Wetlands Ecol Manage (2007) 15:417–439
DOI 10.1007/s11273-007-9040-z

ORIGINAL PAPER

Ordination of breeding birds in relation to environmental gradients in three southeastern United States floodplain forests

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Received: 13 December 2004 / Accepted: 9 April 2007 / Published online: 22 May 2007

Abstract We used an ordination approach to identify factors important to the organization of breeding bird communities in three floodplains: Cache River, Arkansas (AR), Iatt Creek, Louisiana '(LA), and the Coosawhatchie River, South Carolina (SC), USA. We used 5-min point counts to sample birds in each study area each spring from 1995 to 1998, and measured ground-surface elevations and a suite of other habitat variables to investigate bird distributions and community characteristics in relation to important environmental gradients. In both AR and SC, the average number of Neotropical migrant species detected was lowest in semipermanently flooded *Nyssa aquatica* Linnaeus habitats and greatest in the highest elevation floodplain zone. *Melanerpes carolinus* Linnaeus, *Protonotaria citrea* Boddaert, *Quiscalus quiscula* Linnaeus, and other species were more abundant in *N. aquatica* habitats, whereas *Wilsonia citrina* Boddaert, *Oporornis formosus* Wilson, *Vireo griseus* Boddaert, and others were more abundant in drier floodplain zones. In LA, there were no significant differences in community metrics or bird species abundances among forest types. Canonical correspondence analyses revealed that structural development of understory vegetation was the most important factor affecting bird distributions in all three study areas; however, potential causes of these structural gradients differed. In AR and SC, differences in habitat structure were related to the hydrologic gradient, as indexed by ground-surface elevation. In LA, structural variations were related mainly to the frequency of canopy gaps. Thus, bird communities in all three areas appeared to be organized primarily in response to repeated localized disturbance. Our results suggest that regular disturbance due to flooding plays an important role in structuring breeding bird communities in floodplains subject to prolonged inundation, whereas other agents of disturbance (e.g., canopy gaps) may be more important in headwater systems subject to only short-duration flooding. Management for avian community

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integrity in these systems should strive to maintain forest zonation and natural disturbance regimes.

Keywords Breeding birds · Ordination · Forested wetlands · Natural disturbance · Environmental gradients

Introduction

In the southeastern United States, floodplain forests are important habitats for many resident and migratory birds. Also known as bottomland hardwoods, southeastern floodplain forests often support higher overall densities of both breeding and wintering birds than do upland pine and pine/hardwood stands (Dickson 1978a). They also provide stopover habitat for migrants and breeding habitat for a number of bottomland forest specialists (Dickson 1978b, 1991; Pashley and Barrow 1993; Gauthreaux and Belser 2005). Bottomland hardwood forests are a conservation priority for Partners in Flight because they provide habitat for many bird species considered to be declining or vulnerable, including several species of Neotropical migrant warblers, vireos, and flycatchers (Hunter et al. 1993).

One reason for concern is that the acreage of forested wetlands in the Southeast has declined substantially in recent years. Across the southeastern U.S. from Texas to Virginia, losses of forested wetlands averaged nearly 60,000 ha/year between 1940 and 1980, mainly due to conversion to agriculture (Abernethy and Turner 1987). In the Mississippi Alluvial Valley, formerly the largest contiguous area of forested wetlands in the Southeast, roughly 80% of the original acreage of bottomland hardwood wetlands has been cleared and drained for crop production (Tiner 1984). Remaining floodplain forests are mostly in private ownership and many are managed actively for forest products (Brown 1997; Shepard et al. 1998).

To protect and manage bottomland hardwood forests in the Southeast, it is important to understand their ecological functions including the factors affecting their suitability and sustainability as bird habitats. Despite their importance to the regional avifauna, relatively few studies of habitat relationships of birds in bottomland hardwoods have been conducted. Several studies of temporal changes in bird communities after timber harvest or other disturbances have noted the importance of older stands, particularly to Neotropical migrants (Hamel 1989; Mitchell et al. 1989; Buffington et al. 1997). Others have examined the effects of forest loss, fragmentation, and stand width on bottomland bird species (Burdick et al. 1989; Wenny et al. 1993; Sargent et al. 1997; Kilgo et al. 1998; Sallabanks et al. 2000).

Vegetation patterns in bottomland hardwood forests reflect complex spatial variations in the frequency and duration of flooding, sediment deposition, and other factors (Wharton et al. 1982). The effect of these spatial patterns on the abundance and distribution of floodplain bird species has received little attention and may be critical to their effective conservation and management. Wakeley and Roberts (1996) sampled birds along transects across the floodplain of the Cache River, Arkansas, and showed that the distributions of several species were skewed toward either the wetter or drier floodplain zones. Ordination of bird counts revealed that position on the moisture gradient was the factor most closely associated with the distribution of bird species across the floodplain. However, it was not clear whether the results from this one study site could be generalized to other southeastern bottomland systems.

The purposes of the present study were to identify and compare the factors important to the distribution of breeding birds across the floodplains of three rivers in the Southeast using consistent sampling methods and analytical approaches. Specific objectives were to compare the abundance and species richness of breeding birds across floodplain forest zones in three study areas and to identify important environmental gradients affecting the organization of avian communities in southeastern bottomland hardwood forests.

Study areas

Three study areas were selected to represent extensive, relatively mature (>50 years), uneven-aged floodplain forests in the southeastern United States. Study areas were located in the floodplains of the Cache River, Arkansas (AR), Iatt Creek, Louisiana (LA), and the Coosawhatchie River, South Carolina (SC) (Fig. 1).

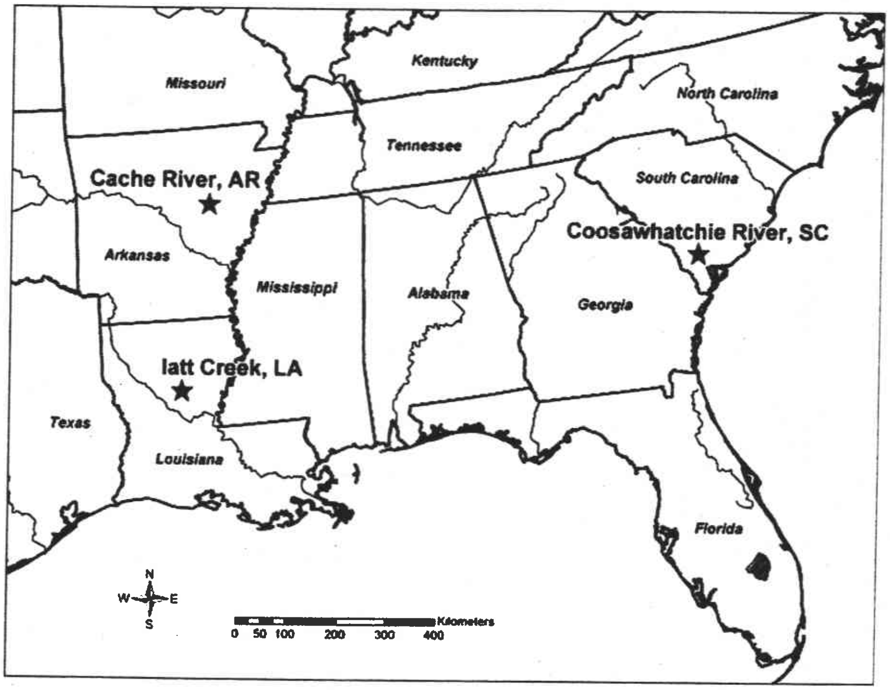

Fig. 1 Locations of the study areas in the southeastern United States

The Cache River study area was located in the Arkansas Game and Fish Commission's Rex Hancock/Black Swamp Wildlife Management Area and the Cache River National Wildlife Refuge in Woodruff County, AR. It consisted of the broad (>2 km wide) forested floodplain of the Cache River, an alluvial stream with a watershed of approximately 2,880 km^2 (Kress et al. 1996). The floodplain contained relatively continuous second-growth forest as much as 80–120 years old (King and Antrobus 2001). The pattern of forest types in the study area mainly reflected the hydrologic gradient (Smith 1996; Wakeley and Roberts 1996). The floodplain supported semipermanently flooded *Nyssa aquatica* L. and *Taxodium distichum* Rich. swamps at the lowest elevations, and seasonally flooded wetlands dominated by *Quercus nuttallii* Palmer, *Q. lyrata* Walt., *Carya aquatica* Michx. f., *Ulmus americana* L., and *Fraxinus* spp. L. at higher elevations. Water levels in the Cache River fluctuate >3 m annually due to backwater flooding caused by constrictions in the floodplain downstream of the study area (Walton et al. 1996). The area where bird and vegetation surveys were performed (ca. 300 ha) had approximately 1.3 m of topographic relief and was flooded continuously for >30 days each year. Previous work at this site showed that ground-surface elevation and annual cumulative flooding duration were highly correlated (range: $r = -0.83$ to -0.91) (Wakeley and Roberts 1996, unpublished data; Richard Day, U.S. Geological Survey, unpublished data). Beyond the forested floodplain the surrounding landscape was largely agricultural.

