

Associations of Breeding Birds with Fire-Influenced and Riparian-Upland Gradients in a Longleaf Pine Ecosystem (Asociaciones de Aves Reproductivas con Áreas Influenciadas por el Fuego y con Gradientes Ribereños-Tierras Altas en un Ecosistema de *Pinus palustris*)

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## ASSOCIATIONS OF BREEDING BIRDS WITH FIRE-INFLUENCED AND RIPARIAN–UPLAND GRADIENTS IN A LONGLEAF PINE ECOSYSTEM

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**ABSTRACT.**—We determined the effects of fire history and a riparian–upland gradient on the breeding bird community at Fort Bragg Military Installation in North Carolina, one of the largest remnant areas of the endangered longleaf pine (*Pinus palustris*) ecosystem. Study sites were classified into two treatments: fire-intense (areas experiencing growing-season burns) and fire-suppressed (areas lacking fires). Within each treatment, bird and vegetation data were recorded at point-count stations positioned at three distances from streamhead pocosins to characterize the riparian–upland habitat gradient: 0, 75, and  $\geq 150$  m. Total bird abundance and species richness varied significantly along the riparian–upland gradient, with pocosins contributing greatly to avian biodiversity. Our data revealed strong effects of fire history and riparian–upland gradient on bird species, which we described in terms of breeding-bird assemblages. Members of the open longleaf assemblage (e.g., Red-cockaded Woodpecker [*Picoides borealis*], Bachman's Sparrow [*Aimophila aestivalis*]) were most common in fire-intense areas and at upland locations. Members of the fire-suppressed assemblage (e.g., Wood Thrush [*Hylocichla mustelina*], Ovenbird [*Seiurus aurocapilla*]) were confined to pocosins in fire-intense areas, but became more abundant in fire-suppressed areas. Members of the pocosin assemblage (e.g., Eastern Towhee [*Pipilo erythrophthalmus*], Common Yellowthroat [*Geothlypis trichas*]) were largely confined to pocosins and, in some cases, were most abundant in fire-intense pocosins. Fire suppression increased structural diversity of vegetation and promoted one breeding-bird assemblage (fire-suppressed), but at the expense of two others (open longleaf, pocosin). Continued management of Fort Bragg to promote longleaf pine restoration is essential for supporting conservation of the open-longleaf bird assemblage; in addition, it will benefit the pocosin assemblage. Received 8 February 2004, accepted 3 January 2006.

**Key words:** breeding birds, fire, longleaf pine, *Pinus palustris*, riparian habitat.

### Asociaciones de Aves Reproductivas con Áreas Influenciadas por el Fuego y con Gradientes Ribereños–Tierras Altas en un Ecosistema de *Pinus palustris*

**RESUMEN.**—Determinamos los efectos de la historia del fuego y de un gradiente entre áreas ribereñas y tierras altas en la comunidad de aves que crían en la Instalación Militar de Fort Bragg en North Carolina, una de las áreas remanentes más grandes del ecosistema amenazado de *Pinus palustris*. Los sitios de estudio fueron clasificados en dos tratamientos: con fuego intenso (áreas quemadas durante

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la estación de crecimiento) y con supresión de fuego (áreas sin fuego). Para cada tratamiento se registraron datos de las aves y la vegetación en estaciones de conteo ubicadas a tres distancias (0, 75, y  $\geq 150$  m) desde los extremos de los cenagales para caracterizar el gradiente ambiental entre el sector ribereño y las tierras altas. La abundancia total de aves y la riqueza de especies variaron significativamente a lo largo de este gradiente, con una alta contribución de los cenagales a la diversidad de aves. Nuestros datos revelaron la existencia de fuertes efectos de la historia del fuego y de los gradientes ambientales sobre las especies de aves, los cuales describimos en términos de los ensambles de aves reproductivas. Los miembros del ensamble de las áreas abiertas de *P. palustris* (e.g., *Picoides borealis*, *Aimophila aestivalis*) fueron más comunes en las áreas con fuego intenso y en las zonas de tierras altas. Los miembros del ensamble de las zonas sin fuego (e.g., *Hylocichla mustelina*, *Seiurus aurocapilla*) estuvieron restringidos a los cenagales en las áreas con fuego intenso, pero fueron más abundantes en las áreas sin fuego. Los miembros del ensamble de los cenagales (e.g., *Pipilo erythrophthalmus*, *Geothlypis trichas*) estuvieron principalmente restringidos a los cenagales y en algunos casos fueron más abundantes en cenagales con fuego intenso. La supresión del fuego incrementó la diversidad estructural de la vegetación y promovió un ensamble de aves reproductivas (el de las zonas sin fuego), pero a costa de otros dos ensambles (el de áreas abiertas de *P. palustris* y el de los cenagales). Es esencial continuar con el manejo de Fort Bragg para promover la restauración de áreas de *P. palustris* para apoyar la conservación del ensamble de aves de este ecosistema. Adicionalmente, esto beneficiará el ensamble de aves de los cenagales.

**PYROCLIMAX LONGLEAF PINE** (*Pinus palustris*) ecosystems dominated much of the southeastern United States until European settlement (Ware et al. 1993). Thereafter, longleaf habitat was lost or degraded by open range hogs and cattle, settlement clearings, naval-stores and timber production, fire suppression policies, and conversion to plantations of other southern pines (Crocker 1979, Frost 1993, Landers et al. 1995). These factors reduced longleaf pine to <3% of its original acreage (Frost 1993, Ware et al. 1993). Most of what habitat remained was highly degraded, largely because of fire suppression. Without regular fires, understory plant species-richness and groundcover biomass decrease, a hardwood midstory develops, and longleaf pine is unable to regenerate and compete with more aggressive southern pine and hardwood species (Brockway and Lewis 1997).

Currently, restoration of longleaf pine systems is a focus of conservation efforts throughout the Southeast (Hermann 1993, Noel et al. 1998). Emphasis is on restoring native vegetation and providing critical habitat for the endangered Red-cockaded Woodpecker (see Appendix for scientific names of this and other study species), typically by using prescribed growing-season

fire. The effects of these restoration efforts on nontarget species are receiving increasing attention (Engstrom 1993, Brennan et al. 1995, Main and Richardson 2002), resulting in better understanding of the avian community associated with longleaf pine forests (Repenning and Labisky 1985, Hamel and Dunning 2000, Kilgo et al. 2000, Rutledge and Conner 2002) and the influence of fire on that community (Hirth et al. 1991; Engstrom et al. 1996, 2005; King et al. 1998; Provencher et al. 2002). The objective of the present study was to describe quantitatively the relationships of breeding-bird assemblages within the Fort Bragg Military Installation in the North Carolina Sandhills, one of the largest remnant areas of longleaf pine, to fire-associated and upland-riparian vegetative gradients. The former gradient has received much more attention than the latter or the interaction between the two. We assessed the breeding-bird assemblages in two fire treatments, fire-intense (areas experiencing growing season burns) and fire-suppressed (areas lacking fires), at three distances from riparian zones of streamhead pocosins: 0, 75, and  $\geq 150$  m (streamhead pocosin is a type of vegetative community in the longleaf pine ecosystem; it is characterized by speciose, dense, shrub-dominated vegetation along

streams). The fire-intense areas were repeatedly subjected to growing-season prescribed burns beginning in 1989, whereas the fire-suppressed areas have lacked growing-season prescribed fires for several decades.

One unique aspect of the present study is that all analyses were performed on two independent data sets using the same comparative study design. Independent data sets are desirable because it is often unknown how much spatio-temporal variation affects the results of a single analysis; hence, the two data sets help separate biological patterns from spurious results. On the basis of observed bird abundance patterns, we delineated species assemblages associated with the vegetative gradients and described differences between these assemblages in their association with fire.

#### METHODS

**Study area.**—Fort Bragg Military Installation is located in the Sandhills physiographic region of North Carolina and includes ~40,000 ha of forest. By the establishment of Fort Bragg in 1917, most of the original longleaf pine had been cut, and now mostly second- and third-growth stands exist. Dormant-season burns were conducted on a five-year rotation before 1989, and wildfires periodically occurred during all seasons (Cantrell et al. 1995). Since 1989, Fort Bragg has adopted a three-year growing-season rotation for prescribed burns to conserve this longleaf pine ecosystem. Because of varying fire frequency, timber history, and soil types, Fort Bragg is a heterogeneous landscape of upland pine, successional communities of mixed pine-hardwood and hardwood stands, seeps, and streamhead pocosins.

