.43	0.16	0.33	0.568
1994	0.19	0.09	1.03	0.10	37.51	0.000
Summer tanager[a]						
1993	0.48	0.10	0.11	0.11	6.08	0.019
1994	0.33	0.11	0.37	0.13	0.06	0.809

[a] Analyzed by year because year-x-treatment interaction was significant ($P < 0.05$).

were analyzed by year for these species. Abundance of all species, except blue-gray gnatcatcher, differed between treatments in ≥1 year (Table 2). Abundance of red-eyed vireo in 1993 was negatively associated with isolation ($F_{1,30}$ = 5.44, P = 0.027) and positively associated with PC1 ($F_{1,30}$ = 8.77, P = 0.006), indicating greater abundance in stands with a closed canopy of larger trees but poorly developed under- and midstories. Abundance of northern cardinal in 1994 was negatively associated with isolation ($F_{1,31}$ = 6.84, P = 0.014) and with PC2 ($F_{1,31}$ = 7.02, P = 0.013) indicating greater abundance in stands with larger trees, poorly developed midstories, but dense understories. No other relationships between habitat variables and species abundances were detected. With the exception of ovenbird and black-and-white warbler (*Mniotilta varia*), both of which were uncommon, all neotropical migrants detected in the study stands (treatment ignored) were midstory and canopy-nesters.

Ten species had greater probabilities of occurrence in FES (Table 3), while red-eyed vireo was the only species more likely to occur in PES. Wood thrush and ovenbird were detected only in PES (Table 3) so convergence could not be attained in the logistic regression analysis, and the chi-square test statistic for the difference between treatments could not be computed. Probability of occurrence of American crow, Carolina wren, and blue grosbeak differed between years, so years were analyzed separately for these species.

Discussion

Total richness and richness of neotropical migrant species were positively associated with stand area for both treatments. Results of previous species-area studies in small stands are conflicting. Loman and Von Schantz (1991) reported greater species richness in smaller stands, whereas Howe (1984) reported a positive relationship between species richness and stand area. Species richness of interior-edge and forest-interior neotropical migrants did not exhibit a stronger relationship with stand size than total species richness, probably because few forest-interior species were detected in the stands.

Total species richness, abundance, and the abundance indices of 3 species were greater in FES than PES. Additionally, for 10 species, probability of occurrence was greater in FES than PES. All species more likely to occur in FES were edge species (i.e., interior-edge or field-edge). This pattern is consistent with the concept of edge effect (i.e., abundance and diversity of species is greater at habitat edges), especially considering that small stands isolated by open land may be comprised, in effect, entirely of edge habitat (Ranney et al. 1981). A core group of interior-edge species (e.g., northern cardinal, Carolina wren, tufted titmouse, blue-gray gnatcatcher) existed in most sites. This group generally was supplemented in FES by interior-edge and field-edge species (e.g., mourning dove, indigo bunting, and northern bob white) and in PES by more area-sensitive interior-edge and interior species (e.g., red-eyed vireo, wood thrush, ovenbird). Other species generally considered to be area-sensitive (e.g., northern parula and Acadian flycatcher; Robbins et al. 1989) also were common in small FES. Thus, the greater species richness and abundance observed in FES resulted from the larger number of field-edge species in FES, relative to the number of forest-interior species in PES.

The presence of an adjacent closed-canopy forest apparently allowed some species to exist in greater abundance in PES than in FES. Abundance of red-eyed vireo and summer tanager, both interior-edge neotropical migrants, was greater in PES than FES (for 1 year); and wood thrush, red-eyed vireo, and ovenbird, all interior-edge or forest interior neotropical migrants, were more likely to be detected in PES than FES. Similarly, Freemark and Collins (1992) reported more area-sensitive species in forest fragments in an area of greater overall forest cover than in fragments in an area with less forest cover. Red-eyed vireo, summer tanager, wood thrush, and ovenbird are sensitive to forest area (Robbins et al. 1989). It is unclear whether they were more abundant in PES because

Table 3. Probabilities of detecting species in various-sized hardwood stands enclosed by pine forest (PES; n = 20) and by field-scrub habitats (FES; n = 15) in South Carolina, 199331994, as estimated by logistic regression analysis, with the Wald χ^2 statistic and probability (P) that the 2 treatments (PES and FES) differ. Species are ordered from those most likely to be detected in PES to those most likely to be detected in FES. Only species detected in 5% of the sites over both years are included.

