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Avian Habitat Use in a Chronosequence of Bottomland Hardwood Forest Restoration Sites

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Abstract - Since the 1950s, anthropogenic activity has caused the loss of millions of hectares of bottomland hardwood forest in the Upper Mississippi River Valley, causing population declines in bird populations. Restoration of these forest stands has been ongoing for the past 2 decades. We assessed bird species presence on sites in the Upper Mississippi River Valley to quantify diversity and relate presence to habitat conditions and sites' age since restoration. We observed higher mean diversities at mature bottomland-forest sites during the spring and autumn, but nested ANOVAs indicated no significant differences among restoration-age categories during spring. During the autumn, the 15–23-y and the mature bottomland-forest categories were significantly different from the <7-y category. Predictive habitat models differed among species, but presence of forest-dwelling birds was positively related to forested conditions, such as tree height and tree density. Overall, our analyses show that a variety of birds use these sites, and we suggest further exploration of how assemblages may change in future surveys.

Introduction

The Upper Mississippi River Valley (UMR) represents a dynamic region in which species diversity and ecosystem function rely heavily on regular flood pulses (Knutson et al. 1996, Romano 2010, Sparks 2010). Many resident and migratory species in this area depend on these annual flood regimes to provide ecosystem services, such as food, habitat, recruitment, and connectivity (Garvey et al. 2010, Romano 2010, Twedt and Loesch 1999). Historically, bottomland hardwood forests dominated the landcover and were represented by millions of hectares of contiguous floodplains. However, there has been significant forest-habitat loss in the UMR attributed to: (1) the development of locks and dams for commercial navigation, which altered the flood regime; and (2) the conversion of bottomland hardwood forests to agriculture and (sub)urbanized areas, which fragmented the historically contiguous landscape (Kirsch et al. 2013, Twedt and Loesch 1999). This fragmentation inhibited vital ecosystem services such as water enhancement and nutrient cycling (King and Keeland 1999). Additionally, historical spring floods typically receded by mid-May, but the systems of locks and dams increased the intensity of flooding in many areas (Knutson and Klaas 1997).

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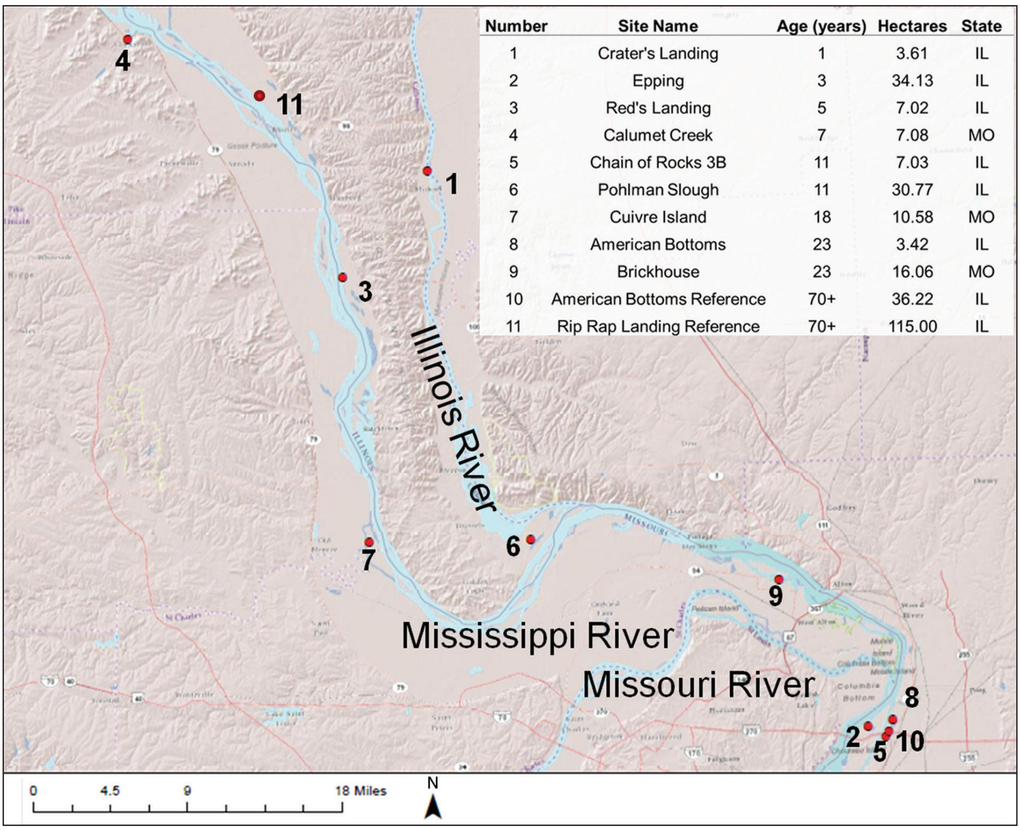
Surveys within the UMR found that floodplain forests provide habitat for ~290 species of birds (Nelson and Wlosinski 1999). Millions of birds annually use these habitats for breeding, migrating, and overwintering. Presently, trends from 1966–2015 show that >33% of UMR birds have experienced population declines due to habitat loss and fragmentation in bottomland forests in the UMR (King et al. 2006, Robinson et al. 1995, Sauer et al. 2017). Some species of conservation concern, such as *Coccyzus erythropthalmus* (Wilson) (Black-billed Cuckoo) and *Setophaga cerulea* (Wilson) (Cerulean Warbler) preferentially use the UMR as a migratory corridor (Kirsch et al. 2013, Knutson et al. 1999, Thompson et al. 2012). As such, some land areas, such as Two Rivers National Wildlife Refuge and Riverlands Migratory Bird Sanctuary, have been designated as Globally Important Bird Areas to facilitate protection of bird species (Jensen 2007, Knutson et al. 1999, Wells et al. 2005).

