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Research Paper

Vegetation associations of riparian birds in successional woodlands along the regulated Missouri River

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ABSTRACT. River regulation by dams on the Missouri River has modified riparian forest successional patterns, with decreases in early and increases in later seral stages and higher occurrence of invasive tree species, including Russian olive (*Elaeagnus angustifolia*) and eastern red cedar (*Juniperus virginiana*). The effects of these altered successional trajectories on bird biodiversity are difficult to quantify because of limited data on bird-habitat associations. We surveyed riparian shrubland and forest bird species across a gradient of riparian forest ages along two segments of the regulated Missouri River in South Dakota and Nebraska, USA and explored relationships between bird abundance and patch- and landscape-scale vegetation characteristics for 46 bird species. Predicted abundances at sites assigned to five vegetation classes, estimated from Bayesian binomial N-mixture models, identified 11 early successional bird species and 19 forest bird species. Abundances of early successional bird species were similar at cottonwood-willow sites and Russian olive sites and were positively correlated with cottonwood (*Populus deltoides*) importance values for only one species, Willow Flycatcher (*Empidonax traillii*). Abundances of forest bird species were similar at sites in the three forest vegetation classes, although Ovenbird (*Seiurus aurocapilla*) and Baltimore Oriole (*Icterus galbula*) showed some affinity for mid- or late successional cottonwood sites over late-successional non-cottonwood sites. Abundances of three forest species, including Baltimore Oriole, were positively correlated with cottonwood or negatively correlated with eastern red cedar importance values. Fifteen species were positively correlated with shrubland land cover, whereas 21 species were positively correlated with forest land cover. For most bird species, correlations were strongest with land cover within a 200-m buffer compared to 400 or 1200 m. These data suggest that the trends in riparian forest change due to river regulation along the middle Missouri River may produce a mix of positive and negative effects on riparian bird species. While management plans to promote regeneration of early successional cottonwood-willow stands are likely to benefit conservation of early successional bird species, Russian olive may also provide suitable bird habitat for the majority those species.

Associations végétales des oiseaux riverains dans les peuplements successionnels le long de la rivière Missouri

RÉSUMÉ. La régulation de la rivière Missouri par des barrages a modifié les schémas de succession des peuplements riverains, en menant à une diminution des premiers stades successionnels et à une augmentation des derniers stades, ainsi qu'à une plus grande présence d'espèces d'arbres envahissantes, notamment l'olivier de Bohême (*Elaeagnus angustifolia*) et le genévrier de Virginie (*Juniperus virginiana*). L'effet de ces processus successionnels sur la biodiversité d'oiseaux est difficile à quantifier en raison du manque de données sur les associations oiseaux-habitat. Nous avons recensé les espèces d'oiseaux de forêts et d'arbustales riveraines le long d'un gradient d'âge des forêts sur deux segments régulés de la rivière Missouri, dans le Dakota du Sud et le Nebraska, aux États-Unis, et examiné les relations entre l'abondance d'oiseaux et les caractéristiques de la végétation aux échelles de la parcelle et du paysage pour 46 espèces d'oiseaux. L'abondance prédite sur les sites assignés à cinq classes de végétation, estimée au moyen de modèles N-mélange binomiaux bayésiens, a mené à la détermination de 11 espèces d'oiseaux de début de succession et de 19 espèces d'oiseaux forestiers. L'abondance des espèces d'oiseaux de début de succession était comparable entre les sites de peupliers deltoïdes-saules et ceux d'oliviers de Bohême, et était corrélée positivement à la valeur de l'importance du peuplier deltoïde (*Populus deltoides*) pour une seule espèce, le Moucherolle des saules (*Empidonax traillii*). L'abondance des espèces d'oiseaux forestiers était similaire entre les sites des trois classes de végétation forestière, bien que la Paruline couronnée (*Seiurus aurocapilla*) et l'Oriole de Baltimore (*Icterus galbula*) aient montré une certaine affinité pour les sites de peupliers deltoïdes de stade de succession intermédiaire ou avancée par rapport aux sites de stade de succession avancée sans peuplier deltoïde. L'abondance de trois espèces forestières, dont l'Oriole de Baltimore, était corrélée positivement avec le peuplier deltoïde ou corrélée négativement avec le degré d'importance du genévrier de Virginie. Quinze espèces étaient corrélées positivement avec les arbustales, tandis que 21 espèces étaient corrélées positivement avec les peuplements forestiers. Pour la plupart des espèces d'oiseaux, les corrélations étaient les plus fortes avec le type de végétation dans une zone tampon de 200 m, par rapport à 400 ou à 1200 m. Ces données indiquent que les tendances de changements de la forêt riveraine, dues à la régulation le long de la rivière Missouri moyenne, peuvent produire un mélange d'effets positifs et négatifs sur les espèces d'oiseaux riverains. Bien que les plans de gestion visant à privilégier la régénération des peuplements de peupliers deltoïdes et de saules de début de succession soient susceptibles de favoriser la conservation des espèces d'oiseaux de début de succession, l'olivier de Bohême peut également fournir un habitat approprié à la majorité de ces espèces.

Key Words: avian biodiversity; hierarchical abundance model; invasive species; land cover; Missouri River; riparian forest; Russian olive; species abundance

INTRODUCTION

Western North American riparian habitats cover small land areas but are disproportionately important habitats for birds (Tubbs 1980, Ohmart 1994, Bennett et al. 2014). In addition, riparian zones support different species assemblages than surrounding uplands and thus contribute to regional biodiversity (Saab 1999, Sabo et al. 2005, Thogmartin et al. 2009). Early seral, shrub-dominated, riparian habitats are important for riparian bird abundance and diversity, but these habitats are declining on many regulated rivers in western North America and are associated with declining populations of early successional bird species (Swanson 1999, Luther et al. 2008, Betts et al. 2010, Swanson et al. 2011). The importance of such early successional vegetation for bird biodiversity represents an underappreciated aspect of riparian forest management (Swanson et al. 2011). Another complication to biodiversity conservation is that altered riparian successional trajectories from river management and land-use change have resulted in the occupation of western riparian habitats by upland or invasive tree species (Friedman et al. 2005, Illeperuma et al. 2023), with varying effects on breeding and migratory bird populations (Cerasale and Guglielmo 2010, Fischer et al. 2012, Sogge et al. 2013).

Riparian forests in the Great Plains region are dominated by plains cottonwood (*Populus deltoides* subsp. *monilifera*) and support among the highest levels of bird diversity of any habitat type in the region (Finch and Ruggiero 1993, Rumble and Gobeille 2004, Gentry et al. 2006, Munes et al. 2015). On the Missouri River, decades of river management by upstream dams have greatly affected native floodplain forests and the processes that sustain them (Johnson 1992, Dixon et al. 2012, 2015, Johnson et al. 2012, 2015). These effects include a reduction in flooding, increased channel incision that isolates the floodplain from the river, and declines in the geomorphic dynamism necessary to create open sediment bars for colonization by riparian pioneer species such as cottonwood and willow (*Salix* spp.). As a result, most floodplain forests are composed of age classes of trees that were established prior to the operation of upstream dams (Dixon et al. 2012, Johnson et al. 2012, Scott et al. 2013), although there is some variation in land-cover trends and age distribution of forests among different reaches of the river (Dixon et al. 2012). Early successional habitats on the Missouri River support high bird densities and species richness, particularly when included within a matrix containing nearby later successional stages (Liknes et al. 1994, Rumble and Gobeille 1998, 2004, Swanson 1999, Munes et al. 2015). Over longer (~50 year) time scales, a continuation of status quo river management is projected to lead to declines in cottonwood forest area, landscape diversity, and abundance of many forest bird species, particularly early successional and cottonwood specialists (Johnson 1992, Rumble and Gobeille 2004, Dixon et al. 2012, Munes 2014).

In addition to the shift toward older forests, river management has also contributed to invasion of floodplain forests by native upland tree species (eastern red cedar *Juniperus virginiana*) and non-native species (e.g., Russian olive *Elaeagnus angustifolia*, and common buckthorn *Rhamnus cathartica*; Katz and Shafroth 2003, Frost and Powell 2011, Greene and Knox 2014, Illeperuma et al. 2023). Control of invasive woody species is a major management focus by natural resource agencies, and there are also some efforts to restore native species such as cottonwood

through planting. Control of invasive woody species may have positive or negative effects on forest birds (Bateman and Paxton 2010, Sogge et al. 2013, Valente et al. 2019) depending on the quality of nesting or foraging habitat provided by these species relative to native tree species. Indeed, there is some evidence that shrub-nesting bird species (e.g., Bell's Vireo *Vireo bellii* and Yellow Warbler *Setophaga petechia*) occur in similar densities in Russian olive and in young native cottonwood-willow stands in Missouri River riparian forests, with Russian olive potentially retaining the structure needed by these species for a longer period of time than the faster growing cottonwood stands (Benson 2011, Munes 2014). Changes in bird distributions in aging riparian forests may be sensitive to the effects of management on invasive woody plant species and the effects of these species on bird abundance and diversity.

Riparian forests along the Missouri River have also declined in area and become increasingly fragmented due to land-use conversion. Dixon et al. (2012) found that riparian forest area declined by 48% and riparian shrubland by 69% from the 1890s to 2006 within our study area, with the most important driver of change being conversion to agricultural cropland (see also Bragg and Tatschl 1977). With forests and shrublands declining in area and becoming more fragmented, landscape-scale factors such as patch size, proximity to neighboring patches, and the total area of forest or shrubland within the surrounding landscape may influence habitat selection and population persistence of different bird species (Andrén 1994). Configuration and area of forest in the landscape generate varied effects on populations and community structure of forest birds, with some studies showing strong effects (Robinson et al. 1995, Saab 1999) and others, particularly in riparian forests, showing weaker landscape-scale influences (Knutson 1995, Sallabanks et al. 2000, Miller et al. 2004). Fahrig (2013) suggested that the total area of suitable habitat within a defined buffer distance around a plot or patch may be a better predictor of local species richness and abundance than patch size and isolation (Trzcinski et al. 1999, Watling et al. 2020), with different species and ecological responses (e.g., fecundity, abundance, and occurrence) varying in their sensitivity to habitat area and the characteristic "scale of effect" over which this response is strongest (Carrara et al. 2015, Moraga et al. 2019). Determining the degree and scale at which riparian birds respond to the abundance of early (shrubland) and later (forest) successional vegetation in the Missouri River floodplain would provide managers with useful information for predicting species occurrence, abundance, and richness beyond that generated from patch-level vegetation characteristics alone.

Given the potential importance of changes in native and invasive woody vegetation for floodplain forest birds, our aim was to explore the influence of riparian vegetation successional stage, species composition, and structure on bird abundance and species richness at both patch and landscape scales along the Missouri River in eastern South Dakota and Nebraska. We also sought to identify bird species associated with early or late successional stages of riparian forest. Description of patch- and landscape-scale vegetation associations for the riparian forest bird community and for individual bird species will provide important data to support conservation and management of this disproportionately important habitat for regional biodiversity.

We hypothesized that bird species richness would be lower in early successional vegetation classes (and Russian olive) than in later successional vegetation classes because of lower structural diversity (Farley et al. 1994, Scott et al. 2003, Knutson et al. 2005) and the absence of cavity-nesting species (Rumble and Gobeille 2004, Bateman and Paxton 2010, Fischer et al. 2012). However, some studies have documented higher or similar bird species richness in early compared to later successional stages (Yahner 2003, Hanowski et al. 2007, Thogmartin et al. 2009). In addition, because early successional study sites in our study area were often bordered by later successional vegetation, mature forest birds may use early successional vegetation for foraging, increasing overall bird species richness there (Liknes et al. 1994, Swanson 1999). Thus, an alternative hypothesis is the presence of similar bird species richness in all successional stages. We also hypothesized that early successional bird species would respond positively to shrubland and negatively to mature forest in the landscape, whereas the opposite would be true for mature forest species (Brawn et al. 2001, Hanberry and Thompson 2019). Finally, we hypothesized that Russian olive and eastern red cedar, both invasive tree species on the middle Missouri River floodplain (Dixon et al. 2012, Illeperuma et al. 2023), would decrease bird abundance and richness in native cottonwood forests (Knopf and Olson 1984, Davis 2005, Bateman and Paxton 2010, Frost and Powell 2011). Some studies, however, suggest positive or non-significant effects of Russian olive or eastern red cedar on breeding bird species richness and abundance in riparian habitats (Fleishman et al. 2003, Heinen and O'Connell 2009, Fischer et al. 2012), so an alternative hypothesis is that species richness and abundance will be similar between Russian olive and cottonwood-willow early successional riparian forest stands and between forest stands with and without eastern red cedar present.

METHODS

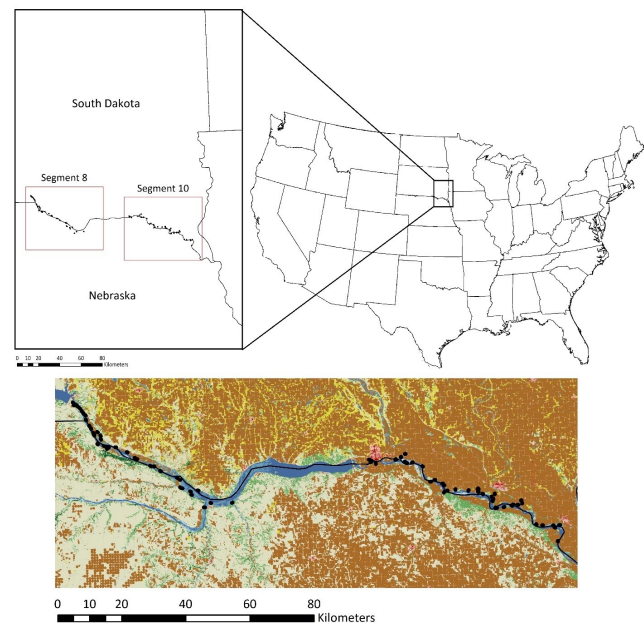
Study area

We surveyed riparian forest and shrubland patches in two segments of the Missouri River (Fig. 1), both of which are included in the Missouri National Recreational River (MNRR) unit of the National Park Service. These segments represent some of the last unimpounded, unchanneled sections of the Missouri River, although the flow and sediment regimes of each are influenced by upstream dams. The upriver MNRR section is 63 km long and extends from Fort Randall Dam downstream to the delta at the confluence of the Niobrara River and Lewis and Clark Lake above Gavins Point Dam (segment 8). The lower MNRR section is 94 km in length and extends downstream from Gavins Point Dam to Ponca, Nebraska (segment 10). The segment numbers used here are based on segments defined by the U.S. Army Corps of Engineers (Jacobson et al. 2010). Each of these segments has substantial remaining patches of floodplain forest of different successional stages and vegetation categories, so they serve as excellent study sites to examine bird-vegetation relationships.

