



Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks



Jennifer L. Reidy^{a,*}, Frank R. Thompson III^b, Sarah W. Kendrick^a

^a Department of Fisheries and Wildlife Sciences, University of Missouri, 302 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA

^b United States Department of Agriculture, Forest Service, Northern Research Station, 202 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA

ARTICLE INFO

Article history:

Received 21 August 2013

Received in revised form 25 October 2013

Accepted 29 October 2013

Keywords:

Bird density

Canopy cover

Distance-based models

Landscape forest cover

Prescribed burns

Tree density

ABSTRACT

Savanna and woodland were once common in the Midwest, but land use changes have led to increasing scarcity of these communities. These transitional habitats are being restored across the Midwest, but few studies have evaluated the response of wildlife to restoration or the vegetative gradient created by management. We conducted point counts for 25 songbirds at sites undergoing savanna or woodland restoration and nearby non-managed forest sites across the Ozark Highlands of Missouri during the 2009–2011 breeding seasons; these sites represented a gradient of canopy cover and tree density from savanna to woodland to forest. We estimated density of 17 species with ≥ 50 detections using distance-based models, which adjust estimates by the detection probability. Bird densities were more strongly related to habitat structure, fire history, and landscape composition than simply whether a site was managed or non-managed. Mature forest species such as Acadian Flycatcher (*Empidonax virens*), Northern Parula (*Setophaga americana*), Red-eyed Vireo (*Vireo olivaceus*), and Worm-eating Warbler (*Helmitheros vermivorum*) were generally more abundant at points with more trees, higher canopy cover, lower shrub density, and less frequent or no fire in the 20 years prior to surveys. Woodland generalists such as Blue-gray Gnatcatcher (*Polioptila caerulea*), Eastern Wood-Pewee (*Contopus virens*), Great Crested Flycatcher (*Myiarchus crinitus*), Summer Tanager (*Piranga rubra*), and Yellow-billed Cuckoo (*Coccyzus americanus*) were generally more abundant at points with less landscape forest cover (10-km scale), more large and fewer small trees, intermediate to high canopy cover, lower shrub density, and recent or frequent fire. Early-successional species such as Eastern Towhee (*Pipilo erythrophthalmus*), Field Sparrow (*Spizella pusilla*), Indigo Bunting (*Passerina cyanea*), Kentucky Warbler (*Geothlypis formosa*), Prairie Warbler (*Setophaga discolor*), White-eyed Vireo (*Vireo griseus*) and Yellow-breasted Chat (*Icteria virens*) were generally more abundant at points with lower canopy cover, recent or frequent fire, and higher shrub density. Brown-headed Cowbirds (*Molothrus ater*) were more abundant at points with intermediate landscape forest cover and lower canopy cover. Restored sites provided breeding habitat for woodland generalists and early-successional species of conservation concern; however, managed landscapes with more open canopy and herbaceous ground cover may be required for species more indicative of open savannas.

© 2013 Published by Elsevier B.V.

1. Introduction

Savanna and woodland are semi-wooded communities composed of a ground layer dominated by grasses and forbs, a sparse understory, and <50% tree canopy cover in savanna and 50–90% canopy cover in woodland (McPherson, 1997; Anderson et al., 1999; Nelson, 2002, 2005). These transitional communities were historically maintained by natural and anthropogenic fire, grazing by native herbivores such as bison (*Bison bison*) and elk (*Cervus canadensis*), and other natural disturbances (Nelson, 2005).

Savanna and woodland occurred across as much as 11–13 million ha of the Midwestern United States prior to European settlement, but fire suppression, overgrazing by livestock, and land conversion over the past two centuries have resulted in most savanna and woodland succumbing to closed-canopy forest or being converted to pasture (Nuzzo, 1986; Anderson, 1998). Midwestern savanna and fire-dependent woodland are considered endangered habitat types (Nigh, 1992; Noss et al., 1995). Missouri once had up to 8.5 million ha of savanna and woodland, and only 2.4 million ha of these communities remain, most in a generally degraded condition (Nelson, 2005).

Interest in restoring savanna and woodland communities continues to grow throughout the Midwest (Au et al., 2008; Mabry et al., 2010), including many areas in Missouri (Nigh, 1992; Nelson,

* Corresponding author. Tel.: +1 5738081505.

E-mail address: jennifer.reidy@gmail.com (J.L. Reidy).

2005). State and federal agencies began restoring savanna and woodland communities in the early 1980s using prescribed fire and mechanical tree thinning (McCarty, 1993) with the primary goal of maintaining the high floristic diversity of these natural communities (McCarty, 1993; U.S. Department of Agriculture, 2005). Increasing emphasis focuses on exploring the importance of restoration sites to wildlife populations (Leach and Ross, 1995).

Breeding birds are an ideal group to study across this habitat gradient, because they are relatively easy to survey and we have existing knowledge of habitat preferences and population trends in other regions or habitat types. Previous studies have documented higher bird diversity at savanna or woodland restoration sites than nearby prairie (Au et al., 2008) or forest sites (Davis et al., 2000; Brawn, 2006; Au et al., 2008). However, Mabry et al. (2010) found that diversity within savanna and woodland sites was dependent on the surrounding landscape. While few birds are considered savanna specialists (Brawn, 2006; Grundel and Pavlovic, 2007a), savanna and woodland provide breeding habitat for some declining, early-successional birds (Davis et al., 2000; Hunter et al., 2001; Brawn, 2006; Barrioz et al., 2013), indicating their potential importance for conservation of rare or declining bird species that rely on disturbance (Brawn et al., 2001).

Savanna and woodland were historically part of a landscape mosaic as Eastern deciduous forests transitioned into Midwestern prairies. However, restoration tends to be small-scale and site-specific (Leach and Ross, 1995; Davis et al., 2000; Mabry et al., 2010) and most studies have focused on management effects independent of the surrounding landscape (Davis et al., 2000). Because wildlife abundance is constrained by a spatial hierarchy that suggests landscape scale effects provide context for effects at the local habitat scale (Thompson et al., 2002), breeding bird communities are likely influenced by both site-level management and the surrounding landscape (Mabry et al., 2010).

Savanna and woodland restoration is occurring throughout the Midwest to promote floristic diversity and enhance biological diversity across the landscape, but little is known about the benefits to breeding birds, particularly within highly forested landscapes. The Ozark Highlands are highly forested and rugged in the east and south of their range, and flatten to rolling plains in the west and north of their range, becoming increasingly fragmented by agriculture (i.e. cropland and pastures; Nigh and Schroeder, 2002). Varying habitat and landscape characteristics presented an opportunity to evaluate the importance of site-level and landscape-level attributes of restored savanna and woodland to breeding birds in this region. By integrating multiple spatial scales, we seek to better inform which habitat and landscape factors influence bird communities in restored savanna and woodland sites and use this information to guide future management and restoration decisions in the Midwest. Our objectives were to determine densities of focal bird species in managed and non-managed sites and to investigate relationships between point-level habitat structure and large-scale landscape composition and bird densities.

2. Methods

2.1. Study areas

We conducted this study across the Ozark Highlands of Missouri (with the exception of one site located ~26 km outside the defined boundary; Fig. 1). The region is an ecotone between the deciduous forests of eastern North America and the prairies of central North America characterized by rolling to rugged terrain dissected by deep river valleys to the east and south and large plains to the west (The Nature Conservancy, 2003). The Ozark Highlands are predominantly composed of oak (*Quercus* spp.)-hickory (*Carya* spp.) and

oak-hickory-pine (*Pinus* sp.) woodland and forest, interspersed with bluestem (*Andropogon gerardii*, *Schizachyrium scoparium*) prairie, fescue (*Festuca* spp.) pasture, and glades dominated by Eastern red cedar (*Juniperus virginiana*; Nelson, 2005). Dominant species of forested upland and mesic slopes include post oak (*Quercus stellata*), blackjack oak (*Quercus marilandica*), white oak (*Quercus alba*), northern red oak (*Quercus rubra*), bitternut hickory (*Carya cordiformis*), shortleaf pine (*Pinus echinata*), and flowering dogwood (*Cornus florida*; Nelson, 2005).

We collaborated with state and federal agencies to identify 18 study areas that included managed sites that were undergoing savanna or woodland restoration and showed a substantial vegetative response to restoration. The primary management tool was prescribed fire, but some managed sites were also treated by tree thinning or herbicides. Managed sites were burned 1–8 times and 1–15 times in the 10 and 20 years, respectively, prior to surveys and ranged in size from 4 to 2324 ha (mean = 208 ha, SD = 361). We also selected non-managed sites on each study area that were forest with no management for >30 years and on similar landforms and within 5 km of managed sites. Ten sites were owned and managed by the Missouri Department of Conservation, six sites by the Missouri Department of Natural Resources, and one site each by The Nature Conservancy and the U.S. Department of Agriculture Forest Service. Local site conditions and degree of management led to highly heterogeneous vegetation structure within managed sites, whereas non-managed sites had largely succeeded to closed-canopy forest and had a more uniform structure characterized by high canopy cover and tree density and little herbaceous ground cover.

2.2. Data collection

2.2.1. Bird surveys

We surveyed abundance of 25 breeding bird species that represented species of regional conservation concern (Partners in Flight, 2012) or that we hypothesized would respond to restoration and were reasonably common. We chose to limit surveys to target species to minimize errors in species identification and allow observers adequate time to record detections and measure distances. We conducted 10-min unlimited-radius point count surveys from late May through early July 2009–2011. We overlaid a grid of points at 250-m intervals over a site and chose a random starting point and subsequent points along transects composed of up to 15 points such that all points were >50 m from the boundary of a managed site. Surveys were conducted with wind speeds <14 kph, little or no precipitation, temperature >10 °C, and between approximately 15 min after sunrise and 1000 h CDT. Each point was surveyed once. Observers recorded the exact time of initial detection and exact distance to individual singing males of target species (Table 1). We measured distances with laser range-finders (Bushnell Yardage Pro, Bushnell, Overland Park, Kansas, USA) but sometimes had to estimate distance when we could not focus the rangefinder on or near the bird because of vegetation or topography. All observers were trained in species identification and distance estimation. Observers recorded multiple individuals of the same species at a point only if they were confident they were different individuals (e.g. simultaneous detections).