To create more suitable habitat for species that utilize the UMR, over the past 2 decades, the US Army Corps of Engineers (USACE) has aided in the restoration of bottomland hardwood forests in the area, which includes ~1.2 million ha (~3 million ac) of floodplain forests (Sparks 2010, Theiling et al. 2015, Twedt and Portwood 1997). Historically, bottomland hardwood forests were primarily a mixture of *Quercus* (oak), *Ulmus* (elm), and *Acer* (maple), which are late-successional species (Hanberry et al. 2012, Romano 2006). Therefore, restorations have included planting of root-production method (RPM) seedlings with highly developed root systems, which increase their survival and initial vertical growth (Dey et al. 2004).

Restoration efforts in the lower Mississippi River Valley have been well described (Hamel 2003; Twedt et al. 2002, 2008). However, restoration sites in the UMR have not received as much research attention, and little is known regarding species composition of the avian assemblages that utilize these areas. This information is critical for informing conservation and management strategies for bird species that have historically used the UMR. We offer one of the first exploratory studies to survey restoration sites in the UMR, the results of which provide new information useful to the conservation and management mission of wildlife refuges and the USACE along the Mississippi Flyway. Our objectives were to (1) quantify species diversity of avian assemblages that were present during spring and autumn, and (2) model bird species presence as a function of habitat conditions. We formulated 2 hypotheses based on our objectives. (1) We expected species diversity to peak in sites that were 15–23 years since restoration. Previous studies have shown that there is higher bird diversity at open woodland sites when compared to grassland and forest sites (Au et al. 2008, Brawn 2006, Davis et al. 2000). This hypothesis also corresponds to the intermediate disturbance hypothesis, which states that there is likely to be greater diversity due to more habitat heterogeneity in habitats with regular disturbances (Connell 1978, Roxburgh et al. 2004). (2) We expected habitat models to generally show that birds associate with vegetation variables present at the sites where they are traditionally present. For example, that there would be a higher likelihood of detecting a Cerulean Warbler at mature bottomland forest sites than at younger, open-woodland sites (Kirsch et al. 2013).

Field Site Description

We surveyed 9 bottomland hardwood-forest restoration sites (1–23 years since restoration) in Illinois and Missouri, located near either the Illinois or Mississippi Rivers (Fig. 1). Four sites (Epping, Chain of Rocks, Earth Day Patch, and American Bottoms) are within the St. Louis metropolitan area and border suburban communities. We selected only sites that were ≥3 ha and planted with RPM seedlings of native oak species. In addition, we surveyed 2 mature (>70 y old) bottomland hardwood-forest sites (American Bottoms and Rip Rap Landing) as references. We collected avian and vegetation data from 5 plots at each site. We used ArcGIS Desktop 10 (ESRI 2010) to randomly select plots with the constraint that points were at least 50-m apart to reduce sampling overlap and, to limit edge effects, could not be within a 30-m buffer zone. All plots were at least 150 m apart in our final plot selection. The Rip Rap Landing site plots were derived from pre-established plots from an earlier study. Following plot selection, we used a GPS receiver (Garmin GPSMAP 62S, Model 010-00868-01, Olathe, KS) to record the locations of sample plots. We marked each plot with a 1.83-m steel t-post.



Number	Site Name	Age (years)	Hectares	State
1	Crater's Landing	1	3.61	IL
2	Epping	3	34.13	IL
3	Red's Landing	5	7.02	IL
4	Calumet Creek	7	7.08	MO
5	Chain of Rocks 3B	11	7.03	IL
6	Pohlman Slough	11	30.77	IL
7	Cuivre Island	18	10.58	MO
8	American Bottoms	23	3.42	IL
9	Brickhouse	23	16.06	MO
10	American Bottoms Reference	70+	36.22	IL
11	Rip Rap Landing Reference	70+	115.00	IL

Figure 1. We chose 9 restoration sites and 2 mature bottomland-forest reference sites for data collection. All sites border along either the Illinois or Mississippi Rivers. Rip Rap Landing covers a large area and includes varying ages of succession. The USACE estimated that ~115 ha at that site is mature bottomland hardwood forest.

Methods

Avian point-count surveys

We used 25-m fixed-radius point-count surveys to survey birds during spring and autumn over 3 sampling periods: 1 May–30 June 2013 (spring), 1 September–31 October 2013 (autumn), and 10 May–30 June 2014 (spring) (Hutto et al. 1986). Due to excessive flooding during spring 2013 and 2014, we could access only 8 of the 11 sites for spring surveys. We visited all plots 3 times during each season to account for variation in arrival timing for different species and because we wanted to survey a variety of species. We conducted bird surveys between 0600 h and 1000 h for a 10-min duration after a 5-min acclimation period. We determined the 25-m boundary using a laser rangefinder (Nikon ProStaff 550, Model 8369, Melville, NY), to prevent sampling outside of the fixed radius (Richter et al. 2010). We avoided surveying birds during inclement weather, such as fog, rain, or high winds.

