RESEARCH ARTICLE

Breeding Bird Assemblages Associated With Stages of Forest Succession in Large River Floodplains

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ABSTRACT: Floodplain forests rival all other habitat types in bird density and diversity. However, major successional changes are predicted for floodplain forests along the Mississippi River in the coming decades; young forests may replace the existing mature silver maple (*Acer saccharinum* L.) forests in some areas. We wanted to assess how the breeding bird community might respond to these changes. We studied stands of young forests along the middle Mississippi River, comparing the breeding bird assemblages among three stages of forest succession: shrub/scrub, young cottonwood (*Populus deltoides* Marshall) and willow (*Salix nigra* Marshall) forests, and mature silver maple dominated forests. We recorded a total of 54 bird species; the most frequently observed species were the indigo bunting (*Passerina cyanea*), red-winged blackbird (*Agelaius phoeniceus*), and yellow-billed cuckoo (*Coccyzus americanus*). Bird species richness differed among the habitat types, with mature forests supporting the largest number of species and the most species of management concern. The shrub/scrub and mature forest bird assemblages were distinct and shared few species, but the young forests had no identifiable bird species assemblage, sharing species found in both of the other habitat types. The bird assemblages we observed in young forests may become more prevalent as aging floodplain forests are replaced with younger stages of forest succession. Under this scenario, we would expect a temporary local decrease in bird species richness and habitat for species of management concern.

Index terms: bird assemblage, cottonwood, floodplain forest, middle Mississippi River, young forest

INTRODUCTION

Floodplain forests rival all other habitat types in bird density and diversity (Best et al. 1995). A number of studies have reported high species richness and high abundances of birds in these habitats (Best et al. 1996, Knutson et al. 1996, Twedt and Portwood 1997, Knutson and Klaas 1998, Twedt et al. 1999). In the western United States, riparian forests provide breeding and migration habitat for an abundance of forest birds, some of which are restricted to these riparian corridors (Sanders and Edge 1998, Skagen et al. 1998, Saab 1999). Unfortunately, floodplain forests in the northern portions of the Mississippi River are now facing a number of ecological challenges.

Managers are concerned because the mature silver maple (*Acer saccharinum* L.) forests that now dominate the floodplain have low tree species diversity compared with historical conditions and low representation of young age classes (Yin et al. 1997, Knutson and Klaas 1998). In addition, many Mississippi River floodplain forests are reaching senescence (Urich et al. 2002). Because silver maple is not a long-lived tree, large areas of floodplain forest are predicted to undergo successional change in the next five to six decades (Urich et al. 2002).

It is unclear whether forests will persist on these sites or whether they will revert to grasslands under the current hydrologic regime (Yin et al. 1997, Urich et al. 2002). One possible scenario is that forest openings will be inundated with mud during a flood. Young cottonwood (*Populus deltoides* Marshall) and willow (*Salix nigra* Marshall) floodplain forests will become established on these mudflats. Another scenario is that shade tolerant trees such as box elder (*Acer negundo* L.) and mulberry (*Morus rubra* L.), along with silver maple will regenerate in the relatively open canopy created by gradual die-off of mature trees. Yet another predicted scenario is that forest openings will be captured by grasses such as reed canary grass (*Phalaris arundinacea* L.), which can out-compete tree seedlings and maintain the site in an open condition indefinitely. We have observed the last scenario in many places in the floodplain north of St. Louis. Site conditions across the floodplain will vary temporally and spatially, as will the successional trajectory at any specific location. Regardless of which scenario predominates, young forest stands are predicted to become more prevalent in the future along the northern portions of the Mississippi River (Urich et al. 2002).

Threats to large floodplain forests are not limited to the Mississippi River; large rivers are facing ecological challenges across the Midwest, nationally, and globally (Hughes et al. 2001, Johnson 2002, Tockner and Stanford 2002). Floodplain forest regeneration and the consequences for birds is an issue deserving study across the Midwest (Dixon et al. 2002). Despite the ecological importance of floodplain forests for birds, few studies have examined how the breeding bird assemblage changes with different stages of floodplain forest succession in the midwestern United States (Twedt et al. 1999). As a result, future changes in the structure and composition of large floodplain forest stands and the associated effects on the breeding bird community are largely unknown.

We identified two sites containing large stands of young cottonwood and willow forests regenerating on abandoned agricultural land along the middle Mississippi River. These sites also supported mature floodplain forests and shrub/scrub habitats adjacent to the young cottonwood and willow stands. The breeding birds occupying these three habitat types may provide a model for how the bird community will respond to projected changes in floodplain forests. Our objectives were: (1) to compare the breeding bird assemblage and environmental factors associated with three stages of forest succession represented at these sites: shrub/scrub, young cottonwood and willow forests, and mature silver-maple dominated forests, and (2) to identify indicator bird species and species of conservation concern associated with each habitat type. We expected that the mature forests would support the largest numbers of species, but that young forests may be associated with some species of management concern.

METHODS

Study area

Harlow Island (500 ha) is located on the Mississippi River, 10 km south of Crystal City, Missouri, in Jefferson County. Wilkinson Island (985 ha) is also located on the Mississippi River, 58 km north of Cape Girardeau, Missouri, in Jackson County, Illinois. Both sites are part of the U.S. Fish and Wildlife Service (USFWS) Mark Twain National Wildlife Refuge Complex and are located within the floodplain of the middle Mississippi River. From a bird habitat perspective, this part of the Mississippi River falls within the Eastern Avifaunal Biome, a region dominated by forests, adjacent to the Prairie Avifaunal Biome to the west (Rich et al. 2004).

Agricultural land on both islands was abandoned after the 1993 flood and acquired by the USFWS; all row crop agriculture ended in 1995. Levees at each location were breached during the 1993 flood, and there are no plans to repair them. Consequently, the sites were subject to water level changes and frequent floods. In 2001, the sites had extensive stands (100–250 ha) of young (< 8 years old) Cottonwood – Black Willow Forest (Global Rank G3G4, Faber-Langendoen 2001). Mature Silver Maple – Elm (Cottonwood) floodplain forests (Global Rank G4, Faber-Langendoen 2001) were also found at these sites, mainly along the levees and in scattered stands.

Catastrophic flooding during 1993 induced considerable physical and biological changes in floodplain forest habitats (Yin 1998). Many forest stands experienced high tree mortality, setting the stage for forest regeneration. The mature forests at our sites were in senescence, with many aging and dead trees and frequent canopy gaps. There were also open shrub/scrub communities characterized by disturbance-associated species such as annual horseweed (*Conyza canadensis* [L.] Cronq.) and Johnson-grass (*Sorghum halepense* [L.] Pers.), mixed with trumpet creeper (*Campsis radicans* [L.] Seemann) vines, and scattered cottonwood and willow trees. We digitized land cover maps defining the three major habitat types present at our study sites (shrub/scrub, young forest, and mature forest) using aerial photographs taken during 2000. We used U.S. Geological Survey National Land Cover Data (<http://landcover.usgs.gov/classes.html>) within a 50-km zone surrounding our study sites to describe the landscape context for our study sites.

Birds and vegetation

We conducted bird surveys using 10-min point counts within a 50-m radius circle (7,854 m^2; 0.8 ha). Surveys were conducted between 05:00-09:00 hours CST from 6 June to 18 July in 2001. Survey points were randomly located in young cottonwood and willow forest (n =20), mature floodplain forest (n =20), and shrub/scrub (n =20); 10 points of each habitat type were surveyed at each study site (Harlow and Wilkinson Islands). Points were > 200 m apart and 50 m from the nearest edge (Ralph et al. 1995). High water levels rendered portions of the plots inaccessible during much of the breeding season. Survey points were limited to accessible portions of the plots and each point was surveyed once.

In 1997, the USFWS conducted point counts using similar protocols (but not the same point locations) at Wilkinson and Harlow Islands; the data were provided to us as a list of relative abundances (Karen Westphall, USFWS, unpubl. data). For purposes of comparison, we present the 1997 data along with our 2001 bird survey data. Bird species names follow the Check-list of North American Birds, 7th ed. (American Ornithologists' Union 1998). Priority bird species were identified based on the USFWS Region 3 Resource Conservation Priority list (U.S. Fish and Wildlife Service 2002b). Additional sources of information on species of conservation concern, including the USFWS (U.S. Fish and Wildlife Service 2002a) and Partners in Flight (Rich et al. 2004), were consulted.