Most fire-intense areas are classified as longleaf pine-scrub oak sandhills (*Pinus palustris* / *Quercus laevis* - *Quercus* [*incana*, *margarettae*] - *Gaylussacia dumosa* / *Aristida stricta* Woodland) or xeric sandhill scrub (*Pinus palustris* / *Quercus laevis* / *Aristida purpurascens* - *Stipulicida setacea* - [*Rhynchospora megalocarpa*, *Selaginella acanthonota*] Woodland) (Schafale and Weakley 1990). Longleaf pine dominates the canopy, and there is virtually no vertical structural diversity. Fire-suppressed areas may have experienced dormant-season burns, but not growing-season fires. These areas can be described as xeric sandhill scrub, dry oak hickory forest (*Quercus falcata* - *Quercus*

*stellata* - *Carya alba* / *Vaccinium* spp. Coastal Plain Forest), and bottomland hardwood communities (Schafale and Weakley 1990). The streamhead pocosin community (Schafale and Weakley 1990) is a linear, densely vegetated feature common to both fire-intense and fire-suppressed areas.

**Study design.**—We sampled the breeding-bird assemblages at two independent sets of permanent point-count stations from 1994 to 1997. The first set (four-year data set) was sampled each breeding season during the study, and the second set (one-year data set) was sampled for one year only, 1996. Krieger (1997) selected sites for the four-year data set ( $n = 65$ ) on the basis of fire history, timber stocking levels, military activity, and presence of pocosins. In 1996, we selected 156 stations to compose the second data set from field-verified geographic-information-system (GIS) spatial data depicting habitat cover types.

All count stations were randomly positioned in areas stratified by fire treatment (intense or suppressed), and at one of three distances (herein termed "location") from a streamhead pocosin: pocosin (0 m), intermediate (75 m), and upland ( $\geq 150$  m). The count stations were  $\geq 200$  m apart.

We collected vegetation-structure and floristics data on 29 attributes (see Table 1) of the ground-cover, under-, mid-, and overstory based on the BBIRD protocol (Martin and Conway 1994). At each count station, we collected these data within four subplots, consisting of nested 5-m-radius and 11.3-m-radius plots. Within the 5-m-radius plots, we collected data on shrubs, tree saplings ( $\leq 8$  cm diameter at breast height [DBH]), litter depth, and groundcover characteristics, and within the 11.3-m-radius plots, we measured trees ( $> 8$  cm DBH) and snags. We also estimated canopy cover and height, aspect, and slope.

During the breeding seasons, we used a 50-m fixed-radius point-count method to census the avifauna at count stations (Hutto et al. 1986). We conducted bird counts from late April or early May to mid-June and during the hours between 0545 and 1000 hours EST. We recorded the birds detected within the 50-m count station by sight and sound for 10 min, and we excluded birds flying over and not stopping within the station. We assumed that detectability of species within the 50-m count stations was uniform across fire treatments and along the three locations from pocosins. We conducted three counts at each count station in 1994, 1995, and 1997.

We conducted two counts in 1996, because of personnel limitations. For each survey, we varied the observer, order, and time of counts to minimize systematic detection biases. We trained observers in bird identification skills and distance estimation for four weeks before the first survey each year.

*Statistical analyses.*—Because most of the bird-count and vegetation data failed to meet the assumptions of normality and homogeneity of variances, we used nonparametric statistical tests. We used the general linear models (GLM) procedure on ranked values for factorial analyses, because most data were unbalanced (i.e., unequal sample sizes) and not from a normal distribution (Zar 1999). We employed Bonferroni multiple-comparison procedures when necessary to control the experiment-wise error rate. We used an alpha level of 0.05 to determine statistical significance. Unless otherwise noted, we performed all analyses with the statistical package SAS, release 6.12 (SAS Institute, Cary, North Carolina).

To examine fire-treatment and location effects on the vegetation, we used a two-way factorial GLM procedure for the 29 vegetation variables. Because we found similar patterns of effects for both the one-year and four-year vegetation data sets, we present only the results of the one-year data set below (see Allen [2001] for four-year results).

For the two bird data sets, we calculated species richness as the number of species detected per count station per survey per year. We defined total bird abundance as the number of individuals detected per count station per survey per year. To test for differences in species richness and total bird abundance, we used three-way factorial tests with year, fire treatment, location, and interaction terms for the four-year data set and two-way factorial tests for the one-year data set (no year term). We defined species relative abundance as the number of individuals of a species per count station per survey per year. We tested for fire treatment and location effects on species relative abundance using two-way factorial tests for 32 species in the four-year data set and 31 species in the one-year data set, thereby testing 34 different species (see Appendix).

For both the four-year and one-year data sets, we employed canonical correspondence analysis (CCA) to describe the bird community

composition and its relationship with the vegetation gradients using PC-ORD (McCune and Mefford 1997). Canonical correspondence analysis is a direct gradient analysis that extracts ordination axes of community variation, which are restricted by being linear combinations of environmental variables, such that community variation is directly related to environmental variation (ter Braak 1986). Ordination of the bird species matrix was performed by reciprocal averaging, and this ordination was constrained by multiple linear regression on the vegetation variables. For the CCA, we centered axis scores and standardized them to unit variance and optimized species scores for axis scaling. We included 31 bird species that were common to both the four-year and one-year data sets in sufficient numbers for each CCA.

## RESULTS

*Vegetation characteristics.*—Most of the vegetation variables for the one-year data set had a significant fire-treatment effect (Table 1). Fire-intense areas had a more open canopy, better-developed groundcover (higher percentages of green and grass cover), reduced midstory (lower shrub, sapling, and small-tree numbers), lower species richness, longleaf pine-dominated overstory, and fewer snags. Fire-suppressed areas had significantly greater abundance of non-longleaf pines and hardwoods (higher numbers of other pine saplings, other pine trees, and other tree species).

Location effects indicating a riparian–upland gradient were abundant, with 25 significant variables (Table 1). From the pocosin to upland habitats, the percentage of grass cover, bare ground, and number of longleaf pine trees increased, and the following variables decreased: slope; canopy cover and height; litter depth; percentages of green, shrub, and fern cover; numbers of shrubs and other pine and hardwood species; and shrub, sapling, and tree species richness.

Fourteen variables exhibited a significant interaction of fire treatment and location effects (Table 1). The patterns revealed by these effects were that fire-intense pocosins had a denser and more diverse shrub layer but less diverse canopy than fire-suppressed pocosins, and that differences in vegetation among locations were less pronounced in fire-suppressed areas than in fire-intense areas.

TABLE 1. Results of two-way factorial tests on vegetation variables measured at Fort Bragg, North Carolina, in the one-year (1996) data set to test for fire-treatment, location, and interaction effects. Means  $\pm$  SE are shown.