Vegetation surveys

We surveyed non-woody vegetation 15 May–1 September 2013 and woody vegetation 15 September–15 November 2013 and in early March 2014 during a single sample visit (Table 1). We created 17.84-m–radius vegetation plots within the 25-m–radius bird-survey plots, (Fig. 2). In the vegetation plots, we recorded tree species, crown density, diameter at breast height (DBH), and abundance for trees that were at least 5 cm in diameter at a height of 1.4 m up from the base of the trunk. We calculated tree dominance by totaling the cross-sectional area of all trees and estimating the total area in which trees occurred per hectare.

Within vegetation plots, we surveyed the shrub and ground vegetation of 4 belts in which we recorded the number of shrub stems that were ≥1 m in height (Fig. 2). We recorded forb and grass data, vegetation height, and litter depth in five 0.5-m^2 quadrats along the belt. We placed the first quadrat 1 m away from the center and

Table 1. We included 12 geographic and vegetation variables in predictive habitat models. We chose them based on parameters that were presumed to be important to a species' presence or absence. * denotes variables with curvilinear relationships with bird species presence, the values of which were squared in the models.

Variable	Description of variable	Measurement format
Landsize	Area of site	Continuous (m^2)
DistEdge*	Distance to edge	Continuous (m)
DistRiver	Distance to nearest river or canal	Continuous (m)
GroundCover*	Ground layer cover	Categorical (midpoint percentage)
DBH	Diameter at breast height (90^{th} percentile)	Continuous (cm)
TreeHeight	Height of tree (90^{th} percentile)	Continuous (m)
LitterDepth	Litter depth	Continuous (cm)
HerbHeight*	Average maximum grass/forb height	Continuous (m)
ShrubHeight*	Average maximum shrub height	Continuous (m)
CrownDensity	Average tree-crown density	Categorical (1 [lowest]–9 [highest])
TreeDom	Tree dominance	Continuous (m^2/ha)
ShrubDensity	Shrub density	Continuous (stems/ha)

spaced subsequent quadrats 3-m apart (Fig. 2). We used general percent-cover estimates for the quadrats using Braun-Blanquet classes (Van Der Maarel 1975).

Data analyses

Following the guidelines set in a previous study in bottomland-hardwood forests, we divided sites into 4 age categories based on vegetative characteristics: <7 years since restoration (grassland-like), 7–14 years since restoration (shrubland-like), 15–23 years since restoration (open woodland-like), and mature bottomland-forest reference sites (forest-like) (Wilson and Twedt 2005). We utilized these categories to identify trends in diversity and apparent frequencies of occurrence for bird species through nested ANOVA measures.

For each plot, we calculated diversity with the following diversity indices:

$$\text{antilog Shannon's} = e(\sum_{i=1}^{R} p_i ln p_i)$$

$$\text{inverse Simpson's} = 1 / (\sum_{i=1}^{R} p_i^2)$$

We chose to calculate the antilog Shannon's and inverse Simpson's diversity indices to facilitate interpretation; if all species had the same number of individuals, diversity would equal richness (Möckel et al. 2016, Pizzio et al. 2016). We performed nested ANOVAs and Tukey–Kramer comparison tests on diversity data to determine differences in diversity as a function of restoration-age category in NCSS 2007 statistical software (Hintze 2007; NCSS, LLC, Kaysville, UT). Survey plots were nested within sites, which were nested within age categories.

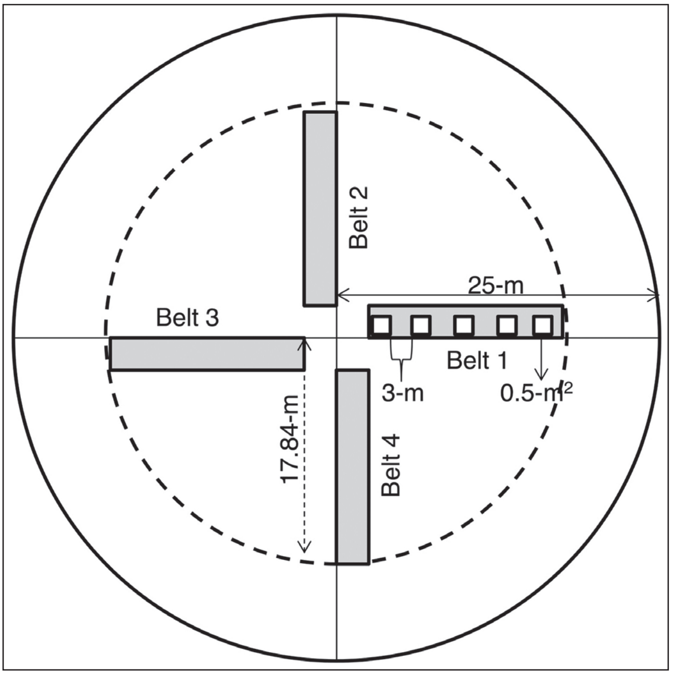


Figure 2. Sample design of the avian and vegetation plots. The outermost circle represents the area in which avian point-count surveys were conducted. We included in statistical analyses all birds seen within the 25-m radius. The inner dotted circle represents the area in which vegetation surveys occurred. We tagged and identified all trees within the 17.84-m radius. We collected shrub data within the belts and forb and vegetation-cover data within each quadrat.

We used logistic regression to create predictive habitat-models, and interpreted the models' ability to effectively estimate selection probabilities (Keating and Cherry 2004). We generated separate models for spring and autumn survey periods. We chose logistic regression because we developed presence/absence models, which employ vegetation and landsize variables to estimate the probability of a species utilizing an area. We considered presence/absence modeling to be the most appropriate because many of the birds surveyed were short-term migrants occupying areas for only short periods, making it challenging to estimate abundances. We squared variables that had a curvilinear relationship with species presence in anticipation that influential variables might not be a predicted indicator due to a lack of a linear response (Austin 2007). We modeled birds that were present in at least 5 of 55 plots within our sites. We present birds with at least 1 significant indicator from their best model.