Stem counts of trees, shrubs, and snags and cover estimates of understory vegetation, forest canopy, and water were taken at the same time and location as the bird point counts within 11.5-m (415 m^2; 0.04 ha) and 5-m (79 m^2; 0.008 ha) radius circles. We estimated the proportion of grass, forb, shrub, and moss cover as well as total green cover within a 5-m circle centered on the bird point count. We also estimated the cover of logs, brush, water, bare ground, and leaf litter within the 5-m circle; litter depth and tree canopy height were also estimated. Details of the vegetation measurements are described in the Breeding Biology Research and Monitoring Database protocol (Martin and Geupel 1993, Martin et al. 1997).

Statistical analyses

We used a number of multivariate analysis methods to describe the similarities and differences in the bird assemblages associated with the three habitat types and to describe the habitats. We investigated the relationships between environmental factors and stages of forest succession using principal component analysis (PCA). Vectors corresponding to environmental factors were interpreted to identify variables that were associated with habitat types using principal component loadings (the correlation between environmental variables and the component axis) and an ordination plot (Appendix A) (Legendre and Legendre 1998). Data were standardized before performing PCA because of differences in measurement scale among the variables. Standardization preserves the relative rank and variance properties of the data and places all data on the same measurement scale (Legendre and Legendre 1998). Large and small snags were combined to reduce redundancy. We report only the first two principal components to simplify interpretation. Differences in our response variables among the assigned habitat types were compared using the nonparametric Kruskal-Wallis test, and values significant at alpha < 0.05 are reported (Zar 1984). Differences in total stem counts of the dominant tree species were compared among habitat types using Fisher's exact test (Zar 1984).

We wanted to focus our analysis on describing the bird assemblages associated with each habitat type, combining the data from the two sites. To this end, we used non-metric multidimensional scaling (NMS) to assess whether or not the bird assemblages were different at the two sites. This non-parametric approach is appropriate for highly skewed species data (Primer – E, Clarke and Warwick 1994). Before ordination, the species matrix was fourth-root transformed to dampen the influence of highly abundant species on the ordination. The Bray-Curtis similarity metric was used to describe and ordinate similarities in bird community structure between sites (Legendre and Legendre 1998).

Indicator species analysis (Dufrene and Legendre 1997) was used to sort the species by habitat type and score their associations with the habitats (PC-ORD, McCune and Mefford 1999, McCune et al. 2002). This analysis provides a statistical basis for assigning a bird species to a primary habitat and defining a bird assemblage for each habitat type. The method uses species abundance data at points and the exclusivity of a species within a habitat type. Indicator values range between 0 (no indication) and 100 (perfect indication). Statistical significance of indicator values was tested using Monte Carlo permutation tests (PC-ORD, McCune and Mefford 1999, McCune et al. 2002).

We used canonical correspondence analysis (CCA, Ter Braak 1986) and an ordination biplot to further assess bird species associations with the habitat types and clarify relations between species and environmental variables (Jongman et al. 1995). Ordination biplots from CCA portray relationships between species, environmental variables, and sample locations simultaneously and they allow a parsimonious visual analysis of these community relationships (Appendix A). Environmental and species data are not standardized before CCA analysis because of a built-in double weighting by sample unit and species totals (McCune et al. 2002). We used presence or absence of bird species data to reduce outliers; redundant environmental variables were removed (leaf litter and canopy height) or combined (small and large snags). We used a Monte Carlo permutation test to measure the significance of the first canonical axis (Ter Braak and Smilauer 1998); we report only two canonical axes to simplify interpretation. Species/environment multiple correlation coefficients indicate the strength of relations with respect to each canonical axis. These, along with ordination plots, were used to interpret results. All ordination plots were drawn using an Excel biplot macro (Smith and Lipkovich 1999); CCA results were obtained from the Excel biplot macro and the computer program CANOCO (Ter Braak and Smilauer 1997).

RESULTS

Vegetation and environmental variables

Within the 50-km zone surrounding Harlow and Wilkinson Islands, the land cover is composed of deciduous or mixed forest (42% and 34%, respectively), grassland or pasture (28% and 36%), cropland (16% and 19%), and woody wetland (2% and 4%). Interpretation of aerial photography revealed that Harlow Island was composed of 245 ha of shrub/scrub, 93 ha of young cottonwood and willow forest, and 149 ha of mature forest. Wilkinson Island was composed of 402 ha of shrub/scrub, 265 ha of young cottonwood and willow forest, and 406 ha of mature forest. Field observations indicated that the three habitat types were similar between the study areas in terms of vegetation structure, composition, and seasonal phenology.

The young forests were dominated by willow, with cottonwood as a subdominant; the mature forests were dominated by silver maple (Table 1; Figure 1). Shrub/scrub habitats had the highest proportions of green ground cover (60%), followed by mature forest (33%) and young forests (18%; Table 1). Stem densities of the smallest shrubs (<2.5 cm dbh) were similar among the habitat types (32-38 stems/0.008 ha), but stem densities of larger shrubs (2.5-8 cm dbh) were highest in young cottonwood and willow habitats (34 stems/0.008 ha). Tree stem density in the 8 to 23 cm size class was highest in young cottonwood and willow habitats (20 stems/0.04 ha), while only the mature forest had stems in the larger size classes. Canopy heights and canopy cover tended to increase from shrub/scrub to young forest to mature forest habitat types (Table 1; Figure 1).

An ordination plot of the vegetation data indicates a gradient corresponding to stages of forest succession (Figure 1). Correlations between the components and the measured variables suggested the following interpretation: High values of PC1 (21.6% of the variability) correspond to high levels of tree height, canopy cover, log cover, number of snags, number of