Vegetation variables	Fire-intense			Fire-suppressed			Significant effects <sup>a</sup>
	Pocosin (n = 19)	Intermediate (n = 20)	Upland (n = 34)	Pocosin (n = 29)	Intermediate (n = 23)	Upland (n = 31)	
Slope	7.3 $\pm$ 0.7	6.7 $\pm$ 0.5	3.6 $\pm$ 0.4	7.6 $\pm$ 1.0	5.3 $\pm$ 0.5	5.2 $\pm$ 0.6	L, I
Canopy cover (%)	74.8 $\pm$ 2.6	73.0 $\pm$ 2.2	64.2 $\pm$ 1.9	88.5 $\pm$ 2.0	79.4 $\pm$ 2.6	84.0 $\pm$ 1.9	T, L, I
Canopy height (m)	21.5 $\pm$ 1.1	18.4 $\pm$ 0.4	17.7 $\pm$ 0.5	19.4 $\pm$ 0.4	17.9 $\pm$ 0.7	17.6 $\pm$ 0.5	L
Litter depth (cm)	3.3 $\pm$ 0.2	3.0 $\pm$ 0.4	2.0 $\pm$ 0.2	3.6 $\pm$ 0.2	2.8 $\pm$ 0.2	3.5 $\pm$ 0.3	T, L, I
Green cover (%)	71.9 $\pm$ 3.3	39.7 $\pm$ 3.4	40.6 $\pm$ 2.7	52.4 $\pm$ 2.8	34.9 $\pm$ 3.7	30.1 $\pm$ 2.2	T, L
Grass cover (%)	13.8 $\pm$ 2.5	18.0 $\pm$ 2.1	22.8 $\pm$ 1.8	6.4 $\pm$ 1.2	12.4 $\pm$ 2.5	9.4 $\pm$ 1.5	T, L
Shrub cover (%)	49.8 $\pm$ 3.2	18.9 $\pm$ 2.1	14.5 $\pm$ 1.1	39.6 $\pm$ 2.7	20.1 $\pm$ 2.8	18.3 $\pm$ 1.4	L, I
Forb cover (%)	2.8 $\pm$ 0.7	33.6 $\pm$ 0.7	4.3 $\pm$ 0.6	2.3 $\pm$ 1.1	3.1 $\pm$ 0.7	3.3 $\pm$ 0.6	T, L
Fern cover (%)	9.5 $\pm$ 2.1	0.6 $\pm$ 0.2	0.5 $\pm$ 0.3	5.6 $\pm$ 1.0	0.8 $\pm$ 0.3	0.3 $\pm$ 0.2	L
Downed logs (%)	3.4 $\pm$ 0.7	2.2 $\pm$ 0.3	1.7 $\pm$ 0.3	5.3 $\pm$ 0.5	4.5 $\pm$ 1.3	4.1 $\pm$ 0.5	T, L
Leaf litter (%)	90.6 $\pm$ 1.5	77.6 $\pm$ 4.6	70.0 $\pm$ 2.6	91.0 $\pm$ 2.1	82.4 $\pm$ 3.9	84.9 $\pm$ 2.7	T, L, I
Bare ground (%)	4.9 $\pm$ 1.0	10.8 $\pm$ 2.0	15.5 $\pm$ 2.0	4.1 $\pm$ 1.1	13.0 $\pm$ 3.7	11.8 $\pm$ 2.7	T, L
Small shrubs <2.5 cm DBH (n)	460.0 $\pm$ 42.4	22.2 $\pm$ 15.9	3.3 $\pm$ 1.4	296.3 $\pm$ 32.6	33.8 $\pm$ 13.2	15.1 $\pm$ 4.0	T, L, I
Large shrubs >2.5 cm DBH (n)	2.0 $\pm$ 1.0	0	0	3.1 $\pm$ 0.6	0	0.2 $\pm$ 0.1	T, L, I
Small saplings <2.5 cm DBH (n)	58.7 $\pm$ 8.2	51.6 $\pm$ 6.7	38.9 $\pm$ 4.9	45.9 $\pm$ 5.4	35.9 $\pm$ 6.9	36.1 $\pm$ 4.1	L
Large saplings >2.5 cm DBH (n)	5.1 $\pm$ 1.1	3.9 $\pm$ 0.8	2.8 $\pm$ 0.7	5.6 $\pm$ 0.7	4.7 $\pm$ 1.4	5.1 $\pm$ 1.0	T, L
Trees 8–23 cm DBH (n)	6.2 $\pm$ 1.1	4.8 $\pm$ 1.0	2.7 $\pm$ 0.5	15.9 $\pm$ 1.5	12.6 $\pm$ 1.4	17.4 $\pm$ 1.6	T, I
Trees >23–38 cm DBH (n)	3.1 $\pm$ 0.3	3.2 $\pm$ 0.3	3.9 $\pm$ 0.3	4.1 $\pm$ 0.3	4.0 $\pm$ 0.3	4.5 $\pm$ 0.4	T
Trees >38 cm DBH (n)	1.7 $\pm$ 0.2	1.3 $\pm$ 0.2	1.2 $\pm$ 0.2	1.7 $\pm$ 0.2	1.2 $\pm$ 0.2	1.0 $\pm$ 0.2	L
Longleaf pine saplings (n)	0.2 $\pm$ 0.1	0.5 $\pm$ 0.2	0.6 $\pm$ 0.2	0.1 $\pm$ 0.1	0.9 $\pm$ 0.4	0.4 $\pm$ 0.2	NS
Other pine saplings (n)	2.0 $\pm$ 0.7	0.3 $\pm$ 0.2	0	1.2 $\pm$ 0.3	0.5 $\pm$ 0.3	1.2 $\pm$ 0.5	T, L, I
Other species saplings (n) <sup>b</sup>	61.6 $\pm$ 8.7	54.7 $\pm$ 6.8	41.0 $\pm$ 5.2	50.2 $\pm$ 5.7	39.2 $\pm$ 6.8	39.5 $\pm$ 4.3	L
Longleaf pine trees (n)	2.9 $\pm$ 0.5	5.3 $\pm$ 0.4	6.7 $\pm$ 0.5	1.6 $\pm$ 0.3	5.0 $\pm$ 0.9	5.5 $\pm$ 0.9	T, L
Other pine trees (n)	4.0 $\pm$ 0.9	0.5 $\pm$ 0.2	0.1 $\pm$ 0.1	7.6 $\pm$ 1.3	5.0 $\pm$ 1.6	7.9 $\pm$ 1.9	T, L, I
Other species trees <sup>b</sup> (n)	3.6 $\pm$ 0.7	3.5 $\pm$ 0.9	0.9 $\pm$ 0.2	11.7 $\pm$ 1.2	7.4 $\pm$ 0.8	9.1 $\pm$ 1.0	T, L, I
Shrub species richness	12.8 $\pm$ 0.5	2.4 $\pm$ 0.7	0.8 $\pm$ 0.2	12.0 $\pm$ 0.5	3.3 $\pm$ 0.7	2.9 $\pm$ 0.6	T, L, I
Sapling species richness	12.4 $\pm$ 0.6	5.7 $\pm$ 0.5	4.0 $\pm$ 0.3	12.4 $\pm$ 0.6	6.7 $\pm$ 0.8	7.6 $\pm$ 0.6	T, L, I
Tree species richness	6.2 $\pm$ 0.4	3.7 $\pm$ 0.5	2.1 $\pm$ 0.2	10.3 $\pm$ 0.5	6.0 $\pm$ 0.5	6.6 $\pm$ 0.5	T, L, I
Snags $\geq$ 12 cm DBH (n)	0.4 $\pm$ 0.2	0.1 $\pm$ <0.1	0.1 $\pm$ <0.1	0.4 $\pm$ 0.1	0.4 $\pm$ 0.2	0.3 $\pm$ 0.1	T

<sup>a</sup> Results of the GLM procedures. Characters represent significant effects at  $P \leq 0.05$ ; T = Treatment effect; L = Location effect; I = Interaction effect; NS = no significant effects found.

<sup>b</sup> Includes all deciduous and non-pine evergreen species.

**Bird species richness and total bird abundance.**—In the four-year data set, species richness and total bird abundance varied among years ( $P < 0.001$ ), with 1995 having larger values (Fig. 1A). There was no fire-treatment effect (Fig. 1B), and no interactions between year, treatment, and location. A location effect was detected for both of these metrics ( $P < 0.001$ ), with pocosins having larger values than the other locations (Fig. 1C). In the one-year data set, species richness varied between treatments ( $P = 0.04$ ), with higher

species richness in fire-suppressed areas (Fig. 1B). Total bird abundance was not different between treatments. A location effect was detected for both total bird abundance and species richness ( $P < 0.001$ ), with pocosins having larger values than the other locations (Fig. 1C). No interaction between treatment and location was detected.

**Breeding-bird assemblages.**—The relative abundance of many species across treatments and locations fell into four patterns, which we defined as four breeding-bird assemblages: open longleaf, fire-suppressed, pocosin, and generalist (Table 2). Three assemblages were identified by a shared association, indicated by a consistent pattern of highest relative abundance, with the fire-intense treatment (open longleaf assemblage), fire-suppressed treatment (fire-suppressed assemblage), or pocosin location (pocosin assemblage). These assemblage categorizations typically were supported by a statistically significant treatment or location effect, as well as by secondary patterns involving additional treatment, location, or interaction effects that were common to the species within an assemblage. The last assemblage, generalist, was identified by the lack of a consistent association with a treatment or location.