We did not propose or run a priori candidate models because of the number of species we surveyed and the lack of detailed descriptions for some bird species. We used SAS 9.3 (SAS Institute, Cary NC) to write a predictive-model logistic procedure to produce all possible models using a combination of all variables for each species in. All of our models reported Akaike information criterion (AIC) values, which represent the quality of a model based on a particular set of variables (Akaike 1974). We recorded the best model for each species, represented by the lowest AIC, and we standardized all associated variables in the best-fitting model by calculating *Z*-scores. We also recorded the apparent frequency of the bird species occurring on a specific plot from the model and performed nested ANOVAs and Tukey–Kramer post hoc tests to compare significant differences in apparent frequencies of occurrence in varying age categories in NCSS 2007 (Hintze 2007).

Results

Species diversity

During the spring 2013 and 2014 field seasons, we observed 65 bird species within 40 sample plots (Table 2). During the autumn 2013 field season, we observed 79 bird species within 55 sample plots (Table 2).

Although we observed higher mean diversities at mature bottomland-forest sites during the spring and autumn, nested ANOVAs indicated no significant differences among restoration-age categories during spring ($F_{3,4}$ = 0.52, P = 0.689 [antilog Shannon's], $F_{3,4}$ = 0.65, P = 0.625 [Simpson's]; Fig. 3a, b). During the autumn, the 15–23-y and the mature bottomland-forest categories were significantly different from the <7-y category ($F_{3,6}$ = 8.18, P = 0.015 [antilog Shannon's], $F_{3,6}$ = 7.96, P = 0.016 [Simpson's]; Fig. 3c, d).

Habitat models

Grassland birds. Spizella pusilla (Wilson) (Field Sparrow) presence during spring was negatively associated with tree height (β = -1.34, P = 0.029), whereas during autumn their presence was associated with distance to the edge of the site (β = 1.13, P = 0.047) and DBH (β = -1.70, P = 0.030) (Table 3).

Table 2. Bird species observed within the 25-m fixed-radius plots during spring (n = 65) and autumn (n = 79). * denotes species seen only in spring, ** denotes species seen only in autumn. [Table continued on following page.]

Order Galliformes
- Family Phasianidae: *Bonasa umbellus* (L.) (Ruffed Grouse)**

Order Columbiformes
- Family Columbidae: *Columba livia* Gmelin (Rock Pigeon)*, *Zenaida macroura* (L.) (Mourning Dove) **

Order Cuculiformes
- Family Cuculidae: *Coccyzus americanus* (L.) (Yellow-billed Cuckoo)**

Order Apodiformes
- Family Apodidae: *Chaetura pelagica* (L.) (Chimney Swift)**
- Family Trochilidae: *Archilochus colubris* (L.) (Ruby-throated Hummingbird)

Order Charadriiformes
- Family Charadriidae: *Charadrius vociferous* L. (Killdeer)**

Order Coraciiformes
- Family Alcedinidae: *Megaceryle alcyon* (L.) (Belted Kingfisher)**

Order Piciformes
- Family Picidae: *Melanerpes erythrocephalus* (L.) (Red-headed Woodpecker), *Melanerpes carolinus* (L.) (Red-bellied Woodpecker), *Sphyrapicus varius* (L.) (Yellow-bellied Sapsucker)**, *Picoides pubescens* (L.) (Downy Woodpecker), *Picoides villosus* (L.) (Hairy Woodpecker), *Colaptes auratus* (L.) (Northern Flicker), *Dryocopus pileatus* (L.) (Pileated Woodpecker)**

Order Passeriformes
- Family Tyrannidae: *Contopus virens* (L.) (Eastern Wood-Pewee), *Empidonax virescens* (Vieillot) (Acadian Flycatcher)**, *Empidonax alnorum* Brewster (Alder Flycatcher)**, *Sayornis phoebe* (Latham) (Eastern Phoebe), *Tyrannus tyrannus* (L.) (Eastern Kingbird)
- Family Laniidae: *Lanius excubitor* Campbell (Northern Shrike)**
- Family Vireonidae: *Vireo bellii* Audubon (Bell's Vireo)**, *Vireo gilvus* Vieillot (Warbling Vireo)**, *Vireo olivaceus* (L.) (Red-eyed Vireo)
- Family Corvidae: *Cyanocitta cristata* (L.) (Blue Jay), *Corvus brachyrhynchos* Brehm (American Crow)
- Family Hirundinidae: *Tachycineta bicolor* (Vieillot) (Tree Swallow), *Riparia riparia* (L.) (Bank Swallow)
- Family Paridae: *Poecile carolinensis* (Audubon) (Carolina Chickadee), *Baeolophus bicolor* L. (Tufted Titmouse)
- Family Sittidae: *Sitta carolinensis* Latham (White-breasted Nuthatch)
- Family Certhiidae: *Certhia americana* Bonaparte (Brown Creeper)**
- Family Troglodytidae: *Thryothorus ludovicianus* (Latham) (Carolina Wren)
- Family Polioptilidae: *Polioptila caerulea* (L.) (Blue-gray Gnatcatcher)**
- Family Turdidae: *Catharus ustulatus* (Tschudi) (Swainson's Thrush), *Hylocichla mustelina* (Gmelin) (Wood Thrush), *Turdus migratorius* L. (American Robin)
- Family Mimidae: *Dumetella carolinensis* (L.) (Gray Catbird)**, *Toxostoma rufum* (L.) (Brown Thrasher), *Mimus polyglottos* (L.) (Northern Mockingbird)
- Family Fringillidae: *Spinus tristis* (L.) (American Goldfinch)
- Family Passerellidae: *Pipilo erythrophthalmus* (L.) (Eastern Towhee), *Spizella passerina* (Bechstein) (Chipping Sparrow), *Spizella pallida* (Clay-colored Sparrow)**, *Spizella pusilla* (Swainson) (Field Sparrow), *Pooecetes gramineus* (Gmelin) (Vesper Sparrow), *Chondestes grammacus* (Say) (Lark Sparrow), *Passerculus sandwichensis* (Gmelin) (Savannah Sparrow), *Ammodramus savannarum* (Gmelin) (Grasshopper Sparrow), *Melospiza melodia* (Wilson) (Song Sparrow), *Melospiza lincolnii* (Audubon) (Lincoln's Sparrow)**, *Junco hyemalis* (L.) (Dark-eyed Junco)**
- Family Icteriidae: *Icteria virens* (L.) (Yellow-breasted Chat)
- Family Icteridae: *Sturnella magna* (L.) (Eastern Meadowlark), *Icterus spurius* (L.) (Orchard Oriole)*, *Icterus galbula* (L.) (Baltimore Oriole)*, *Agelaius phoeniceus* (L.) (Red-winged Blackbird), *Molothrus ater* (Boddaert) (Brown-headed Cowbird), *Euphagus cyanocephalus* (Wagler) (Brewer's Blackbird)