Land-cover mapping

We classified land use and land cover using a system designed for the vegetation types encountered along the Missouri River (Dixon et al. 2012, Scott et al. 2013). Woody vegetation included shrubland, woodland, and closed-canopy forest. To stratify bird

Fig. 1. Study areas (segments 8 and 10) within the Missouri National Recreational River along the South Dakota-Nebraska border. Bird survey sites ($N = 78$ sites with two survey points per site) and regional land cover from the 2008 U.S. Geological Survey National Land Cover Database are depicted on the bottom map. Brown = cultivated cropland, yellow = pasture or hay, tan = grassland, blue = water and wetlands, red = urban and other developed lands, and green = forests (<https://www.mrlc.gov/data/legends/national-land-cover-database-class-legend-and-description>).



sampling by dominant vegetation and successional stage, we mapped all patches of riparian woody vegetation within the river valley using 2006 historical aerial imagery from the National Agriculture Imagery Program (<http://datagateway.nrcs.usda.gov/>; Dixon et al. 2012).

We assigned an age class (relative to the year 2007) and species composition category to each woody vegetation patch using a combination of field reconnaissance from 2006 to 2008; aerial photography from the late 1990s, mid-1980s, and 1950s; and the 1890s Missouri River Commission maps (Dixon et al. 2012). Age classes included sapling (< 10 yr), pole (10–24 yr), intermediate (25–49 yr), mature (50–114 yr), and old (> 114 yr). These break points correspond roughly to the 1997 Missouri River high flow event, the National High Altitude Photography (U.S. Department of Agriculture) imagery available for the early to mid-1980s, the completion of dam construction during the mid-1950s, and the availability of land-use and land-cover maps from the 1890s Missouri River Commission, respectively (Dixon et al. 2012).

Riparian vegetation species composition categories were cottonwood and non-cottonwood. Cottonwood patches were those with woody vegetation composed of at least 15% cottonwood by aerial cover. Older non-cottonwood patches (post-cottonwood) were mature–old forest and woodland, which

had theoretically started as cottonwood but with 2006 aerial cover of cottonwood < 15% due to mortality of cottonwood trees and recruitment of later successional species, primarily green ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), hackberry (*Celtis occidentalis*), and box elder (*Acer negundo*; Johnson et al. 1976, Johnson 1992, Dixon et al. 2010). Although American elm remains a common species in older stands, its abundance (and the frequency of large trees) has declined sharply over the last 50 years because of widespread mortality from infection by *Ophiostoma novo-ulmi*, the fungus that causes Dutch elm disease (Johnson et al. 2012). The transition from cottonwood to post-cottonwood forest usually occurs between 80 and 150 years after initial seedling recruitment (Dixon et al. 2012). The post-cottonwood species composition category is roughly analogous to the “equilibrium” forest in the model of Missouri River vegetation succession presented by Johnson (1992). Sapling, pole, and intermediate-aged non-cottonwood patches comprised a variety of woody vegetation types that result from colonization of sandbar, grassland, or abandoned agricultural habitat by species such as willow spp., eastern red cedar, and Russian olive.

For the landscape analyses, we simplified the land-use and land-cover map of Dixon et al. (2012) by reclassifying land cover into three broad classes representing woody vegetation structure and successional stage: shrubland, forest, and other. The new forest class comprised forest, woodland, planted trees, upland forest, and managed forest or cabin areas, whereas the new shrubland class comprised cottonwood shrubland, non-cottonwood shrubland, and riparian low woody vegetation. Detailed descriptions of these land-cover classes are provided by Dixon et al. (2012).

Bird surveys

We surveyed birds during the breeding season (late May–early July) in 2009 and 2010 as described in detail by Benson (2011) and Munes et al. (2015). We chose 79 sites stratified by age class and species composition category identified during land-cover mapping (Dixon et al. 2012). At each site, we randomly placed two bird survey points (156 total points, as two sites only had a single bird survey point) at least 200 m apart and, where possible, at least 50 m from the woodland edge. We were able to place survey points at least 250 m apart and > 50 m from the woodland edge in most sites. We assumed the absence of a social stimulation effect in our bird surveys (i.e., the presence of a bird at one survey point did not influence the presence of another individual of the same species at an adjacent survey point, outside of shared vegetation preferences). We surveyed each point twice in both years, once each during the first (25 May–14 June) and second (15 June–8 July) half of the breeding season, with successive counts separated by at least 10 d. We surveyed each point for a 10-min period during the morning (sunrise to 11:00 CST) and recorded all birds observed by sight or sound and estimated their distance from the observer at first detection using laser rangefinders to verify distance estimates. All observers completed a several-day training period before surveys to ensure competency in visual and aural identification of breeding birds of the region.

For the analyses, we excluded sites for which vegetation sampling could not be completed because of property access issues. The resulting bird data set comprises 74 sites, all but one of which had two bird survey points, for a total of 147 points. Each point was surveyed twice in each of two years, for a total of 588 bird surveys.

We also excluded detections of species that do not breed locally in forest and shrubland land-cover classes (i.e., passage migrants and species breeding primarily in open sandbar, riverbank, wetland, and grassland), nocturnal species, species most commonly observed as flyovers (crows, raptors), and any species with fewer than 15 observations. In addition, we grouped Eastern Towhee (*Pipilo erythrophthalmus*) and Spotted Towhee (*Pipilo maculatus*) together and refer to them as “Rufous-sided Towhee” (*Pipilo* spp.) in the analyses because the two species could not be reliably separated by song within the study area due to extensive hybridization (Tallman et al. 2002). This procedure yielded a total of 46 “species” of birds, which represents most individuals and species found in riparian forests along the Missouri River (Table A1.1 in Appendix 1).

Vegetation surveys

We sampled trees (woody stems ≥ 10 cm diameter at breast height [dbh]) and shrubs (woody stems < 10 cm dbh and ≥ 1 m tall) within the 74 study sites using methods described by Dixon et al. (2010, 2015) and Boever et al. (2019). Tree species composition, density, and basal area were characterized using the point-centered quarter method (Cottam and Curtis 1956) at 40 points per stand or, for some sparse or young stands, using fixed-radius (15 m) circular plots (12 per stand). Shrub density and cover were sampled using the line-strip method (Lindsey 1955, Johnson et al. 1976), with twelve 2 $\times$ 10-m belt transects sampled per stand.

Importance values (IVs) were calculated separately for each tree species and shrub species as the sum of relative density, relative dominance, and relative frequency (Curtis and McIntosh 1951). For trees, we calculated dominance using basal area; for shrubs, we used shrub cover. For species that occurred as both trees and shrubs, we calculated both a tree IV and a shrub IV.

Abundance modelling by vegetation class

We classified the study sites based on vegetation characteristics and estimated the abundance of each bird species across vegetation classes. To begin, we first classified the 74 study sites for which we had vegetation data using hierarchical clustering based on species-specific stem densities and tree basal areas (see Appendix 2). Hierarchical clustering of sites resulted in clusters that reflected site differences in both age and species composition. After inspecting the resulting dendrogram (Fig. A2.1 in Appendix 2), we divided sites into five classes corresponding generally to early successional cottonwood-willow, Russian olive, mid-successional cottonwood, transitional cottonwood (containing large cottonwoods and various later successional species), and post-cottonwood equilibrium (“equilibrium” as in Johnson 1992) forest. Here, we refer to sites in the first two classes as “early successional sites”, sites in the other three classes as “forest” or “mid- to late successional sites”, and sites in the last two classes as “late successional sites.” Analysis was performed in R version 4.2.3 (R Core Team 2023) using the vegan package (Oksanen et al. 2020).

We modelled bird abundance using binomial N-mixture models to account for imperfect detection (Royle 2004) in a Bayesian framework using Stan in R (Carpenter et al. 2017, Kellner et al. 2022, Stan Development Team 2023). The goal of our models was to explore the distribution of each bird species by estimating its abundance across the five vegetation classes identified in the previous step. With two years of bird surveys, we lacked sufficient

data to fit a generalized model for open populations (e.g., Dail and Madsen 2011, Hostetler and Chandler 2015). Instead, we opted for a “stacked” approach by treating point-years as our sampling unit rather than points. With this approach, we had 294 “sites” (point-years) visited twice each. To account for the pseudoreplication the stacking of years may have introduced, we considered models that included point as a random effect. We also considered models with a restricted spatial regression component (Hodges and Reich 2010, Hughes and Haran 2013) to account for spatial autocorrelation between neighboring points, an approach that has demonstrated effectiveness for complex data sets with sparse detections (Broms et al. 2014). The ability to incorporate random effects and spatial correlation into the model structure is one of the primary reasons we opted to use the Bayesian model-fitting framework implemented in the *ubms* package (Kellner et al. 2022) as opposed to the maximum-likelihood framework implemented in the popular unmarked package (Fiske and Chandler 2011).

For each species, we first identified a top model for the observation process by comparing six candidate observation models (Table 1) in a forward selection procedure. Candidate observation models included all combinations of observer (a categorical variable with three levels), and the (standardized) day of the year, either by itself or as a second-order polynomial. If one of the single-variable observation models, including either observer or date, fit better than the intercept-only model, we retained it and compared its fit to that of the two two-variable observation models. After identifying the top observation model, we compared three candidate models for the state process, abundance (Table 1). All state models included vegetation class, a categorical variable with five levels. One model also included a random effect of point to address the issue of non-independence among point-years, while another included a restricted spatial regression component with a 1000-m threshold.

We fit each model using four Markov chain Monte Carlo chains run for 3000 iterations, with the first 1000 iterations as warm-up. We assessed chain convergence for each estimated parameter using the potential scale reduction factor $\hat{R}$ and diagnostic estimated sample size (ESS; Vehtari et al. 2021). We considered the chains to have converged if $\hat{R}$ was close to 1, ESS was > 400 (Vehtari et al. 2021), and no divergent transitions were found. In the case of divergent transitions, we attempted to fit the model again after increasing the target average acceptance probability from 0.8 to 0.9 or 0.95. If $\hat{R}$ or ESS diagnostics indicated chains did not converge for a given model, we attempted to fit the model again with more post-warm-up iterations. If chains did not converge, we excluded that model from our candidate model set for that species. We assessed model goodness-of-fit with posterior predictive checks based on Pearson’s chi-square (Kellner et al. 2022).

We compared models using leave-one-out cross-validation (Vehtari et al. 2017) via the *loo* package in R (Vehtari et al. 2022). We considered one model a better fit than another if the expected log predictive density (ELPD) differed by ≥ 4 and the ELPD was at least twice the standard error of the difference, although we should point out that the choice of such thresholds is somewhat arbitrary and not generally agreed upon. To assess whether our choice of thresholds to assess model convergence, measure goodness-of-fit, and perform model selection affected the results

Table 1. A priori candidate models fitted using binomial N-mixture models to estimate bird abundance at sites in five vegetation classes. Observation models included no covariates on the state submodel. State models included the observation submodel from the top observation model. λ = state submodel; p = observation submodel; . = intercept only (no covariates); Observer = the observer who conducted the survey, a categorical variable with three levels; Date = day of the year, standardized; Date² = square of Date; Class = vegetation class, a categorical variable with five levels; Point = identifier for the point count location, a categorical variable with 74 levels; RSR1000 = restricted spatial regression with a distance threshold of 1000 m to consider sites neighbors.

Observation models	State models
$\lambda(.) p(.)$	$\lambda(\text{Class}) p(\text{Top submodel})$
$\lambda(.) p(\text{Observer})$	$\lambda(\text{Class} + (1 \text{Point}) p(\text{Top submodel})$
$\lambda(.) p(\text{Date})$	$\lambda(\text{Class} + \text{RSR1000}) p(\text{Top submodel})$
$\lambda(.) p(\text{Date} + \text{Date}^2)$	
$\lambda(.) p(\text{Observer} + \text{Date})$	
$\lambda(.) p(\text{Observer} + \text{Date} + \text{Date}^2)$	

of our analyses, we compared the predicted abundance estimates for a selection of species using fitted models with various outcomes (converged, not converged, good fit, poor fit, large difference in ELPD, small difference in ELPD). In most cases, the predicted abundance estimates were very similar, and the relative abundances across the five vegetation categories—the estimation of which was our main modeling goal—were almost identical. For these reasons, we are confident that our modeling approach was sufficient to meet our goals.

Once we had identified a top model for a species, we used the model to predict mean abundance and 95% credible intervals for the five vegetation classes. We visually inspected abundance plots and classified each species as an “early successional species” if it was more abundant in one or both of the early successional vegetation classes, or a “forest species” if it was more abundant in one or more of the forest vegetation classes.

Patch-scale correlations

The abundance models gave us an overview of how riparian bird species are distributed across the vegetation successional stages. To further explore the effects of vegetation structure and species composition on bird abundances, we estimated Spearman’s correlation coefficients between bird abundance and a suite of vegetation structure and species composition variables. Here, we defined bird abundance as the raw maximum number of birds observed at a point across the four visits over two years. For all species, we estimated correlations with vegetation using three structural variables: total tree density, total shrub cover, and the 98th percentile of tree dbh (dbh P98, as a rough proxy for stand age). We did not include basal area because it was highly correlated with other variables. For early successional species only, we estimated correlations with cottonwood, Russian olive, and eastern red cedar IVs, both for shrubs and trees. For forest bird species only, we estimated correlations with tree IVs for cottonwood, eastern red cedar, and a group we termed “late successional tree species” consisting of green ash, American elm, box elder, hackberry, and white mulberry (*Morus alba*).