		Size (ha)						
Species	**Treatment**	0.5	**1.0**	2.5	5.0	**10.0**	χ^2	P
Red-eyed vireo	PES	0.65	*0.65*	0.67	0.70	0.76	11.20	***0.001***
(*Vireo olivaceous*)	FES	0.22	*0.23*	0.24	0.27	0.33		
Summer tanager"	PES	0.25	*0.30*	0.49	0.77	0.97	0.54	0.46
(*Piranga rubra*)	FES	0.18	*0.22*	0.39	0.69	0.95		
Northern flicker	PES	0.09	0.10	0.12	0.16	0.30	0.09	0.76
(*Colaptes auratus*)	FES	0.06	0.07	0.08	0.12	0.22		
Blue-gray gnatcatcher	PES	0.73	0.74	0.77	0.80	0.86	0.07	0.79
(*Polioptila caerulea*)	FES	0.71	0.72	0.74	0.78	0.84		
Rufous-sided towhee"	PES	0.24	0.28	0.42	0.65	0.88	0.00	0.94
(*Pipilo erythrophthalmus*)	FES	0.23	0.27	0.41	0.63	0.88		
Wood thrush[b]	PES	0.05	0.05	0.08	0.14	0.37	NA	NA
(*Hylocichla mustelina*)	FES	0.00	0.00	0.00	0.00	0.00		
Ovenbird[b]	PES	0.07	0.07	0.08	0.09	0.12	NA	NA
(*Seiurus aurocapillus*)	FES	0.00	0.00	0.00	0.00	0.00		
Eastern wood pewee[a,b]	PES	0.00	0.00	0.00	0.00	0.00	NA	NA
(*Contopus virens*)	FES	0.01	0.03	0.42	0.19	0.00		
Brown-headed cowbird"	PES	0.04	0.05	0.09	0.22	0.55	0.01	0.92
(*Molothrus ater*)	FES	0.04	0.06	0.10	0.23	0.58		
Northern parula	PES	0.23	0.24	0.26	0.30	0.40	0.11	0.74
(*Parula americana*)	FES	0.27	0.27	0.30	0.35	0.45		
Carolina chickadee	PES	0.18	0.19	0.25	0.38	0.66	0.42	0.52
(*Parus carolinensis*)	FES	0.24	0.26	0.33	0.47	0.74		
Blue jay[a]	PES	0.39	0.41	0.49	0.61	0.78	0.99	0.32
(*Cyanocitta cristata*)	FES	0.53	0.62	0.63	0.74	0.86		
Pileated woodpecker	PES	0.35	0.36	0.40	0.47	0.60	0.98	0.32
(*Dryocopus pileatus*)	FES	0.59	0.61	0.64	0.70	0.81		
Pine warbler	PES	0.04	0.05	0.05	0.07	0.10	1.61	0.20
(*Dendroica pinus*)	FES	0.17	0.18	0.20	0.24	0.34		
Downy woodpecker[a]	PES	0.1 1	0.12	0.16	0.22	0.29	1.79	0.18
(*Picoides pubescens*)	FES	0.22	0.24	0.30	0.40	0.49		
American crow								
1993	PES	0.09	0.10	0.13	0.21	0.44	2.14	0.14
(*Corvus brachyrhynchos*)	FES	0.26	0.28	0.35	0.49	0.75		
1994	PES	0.00	0.00	0.00	0.00	0.01	0.91	0.34
	FES	0.07	0.08	0.12	0.2 1	0.51		
Yellow-throated vireo	PES	0.1 1	0.11	0.12	0.14	0.20	2.42	0.12
(*Vireo flavifrons*)	FES	0.32	0.33	0.36	0.40	0.49		
Acadian flycatcher"	PES	0.02	0.03	0.09	0.22	0.06	2.91	0.09
(*Empidonax virescens*)	FES	0.06	0.13	0.25	0.49	0.17		
Red-bellied woodpecker"	PES	0.26	0.31	0.51	0.86	*1 .00*	3.26	0.07
(*Melanerpes carolinus*)	FES	0.53	0.58	0.76	0.95	1 .00		
Blue grosbeak								
1993	PES	0.09	0.09	0.10	0.10	0.1 1	4.23	0.04
(*Guiraca caerulea*)	FES	0.42	0.42	0.43	0.44	0.46		
1994[b]	PES	0.05	0.05	0.05	0.05	0.05	NA	NA
	FES	0.28	0.28	0.28	0.28	0.28		
Great-crested flycatcher	PES	0.50	0.53	0.60	0.72	0.88	4.24	0.04
(*Myiarchus crinitus*)	FES	0.75	0.77	0.82	0.89	0.96		
Yellow-billed cuckoo	PES	0.38	0.40	0.49	0.64	0.86	5.06	0.02
(*Coccyzus americanus*)	FES	0.68	0.70	0.77	0.86	0.95		
Northern cardinal"	PES	0.52	0.57	0.69	0.84	0.95	6.00	0.01
(*Cardinalis cardinalis*)	FES	0.87	0.89	0.93	0.97	0.99		