Table 2, continued.

Family Parulidae: *Seiurus aurocapilla* (L.) (Ovenbird)**, *Helmitheros vermivorum* (Gmelin) (Worm-eating Warbler)*, *Parkesia noveboracensis* (Gmelin) (Northern Waterthrush)**, *Vermivora cyanoptera* (L.) (Blue-winged Warbler), *Mniotilta varia* (L.) (Black-and-white Warbler), *Protonotaria citrea* (Boddaert) (Prothonotary Warbler)*, *Oreothlypis peregrina* (Wilson) (Tennessee Warbler), *Oreothlypis celata* (Say) (Orange-crowned Warbler)*, *Geothlypis formosa* (Wilson) (Kentucky Warbler)*, *Geothlypis trichas* (L.) (Common Yellowthroat), *Setophaga ruticilla* (L.) (American Redstart), *Setophaga cerulea* (Wilson) (Cerulean Warbler), *Setophaga americana* (L.) (Northern Parula), *Setophaga fusca* (Muller) (Blackburnian Warbler), *Setophaga striata* (Forster) (Blackpoll Warbler), *Setophaga caerulescens* (Gmelin) (Black-throated Blue Warbler)*, *Setophaga coronata* (L.) (Yellow-rumped Warbler), *Setophaga magnolia* (Wilson) (Magnolia Warbler), *Setophaga petechia* (L.) (Yellow Warbler), *Setophaga discolor* (Vieillot) (Prairie Warbler)*, *Setophaga dominica* (L.) (Yellow-throated Warbler)*, *Cardellina canadensis* (L.) (Canada Warbler)**, *Cardellina pusilla* (Wilson) (Wilson's Warbler)

Family Cardinalidae: *Piranga rubra** (L.) (Summer Tanager), *Piranga olivacea* (Gmelin) (Scarlet Tanager), *Cardinalis cardinalis* (L.) (Northern Cardinal), *Pheucticus ludovicianus* (L.) (Rose-breasted Grosbeak), *Passerina cyanea* (L.) (Indigo Bunting)*