When we estimated correlations, we suspected that the signature of early vs. late successional vegetation would obscure other interesting patterns. For example, cottonwood shrub IV is very low in equilibrium forests, whereas eastern red cedar shrub IV is very high. This situation would manifest as a positive correlation between forest bird abundance and cedar shrub IV, even though forest birds may be more abundant in forests with low cedar shrub IV than in forests with high cedar shrub IV. For this reason, we used only early successional sites for correlations with early successional bird species, and only forest sites for correlations with forest bird species.

Correlations were estimated using the correlation package in R (Makowski et al. 2020, 2022). We used Holm's (1979) method to adjust the confidence intervals to control the family-wise error rate for all bird-vegetation correlations. We considered a correlation significant if its 95% confidence interval did not overlap zero.

Landscape-scale correlations

In addition to relationships between bird abundance and vegetation at the vegetation patch scale, we wanted to explore relationships at the landscape scale. For this analysis, we used our land-cover map to measure the proportion of area in each of two land-cover classes, forest and shrubland, surrounding each bird survey point. We then related these proportions of forest and shrubland area to point-level bird abundances as defined above, using Spearman's correlation coefficients.

We carefully considered the choice of a buffer distance at which to summarize land cover. Other studies have used a range of buffer distances for representing landscape context: 100 m (Miller et al. 2004), ~500 m (Smith et al. 2011, Carrara et al. 2015), 800–1500 m (Knutson 1995, Saab 1999, Miller et al. 2004, Fletcher and Hutto 2008, Smith et al. 2011, Carrara et al. 2015), or ≥ 10 km (Robinson et al. 1995, Trzcinski et al. 1999, Smith et al. 2011). The buffer distance at which the ecological response to landscape composition is strongest (the scale of effect), may vary among species, the ecological response of interest (e.g., fecundity, abundance, occurrence), and even between different geographic settings for a given species (Smith et al. 2011, Carrara et al. 2015, Moraga et al. 2019). Given these uncertainties, some scientists recommend estimating the scale of effect empirically by evaluating a range of scales, rather than choosing a single one a priori (Jackson and Fahrig 2015, Moraga et al. 2019, Martin et al. 2021). We used this empirical, exploratory approach in our analysis.

We chose to compare buffer distances of 200, 400, and 1200 m around each bird survey point based on the characteristics of riparian areas in the study area. The 200-m and 400-m buffers may mostly or partly reflect the vegetation within the focal patch, but they are also likely to capture the influence of adjacent land cover and neighboring patches because riparian forest and shrubland patches were frequently narrow and fragmented within the study area, and survey points were often < 100 m from the patch edge. We estimated six correlations (two land-cover classes at three buffer distances) per species and adjusted the confidence intervals using Holm's (1979) method.

After estimating landscape-scale correlations, we identified the buffer distance with the strongest correlation between abundance and forest land cover and the buffer distance with the strongest

correlation between abundance and shrubland land cover for each species. We plotted those two correlations against each other and visually inspected the ordination to identify groups of bird species that responded to landscape similarly. These groups included forest landscape specialists, forest landscape associates, riparian landscape generalists, early successional landscape associates, and early successional landscape specialists.

Bird species richness

We examined the relationships of bird species richness with forest and shrubland land cover by estimating Spearman's correlation coefficients between richness and the proportion of surrounding area in each land-cover class within 200-, 400-, and 1200-m buffers around each survey point. We used the same methods as with the patch- and landscape-scale correlations. We used one-way analysis of variance (ANOVA) to assess whether bird species richness varied among the five vegetation classes identified by our site classification. When ANOVA indicated significant differences, we used post-hoc pairwise *t*-tests with the Holm correction for multiple comparisons.

RESULTS

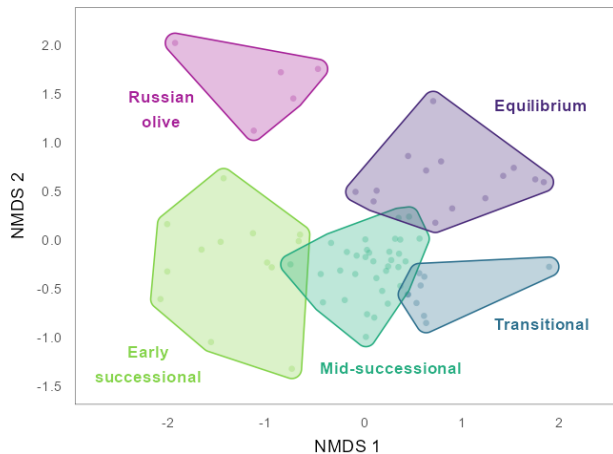
We observed 50 species of forest and shrubland breeding birds, accounting for 11,675 detections in 588 surveys of 147 points at 74 sites. The most commonly detected species were House Wren (*Troglodytes aedon*; 1257 detections in 474 surveys), Yellow Warbler (1124, 413), Mourning Dove (*Zenaida macroura*; 806, 463), and Baltimore Oriole (*Icterus galbula*; 798, 392; Table A1.1 in Appendix 1). The least commonly detected species included in our analyses were Chipping Sparrow (*Spizella passerina*; 26), Scarlet Tanager (*Piranga olivacea*; 24), Yellow-billed Cuckoo (*Coccyzus americanus*; 16), and Yellow-throated Vireo (*Vireo flavifrons*; 16; Table A1.1 in Appendix 1). Another four species were detected six or fewer times each and were not included in our correlation analyses or abundance modeling: Eastern Phoebe (*Sayornis phoebe*), Black-billed Cuckoo (*Coccyzus erythrophthalmus*), Ruby-throated Hummingbird (*Archilochus colubris*), and Yellow-breasted Chat (*Icteria virens*).

Abundance modelling by vegetation class

Site classification based on ordination of vegetation characteristics and cluster analysis yielded five vegetation classes, which we labeled early successional cottonwood-willow, Russian olive, mid-successional cottonwood, transitional cottonwood (containing large cottonwoods and various later successional species), and post-cottonwood equilibrium forest (Fig. 2). Early and mid-successional classes tended to have higher woody stem densities (Fig. A2.2 in Appendix 2) and absolute tree basal areas (Fig. A2.3 in Appendix 2) of plains cottonwood, willow spp., and Russian olive. Mid- and late successional sites tended to have higher densities and basal areas of ash, elm, box elder, eastern red cedar, and common buckthorn.

Model fitting and selection yielded a top observation model for each bird species (see Appendix 3). The top observation model included observer for 18 species and no covariates for the other 28 species. Date was not included in the top model for any species. The estimated probability of detection varied among species and observers, with mean detection probability averaged across the three observers ranging from 0.07 to 0.29 (median 0.18). The top state model included a random effect of point for 20 species and

Fig. 2. Ordination of sites based on the first two axes of a non-metric multidimensional scaling of vegetation characteristics at 74 sites based on a combination of tree species-specific stem densities and basal areas. Five classes identified by agglomerative hierarchical clustering are shown with convex hulls. These classes correspond to early successional cottonwood-willow, Russian olive, mid-successional cottonwood, transitional cottonwood, and post-cottonwood “equilibrium” forest.



a restricted spatial regression component for four species. The other 22 species contained neither effect. For all species, abundance estimates did not differ greatly among the three candidate state models. Goodness-of-fit, as measured by posterior predictive P -values, was satisfactory for most species ($P < 0.1$); models for four species (American Robin *Turdus migratorius*, Brown-headed Cowbird *Molothrus ater*, Common Grackle *Quiscalus quiscula*, and Mourning Dove) showed relatively poor fit ($P > 0.9$). The abundance estimates generated by those models, however, revealed patterns of relative abundance across vegetation types that were consistent with the data and what we would expect for those species, so we included them in our results.

We grouped the bird species into three classes, early successional, forest, and other, based on their signature of predicted abundances across the five vegetation classes (Fig. 3). Early successional bird species were most abundant in the early successional cottonwood-willow and Russian olive vegetation classes, and comparatively less abundant in the forest classes. Eleven species fell into this category, including Bell’s Vireo, Orchard Oriole (*Icterus spurius*), and Willow Flycatcher (*Empidonax traillii*). Abundances tended to be similar in early successional cottonwood-willow and Russian olive vegetation classes, but the credible intervals for the Russian olive were wide for some species, in part because of the smaller number of sites in that class.

Forest bird species were most abundant in one or more of the forest vegetation classes, mid-successional cottonwood, transitional cottonwood, or post-cottonwood equilibrium forest, and comparatively less abundant in the early successional cottonwood-willow and Russian olive classes. Nineteen species

fell into this category, including most of the woodpeckers and secondary cavity nesters, such as Great Crested Flycatcher (*Myiarchus crinitus*), House Wren, Black-capped Chickadee (*Parus atricapillus*), and White-breasted Nuthatch (*Sitta carolinensis*). Most species were approximately equally abundant in all three forest age classes. Breaking this trend, Ovenbird (*Seiurus aurocapilla*) was more abundant in mid-successional cottonwood than in the other two forest classes, whereas Baltimore Orioles were somewhat less abundant in equilibrium forest than in the other two forest classes.

Other bird species had similar densities in at least one of the early and mid- to late successional vegetation classes, with no clear early successional or forest signature. Some notable patterns among these species include: American Robin less abundant in Russian olive than early successional cottonwood-willow, and Scarlet Tanager more abundant in Russian olive than early successional cottonwood-willow.

Patch-scale correlations

Correlations between bird abundance and vegetation at early successional cottonwood-willow and Russian olive sites varied among bird species (Fig. 4; Fig. A4.1 in Appendix 4). Relatively few species showed significant correlations between abundance and total structure variables: Yellow Warbler abundance was positively correlated with higher tree density, Eastern Kingbird (*Tyrannus tyrannus*) abundance was positively correlated with higher dbh P98, and Red-winged Blackbird (*Agelaius phoeniceus*) abundance was negatively correlated with both variables. No species abundances were correlated with total shrub cover. Only Willow Flycatcher abundance was correlated with cottonwood shrub IV (a positive association), and no species were correlated with cottonwood tree IV. American Goldfinch (*Spinus tristis*) and Field Sparrow (*Spizella pusilla*) abundances were positively correlated with Russian olive tree IV, whereas Eastern Kingbird and Orchard Oriole abundances were positively correlated with both Russian olive shrub and tree IVs. Eastern Kingbird and Field Sparrow abundances were correlated with eastern red cedar tree IV, whereas Lark Sparrow (*Chondestes grammacus*) and Willow Flycatcher abundances were positively correlated with cedar shrub IV. The only species to show a negative association with eastern red cedar IV or Russian olive IV was Red-winged Blackbird, which was negatively associated with tree IVs for both invasive tree species.

At forest sites, most forest bird species showed at least one significant correlation between abundance and one of the total structure variables (Fig. 5; Fig. A4.2 in Appendix 4). Two-thirds of species were negatively associated with tree density, more than one-third were positively associated with dbh P98, and several species were positively associated with shrub cover. No species were correlated with total herbaceous cover. Abundances of 12 of 19 species were positively correlated with late successional tree species IV, whereas seven were positively correlated with common buckthorn shrub IV. Eastern red cedar tree IV was negatively correlated with the abundance of Baltimore Orioles and Red-bellied Woodpeckers (*Melanerpes carolinus*) and positively correlated with Northern Cardinal (*Cardinalis cardinalis*) abundance. Baltimore Oriole and Spotted/Eastern Towhees were the only late successional bird species to show positive correlations with cottonwood tree IV, whereas eight species showed negative correlations.

Fig. 3. Predicted abundance estimates (number of birds per point) and Bayesian 95% credible intervals for the 46 most common riparian bird species detected. Bird species names are provided in Appendix 1. Estimates were derived from binomial N-mixture models implemented in a Bayesian framework using Stan.