The Iatt Creek study area was located in the Kisatchie National Forest in Winn Parish, LA. Iatt Creek dominates a minor alluvial floodplain (Hodges 1998) characterized by frequent, short-duration (1–5 day) flooding in response to local rainfall events within its approximately 210-km^2 watershed (Meier et al. 1999; Baker et al. 2006). Within the study area, the main stream and a number of secondary channels and sloughs formed a braided pattern on the floodplain. Topographic relief in the area where bird and vegetation surveys were done (ca. 300 ha) was approximately 10 m including the active floodplain and terraces dominated mainly by uneven-aged hardwoods about 70 years old (Gardiner et al. 1996). Distribution of tree species and plant communities across the study site were not strongly related to elevation gradients (Meier et al. 1999). Dominant tree species included *Liquidambar styraciflua* L., *Q. nigra* L., *N. sylvatica* Marsh., *Fagus grandifolia* Ehr., and *Pinus taeda* L. Surrounding upland areas were dominated by even-aged *P. taeda* and *P. echinata* Mill. plantations.

The Coosawhatchie River study area was located in Jasper County, SC, on land owned and managed for forest products by MeadWestvaco Corporation. The Coosawhatchie River is a braided, blackwater river with a drainage area of roughly 1,000 km^2 upstream of the study area (Eisenbies and Hughes 2000). Within the area where bird and vegetation surveys were performed (ca. 350 ha), the floodplain had about 2 m of topographic relief and was roughly 1.6 km wide. Most areas of the floodplain were flooded >30 days each year. Vegetation patterns mainly reflected the hydrologic gradient (Burke et al. 2000, 2003), and between 1994 and 1997, river level and water-table elevation ranged in correlation between 0.56 and 0.97 (Burke et al. 2003). Due to the anastomosing stream channels, plant communities were disjunct and transitions were relatively abrupt. Dominant tree species included *N. aquatica*, *N. sylvatica* var. *biflora* Walt., and *T. distichum* at the lowest elevations. Intermediate elevations were dominated by *Q. laurifolia* Michx., *Q. lyrata*, *L. styraciflua*, and *Acer rubrum* L. Higher elevations also supported *Q. nigra*, *Q. falcata* var. *pagodaefolia* Michx., and *P. taeda* (Burke et al. 2000). Adjacent areas were dominated by forest, regenerating clearcuts, and even-aged pine plantations.

Methods

Bird surveys

From 1995 to 1998, we used 5-min point counts, one count per year, to sample breeding birds in each study area (Ralph et al. 1995; Hamel et al. 1996). Point-count surveys were conducted by four observers at permanently marked sampling points systematically arranged in a grid pattern with 250-m spacing between points. The Cache River study area contained 47 points, Iatt Creek 44, and the Coosawhatchie River 59. Only birds seen or heard within 50 m of the sampling point were used in this analysis and counts were averaged over the 4 years of the study. Counts were made by a single observer in the morning, generally between sunrise and 10:00 local standard time or until activity declined noticeably. Point counts were conducted at approximately the same time each year, during May or June, by the same four observers. Bird species were categorized as Neotropical migrants or year-round residents based on Finch (1991) and local field guides. The use of common names is well established in the ornithological sciences (American Ornithologists' Union 1998); therefore, common names are used throughout the text. Scientific names with full authorities of birds detected in this study are listed in Table 1.

Differences in detectability of bird species in different habitats or with increasing distance from an observer can potentially bias estimates of abundance, species richness, and habitat use (Burnham 1981; Nichols et al. 2000; Thompson 2002). We used data from the 25 most abundant bird species in each study area to check for significant declines in detectability with distance from the observer within the 50-m fixed-radius plot by comparing the average density of birds detected within 25 m of the sampling point (area = 0.196 ha) with that in the zone 25–50 m from the sampling point (area = 0.589 ha). Comparisons were done separately for each study area and species using paired *t*-tests (Zar 1984) with the experiment-wise error rate set at $\alpha = 0.10$ (Bonferroni sequential test; Rice 1989). Differences among the four observers were further controlled by having the surveyors sample all vegetative community types along the environmental gradient at each site, and by employing experienced birders with excellent hearing and vision (Verner and Milne 1989; Gutzwiller and Barrow 2001).

Vegetation sampling

Vegetation sampling served two purposes: (1) to classify forest types in the vicinity of bird sampling points and (2) to describe habitat features and gradients that may have influenced bird distributions across the floodplains. Classification of forest types was based on species composition and basal area of trees $\geq$10 cm in diameter at breast height (DBH) within a 0.04-ha (11.3-m radius) circular plot surrounding each sampling point (James and Shugart 1970). Basal areas for each species in each plot were calculated from diameter measurements made during summer of 1995.

We measured habitat characteristics thought to be important to birds of bottomland hardwoods (Pashley and Barrow 1993) around bird sampling points using a sampling design similar to that of Gutzwiller et al. (1994). During the spring and summer of 1998, we

Table 1 Number of individual birds, number of bird species, and total number of individuals detected within 50 m of each sampling point during one 5-min point count each spring from 1995 to 1998 in three southeastern U.S. bottomland hardwood forests

Species	Abbreviation	Cache River, AR (n = 47)	Iatt Creek, LA (n = 44)	Coosawhatchie River, SC (n = 59)
Double-crested Cormorant *Phalacrocorax auritus* (Lesson)[a]	DCCO	–	–	1
Great Blue Heron *Ardea herodias* Linnaeus	GTBH	–	2	–
Great Egret *Ardea alba* (Linnaeus)	GREG	–	–	2
Little Blue Heron *Egretta caerulea* (Linnaeus)	LBHE	–	1	–
Yellow-crowned Night-Heron *Nyctanassa violacea* (Linnaeus)	YCNH	–	3	–
White Ibis *Eudocimus albus* (Linnaeus)	WHIB	–	–	53
Wood Duck *Aix sponsa* (Linnaeus)	WODU	5	–	2
Red-shouldered Hawk *Buteo lineatus* (Gmelin)	RSHA	–	2	4
Mourning Dove *Zenaida macroura* (Linnaeus)	MODO	2	1	1
Yellow-billed Cuckoo[b] *Coccyzus americanus* (Linnaeus)	YBCU	18	8	23
Barred Owl *Strix varia* Barton	BAOW	–	4	–
Chimney Swift[b] *Chaetura pelagica* (Linnaeus)	CHSW	7	–	2
Ruby-throated Hummingbird[b] *Archilochus colubris* (Linnaeus)	RTHU	3	4	5
Red-headed Woodpecker *Melanerpes erythrocephalus* (Linnaeus)	RHWO	5	1	4
Red-bellied Woodpecker *Melanerpes carolinus* (Linnaeus)	RBWO	75	24	100
Downy Woodpecker *Picoides pubescens* (Linnaeus)	DOWO	72	10	61
Hairy Woodpecker *Picoides villosus* (Linnaeus)	HAWO	7	–	4
Northern Flicker *Colaptes auratus* (Linnaeus)	YSFL	2	2	9
Pileated Woodpecker *Dryocopus pileatus* (Linnaeus)	PIWO	8	4	10
Eastern Wood-Pewee[b] *Contopus virens* (Linnaeus)	EAWP	12	1	8
Acadian Flycatcher[b] *Empidonax virescens* (Vieillot)	ACFL	105	84	212

Table 1 continued

Species	Abbreviation	Cache River, AR ($n = 47$)	Iatt Creek, LA ($n = 44$)	Coosawhatchie River, SC ($n = 59$)
Eastern Phoebe *Sayornis phoebe* (Latham)	EAPH	1	–	–
Great Crested Flycatcher[b] *Myiarchus crinitus* (Linnaeus)	GCFL	40	21	106
Blue Jay *Cyanocitta cristata* (Linnaeus)	BLJA	7	14	–
American Crow *Corvus brachyrhynchos* Brehm	AMCR	3	7	15
Fish Crow *Corvus ossifragus* Wilson	FICR	–	–	1
Carolina Chickadee *Poecile carolinensis* (Audubon)	CACH	91	25	63
Tufted Titmouse *Baeolophus bicolor* (Linnaeus)	ETTI	116	56	159
White-breasted Nuthatch *Sitta carolinensis* Latham	WBNU	76	4	41
Carolina Wren *Thryothorus ludovicianus* (Latham)	CARW	19	30	98
Blue-gray Gnatcatcher[b] *Polioptila caerulea* (Linnaeus)	BGGN	171	43	248
Wood Thrush[b] *Hylocichla mustelina* (Gmelin)	WOTH	7	–	–
Gray Catbird[b] *Dumetella carolinensis* (Linnaeus)	GRCA	–	–	1
Brown Thrasher *Toxostoma rufum* (Linnaeus)	BRTH	–	1	1
White-eyed Vireo[b] *Vireo griseus* (Boddaert)	WEVI	1	18	55
Yellow-throated Vireo[b] *Vireo flavifrons* Vieillot	YTVI	2	16	40
Red-eyed Vireo[b] *Vireo olivaceus* (Linnaeus)	REVI	16	113	221
Northern Parula[b] *Parula americana* (Linnaeus)	NOPA	6	16	158
Blackburnian Warbler[b] *Dendroica fusca* (Müller)	BLBW	–	1	–
Yellow-throated Warbler[b] *Dendroica dominica* (Linnaeus)	YTWA	10	–	27
Pine Warbler *Dendroica pinus* (Wilson)	PIWA	–	5	19
American Redstart[b] *Setophaga ruticilla* (Linnaeus)	AMRE	–	11	10
Prothonotary Warbler[b] *Protonotaria citrea* (Boddaert)	PROW	156	1	41