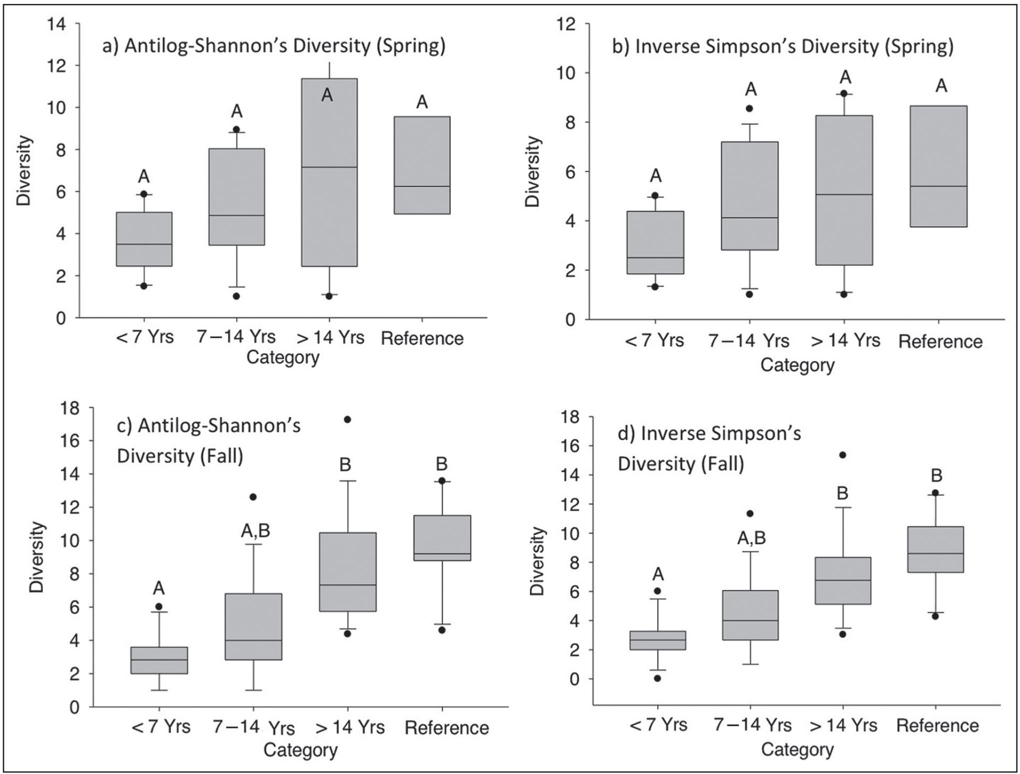


Figure 3. Diversity indices for each restoration category during spring and autumn surveys. Median (bar), 10th (lower error bar), 25th (lower box), 75th (upper box), and 90th (upper error bar) percentiles are included. Outliers are represented with black dots. Points with the same letter represent no significant difference between means, which is based on Tukey–Kramer post hoc tests at $P = 0.05$.

Table 3. The following are the best habitat models for species as determined by the lowest AIC value and regression analyses. Variables that are significant at $P = 0.05$ are designated with (*). All variables have been standardized.

Common Name	Model
Spring	
Grassland Birds	
Field Sparrow	TreeHeight (-1.34*)
Shrubland Birds	
Common Yellowthroat	GroundCover (1.42*) TreeHeight (-2.16) ShrubHeight (-3.64) ShrubDensity (1.51) ShrubHeight2 (1.89)
Red-winged Blackbird	TreeDom (-7.59*)
Open Woodland Birds	
American Goldfinch	DistEdge (4.62*) TreeDom (-2.54) DistEdge^2 (-4.27*) HerbHeight^2 (0.41)
American Robin	CrownDensity (0.96*) TreeDom (1.41) ShrubDensity (0.81*)
Indigo Bunting	DistRiver (-0.94*) GroundCover (0.60*) ShrubDensity (-0.61*) HerbHeight^2 (0.76*)
Northern Cardinal	LitterDepth (1.10*)
Summer Tanager	ShrubDensity (0.46*)
Yellow Warbler	DistRiver (-1.96) GroundCover (1.62*) LitterDepth (0.78) TreeDom (1.89) ShrubDensity (1.42)
Forest Birds	
Northern Parula	DistRiver (-3.32) GroundCover (1.21) TreeDom (3.12*) ShrubDensity (1.10) HerbHeight2 (1.27)
Autumn	
Grassland Birds	
Field Sparrow	DistEdge (1.13*) DBH (-1.70*)
Shrubland Birds	
Yellow-breasted Chat	DBH (0.30) ShrubDensity (-0.39) GroundCover (0.77*)
Open Woodland Birds	
Eastern Phoebe	DBH (0.97*) TreeDom (-0.71)
Gray Catbird	Landsize (-1.64) DBH (1.37*) ShrubDensity (0.77)
Hermit Thrush	Landsize (-2.42) BH (4.54*) TreeHeight (-3.61*) ShrubHeight^2 (-7.91)
Northern Cardinal	Landsize (-3.52*) DBH (6.52*) TreeHeight (-2.41*)
Northern Flicker	GroundCover (-0.48) TreeDom (0.48*)
Red-headed Woodpecker	DistRiver (0.73) GroundCover (-1.87) TreeHeight (1.50*) LitterDepth (-1.24) CrownDensity (1.55) TreeDom (-0.98) HerbHeight^2 (0.94)
Forest Birds	
Carolina Chickadee	DBH (1.78*) LitterDepth (-0.77) CrownDensity (-0.29) DistEdge^2 (-1.72*) ShrubHeight^2 (0.39)
Downy Woodpecker	TreeHeight (0.71*) HerbHeight (0.47) ShrubDensity (0.52) GroundCover^2 (-1.34*)
Eastern Wood-Pewee	DistRiver (0.44*) GroundCover (0.59*) TreeHeight (0.35) ShrubHeight (-2.48*) ShrubHeight2 (2.47*)
Northern Parula	TreeDom (0.54*)
Red-eyed Vireo	DistRiver (-0.59) DBH (-0.69) TreeHeight (1.12*) HerbHeight (0.36)
White-breasted Nuthatch	Landsize (-1.77) TreeHeight (0.98*) HerbHeight^2 (-0.69)
White-throated Sparrow	DistRiver (0.65*) DBH (4.04*) TreeHeight (-1.85) CrownDensity (-0.43) TreeDom (-2.46*)

Shrubland birds. We detected no particular trends for shrubland birds. During spring, *Geothlypis trichas* (L.) (Common Yellowthroat) presence was associated with groundcover (β = 1.42, P = 0.039), and *Agelaius phoeniceus* (L.) (Red-winged Blackbird) presence was associated with tree dominance (β = -7.59, P = 0.044) (Table 3). During autumn, *Icteria virens* (L.) (Yellow-breasted Chat) had a positive association with the curvilinear relationship to groundcover (β = 0.77, P = 0.026); Table 3).

Open woodland birds. During autumn, the presence of many open-woodland birds was positively associated with DBH (Table 3). Additionally, tree height differed and had significant negative associations with *Catharus guttatus* (Pallas) (Hermit Thrush) (β = -3.61, P = 0.043) and *Cardinalis cardinalis* (L.) (Northern Cardinal) during the autumn (β = -2.41, P = 0.036), but was positively associated with *Melanerpes erythrocephalus* (L.) (Red-headed Woodpecker) (β = 1.50, P = 0.044 (Table 3). Further, during spring, some open-woodland birds exhibited associations with shrub density (Table 3).