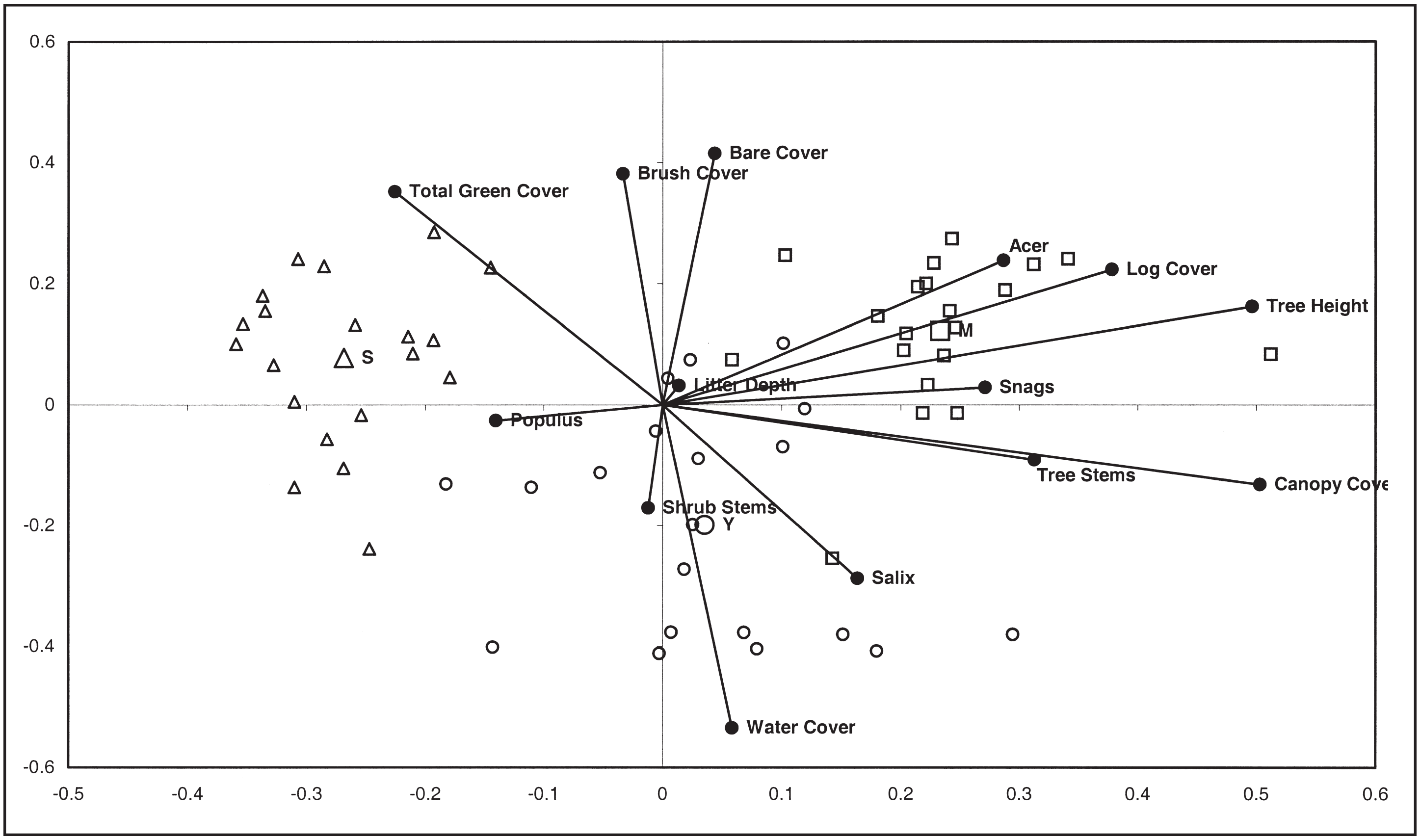

Figure 1. Principal components analysis of the environmental variables with respect to survey points showing the distribution of mature forest (squares, M), young forest (circles, Y), and shrub/scrub (triangles, S) habitats, 2001. Large symbols approximate the centroid of the points representing each habitat type. The length and angle of the line corresponding to the environmental variable represents its contribution to the first or second principal component. See Appendix A for details regarding interpretation of ordination plots.

silver maple stems; low levels of total green cover were negatively related to this pattern (Table 2, Figure 1). PC2 (17.7% of the variability) expressed a trend for high levels of bare ground, brush cover, total green cover, and low water levels (indicator for elevation). Mature forests tended to have higher values of PC1 and PC2, while shrub habitats tended to have lower values for PC1 and higher values for PC2 (Figure 1). Younger forests were associated with the vertical axis (0) for PC1 and had lower values for PC2.

Bird assemblages

We recorded 54 bird species during the point count surveys in 2001 (Appendix B). Ordination (NMDS) plots of the bird assemblages did not differentiate between the two sites, substantiating that they were comparable for our purposes; data from the two sites were pooled for all subsequent analyses. Bird species richness per survey point differed among the habitat types ($P < 0.0001$, KW = 30.9), with mature forests supporting the largest number of species (mean = 12.2, 0.5 SE, n = 20), followed by young cottonwood and willow forests (mean = 7.4, 0.6 SE, n = 20) and shrub/scrub habitats (mean = 7.3, 0.5 SE, n = 20). Fifty-one bird species were recorded during bird surveys conducted by the USFWS in 1997: 44 species at Wilkinson Island, and 35 species at Harlow Island (Appendix B). Six species were recorded in 1997 that were not found in 2001, and eight species were recorded in 2001 but not in 1997 (Appendix B).

The most frequently observed species were the indigo bunting (*Passerina cyanea)*, red-winged blackbird (*Agelaius phoeniceus),* and yellow-billed cuckoo (*Coccyzus americanus;* Appendix B). Indicator species analysis revealed that the common yellowthroat (*Geothlypis trichas)*, song sparrow (*Melospiza melodia),* and yellow-breasted chat (*Icteria virens)* were indicative of the shrub/scrub habitats (Table 3). Eleven species of forest-nesting birds were indicative of the mature forest, and no species were associated with the young forest habitats alone. The red-winged blackbird, yellow-billed cuckoo, and downy woodpecker (*Picoides pubescens)* showed some affinity for young forests but were also associated with one of the other two habitat types.

The CCA ordination of the bird data also indicated that the shrub/scrub and mature forest bird assemblages were distinct and shared few species, but the young forests had no identifiable bird species assemblage, sharing species found in both of the other habitat types (Figure 2). The first canonical axis was dominated by tree height and canopy cover (Table 2). These environmental variables were positively related to mature forests and negatively related to shrub habitats. The second canonical axis

Table 1. Mean (SE) of environmental variables measured at survey points within shrub/scrub, young, and mature forest habitats at Harlow and Wilkinson Islands, U.S. Fish and Wildlife Service, Mark Twain National Wildlife Refuge Complex, 2001.

Environmental variable	Shrub/scrub (n = 20)	Young forest (n = 20)	Mature forest (n = 20)	P-value[a]
Litter depth (mm)	0	2 (1.1)	3 (2.1)	0.56
Total green cover [b]	60 (9.1)	18 (5.6)	33 (5.7)	0.002
Grass [b]	13 (4.2)	0	2 (1.5)	0.003
Forb [b]	36 (7.2)	11 (4.8)	22 (4.1)	0.004
Shrub [b]	13 (5.0)	6 (2.5)	10 (2.4)	0.09
Moss [b]	0	0.3 (0.2)	0	e
Leaf litter cover [b]	2 (1.7)	7 (4.8)	6 (4.0)	0.18
Log cover [b]	0	0	11 (1.6)	e
Brush cover [b]	48 (5.9)	20 (5.8)	46 (5.0)	0.001
Water cover [b,c]	11 (6.6)	48 (10.9)	9 (5.8)	0.002
Bare ground cover [b]	52 (9.3)	37 (9.0)	60 (7.3)	0.2
Shrubs (stem count within 0.008 ha)				
# stems <2.5 cm dbh	34 (19.8)	38 (12.4)	32 (6.0)	0.08
# stems 2.5-8 cm dbh	4 (1.0)	34 (5.7)	14 (2.4)	< 0.001
Trees (stem count within 0.04 ha)				
# stems 8-23 cm dbh	3 (1.0)	20 (4.2)	6 (1.4)	<0.001
# stems 24-38 cm dbh	0	0	6 (1.0)	e
# stems > 38 cm dbh	0	0	3 (1.0)	e
Dominant tree spp. (within 0.04 ha)[d]				< 0.001
Acer saccharinum L.	1	0	10	
Populus deltoides Marsh.	7	6	3	
Salix spp.	2	14	7	
Snags (stem count within 0.04 ha)				
#stems <12 cm dbh	0	3 (1.7)	4 (1.5)	0.18
#stems >12 cm dbh	0	0	2 (0.5)	e
Canopy height (m)	4 (0.7)	9 (0.6)	20 (1.0)	< 0.001
Canopy cover (%)	12 (3.6)	86 (1.4)	88 (1.1)	< 0.001

[a] *P* -values for the null hypothesis that means do not differ among habitat types (Kruskal-Wallis test, P <0.05).

[b] Variables are presented as % cover within 0.008 ha. Total green cover is the % ground cover < 50 cm high. Variables were rounded to the nearest 5% and vegetation layers were evaluated independently; means will not total 100%.

[c] Water coverage was a function of flooding and is an indicator of elevation differences. Flooding and standing water also affected the amount of ground cover < 50 cm high.

[d] Counts of dominant canopy tree species by habitat. Chi-square probability that frequencies of each tree species differed by habitat was <0.0001, Fisher's exact test.

Table 2. Correlation between environmental variables and principal components (PC1 and PC2) and canonical axes (CA1 and CA2), eigenvalues, proportion of variance explained, and bird species-environment correlations for environmental variables at Harlow Island, Missouri and Wilkinson Island, Illinois, 2001.