continued

Table 3 (continued).

Species	Treatment	Size (ha) 0.5	1.0	2.5	5.0	10.0	χ^2	*P*
Carolina wren'								
1993	PES	0.14	0.22	0.60	0.94	1.00	6.35	0.01
(*Thryothorus ludovicianus*)	FES	0.84	0.90	0.98	1.00	1.00		
1994	PES	0.15	0.21	0.43	0.70	0.72	1.33	0.25
	FES	0.32	0.41	0.66	0.86	0.87		
Tufted titmouse[a]	PES	0.47	0.55	0.75	0.92	0.99	6.57	0.01
(*Parus bicolor*)	FES	0.82	0.87	0.94	0.98	1.00		
White-eyed vireo	PES	0.24	0.24	0.25	0.26	0.27	6.91	0.01
(*Vireo griseus*)	FES	0.77	0.77	0.77	0.78	0.80		
Mourning dove	PES	0.31	0.32	0.34	0.39	0.48	7.10	0.01
(*Zenaida macroura*)	FES	0.77	0.78	0.80	0.83	0.87		
indigo bunting	PES	0.10	0.10	0.09	0.08	0.06	7.51	0.01
(*Passerina cyanea*)	FES	0.70	0.69	0.67	0.64	0.56		
Northern bobwhite	PES	0.05	0.06	0.08	0.14	0.38	10.60	0.001
(*Colinus virginianus*)	FES	0.75	0.77	0.83	0.90	0.97		

"The best-fit logistic regression equation included a quadratic term (i.e., area^2).

[b] Convergence could not be attained in logistic regression analysis, so the Wald chi-square could not be calculated. Logistic regression analyses were conducted separately for each treatment.

the pine forest reduced negative edge effects, or because the species were able to exploit the surrounding habitat. However, all 4 species were recorded in the pine stands surrounding PES, but not in the fields surrounding FES (J. C. Kilgo, U.S. For. Serv., Aiken, S.C., unpubl. data).

