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Effects of pine-oak woodland restoration on breeding bird densities in the Ozark-Ouachita Interior Highlands

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ABSTRACT

Restoration is underway to restore lost or degraded remnants of savanna and woodland in the Midwestern United States in the hopes of restoring floristic and wildlife diversity. Information is needed on the effects of pine savanna-woodland restoration on bird abundance to inform management decisions. We conducted point-count surveys for 19 bird species across the gradient of savanna, woodland, and forest in restored and non-restored areas throughout the Ozark-Ouachita Highlands in parts of Missouri, Arkansas, and Oklahoma during the 2013–2015 breeding seasons. We estimated densities of 16 species using distance sampling to account for detection probability, and we determined relationships of bird abundance with management and vegetation variables by evaluating support for *a priori* models. Densities of early-successional and generalist species were positively related, and interior-forest species negatively related, to restoration. Densities of Brown-headed Nuthatch (*Sitta pusilla*), Eastern Towhee (*Pipilo erythrophthalmus*), Eastern Wood-Pewee (*Contopus virens*), Pine Warbler (*Setophaga pinus*), Prairie Warbler (*Setophaga discolor*), Red-headed Woodpecker (*Melanerpes erythrocephalus*), White-eyed Vireo (*Vireo griseus*), and Yellow-breasted Chat (*Icteria virens*) were positively related to prescribed fire activity. Blue-winged Warbler (*Vermivora cyanoptera*), Kentucky Warbler (*Geothlypis formosa*), and Yellow-breasted Chat densities were positively related to tree thinning. Many species had higher densities in areas with less canopy cover, tree density, and forest cover. Acadian Flycatcher (*Empidonax virescens*), Black-and-white Warbler (*Mniotilta varia*), Ovenbird (*Seiurus aurocapilla*), Wood Thrush (*Hylocichla mustelina*), and Worm-eating Warbler (*Helmitheros vermivorum*) were negatively related to one or more aspects of restoration treatment and generally preferred areas with greater tree density and canopy cover. Summer Tanagers (*Piranga rubra*) were abundant but density was not strongly related to management or vegetation variables. Restoration provided breeding habitat for disturbance-dependent species and woodland generalists, many of which are species of conservation concern, but canopy cover generally remained too great for species that require more open savanna.

1. Introduction

Savanna and woodland are vegetation communities characterized by variable but open canopy cover, a sparse midstory, and a dense understory consisting of grasses, forbs, and shrubs (McPherson 1997, Nelson 2002). Savanna is generally defined by < 30% canopy cover and widely spaced trees while woodland ranges from 30 to 90% canopy cover (Nelson 2002). Both communities have a rich herbaceous ground layer, as ample sunlight permeates the open canopy, as well as an open midstory that distinguishes them from mature forest (Nelson 2002). The open quality of savanna and woodland was historically created and maintained by anthropogenic fire; grazing by large, native ungulates; and other natural disturbances such as wind throw and insect or disease outbreak (McCarty 1993, Nelson 2002, Dey and Kabrick 2015). Fire, however, is particularly important in maintaining the open midstory that is characteristic of these communities (Lorimer 2001, Peterson and Reich 2001, McCarty 2002, Cunningham 2007). Without disturbance to halt understory growth, savannas and woodlands, as well as other open ecosystems such as grasslands, transition to closed forests with dense midstories and few canopy gaps (Hanberry and Abrams 2018).

Historically, savanna-woodland covered 13–33 million ha in the Midwestern US, but this was reduced to only 2600 ha after European settlement (Nuzzo 1986, Hanberry and Abrams 2018). The region lost nearly all savanna and woodland due to extensive timber harvest,

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conversion to agricultural land, or succession to closed-canopy forest following extended periods of fire suppression (Schroeder 1981, Nuzzo 1986, Cutter and Guyette 1994, Cunningham 2007). The loss of savannas and woodlands has likely contributed to the decline of many disturbance-dependent bird species (Brawn et al. 2001, Hunter et al. 2001). Grassland and shrubland obligates are among the species experiencing the worst population declines in North America, at least partly in response to decreased or degraded habitat (Brawn et al. 2001, Hunter et al. 2001, Brennan and Kuvlesky 2005, Sauer and Link 2011).