	Principal components analysis		Canonical correspondence analysis	
Environmental variable	PC1	PC2	CA1	CA2
Litter depth	0.01	0.03	0.11	0.56
Total green cover	-0.23	0.35	0.35	0.45
Log cover	0.38	0.22	-0.6	0.23
Brush cover	-0.03	0.38	-0.08	-0.17
Water cover	0.06	-0.53	0.03	-0.25
Bare cover	0.04	0.42	-0.18	0.23
Shrub stems	-0.01	-0.17	0.04	-0.09
Tree stems	0.31	-0.09	-0.42	0.21
Salix spp.	0.16	-0.29	-0.17	-0.28
Populus deltoides Marshall	-0.14	-0.03	0.28	0.11
Acer saccharinum L.	0.29	0.24	-0.49	0.26
Snags	0.27	0.03	-0.26	-0.02
Canopy height	0.5	0.16	-0.92	0.17
Canopy cover	0.5	-0.13	-0.82	0.12
Eigenvalue	3.03	2.48	0.31	0.23
Proportion of variance	21.60%	17.70%	20.60%	15.20%
Species-environment correlation	-	-	0.9	0.89

was dominated by litter depth and green cover, and to a lesser extent water cover (elevation) and presence of silver maple. The proportion of variance explained was 20.6% and 15.2% for each canonical axis (Table 2). Even though less than half of the total variance was explained (cumulative variance of first two axes = 35.8%), this is typical of species/habitat data and ordination is still informative (Ter Braak and Smilauer 1998). Species and environment correlations (0.90 and 0.89, respectively) suggested strong relations with each canonical axis (Table 2). A Monte Carlo permutation test verified the significance of the first canonical axis (*F*-ratio = 3.32, *P*-value = 0.002).

The shrub/scrub bird assemblage derived from the CCA ordination included the yellow-breasted chat, song sparrow, common yellowthroat, and willow flycatcher (*Empidonax traillii;* Figure 2). Of the species found primarily in this habitat, the wood duck (*Aix sponsa)* and dickcissel (*Spiza americana)* were species of high management concern to the USFWS (Appendix B), although the wood duck's nest requirements led us to suspect that they were breeding in the mature forests and merely more visible as they traversed the shrub/scrub. Trumpet creeper was the dominant vine in shrub/scrub habitats and was a popular nesting substrate for the indigo bunting, common yellowthroat, and yellow-breasted chat. Johnson-grass, an exotic invasive species, dominated large areas of the shrub/scrub habitat type and supported few birds.

The mature forest bird assemblage derived from the CCA ordination included many bird species, including the great crested flycatcher (*Myiarchus crinitus)*, American robin (*Turdus migratorius*), American redstart (*Setophaga ruticilla*), wild turkey (*Meleagris gallopavo)*, house wren (*Troglodytes aedon)*, downy woodpecker, tufted titmouse (*Baeolophus bicolor)*, eastern wood-peewee (*Contopus virens)*, white-breasted nuthatch (*Sitta carolinensis*), blue-gray gnatcatcher (*Polioptila caerulea*), and brown-headed cowbird (*Molothrus ater;* Figure 2). Bird species of management concern in mature forests included the red-headed woodpecker (*Melanerpes erythrocephalus)*, northern flicker (*Colaptes auratus)*, Kentucky warbler *(Oporornis formosus)*, Acadian flycatcher (*Empidonax virescens)*, prothonotary warbler (*Protonotaria citrea)*, and wood thrush (*Hylocichla mustelina;* Appendix B).

The young forest sites shared many species with either the shrub/scrub habitats or the mature forests; no unique bird assemblage could be defined from the indicator species analysis or the CCA ordination biplot (Figure 2, Table 3). The orchard oriole (*Icterus spurius)* was a species of management concern that achieved relatively high abundances in young forests; the

Table 3. Bird species that can be considered habitat indicators, ranked by habitat type and habitat indicator values (% of perfect indication, P < 0.05); generalist species (P > 0.05) are not listed. Species associated with more than one habitat type are listed with dual associations.

Species[a]	Indicator value (%)	*P* -value	Habitat[b]
Common Yellowthroat	58	0.001	S
Yellow-breasted Chat	42	0.001	S
Song Sparrow	32	0.004	S
American Goldfinch	25	0.03	S/M
Red-winged Blackbird	44	0.001	Y/S
Yellow-billed Cuckoo	30	0.014	Y/M
Downy Woodpecker	31	0.017	M/Y
Gray Catbird	50	0.001	M
Eastern Wood-Pewee	46	0.001	M
Northern Cardinal	43	0.004	M
Northern Flicker	36	0.002	M
Red-eyed Vireo	36	0.007	M
Tufted Titmouse	33	0.007	M
House Wren	27	0.019	M
White-eyed Vireo	27	0.028	M
Blue-gray Gnatcatcher	26	0.016	M
Great Crested Flycatcher	25	0.006	M
White-breasted Nuthatch	25	0.008	M

[a]Bird species names follow the Check-list of North American Birds, 7th ed.

[b]Habitat types: S=shrub/scrub, Y=young forest, M=mature forest.

field sparrow (*Spizella pusilla*) was also represented in low abundance in young forests (Appendix B).

DISCUSSION

The rarity of wooded wetlands within 50 km of our study sites is generally indicative of the status of floodplain forests as an uncommon habitat type in most landscapes (Noss et al. 1995). Yin (1999) estimated that there were 123,000 ha of floodplain forests in the Upper Mississippi River Valley in 1989, an estimated reduction of 40% or more from presettlement conditions (Knutson and Klaas 1998). The general scarcity of young cottonwood and willow stands along the Upper Mississippi River (Urich et al. 2002) makes the stands at Harlow and Wilkinson Islands important as representatives of a limited habitat type, and one that could become more common in the future.

The forests of our study sites have grown at rapid rates, reaching up to 9 m in height in less than a decade. The young forests, however, have low tree species and structural diversity, which may account for the lower bird species richness compared with mature forests (Scott et al. 2003). Structural diversity increases as succession proceeds; trees become taller, and additional species, such as silver maple and sycamore (*Platanus occidentalis* L.), increase in dominance. Our bird species assemblages were similar to those described by Twedt et al. (1999) working in the Mississippi Alluvial Valley; they also found more bird species of management concern inhabiting mature floodplain forests than young forests.

The observation that the young forests were less diverse than mature floodplain forests and supported fewer high priority bird species is important because widespread floodplain forest regeneration will be required over the next decades to replace the senescing silver maple forests (Urich et al. 2002). The bird assemblage we observed in young forests may become more prevalent as many aging floodplain forests are replaced with younger stages of forest succession. Assuming young forests will become more prevalent, we would predict a temporary local decrease in bird species richness and habitat for species of management concern along the Mississippi River. However, a young forest is a necessary time step on the path towards a mature forest. Over time we expect that these young forests will mature into forests rich in bird species.

Foresters can focus stand management on either fast-growing tree species or slower growing hardwoods. The fastest reforestation method resulting in a mature forest with native tree species diversity and structural diversity is predicted to best meet the needs of bird species of management concern. For example, Twedt and Portwood (1997) recommend fast-growing young cottonwood and willow trees for reforestation efforts because they provide habitat suitable for forest birds faster than slower-growing tree species like oaks and hickory (*Quercus* and *Carya* spp., respectively). Including a component of hickory and silver maple trees, however, may provide better foraging habitat for some bird species, including cerulean warblers (*Dendroica cerulea)* and yellow-throated warblers (*D. dominica*) (Gabbe et al. 2002). Long-term management should strive toward diversifying forest age structure and species composition across the region, creating a shifting mosaic of floodplain forests of different ages and tree species. These actions will best restore and sustain forest habitats needed by many bird species, including those most in need of management. Similar forest planning may also be needed for other large rivers in the region.