2.2.2. Vegetation surveys

We sampled habitat structure at each survey location by measuring canopy cover, percent ground cover, leaf litter depth, shrub density, and tree density following a modified BBIRD protocol (Martin et al., 1997). We developed our vegetation sampling design to provide a comprehensive overview of habitat structure using standard protocols. We calculated point-level canopy cover as the average of four spherical densiometer readings (one in each

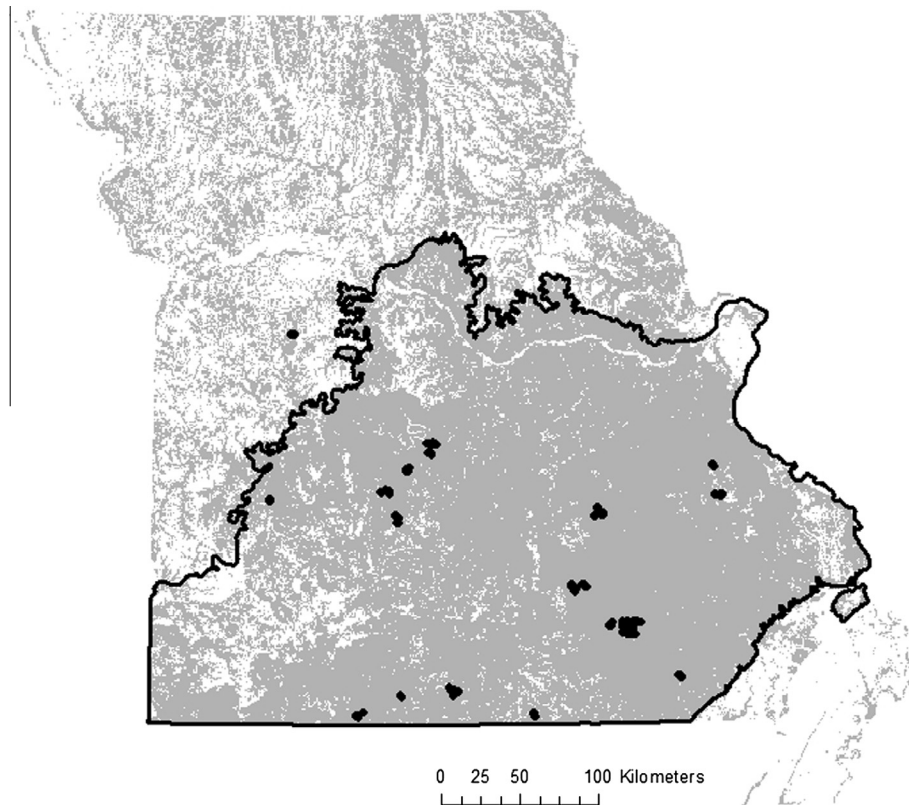


Fig. 1. Locations (black circles) of sites within the Ozark Highlands (black outline) in Missouri surveyed between late May and early July 2009–2011. Forest land cover is gray and all other land cover or use is white.

Table 1
Number of singing males detected (Det.) of 25 focal species, and predicted densities (singing males/ha), standard errors (SE), and 95% confidence limits (LCL, UCL) from a model with landscape and type (managed or non-managed) variables of 17 modeled species detected during point counts in the Missouri Ozark Highlands, 2009–2011.

Species	Managed points (n = 565)					Non-managed points (n = 362)				
	Det.	Density	SE	LCL	UCL	Det.	Density	SE	LCL	UCL
Northern bobwhite (<i>Colinus virginianus</i>)	1	–	–	–	–	1	–	–	–	–
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>) ^a	97	0.12	0.02	0.09	0.15	26	0.06	0.01	0.04	0.09
Red-headed woodpecker (<i>Melanerpes erythrocephalus</i>)	13	–	–	–	–	9	–	–	–	–
Eastern Wood-Pewee (<i>Contopus virens</i>)	488	0.39	0.03	0.34	0.46	255	0.32	0.03	0.27	0.38
Acadian Flycatcher (<i>Empidonax virens</i>)	261	0.37	0.03	0.32	0.44	298	0.62	0.05	0.52	0.73
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	57	0.09	0.02	0.06	0.14	12	0.03	0.01	0.02	0.06
Eastern kingbird (<i>Tyrannus tyrannus</i>)	6	–	–	–	–	0	–	–	–	–
White-eyed Vireo (<i>Vireo griseus</i>) ^a	74	0.32	0.07	0.21	0.48	16	0.18	0.06	0.09	0.33
Red-eyed vireo (<i>Vireo olivaceus</i>) ^a	425	0.91	0.08	0.77	1.08	279	1.22	0.13	0.99	1.50
Blue-gray Gnatcatcher (<i>Poliptila caerulea</i>) ^a	270	1.17	0.12	0.96	1.42	125	0.95	0.12	0.75	1.21
Wood thrush (<i>Hylocichla mustelina</i>)	11	–	–	–	–	16	–	–	–	–
Brown thrasher (<i>Toxostoma rufum</i>)	0	–	–	–	–	3	–	–	–	–
Worm-eating Warbler (<i>Helmitheros vermivorum</i>)	38	0.05	0.01	0.03	0.09	73	0.14	0.03	0.09	0.22
Blue-winged warbler (<i>Vermivora pinus</i>)	14	–	–	–	–	10	–	–	–	–
Common yellowthroat (<i>Geothlypis trichas</i>) ^a	5	–	–	–	–	4	–	–	–	–
Kentucky Warbler (<i>Oporornis formosus</i>)	58	0.14	0.02	0.10	0.20	72	0.27	0.04	0.19	0.37
Northern parula (<i>Setophaga americana</i>) ^a	88	0.15	0.03	0.11	0.21	85	0.23	0.05	0.16	0.35
Prairie Warbler (<i>Setophaga discolor</i>)	198	0.12	0.02	0.09	0.16	56	0.05	0.01	0.03	0.07
Yellow-breasted Chat (<i>Icteria virens</i>)	196	0.22	0.02	0.18	0.26	70	0.15	0.02	0.11	0.19
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	62	0.07	0.01	0.04	0.10	17	0.03	0.01	0.02	0.05
Field Sparrow (<i>Spizella pusilla</i>)	76	0.11	0.02	0.07	0.17	8	0.03	0.01	0.01	0.06
Summer Tanager (<i>Piranga rubra</i>)	257	0.48	0.05	0.40	0.58	101	0.30	0.04	0.23	0.39
Indigo Bunting (<i>Passerina cyanea</i>) ^a	515	1.13	0.10	0.96	1.34	84	0.35	0.05	0.27	0.46
Brown-headed Cowbird (<i>Molothrus ater</i>)	139	0.18	0.04	0.13	0.27	72	0.15	0.03	0.10	0.23
Orchard oriole (<i>Icterus spurius</i>)	0	–	–	–	–	3	–	–	–	–

^a Recorded in 2010 and 2011 only.

cardinal direction) at the point. We estimated percent herbaceous ground cover in a 5-m radius around the point. We averaged litter depth recorded 2 m from the point in each cardinal direction. We

counted woody stems <2.5-cm wide at 0.5 m above ground in a 5-m radius and converted this count to density of stems/ha (shrub density); at points with extremely high stem counts, we reduced

the sampled area to a 1-m radius. We measured diameter-at-breast height (DBH) of stems >2.5 cm DBH in an 11.3-m radius and recorded trees as deciduous, evergreen (cedars and pines), or snag. We calculated densities of seedlings and saplings (2.5–12.5 cm DBH), pole timber (12.5–27.5 cm DBH), and saw timber (>27.5 cm DBH), and density of dead trees (snags) >12.5 cm DBH. We also calculated percent tree stocking (hereafter stocking) from DBH values for deciduous trees, evergreen trees, and total live trees using equations for upland oaks and hickories and shortleaf pine (Johnson et al., 2009). Stocking represents the percentage of a plot covered by tree canopies predicted from DBH values and can be >100% because canopies can overlap.

2.2.3. Landscape composition

We calculated percent landscape forest cover within a 10-km radius around each point, and mean canopy cover within 100 m of each point using Fragstats v3 (McGarigal et al., 2002) and the 2006 National Land Cover Dataset (NLCD; Fry et al., 2011) in ArcMap 10 (ESRI, Redlands, California, USA). We categorized the landform at each point as ridge, north- or east-facing slope, south- or west-facing slope, bottomland, and upland drainage based on a digital elevation model using ArcMap 10.

2.2.4. Fire history

We obtained the fire history of each site from local managers for the 20 years prior to surveys. Non-managed sites had no management for 30 years prior to the study and most had not experienced fire in >50 years. We categorized the number of years since the last burn as 0, 1–2, 3–4, 5–20, and >20 years because we did not necessarily hypothesize effects to be linear and we did not know the exact years since burned for plots >20 years. We classified years since last burn as 0 if the site burned between the previous fall and spring of the survey year. We also summed the number of burns at each point 10 and 20 years prior to the survey.

2.3. Data analysis

We used a model selection approach to compare candidate models and evaluate support for the effects of management, habitat, and landscape factors on the density of each species. We developed hierarchical distance-based density models in the R package “unmarked” that uses distance sampling to estimate a detection function and Poisson regression to consider covariate effects on density (Royle et al., 2004; Fiske and Chandler, 2011). The assumptions of distance sampling are individuals at distance zero are always detected, individuals are detected at their initial location, and distances to the detected individuals are accurately estimated (Buckland et al., 2001), which we addressed through observer training. We only included target species with >50 detections. We binned detection distances into 20-m intervals to a maximum distance of 100 m. We evaluated multi-collinearity and did not include variables in individual models that resulted in tolerance values <0.4 (Allison, 1999) in SAS 9.3 (SAS Institute Inc., North Carolina, USA). We standardized all continuous variables to a mean of zero and a SD of one to facilitate model convergence (SAS 9.3). We constructed and evaluated candidate models in multiple steps (described below) for each species to reduce the number of total models fit.