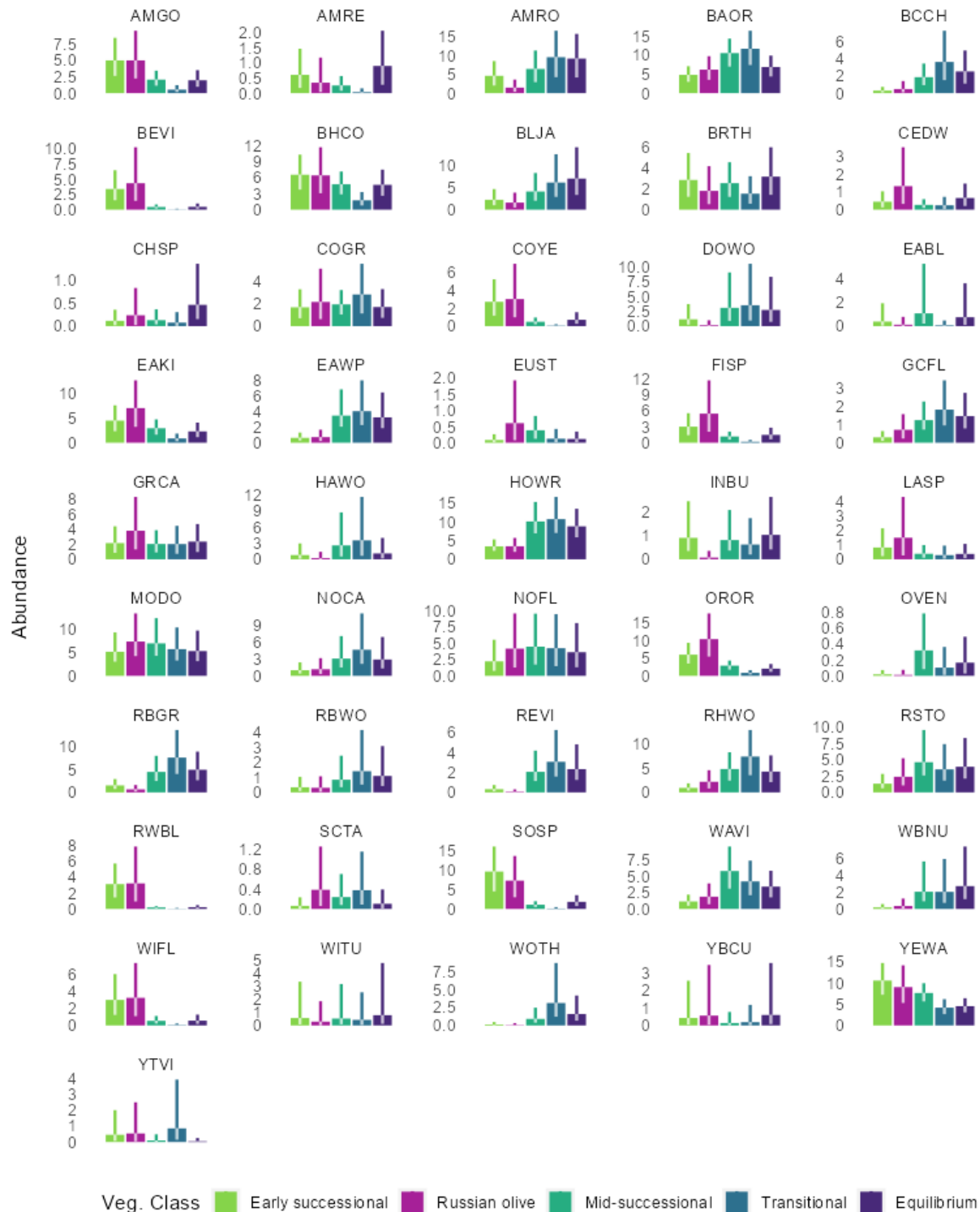
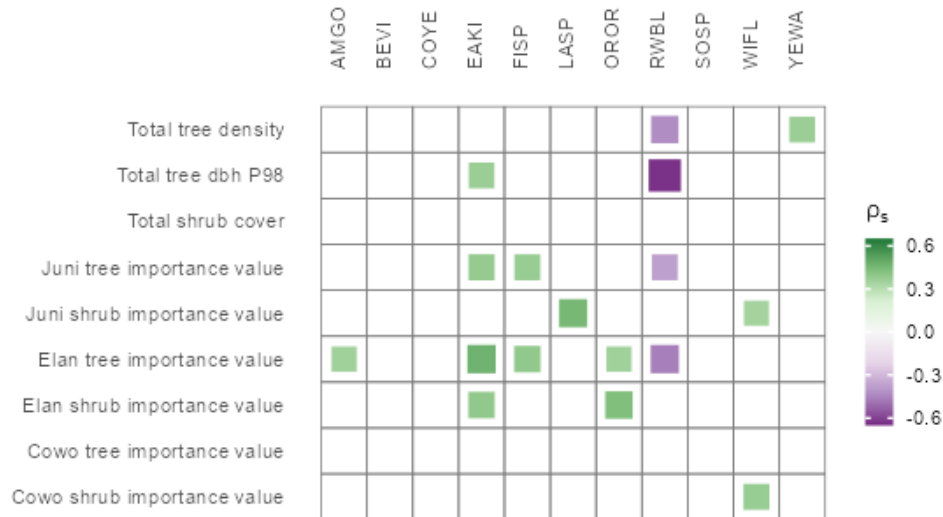


Fig. 4. Correlations between vegetation characteristics and bird abundances for bird species positively associated with shrubland land cover. Bird species names are provided in Appendix 1. Spearman's correlation coefficients are shown, with larger, darker squares indicating greater correlation, and color indicating the direction of the relationship (green = positive, purple = negative). Only significant correlation coefficients are shown (those whose 95% confidence intervals did not overlap 0). Total tree dbh P98 refers to the 98th percentile for tree diameter at breast height (DBH) measurements. For tree and shrub importance values, Juni = eastern red cedar, Elan = Russian olive, and Cowo = cottonwood.



Landscape-scale correlations

Fifteen bird species showed significant positive relationships between abundance and shrubland land cover within one or more distance buffers (Fig. 6; Table A4.1 in Appendix 4). Eight species, which we classified as early successional landscape specialists, also showed large ($\rho_s < -0.4$) significant negative relationships with forest land cover. These species included Bell's Vireo, Field Sparrow, Orchard Oriole, Willow Flycatcher, Eastern Kingbird, Brown-headed Cowbird, Red-winged Blackbird, and Song Sparrow (*Melospiza melodia*). The remaining seven species, which we classified as early successional landscape associates, showed either weaker negative ($\rho_s > -0.4$) or nonsignificant relationships with forest land cover.

Among the eight early successional landscape specialists, the strongest relationship for all species was at 200 m for both the shrubland and forest land-cover correlations (Table A4.1 in Appendix 4). Among the seven early successional landscape associates, most of the strongest correlations for each species were at 200 m, with the following exceptions. Yellow Warbler had its strongest relationship with shrubland cover at 1200 m, whereas Brown Thrasher (*Toxostoma rufum*) and American Redstart (*Setophaga ruticilla*) had their strongest relationships with shrubland cover at 400 m (Table A4.1 in Appendix 4).

Twenty-one bird species showed significant positive correlations between abundance and forest land cover within one or more distance buffers (Fig. 6; Table A4.1 in Appendix 4). Six species, which we classified as forest landscape specialists, also showed large ($\rho_s < -0.4$) significant negative relationships with shrubland land cover. These species included Red-eyed Vireo (*Vireo olivaceus*), Red-headed Woodpecker (*Melanerpes erythrocephalus*),

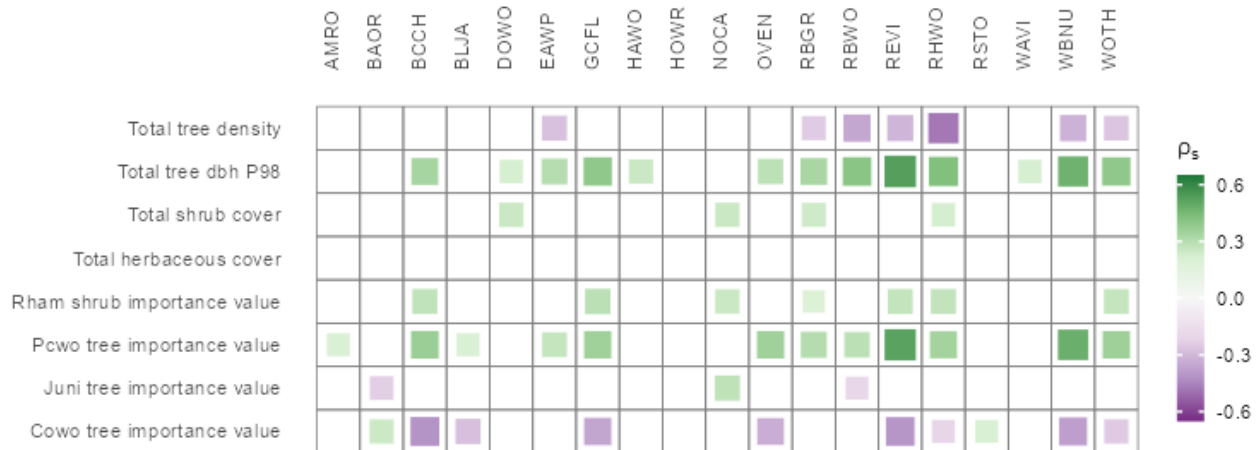
Eastern Wood-Pewee (*Contopus virens*), Rose-breasted Grosbeak (*Phœucticus ludovicianus*), White-breasted Nuthatch, and Black-capped Chickadee. The remaining 15 species, which we classified as forest landscape associates, showed either weaker negative ($\rho_s > -0.4$) or nonsignificant relationships with shrubland land cover.

Among the six forest landscape specialists, the strongest relationship for all species was at 200 m for both the shrubland and forest land cover, except for Black-capped Chickadee, which showed the strongest negative relationship with shrubland cover at 1200 m (Table A4.1 in Appendix 4). Among the 15 forest landscape associates, there was more variability for the buffer distance showing the strongest relationship. Nine species showed the strongest relationship with forest cover at 200 m, whereas four and two species showed the strongest relationship at 400 m and 1200 m, respectively (Table A4.1 in Appendix 4). Among those six species, three of which were woodpecker species, five showed a significant negative relationship with shrubland cover ($\rho_s < -0.4$), two at 200 m, two at 400 m, and one at 1200 m (Table A4.1 in Appendix 4).

Bird species richness

Riparian bird species richness at survey points was significantly positively correlated with the proportion of forest land cover at all three buffer distances (Table A5.1 in Appendix 5). The relationship was similar at all buffer distances, with the strongest at 400 m ($\rho_s = 0.21$, $P < 0.001$). There were no significant relationships between shrubland cover on the landscape and bird species richness at any of the buffer distances (Table A5.1 in Appendix 5). Mean bird species richness ranged from 25.2 species on early successional cottonwood-willow sites to 29.7 species on equilibrium sites (Fig. A5.1 in Appendix 5). There was a

Fig. 5. Correlation between vegetation characteristics and bird abundances for bird species positively associated with forest land cover. Bird species names are provided in Appendix 1. Spearman's correlation coefficients are shown, with larger, darker squares indicating greater correlation, and color indicating the direction of the relationship (green = positive, purple = negative). Only significant correlation coefficients are shown (those whose 95% confidence intervals did not overlap 0). Total tree dbh P98 refers to the 98th percentile for tree diameter at breast height (DBH) measurements. For tree importance values, Rham = common buckthorn, Juni = eastern red cedar, Elan = Russian olive, and Pcow = a group of late successional ("post-cottonwood") tree species.



statistically significant difference in richness between at least two vegetation classes ($F_{4,69} = 3.719$, $P = 0.008$), with early successional cottonwood-willow sites being less species rich than both mid-successional ($P = 0.028$) and equilibrium ($P = 0.033$) sites.

DISCUSSION

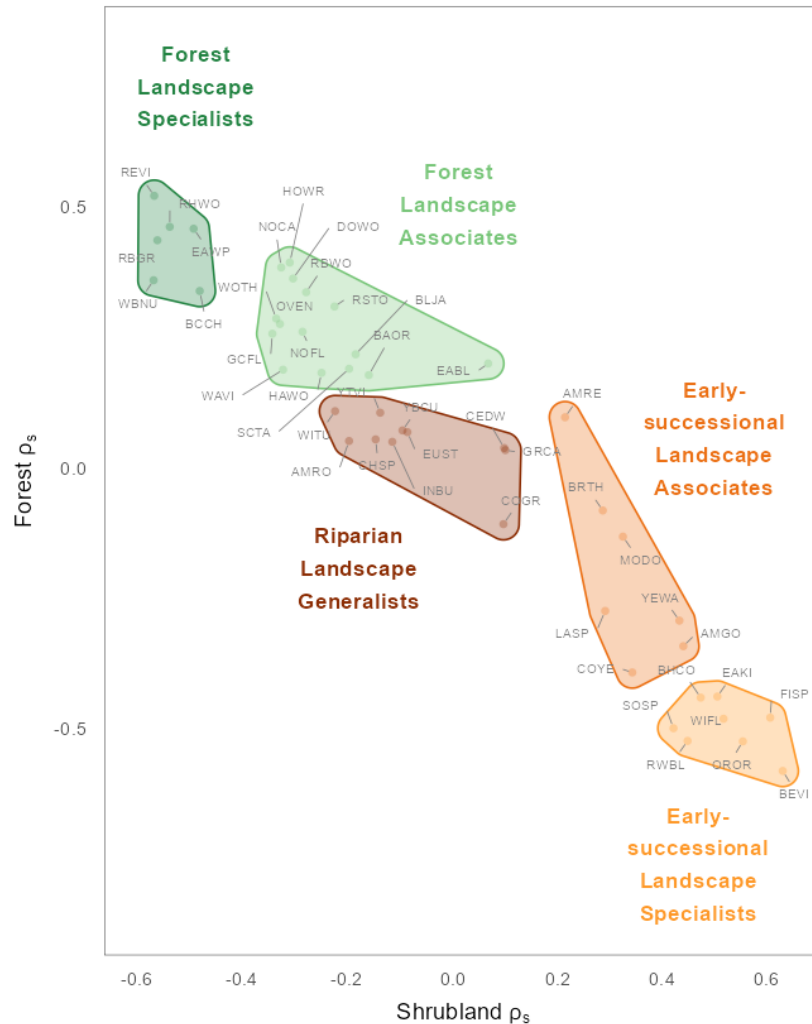
Both patch- and landscape-scale vegetation characteristics were associated with riparian bird abundance in Missouri River riparian forests. Bird species varied in abundance across the five classes of sites defined by patch-level vegetation characteristics. We used those patterns of variation to identify 15 species relatively more abundant in early successional vegetation patches and 21 species more abundant in mid- to late successional (forest) patches. These latter species include several that are habitat specialists in the region or whose populations have decreased in recent decades, including Bell's Vireo, Willow Flycatcher, Yellow-billed Cuckoo, Red-headed Woodpecker, Baltimore Oriole, Wood Thrush (*Hylocichla mustelina*), and Ovenbird (Sauer et al. 2017).

The patch- and landscape-scale analyses were generally similar in defining vegetation associations for riparian birds. Seven species were classified as "other" at the patch scale because they occurred in similar abundance in at least one early and one mid- to late successional vegetation class, and classified as landscape associates or specialists using the landscape-scale correlations. These species included those that nest in forest or forest edge but forage in early successional habitat (Northern Flicker *Colaptes auratus*, Eastern Bluebird *Sialia sialis*, and Scarlet Tanager) and those that nest in a variety of habitats (Mourning Dove, American Redstart, Brown-headed Cowbird, and Brown Thrasher). One species, American Robin, was categorized as a forest species in

the patch-scale abundance modelling but as a riparian landscape generalist using landscape-scale correlations.