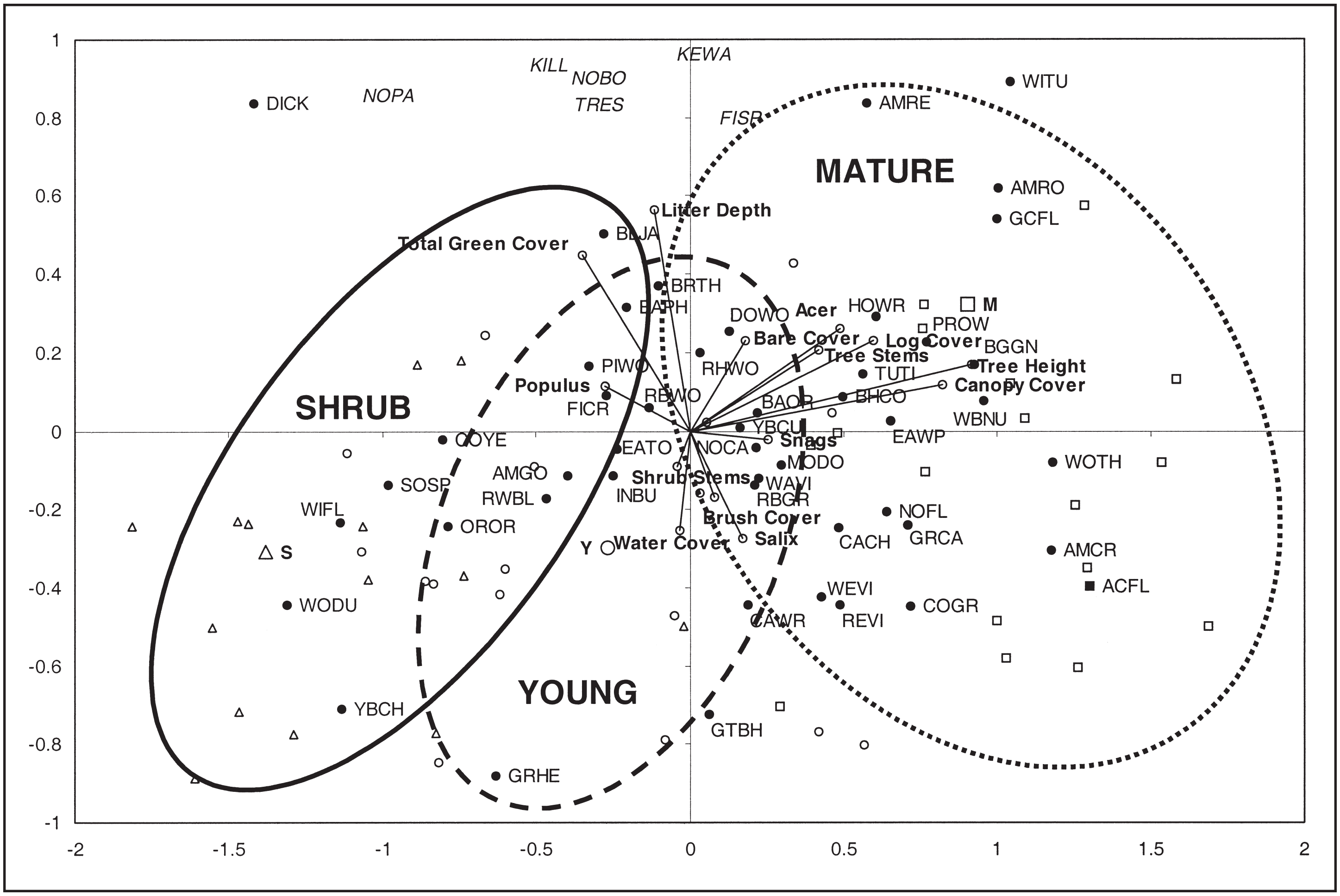

Figure 2. Canonical correspondence analysis ordination plot illustrating how the bird species are related to environmental factors and survey points in shrub/scrub, young forest, and mature forest habitats at Harlow Island, Missouri and Wilkinson Island, Illinois during 2001. Ellipses, drawn by the authors, approximate the region of the graph associated with each habitat type and help clarify plot interpretation. Bird species codes are defined in Appendix B; species in italics (top of plot) were moved closer to the origin in order to be displayed at this scale.

Landscape context and natural plant succession at our study sites seemed to favor the development of forests rather than grasslands. We found the scrub/shrub plant communities at both study sites to be monotypic stands of grasses and forbs, with scattered shrubs dominated by non-native, disturbance-associated species. The grassland bird assemblage was equally depauperate. Among the three habitat types, the shrub/scrub areas occupied the largest areas (245 and 402 ha), so it is unlikely that grassland birds were missing because the sites were too small to support them. However, because bird species associated with shrub/scrub habitats are of management concern nationally (Thompson and DeGraaf 2001), these habitats may be serving an important role in the short term. A long-term management strategy of floodplain forest regeneration is compatible with the short-term existence of shrub/scrub habitat as an intermediate stage.

Small changes in elevation may have influenced succession at our sites. Our ordination plots indicated that young forests were established on areas more subject to flooding (lower in elevation) than the other two habitat types. The shrub/scrub and mature forest areas were associated with slightly higher elevations. During flooding, the low-lying former agricultural areas were covered with mud flats that provided ideal conditions for tree seedling establishment. The higher open areas did not benefit from inundation and were captured by disturbance-associated forbs and shrubs rather than trees. Elevation differences appeared to be especially important for species of concern such as the dickcissel, Kentucky warbler, and field sparrow, which were associated with higher elevation and also green ground cover and deeper litter (Figure 2). These species are all ground nesters and unlikely to be found nesting in low areas subject to frequent floods. In contrast, the herons, wood duck, orchard oriole, Acadian flycatcher, and yellow-breasted chat were associated with wetter conditions. Of these, only the yellow-breasted chat nests low enough to be directly affected by flooding.

The mosaic of habitats at our sites, resulting from differences in elevation and flood potential, created structural and habitat diversity that supported a variety of bird species. The abundance of large dead snags present in the mature forests are especially important to large-bodied cavity nesters, including red-headed woodpeckers, northern flickers, red-bellied woodpeckers (*Melanerpes carolinus*), and pileated woodpeckers (*Dryocopus pileatus*) (Renken and Wiggers 1993, Conner et al. 1994, Ingold 1994, Knutson et al. 1996, Twedt and Henne-Kerr 2001). The prothonotary warbler also requires cavities for nesting (Petit 1999). Our data may under represent the prothonotary warbler, a species associated with flooded forests, because high water prevented us from surveying some portions of the mature forest stands. The lack of a hardwood component to our mature forests may explain the absence of the cerulean warbler and yellow-throated warbler – species usually detected in floristically diverse floodplain forests (Gabbe et al. 2002). The cerulean warbler is also area-sensitive; these forests may be too small to support this species (Hamel 2000).

The bird assemblages and the associated habitat types we identified provide a model for how the bird assemblages may change during the stages of floodplain forest succession. However, managers may question whether our findings are generally applicable to other large river forests in the central United States. Admittedly, our data set was limited in time and space. Bird abundances can be influenced by climatic conditions (Knutson and Klaas 1997) and abundances can vary from year to year or from one site to another, even if the vegetation appears similar. The general agreement of our data with relative abundance estimates from 1997 at the same sites provides some evidence that annual climatic conditions did not greatly alter the assemblage of species.

The bird species assemblages at our sites were comparable to those observed along the Upper Mississippi River farther north in Iowa, Minnesota, and Wisconsin (Knutson and Klaas 1997) and along the Cache River in Illinois (Knutson et al. 1996). Our observations were also in general agreement with habitat associations and indicator bird species identified by Twedt et al. (1999) to the south in the Mississippi Alluvial Valley, supporting the generality of the associations between bird species and habitat types we identified. The similarities among floodplain bird species assemblages observed over a wide latitudinal range from Louisiana to Minnesota suggest that our findings are generally applicable to large river floodplain forests across the midwestern United States.

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LITERATURE CITED

American Ornithologists' Union. 1998. Check-list of North American birds, 7th ed. American Ornithologists' Union, Washington, D.C.

Best, L.B., K.E. Freemark, J.J. Dinsmore, and M. Camp. 1995. A review and synthesis of habitat use by breeding birds in agricultural landscapes of Iowa. American Midland Naturalist 134:1-29.

Best, L.B., K.E. Freemark, B.S. Steiner, and T.M. Bergin. 1996. Life history and status classifications of birds breeding in Iowa. Journal of the Iowa Academy of Science 103:34-45.

Clarke, K.R., and R.M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratories, Plymouth, U.K.

Conner, R.N., S.D. Jones, and G.D. Jones. 1994. Snag condition and woodpecker foraging ecology in a bottomland hardwood forest. Wilson Bulletin 106:242-257.

Dixon, M.D., M.G. Turner, and C.F. Jin. 2002. Riparian tree seedling distribution on Wisconsin River sandbars: controls at different spatial scales. Ecological Monographs 72:465-485.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345-366.

Faber-Langendoen, D. (ed.). 2001. Plant communities of the Midwest: classification in an ecological context. Association for Biodiversity Information, Arlington, Va. Available online <http://www.natureserve.org/publications/plantCommunitiesmidwest.jsp>.

Gabbe, A.P., S.K. Robinson, and J.D. Brawn. 2002. Tree-species preferences of foraging insectivorous birds: implications for floodplain forest restoration. Conservation Biology 16:462-470.