Table 1 continued

Species	Abbreviation	Cache River, AR (n = 47)	Iatt Creek, LA (n = 44)	Coosawhatchie River, SC (n = 59)
Swainson's Warbler[b] *Limnothlypis swainsonii* (Audubon)	SWWA	–	–	1
Ovenbird[b] *Seiurus aurocapillus* (Linnaeus)	OVEN	–	–	1
Louisiana Waterthrush[b] *Seiurus motacilla* (Vieillot)	LOWA	–	2	3
Kentucky Warbler[b] *Oporornis formosus* (Wilson)	KEWA	–	5	18
Common Yellowthroat[b] *Geothlypis trichas* (Linnaeus)	COYE	–	–	7
Hooded Warbler[b] *Wilsonia citrina* (Boddaert)	HOWA	1	37	60
Yellow-breasted Chat[b] *Icteria virens* (Linnaeus)	YBCH	–	2	–
Summer Tanager[b] *Piranga rubra* (Linnaeus)	SUTA	12	13	23
Northern Cardinal *Cardinalis cardinalis* (Linnaeus)	NOCA	22	43	61
Indigo Bunting[b] *Passerina cyanea* (Linnaeus)	INBU	11	1	6
Eastern Towhee *Pipilo erythrophthalmus* (Linnaeus)	RSTO	–	–	3
Red-winged Blackbird *Agelaius phoeniceus* (Linnaeus)	RWBL	24	–	–
Common Grackle *Quiscalus quiscula* (Linnaeus)	COGR	261	–	–
Brown-headed Cowbird *Molothrus ater* (Boddaert)	BHCO	11	–	2
Total number of birds (all years)		1,385	636	1,990
Birds/sampling point/year (mean ± SD)		7.37 ± 14.78	3.61 ± 6.00	8.43 ± 15.78
Number of bird species		36	39	46
Number of Neotropical migrant species		17	19	23
Number of resident species		19	20	23

Common and scientific names and authorities according to the American Ornithologists' Union (1998)

[a] Author's name listed in parentheses indicates a species originally described in a different genus than currently assigned (AOU 1998)

[b] Neotropical migrant

established four 48-m transects that radiated outward from each sampling point. The first transect was established by stretching a 50-m tape along a random compass bearing and the remaining transects were located at 90° intervals. Along each transect, a series of four 3 × 10-m plots was established such that the transect formed the centerline of the long axis of each plot. A 2-m gap was left between plots. Thus, plots extended from 2–12, 14–24, 26–36, and 38–48 m along each transect, for a total of 16 plots per sampling point. Within each plot, we recorded presence of trees and snags in four diameter classes (<5, 5–15, 15–30, and ≥30 cm), *Sabal minor* Jacq., *Arundinaria gigantea* Walt., *Tillandsia usneoides* L., vine tangles >15 cm in diameter (estimated visually), sloughs (linear channels or drainage ways, whether or not they currently contained water), and gaps in the tree canopy >10 m^2 in size. In addition, we visually estimated percent cover of the tree canopy above each plot and percent foliage volume within four strata (0–0.5, 0.5–2, 2–12 m, and from 12 m to the maximum height of the canopy). To reduce bias in estimates of percentages, data were categorized into the following classes: 0–5, 5–25, 25–50, 50–75, 75–95, and 95–100%. Midpoints of cover classes were used in subsequent analyses (Daubenmire 1959; Bonham 1989). In addition, canopy height was determined by visually estimating the height of the closest dominant tree to the midpoint of each transect; estimates were checked periodically with a clinometer. Ground surface elevation at each bird sampling point was determined by standard surveying techniques.

Analysis

We used TWINSPAN (Hill 1979) to classify forest types at bird sampling points based on basal area of tree species within 0.04-ha plots. TWINSPAN is a divisive clustering procedure suited to analysis of communities that are distributed along an environmental gradient. Analyses were performed with PC-ORD software (McCune and Mefford 1997).

We used univariate testing as a prelude to more comprehensive multivariate analyses. Analysis of variance (PROC GLM; SAS Institute, Inc., 2004) or a *t*-test (PROC TTEST) was used to test for differences in mean bird-community metrics (i.e., number of species and number of birds per point for Neotropical migrants, residents, and all species combined) and abundances of individual bird species among forest types. Only the 25 most abundant bird species in each study area were tested. We used the sequential Bonferroni procedure (Rice 1989) to test for significance under the conservative null hypothesis that the probability of making one or more type I errors across all simultaneous tests did not exceed $\alpha = 0.10$. The sequential Bonferroni procedure does not require independence, but it does not take possible correlations among species into consideration.

We calculated 21 habitat variables from elevation data and vegetation measurements made in radial transects at each sampling point (Table 2). For trees, snags, *S. minor*, *A. gigantea*, *T. usneoides*, vines, sloughs, and canopy gaps, frequencies were calculated based on presence or absence in the 16 vegetation plots per bird sampling point. Mean canopy cover and foliage volumes were calculated by averaging the midpoints of cover or volume classes across the 16 plots. Mean canopy height was calculated as the average of four measurements per sampling point.

We used canonical correspondence analysis (CCA) (ter Braak 1986; ter Braak and Prentice 1988; Palmer 1993) to examine relationships between bird community composition and environmental gradients for each study area separately and for all three study areas combined. Canonical correspondence analysis is a form of direct gradient analysis that calculates a set of ordination axes based on a primary matrix of bird abundances at each sampling point. However, unlike various forms of indirect gradient analysis (e.g., correspondence analysis, multidimensional scaling), the axes in CCA are constrained by a multiple regression on a secondary matrix of environmental variables. Therefore, the procedure identifies gradients in the bird community that may be attributed to variations in habitat characteristics. Advantages of CCA include simultaneous ordering of sites and species, and good performance when species have nonlinear and unimodal responses to environmental gradients (Palmer 1993).

For each CCA, the bird species matrix consisted of mean counts of each species at each sampling point over the 4 years of the study. Before analysis, we eliminated observations of waterfowl, wading birds, wide-ranging species (e.g., hawks, crows), and fly-overs that were not known to use the habitat within 50 m of a sampling point. Canonical correspondence analysis is sensitive to rare species, which can have a disproportionate effect on the ordination. Therefore, we eliminated rare species (i.e., those detected at <3 sampling points) and accepted PC-ORD defaults for downweighting of uncommon species (McCune and Mefford 1997). Monte Carlo tests ($n = 1000$) were used to evaluate

Table 2 Habitat variables measured at each bird sampling point

Abbreviation	Description
TREES < 5 cm	Frequency (out of 16 plots) of live woody stems >1.4 m tall but < 5 cm DBH
TREES 5–15 cm	Frequency of live woody stems ≥5 and < 15 cm DBH
TREES 15–30 cm	Frequency of live woody stems ≥15 and < 30 cm DBH
TREES >30 cm	Frequency of live woody stems ≥30 cm DBH
SNAGS < 5 cm[a]	Frequency of dead woody stems >1.4 m tall but < 5 cm DBH
SNAGS 5–15 cm[a]	Frequency of dead woody stems ≥5 and < 15 cm DBH
SNAGS 15–30 cm[a]	Frequency of dead woody stems ≥15 and < 30 cm DBH
SNAGS >30 cm[a]	Frequency of dead woody stems ≥30 cm DBH
PALM	Frequency of *S. minor*
CANE	Frequency of *A. gigantea*
MOSS	Frequency of *T. usneoides*
VINES	Frequency of vine tangles >15 cm in diameter
SLOUGH	Frequency of sloughs, channels, and drainageways
GAPS	Frequency of canopy gaps >10 m^2 in a relatively continuous tree canopy. Interconnected spaces between widely spaced trees in certain *N. aquatica* and *T. distichum* stands were not counted as gaps.
CANOPY COV	Mean percent canopy cover
FOL 0–0.5 m	Mean percent foliage volume in the 0–0.5 m stratum
FOL 0.5–2 m	Mean percent foliage volume in the 0.5–2 m stratum
FOL 2–12 m	Mean percent foliage volume in the 2–12 m stratum
FOL >12 m	Mean percent foliage volume in the >12 m stratum
CANOPY HT	Mean canopy height (m)
ELEV[b]	Ground-surface elevation at the sampling point (m)

[a] Variables included in the regional analysis, but dropped from analyses of individual study areas

[b] Standardized to a mean of 0 and variance of 1 for analyses involving all three study areas combined

the significance of CCA axes. Scores plotted in CCA diagrams are linear combinations of environmental variables (LC scores; Palmer 1993; McCune 1997). Arrows shown in figures represent the direction of change in each habitat variable across the CCA ordination diagram (Kent and Coker 1992; Palmer 1993). The value of a variable increases in the direction of the arrow's head and decreases in the direction of its tail, which also extends through the origin. The length of an arrow indicates the relative importance of that variable, and the angle between arrows indicates the strength of correlations between variables. The arrows can be interpreted as secondary axes and thus help to explain the distribution of bird species in relation to environmental gradients (Kent and Coker 1992).