Seven species, including the Red-cockaded Woodpecker and Bachman's Sparrow, were included in the open longleaf assemblage. These species were more common in fire-intense areas, and most also favored upland locations (Fig. 2A), thus exhibiting significant effects of both fire treatment and location (Table 2). The Prairie Warbler was exceptional within this assemblage in tending to be more common in pocosins than in uplands (Table 2).

Seven species, including the Wood Thrush and Ovenbird, were associated with fire-suppressed habitats. Secondary patterns characteristic of this assemblage were that these species were most common in pocosins, but spread to other locations in fire-suppressed areas (Fig. 2B), thus often exhibiting significant location and interaction effects, as well as fire-treatment effects (Table 2).

Six species were included in the pocosin assemblage, including the Eastern Towhee and Common Yellowthroat. All these species reached peak numbers in pocosins, and most were rare to nonexistent at upland locations, regardless of fire treatment (Fig. 2C and Table 2). Beyond an association with pocosins, the

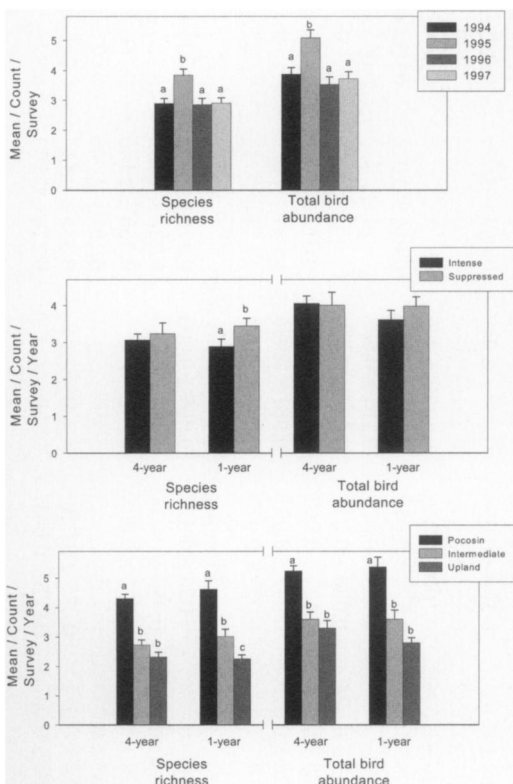


FIG. 1. Species richness and total bird abundance in the four-year and one-year data sets by year (A), fire treatment (B), and location (C) at Fort Bragg, North Carolina. Mean values  $\pm$  SE are indicated. Different letters within each bar group indicate significant differences by Bonferroni MCPs. Sample sizes are as follows. (A) Four-year: 65; (B) four-year: intense = 48, suppressed = 17; one-year: intense = 73, suppressed = 83; (C) four-year: pocosin = 22, intermediate = 21, upland = 22; one-year: pocosin = 48, intermediate = 43, upland = 65.

TABLE 2. Results of two-way factorial tests on relative abundance of the breeding birds of Fort Bragg, North Carolina, in four-year (1994–1997) and one-year (1996) data sets to test for fire-treatment, location, and interaction effects. For each species, the top row represents the four-year and the bottom row the one-year data set. Means  $\pm$  SE are shown. The highest abundance value for each species in each data set is indicated by bold type to highlight patterns in the data. Species are presented by assemblage (see text) and, within assemblages, in order of highest abundance value. See Appendix for scientific names of bird species.

Bird species	Fire-intense				Fire-suppressed				Significant effects <sup>a</sup>
	Four-year data set:		Pocosin (n = 16) (n = 20)	Upland (n = 16) (n = 34)	Pocosin (n = 6) (n = 29)	Intermediate (n = 5) (n = 23)	Upland (n = 6) (n = 31)		
	One-year data set:	(n = 19)							
Open longleaf assemblage									
Pine Warbler	0.419 ± 0.061	0.654 ± 0.110	0.862 ± 0.075	0.236 ± 0.063	0.325 ± 0.131	0.528 ± 0.123	T, L		
Brown-headed Nuthatch	0.105 ± 0.048	0.450 ± 0.149	0.412 ± 0.088	0.103 ± 0.058	0.391 ± 0.137	0.113 ± 0.038	T, L		
	0.083 ± 0.039	0.276 ± 0.072	0.503 ± 0.100	0.014 ± 0.014	0.042 ± 0.042	0.139 ± 0.123	T, L		
	0.158 ± 0.077	0.275 ± 0.099	0.382 ± 0.099	0.052 ± 0.029	0.130 ± 0.056	0.210 ± 0.100	T		
Red-cockaded Woodpecker	0.169 ± 0.085	0.143 ± 0.085	0.411 ± 0.082	0.014 ± 0.014	0	0	T, L, I		
Prairie Warbler	0	0.025 ± 0.025	0.324 ± 0.099	0	0.022 ± 0.022	0.032 ± 0.022	T, L, I		
	0.260 ± 0.061	0.198 ± 0.048	0.120 ± 0.032	0	0.017 ± 0.017	0.111 ± 0.080	T		
Bachman's Sparrow	0.289 ± 0.103	0.100 ± 0.058	0.088 ± 0.049	0.052 ± 0.029	0.087 ± 0.068	0.032 ± 0.022	T		
	0.091 ± 0.032	0.164 ± 0.046	0.221 ± 0.062	0	0	0	T		
	0.026 ± 0.026	0.100 ± 0.046	0.103 ± 0.055	0	0.065 ± 0.065	0	T		
Chipping Sparrow	0.026 ± 0.017	0.172 ± 0.049	0.182 ± 0.055	0.014 ± 0.014	0.058 ± 0.058	0.069 ± 0.040	T, L		
Eastern Wood-Pewee	0	0.025 ± 0.025	0.191 ± 0.063	0	0.065 ± 0.036	0.065 ± 0.038	L		
	0.049 ± 0.024	0.086 ± 0.031	0.076 ± 0.020	0	0	0.042 ± 0.042	T		
Red-headed Woodpecker	0.105 ± 0.061	0.125 ± 0.062	0.132 ± 0.049	0.017 ± 0.017	0.087 ± 0.040	0.065 ± 0.031	NS		
	0.026 ± 0.010	0.042 ± 0.031	0.081 ± 0.034	0	0	0.014 ± 0.014	T		
	0	0.025 ± 0.025	0.103 ± 0.055	0	0.022 ± 0.022	0.032 ± 0.022	NT		
Fire-suppressed assemblage									
Red-eyed Vireo	0.156 ± 0.038	0.036 ± 0.017	0.005 ± 0.005	0.375 ± 0.105	0.308 ± 0.119	0.104 ± 0.089	T, L		
Acadian Flycatcher	0.184 ± 0.134	0.050 ± 0.034	0.015 ± 0.015	0.224 ± 0.059	0.130 ± 0.056	0.113 ± 0.038	T		
	0.068 ± 0.039	0.005 ± 0.005	0	0.368 ± 0.160	0.150 ± 0.113	0	T, L		
	0.053 ± 0.053	0	0	0.103 ± 0.046	0.022 ± 0.022	0.048 ± 0.027	T		
Ovenbird	0.034 ± 0.014	0.018 ± 0.010	0	0.333 ± 0.113	0.225 ± 0.089	0.104 ± 0.068	T, L		
	0.184 ± 0.069	0.075 ± 0.041	0	0.224 ± 0.073	0.326 ± 0.116	0.161 ± 0.049	T		





TABLE 2. Continued.