Hamel, P.B. 2000. Cerulean Warbler (*Dendroica cerulea*). Pp. 1-20 *in* A. Poole and F. Gill, eds., The Birds of North America No. 511. Academy of Natural Sciences, Philadelphia, Pa.

Hughes, F.M.R., W.M. Adams, E. Muller, C. Nilsson, K.S. Richards, N. Barsoum, H. Decamps, R. Foussadier, J. Girel, H. Guilloy, A. Hayes, M. Johansson, L. Lambs, G. Pautou, J.L. Peiry, M. Perrow, F. Vautier, and M. Winfield. 2001. The importance of different scale processes for the restoration of floodplain woodlands. Regulated Rivers: Research & Management 17:325-345.

Ingold, D.J. 1994. Nest-site characteristics of Red-bellied and Red-headed Woodpeckers and Northern Flickers in east-central Ohio. Ohio Journal of Science 94:2-7.

Johnson, W.C. 2002. Riparian vegetation diversity along regulated rivers: contribution of novel and relict habitats. Freshwater Biology 47:749-759.

Jongman, R.H.G., C.J.F. Ter Braak, and O.F.R. Van Tongeren. 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge, U.K.

Knutson, M.G., J.P. Hoover, and E.E. Klaas. 1996. The importance of floodplain forests in the conservation and management of neotropical migratory birds in the Midwest. Pp. 168-188 *in* F.R. Thompson, ed., Management of Midwestern landscapes for the conservation of neotropical migratory birds. General Technical Report NC-187. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn.

Knutson, M.G., and E.E. Klaas. 1997. Declines in abundance and species richness of birds following a major flood on the Upper Mississippi River. Auk 114:367-380.

Knutson, M.G., and E.E. Klaas. 1998. Floodplain forest loss and changes in forest community composition and structure in the Upper Mississippi River: a wildlife habitat at risk. Natural Areas Journal 18:138-150.

Legendre, P., and L. Legendre. 1998. Numerical Ecology, 2nd English ed. Elsevier, New York.

Martin, T.E., and G.R Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507-519.

Martin, T.E., C.R. Paine, C.J. Conway, W.M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD field protocol. Montana Cooperative Fish and Wildlife Research Unit, University of Montana, Missoula.

McCune, B., J.B. Grace, and D.L. Urban. 2002. Analysis of ecological communities. MJM Software Design, Glenenden Beach, Ore.

McCune, B., and M.J. Mefford. 1999. Multivariate analysis of ecological data, Version 4. MJM Software Design, Glenenden Beach, Ore.

Noss, R.F., E.T. LaRoe, III, and J.M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biological Report 28, U.S. Department of the Interior, National Biological Service, Washington, D.C.

Petit, L.J. 1999. Prothonotary Warbler (*Protonotaria citrea*). Pp. 1-24 *in* A. Poole and F. Gill, eds., The Birds of North America No. 408. Academy of Natural Sciences, Philadelphia, Pa.

Ralph, C.J., S. Droege, and J.R. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications. Pp. 161-175 *in* C.J. Ralph, S. Droege, and J.R. Sauer, eds., Monitoring bird populations by point counts. Pacific Southwest Research Station, Albany, Calif.

Renken, R.B., and E.P. Wiggers. 1993. Habitat characteristics related to Pileated Woodpecker densities in Missouri. Wilson Bulletin 105:77-83.

Rich, T.D., C.J. Beardmore, H. Berlanga, P.J. Blancher, M.S. Bradstreet, G.S. Butcher, D. Demarest, E.H. Dunn, W.C. Hunter, D. Inigo-Elias, J.A. Kennedy, A. Martell, A. Panjabi, D.N. Pashley, K.V. Rosenberg, C. Rustay, S. Wendt, and T. Will. 2004. Partners in Flight, North American landbird conservation plan. Cornell Lab of Ornithology, Ithaca, N.Y.

Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications 9:135-151.

Sanders, T.A., and W.D. Edge. 1998. Breeding bird community composition in relation to riparian vegetation structure in the western United States. Journal of Wildlife Management 62:461-473.

Scott, M.L., S.K. Skagen, and M.F. Merigliano. 2003. Relating geomorphic change and grazing to avian communities in riparian forests. Conservation Biology 17:284-296.

Skagen, S.K., C.P. Melcher, W.H. Howe, and F.L. Knopf. 1998. Comparative use of riparian corridors and grasses by migrating birds in southeast Arizona. Conservation Biology 12:896-909.

Smith, E.P., and I.A. Lipkovich. 1999. Biplot macro. Statistics Department of Virginia Tech, Blacksburg, Va. Available online <http://www.stat.vt.edu/facstaff/epsmith.html>.

Ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179.

Ter Braak, C.J.F., and P. Smilauer. 1997. CANOCO for Windows, Version 4.5. Biometris - Plant Research International, Wageningen, The Netherlands.

Ter Braak, C.J.F., and P. Smilauer. 1998. CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination, Version 4. Microcomputer Power, Ithaca, N.Y.

Thompson, F.R., III, and R.M. DeGraaf. 2001. Conservation approaches for woody, early successional communities in the eastern United States. Wildlife Society Bulletin 29:483-494.

Tockner, K., and J.A. Stanford. 2002. Riverine flood plains: present state and future trends. Environmental Conservation 29:308-330.

Twedt, D.J., and J.L. Henne-Kerr. 2001. Artificial cavities enhance breeding bird densities in managed cottonwood forests. Wildlife Society Bulletin 29:680-687.

Twedt, D.J., and J. Portwood. 1997. Bottomland hardwood reforestation for neotropical migratory birds: are we missing the forest for the trees? Wildlife Society Bulletin 25:647-652.

Twedt, D. J., R.R. Wilson, J.L. Henne-Kerr, and R.B. Hamilton. 1999. Impact of forest type and management strategy on avian densities in the Mississippi Alluvial Valley, USA. Forest Ecology and Management 123:261-274.

U.S. Fish and Wildlife Service. 2002a. Birds of Conservation Concern. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, Va.

U.S. Fish and Wildlife Service. 2002b. Fish and Wildlife Resource Conservation Priorities, Region 3, Version 2. U.S. Fish and Wildlife Service, Region 3, Fort Snelling, Minn. Available online <http://midwest.fws.gov/pdf/priority.pdf> (27 October 2003).

Urich, R., G. Swenson, and E. Nelson (eds.), 2002. Upper Mississippi River and Illinois River floodplain forests. Upper Mississippi River Conservation Committee, Rock Island, Ill.

Yin, Y. 1998. Flooding and forest succession in a modified stretch along the Upper Mississippi River. Regulated Rivers: Research and Management 14:217-225.

Yin, Y. 1999. Floodplain forests. Pp. 9-1 to 9-9 *in* K. Lubinski and C. H. Theiling, eds., Ecological status and trends of the Upper Mississippi River System 1998: a report of the Long Term Resource Monitoring Program. U.S. Geological Survey, La Crosse, Wis.

Yin, Y., J.C. Nelson, and K.S. Lubinski. 1997. Bottomland hardwood forests along the Upper Mississippi River. Natural Areas Journal 17:164-173.

Zar, J.H. 1984. Biostatistical Analysis, 2nd ed. Prentice Hall, Englewood Cliffs, N.J.

APPENDIX A

Guidelines for interpretation of ordination plots.

The general structure of an ordination plot includes points designating species, vectors representing environmental variables, and ordination axes (Figure A). Points designating sampling locations can also be displayed but are not shown in the example below. The following is a brief set of general rules for interpreting ordination plots.