Initially, we combined data from all three study areas in a single CCA to identify habitat gradients that might be important to the organization of bottomland bird communities at a regional level. We then analyzed data from each study area separately to check for consistency with the regional results and to identify important gradients at the local level. For the regional analysis, ground-surface elevations were made comparable by first standardizing them within study areas to a mean of zero and variance of one. For analyses involving individual study areas and, thus, smaller samples of bird counts (*n* = 44–59 sampling points), we reduced the number of habitat variables entered into the CCA (Table 2) by dropping the snag variables, which had not been shown to be important at the regional level. Other

Table 3 Means of habitat variables measured in three southeastern U.S. bottomland hardwood forests

Abbreviation	Study area		
	Cache River, AR	Iatt Creek, LA	Coosawhatchie River, SC
TREES < 5 cm	65.2 b	81.1 a	67.1 b
TREES 5–15 cm	59.1	61.9	57.7
TREES 15–30 cm	40.7 a	29.5 b	46.8 a
TREES >30 cm	55.6 a	35.0 b	55.2 a
SNAGS < 5 cm	22.4 a	9.0 b	17.1 a
SNAGS 5–15 cm	8.7 a	3.7 b	12.0 a
SNAGS 15–30 cm	1.2 b	2.3 b	5.2 a
SNAGS >30 cm	1.3	1.3	1.4
PALM	0.0 b	0.0 b	3.1 a
CANE	0.0 b	33.2 a	6.4 b
MOSS	0.0 b	0.1 b	7.7 a
VINES	17.2	25.6	19.5
SLOUGH	6.6 b	18.8 a	15.0 ab
GAPS	6.8 b	25.2 a	6.1 b
CANOPY COV	74.2 b	82.1 a	83.3 a
FOL 0–0.5 m	7.1 b	22.1 a	23.9 a
FOL 0.5–2 m	13.2 b	26.3 a	13.1 b
FOL 2–12 m	33.4 a	35.7 a	24.1 b
FOL >12 m	48.3 a	41.9 a	28.8 b
CANOPY HT	30.3 a	29.9 ab	28.0 b
ELEV	54.4 a	37.5 b	4.7 c

Significant differences between study areas are indicated by different letters (ANOVA with Tukey tests, $P < 0.05$)

variables were eliminated from an individual CCA if they did not vary across a site (e.g., CANE, PALM, and MOSS were zero throughout the AR study area).

Results

Comparisons of habitat variables among the three study areas tended to highlight differences between the Iatt Creek, LA, study area and the other two sites (Table 3). On average, Iatt Creek had more small trees (<15 cm) and shrubs <5 cm DBH but fewer larger trees (≥15 cm) than either the AR or SC study areas. In addition, canopy gaps and *A. gigantea* thickets were more abundant, and smaller snags (<15 cm) less abundant, at the LA study area. Both the AR and SC bottomlands were subject to prolonged winter and early spring flooding in most years and, with few exceptions, were fairly similar in habitat structure (Table 3). Mean foliage volume in the lowest stratum (0–0.5 m) was less in AR than in SC, but foliage volumes in the upper strata were greater. Average canopy cover was greater in SC. In addition, *S. minor*, *A. gigantea*, and *T. usneoides* were all present on the SC study area and absent from the AR site.

Vegetation classification

We used the results of TWINSPAN analysis of tree basal-area measurements from each study area to identify forest types that could be distinguished readily in the field. In general, we named forest types for the tree species that accounted for most of the basal area. At the AR study area, only two forest types were identified: (1) *N. aquatica*, which also contained scattered large *T. distichum*, and (2) mixed hardwoods, which was dominated by *Quercus* spp., *Fraxinus* spp., and *U. americana*. Three forest types were differentiated at the LA study area: (1) *F. grandifolia*, (2) *L. styraciflua*, and (3) *P. taeda*/*Q. f.* var. *pagodaefolia*. At the SC study area, four types were identified: (1) *N. aquatica*, (2) *Q. laurifolia*, (3) *N. s.* var. *biflora*/*L. styraciflua*, and (4) *P. taeda*/*L. styraciflua*.

Bird counts

Comparisons of the density of bird detections within 0–25 and 25–50 m from the observer yielded only four significant differences. In two of these tests (Prothonotary Warbler in AR and Yellow-billed Cuckoo in LA), apparent bird densities within the zone 25–50 m from the observer were greater than those within 25 m. Apparently, some birds either moved farther away or were less likely to vocalize in close proximity to the observer. Only one species, the Blue-gray Gnatcatcher, had a lower density of detections in the farther zone (two significant tests, in AR and SC). Therefore, there was no evidence to suggest that detectability of most bird species declined appreciably within the 50-m fixed radius that we used for point counts. Furthermore, all of the habitats sampled were mature forests and we considered it unlikely that detectability varied appreciably within or among study areas. Therefore, we chose not to adjust bird counts based on estimated detection functions (Burnham et al. 1980; Hutto and Young 2002).

During spring of 1995–1998, we counted 4,011 individuals of 57 bird species on the three study areas combined (Table 1). We observed 26 species of Neotropical migrants on one or more of the three study areas, although individuals of at least two species (i.e., Ovenbird and Blackburnian Warbler) probably were in migration to more northerly breeding areas. Within study areas, the numbers of Neotropical migrant and resident species were about equal. More species (46) and more Neotropical migrant species (23) were counted at the SC study area than in AR or LA; however, the number of sampling points was greater at SC than at the other two sites.

Species composition of the breeding bird community was similar at the three study areas, although a few species were clearly more abundant in one or two areas. For example, Prothonotary Warblers were common at the AR and SC study areas and nearly absent in LA (Table 1), perhaps reflecting the wetter conditions at the first two sites. The abundance of Red-winged Blackbirds, Common Grackles, and Brown-headed Cowbirds at the AR site probably was due to the presence of agricultural land surrounding the forested floodplain.

Twenty-four of the 57 bird species (42%) were detected on all three study areas (Table 1). Eliminating water birds and wide-ranging species such as hawks, owls, and crows from the data set increased the percentage of species common to all three areas to 52% (24 of 46). In pairwise comparisons, the LA and SC study areas were most similar with 71% (30 of 42) of species in common. Despite their closer proximity, the AR and LA study areas had only 63% (26 of 41) of species in common, while AR and SC had 66% (29 of 44) in common. These results reflect differences in landscape context; both LA and SC were in predominantly forested landscapes whereas AR was in an agricultural landscape.

Differences in bird communities among forest types

There were a number of differences in bird community composition and abundance among forest types at the AR and SC study areas, but not at the LA study area. In AR, the average number of bird species detected per point in mixed hardwoods was not significantly different from that in *N. aquatica* forests (Table 4). However, greater numbers of individuals were detected at points classified as *N. aquatica* (sequential Bonferroni test, table-wide $\alpha = 0.10$). The number of species of Neotropical migrants per point was greater in mixed hardwoods than in *N. aquatica* forests, whereas the number of individuals of resident bird species per point was greater in *N. aquatica* than in mixed hardwoods. Overall, a mean of 11.7 species were detected per sampling point, of which 5.1 were Neotropical migrants.

Among individual bird species, Blue-gray Gnatcatchers, Common Grackles, and Prothonotary Warblers were significantly more abundant in *N. aquatica* habitats than in mixed hardwood forests in AR (Table 4). In contrast, Indigo Buntings and Red-eyed Vireos were more abundant in mixed hardwood forests.

At the Iatt Creek, LA, study area, there were no significant differences in the number of bird species or individuals counted in the different forest types (Table 5). Overall, 7.7 species were detected per sampling point, of which 4.7 were Neotropical migrants.

At the Coosawhatchie River, SC, the mean number of bird species detected per point ranged from 12.7 to 15.9 across forest types, and the number of Neotropical migrant species ranged from 6.8 to 9.9 (Table 6).