Bird species	Fire-intense			Fire-suppressed			Significant effects <sup>a</sup>
	Pocosin (n = 16)	Intermediate (n = 20)	Upland (n = 16)	Pocosin (n = 29)	Intermediate (n = 23)	Upland (n = 31)	
Four-year data set: One-year data set:	(n = 19)	(n = 16)	(n = 34)	(n = 29)	(n = 23)	(n = 31)	
Blue Jay	0.039 ± 0.025	<b>0.102</b> ± 0.030	0.068 ± 0.025	0.069 ± 0.045	0.067 ± 0.049	0.083 ± 0.030	NS
Red-bellied Woodpecker	0.026 ± 0.026	0.075 ± 0.055	0.044 ± 0.025	0.052 ± 0.029	<b>0.130</b> ± 0.072	0.081 ± 0.034	NS
	0.047 ± 0.017	0.057 ± 0.032	0.049 ± 0.020	0.083 ± 0.054	<b>0.100</b> ± 0.100	0	NS
	0.079 ± 0.043	0.050 ± 0.034	0.015 ± 0.015	0.034 ± 0.024	0.043 ± 0.030	<b>0.081</b> ± 0.034	NS
Northern Flicker	0.031 ± 0.012	0.026 ± 0.010	<b>0.044</b> ± 0.016	0.042 ± 0.026	0	0.021 ± 0.021	NS
	0.053 ± 0.036	<b>0.075</b> ± 0.055	0.029 ± 0.020	0.017 ± 0.017	0.043 ± 0.030	0.032 ± 0.032	NS
Unclassified							
Blue-gray Gnatcatcher	0.526 ± 0.058	0.203 ± 0.045	0.073 ± 0.039	<b>0.799</b> ± 0.064	0.750 ± 0.151	0.458 ± 0.165	T, L
Brown-headed Cowbird	<b>0.763</b> ± 0.159	0.300 ± 0.092	0.147 ± 0.045	0.517 ± 0.091	0.217 ± 0.069	0.258 ± 0.086	L
	0.143 ± 0.038	0.102 ± 0.035	0.021 ± 0.012	0.097 ± 0.033	<b>0.292</b> ± 0.085	0	L, I
Yellow-throated Warbler	0.053 ± 0.036	0.075 ± 0.041	0.029 ± 0.021	0.086 ± 0.036	0.087 ± 0.040	<b>0.097</b> ± 0.036	NS
	0.055 ± 0.022	0.021 ± 0.009	0	<b>0.083</b> ± 0.057	0.050 ± 0.020	0.028 ± 0.028	L
Indigo Bunting	0.053 ± 0.036	0.075 ± 0.041	0	0.138 ± 0.042	<b>0.174</b> ± 0.087	0.016 ± 0.016	L
	<b>0.055</b> ± 0.019	0.023 ± 0.013	0.005 ± 0.005	0	0	0.028 ± 0.018	NT
American Goldfinch	<b>0.105</b> ± 0.061	0.075 ± 0.055	0.015 ± 0.015	0.017 ± 0.017	0.065 ± 0.048	0.016 ± 0.016	NS
	0.044 ± 0.019	0.036 ± 0.013	0.016 ± 0.011	0.028 ± 0.028	0	<b>0.083</b> ± 0.083	NS
Mourning Dove	0	0	<b>0.044</b> ± 0.032	0	0.043 ± 0.030	0.016 ± 0.016	NT
	<b>0.070</b> ± 0.027	0.052 ± 0.018	0.047 ± 0.015	0	0.017 ± 0.017	0.028 ± 0.028	T
Eastern Bluebird	<b>0.079</b> ± 0.058	0.075 ± 0.055	0	0.034 ± 0.024	0.022 ± 0.022	0.048 ± 0.036	NS
	0.026 ± 0.015	<b>0.052</b> ± 0.018	0.049 ± 0.024	0	0.017 ± 0.017	0	T
	0	0	0.015 ± 0.015	0	<b>0.022</b> ± 0.022	0	NT

<sup>a</sup> Results of GLM procedures on the ranked values of relative abundance. Characters represent significant effects: T = Treatment effect; L = Location effect; I = Interaction effect; NS = no significant effects found; NT = insufficient observations for statistical analysis.

<sup>b</sup> Inclusion in assemblage was not supported by CCA.

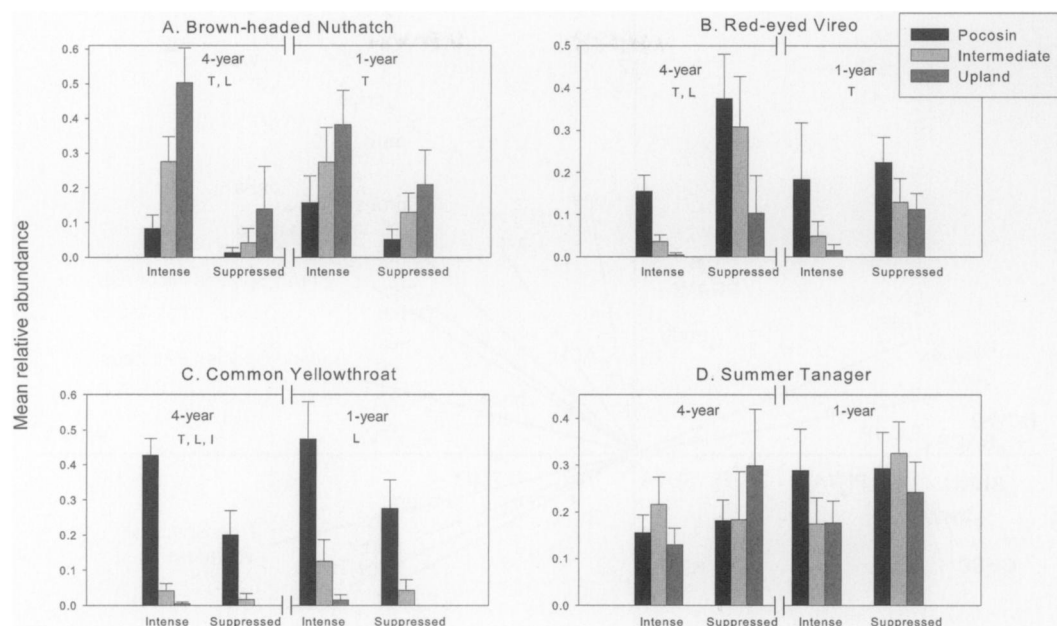


FIG. 2. Relative abundance patterns by fire treatment and location of representative species of the bird assemblages of Fort Bragg, North Carolina, for the four-year and one-year data sets. Mean values  $\pm$  SE are indicated. (2A) Brown-headed Nuthatch from the open longleaf assemblage, (2B) Red-eyed Vireo from the fire-suppressed assemblage, (2C) Common Yellowthroat from the pocosin assemblage, and (2D) Summer Tanager from the generalist assemblage. Significant effects indicated by: T = treatment, L = location, I = Interaction.

only characteristic of this assemblage was a tendency toward higher abundance in fire-intense pocosins (resulting in three significant treatment effects), but this pattern was not consistent (Table 2).

Species such as the Red-bellied Woodpecker and Summer Tanager can be described as forest generalists, in that they were ubiquitous throughout the study area (Fig. 2D), and hence were characterized by a lack of treatment or location effects (Table 2). We include the Great Crested Flycatcher in the generalist assemblage because it fits this pattern, even though a location effect was detected in the four-year data (Table 2).

The remaining seven species were not classified because they did not fit these patterns, often (e.g., Indigo Bunting), but not always (e.g., Blue-gray Gnatcatcher), because we obtained too few observations of them (Table 2).

The data sets varied somewhat in which species had statistically significant fire-treatment or location effects, but the relative abundance

patterns in the two data sets were nearly identical (see Allen [2001] for comparisons of relative abundance by treatments and by locations). There were only three clear discrepancies between the two data sets: (1) the Blue-gray Gnatcatcher was more common in fire-suppressed areas in the four-year data but not in the one-year data, a finding that prevented us from categorizing it; (2) the Great Crested Flycatcher decreased from upland to pocosin in the four-year data but not in the one-year data, a finding we chose to ignore in classifying it as a generalist; and (3) the Pine Warbler reached its highest abundance in uplands in the four-year data and in intermediate sites in the one-year data, which constitutes a minor violation of the secondary location effect characteristic of the longleaf assemblage, but not of the primary effect of association with fire-intense habitat.