Forest birds. Several models for forest birds showed significant relationships with tree variables. Three of the autumn forest-bird models had positive associations with tree height: *Picoides pubescens* (L.) (Downy Woodpecker) (β = 0.71, P = 0.008), *Vireo olivaceus* (L.) (Red-eyed Vireo) (β = 1.12, P = 0.025), and *Sitta carolinensis* Latham (White-breasted Nuthatch) (β = 0.98, P = 0.003) (Table 3). In both the spring and autumn, *Setophaga americana* (L.) (Northern Parula) displayed significant associations with tree dominance (β = 3.12 [spring], β = 0.54 [autumn], P < 0.05) (Table 3). *Poecile carolinensis* (Audubon) (Carolina Chickadee) (β = 1.78, P < 0.001) and *Zonotrichia albicollis* (Gmelin) (White-throated Sparrow) (β = 4.04, P = 0.008) had significant associations with DBH (Table 3).

Apparent frequencies of occurrence

Nested ANOVAs indicated that during spring, no bird models exhibited significant differences in apparent frequencies of occurrence in varying age categories. Analyses of autumn data indicated significant differences in 5 bird species (Fig. 4). Carolina Chickadees were more likely to occur in sites 15–23 y of age ($F_{3,7}$ = 2.77, P = 0.018), Downy Woodpeckers were more likely to be encountered in mature bottomland-forest sites compared to restoration sites that were 7–14 y old ($F_{3,7}$ = 8.24, P < 0.001), *Colaptes auratus* (L.) (Northern Flicker) were more likely to occur on mature bottomland-forest sites than on restoration sites between 1–14 y of age ($F_{3,7}$ = 5.47, P < 0.001), and both Red-headed Woodpeckers and Northern Parulas were more likely to occur in mature bottomland-forest reference sites than in restoration sites (Fig. 4).

Discussion

Species diversity

Nested ANOVAs resulted in no significant differences in diversity measurements at different age categories during spring and only significant differences with the youngest age category (<7 years) in relation to all other categories during autumn.

This result contrasted with our original hypothesis that sites of ages 15–23 y since restoration would have the highest diversity; however, we had a limited number of sites. Other studies have found diversity tends to increase with age of forest sites (Gram et al. 2003, Johnston and Odum 1956, Kricher 1973).