Table 4 Average number of bird species and individuals ±SE counted at sampling points in relation to forest types at the Cache River, AR, during spring 1995–1998

Community characteristic or bird species	Forest type	
	N. aquatica ($n = 26$)	Mixed hardwoods ($n = 20$)
Community characteristics		
Number of species (per point)[a]	11.04 ± 0.43	12.30 ± 0.55
Number of individuals (per point)[b]	8.13 ± 0.40 a	6.16 ± 0.32 b
Number of neotropical migrant species (per point)[a]	4.38 ± 0.24 b	5.90 ± 0.35 a
Number of neotropical migrant individuals (per point) [b]	3.15 ± 0.17	2.85 ± 0.17
Number of resident species (per point) [a]	6.65 ± 0.29	6.40 ± 0.31
Number of resident individuals (per point) [b]	4.98 ± 0.33 a	3.31 ± 0.25 b
Bird species abundances		
Blue-gray Gnatcatcher	1.06 ± 0.08 a	0.66 ± 0.10 b
Red-eyed Vireo	0.00 ± 0.00 b	0.19 ± 0.04 a
Prothonotary Warbler	1.13 ± 0.10 a	0.49 ± 0.07 b
Indigo Bunting	0.01 ± 0.01 b	0.13 ± 0.03 a
Common Grackle	2.13 ± 0.31 a	0.49 ± 0.10 b

Bird counts that differed significantly between forest types are indicated by different letters (sequential Bonferroni test, table-wide $\alpha = 0.10$; T-test, $P < 0.05$)

[a] Species were accumulated over the 4 years of study before being averaged across points

[b] Average number of individual birds/point/year

Table 5 Average number of bird species and individuals ±SE counted at sampling points in relation to forest types at Iatt Creek, LA, during spring 1995–1998

Community characteristic	Forest type		
	F. grandifolia ($n = 9$)	*L. styraciflua* ($n = 23$)	*P. taeda/Q. f.* var *pagodaefolia* ($n = 11$)
Number of species (per point) [a]	7.33 ± 0.78	8.39 ± 0.45	7.45 ± 0.69
Number of individuals (per point) [b]	3.03 ± 0.29	3.68 ± 0.21	3.39 ± 0.47
Number of neotropical migrant species (per point) [a]	4.44 ± 0.34	4.96 ± 0.30	4.55 ± 0.51
Number of neotropical migrant individuals (per point) [b]	2.11 ± 0.20	2.32 ± 0.18	2.11 ± 0.34
Number of resident species (per point) [a]	2.89 ± 0.51	3.43 ± 0.31	2.91 ± 0.46
Number of resident individuals (per point) [b]	0.92 ± 0.18	1.37 ± 0.15	1.27 ± 0.24

There were no significant differences in counts among forest types (sequential Bonferroni test, table-wide $\alpha = 0.10$)

[a] Species were accumulated over the 4 years of study before being averaged across points

[b] Average number of individual birds/point/year

Sampling points in each forest type differed in the number of individual birds counted, and in the number of Neotropical migrant species and individuals. In all these cases, greater numbers were detected in *P. taeda/L. styraciflua* and *N. s.* var. *biflora/L. styraciflua* habitats than in the remaining forest types. Overall number of bird species, number of resident species, and number of resident individuals were also highest in *P. taeda/L. styraciflua* habitats, but not significantly so. Individual bird species that were significantly more abundant in *P. taeda/L. styraciflua* areas than in other habitats included Hooded Warblers, Kentucky Warblers, and White-eyed Vireos (Table 6). Red-bellied Woodpeckers were significantly more abundant in *N. aquatica* habitats.

Ordination results

Canonical correspondence analysis of bird counts from all three study areas combined produced three significant axes ($P = 0.001$ for each axis) that explained 12.8% (Axis 1), 4.6% (Axis 2), and 2.2% (Axis 3) of the total variance in the data set. Six sampling points were dropped from the analysis due

Table 6 Average number of bird species and individuals ±SE counted at sampling points in relation to forest types at the Coosawhatchie River, SC, during spring 1995–1998

Community characteristic or bird species	Forest type			
	N. aquatica ($n = 6$)	*Q. laurifolia* ($n = 21$)	*N. s.* var. *biflora*/*L. styraciflua* ($n = 24$)	*P. taeda*/*L. styraciflua* ($n = 8$)
Community characteristics				
Number of species (per point)[a]	12.67 ± 0.61	12.76 ± 0.46	12.96 ± 0.76	15.88 ± 1.23
Number of individuals (per point)[b]	7.83 ± 0.27 ab	7.51 ± 0.30 b	7.50 ± 0.36 b	9.63 ± 0.89 a
Number of neotropical migrant species (per point)[a]	6.83 ± 0.60 b	7.24 ± 0.34 b	8.17 ± 0.46 ab	9.88 ± 0.85 a
Number of neotropical migrant individuals (per point)[b]	4.92 ± 0.40 b	4.81 ± 0.22 b	5.21 ± 0.25 ab	6.56 ± 0.62 a
Number of resident species (per point)[a]	5.83 ± 0.60	5.52 ± 0.36	4.79 ± 0.42	6.00 ± 0.96
Number of resident individuals (per point) [b]	2.92 ± 0.28	2.70 ± 0.20	2.29 ± 0.22	3.06 ± 0.51
Bird species abundances				
Red-bellied Woodpecker	0.67 ± 0.22 a	0.56 ± 0.08 ab	0.26 ± 0.04 b	0.28 ± 0.07 b
White-eyed Vireo	0.00 ± 0.00 b	0.05 ± 0.04 b	0.26 ± 0.07 b	0.69 ± 0.15 a
Kentucky Warbler	0.00 ± 0.00 b	0.00 ± 0.00 b	0.07 ± 0.02 b	0.28 ± 0.10 a
Hooded Warbler	0.00 ± 0.00 b	0.11 ± 0.06 b	0.27 ± 0.07 b	0.69 ± 0.19 a

Bird counts that differed significantly among forest types are indicated by different letters (sequential Bonferroni test, table-wide $\alpha = 0.10$; Tukey tests, $P < 0.05$)

[a] Species were accumulated over the 4 years of study before being averaged across points.

[b] Average number of individual birds/point/year

to missing data. The first CCA axis tended to separate bird counts made at the AR study area from those made in LA and SC (Fig. 2a). Neither the second axis nor the third axis produced any appreciable separation of bird counts from LA and SC. Therefore, CCA reflected the similarity of bird communities at the LA and SC study areas, and accentuated the differences with the AR site.

Reasons for the separation of the AR samples from those of LA and SC are revealed in a plot of bird species on the same two CCA axes (Fig. 2b). Species that were only detected at the AR site (e.g., Wood Thrushes) (see Table 1) or were more abundant at that site (e.g., Prothonotary Warblers) plotted at the left end of Axis 1, whereas species that were detected mainly at the other two sites (e.g., Louisiana Waterthrushes) plotted at the right end of Axis 1. In Fig. 2b and all subsequent ordination diagrams, arrows are shown only for those variables whose correlations with one or both axes exceed |0.5| (i.e., $r^2 > 0.25$).

Canonical correspondence analysis of bird counts from all three study areas combined (Fig. 2b) indicated that a suite of correlated habitat variables reflecting understory development (FOL 0–0.5 m, FOL 0.5–2 m, TREES < 5 cm, and VINES) was an important influence on bird distributions within the relatively mature floodplain forests we studied. Habitats with greater understory development were favored by species such as Kentucky Warblers, Common Yellowthroats, and White-eyed Vireos. Other important gradients included variations in average canopy height (CANOPY HT) and coverage (CANOPY COV).

Cache River

Ordinations of bird counts from individual study areas did not necessarily follow the pattern established by the analysis of data from all study areas combined. At the AR study area, CCA produced only one significant axis ($P = 0.001$, $n = 42$, after elimination of one outlier and four points with missing data) that explained 13.6% of the variance in the data set. For consistency in the presentation of results across study sites, both Axis 1 and Axis 2 ($P = 0.66$) are shown in Fig. 3.