*Ordination of bird species assemblages.*—Figures 3 and 4 show ordination along the first two axes of the 31 breeding-bird species included in the CCA for both the four-year and one-year data

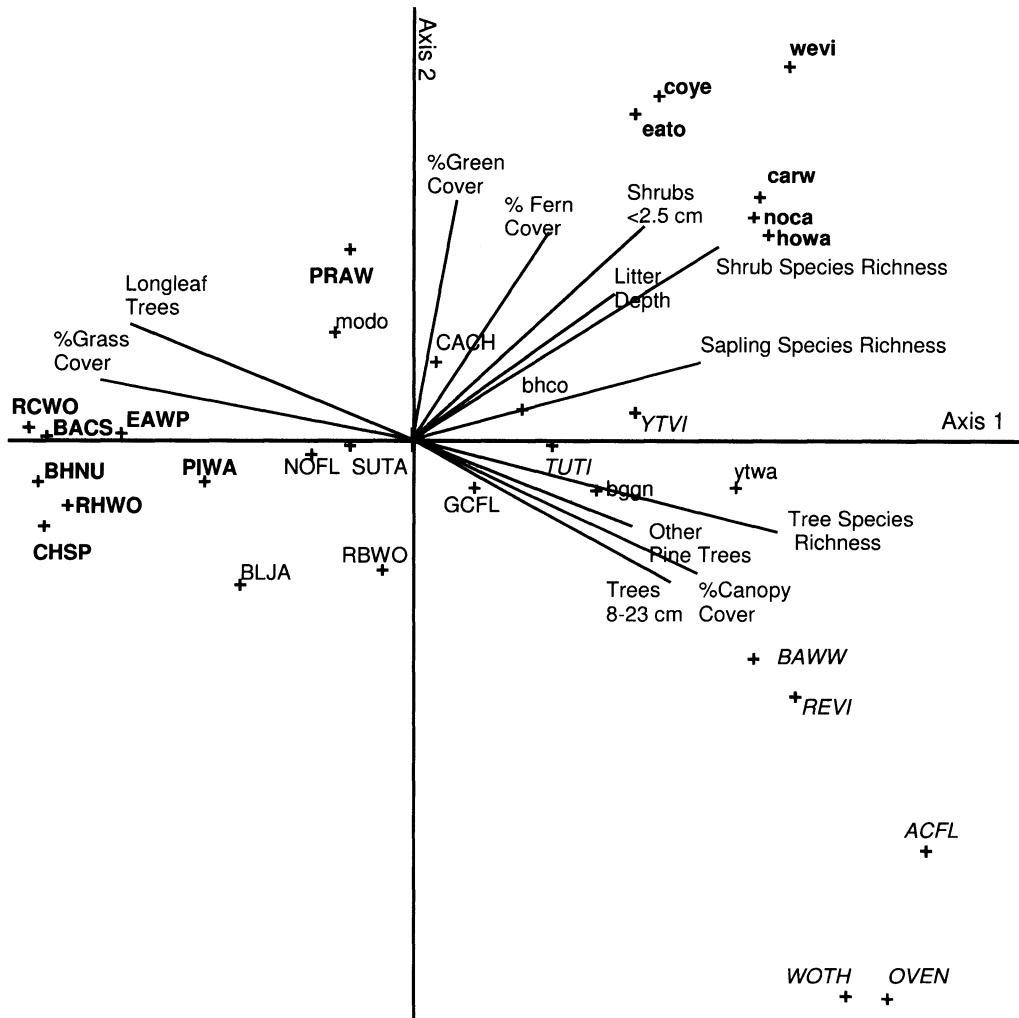


FIG. 3. Biplot of canonical correspondence analysis for the ordination of the breeding-bird community of Fort Bragg, North Carolina, in relation to habitat variables for the four-year data set ( $n = 65$ ). Species within an assemblage are indicated by different text formats (fire-intense: bold, upper case; fire-suppressed: italics, upper case; pocosin: bold, lower case; generalist: upper case; unclassified: lower case). See Appendix for species codes.

sets. These CCAs directly linked the results for the vegetation and bird-distribution patterns. The ordinations for the four-year and one-year data sets were not identical, but resulted in similar patterns. The first axis separated the open-longleaf bird-species assemblage from the other bird assemblages. The second axis separated the fire-suppressed and pocosin assemblages from one another and, in the one-year data set, provided some separation within the open longleaf assemblage as well. The open

longleaf assemblage was associated with open longleaf pine forest with a high proportion of grass cover, features of fire-intense uplands. The fire-suppressed bird species assemblage was associated with high tree species richness, high number of pine trees other than longleaf, high number of non-pine trees, and closed canopy forest with many small trees (8–23 cm DBH). Species in the pocosin assemblage were associated with high numbers of shrub and sapling species, high proportions of green cover

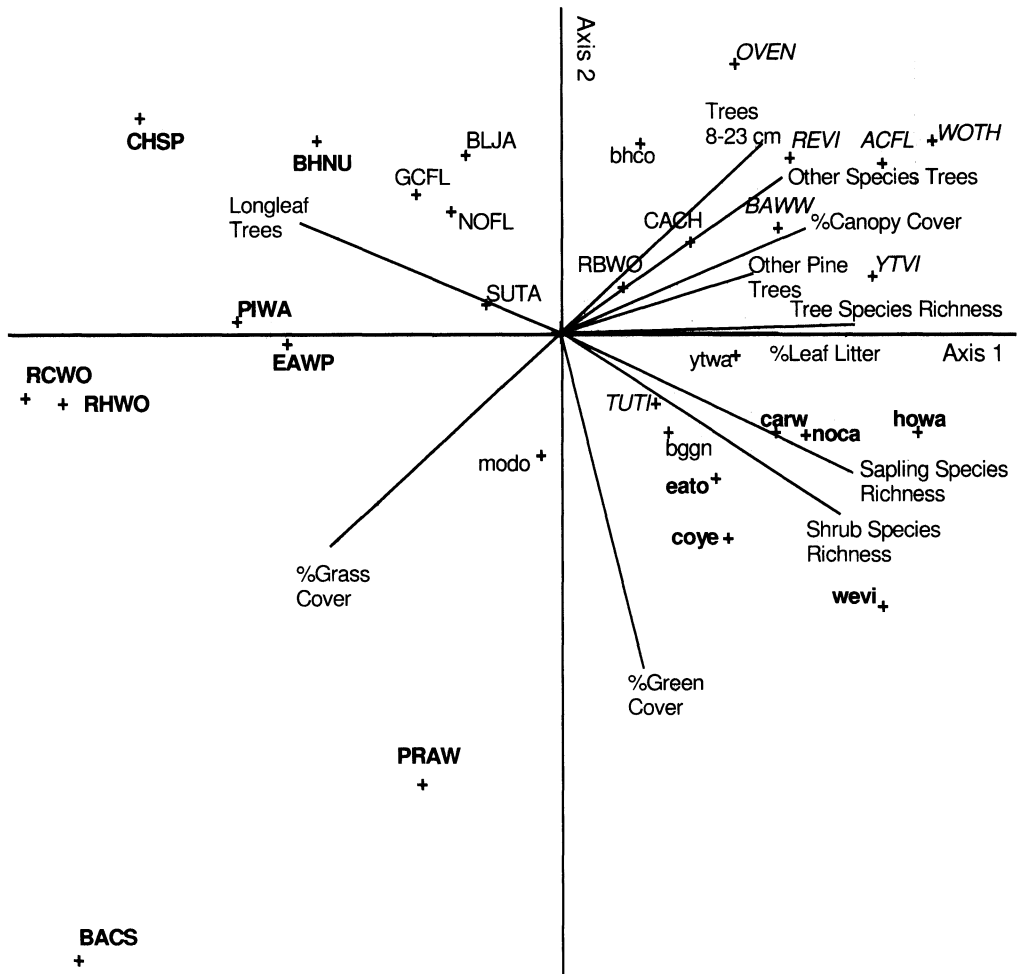


FIG. 4. Biplot of canonical correspondence analysis for the ordination of the breeding-bird community of Fort Bragg, North Carolina, in relation to habitat variables for the one-year data set ( $n = 155$ ). Species within an assemblage are indicated by different text formats (fire-intense: bold, upper case; fire-suppressed: italics, upper case; pocosin: bold, lower case; generalist: upper case; unclassified: lower case). See Appendix for species codes.

and fern cover, and high litter depth, which reflect effects of fire on pocosin vegetation.