We first compared support for half-normal, hazard, and uniform key detection functions based on Akaike's information criterion adjusted for small sample sizes (AIC_c); these are three standard distance-based detection functions used with point counts (Buckland et al., 2001). We then used the most-supported key function and evaluated support for all singular and additive combinations of day of year (day), minutes since sunrise (mins), temperature (temp), and observer (obs), and a null model consisting of an

intercept for a total of 16 possible detection models. We evaluated day, mins, and temp because of their potential influence on singing rates and hence, detectability. We carried forward all variables and the most-supported detection function from the most-supported model and any additional variables from models with substantial support ($\Delta AIC_c < 1$).

We compared support among habitat or landscape variables that measured similar characteristics and retained the most-supported variable in candidate models; this allowed us to eliminate redundancy among variables while enabling us to consider competing and sometimes novel measures of the same characteristics. These groups of similar variables included: linear and quadratic measures of percent forest cover in the landscape as measures of landscape-level forest cover; linear and quadratic stocking, stocking by deciduous and evergreen forest classes, and tree density by size class as measures of tree structure; linear and quadratic canopy cover measured by spherical densiometer and linear and quadratic mean canopy cover within a 100-m radius derived from NLCD as measures of canopy cover; linear and quadratic measures of shrub density; and years since last burn, number of burns in 10 years prior, and number of burns in 20 years prior as measures of fire history. We then brought forward the most-supported variable representing forest cover, tree structure, canopy cover, shrub density, and fire history for each species. We also considered snag density, proportion of herbaceous ground cover, and litter depth if we hypothesized a species was influenced by those variables based on foraging and nesting habits and our literature review. We developed species-specific sets of candidate models that included the most-supported detection function, variables used to model detectability, and single and additive combinations of the selected habitat and landscape variables for the density portion of the model, which resulted in a final set of up to 27 candidate models for each species (Table A1). All models included forest cover and landform to control for these landscape features while evaluating relationships between habitat and management-related factors and bird density. We included a null habitat model in the candidate set that consisted of the supported detection covariates and only an intercept for the density model. We also included a “type” model that included the landscape variables (forest cover and landform) and a binomial variable indicating whether the point was managed or not.

We ranked candidate models for each species by AIC_c and evaluated goodness-of-fit for the most-supported model with the Freeman-Tukey test based on a parametric bootstrap for 100 simulations (Fiske and Chandler, 2011; Sillett et al., 2012). We report model-averaged predictions of bird density for managed and non-managed points and as a function of covariates that had large effect sizes from a confidence set of models with $\Delta AIC_c < 4$ (Burnham and Anderson, 2002). We considered effect sizes large if model-averaged predictions of density varied >20% from the 1st–99th percentile of observed values for a covariate. We used this approach to focus our inference because of the many species, models, and variables. This approach also incorporated model selection uncertainty, focused on effects that we judged large enough to potentially have biological importance, excluded predictions for outlier values for covariates, and avoided significance testing of model coefficients (Burnham and Anderson, 2002). To evaluate the hypothesis that birds were responding to the individual components of habitat structure as opposed to the holistic summation of management effects captured by whether a site was managed or not, we compared the most-supported model based on habitat variables to the type model with an evidence ratio based on Akaike weights; evidence ratios provide an easy interpretation of the likelihood for one model over another (Burnham and Anderson, 2002). We also report the total number of individual males detected of all focal species in managed and non-managed

sites to provide comparative data for studies that do not estimate detectability, and because not all species met the minimum sample size to estimate density.

3. Results

We surveyed 565 points in managed sites (170, 122, and 273 in 2009, 2010, and 2011, respectively) and 362 points in non-managed sites (145, 124, and 93 in 2009, 2010, and 2011, respectively) on 18 study areas. Survey points spanned the gradient from open savanna with 0% canopy cover to forest with 100% canopy cover. There was substantial overlap in structure between managed and non-managed points, but managed points generally had lower stocking, tree density, canopy cover, and litter depth, and greater herbaceous cover and shrub density than non-managed points (Table 2).

We rarely detected 8 of the 25 target species (Table 1). We detected more Red-headed Woodpecker (*Melanerpes erythrocephalus*), Eastern Kingbird (*Tyrannus tyrannus*), and Blue-winged Warbler (*Vermivora pinus*) and fewer Brown Thrasher (*Toxostoma rufum*), Orchard Oriole (*Icterus spurius*), and Wood Thrush (*Hylocichla mustelina*) males at managed points, whereas we detected similar numbers of Northern Bobwhite (*Colinus virginianus*) and Common Yellowthroat (*Geothlypis trichas*) at managed and non-managed points. Eastern Kingbird was not detected at non-managed points and Brown Thrasher and Orchard Oriole were not detected at managed points.

We fit density models to 17 species with >50 detections (Table 3). There was no evidence of lack of fit for the most-supported model for 16 of the 17 species based on goodness-of-fit tests ($P > 0.10$); however, the goodness-of-fit test for Field Sparrow failed to integrate, likely due to sparse data. Detectability was related to observer for the 10 species in which we were able to include it (Table 3). Support for effects of temp, mins, and day on detectability varied by species, but at least two of these factors were supported for each species (Table 3).

We found relationships between bird density and habitat and landscape variables for all species, but in all cases there was more than one model with $\Delta AIC_c < 4$ so we model-averaged density predictions (Tables 3 and A1). Support for the top model with habitat

and landscape variables had >14 times the support than the management type model for all species except Kentucky Warbler, which was 2.27, based on evidence ratios. We included forest cover in all models except the null for every species, but could only include landform in all models for nine species because of convergence problems presumably caused by model complexity for species with low numbers of detections (Table A1). Therefore, we evaluated landform as a competing model for these eight species. The null, landform, and management type models tended to receive little or no support by themselves for most species; however, landform was supported in combination with measures of vegetation structure (Table 3). The quadratic form of landscape forest cover was supported over the linear form for 10 species (Table A1). Landscape forest cover was a strong predictor of density for all species except Acadian Flycatcher (Table 4). Predicted densities of woodland generalists (Blue-gray Gnatcatcher, Eastern Wood-Pewee, Great Crested Flycatcher, Summer Tanager, and Yellow-billed Cuckoo) declined with increasing forest cover (Fig. 2). Densities of mature forest species generally increased (Northern Parula, Red-eyed Vireo, and Worm-eating Warbler) or were unaffected (Acadian Flycatcher) with increasing forest cover (Fig. 2). Increasing forest cover had mixed effects on densities of early-successional species: Eastern Towhee, Prairie Warbler, and Yellow-breasted Chat increased; Indigo Bunting and Kentucky Warbler decreased; and Field Sparrow and White-eyed Vireo peaked at intermediate levels of forest cover (Fig. 2). Density was related to landform for seven species for which it was included in all models (Fig. A1).

Tree density or stocking was in the top model for 10 species (Table 3) and showed large effects on the densities of 14 species (Table 4). Density of Yellow-breasted Chat was negatively related, and Red-eyed Vireo positively related, to tree density in all size classes (Fig. 3A–C). Densities of Eastern Wood-Pewee, Field Sparrow, Indigo Bunting, and Summer Tanager were negatively related to sapling density (Fig. 3A); density of Summer Tanager was also negatively related to pole timber density (Fig. 3B); and density of Eastern Wood-Pewee was positively related, and Indigo Bunting and Kentucky Warbler negatively related, to saw timber density (Fig. 3C). Four species showed strong relationships between density and stocking by deciduous or evergreen trees: densities of Acadian Flycatcher and Northern Parula were positively, and

Table 2
Descriptive statistics for survey conditions and vegetation and landscape characteristics of point locations in a study of breeding bird densities across a savanna, woodland, forest gradient in the Missouri Ozark Highlands, 2009–2011. See methods for description of variables.

Variable ^a	Managed points (n = 565)				Non-managed points (n = 362)				P ^b
	Mean	SD	Min ^b	Max ^b	Mean	SD	Min ^a	Max ^a	
Temperature (°C)	23.20	3.79	11.11	31.67	21.96	4.33	7.22	30.00	
Minutes since sunrise	135.78	72.76	13.00	259.00	129.54	71.71	17.00	262.00	
Day of year	169.93	10.25	149.00	189.00	167.80	8.81	150.00	187.00	
Percent forest	76.44	13.38	26.94	93.18	76.14	16.90	27.10	93.85	0.7654
Deciduous stocking (%)	66.97	38.84	0.00	167.23	82.19	37.12	4.03	169.95	<0.0001
Evergreen stocking (%)	8.50	19.61	0.00	75.86	5.16	16.45	0.00	81.57	0.0139
Total stocking (%)	75.47	44.19	0.24	175.53	87.35	39.81	4.17	196.43	<0.0001
Shrubs ha ⁻¹	1511.58	2185.72	0	9779	1363.13	1809.48	50	9250	0.3932
Sapling ha ⁻¹	371.77	381.30	0.00	1500	665.95	434.44	0.00	1975	<0.0001
Pole timber ha ⁻¹	198.36	142.05	0.00	625	204.70	152.83	0.00	725	0.5206
Saw timber ha ⁻¹	99.82	71.04	0.00	275	110.22	72.57	0.00	325	0.0313
Snag ha ⁻¹	22.04	38.49	0.00	175	19.41	32.36	0.00	125	0.2812
Point-level canopy cover (%)	77.46	27.86	0.00	100.00	89.04	18.46	0.00	100.00	<0.0001
Canopy cover mean (%)	82.99	10.23	41.62	93.51	85.14	7.77	48.48	93.06	0.0007
Burns10	2.54	1.49	0.00	8.00	0.00	0.00	0.00	0.00	<0.0001
Burns20	4.06	2.69	0.00	15.00	0.00	0.00	0.00	0.00	<0.0001
Herbaceous ground cover (%)	28.11	25.27	0.00	95.75	18.79	21.16	0.00	92.50	<0.0001
Litter depth (mm)	14.78	14.38	0.00	58.75	26.49	16.81	0.00	71.25	<0.0001

^a Minimum and maximum values based on the 1st and 99th percentile of values.