The eight species of early successional landscape specialists showed significant positive associations with shrubland and strong significant negative abundance relationships with forest land cover. The six species of forest landscape specialists showed the reverse pattern, with positive associations with forest and strong negative associations with shrubland land cover. For most of these species, positive abundance relationships with riparian vegetation type (forest or shrubland) and negative abundance relationships with the other vegetation type were strongest at the smallest landscape scale of 200 m and declined as buffer distance increased. This result is consistent with those from some other studies of early successional bird species (Askins et al. 2007), including data from farther upstream along the Missouri River and its tributaries in Montana (Fletcher and Hutto 2008). Lehen and Rodewald (2009) and Roberts and King (2017) found that shrubland bird abundance increased with patch size for small (< 16 ha) shrubland patches. Moreover, bird abundance increased in patch centers relative to edge in some studies (Schlossberg and King 2008), suggesting that patch-scale vegetative characteristics are also important to shrubland birds. Other studies also document limited effects of mature forest on shrubland bird occurrence or abundance at larger buffer radii (Askins et al. 2007, Shake et al. 2012). Landscape-scale variables, however, were more important than patch-scale variables for explaining riparian forest bird occupancy in some other studies, but these studies dealt largely with mature forest species and did not measure local-scale associations (Rodewald and Bakermans 2006) or found stronger local- than landscape-scale effects for some shrubland bird species (Saab 1999). For example, landscape variables (1000-m buffer)

Fig. 6. Ordination of bird species along two axes representing the estimated Spearman's correlation coefficient between species abundance and proportion of shrubland cover (x-axis) and species abundance and proportion of forest cover (y-axis) within a buffer area at 148 sites. The proportion of land cover was measured within three buffer distances: 200, 400, and 1200 m. Only the strongest of the three correlations is shown. Bird abundance was calculated as the maximum number of individuals seen at a point during four visits over two years. Bird species names are provided in Appendix 1. Birds were categorized as forest associates if they had a significant positive correlation with forest land cover and as forest specialists if they also showed a significant and large negative correlation with shrubland land cover. Birds were categorized as shrubland associates if they had a significant positive correlation with shrubland land cover and as shrubland specialists if they also showed a significant and large negative correlation with forest land cover. Significant correlations were those whose 95% confidence intervals did not overlap 0.



were the most frequent predictors of mature forest bird occurrence in Idaho riparian habitats, with micro- and macrohabitat variables of secondary importance (Saab 1999). Habitat loss and fragmentation of riparian forests at the landscape scale (1000-m buffer) in central Montana explained more unique variation in riparian forest bird occurrence than did local-scale disturbance (Fletcher and Hutto 2008). Landscape patterns (1000-m buffer) also explained more variation in bird communities than did forest patch width in Ohio riparian forests (Rodewald and Bakermans 2006). The presence of mature forest birds also generally increased with the percentage of forest on the landscape (1400-m buffer) in eastern Ontario (Villard et al. 1999). The reasons for the weaker correlations

at broader landscape scales for mature forest birds in our study are uncertain but perhaps relate to riparian forest habitats in the region being narrow, with relatively high amounts of edge (Gentry et al. 2006). However, other riparian systems in western North America, with narrow riparian areas, fail to show a similar pattern (Saab 1999, Fletcher and Hutto 2008). The responses of abundance to vegetative characteristics at the patch scale along with the greatest responses at the smallest (200-m radius) landscape scale for most bird species suggests that the local, or patch, scale is most important to defining bird abundance in middle Missouri River riparian forests. These data, along with other regional studies (Swanson 1999, Gentry et al. 2006, Munes

et al. 2015), suggest that management plans preserving even relatively small areas of riparian forest or shrublands in this area should benefit breeding riparian birds.

Riparian bird species richness was lower in early successional cottonwood-willow vegetation than in mid-successional and transitional cottonwood forest classes, so our hypothesis of higher species richness in later successional stages was partially supported. These results differ from those from previous studies of riparian birds along the Missouri River below the mainstem dams that suggest that early successional vegetation, especially when bordered by mature cottonwood forest, supports high avian species richness (Liknes et al. 1994, Swanson 1999). In reservoir stretches of the Missouri River above the dams, early successional vegetation exists primarily as very narrow strips next to later seral stages, with bird species richness tending to increase in late intermediate and mature seral stages (Rumble and Gobeille 1998, 2004). Thus, the narrow riparian forests above the dams on the Missouri River may show different relationships with bird species richness than in the more extensive riparian forests along unpounded sections of the river, like those in our study. Likewise, bird species richness was positively related to structural complexity of riparian vegetation along the upper Missouri River in central Montana, with highest values in cottonwood-shrub and mature cottonwood successional stages when an understory layer was present (Scott et al. 2003). Other studies also documented variable trends in riparian bird species richness and diversity with successional stage. For example, on the lower Missouri River, Thogmartin et al. (2009) found the highest bird diversity in mature riparian forest relative to wet prairie and early successional forest (< 10 yr old), although early successional and mature riparian forests did not differ significantly. Bird species richness was also higher in mature riparian forest than in early successional cottonwood-willow forest and scrub/shrub habitat on the Mississippi River (Knutson et al. 2005). In contrast, riparian bird species richness increased with willow, shrub, and herbaceous cover, characteristics associated with early successional riparian vegetation, in the Sierra Nevada mountains of northern California (Cole et al. 2019). Bird abundance and diversity also tended to be higher in early successional riparian vegetation than in mature and urban riparian vegetation in the Ziarat watershed in Iran (Roshan et al. 2017). Collectively, these studies suggest that the relationship between bird species richness and vegetation succession in riparian habitats is difficult to generalize and may be dependent on the specific riparian systems and bird communities involved. Such a conclusion complicates management of riparian systems for bird species richness and diversity and highlights the need for local information in developing specific management plans.

Bird richness and abundance are often associated with vegetation characteristics at both local and landscape scales. Thirteen forest bird species, including most of the cavity nesting species, were positively correlated with tree diameter; seven of them were also negatively correlated with tree density, suggesting that these species prefer structurally mature stands. For several forest species (Red-headed and Downy (*Dryobates pubescens*) woodpeckers, Northern Cardinal, and Rose-breasted Grosbeak), abundance was positively associated with total shrub cover at the patch scale, suggesting that they prefer the presence of a shrubby understory in riparian forests. Among early successional species, only three

showed any correlation with vegetation structure variables. Scott et al. (2003) documented that individual bird species differed in abundance among vegetation classes in central Montana riparian forests, with 17 species, including Cedar Waxwing (*Bombycilla cedrorum*), American Goldfinch, Common Yellowthroat (*Geothlypis trichas*), Spotted Towhee, Black-headed Grosbeak (*Pheucticus melanocephalus*), Song Sparrow, and Red-eyed Vireo, most common in cottonwood-shrub vegetation, and six species (including Baltimore Oriole, Common Grackle, Mourning Dove, Northern Flicker, and Eastern Kingbird) most common in cottonwood forests without a shrubby understory layer. Litvaitis (1993) found declines in bird abundance with forest maturation after farm abandonment in New England deciduous forest for 18 of 26 species of migratory passerines. Of these 18 species, 8 were associated with early successional vegetation; among these species were several warbler species, including American Redstart (Litvaitis 1993). Landscape-scale predictors of high bird species richness in riparian forests of the Snake River in central Idaho included natural and heterogeneous landscapes, large cottonwood patches, proximity to other patches, and microhabitats with open canopies (Saab 1999).

Early successional bird species showed mostly positive or neutral responses to invasive Russian olive trees or shrubs at the patch scale (Fig. 4; Fig. A4.1 in Appendix 4). This result is consistent with results from some other studies in western North America (Fleishman et al. 2003, Fischer et al. 2012). The only early successional bird species we found to be negatively associated with Russian olive IV was Red-winged Blackbird, but the relationship was only with tree IV, not shrub IV. Indeed, Red-winged Blackbird is an indicator species for wet prairie or young cottonwood/early successional cottonwood-willow vegetation on the lower Missouri and middle Mississippi rivers (Knutson et al. 2005, Thogmartin et al. 2009). Of the 15 species we found positively associated with early successional cottonwood-willow or Russian olive vegetation at the patch or landscape scale, 4 demonstrated significant regional (Central Region of the U.S. Fish and Wildlife Service's Breeding Bird Survey) population declines in both 1966–2015 and 2005–2015 (Sauer et al. 2017). These species included Eastern Kingbird, Brown Thrasher, Common Yellowthroat, and Field Sparrow. In our study area, population declines of early successional bird species could result from the cessation of regular flooding and the decline in regeneration of early successional vegetation since upstream Missouri River dams closed in the 1950s (Hesse 1996, Dixon et al. 2012). Declining populations of early successional bird species along with a reduction in early successional vegetation is consistent with the study by Betts et al. (2010), who showed that early succession-associated bird species in western Oregon deciduous forests were those showing the greatest population declines. Collectively, these data underscore the importance of early successional riparian vegetation to maintenance of regional biodiversity. However, our data suggest that expanding Russian olive vegetation in western North America (Jarnevich and Reynolds 2011, West et al. 2020) can help offset losses of cottonwood-willow early successional riparian vegetation for many of these early successional bird species, so management plans to remove Russian olive without re-establishment of native early successional vegetation will likely affect early successional riparian bird communities negatively (Fischer et al. 2012, Valente et al. 2019).

The only forest bird species to show a positive relationship with eastern red cedar, Northern Cardinal, nests in cedars (D. Swanson, *personal observation*). Of the two species showing negative associations with cedar, Baltimore Orioles were positively associated with cottonwoods and Red-bellied Woodpeckers are cavity nesters. Davis (2005) suggested that replacement of cottonwood-willow forests with eastern red cedar and Russian olive in riparian forest in the central United States may eventually result in the loss of cavity nesting species from riparian habitats, so our data are consistent with this suggestion. Eastern red cedar reaches the northwest extent of its range in southeastern South Dakota, occurring naturally in upland areas, but has markedly increased its coverage in South Dakota and throughout the midwestern United States in recent decades (Schmidt and Leatherberry 1995, Briggs et al. 2002, Meneguzzo and Liknes 2015), including invasion of the cottonwood-dominant riparian forests along the Missouri River in eastern South Dakota (Spencer et al. 2009, Greene and Knox 2014, Illeperuma et al. 2023). Effects of increasing red cedar coverage on woodland bird community structure in the central United States are varied, with both negative (Frost and Powell 2011) and non-significant (Heinan and O'Connell 2009) effects on species richness. Effects of high red cedar densities in central U.S. woodlands on individual species abundances are also varied, with positive, negative, and non-significant responses (Heinen and O'Connell 2009, Frost and Powell 2011). In addition, red cedar may have benefits for populations of wintering birds in our study region (Swanson et al. 2020). Collectively, these data suggest that removal of invasive eastern red cedar from riparian forests may benefit some species but negatively affect others, so management plans for eastern red cedar should consider these varying effects on riparian bird communities before proceeding.

The presence of positive associations and lack of negative associations between bird abundances and common buckthorn shrub IV is perhaps not surprising. Five of the seven species with positive associations to buckthorn shrub IV have been documented to feed on buckthorn berries (Craves 2015). There is relatively little information on the effects of buckthorn abundance on birds, and the results are mixed, sometimes even within species. For example, Labbé and King (2020) found that female gray catbird body condition was negatively related to *Rhamnus* abundance, whereas male body condition was positively related. Smith et al. (2013) found that fruits of native shrubs have greater nutritional value than invasives, including common buckthorn, and that midge (Chironomidae) abundance was lower on *Rhamnus cathartica* than on native shrubs. Given the potential negative effects of this invasive shrub on habitat quality and thus bird populations, additional studies are warranted.

Nine of the 21 species associated with forest at patch or landscape scales showed regional (Central Region of the U.S. Fish and Wildlife Service's Breeding Bird Survey) population declines from 1966–2015, but eight also showed increasing populations over this same time period (Sauer et al. 2017). For both species with significantly decreasing or increasing populations during 1966–2015, population trends for most species tended to become non-significant (i.e., stable) during the more recent 2005–2015 time period (Sauer et al. 2017). If we limit comparisons to woodpeckers and secondary cavity nesters, groups that are tied to mature forest because of the need for large or dead trees, a similar picture

emerges. Two woodpeckers showed declining regional populations over the 1966–2015 period (Northern Flicker, Red-headed Woodpecker), but three (Downy, Hairy [*Dryobates villosus*], and Red-bellied woodpeckers) showed increasing or stable regional populations (Sauer et al. 2017). Similarly, two secondary cavity-nesting species (Black-capped Chickadee, Great Crested Flycatcher) showed population declines from 1966–2015, but two (House Wren, White-breasted Nuthatch) showed population increases (Sauer et al. 2017). These data suggest that maturation of riparian forests is not a general factor influencing recent regional population trends of birds associated with later seral riparian forest stages.

CONCLUSIONS

Our hypotheses regarding riparian bird species richness and individual species vegetation associations were partly supported. Bird species richness was lower for the early successional cottonwood-willow vegetation class than for mid-successional and transitional cottonwood forest classes, supporting our hypothesis of higher species richness in later seral stages. Higher bird species richness with forest, but not shrubland, area on the landscape is also consistent with this hypothesis. Bird species richness did not differ between Russian olive and other vegetation classes, however, which was not consistent with the hypothesis of reduced species richness in woodlands dominated by invasive tree species. Our hypothesis that early successional birds would be positively associated with shrubland area on the landscape and negatively associated with forest area on the landscape, and vice versa for mature forest birds, was supported. Relationships were typically strongest at the smallest landscape scale that we used (200 m radius), suggesting that local, patch-scale conditions were important in defining bird-vegetation associations in Missouri River riparian forests. Finally, Russian olive and eastern red cedar showed both positive and negative effects on different bird species at the patch scale, suggesting that these invasive tree species do not produce general negative effects on abundance across the Missouri River riparian bird community. Management plans for these riparian systems often target invasive tree species removal (Huddle et al. 2011), but our data suggest that such plans for riparian birds need to consider differing effects on individual bird species, the scale of those effects (with patch-scale effects predominating), and the potential for invasive tree species to provide ecological functions that can support riparian bird conservation. Regarding early successional vegetation, which is the most imperiled riparian habitat along the middle Missouri River (Dixon et al. 2012), management plans to promote regeneration of early successional cottonwood-willow habitats are likely to benefit conservation of early successional bird species, but Russian olive also appears to positively affect this bird species group.