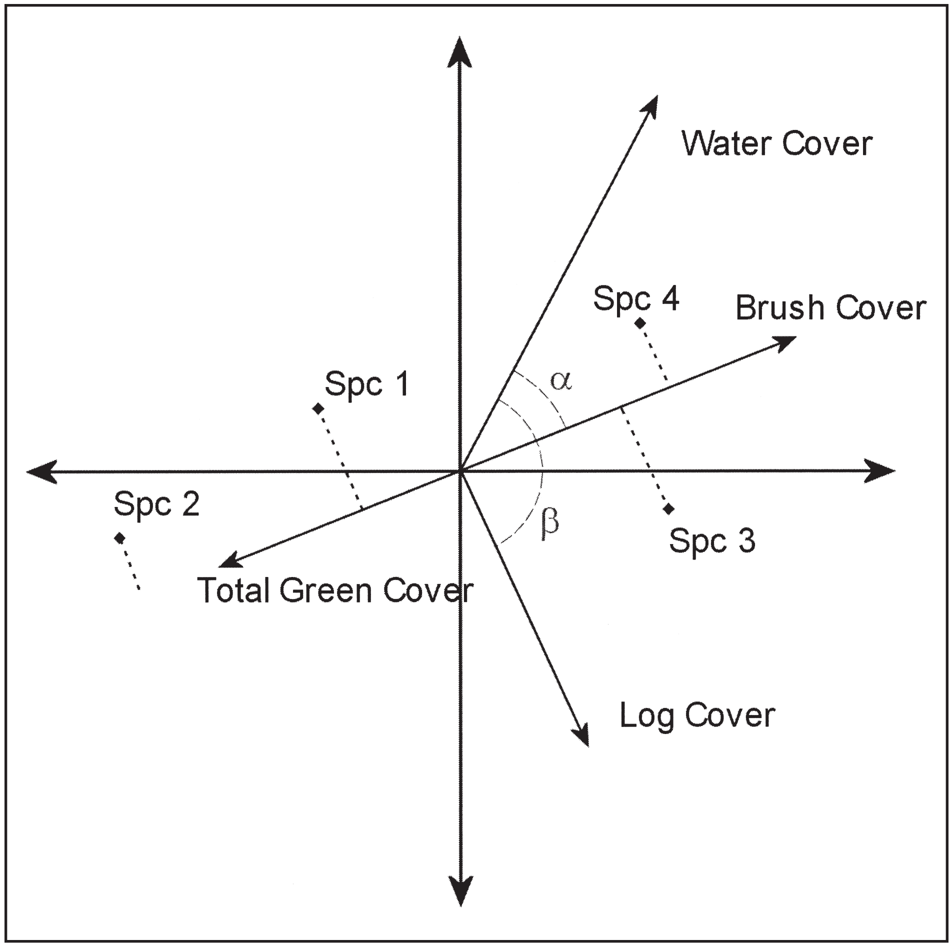

Figure A. Hypothetical ordination plot demonstrating relationships between species, environmental factors, and ordination axes.

1) The longer the vector corresponding to environmental variables, the more variation in this variable is associated with the species composition of this community.

    i) Example: Variation in Water Cover has the strongest association with the species composition of this community, followed by Brush Cover.

2) The angle between two environmental vectors represents the correlation between them.

    a) Two vectors (environmental variables) have a strong positive correlation when the angle between them is small.

        i) Example: Water Cover has a stronger positive correlation with Brush Cover, than with Log Cover (angle α is smaller than angle β, Log Cover has a negative correlation with Water Cover).

    b) Perpendicular vectors are uncorrelated (r = 0).

        i) Example: Log Cover and Brush Cover are not correlated.

    c) Two vectors have a strong negative correlation when the angle between them is near 180° (parallel but in opposite directions).

        i) Example: Brush Cover and Total Green Cover have a strong negative correlation.

3) The angle between an environmental vector and an ordination axis represents the correlation between them, as described above.

4) The distance between two points (species or sample) is proportional to the dissimilarity between the two entities (McCune and Grace 2002).

    i) Example: Species 2 is more similar to Species 1 than Species 3.

5) A perpendicular line between a point (species or sample) and a vector (environmental variable) shows the relative association between the species and the environmental variable for each point.

    i) Species 4 is associated with higher proportions of brush cover than the other species. Species 2 is associated with lower proportions of brush cover. The reverse is true for Total Green Cover.

APPENDIX B

Relative abundances (SE) of bird species per survey point (0.8 ha) and P-values < 0.05 for differences in relative abundances among shrub/scrub, young forest, and mature forest habitats at Harlow and Wilkinson Islands, Mark Twain National Wildlife Refuge, 2001. P-values > 0.05 are not reported. Data from 1997 are given for comparison; species are listed in taxonomic order. Bird species names follow the Check-list of North American Birds, 7th ed. (American Ornithologists' Union 1998).

Species	Species Code	1997 Forest and old field[a] (n =50)	2001 Shrub/ Scrub (n =20)	2001 Young forest (n =20)	2001 Mature Forest (n =20)	2001 P -value[b]
Great Blue Heron *Ardea herodias*	GTBH	0.9	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	
Green Heron *Butorides virescens*	GRHE	0.04	0.1 (0.1)	0.1 (0.1)	0	
Wood Duck [c] *Aix sponsa*	WODU	0.1	0.2 (0.2)	0	0	
Red-tailed Hawk *Buteo jamaicensis*	RTHA	0.1	0	0	0	
American Kestrel *Falco sparverius*	AMKE	0.02	0	0	0	
Wild Turkey *Meleagris gallopavo*	WITU	0	0	0	0.1 (0.1)	
Northern Bobwhite *Colinus virginianus*	NOBO	0.04	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	
Killdeer *Charadrius vociferus*	KILL	0.1	0.1 (0.1)	0	0.1 (0.1)	
Mourning Dove *Zenaida macroura*	MODO	0.1	0.1 (0.1)	0.1 (0.1)	0.3 (0.1)	
Black-billed Cuckoo [c] *Coccyzus erythropthalmus*	BBCU	0.02	0	0	0	
Yellow-billed Cuckoo *Coccyzus americanus*	YBCU	0.1	0.2 (0.1)	0.8 (0.2)	0.5 (0.1)	0.01
Belted Kingfisher *Ceryle alcyon*	BEKI	0.02	0	0	0	
Red-headed Woodpecker [c] *Melanerpes erythrocephalus*	RHWO	0.5	0.1 (0.1)	0.1 (0.1)	0.3 (0.2)	
Red-bellied Woodpecker *Melanerpes carolinus*	RBWO	0.2	0.1 (0.1)	0.1 (0.1)	0.3 (0.1)	
Downy Woodpecker *Picoides pubescens*	DOWO	0.1	0.2 (0.1)	0.4 (0.1)	0.7 (0.1)	0.01
Northern Flicker [c] *Colaptes auratus*	NOFL	0	0.1 (0.1)	0	0.6 (0.2)	0.001

continued

Species	Species Code	1997 Forest and old field[a] (*n* =50)	2001 Shrub/ Scrub (*n* =20)	2001 Young forest (*n* =20)	2001 Mature Forest (*n* =20)	2001 *P* -value[b]
continued						
Pileated Woodpecker *Dryocopus pileatus*	PIWO	0.1	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	
Eastern Wood-Pewee *Contopus virens*	EAWP	0.3	0.1 (0.1)	0	0.7 (0.2)	<0.001
Acadian Flycatcher [c] *Empidonax virescens*	ACFL	0	0	0	0.2 (0.1)	
Willow Flycatcher *Empidonax traillii*	WIFL	0	0.2 (0.1)	0.1 (0.1)	0	
Great Crested Flycatcher *Myiarchus crinitus*	GCFL	0.4	0	0	0.3 (0.1)	0.005
Eastern Phoebe *Sayornis phoebe*	EAPH	0.2	0.1 (0.1)	0	0.1 (0.1)	
White-eyed Vireo *Vireo griseus*	WEVI	0.1	0.2 (0.1)	0.1 (0.2)	0.6 (0.2)	0.01
Warbling Vireo *Vireo gilvus*	WAVI	0.1	0.1 (0.1)	0.8 (0.2)	0.5 (0.2)	0.02
Red-eyed Vireo *Vireo olivaceus*	REVI	0.2	0.1 (0.1)	0.4 (0.2)	0.7 (0.2)	0.01
Blue Jay *Cyanocitta cristata*	BLJA	0.1	0.2 (0.1)	0.3 (0.1)	0.6 (0.2)	
American Crow *Corvus brachyrhynchos*	AMCR	0.1	0	0	0.1 (0.1)	
Fish Crow *Corvus ossifragus*	FICR	0.04	0.1 (0.1)	0	0.1 (0.1)	
Tree Swallow *Tachycineta bicolor*	TRSW	0.04	0.1 (0.1)	0	0.2 (0.2)	

continued

[a]Numbers and relative abundances of bird species per 0.8 ha (50-m radius circle), Harlow and Wilkinson Island survey data, U. S. Fish and Wildlife Service, Mark Twain National Wildlife Refuge Complex, 1997. Ten-minute point counts conducted in June 1997; 16 points were in forest and 2 points in old field (grassland/fallow field) habitats (*n* =18) at Harlow Island, 27 points were in forest and 5 points in old field habitats (*n* =32) at Wilkinson Island (Karen Westphall, unpubl. data).