^b Based on ANOVA run in SAS 9.3.

Table 3

Number of parameters (K), Akaike weight (w_i) based on Akaike's Information Criteria, and P -value from Freeman-Tukey goodness-of-fit test for the top-ranked habitat (λ) and detection (σ) model predicting density of singing males of 17 species in the Missouri Ozark Highlands, 2009–2011. See Table A1 for full model results.

Species	Model ^a	K	w_i	P
Yellow-billed Cuckoo ^{b,c}	$\lambda(\text{forest}^2 + \text{stocking}^2 + \text{shrub} + \text{burns}) \sigma(\text{temp} + \text{day})$	15	0.48	0.43
Eastern Wood-Pewee	$\lambda(\text{forest} + \text{landform} + \text{tree size} + \text{burns20}) \sigma(\text{obs} + \text{mins} + \text{day})$	20	0.51	0.72
Acadian Flycatcher	$\lambda(\text{forest}^2 + \text{landform} + \text{tree group} + \text{canopy}^2 + \text{shrub} + \text{burns}) \sigma(\text{obs} + \text{temp} + \text{mins})$	26	0.77	0.61
Great Crested Flycatcher ^{b,c}	$\lambda(\text{forest} + \text{canopy mean}^2 + \text{burns20}) \sigma(\text{temp} + \text{mins})$	8	0.27	0.42
White-eyed Vireo	$\lambda(\text{forest}^2 + \text{landform} + \text{stocking}^2 + \text{canopy}^2 + \text{shrub}^2 + \text{burns}) \sigma(\text{obs} + \text{day})$	25	0.48	0.47
Red-eyed Vireo	$\lambda(\text{forest}^2 + \text{landform} + \text{tree size} + \text{canopy mean} + \text{shrub} + \text{burns}) \sigma(\text{obs} + \text{temp} + \text{day})$	26	0.44	0.70
Blue-gray Gnatcatcher	$\lambda(\text{forest} + \text{landform} + \text{tree group} + \text{burns20}) \sigma(\text{obs} + \text{mins} + \text{day})$	18	0.15	0.26
Worm-eating Warbler ^{b,c}	$\lambda(\text{forest} + \text{canopy}^2 + \text{shrub}^2 + \text{burns10}) \sigma(\text{temp} + \text{day})$	11	0.55	0.47
Kentucky Warbler ^c	$\lambda(\text{forest}^2 + \text{burns10} + \text{herbaceous}) \sigma(\text{obs} + \text{temp} + \text{day})$	13	0.20	0.51
Northern Parula	$\lambda(\text{forest}^2 + \text{landform} + \text{canopy} + \text{shrub}^2) \sigma(\text{obs} + \text{mins})$	17	0.36	0.51
Prairie Warbler ^b	$\lambda(\text{forest} + \text{landform} + \text{canopy}^2 + \text{burns}) \sigma(\text{temp} + \text{day})$	18	0.40	0.34
Yellow-breasted Chat ^c	$\lambda(\text{forest} + \text{tree size} + \text{canopy}^2 + \text{shrub}^2 + \text{burns}) \sigma(\text{obs} + \text{temp})$	22	0.63	0.53
Eastern Towhee ^{b,c}	$\lambda(\text{forest} + \text{tree group} + \text{canopy mean}^2 + \text{shrub}^2 + \text{burns20}) \sigma(\text{temp} + \text{day})$	12	0.53	0.38
Field Sparrow ^{b,c}	$\lambda(\text{forest}^2 + \text{canopy} + \text{shrub} + \text{burns}) \sigma(\text{temp} + \text{mins} + \text{day})$	14	0.48	–
Summer Tanager ^c	$\lambda(\text{forest}^2 + \text{tree size} + \text{shrub} + \text{burns}) \sigma(\text{obs} + \text{day})$	19	0.34	0.58
Indigo Bunting	$\lambda(\text{forest}^2 + \text{landform} + \text{tree size} + \text{canopy}^2 + \text{burns}) \sigma(\text{obs} + \text{temp} + \text{mins} + \text{day})$	27	0.26	0.28
Brown-headed Cowbird ^b	$\lambda(\text{forest}^2 + \text{landform} + \text{canopy}) \sigma(\text{mins} + \text{day})$	13	0.23	0.36

^a obs = Observer; temp = temperature; mins = minutes since sunrise; day = day of year; forest = percent forest cover in a 10-km radius of the point; forest2 = forest + forest²; landform = landform type; stocking = percent stocking of live trees at a point; stocking² = stocking + stocking²; tree group = percent deciduous stocking + percent evergreen stocking; tree size = sapling ha⁻¹ + pole timber ha⁻¹ + saw timber ha⁻¹; snag density = snag ha⁻¹; canopy = point-level canopy cover; canopy² = canopy + canopy²; canopy mean = mean canopy cover in a 100-m radius of a point; canopy mean² = canopy mean + canopy mean²; shrub = small woody stem density; burns = years since burned; burns10 = total burns 10 years prior to study; burns20 = total burns 20 years prior to study.

^b Observer not included in detection model set.

^c Landform included as competing model.

Table 4

Summary of effects of landscape and habitat variables on predicted densities of 17 species surveyed in the Missouri Ozark Highlands, 2009–2011. Symbols indicate a positive (+), negative (–), quadratic (□), or no (×) effect. Blanks indicate variable was not evaluated.

Species	Forest cover	Sapling density	Pole timber density	Saw timber density	Stocking	Canopy cover	Shrub density	Fire frequency ^a
Yellow-billed Cuckoo	□				–	□	–	+
Eastern Wood-Pewee	–	–	×	+		+	×	+
Acadian Flycatcher	×				± ^b	+	–	–
Great Crested Flycatcher	–				×	□	□	+
White-eyed Vireo	□				–	□	+	□
Red-eyed Vireo	+	+	+	+		+	–	–
Blue-gray Gnatcatcher	–				– ^b	×	×	+
Worm-eating Warbler	+				□	+	–	–
Kentucky Warbler	–	×	×	–		×	×	–
Northern Parula	□				± ^b	+	□	×
Prairie Warbler	+				×	–	×	+
Yellow-breasted Chat	+	–	–	–		–	+	□
Eastern Towhee	+				± ^b	□	+	–
Field Sparrow	□	–	×	×		–	+	+
Summer Tanager	□	–	–	×		×	–	+
Indigo Bunting	–	–	×	–		×	×	+
Brown-headed Cowbird	□	×	×	×		–	×	×

^a Fire frequency is + if density response was positively related to frequency or recency of fire.

^b Acadian Flycatcher responded positively and negatively to increased deciduous and evergreen stocking, respectively; Blue-gray Gnatcatcher responded negatively to evergreen stocking; Northern Parula responded positively to deciduous stocking; and Eastern Towhee responded negatively and positively to increased deciduous and evergreen stocking.

Eastern Towhee negatively, related to higher deciduous stocking (Fig. 4A), whereas density of Eastern Towhee was positively, and Acadian Flycatcher and Blue-gray Gnatcatcher were negatively, related to higher evergreen stocking (Fig. 4B). The quadratic form of stocking was supported for four species. Densities of White-eyed Vireo and Yellow-billed Cuckoo had an overall negative relationship with stocking, whereas Worm-eating Warbler density peaked at intermediate levels of stocking (Fig. 4C). Snag density was not related to the densities of five species for which we evaluated it (Table A1).

A measure of canopy cover was in the top model for 12 species (Table 3) and had large effects on the densities of 13 species (Table 4). Quadratic forms of point-level canopy cover or mean canopy cover were supported for seven and three species, respectively

(Table A1). Densities of early-successional species generally peaked at low or intermediate levels of point-level canopy cover (Fig. 5A) or mean canopy cover (Fig. 5B). Densities of mature forest species tended to show a positive response to increasing point-level canopy cover (Fig. 5A) or mean canopy cover (Fig. 5B). Densities of woodland generalists peaked at intermediate levels of point-level canopy cover (Fig. 5A) or high levels of mean canopy cover (Fig. 5B).