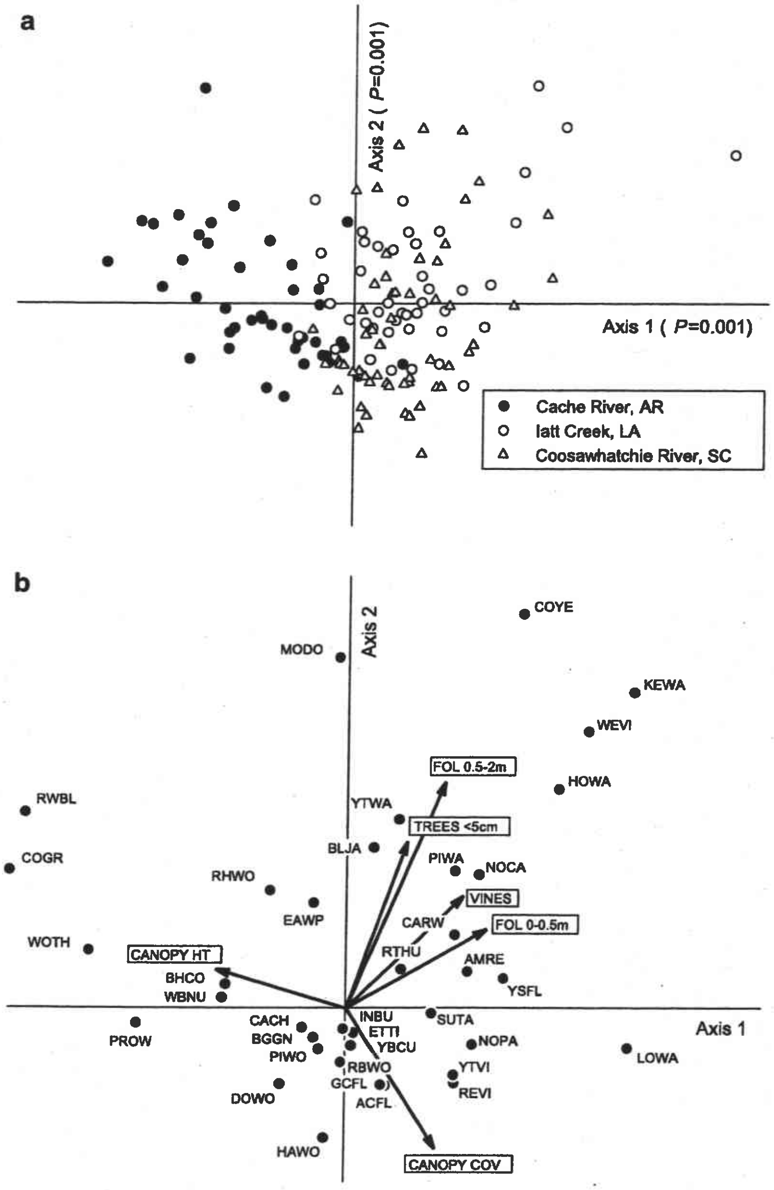

Fig. 2 Results of canonical correspondence analysis (CCA) of bird counts made in mature floodplain forests at three study areas in the southeastern USA: (**A**) plot of samples (n = 144), and (**B**) biplot of bird species and habitat variables in relation to the first two CCA axes. See Table 1 for abbreviations of bird species names and Table 2 for abbreviations of habitat variables

Figure 3a shows the ordination of bird count data at the Cache River with the sampling points coded according to forest types. Axis 1 clearly reflects the hydrologic gradient and separates counts made in *N. aquatica* forests from those made in mixed hardwood forests. Elevation of the sampling point (ELEV) was an important variable (Fig. 3b), as were foliage volume in the 2–12-m layer (FOL 2–12 m), frequency of trees 5–15 cm DBH (TREES 5–15 cm), and frequency of vines (VINES), all of which attained higher values in the mixed hardwood forests at higher elevations in the floodplain. On the other hand, average canopy height (CANOPY HT) was strongly negatively correlated with Axis 1, reflecting the greater average height of the *N. aquatica* and *T. distichum* trees at lower elevations in the floodplain (Fig. 3b). The frequency of canopy gaps (GAPS) was correlated with both Axis 1 and the nonsignificant Axis 2.

Bird species that plotted mainly at the left (lower elevation) end of Axis 1 included Red-winged Blackbirds, Blue Jays, Common Grackles, Prothonotary Warblers, Eastern Wood-Pewees, Blue-gray Gnatcatchers, and Yellow-throated Warblers (Fig. 3b). These species tend to prefer more open (e.g., Red-winged Blackbirds and Common Grackles) or wetter habitats (Prothonotary Warblers and Yellow-throated Warblers). Species that were more common at the right (higher elevation) end of Axis 1 tend to prefer forest conditions with denser canopy cover and included Northern Parulas, Hairy Woodpeckers, Indigo Buntings, Ruby-throated Hummingbirds, and Red-eyed Vireos. Apparently, the bird community at the Cache River, AR, study area was organized mainly in response to the wetness gradient, perhaps because of individual species preferences for the structural characteristics or resources available in the forest type present at lower versus higher elevations on the floodplain.

Iatt Creek

Canonical correspondence analysis of bird counts at the LA study area produced two significant axes. Axis 1 ($P = 0.001$) accounted for 12.0% of the total variance in the data, and Axis 2 ($P = 0.002$) accounted for 7.5% of the variance ($n = 43$; after elimination of one outlier). Figure 4a shows a plot of bird-count samples in relation to CCA axes, with

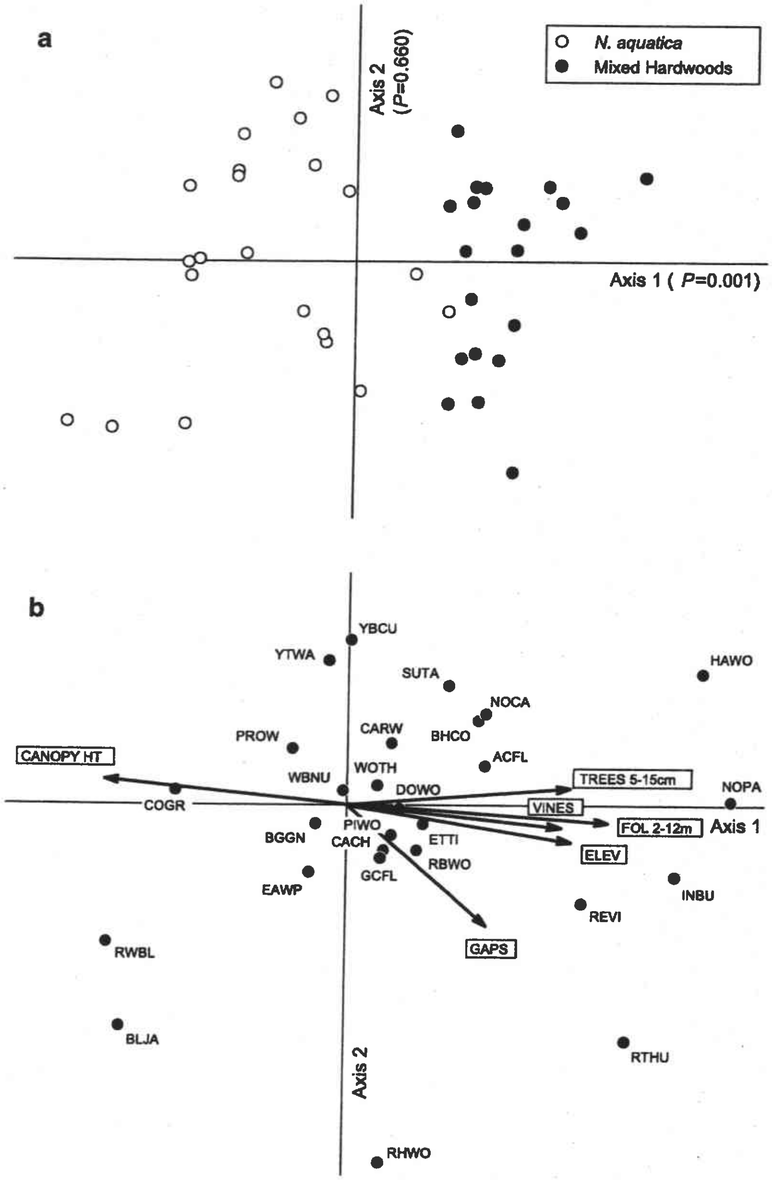

Fig. 3 Results of canonical correspondence analysis (CCA) of bird counts made at the Cache River, AR, study area: (**A**) plot of samples ($n = 42$) coded according to forest types, and (**B**) biplot of bird species and habitat variables in relation to CCA axes. Axis 2 was not significant but was retained for consistency with other analyses. See Table 1 for abbreviations of bird species names and Table 2 for abbreviations of habitat variables