[b]*P* -values given for relative abundances that differ among habitat types in 2001 survey (Kruskal-Wallis test, $P < 0.05$); statistically non-significant *P* -values are not reported. If two habitats have 0 values, *P* -values are not reported.

[c]Resource Conservation Priority species in U. S. Fish and Wildlife Service Region 3 (U.S. Fish and Wildlife Service 2002b).

Relative abundances (SE) of bird species per survey point (0.8 ha) and P-values < 0.05 for differences in relative abundances among shrub/scrub, young forest, and mature forest habitats at Harlow and Wilkinson Islands, Mark Twain National Wildlife Refuge, 2001. P-values > 0.05 are not reported. Data from 1997 are given for comparison; species are listed in taxonomic order. Bird species names follow the Check-list of North American Birds, 7th ed. (American Ornithologists' Union 1998).

Species	Species Code	1997 Forest and old field[a] (n =50)	2001 Shrub/ Scrub (n =20)	2001 Young forest (n =20)	2001 Mature Forest (n =20)	2001 P -value[b]
continued						
Barn Swallow *Hirundo rustica*	BASW	0.02	0	0	0	
Carolina Chickadee *Poecile carolinensis*	CACH	0.1	0.2 (0.1)	0.7 (0.2)	0.7 (0.2)	0.04
Tufted Titmouse *Baeolophus bicolor*	TUTI	0.1	0.1 (0.1)	0.2 (0.1)	0.8 (0.2)	0.003
White-breasted Nuthatch *Sitta carolinensis*	WBNU	0.1	0	0	0.4 (0.2)	
Carolina Wren *Thryothorus ludovicianus*	CAWR	0.1	0	0.1 (0.1)	0	
House Wren *Troglodytes aedon*	HOWR	0.6	0.1 (0.1)	0.1 (0.1)	0.6 (0.2)	0.008
Blue-gray Gnatcatcher *Polioptila caerulea*	BGGN	0.1	0	0.1 (0.1)	0.5 (0.2)	0.007
Wood Thrush [c] *Hylocichla mustelina*	WOTH	0	0	0	0.1 (0.1)	
American Robin *Turdus migratorius*	AMRO	0	0	0	0.2 (0.1)	
Gray Catbird *Dumetella carolinensis*	GRCA	0.2	0	0.2 (0.1)	0.9 (0.2)	<0.001
Brown Thrasher *Toxostoma rufum*	BRTH	0	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	
European Starling *Sturnus vulgaris*	EUST	0.1	0	0	0	
Northern Parula *Parula americana*	NOPA	0	0.1 (0.1)	0	0.1 (0.1)	
Cerulean Warbler [c] *Dendroica cerulea*	CERW	0.1	0	0	0	
American Redstart *Setophaga ruticilla*	AMRE	0	0	0	0.1 (0.1)	
Prothonotary Warbler [c] *Protonotaria citrea*	PROW	0.4	0	0.1 (0.1)	0.3 (0.1)	

continued

Species	Species Code	1997 Forest and old field[a] (n =50)	2001 Shrub/ Scrub (n =20)	2001 Young forest (n =20)	2001 Mature Forest (n =20)	2001 P -value[b]
continued						
Kentucky Warbler [c] *Oporornis formosus*	KEWA	0.1	0	0	0.1 (0.1)	
Common Yellowthroat *Geothlypis trichas*	COYE	1	2.5 (0.3)	0.5 (0.2)	0.3 (0.1)	<0.001
Yellow-breasted Chat *Icteria virens*	YBCH	0.1	0.7 (0.2)	0.1 (0.1)	0	<0.001
Eastern Towhee *Pipilo erythrophthalmus*	EATO	0	0.2 (0.1)	0.1 (0.1)	0.2 (0.1)	
Field Sparrow [c] *Spizella pusilla*	FISP	0.02	0	0.1 (0.1)	0	
Song Sparrow *Melospiza melodia*	SOSP	0.6	0.5 (0.1)	0.1 (0.1)	0.1 (0.1)	0.003
Northern Cardinal *Cardinalis cardinalis*	NOCA	0.1	0.4 (0.2)	0.4 (0.1)	1.1 (0.2)	0.03
Rose-breasted Grosbeak *Pheucticus ludovicianus*	RBGR	0	0	0	0.1 (0.1)	
Indigo Bunting *Passerina cyanea*	INBU	1.7	3.6 (0.4)	2.7 (0.3)	2.3 (0.2)	0.01
Dickcissel [c] *Spiza americana*	DICK	0.4	0.3 (0.2)	0	0	
Red-winged Blackbird *Agelaius phoeniceus*	RWBB	1.2	3.7 (0.4)	4.7 (2.2)	0.8 (0.3)	<0.001
Eastern Meadowlark [c] *Sturnella magna*	EAME	0.02	0	0	0	
Common Grackle *Quiscalus quiscula*	COGR	0.4	0	2.2 (2.1)	0.2 (0.1)	

continued

[a]Numbers and relative abundances of bird species per 0.8 ha (50-m radius circle), Harlow and Wilkinson Island survey data, U. S. Fish and Wildlife Service, Mark Twain National Wildlife Refuge Complex, 1997. Ten-minute point counts conducted in June 1997; 16 points were in forest and 2 points in old field (grassland/fallow field) habitats (n =18) at Harlow Island, 27 points were in forest and 5 points in old field habitats (n =32) at Wilkinson Island (Karen Westphall, unpubl. data).

[b]P -values given for relative abundances that differ among habitat types in 2001 survey (Kruskal-Wallis test, P < 0.05); statistically non-significant P -values are not reported. If two habitats have 0 values, P -values are not reported.

[c]Resource Conservation Priority species in U. S. Fish and Wildlife Service Region 3 (U.S. Fish and Wildlife Service 2002b).

Relative abundances (SE) of bird species per survey point (0.8 ha) and P-values < 0.05 for differences in relative abundances among shrub/scrub, young forest, and mature forest habitats at Harlow and Wilkinson Islands, Mark Twain National Wildlife Refuge, 2001. P-values > 0.05 are not reported. Data from 1997 are given for comparison; species are listed in taxonomic order. Bird species names follow the Check-list of North American Birds, 7th ed. (American Ornithologists' Union 1998).

Species	Species Code	1997 Forest and old field[a] (n =50)	2001 Shrub/ Scrub (n =20)	2001 Young forest (n =20)	2001 Mature Forest (n =20)	2001 P-value[b]
continued						
Brown-headed Cowbird *Molothrus ater*	BHCO	0.1	0.1 (0.1)	0.2 (0.1)	0.6 (0.2)	0.05
Orchard Oriole [c] *Icterus spurius*	OROR	0.1	0.5 (0.2)	0.6 (0.2)	0	0.01
Baltimore Oriole *Icterus galbula*	BAOR	0.4	0.1 (0.1)	0.5 (0.2)	0.6 (0.1)	0.03
American Goldfinch *Carduelis tristis*	AMGO	0.1	0.6 (0.2)	0	0.4 (0.2)	0.009

[a]Numbers and relative abundances of bird species per 0.8 ha (50-m radius circle), Harlow and Wilkinson Island survey data, U. S. Fish and Wildlife Service, Mark Twain National Wildlife Refuge Complex, 1997. Ten-minute point counts conducted in June 1997; 16 points were in forest and 2 points in old field (grassland/fallow field) habitats (n =18) at Harlow Island, 27 points were in forest and 5 points in old field habitats (n =32) at Wilkinson Island (Karen Westphall, unpubl. data).

[b]P-values given for relative abundances that differ among habitat types in 2001 survey (Kruskal-Wallis test, $P < 0.05$); statistically non-significant P-values are not reported. If two habitats have 0 values, P-values are not reported.

[c]Resource Conservation Priority species in U. S. Fish and Wildlife Service Region 3 (U.S. Fish and Wildlife Service 2002b).