Shrub density was in the top model for 10 species (Table 3) and had large effects on the densities of 11 species (Table 4). The quadratic form was supported over the linear for seven species (Table A1). Densities of mature forest and woodland generalist species had a generally negative relationship with shrub density (although Great Crested Flycatcher and Northern Parula densities

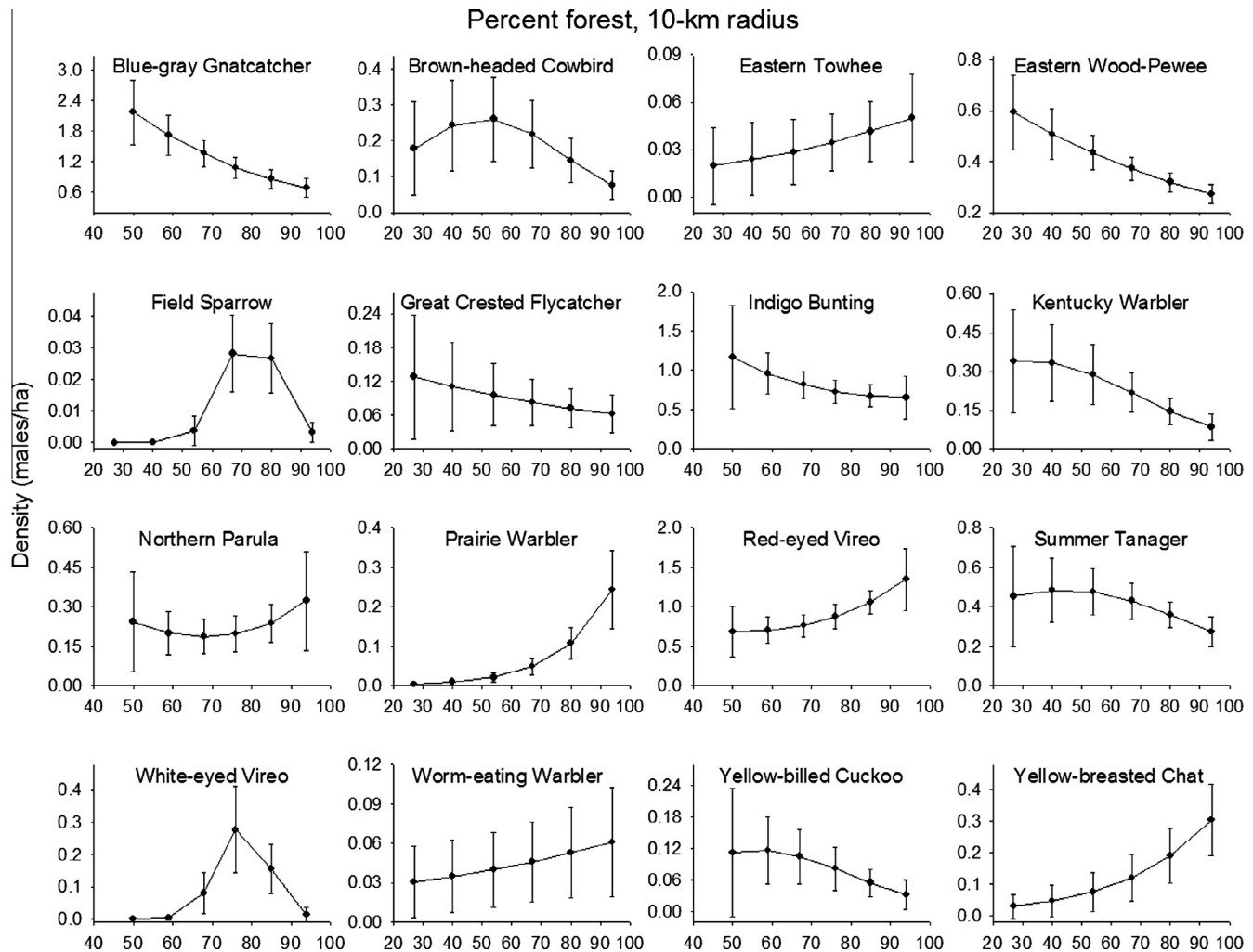


Fig. 2. Predicted density and 95% confidence intervals of 16 focal species across a gradient of forest cover in a 10-km radius at points surveyed in the Missouri Ozark Highlands, late May–early July 2009–2011.

peaked at intermediate values), whereas four early-successional species had a positive relationship (Fig. 6). The response of early-successional species was weaker than other species.

Densities were related to fire history for all species except Brown-headed Cowbird and Northern Parula (Fig. 7 and Table 4); years since burned, number of burns in 10 years prior, and number of burns in 20 years prior were in the top model for nine, two, and four species, respectively (Table 3). We were not able to examine years since burned for Eastern Towhee due to model complexity. Densities of Summer Tanager and Yellow-billed Cuckoo and early-successional species peaked between 1 and 4 years since burned (Fig. 7A), whereas Acadian Flycatcher and Red-eyed Vireo densities peaked at points that had not been burned in at least five years (Fig. 7A). Field Sparrow was the only species whose density peaked in the year following a burn (Fig. 7A). White-eyed Vireo and Yellow-breasted Chat reached the highest densities several years post-fire (Fig. 7A). Kentucky and Worm-eating Warblers showed a negative response to number of burns in 10 years prior to the study (Fig. 7B). Densities of three woodland generalists and Brown-headed Cowbird were positively related to number of burns in 20 years prior, whereas Eastern Towhee density declined (Fig. 7C).

Herbaceous cover was related to density of two species and litter depth was related to density of one species (Table A1). Density

of Kentucky Warbler increased 24% (0.16, 95% CI [0.10–0.22] to 0.20, 95% CI [0.09–0.31]), whereas density of White-eyed Vireo decreased by 26% (0.29, 95% CI [0.14–0.44] to 0.23, 95% CI [0.04–0.42]) over the range of herbaceous cover. Eastern Towhee density decreased 23% (0.04, 95% CI [0.02–0.06] to 0.03, 95% CI [0.01–0.05]) over the range of litter depth.

4. Discussion

We examined the effects of restoration management on a diverse array of songbirds by evaluating support for relationships between habitat and landscape attributes and bird densities using models that simultaneously account for factors that may affect species' detection. In general, managed sites supported higher densities of early-successional and woodland generalist species than birds associated with open savanna habitats such as Eastern Kingbirds, consistent with other studies of restoration effects in forested landscapes (Comer et al., 2011; Barrioz et al., 2013) and contrary to studies in less-forested landscapes that concluded the bird community was composed primarily of grassland-adapted species (Grundel and Pavlovic, 2007a). These results paired with the effect of landscape forest cover on the densities of 16 of 17 species, imply that breeding bird communities are at least partially landscape dependent.

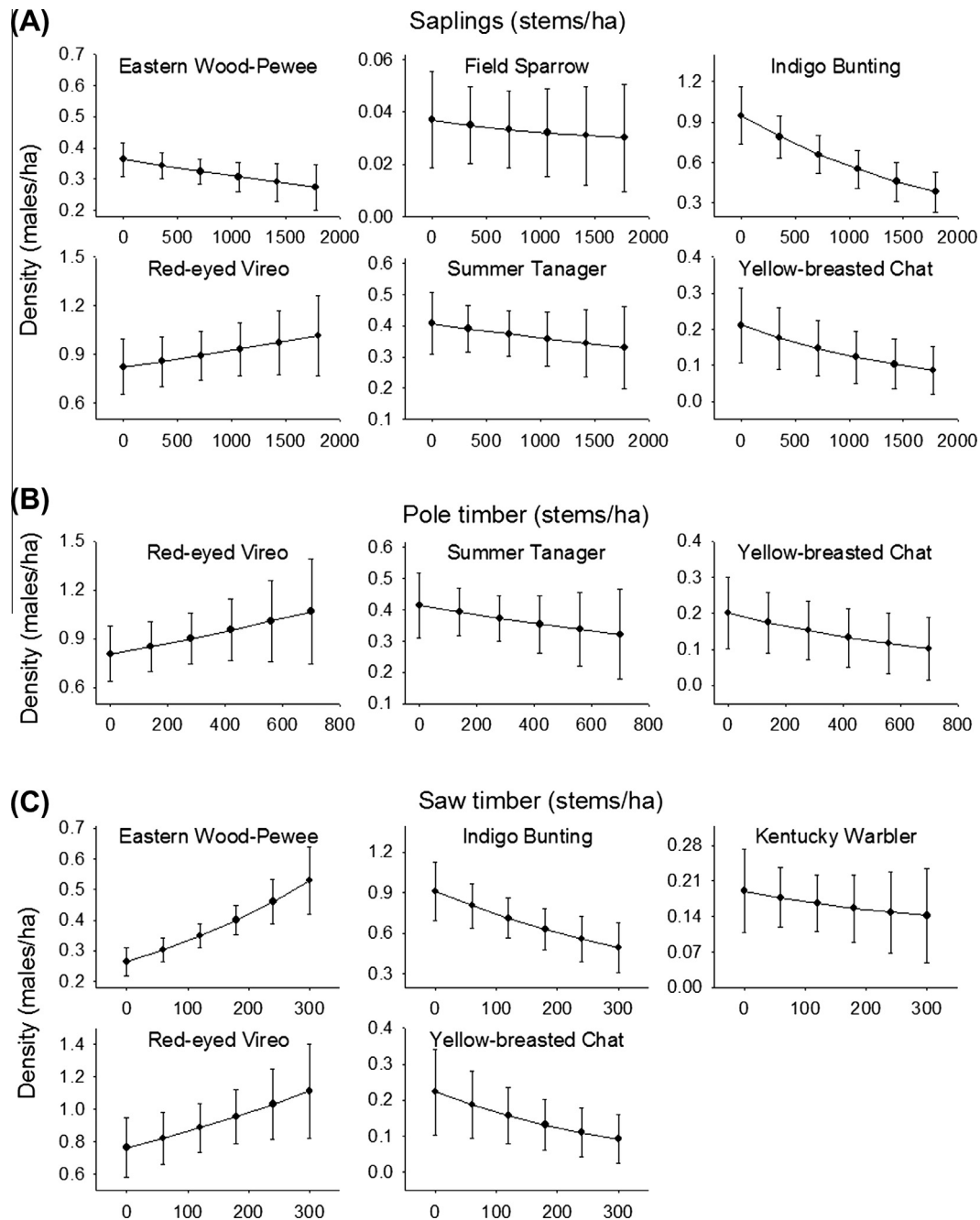


Fig. 3. Predicted density and 95% confidence intervals of seven focal species across the observed range of tree density by size class: (A) sapling, (B) pole timber and (C) saw timber at points surveyed in the Missouri Ozark Highlands, late May–early July 2009–2011.

Managed and control sites differed structurally, but management status alone was a poor predictor of bird densities at our sites. Managed points had lower overall tree density, sapling density, canopy cover, and litter depth, and higher shrub density and percent herbaceous ground cover than adjacent non-managed points, indicating that to some degree, managed sites had the desired response to restoration. However, densities of mid- and large-size trees, snags, and mean canopy cover were similar at managed and non-managed points. This suggests that, on average, the effects of restoration were mostly limited to the ground and understory vegetation. Heterogeneity in structure within managed sites was great and likely a result of variable intensity and coverage of prescribed fires in large management units. The overlap in vegetative characteristics at our managed and non-managed points

may explain the lack of support for management type effects compared to support for relationships with measured structural or compositional characteristics of the habitat and landscape.