Management implications

We did not find evidence in our study to clearly support or reject the "forest-buffer hypothesis." The presence of a surrounding pine forest apparently increased the suitability of PES for some area-sensitive species. However, PES were less suitable for several edge species and had lower total abundance and species richness than FES. Forest-dwelling, neotropical-migrant species richness was not different between treatments, and some neotropical migrants (e.g., wood thrush, summer tanager, red-eyed vireo) were more abundant or found exclusively in PES. Thus, management recommendations depend on the suite of species desired: conversion of agricultural habitat to pine forest likely will increase the suitability of neighboring hardwood remnants for a few species of neotropical migrants that inhabit hardwood forests, whereas clearing of pine forest likely will increase the suitability of remaining hardwoods for edge species. Nesting success of neotropical migrants in these stands is unknown. However, nesting success of a resident species, northern cardinal, did not differ between treatments (Sargent 1996). Our findings should be viewed with caution until information on the effect of surrounding habitat type on nesting success of neotropical migrants is available.

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Literature cited

AMBUEL, B., AND S. A. TEMPLE. 1983. Areadependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057–1068.

BLAKE., J. G., AND J. R. KARR. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68: 1724-1734.

Blondel, J., C. Ferry, and B. Frochot. 1981. Point counts with unlimited distance. Pages 414-420 in C. J. Ralph and J. M. Scott, eds. Estimating numbers of terrestrial birds. Stud. in Avian Biol. 6.

Forman, R. T. T., A. E. Galli, and C. F. Leck. 1976. Forest size and avian diversity in New Jersey woodlots with some land use implications. Oecologia 26: 1-8.

Freemark, K., and B. Collins. 1992. Landscape ecology of birds breeding in temperate forest fragments. Pages 443-454 in J. M. Hagan and D. W. Johnston, eds. Ecology and conservation of neotropical migrant landbirds. Smithsonian Inst. Press. Washington, D.C.

Harris, L. D. 1984. The fragmented forest. Univ. Chicago Press. Chicago, Ill. 21 lpp.

Howe, R. W. 1984. Local dynamics of bird assemblages in small forest habitat islands in Australia and North America. Ecology 65:1585-1601.

Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk 103:593-602.

James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727-736.

Loman, J., and T. V. Von Schantz. 1991. Birds in a farmland-more species in small than in large habitat island. Conserv. Biol. 5:176-188.

Lynch, J. F., AND D. F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. Biol. Conserv. 28:287-324.

Noon, B. R. 1981. Techniques for sampling avian habitats. Pages 42-51 in D. E. Capen, ed. The use of multivariate statistics in studies of wildlife habitat. U.S.D.A. For. Serv. Gen. Tech. Rep. RM-87.

Ralph, C. J., S. Droege, and J. R. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications. Pages 161-168 *in* C. J. Ralph, J. R. Sauer, and S. Droege, eds. Monitoring bird populations by point counts. U.S.D.A. For. Serv. Gen. Tech. Rep. PSW-GTR-149.

Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67-95 in R. L. Burgess and D. M. Sharpe, eds. Forest is land dynamics in man-dominated landscapes. Springer-Verlag, New York, N.Y.

Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic states. Wildl. Monogr. 103:1-34.

Sargent, R. A. 1996. The nesting ecology of songbirds in the fragmented landscape of South Carolina. Ph.D. Diss., Univ. Georgia, Athens. 68pp.

SAS Institute, Inc. 1990. SAS user's guide: version 6.02. SAS Inst., Inc., Cary, N.C.

Tansey, J. B., and C. C. Hutchins, Jr. 1988. South Carolina's forests. U.S.D.A. For. Serv. Resour. Bull. SE-103.

Whipple, S. A., L. H. Wellman, and B. J. Good. 1981. Classification of hardwood and swamp forests of the Savannah River Plant, South Carolina. Publ. SRO-NERP-6, Natl. Environ. Res. Park Program. Savannah River Ecol. Lab., Aiken, S.C. 36pp.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna on the eastern deciduous forest. Pages 125-292 *in* R. L. Burgess and D. M. Sharpe, eds. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, N.Y.

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