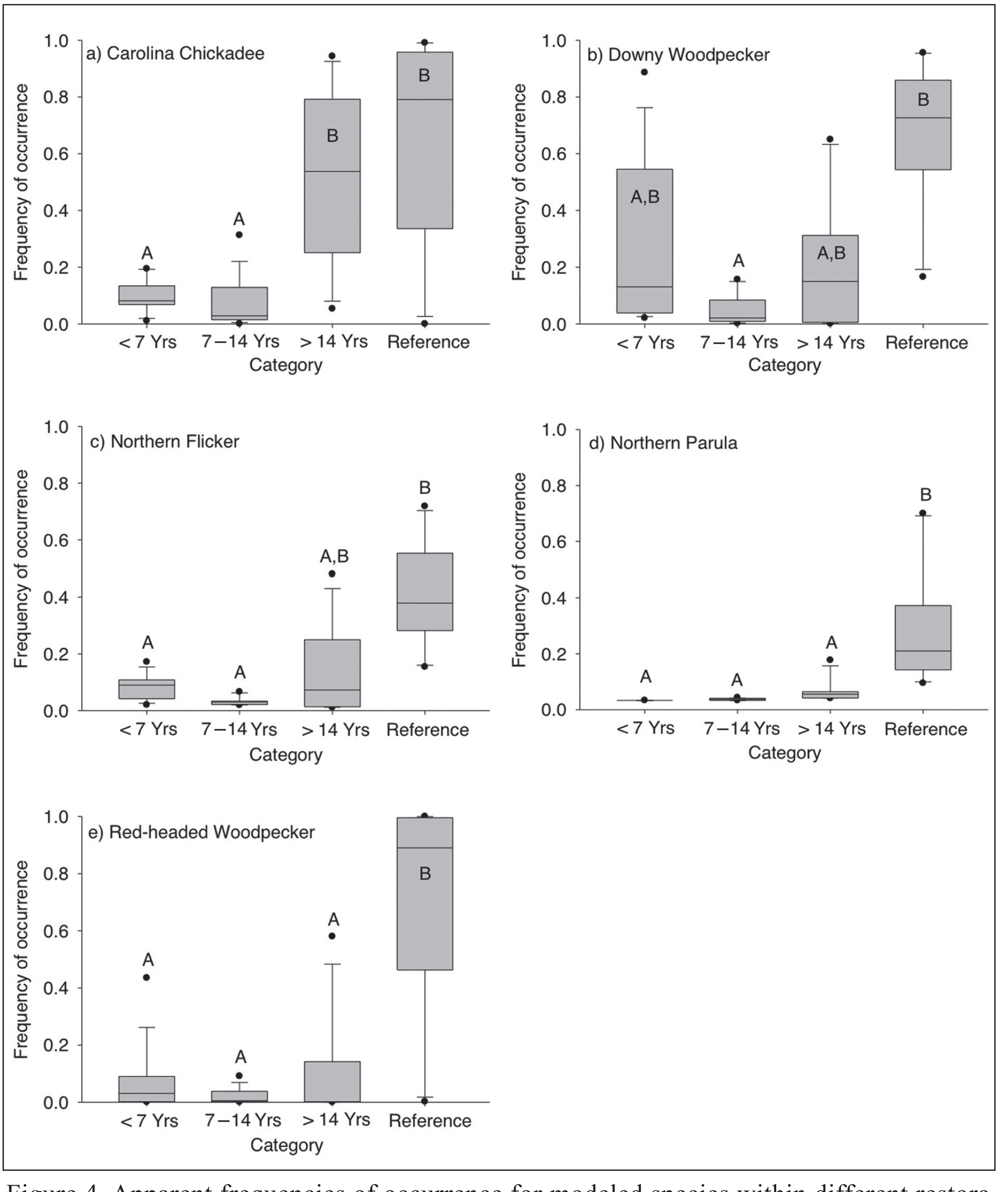


Figure 4. Apparent frequencies of occurrence for modeled species within different restoration-age categories. Median (bar), 10th (lower error bar), 25th (lower box), 75th (upper box), and 90th (upper error bar) percentiles are included. Outliers are represented with black dots. Points with the same letter represent no significant difference between means, which is based on Tukey–Kramer post hoc tests at $P = 0.05$.

Habitat models

Our predictive models for presence of Field Sparrow, Indigo Bunting, Northern Parula, and Red-eyed Vireo supported results reported in previous studies. In spring, The Field Sparrow's negative relationship with tree height, and in autumn, their positive association with distance to edge, and negative association with DBH was indicative of their preference for grasslands (Best 1977, Reidy et al. 2014). Previous literature showed that Indigo Buntings prefer areas with high herbaceous cover, which corresponds to the positive associations with groundcover and the curvilinear relationship to herbaceous height (Reidy et al. 2014, Stauffer and Best 1980). Northern Parula models also exhibited a significant positive association with tree dominance, which was supported by studies that indicated their preference for mature forests (Reidy et al. 2014, Rodewald and Brittingham 2007). Tree height was a significant positive indicator in the Red-eyed Vireo model. This finding was seen in previous studies that have noted that Red-eyed Vireos inhabit mature forests (James 1971, Reidy et al. 2014).

Some species, such as the American Goldfinch, Hermit Thrush, Summer Tanager, and Eastern Wood-Pewee, had models that were not supported by current literature. Our American Goldfinch model showed a significant positive association with distance to edge, but previous studies did not include this as an indicator variable. A number of other studies showed that American Goldfinches are primarily influenced by the presence of shrubs and the lack of saplings and mature trees (Mabry 2013, Stauffer and Best 1980). The Hermit Thrush model showed a significant positive association with DBH, but a significant negative association with tree height. Previous observations have noted that Hermit Thrushes inhabit forested areas, which corresponded to the association with DBH but did not correspond with the tree-height relationship (Dellinger et al. 2012, Morse 1971). The Summer Tanager model included only shrub density as a positive significant indicator of presence. This result is in direct contrast with a previous study that showed that increasing shrub density had a negative effect on the presence of Summer Tanagers (Reidy et al. 2014). The Eastern Wood-Pewee model included a negative association with shrub height, which contrasted with a previous study that indicated a negative relationship with ground cover (Reidy et al. 2014).

We expected our data to be concordant with known habitat relationships, but had mixed results. There are several potential reasons on why some of the models described may not be supported by literature. For example, the autumn models included younger birds, which may prefer different habitat when compared to their adult counterparts. One example is post-fledging Wood Thrushes, which occupied early successional oak–*Carya* (hickory) forests rather than mature forests where adults were typically found (Anders et al. 1998). Some additional species, such as the Red-winged Blackbird, American Robin, Northern Cardinal, and White-throated Sparrow, had unusual indicators in their models but are considered to be generalist species (Blackwell and Dolbeer 2001, Dellinger et al. 2007, Kilgo et al. 1998, Rousseau et al. 2012, Whittaker and Marzluff 2009). Therefore, they are less responsive to habitat structure and do not necessarily produce predictive models indicative of their typical preference (Carrara et al. 2015, Hinsley et al. 2009, Julliard et al. 2006).

Apparent frequencies of occurrence

Many of our models for bird species occurrence did not have significant differences in apparent frequency of occurrence when comparing restoration-age category, and only 5 species had any significant difference among age categories. Therefore, this finding may suggest that many of the species did not preferentially choose habitats during the surveying periods. Part of our sampling period included migration. During migration, habitat use tends to be more variable for bird species (Faaborg et al. 2010a, b; Petit 2000).

Conclusions

This study was one of the first times our restoration sites were surveyed to determine which bird species were utilizing these areas. Our results indicated that bottomland-hardwood forest-restoration sites provide habitat for a variety of birds from grassland specialists to forest specialists, with older sites having greater bird diversity. We detected several species of conservation concern during our surveys, such as Cerulean Warblers and *Vireo bellii* Audubon (Bell's Vireo) (Table 2). Our habitat models, while useful for exploration, did not result in discernible patterns or trends and therefore are of limited value for informing managers on management interventions they can use to increase and maintain bird populations at our sites. To better understand restoration efforts in the UMR, we recomend using our data as a baseline for future studies to determine if there are shifts in bird assemblages in these areas. We further recommend the inclusion of more-robust surveying techniques and the inclusion of more sites to provide data for better population estimates for surveyed bird species. Due to high likelihoods of flooding at our sites during spring, we also recommend that future research focuses on the breeding season and autumn migration.

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