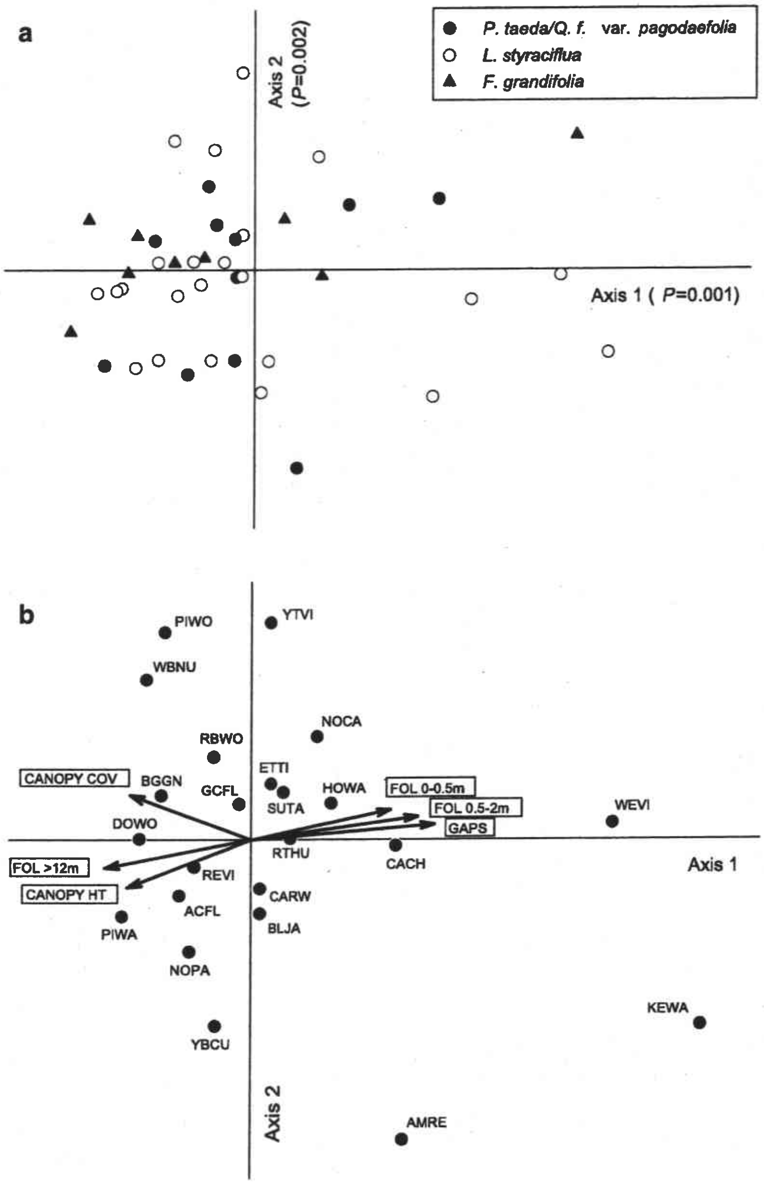

Fig. 4 Results of canonical correspondence analysis (CCA) of bird counts made at the Iatt Creek, LA, study area: (**A**) plot of samples ($n = 43$) coded according to forest types, and (**B**) biplot of bird species and habitat variables in relation to CCA axes. See Table 1 for abbreviations of bird species names and Table 2 for abbreviations of habitat variables

the sampling points coded according to forest types. The lack of obvious pattern in the CCA diagram indicates that forest types were not an important factor in the organization of the Iatt Creek bird community.

The frequency of canopy gaps (GAPS) and the average volume of foliage in the two lowest strata (FOL 0–0.5 m, FOL 0.5–2 m) were important variables in the ordination of bird counts at Iatt Creek and were positively correlated with Axis 1 (Fig. 4b). Variables that were negatively correlated with Axis 1 included two that reflected more continuous canopy coverage (CANOPY COV and FOL >12 m) and one indicating greater canopy height (CANOPY HT). Despite the significance of Axis 2 to the ordination, none of the habitat variables we measured was strongly correlated with it. Variables having the highest correlations with Axis 2 were VINES ($r = -0.47$) and ELEV ($r = -0.41$).

Bird species associated with the right end of Axis 1 (i.e., more frequent canopy gaps, more abundant understory foliage) at Iatt Creek were Kentucky Warblers, White-eyed Vireos, American Redstarts, and Carolina Chickadees (Figure 4b). Those associated with the left end of Axis 1 (i.e., more continuous and abundant canopy-level foliage, taller trees) were Pine Warblers, Downy Woodpeckers, White-breasted Nuthatches, Blue-gray Gnatcatchers, and Pileated Woodpeckers.

Coosawhatchie River

Canonical correspondence analysis of bird counts at the SC study area produced two axes. Axis 1 ($P = 0.001$) explained 14.6% of the variance and Axis 2 ($P = 0.059$) explained 5.5% of the variance in the data set ($n = 57$, after elimination of two points with missing habitat data). A plot of bird-count samples in relation to CCA axes (Fig. 5a) separated counts made in *N. aquatica* forests (left end of Axis 1) from those made in *P. taeda*/*L. styraciflua* stands (right end of Axis 1). Counts made in *Q. laurifolia* forests plotted mostly to the left, whereas counts made in *N. s.* var. *biflora*/*L. styraciflua* forests were widely scattered along Axis 1.

Axis 1 was correlated with ELEV, with higher elevations toward the right of the ordination diagram

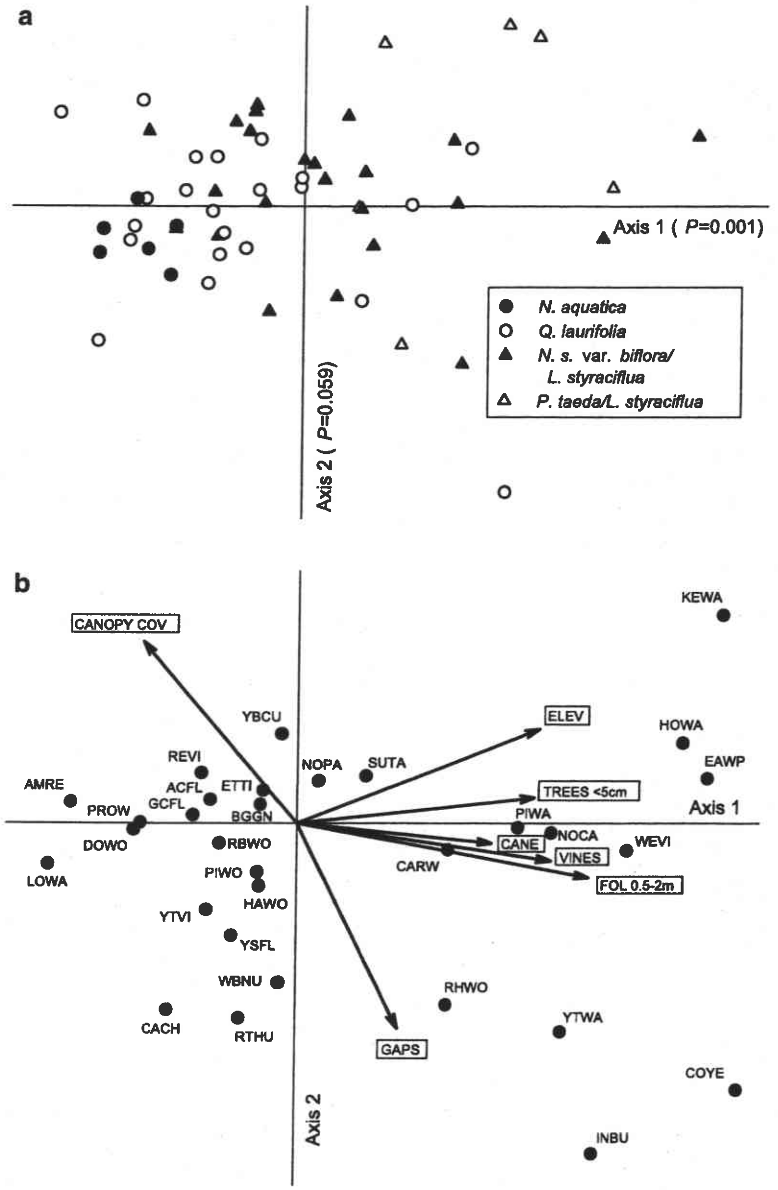

Fig. 5 Results of canonical correspondence analysis (CCA) of bird counts made at the Coosawhatchie River, SC, study area: (**A**) plot of samples ($n = 57$) coded according to forest types, and (**B**) biplot of bird species and habitat variables in relation to CCA axes. See Table 1 for abbreviations of bird species names and Table 2 for abbreviations of habitat variables

(Fig. 5b). In addition, the average volume of foliage in the 0.5–2-m layer (FOL 0.5–2 m), frequency of trees <5 cm DBH (TREES < 5 cm), and frequencies of vine tangles (VINES) and *A. gigantea* (CANE) all increased toward the right of the diagram. Bird species associated with the right end of Axis 1 included Eastern Wood-Pewees, Hooded Warblers, and Kentucky Warblers, whereas those associated with the left end included Louisiana Waterthrushes and American Redstarts (Fig. 5b).

Axis 2 of the CCA was correlated negatively with the frequency of canopy gaps (GAPS) and positively with increased canopy cover (CANOPY COV) (Fig. 5b). Bird species that were associated with greater frequency of gaps included Indigo Buntings, Common Yellowthroats, and Yellow-throated Warblers. Birds associated with higher values of canopy cover and fewer gaps included Yellow-billed Cuckoos and Red-eyed Vireos.

Discussion

Habitat selection by birds is thought to be a hierarchical process involving the selection of landscapes, habitat patches within landscapes, and microhabitat features within patches (Hildén 1965; Klopfer and Ganzhorn 1985). Behavioral stimuli that are important to habitat choice at one level may or may not be relevant at another. Because of this underlying behavioral variability, conclusions drawn from a study of habitat selection depend upon the spatial scale at which the study was conducted (Johnson 1980; Wiens and Rotenberry 1981; Gutzwiller and Anderson 1987; Wiens 1989). Our study focused on the bird communities of floodplain forests in the southeastern United States. Many of the bird species we studied have much wider distributions and occupy other habitats, particularly other forest types, in the region. In some cases, our study areas represented the wetter end of a species' distributional limits (e.g., Smith 1977). Therefore, our results pertain mainly to floodplain forests and the relatively subtle variations in habitat characteristics within them.