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Appendix 1. Bird species.

Bird species included in the analysis are listed in Table A1.1. Species not included in the analysis, e.g. migrants, non-forest species, and those with too few detections, are not included. The superscripts refer to those species with significantly declining populations over the 1966-2015 period, but not over the 2005-2015 period¹, or to species with significantly declining populations over both periods², according to Breeding Bird Survey (BBS) data for the Central BBS Region (Sauer et al. 2017).

Table A1.1. Bird species detected on surveys, with total number of observations and frequencies of detection (out of 588 total surveys) during the study.

Common Name	Scientific Name	Species Code	Number of detections	Number of surveys detected on
American Goldfinch	<i>Spinus tristis</i>	AMGO	265	168
American Redstart	<i>Setophaga ruticilla</i>	AMRE	78	52
American Robin	<i>Turdus migratorius</i>	AMRO	280	206
Baltimore Oriole ¹	<i>Icterus galbula</i>	BAOR	798	392
Bell's Vireo	<i>Vireo bellii</i>	BEVI	228	136
Black-capped Chickadee ¹	<i>Poecile atricapillus</i>	BCCH	182	130
Blue Jay ¹	<i>Cyanocitta cristata</i>	BLJA	335	238
Brown Thrasher ²	<i>Toxostoma rufum</i>	BRTN	206	158
Brown-headed Cowbird	<i>Molothrus ater</i>	BHCO	348	222
Cedar Waxwing	<i>Bombycilla cedrorum</i>	CEDW	70	48
Chipping Sparrow	<i>Spizella passerina</i>	CHSP	26	20
Common Grackle ¹	<i>Quiscalus quiscula</i>	COGR	191	114
Common Yellowthroat ²	<i>Geothlypis trichas</i>	COYE	144	95
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO	93	87
Eastern Bluebird	<i>Sialia sialis</i>	EABL	30	26
Eastern Kingbird ²	<i>Tyrannus tyrannus</i>	EAKI	243	171
Eastern Wood-Pewee ¹	<i>Contopus virens</i>	EAWP	392	273
European Starling ²	<i>Sturnus vulgaris</i>	EUST	74	32
Field Sparrow ²	<i>Spizella pusilla</i>	FISP	221	152

Gray Catbird	<i>Dumetella carolinensis</i>	GRCA	150	115
Great Crested Flycatcher ¹	<i>Myiarchus crinitus</i>	GCFL	158	132
Hairy Woodpecker	<i>Picoides villosus</i>	HAWO	47	44
House Wren	<i>Troglodytes aedon</i>	HOWR	1257	474
Indigo Bunting	<i>Passerina cyanea</i>	INBU	90	77
Lark Sparrow ¹	<i>Chondestes grammacus</i>	LASP	56	43
Mourning Dove ¹	<i>Zenaida macroura</i>	MODO	806	463
Northern Cardinal	<i>Cardinalis cardinalis</i>	NOCA	248	190
Northern Flicker ²	<i>Colaptes auratus</i>	NOFL	160	133
Orchard Oriole ¹	<i>Icterus spurius</i>	OROR	439	261
Ovenbird ¹	<i>Seiurus aurocapilla</i>	OVEN	101	69
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	RBWO	85	75
Red-eyed Vireo	<i>Vireo olivaceus</i>	REVI	210	163
Red-headed Woodpecker ¹	<i>Melanerpes erythrocephalus</i>	RHOW	326	243
Red-winged Blackbird ¹	<i>Agelaius phoeniceus</i>	RWBL	278	103
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	RBGR	450	299
Rufous-sided Towhee	<i>Pipilo spp.</i>	RSTO	376	256
Scarlet Tanager	<i>Piranga olivacea</i>	SCTA	24	20
Song Sparrow	<i>Melospiza melodia</i>	SOSP	182	122
Warbling Vireo	<i>Vireo gilvus</i>	WAVI	331	241
White-breasted Nuthatch	<i>Sitta carolinensis</i>	WBNU	148	126
Wild Turkey	<i>Meleagris gallopavo</i>	WITU	33	31
Willow Flycatcher	<i>Empidonax traillii</i>	WIFL	139	94
Wood Thrush ¹	<i>Hylocichla mustelina</i>	WOTH	97	78
Yellow Warbler	<i>Setophaga petechia</i>	YWAR	1124	413
Yellow-billed Cuckoo ¹	<i>Coccyzus americanus</i>	YBCU	16	15
Yellow-throated Vireo	<i>Vireo flavifrons</i>	YTVI	16	15

Appendix 2. Site classification.

To classify our study sites, we first created two site by tree/shrub species matrices, one for basal area and one for stem density. Within each dataset, we excluded rare species (those which occurred on fewer than 5% of sites) and scaled the values from 0 to 1 by dividing by the maximum value in the dataset. This yielded a 74 site by 23 species matrix for stem density and a 74 site by 13 species matrix for basal area. We then combined the two datasets to form a 74 x 36 site by “species” matrix and calculated the Bray-Curtis dissimilarity matrix. We conducted an agglomerative cluster analysis of sites using Ward's minimum variance method, assessed the optimal number of clusters according to silhouette widths and Mantel statistics, and assigned sites to the newly defined clusters. Visual inspection of the resulting cluster dendrogram (Fig. A2.1), combined with silhouette widths and Mantel tests, yielded an optimal number of five vegetation categories (Fig. 2). The five successional vegetation categories corresponded to these habitat classes: early successional cottonwood-willow, Russian olive, mid-successional cottonwood forest, transitional cottonwood (containing a few large cottonwoods and various later-successional species), and post-cottonwood equilibrium ("equilibrium" sensu Johnson 1992). Analysis was conducted in R (R Core Team 2023) using the vegan package (Oksanen et al. 2020).

Vegetation classes differed in density and basal area of various shrub and tree species or species groups (Figs. A2.2, A2.3).

Figure A2.1. Cluster dendrogram of bird survey sites based on a combination of stem density and basal area of woody plant species. Colors represent the forest type and age class, based on historical aerial imagery, assigned to each site during land-use and land-cover mapping. The red dashed line shows where the dendrogram was cut to form the five habitat classes (Fig. 2) for which bird abundance was estimated (Fig. 3). Colors represent the forest type (CW = cottonwood, NonCW = Non-cottonwood) and age class each site was assigned during land-use and land-cover mapping.

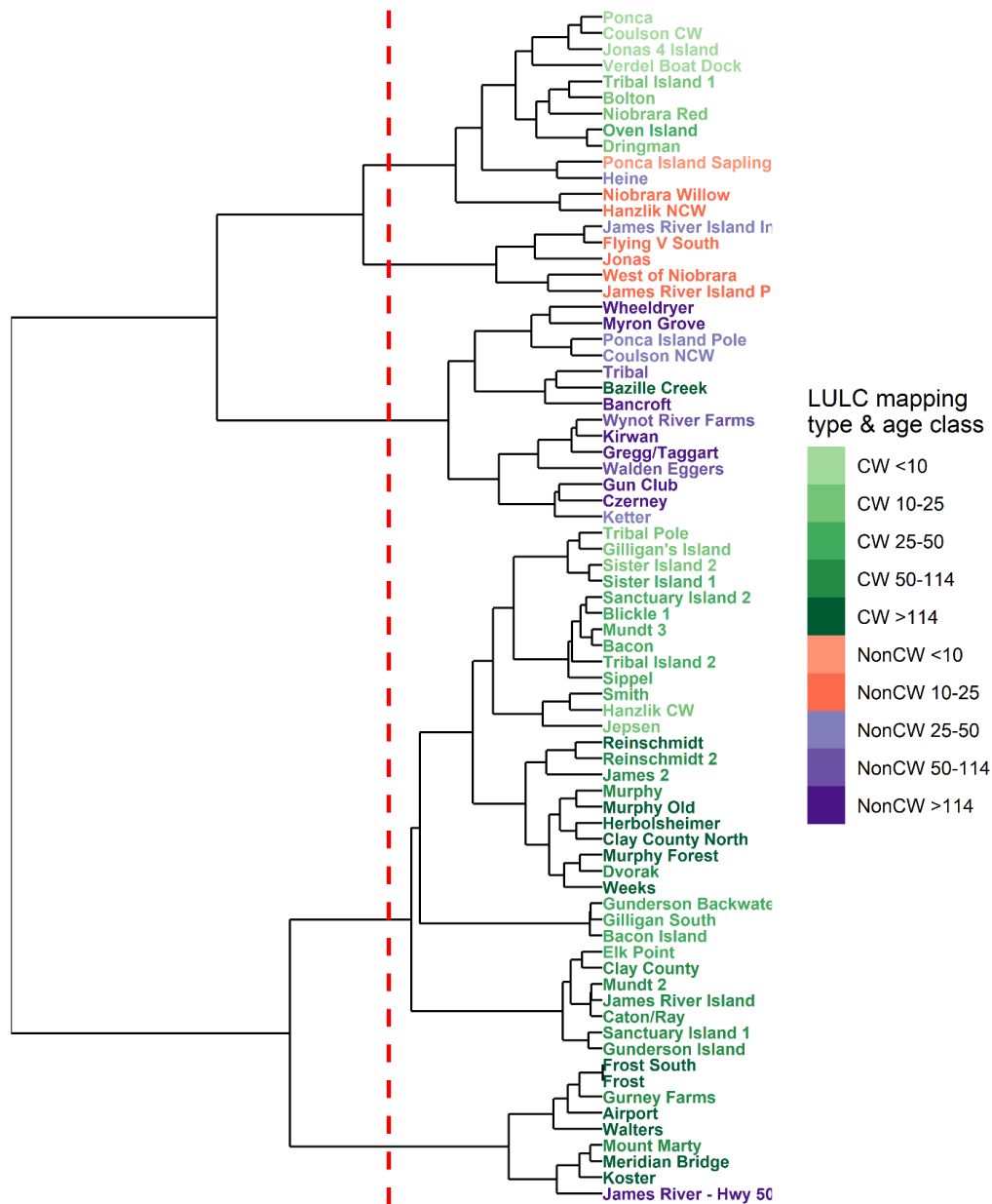


Figure A2.2. Box plots depicting stem density of six of the most common woody plant species or species groups found at bird survey sites. Densities are shown for each of the five habitat types recovered by cluster analysis.

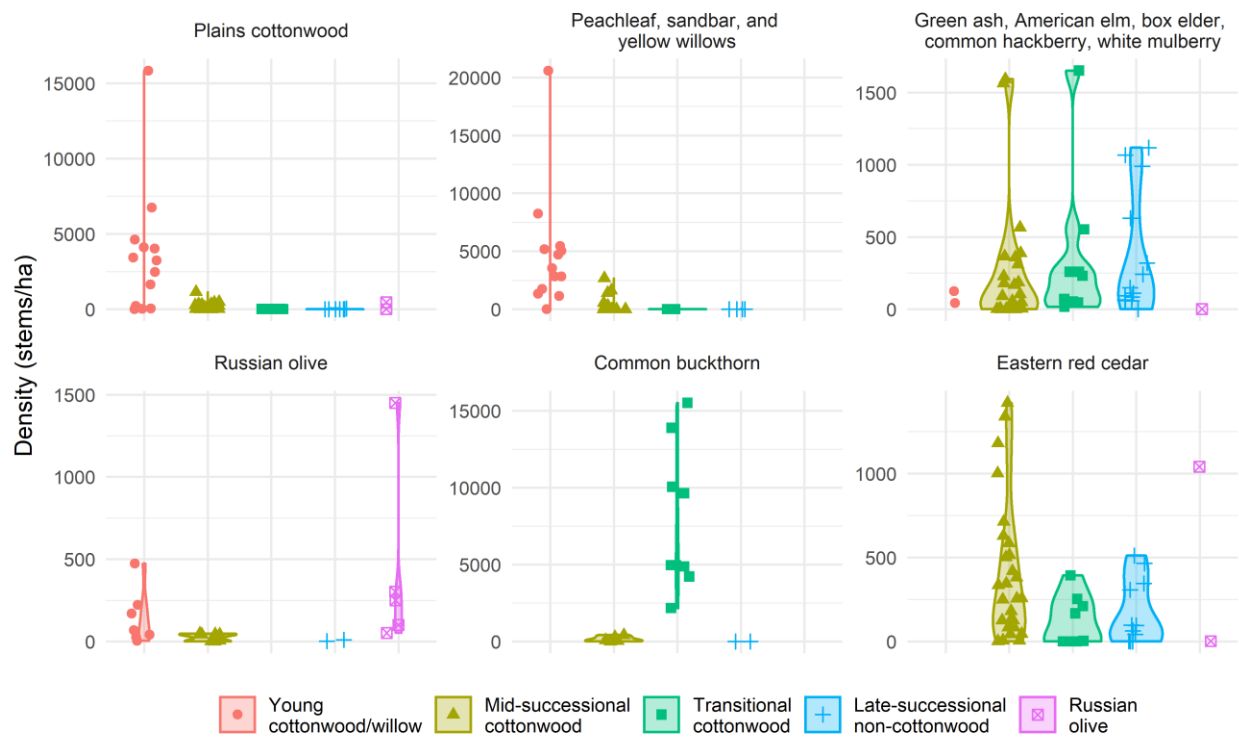
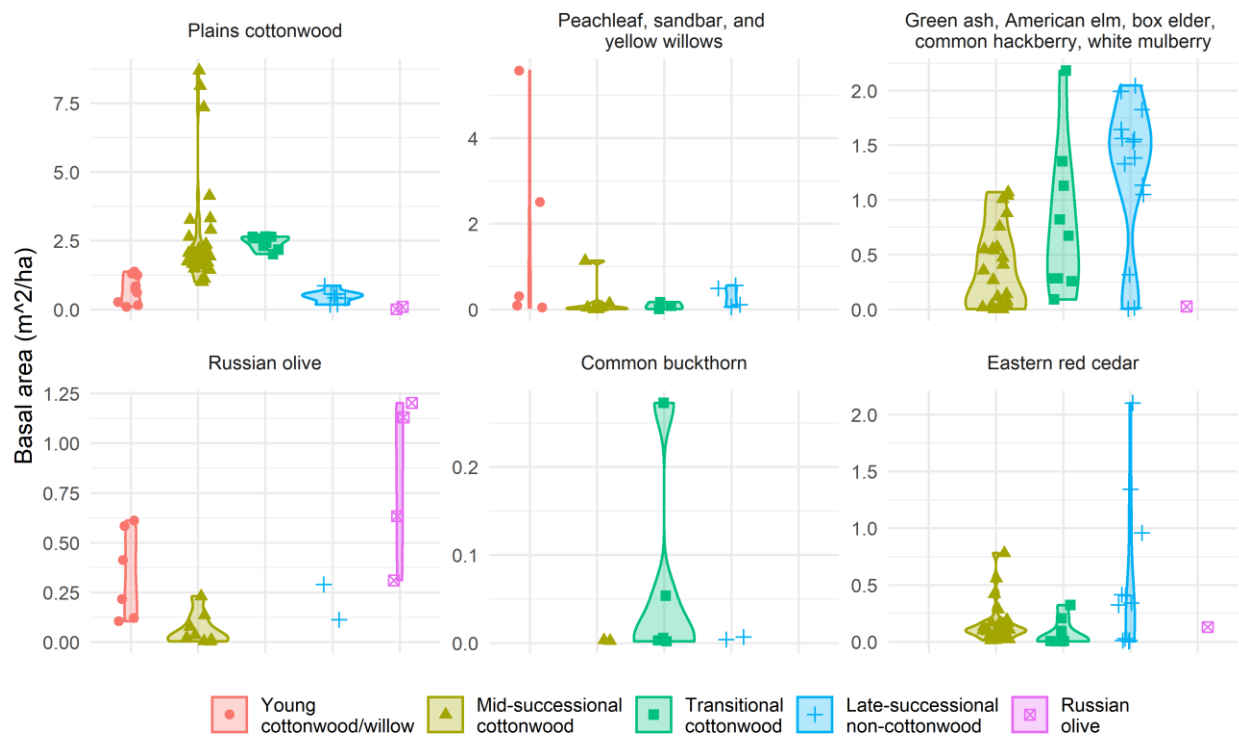