Land managers seeking to restore savanna and woodland often gauge management goals by achieving certain criteria, typically defined by canopy cover or tree density (Anderson, 1998). However, summarizing our results by evaluating the influence of canopy cover or tree density is difficult because relationships between habitat and landscape variables and bird density were not necessarily supported across an entire species guild (i.e. mature forest vs. early-successional species). For example, not all mature forest species showed significant effects of canopy cover or tree structure, and those that were affected did not all increase with these covariates as we predicted. Additionally, multiple

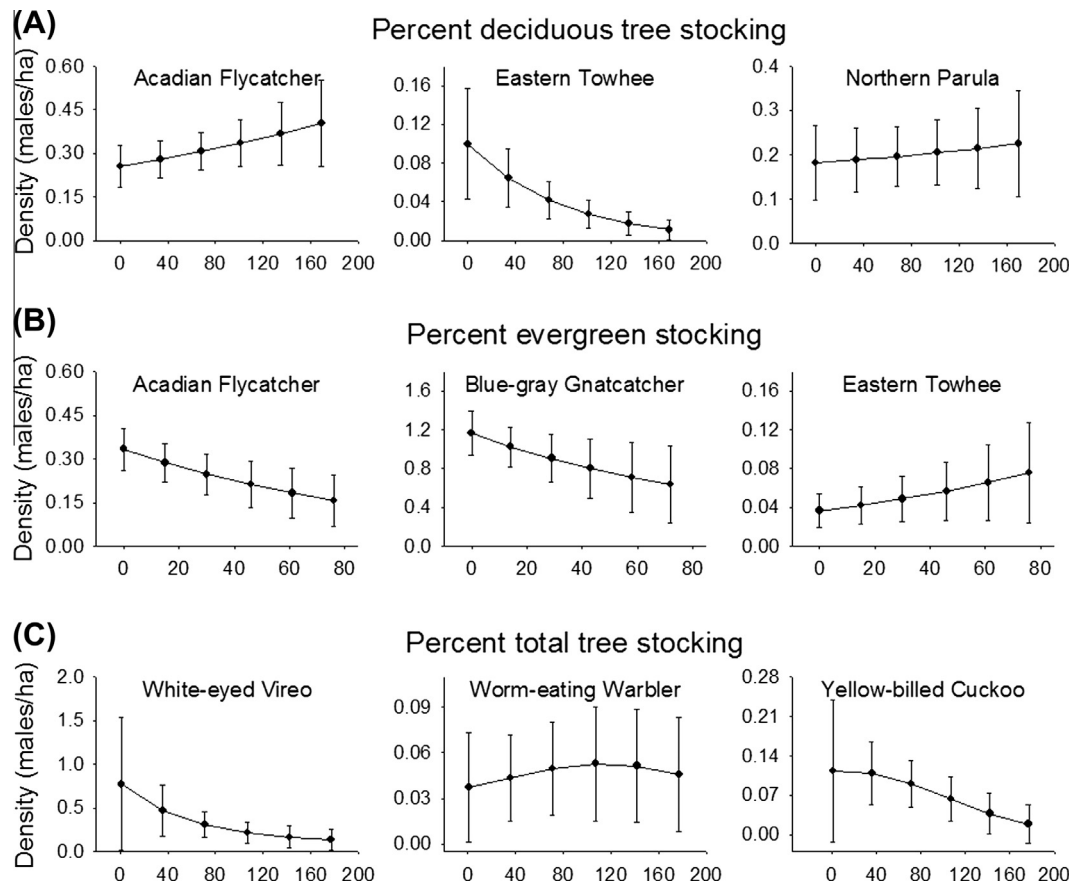


Fig. 4. Predicted density and 95% confidence intervals of four focal species across the observed range of percent stocking by two main tree groups, (A) deciduous and (B) evergreen, and three focal species across the observed range of (C) total stocking measured at points surveyed in the Missouri Ozark Highlands, late May–early July 2009–2011.

characteristics of the habitat structure influenced predicted densities for most modeled species, sometimes in seemingly contradictory ways. Several species had opposite responses to canopy cover and landscape forest cover. In general, early-successional species responded negatively to canopy cover and positively to forest cover, suggesting an overall positive impact of canopy gaps and forest fragmentation within a forested landscape for these species. However, Eastern Wood-Pewee showed the opposite response, with peak densities at high levels of canopy cover and low levels of forest cover, indicating this species may be best adapted to open wooded habitats at the landscape scale. Eleven of 17 species' densities peaked at intermediate levels of canopy cover, including early-successional and mature forest species, demonstrating that restored sites provide preferred habitat for a diverse group of breeding birds.

We found strong support for relationships between tree and shrub density and densities of several bird species. A simple measure of tree structure, such as stocking, did not explain variation in bird density as well as more complex measures such as stocking by deciduous or evergreen tree classes or density by tree size class for most species. For example, Acadian Flycatcher and Northern Parula were positively related to increasing deciduous stocking and, similar to Blue-gray Gnatcatcher, negatively related to evergreen stocking, whereas Eastern Towhee had an opposite response to stocking of deciduous and evergreen trees, an example of potential outcomes if land managers desire to provide breeding habitat suitable to these species. Additionally, density of trees by size class was important for several species, particularly the smallest and largest size classes. Eastern Wood-Pewee density increased with

higher density of large trees and given the observed response to other habitat variables and percent landscape forest cover, this species seemed to be more abundant in less forested landscapes, favoring habitat with large trees that provide high canopy cover and multiple burns that open the understory. We also detected opposite relationships between sapling and shrub densities with bird density, with five of six species' densities negatively related to saplings and positively related to shrubs. Our managed sites often supported high shrub density, and therefore provided habitat for early-successional species, most of which nest in shrubs; densities of all early-successional species increased in response to shrub density.

Fire is the primary management tool used by land managers to reduce tree density and canopy cover and increase herbaceous ground cover, and understanding how different species respond to varying fire histories is important for guiding management decisions based on desired outcomes. Several previous studies have documented species-specific effects of prescribed burns (Artman et al., 2001; Brawn, 2006; Grundel and Pavlovic, 2007b; Barrioz et al., 2013). Fire history was a strong predictor for all but two of our focal species and most responded positively to sites with at least one burn in the 20 years prior to the study. This suggests that fire history caused changes in the vegetative community or structure in ways we did not measure or evaluate or captured multiple structural features, a finding similar to Grundel and Pavlovic (2007b). Some species responded to conditions based on the number of years since the most recent burn, whereas others had stronger relationships with the total number of burns in the preceding 10 or 20 years. Only Field Sparrow density peaked in the year

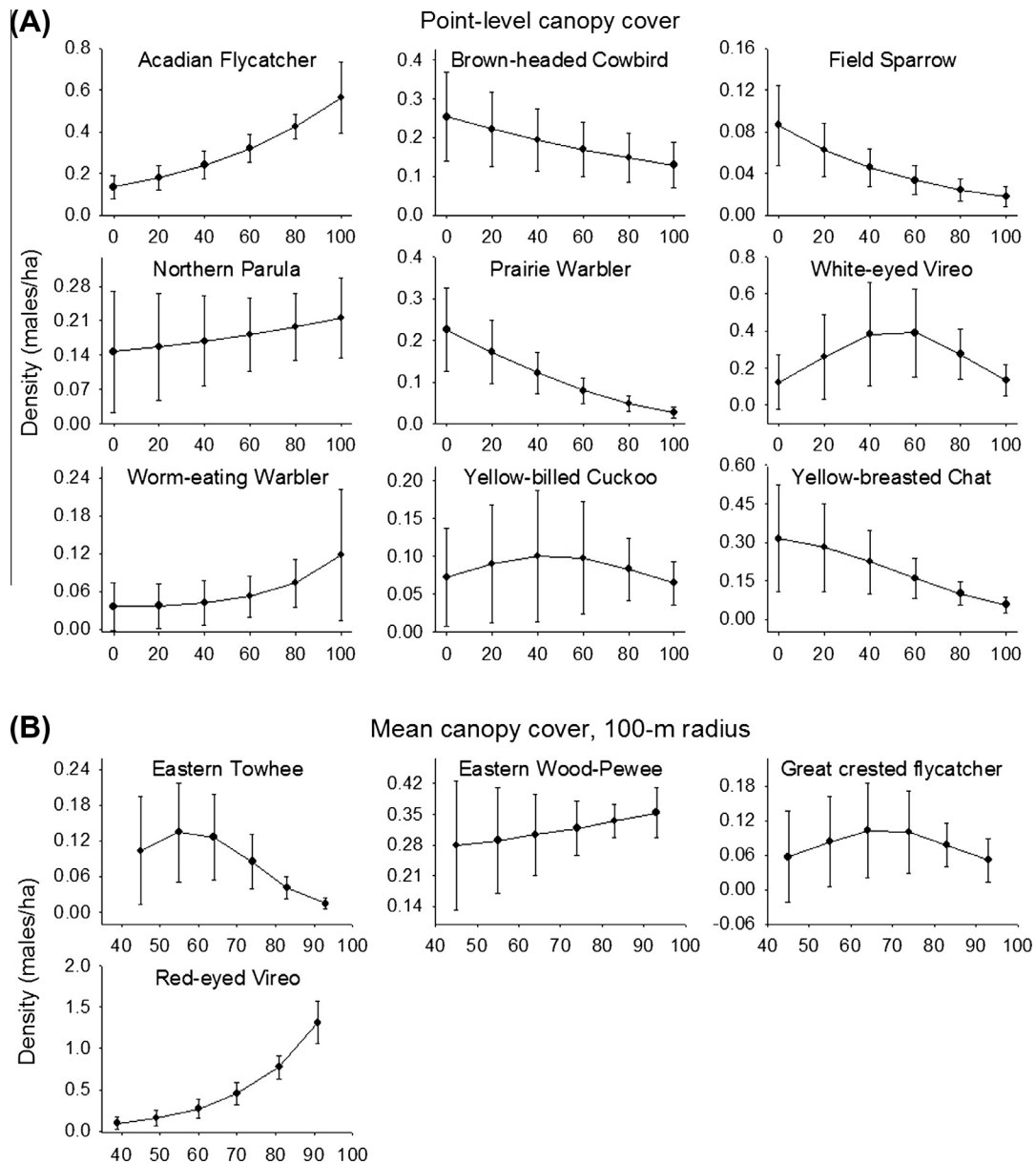


Fig. 5. Predicted density and 95% confidence intervals of 13 focal species across the observed range of (A) canopy cover measured at each point and (B) mean canopy in a 100-m radius of points surveyed in the Missouri Ozark Highlands, late May–early July 2009–2011.