Generally, CCA supported our assemblage categorizations based on abundance data, but it does suggest that the Prairie Warbler occupies a unique position within the longleaf assemblage, and that the Tufted Titmouse (and perhaps Yellow-throated Vireo) might better be classified as a generalist than as a part of the fire-suppressed assemblage (Figs. 3 and 4). For species located near the center of the CCA biplot, we inspected the correlation coefficients between the species and ordination axes to

ascertain whether these species are generalists or whether their relationship to each axis caused them to be positioned near the biplot center. For both data sets, the Mourning Dove (an unclassified species), Northern Flicker, Red-bellied Woodpecker, Summer Tanager, Blue Jay, and Carolina Chickadee had relatively low correlations with the first two axes, supporting their classification as generalists (Figs. 3 and 4). For the four-year data set, the Great Crested Flycatcher and Tufted Titmouse showed some correlation with the first axis. The Blue-gray Gnatcatcher showed some correlation with the

first axis for both data sets and, in the one-year data set, with the second axis as well. These three species, along with perhaps the Yellow-throated Vireo and Yellow-throated Warbler, may form a fifth assemblage of nongeneralists that are associated with more structurally complex vegetation in ways other than those characteristic of the pocosin and fire-suppressed assemblages.

## DISCUSSION

*Effects of habitat structure.*—Differences in vegetation between fire treatments were not surprising, because study sites were chosen on the basis of past management and the assumption that fire history would be reflected in the current vegetation structure and plant species composition. The vegetation varied from open, park-like longleaf pine habitats in the fire-intense uplands to structurally and floristically diverse vegetation in the pocosin and fire-suppressed habitats. Regardless of fire treatment, pocosin habitats provided the most diverse and dense vegetation. Furthermore, pocosins interspersed in fire-intense, open longleaf habitat exhibited the densest shrub layer with the highest shrub species richness, most likely because of the ability of fire to maintain a more open canopy.

Total bird abundance and species richness were highest in the complex pocosin habitats. Higher bird species richness and total bird abundance are often associated with complex vegetation structure and greater floristic diversity (Stauffer and Best 1980, Szaro 1980, Thurmond et al. 1995). In the longleaf pine ecosystem, the distinctive streamhead pocosins may add to avian biodiversity and enable higher bird numbers by providing additional niches, and perhaps foraging and nesting resources, for species found in the uplands.

Although fire-suppressed habitats had more complex vertical structure (i.e., a developed midstory) than the fire-intense longleaf pine habitats, the fire-suppressed habitats did not have significantly greater total bird abundance. Similarly, species richness was not greater in the fire-suppressed habitats in the four-year data set, though it was slightly higher in the one-year data. Engstrom et al. (2005) found that breeding bird species richness in the Wade Tract, an old-growth longleaf pine stand in Georgia, was comparable to that in vertically

diverse southern hardwood forests, and was higher than the richness in other regional longleaf pine stands. If the Fort Bragg stands mature toward old growth, they may have the potential to support bird species richness comparable to that on the Wade Tract. Despite the increase in structural diversity of vegetation, succession of fire-intense longleaf pine stands to mixed pine-hardwood stands through fire suppression does not appear to increase bird diversity in this longleaf pine system, though it influences the composition of the breeding-bird community.

*Breeding-bird assemblages.*—We were unable to clearly characterize the positions in the community of three common species, the Tufted Titmouse, Blue-gray Gnatcatcher, and Great Crested Flycatcher, other than to state that they appear to be associated with more structurally complex vegetation in similar ways. For the remaining species, our data revealed strong effects of fire history and location with respect to pocosins on the distribution of breeding bird species; the pattern observed can be described in terms of four breeding-bird species assemblages.

Five of the eight species included in the open longleaf assemblage (Red-cockaded Woodpecker, Brown-headed Nuthatch, Pine Warbler, Prairie Warbler, and Bachman's Sparrow) are considered endemics of or are strongly associated with open pine forests of the Southeast (Jackson 1988). The dependence of the Red-cockaded Woodpecker (Conner et al. 2001) and Bachman's Sparrow (Dunning 1993) on growing-season fire to maintain suitable habitat conditions is well established. Similar to data in Wilson et al. (1995), our data suggest that the Brown-headed Nuthatch also benefits from the effects of this fire regime, which maintains the open, mature pine forests that this species favors (Withgott and Smith 1998). Even though the Pine Warbler is abundant in pine forests not maintained by fire, such as older pine plantations (Repenning and Labisky 1985), it is negatively affected by hardwood encroachment resulting from fire suppression (Engstrom et al. 1984, Wilson et al. 1995), and generally it is most abundant where understory is sparse (Rodewald et al. 1999), a characteristic associated with fire-maintained pine forests. The Prairie Warbler's link to early successional stages created by fire in several habitat types is well known (Nolan 1978, Wilson et al. 1995), but its ties to open pine systems, though long

documented (Meyers and Odum 2000), is not as well appreciated. In the present study, its position in niche space was somewhat removed from the other members of its assemblage (Figs. 3 and 4), reflecting its association with dense patches of regenerating pines or scrub oaks. The three other species in the open longleaf assemblage (Chipping Sparrow, Eastern Wood Pewee, and Red-headed Woodpecker) are not limited to pine forests throughout their ranges, but clearly they are common members of this assemblage in southern pine forests (Dickson and Segelquist 1979, Wilson et al. 1995, Hamel and Dunning 2000, Engstrom et al. 2005).

Members of the fire-suppressed bird assemblage in other forested systems are typically associated with mixed pine-hardwood or hardwood stands that have greater vertical structural complexity and canopy closure than open longleaf pine stands. Conner and Dickson (1997) describe an association of the Red-eyed Vireo and Black-and-white Warbler with deciduous foliage in the mid- and overstory, a defining characteristic of the fire-suppressed habitats in the present study. Other studies have documented that some of these species benefit from fire exclusion in southern pine ecosystems (Engstrom et al. 1984, Wilson et al. 1995).

Most members of the fire-suppressed assemblage occurred at varying abundance levels in the fire-intense pocosins, albeit typically at lower abundances than in fire-suppressed pocosins (Table 2). One notable exception may be the Wood Thrush, a forest interior species, which was virtually nonexistent at every location in fire-intense areas. Brennan et al. (1995) reported a similar pattern for this species in Mississippi. At Fort Bragg, the presence of other species with very low abundance in fire-intense pocosins—namely the Ovenbird, Yellow-throated Vireo, Acadian Flycatcher, and Black-and-white Warbler—may depend on the existence of fire-suppressed areas. Conversely, Red-eyed Vireos likely would maintain a presence within pocosins in burned areas.

Other studies link five of the six species of the pocosin assemblage (Carolina Wren, White-eyed Vireo, Common Yellowthroat, Northern Cardinal, and Eastern Towhee) with shrubby patches and a dense understory (Engstrom et al. 1984, Wilson et al. 1995, Conner and Dickson 1997). Fire appears to promote the type of vegetation these species prefer, and this type of

vegetation does not develop outside of pocosins, even in the absence of fire within the study area. The Hooded Warbler, the final species in this assemblage, has been described as an eastern deciduous forest bird associated with older forest age classes (Conner and Dickson 1997) and the development of a sapling subcanopy (Engstrom et al. 1984). Yet, in the present study, its distribution is almost exclusively limited to pocosins, which suggests an association with mesic habitats, thereby supporting the results of Smith (1977), who termed it an obligatory moist-forest species.

Members of the generalist assemblage are either canopy species (Blue Jay and Summer Tanager) or cavity nesters (Northern Flicker, Red-bellied Woodpecker, and Carolina Chickadee). Canopy species may be minimally affected by vegetation changes as long as overstory pine or hardwood trees exist for foraging and nesting requirements (Engstrom et al. 1984). For cavity nesters, the distribution of suitable cavities may be a more important habitat component than structural and floristic differences in vegetation associated with fire treatment and location.