Figure A2.3. Box plots depicting basal area of six of the most common woody plant species or species groups found at bird survey sites. Basal areas are shown for each of the five habitat types recovered by cluster analysis.



Appendix 3. Abundance models.

The following tables give more information about the top model chosen for each species (Table A3.1) and the model selection process (Table A3.2).

Table A3.1. Top abundance models for each species. The top submodel for the observation process (detection) and the state process (abundance) was chosen using a model selection approach. All three possible state submodels included vegetation class (Class) as a predictor. Alternative state submodels included either a random effect of point (1|Point, to account for treating point-years as the sampling unit) or a restricted spatial regression component (RSR, with a 1000 m threshold, to account for spatial autocorrelation in counts). The estimated probability of detection p is given, or three estimates are given for those species which included observer in the observation submodel. Posterior predictive (Bayesian) P -values indicate goodness-of-fit, with values closest to 0.5 indicating the best fit. Species were classified based on their relative abundance in the five vegetation classes as early successional, forest, or other.

Common Name	Top state submodel	Top observation submodel	Estimated detection probability	Posterior predictive P -value	Vegetation class signature
American Goldfinch	$\lambda(\text{Class}+(1 \text{Point}))$	$p(\text{Observer})$	0.12, 0.23, 0.21	0.22	Early successional
American Redstart	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.14	0.5	Other
American Robin	$\lambda(\text{Class})$	$p(.)$	0.085	0.016	Forest
Baltimore Oriole	$\lambda(\text{Class}+\text{RSR})$	$p(\text{Observer})$	0.21, 0.093, 0.11	0.18	Forest
Bell's Vireo	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.22	0.64	Early successional
Black-capped Chickadee	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.15	0.29	Forest
Blue Jay	$\lambda(\text{Class})$	$p(\text{Observer})$	0.21, 0.084, 0.11	0.28	Forest
Brown Thrasher	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.12	0.44	Other
Brown-headed Cowbird	$\lambda(\text{Class}+(1 \text{Point}))$	$p(\text{Observer})$	0.069, 0.16, 0.17	0.019	Other
Cedar Waxwing	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.16	0.35	Other
Chipping Sparrow	$\lambda(\text{Class})$	$p(.)$	0.29	0.24	Other
Common Grackle	$\lambda(\text{Class}+(1 \text{Point}))$	$p(\text{Observer})$	0.12, 0.074, 0.089	0.063	Other
Common Yellowthroat	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.16	0.51	Early successional
Downy Woodpecker	$\lambda(\text{Class})$	$p(.)$	0.091	0.62	Forest
Eastern Bluebird	$\lambda(\text{Class})$	$p(.)$	0.13	0.32	Other
Eastern Kingbird	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.12	0.19	Early successional
Eastern Wood-Pewee	$\lambda(\text{Class})$	$p(\text{Observer})$	0.33, 0.17, 0.2	0.48	Forest

European Starling	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.15	0.23	Other
Field Sparrow	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.15	0.51	Early successional
Gray Catbird	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.099	0.23	Other
Great Crested Flycatcher	$\lambda(\text{Class})$	$p(.)$	0.26	0.42	Forest
Hairy Woodpecker	$\lambda(\text{Class})$	$p(.)$	0.07	0.42	Forest
House Wren	$\lambda(\text{Class})$	$p(\text{Observer})$	0.29, 0.26, 0.22	0.82	Forest
Indigo Bunting	$\lambda(\text{Class})$	$p(\text{Observer})$	0.11, 0.36, 0.35	0.24	Other
Lark Sparrow	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.12	0.34	Early successional
Mourning Dove	$\lambda(\text{Class})$	$p(.)$	0.24	0.96	Other
Northern Cardinal	$\lambda(\text{Class})$	$p(\text{Observer})$	0.26, 0.15, 0.068	0.53	Forest
Northern Flicker	$\lambda(\text{Class}+(1 \text{Point}))$	$p(\text{Observer})$	0.057, 0.11, 0.093	0.20	Other
Orchard Oriole	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.19	0.56	Early successional
Ovenbird	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.23	0.64	Forest
Red-bellied Woodpecker	$\lambda(\text{Class})$	$p(\text{Observer})$	0.097, 0.35, 0.34	0.38	Forest
Red-eyed Vireo	$\lambda(\text{Class})$	$p(.)$	0.22	0.45	Forest
Red-headed Woodpecker	$\lambda(\text{Class}+\text{RSR})$	$p(\text{Observer})$	0.16, 0.096, 0.14	0.84	Forest
Red-winged Blackbird	$\lambda(\text{Class}+(1 \text{Point}))$	$p(.)$	0.25	0.45	Early successional
Rose-breasted Grosbeak	$\lambda(\text{Class}+\text{RSR})$	$p(\text{Observer})$	0.22, 0.16, 0.14	0.78	Forest
Rufous-sided Towhee	$\lambda(\text{Class})$	$p(\text{Observer})$	0.24, 0.12, 0.18	0.27	Forest
Scarlet Tanager	$\lambda(\text{Class})$	$p(.)$	0.25	0.19	Other
Song Sparrow	$\lambda(\text{Class})$	$p(.)$	0.12	0.27	Early successional
Warbling Vireo	$\lambda(\text{Class}+\text{RSR})$	$p(.)$	0.14	0.53	Forest
White-breasted Nuthatch	$\lambda(\text{Class})$	$p(.)$	0.18	0.51	Forest
Wild Turkey	$\lambda(\text{Class})$	$p(\text{Observer})$	0.035, 0.31, 0.51	0.82	Other
Willow Flycatcher	$\lambda(\text{Class}+(1 \text{Point}))$	$p(\text{Observer})$	0.28, 0.079, 0.092	0.72	Early successional
Wood Thrush	$\lambda(\text{Class})$	$p(.)$	0.18	0.21	Forest
Yellow Warbler	$\lambda(\text{Class}+(1 \text{Point}))$	$p(\text{Observer})$	0.3, 0.15, 0.19	0.48	Early successional
Yellow-billed Cuckoo	$\lambda(\text{Class})$	$p(\text{Observer})$	0.058, 0.51, 0.19	0.56	Other
Yellow-throated Vireo	$\lambda(\text{Class})$	$p(.)$	0.18	0.32	Other

Table A3.2. Model selection results for state submodels using the R package ubms. Species names are given in Table A1.1. Each species was analyzed separately. ELPD is the expected log pointwise predictive density and refers to the expected predictive accuracy of the model. Δ ELPD is the difference in ELPD between the given model and the model with the lowest ELPD. SE of Δ ELPD is the standard error of that difference. For the species with no ELPD given, only one model could be fitted, so no model selection was performed. See Table A3.1 for explanation of the state submodels. Only models which could be successfully fitted are included in this table. In some cases, indicated with footnotes, the model with the highest ELPD had a low posterior predictive p-value, in which case that model was not used and the model with the next highest ELPD was considered instead. In those cases, additional model selection comparisons were made (not shown) to assess the Δ ELPD and SE of Δ ELPD for those model sets.

Species	State submodel	ELPD	N. Param.	Δ ELPD	SE of Δ ELPD	Weight
AMGO [‡]	Class+RSR1000	-511.8	18.1	0.0	0.00	0.55
	Class+(1 point)	-515.0	64.7	-3.2	7.63	0.45
	Class	-531.8	10.5	-20.0	9.34	0.00
AMRE	Class+(1 point)	-190.4	35.6	0.0	0.00	0.79
	Class+RSR1000	-212.2	13.9	-21.9	12.64	0.21
	Class	-235.3	8.5	-45.0	13.98	0.00
AMRO	Class	-553.4	6.1	0.0	0.00	0.57
	Class+RSR1000	-553.8	12.7	-0.3	2.49	0.43
BAOR	Class+RSR1000	-859.7	25.8	0.0	0.00	0.33
	Class	-880.5	8.9	-20.8	7.11	0.06
BCCH	Class+(1 point)	-390.8	52.5	0.0	0.00	0.94
	Class	-402.2	7.5	-11.4	5.41	0.06
BEVI	Class+(1 point)	-354.4	52.2	0.0	0.00	0.89
	Class+RSR1000	-389.3	20.7	-34.9	11.88	0.11
	Class	-409.5	7.0	-55.1	15.75	0.00
BHCO	Class+(1 point)	-627.7	74.5	0.0	0.00	0.49
	Class+RSR1000	-629.8	23.8	-2.1	9.02	0.51
	Class	-655.7	12.0	-28.0	12.07	0.00
BLJA	Class	-567.1	8.4	0.0	0.00	0.55
	Class+RSR1000	-567.8	14.4	-0.8	3.38	0.45
BRTH	Class+(1 point)	-433.2	47.6	0.0	0.00	0.89
	Class+RSR1000	-447.7	16.5	-14.5	7.26	0.11
	Class	-455.4	7.8	-22.2	6.99	0.00
CEDW [†]	Class+(1 point)	-219.9	48.1	0.0	0.00	0.73
	Class	-250.1	11.3	-30.2	18.90	0.27
CHSP	Class+RSR1000	-105.0	11.3	0.0	0.00	0.59
	Class	-105.9	7.4	-0.9	3.78	0.41

COGR	Class+(1 point)	-435.2	77.8	0.0	0.00	0.77
	Class	-477.5	14.7	-42.3	18.38	0.23
	Class+RSR1000	-479.4	27.5	-44.2	17.88	0.00
COYE	Class+(1 point)	-298.1	47.3	0.0	0.00	1.00
	Class	-325.1	7.1	-27.0	8.05	0.00
DOWO	Class	-263.7	3.9	0.0	0.00	0.92
	Class+RSR1000	-265.5	8.8	-1.8	2.11	0.08
EABL	Class	-	-	-	-	-
EAKI	Class+(1 point)	-499.6	54.7	0.0	0.00	1.00
	Class	-516.8	7.2	-17.2	5.66	0.00
EAWP	Class+RSR1000	-579.0	14.2	0.0	0.00	0.94
	Class	-583.6	8.0	-4.6	3.24	0.06
EUST [†]	Class+(1 point)	-231.7	67.7	0.0	0.00	0.65
	Class	-287.5	15.3	-55.9	48.00	0.35
FISP	Class+(1 point)	-401.3	55.2	0.0	0.00	1.00
	Class	-443.1	7.1	-41.8	8.63	0.00
GCFL	Class+RSR1000	-359.5	10.6	0.0	0.00	0.91
	Class	-364.7	5.6	-5.2	3.88	0.09
GRCA	Class+(1 point)	-373.1	49.0	0.0	0.00	0.87
	Class+RSR1000	-382.8	16.1	-9.7	5.80	0.13
	Class	-383.8	7.0	-10.7	4.99	0.00
HAWO	Class	-	-	-	-	-
HOWR	Class+RSR1000	-972.8	14.7	0.0	0.00	0.72
	Class	-975.3	7.6	-2.5	3.40	0.28
INBU	Class	-	-	-	-	-
LASP	Class+(1 point)	-177.4	36.2	0.0	0.00	1.00
	Class	-187.7	7.5	-10.2	5.03	0.00
MODO	Class	-836.5	5.0	0.0	0.00	0.59
	Class+RSR1000	-837.1	10.3	-0.5	2.39	0.41
NOCA	Class+RSR1000	-451.3	13.5	0.0	0.00	0.84
	Class	-461.7	8.4	-10.4	5.93	0.16
NOFL [‡]	Class+(1 point)	-387.9	23.4	0.0	0.00	0.99
	Class	-389.1	7.9	-1.3	1.33	0.00
	Class+RSR1000	-390.8	12.5	-3.0	2.29	0.00
OROR	Class+(1 point)	-610.2	56.6	0.0	0.00	0.85
	Class+RSR1000	-627.9	15.4	-17.7	7.74	0.15
	Class	-645.4	7.4	-35.1	7.79	0.00
OVEN	Class+(1 point)	-192.0	40.3	0.0	0.00	0.56
	Class+RSR1000	-196.7	14.9	-4.7	7.94	0.44