following a burn, but densities of many species were similar 0–4 years post-burn. The positive relationship of most birds to some fire was likely indicative of the ecology of oak-dominated savanna, woodland, and forest in these landscapes, which are generally adapted to frequent low-intensity fires (Johnson et al., 2009). Densities of woodland generalists and most early-successional species responded positively to fire, whereas that of mature forest birds responded negatively. Species that nest on or near the ground (Eastern Towhee, Kentucky Warbler, Worm-eating Warbler) declined the most with frequent burns. Frequent burns reduce the necessary dense shrub layer used by Eastern Towhees and Kentucky Warblers and removes the dense leaf litter in mature forests used by nesting Worm-eating Warblers.

We detected few species considered indicators of open savanna or woodland, including Blue-winged Warblers, Brown Thrashers, Eastern Kingbirds, Orchard Orioles, Northern Bobwhites, and Red-headed Woodpeckers (Grundel and Pavlovic, 2007a). We suggest this is in part because current stocking is still greater than it

was historically on many sites. Many of our study sites may not have achieved the open canopy conditions necessary to attract birds such as Red-headed Woodpecker or restored patches may not be large enough or common enough in the landscape to attract and sustain species. We observed a range of 0–100% canopy cover at the point level, but mean canopy cover at the 100-m scale was generally high, demonstrating that even at a fairly small scale, our sites supported a high degree of canopy cover. Our managed sites represented the largest restored patches undergoing savanna or woodland management in the study area and were substantially larger than in other similar studies (Davis et al., 2000; Mabry et al., 2010; Comer et al., 2011). However, managed sites within a forested landscape may need to be much larger to provide suitable breeding habitat for species adapted to more open habitats. Additionally, our sites generally supported low levels of herbaceous grasses and forbs and may require more intensive management such as more frequent fire and mechanical thinning to achieve the grassy, open habitat structure preferred by Eastern Kingbird,

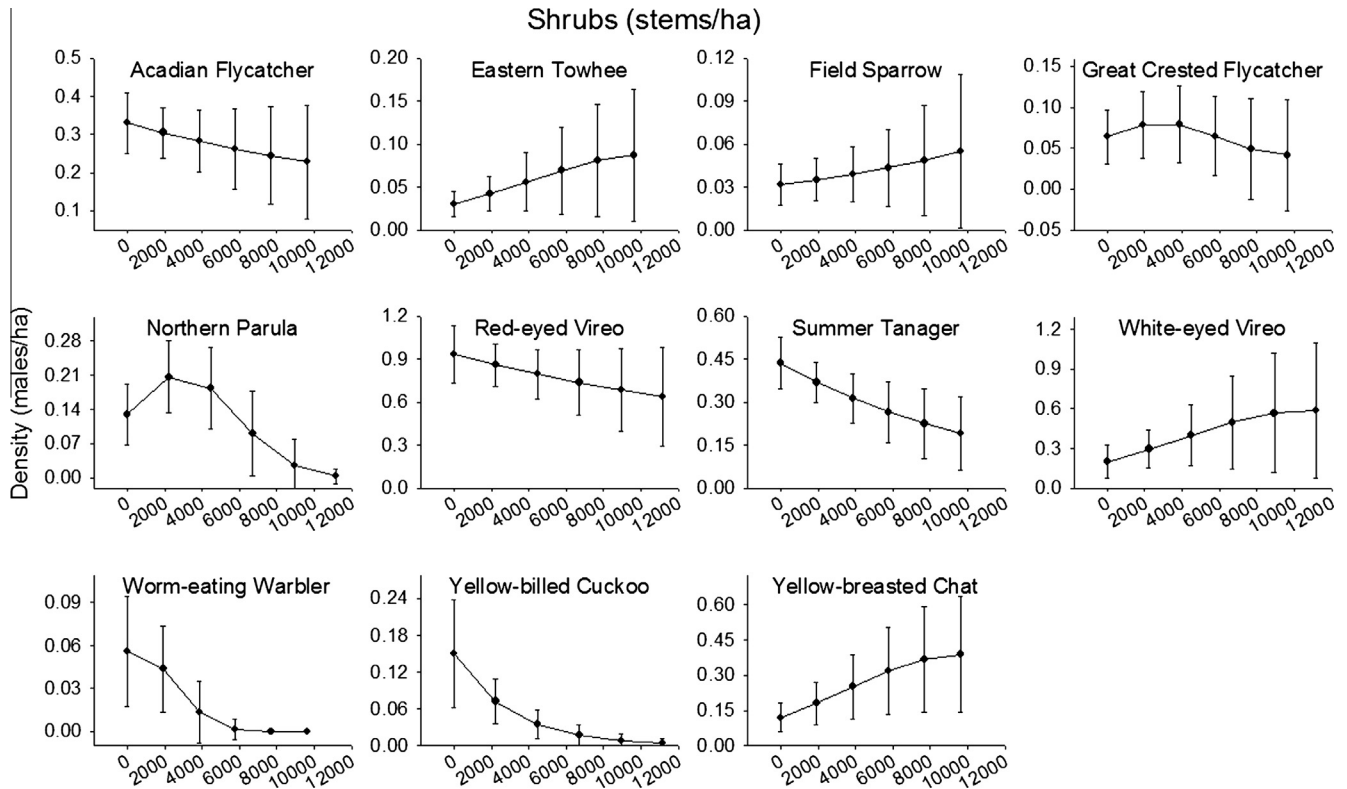


Fig. 6. Predicted density and 95% confidence intervals of 11 focal species across a gradient of shrub density at points surveyed in the Missouri Ozark Highlands, late May–early July 2009–2011.

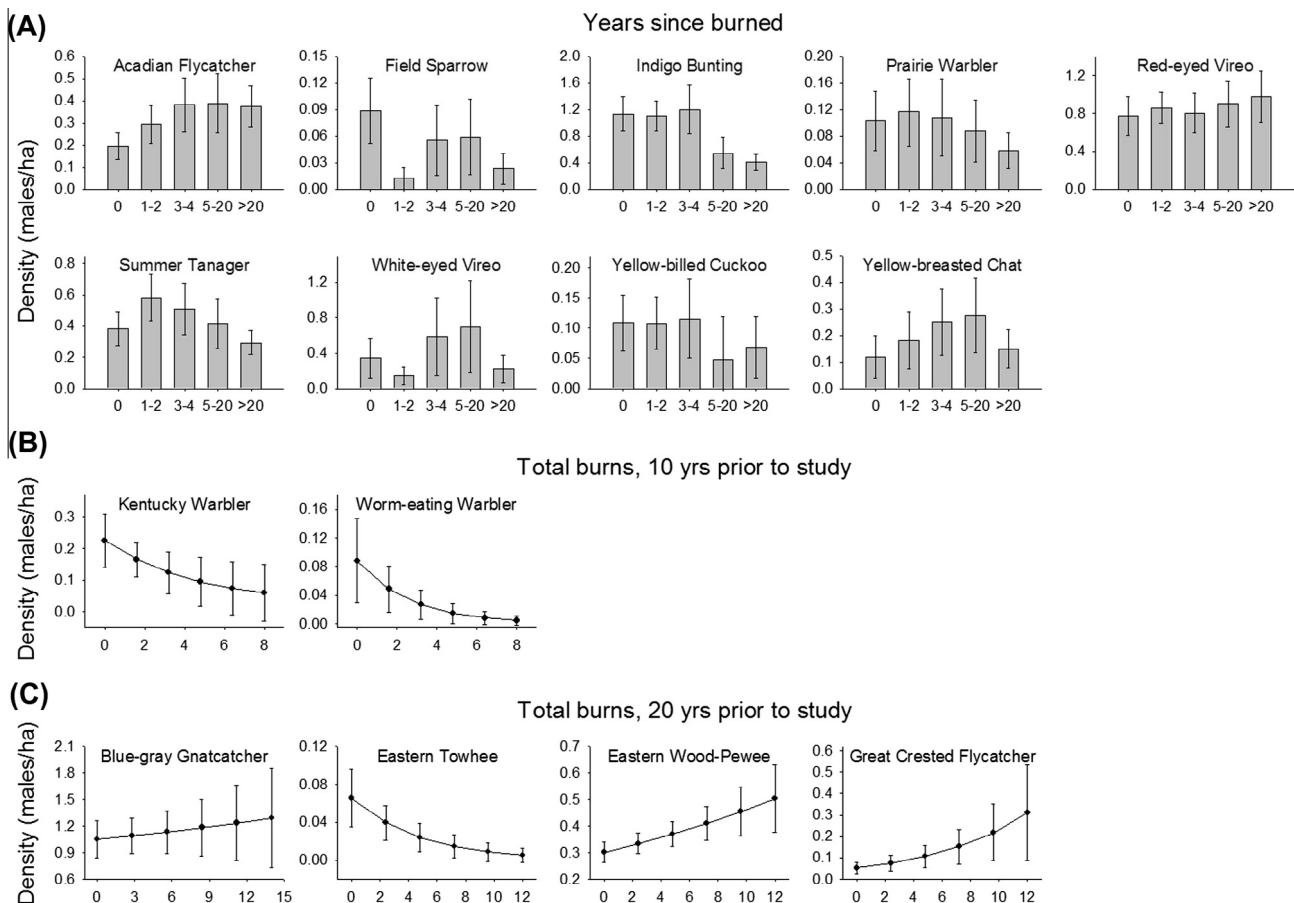


Fig. 7. Predicted density and 95% confidence intervals of 15 focal species for (A) years since burned, (B) total numbers of burns 10 years prior to surveys and (C) total numbers of burns 20 years prior to surveys in the Missouri Ozark Highlands, late May–early July 2009–2011.