We believe that the assemblages we describe reflect true ecological relationships rather than anomalies of our censusing results. First, the same abundance patterns, and relationships to vegetation, emerged from two independent data sets. Second, these patterns persisted across years for the seven species with sufficient observations to test for a year interaction with treatment and location effects (i.e., no significant year interactions found; Allen 2001). Third, a recent study in Florida longleaf forest produced remarkably similar results. Using a well-replicated experimental design, Provencher et al. (2002) examined changes in bird abundance in response to removal of midstory hardwoods by three treatments, one of which was growing-season burning. Several species in our open longleaf assemblage (Red-cockaded Woodpecker, Red-headed Woodpecker, Bachman's Sparrow, Brown-headed Nuthatch) and pocosin assemblage (Eastern Towhee) responded positively to hardwood removal, whereas the only species to respond negatively was the Tufted Titmouse (Provencher et al. 2002), which was not associated with features of open longleaf pine stands in our data.

*Limitations of the data.*—The possibility exists of overestimating environmental effects if

samples are not spatially segregated to ensure independence. In the present study, count stations were  $\geq 200$  m apart, the standard for most bird studies until recently. On the basis of recent work on three species in the Appalachian mountains, Lichstein et al. (2002a, b) suggested that larger distances (e.g., 750 m) may be needed to ensure independence. This is particularly so for species that exhibit strongly clumped distributions (e.g., Red-cockaded Woodpecker). In the specific case of the warblers studied by Lichstein et al. (2002b), adjusting for spatial autocorrelation decreased the magnitude of habitat effects, yet it did not change the fundamental species-habitat relationships inferred prior to such adjustments. Lichstein et al. (2002b) also reasoned that designing studies with widely spaced stations may not be practical or appropriate for all landscapes because it might reduce the benefits accrued from having higher sample sizes and from detecting important relationships at smaller scales. In our data, non-independence from spatial autocorrelation is more likely to affect fire treatment than location effects because the spatial scale of the relevant vegetation gradient is much smaller in the latter case. Further research in southern pine forests is needed to identify critical distance thresholds for ensuring sampling independence in these systems and for guiding the design of future bird-abundance studies.

Detectability of species across various distances can vary across different habitat types. For example, certain species may be harder to detect in dense habitats, such as the streamhead pocosins in this longleaf pine system. Because we used a 50-m fixed-radius distance for count stations, we assumed that detectability of species within stations was uniform. Recent work by Lichstein et al. (2002a) found that detection probabilities for  $>20$  species of forest birds were fairly uniform up to  $\leq 75$  m, which suggests that our 50-m uniform detectability assumption was reasonable. However, we cannot rule out the possibility that detectability was lower in pocosins than in the much more open upland locations. In our data, pocosins were significantly associated with the highest avian richness and total bird abundance, and several species were mainly associated with this unique habitat type. Thus, it is possible that our inferences about species-habitat relationships in pocosins were conservative because we may have underestimated their strength.

An association of a particular fire treatment or location with the relative abundance of a particular species does not necessarily indicate that such habitat is of high quality or can support reproductively sustaining populations (Van Horne 1983). Possibly, some species are more abundant in one fire treatment or location but have greater reproductive success in another. This seems unlikely for most of the relationships reported here, judging from what is known of the ecology of the species involved; still, demographic data are needed to confirm inferences based on abundance data.

#### CONSERVATION IMPLICATIONS

The effects on the avian community of efforts to restore longleaf pine ecosystems using growing-season prescribed fires can readily be described in terms of the bird species assemblages we have defined. These efforts have a positive effect on the open longleaf assemblage, a positive or neutral effect on the pocosin assemblage, a neutral effect on the generalists, and a negative effect on the fire-suppressed assemblage. Some members of the latter group, such as the Wood Thrush, would most likely be eliminated in the absence of fire-suppressed areas, whereas others, like the Red-eyed Vireo, might decline in overall abundance and become restricted to pocosins. How are priorities resolved among species with conflicting habitat requirements? The open longleaf assemblage includes species with high conservation priority (Red-cockaded Woodpecker and Bachman's Sparrow). On the other hand, there also is much concern about population declines of Neotropical migratory landbirds, including some of the species in the fire-suppressed assemblage (Wood Thrush, Acadian Flycatcher, Black-and-white Warbler, Ovenbird). Hunter et al. (1994) assert that conservation is best accomplished using a regional perspective, and that one need not manage for different bird assemblages in the same locale. Longleaf forests represent one of the most endangered ecosystems in the Southeast (Frost et al. 1986), and Fort Bragg is one of the few large areas of public land on which it occurs. Hence, continued management of Fort Bragg for the open longleaf pine community, even if it causes a decline or elimination of some species from the fire-suppressed assemblage, is well justified.



Management of species in the fire-suppressed assemblage should be focused in other regional locations where mixed pine-hardwood, hardwood, or bottomland hardwood forests exist and are the appropriate historical forest types. For example, the Wood Thrush is a relatively common member of bird species assemblages in eastern deciduous hardwood forests. It would be best to manage for this species in these forests, rather than suppressing fire to retain it at higher abundance levels on Fort Bragg.

It is perhaps surprising that fire suppression benefits so few bird species and application of growing-season fire benefits so many, given the more complex vertical structure of the midstory and canopy found in fire-suppressed habitats. In particular, one might not have anticipated the positive effects of fire on some pocosin species, the neutral effects on the species grouped as generalists, or the similar level of species richness as compared with the vertically complex fire-suppressed habitats. Furthermore, if longleaf stands at Fort Bragg are managed for development of old-growth attributes with a spatially and vertically diverse ground layer, avian richness may increase and potentially exceed that of comparable southern hardwood forests, particularly for ground- and shrub-dependent species (Dickson and Segelquist 1979, Engstrom et al. 2005). Thus, the use of growing-season prescribed fires and possibly the promotion of old-growth longleaf, practices often viewed as single-species management to benefit Red-cockaded Woodpeckers, likely will promote the avian assemblage characteristic of longleaf ecosystems.

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APPENDIX. Scientific names and species codes of breeding birds recorded at Fort Bragg, North Carolina.

Common name	Scientific name	Species code
Mourning Dove	<i>Zenaida macroura</i>	MODO
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	RHWO
Red-bellied Woodpecker	<i>M. carolinus</i>	RBWO
Red-cockaded Woodpecker	<i>Picoides borealis</i>	RCWO
Northern Flicker	<i>Colaptes auratus</i>	NOFL
Eastern Wood-Pewee	<i>Contopus virens</i>	EAWP
Acadian Flycatcher	<i>Empidonax virescens</i>	ACFL
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	GCFL
White-eyed Vireo	<i>Vireo griseus</i>	WEVI
Yellow-throated Vireo	<i>V. flavifrons</i>	YTVI
Red-eyed Vireo	<i>V. olivaceus</i>	REVI
Blue Jay	<i>Cyanocitta cristata</i>	BLJA
Carolina Chickadee	<i>Poecile carolinensis</i>	CACH
Tufted Titmouse	<i>Baeolophus bicolor</i>	TUTI
Brown-headed Nuthatch	<i>Sitta pusilla</i>	BHNU
Carolina Wren	<i>Thryothorus ludovicianus</i>	CAWR
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	BGGN
Eastern Bluebird	<i>Sialia sialis</i>	EABL
Wood Thrush	<i>Hylocichla mustelina</i>	WOTH
Yellow-throated Warbler	<i>Dendroica dominica</i>	YTWA
Pine Warbler	<i>D. pinus</i>	PIWA
Prairie Warbler	<i>D. discolor</i>	PRAW
Black-and-white Warbler	<i>Mniotilta varia</i>	BAWW
Ovenbird	<i>Seiurus aurocapilla</i>	OVEN
Common Yellowthroat	<i>Geothlypis trichas</i>	COYE
Hooded Warbler	<i>Wilsonia citrina</i>	HOWA
Summer Tanager	<i>Piranga rubra</i>	SUTA
Northern Cardinal	<i>Cardinalis cardinalis</i>	NOCA
Indigo Bunting	<i>Passerina cyanea</i>	INBU
Brown-headed Cowbird	<i>Molothrus ater</i>	BHCO
American Goldfinch	<i>Carduelis tristis</i>	AMGO
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	EATO
Bachman's Sparrow	<i>Aimophila aestivalis</i>	BACS
Chipping Sparrow	<i>Spizella passerina</i>	CHSP