Bird distributions across forest types

We identified a number of bird community characteristics and individual species abundances that differed among mature floodplain forest types, particularly at the AR and SC study areas. In both areas, for example, species richness of Neotropical migrants was greatest in the highest and driest forest type (i.e., mixed hardwoods in AR and *P. taeda*/*L. styraciflua* in SC) and least in *N. aquatica* habitats. Neotropical migrants that were rare in or absent from *N. aquatica* forests at one or both sites, but relatively common in drier forests, included several species that primarily nest near or on the ground, such as Indigo Buntings, Hooded and Kentucky Warblers, and White-eyed Vireos (DeGraaf et al. 1985; McDonald 1998). In *N. aquatica* habitats, nearly year-round flooding results in a relatively sparse woody understory and may make the ground unavailable to birds throughout the spring nesting period, thus possibly limiting foraging opportunities for these and other foliage gleaners, and nesting opportunities for these and other ground-nesting species.

A number of other species were more abundant in *N. aquatica* forests than in one or more of the higher elevation forest types, although results were not necessarily consistent among study areas. Numbers of Prothonotary Warblers, Blue-gray Gnatcatchers, and Common Grackles were higher in *N. aquatica* forests than in mixed hardwoods in AR, and the number of Red-bellied Woodpeckers was higher in *N. aquatica* forests in SC. Prothonotary Warblers are wet forest specialists; they nest in abandoned tree cavities, generally located over or near standing water (Petit 1999). Prothonotary Warblers were also most abundant in *N. aquatica* forest in SC, but differences in abundance among forest types were not significant, perhaps reflecting the greater interspersion of forest types there. Blue-gray Gnatcatchers were common on all three study sites. They use a wide range of forested and shrub habitats (Ellison 1992) and were significantly more common in *N. aquatica* forest only in the AR study area. Common Grackles, which were present only at the AR site and reflected its agricultural landscape, often inhabit open woods, swamps, and forest edges along waterways but avoid continuous forests (Peer and Bollinger 1997).

Vegetation patterns at the AR and SC sites were typical of southeastern forested wetlands, the result of spatial variations in the frequency and duration of flooding and differences in the tolerance of plant species for prolonged soil anoxia (Wharton et al. 1982; Smith 1996; Burke et al. 2000). Therefore, in

AR and SC, hydrologic variations appeared to be the ultimate cause of the observed spatial variations in bird communities. Vegetation zonation reflected the hydrologic gradient, and bird distributions, at least in part, reflected the vegetation pattern.

In contrast, our results suggest that forest types were largely irrelevant to the distribution of birds at our Iatt Creek, LA, study area. We identified no significant differences in abundance or diversity of bird species among forest types. The LA study area was different from the other areas in that flooding was frequent but of short duration (1–5 days). Flooding episodes that passed so quickly may have had little direct influence on most bird species nor on floodplain plant communities. Thus, forest types along the elevational gradient on the LA study area may not have been different enough in their structure or resource availability to engender different responses in their bird communities.

Environmental gradients

Ordinations presented in this paper resulted in consistently low percentages of explained variance, ranging from 17.4% to 20.1% for Axes 1 and 2 combined. Possible explanations include ''noise'' in the data and problems due to relatively short environmental gradients. Noise results when species or environmental data are affected by random variations or measurement errors, or when irrelevant variables are included in the environmental data set (McCune 1997). The mobility of birds and difficulties in detecting individuals can cause variability in counts. Fortunately, CCA is fairly robust to species and environmental data that contain noise (Gauch 1982a; Palmer 1993; McCune 1997). Gauch (1982b) found that much of the underlying structure of a data set is recovered in the first few ordination axes, whereas noise in the data tends to be deferred to later axes. Therefore, ordination is reliable in interpreting species–environment relationships even when the proportion of variance explained by the first few axes is small. Kenkel and Orlóci (1986) found that ordination methods performed best when species turnover was not great. Most of the bird species we observed were present throughout the environmental gradients we identified and community variations were due mainly to shifts in abundance, rather than complete turnover of species.

Ordination of bird counts from all three study areas combined suggested that a suite of variables describing understory structure (i.e., abundance of foliage within 2 m of the ground, frequency of vines and woody stems <5 cm DBH) was an important factor affecting bird distributions across these forested floodplains. This theme was echoed in the separate ordinations for each study site, which revealed differences in the apparent causes of variation in understory development.

At the Cache River, AR, study area, only one axis was significant in the ordination and that axis mainly described a hydrologic gradient, indicated by correlation with ground-surface elevation. Other correlated variables included understory and midstory characteristics (e.g., frequency of vine tangles and trees 5–15 cm DBH, volume of foliage in the 2–12 m layer).

At the Cache River, the elevation gradient is the dominant feature of the landscape. A transect extending across the floodplain traverses a broad zone of seasonally flooded forest containing a mixture of *Quercus* spp., *Carya* spp., *Fraxinus* spp., and *U. americana* before dropping noticeably into a zone of semipermanently flooded *N. aquatica* and *T. distichum* trees. Understory development is greater in the higher elevation zone that is subject to shorter periods of winter and early spring flooding (Wakeley and Roberts 1996). Our results indicate that bird species are distributed across the Cache River floodplain primarily in response to the hydrologic gradient acting either directly through avoidance of flooded areas during the breeding season, or indirectly through selection of habitats having greater structural development of understory and midstory vegetation.

Ordination of Coosawhatchie River, SC, bird counts produced two significant axes, the first related to elevation and the second related to the frequency of canopy gaps. Important structural characteristics of the forest understory (i.e., frequency of vines, *A. gigantea*, and woody stems <5 cm DBH, and the volume of foliage in the 0.5–2 m layer) were all correlated with Axis 1. Therefore, the bird community at the Coosawhatchie River was organized mainly in response to the hydrologic gradient, while the frequency of canopy gaps played a secondary role.

The Iatt Creek, LA, site was distinct among our study areas in that it was a narrow floodplain dominated by a small, low-order stream with flashy hydrology. Flooding events were frequent but brief. Ordination of bird counts produced two significant axes but only Axis 1 was highly correlated ($|r| > 0.5$) with measured habitat variables. These habitat variables included the frequency of canopy gaps and foliage volumes in the 0–0.5 m and 0.5–2 m strata. Variables that were negatively correlated with Axis 1 included canopy coverage, canopy height, and foliage volume in the >12 m layer. Therefore, Axis 1 apparently reflected differences in bird communities between those areas of the floodplain with continuous canopies and less understory development, and those areas with greater numbers of canopy gaps and increased structural development of the understory. At Iatt Creek, the absence of prolonged flooding apparently resulted in other factors, such as the presence of canopy gaps, assuming greater importance to the distribution of floodplain birds. Gaps in the forest canopy allow additional light penetration, affecting microclimates and stimulating the development of understory vegetation (Runkle 1982, 1985; Brokaw 1985). Birds may respond to the added structural diversity and localized abundance of arthropods and other foods in gaps (Schemske and Brokaw 1981; Blake and Hoppes 1986; Levey 1988; Gorman 1999; Moorman 1999).

Conclusions

Ordination is a correlation approach and cannot identify cause-and-effect relationships with certainty. However, a common theme across all three study areas was the importance of understory vegetation structure to the organization of bird communities in these mature southeastern floodplain forests. Variations in understory structure at our sites may have had different causes (i.e., flooding gradients in AR and SC, and frequency of canopy gaps in LA). Thus, all three bird communities appeared to be organized at least partly in response to periodic habitat disturbance that may have been fairly widespread (flooding) or highly localized (canopy gaps produced by falling trees or other factors). Sites that were affected by long-duration flooding showed less response to gaps, perhaps because they were too wet for substantial understory vegetation development (Guilfoyle et al. 2005).

Disturbance at various spatial scales is an important influence on the organization of natural communities (Sousa 1984; Pickett and White 1985; Urban et al. 1987; Turner et al. 1997). Wiens (1989) suggested that repeated disturbance can alter community-development trajectories toward different end states than would be achieved in the absence of disturbance. For communities subject to frequent disturbance, the normal state is one of recovery from the last episode of disturbance (Reice 1994). Our results suggest that regular flooding disturbance is fundamental to the organization of breeding bird communities in floodplain systems subject to prolonged inundation, whereas other agents of disturbance (e.g., tree falls) may be more important in headwater systems subject only to short-duration flooding.

Diking or leveeing of floodplain forests may have deleterious effects on avian communities by altering the hydrologic forces that maintain forest zones and gradients in habitat structure. Therefore, management of floodplain forests to maintain avian community integrity may require the continued maintenance or restoration of natural flooding regimes and other sources of natural disturbance.

Acknowledgments We thank MeadWestvaco Corporation for permitting us access to the Coosawhatchie River site, Arkansas Game and Fish Commission and the Cache River National Wildlife Refuge for use of the Cache River site, and Kisatchie National Forest for use of the Iatt Creek Site. We thank Chris Woodson for assistance with bird counts; John McCoy, Troy Mallach, and Richard Day for help with vegetation sampling; and Sammy King for advice and logistical support. Rassa Dale, Richard Kasul, and Chester Martin provided valuable comments on the manuscript. This work was funded by the Wetlands Research Program of the U.S. Army Corps of Engineers, the U.S. Forest Service, and the U.S. Geological Survey, Biological Resources Division. Permission to publish this paper was granted by the Chief of Engineers.

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