Orchard Oriole, and Northern Bobwhite. Alternatively, species such as Northern Bobwhite and Brown Thrasher require a patchy landscape comprised of diverse habitats to satisfy their nesting and foraging needs, so a network of many small restored sites neighboring both forest and fields would likely benefit these species.

5. Conclusions

The complexity of the savanna-woodland-forest community gradient makes it difficult to generalize effects of savanna and woodland restoration on birds, especially when abundance is affected by both local habitat structure and landscape composition. Savanna and woodland restoration sites supported higher densities of several of our focal species. While our results do not suggest that any species prefers savanna or woodland at our sites, we did find evidence that in this highly forested landscape, restoration is providing additional habitat for woodland generalists and early-successional species, some of which are of conservation concern. Previous Midwestern studies have also found positive effects of restoration on species richness and diversity (Davis et al., 2000; Au et al., 2008) and densities of many early-successional species (Brawn, 2006). However, if land managers want to attract species specific to open habitats like Red-headed Woodpecker or Northern Bobwhite (both species of conservation concern associated with savanna-woodland), additional management to open the canopy and increase herbaceous ground cover across larger patches and landscapes may be necessary. If land managers seek to provide breeding habitat to a diverse suite of birds in areas being restored to savanna or woodland within forested landscapes, we suggest maintaining low stocking on some sites and a variable fire regime across the landscape to provide areas ranging from grass and forb ground cover to shrub cover. We and others in the Midwest have found substantial and varying support for a number of habitat relationships at multiple scales (Artman et al., 2001; Grundel and Pavlovic, 2007b; Au et al., 2008). Therefore, we suggest future studies take an experimental approach focused on a few variables, such as fire frequency, shrub density, and canopy cover or stocking, to control confounding factors and allow for stronger inference. Additionally, future research should also address the effects of restoration on demographics, such as nest survival, fecundity, site fidelity, and post-breeding habitat use.

Acknowledgements

We are grateful to A. Vaughan, K. McCarty, T. Nigh, D. Ladd, and P. Nelson for assistance with site selection and other support. We thank W. Dijak for calculating landscape metrics and W.A. Cox, J. Fitzgerald, D.T. Jones-Farrand, and R. Stanton for reviewing earlier drafts of this manuscript. We thank S. Caird, R. Evans, and M. Wickens for assisting in data collection. Funding or other support was provided by U.S. Department of Agriculture Forest Service Northern Research Station and Mark Twain National Forest, the Missouri Department of Natural Resources, the Missouri Department of Conservation, and The Nature Conservancy.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.10.042>.

References

Allison, P.D., 1999. Logistic Regression Using SAS®: Theory and Application. SAS Institute, Cary, North Carolina, USA.

- Anderson, R.C., 1998. Overview of Midwestern oak savannas. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 86, 1–18.
- Anderson, R.C., Fralish, J.S., Baskin, J.M. (Eds.), 1999. *Savannas, Barrens and Rock Outcrop Plant Communities of North America*. Cambridge University Press, New York.
- Artman, V.L., Sutherland, E.K., Downhower, J.F., 2001. Prescribed burning to restore mixed-oak communities in southern Ohio: effects on breeding bird populations. *Conservation Biology* 15, 1423–1434.
- Au, L., Andersen, D.E., Davis, M., 2008. Patterns in bird community structure related to restoration of Minnesota dry oak savannas and across a prairie to oak woodland ecological gradient. *Natural Areas Journal* 28, 330–341.
- Barrioz, S., Keyser, P., Buckley, D., Buehler, D., Harper, C., 2013. Vegetation and avian response to oak savanna restoration in the mid-south USA. *American Midland Naturalist* 169, 194–213.
- Brawn, J.D., 2006. Effects of restoring oak savannas on bird communities and populations. *Conservation Biology* 20, 460–469.
- Brawn, J.D., Robinson, S.K., Thompson III, F.R., 2001. The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics* 32, 251–276.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. *Introduction to Distance Sampling*. Oxford University Press, New York, New York, USA.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Verlag, New York, New York, USA.
- Comer, C.E., Bell, A.L., Oswald, B.P., Conway, W.C., 2011. Vegetation and avian response to prescribed fire on glade habitats in the Missouri Ozarks. *American Midland Naturalist* 165, 91–104.
- Davis, M.A., Peterson, D.W., Reich, P.B., Crozier, M., Query, T., Mitchell, E., Huntington, J., Bazakas, P., 2000. Restoring savanna using fire: Impact on the breeding bird community. *Restoration Ecology* 8, 30–40.
- Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43, 1–23.
- Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N., Wickham, J., 2011. Completion of the 2006 national land cover database for the conterminous united states. *PE&RS* 77, 858–864.
- Grundel, R., Pavlovic, N.B., 2007a. Distinctiveness, use, and value of Midwestern oak savannas and woodlands as avian habitats. *Auk* 124, 969–985.
- Grundel, R., Pavlovic, N.B., 2007b. Response of bird species densities to habitat structure and fire history along a Midwestern open-forest gradient. *Condor* 109, 734–749.
- Hunter, W.C., Buehler, D.A., Canterbury, R.A., Confer, J.L., Hamel, P.B., 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin* 29, 440–455.
- Johnson, P.S., Shifley, S.R., Rogers, R., 2009. *The Ecology and Silviculture of Oaks*. CABI Publishing, New York, New York, USA.
- Leach, M.K., Ross, L. (Eds.), 1995. *Midwest Oak Ecosystems Recovery Plan: a Call to Action*. U.S. Environmental Protection Agency Great Lakes National Program Office, Chicago, Illinois, USA.
- Mabry, C.M., Brudvig, L.A., Atwell, R.C., 2010. The confluence of landscape context and site-level management in determining Midwestern savanna and woodland breeding bird communities. *Forest Ecology and Management* 260, 42–51.
- Martin, T.E., Paine, C.R., Conway, C.J., Hochachka, W.M., Allen, P., Jenkins, W., 1997. *BBIRD Field Protocol*. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA.
- McCarty, K., 1993. Restoration in Missouri savannas. In: 1993 Proceedings of the Midwest Oak Savanna Conferences. Environmental Protection Agency Online: <<http://www.epa.gov/ecopage/upland/oak/oak93>>.
- McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. FRAGSTATS v3: Spatial pattern analysis program for categorical maps: <<http://www.umass.edu/landeco/research/fragstats/fragstats.html>>.
- McPherson, G.R., 1997. *Ecology and Management of North American Savannas*. University of Arizona Press, Tucson, Arizona.
- Nelson, P.W., 2002. Classification and characterization of savannas and woodlands in Missouri. In: Hartman, G., Holst, S., Palmer, B. (Eds.), *Proceedings of SRM 2002: Savanna/Woodland Symposium*. Conservation Commission of the State of Missouri, Jefferson City, Missouri, USA. pp. 959–987.
- Nelson, P.W., 2005. *The Terrestrial Natural Communities of Missouri*. Missouri Natural Areas Committee, Jefferson City, Missouri, USA.
- Nigh, T.A., 1992. The forests prior to European settlement. In: Journef, A.R.P., Spratt, H.P. (Eds.), *Towards a Vision for Missouri's Public Forests*. Southeast Missouri State University, Cape Girardeau, Missouri, USA. pp. 6–13.
- Nigh, T.A., Schroeder, W.A., 2002. *Atlas of Missouri Ecoregions*. Missouri Department of Conservation, Jefferson City, Missouri, USA.
- Noss, R.F., LaRoe III, E.T., Scott, J.M., 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. *Biological Report* 28, National Biological Service, Washington, D.C. <<http://biology.usgs.gov/pubs/ecosys/>> (accessed 15.07.13).
- Nuzzo, V., 1986. Extent and status of Midwest oak savanna: presettlement and 1985. *Natural Areas Journal* 6, 6–36.
- Partners in Flight Science Committee, 2012. *Species Assessment Database*, version 2012. <<http://rmbp.org/pifassessment/>> (accessed 15.07.13).
- Royle, J.A., Dawson, D.K., Bates, S., 2004. Modeling abundance effects in distance sampling. *Ecology* 85, 1591–1597.

- Sillett, T.S., Chandler, R.B., Royle, J.A., Kéry, M., Morrison, S.A., 2012. Hierarchical distance-sampling models to estimate population size and habitat-specific abundance of an island endemic. *Ecological Applications* 22, 1997–2006.
- The Nature Conservancy, Ozarks Ecoregional Assessment Team, 2003. Ozarks Ecoregional Conservation Assessment. The Nature Conservancy Midwestern Resource Office, Minneapolis, Minnesota, USA.
- Thompson III, F.R., Donovan, T.M., DeGraaf, R.M., Faaborg, J., Robinson, S.K., 2002. A multi-scale perspective of the effects of forest fragmentation on birds in Eastern forests. *Studies in Avian Biology* 25, 8–19.
- U.S. Department of Agriculture, 2005 Land and Resource Management Plan: 2005 Forest Plan: Mark Twain National Forest, U.S. Department of Agriculture, Forest Service, Eastern Region, Milwaukee, Wisconsin, USA.