	Class	-249.7	5.6	-57.8	9.72	0.00
RBGR	Class+RSR1000	-617.3	15.4	0.0	0.00	1.00
	Class	-633.7	7.2	-16.4	4.87	0.00
RBWO	Class	-238.3	8.0	0.0	0.00	0.63
	Class+RSR1000	-239.5	13.5	-1.2	3.32	0.37
REVI	Class	-	-	-	-	-
RHOW	Class+RSR1000	-535.4	12.0	0.0	0.00	1.00
	Class+(1 point)	-546.6	21.5	-11.2	3.77	0.00
	Class	-551.6	4.7	-16.4	4.38	0.00
RSTO	Class+RSR1000	-602.3	15.1	0.0	0.00	0.58
	Class	-602.8	8.0	-0.5	2.77	0.42
RWBL	Class+(1 point)	-346.9	64.3	0.0	0.00	0.97
	Class	-453.0	13.2	-106.2	20.36	0.03
SCTA	Class	-	-	-	-	-
SOSP	Class	-340.1	4.6	0.0	0.00	0.51
	Class+RSR1000	-340.2	9.5	0.0	2.35	0.49
WAVI	Class+RSR1000	-543.2	9.8	0.0	0.00	1.00
	Class	-551.6	5.6	-8.4	3.68	0.00
WBNU	Class	-	-	-	-	-
WIFL	Class+(1 point)	-277.8	42.2	0.0	0.00	0.87
	Class+RSR1000	-291.3	15.0	-13.4	6.60	0.13
	Class	-293.3	8.6	-15.5	5.92	0.00
WITU	Class	-113.5	6.4	0.0	0.00	1.00
	Class+RSR1000	-116.7	10.0	-3.2	1.24	0.00
WOTH	Class	-	-	-	-	-
YBCU	Class	-	-	-	-	-
YEWA	Class+(1 point)	-947.6	78.3	0.0	0.00	0.80
	Class+RSR1000	-976.3	31.4	-28.8	10.53	0.20
	Class	-1028.1	10.7	-80.5	12.85	0.00
YTVI	Class	-	-	-	-	-

† The SE of the difference in ELPDs was greater than our cutoff, so the model with the next lowest ELPD was chosen. That model, however, had a low goodness-of-fit score, so it was removed from contention and the random effect model was chosen instead.

‡ The model containing the restricted spatial regression had a low goodness-of-fit, so it was removed from contention and the model with the next lowest ELPD was chosen instead.

Appendix 4. Correlations.

Correlations between bird abundances and land cover proportions at various buffer distances, along with species classifications based on those correlations are given in Table A4.1.

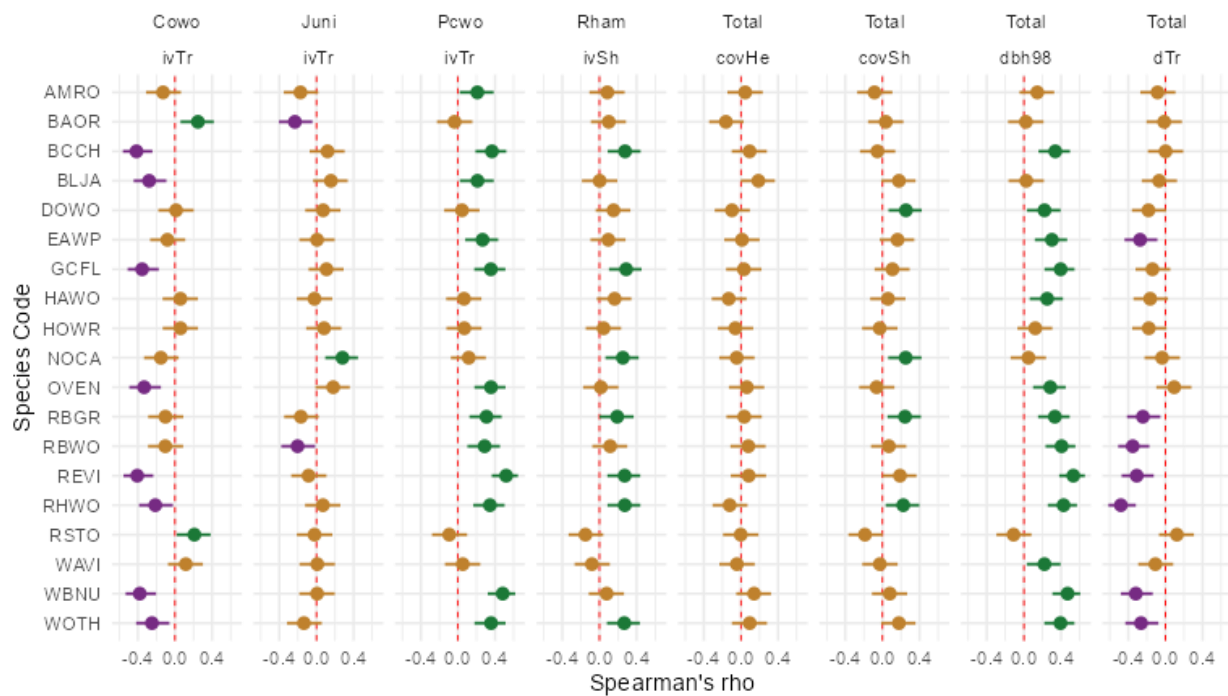
Correlations between bird abundances and vegetation characteristics for early successional bird species are shown in Figure A4.1, while those for forest bird species are shown in Figure A4.2.

Table A4.1. Correlations between bird abundance and the proportion of shrubland and forest land cover classes within 200, 400, and 1200 m buffers of points. Bird abundance was calculated as the maximum number of individuals detected at a point across four visits over two years. Land cover was calculated as the proportion of area of a given land cover type, forest or shrubland, within the buffer distance. Land cover data from our land cover mapping. We considered a correlation statistically significant if its 95% confidence interval did not overlap 0 and denote them in blue font. The strongest significant correlation with each land cover type is indicated with bold font. Birds were classified as early successional (ES) associates if they showed a positive significant correlation with shrubland land cover and early successional specialists if they also showed a large significant negative correlation with forest land cover. Birds were classified as forest (F) associates if they showed a positive significant correlation with forest land cover and forest specialists if they also showed a large significant negative correlation with shrubland land cover.

Species	Forest 200 m	Forest 400 m	Forest 1200 m	Shrub 200 m	Shrub 400 m	Shrub 1200 m	Landscape Classification
American Goldfinch	-0.34	-0.23	0.01	0.44	0.36	0.33	ES Associate
American Redstart	0.06	0.03	0.09	0.14	0.22	0.13	ES Associate
American Robin	0.05	-0.01	-0.01	-0.20	-0.14	-0.18	Generalist
Baltimore Oriole	0.18	0.11	-0.08	-0.15	-0.11	-0.02	F Associate
Bell's Vireo	-0.58	-0.50	-0.23	0.63	0.54	0.40	ES Specialist
Black-capped Chickadee	0.34	0.32	0.16	-0.41	-0.44	-0.48	F Specialist
Blue Jay	0.22	0.15	0.05	-0.19	-0.17	-0.06	F Associate
Brown Thrasher	-0.08	-0.08	-0.03	0.26	0.29	0.29	ES Associate
Brown-headed Cowbird	-0.44	-0.39	-0.21	0.48	0.45	0.37	ES Specialist
Cedar Waxwing	0.01	0.04	0.01	0.10	0.03	0.05	Generalist
Chipping Sparrow	0.00	0.01	0.06	-0.09	-0.14	-0.09	Generalist
Common Grackle	-0.05	-0.07	-0.12	0.10	0.09	0.08	Generalist
Common Yellowthroat	-0.39	-0.30	-0.12	0.34	0.32	0.29	ES Associate
Downy Woodpecker	0.36	0.33	0.18	-0.30	-0.22	-0.11	F Associate
Eastern Bluebird	0.19	0.18	0.20	-0.01	0.01	0.08	F Associate

Eastern Kingbird	-0.44	-0.42	-0.20	0.51	0.43	0.37	ES Specialist
Eastern Wood-Pewee	0.46	0.37	0.08	-0.49	-0.41	-0.22	F Specialist
European Starling	0.03	0.03	0.07	-0.08	-0.04	0.03	Generalist
Field Sparrow	-0.48	-0.43	-0.12	0.61	0.55	0.37	ES Specialist
Gray Catbird	-0.03	-0.03	0.03	0.10	0.07	0.06	Generalist
Great Crested Flycatcher	0.26	0.26	0.19	-0.31	-0.34	-0.28	F Associate
Hairy Woodpecker	0.18	0.19	0.05	-0.24	-0.25	-0.11	F Associate
House Wren	0.39	0.36	0.16	-0.30	-0.25	-0.12	F Associate
Indigo Bunting	0.00	0.01	0.05	-0.02	0.01	-0.11	Generalist
Lark Sparrow	-0.27	-0.27	-0.19	0.30	0.27	0.17	ES Associate
Mourning Dove	-0.13	-0.09	0.07	0.33	0.27	0.27	ES Associate
Northern Cardinal	0.38	0.34	0.10	-0.33	-0.30	-0.10	F Associate
Northern Flicker	0.25	0.26	0.24	-0.29	-0.25	-0.10	F Associate
Orchard Oriole	-0.52	-0.42	-0.05	0.56	0.54	0.37	ES Specialist
Ovenbird	0.23	0.18	0.28	-0.32	-0.33	-0.29	F Associate
Red-bellied Woodpecker	0.33	0.34	0.17	-0.25	-0.22	-0.27	F Associate
Red-eyed Vireo	0.52	0.45	0.20	-0.57	-0.50	-0.46	F Specialist
Red-headed Woodpecker	0.46	0.44	0.21	-0.54	-0.50	-0.36	F Specialist
Red-winged Blackbird	-0.52	-0.42	-0.23	0.46	0.41	0.29	ES Specialist
Rose-breasted Grosbeak	0.44	0.35	0.09	-0.56	-0.46	-0.29	F Specialist
Rufous-sided Towhee	0.29	0.31	0.22	-0.22	-0.17	-0.10	F Associate
Scarlet Tanager	0.19	0.18	0.11	-0.19	-0.19	-0.13	F Associate
Song Sparrow	-0.50	-0.40	-0.17	0.42	0.38	0.32	ES Specialist
Warbling Vireo	0.19	0.15	0.07	-0.32	-0.25	-0.24	F Associate
White-breasted Nuthatch	0.36	0.31	0.15	-0.57	-0.51	-0.38	F Specialist
Wild Turkey	0.11	0.09	0.03	-0.06	-0.08	-0.22	Generalist
Willow Flycatcher	-0.48	-0.40	-0.06	0.52	0.44	0.36	ES Specialist
Wood Thrush	0.29	0.24	0.05	-0.33	-0.33	-0.31	F Associate
Yellow Warbler	-0.29	-0.22	-0.15	0.41	0.38	0.44	ES Associate
Yellow-billed Cuckoo	0.04	0.07	0.07	0.02	0.04	-0.09	Generalist
Yellow-throated Vireo	0.04	0.05	0.11	-0.01	-0.04	-0.13	Generalist

Fig A4.2. Forest bird–vegetation correlations. Spearman’s rank correlation coefficient between bird abundances and selected vegetation measurements of interest. Point estimates and 95% confidence intervals are shown, with the vertical reference lines indicating zero correlation. Yellow confidence intervals overlap zero. Vegetation measurements include total tree density (Total dTr), total shrub cover (Total covSh), the 98th percentile of tree diameter at breast height (DBH) (Total dbh98), cottonwood (Cowo) tree importance value, late successional (Pcwo) tree importance value, eastern red cedar (Juni) tree importance value, and common buckthorn (Rham) shrub importance value. Bird species names are provided in Appendix 1.



Appendix 5. Bird species richness.

Additional results from the bird species richness analysis, including correlation between bird species richness and land cover composition (Table A5.1) and mean species richness for sites in the five vegetation classes (Fig. A5.1).

Table A5.1. Spearman's correlation coefficients (ρ_s) and P -values for relationships between point-level bird species richness and forest or shrubland on the landscape at 200, 400 and 1200 buffers surrounding riparian bird survey points in the Missouri National Recreational River.

Buffer	Forest ρ_s	Forest P	Shrubland ρ_s	Shrubland P
200 m	0.19	0.001	-0.11	0.051
400 m	0.21	< 0.001	-0.06	0.288
1200 m	0.18	0.002	-0.04	0.459

Figure A5.1. Bird species richness for each of the five vegetation categories recovered by cluster analysis. Large dots are means, lines are 95% confidence intervals, and small dots are bird survey points. For each point, abundance was calculated as the maximum number of individuals seen at the point across four visits over two years. Only shrub/forest associated breeding species are included. There was a statistically significant difference in richness between at least two vegetation classes ($F_{4,69} = 3.719$, $P = 0.008$), with early successional cottonwood-willow sites being less species rich than both mid-successional ($P = 0.028$) and equilibrium ($P = 0.033$) sites.