Savanna and woodland are ecotonal or transitional communities that contain characteristics of both grasslands and forests (Temple 1998). This vegetation gradient allows bird species from normally distinct vegetation communities to coexist and results in increased species richness and diversity (Temple 1998, Grundel and Pavlovic 2007, Barrioz et al. 2013). Although there are few true savanna or woodland specialists (Davis et al. 2000), overall species diversity is greater in restored savanna and woodland when compared to prairie or forest (Brawn 2006, Au et al. 2008, Reidy et al. 2014) because both woodland generalists and early-successional species are able to utilize the same area (Vander Yacht et al. 2016). Savanna and woodland are likely to serve as vital habitat for declining early-successional or disturbance-dependent species such as Prairie Warblers (*Setophaga discolor*) and Blue-winged Warblers (*Vermivora cyanoptera*) as well as savanna-dependent species like the Bachman's Sparrow (*Peucaea aestivalis*) without negative effects on many other co-occurring species (Davis et al. 2000, Hunter et al. 2001, Askins et al. 2007, Vander Yacht et al. 2016).

There is growing interest in restoring lost and degraded remnants of savanna and woodland in the central United States, including the Ozark and Ouachita Mountains. These communities are more sustainable and biologically diverse than many closed-canopy forests in the region, and providing healthy savanna-woodland could be an efficient conservation strategy for avian communities (The Nature Conservancy 2003, Hedrick et al. 2007, Ouachita National Forest 2010, Mark Twain National Forest 2011, Hanberry and Abrams 2018). Shortleaf pine (*Pinus echinata*) was historically common in the Ozark Plateau and Ouachita Mountains (McWilliams et al. 1986, Nelson 1997). It covered nearly 2.7 million hectares in Missouri alone and often occurred in woodlands and savannas (Liming 1946, Martin and Presley 1958, Batek 1994, Nelson 1997). Most previous research in Missouri and nearby Midwestern states has focused on the restoration of oak savanna and woodland (Artman et al. 2001, Hartung and Brawn 2005, Brawn 2006, Reidy et al. 2014) with comparatively few studies examining the effects of pine restoration (Wilson et al. 1995, Masters 2007). Management efforts have increased in the central US, especially in the Ouachita Mountains, to restore pine savanna and woodland, but it is still unclear how the type, extent, and frequency of treatments and the resulting vegetation structure affect breeding birds.

Prescribed fire and tree thinning are used to restore pine savanna-woodland in the Ozark-Ouachita Highlands (Ouachita National Forest 2010, Mark Twain National Forest 2011), but studies exploring the combined effects of burning and thinning on birds are relatively rare. Understanding these treatment effects in a restoration context could lead to more effective management for focal species or the community as a whole. Varied amounts of management in the landscape provided an excellent opportunity to study bird response to restoration at a large, operational scale. We surveyed birds and measured site- and landscape-level characteristics in areas with varied levels of prescribed fire and tree thinning or no management over the last ten years. Our objective was to determine densities of select bird species in relation to restoration management and vegetation characteristics. We hypothesized that early-successional, disturbance-dependent, and generalist species would be positively related to restoration because vegetation needed for both nesting and foraging would be created while interior-forest species would respond negatively to restoration as closed-canopy conditions were lost.

2. Methods

2.1. Study area

We conducted this study throughout the Ozark-Ouachita Interior Highlands in parts of Missouri, Arkansas, and Oklahoma. This region is comprised of the Ozark Mountains to the north and the Ouachita Mountains to the south. The Ozarks are characterized by rolling to rugged terrain with diverse karst landscapes resulting in an abundance of exposed rock, caves, and spring systems amid the steep hills and valleys (Missouri Department of Natural Resources 2016, The Nature Conservancy 2003) while the Ouachitas consist mainly of sandstone, shale, and novaculites that are more resistant to weather and erosion (Foti and Glenn 1991). Both the Ozark and Ouachita Mountains are dominated by oak-hickory, pine-oak, and mixed-oak woodland and forest communities (Nelson 2012, Ouachita National Forest 2010). Common upland tree species include post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), white oak (*Q. alba*), northern red oak (*Q. rubra*), hickory (*Carya* spp.), shortleaf pine (*Pinus echinata*), and flowering dogwood (*Cornus florida*) with open woodland and savanna containing bluestem grasses (*Andropogon gerardii, Schizachyrium scoparium*), sedges (*Cyperaceae* spp.), woody shrubs such as fragrant sumac (*Rhus aromatic*) and blackberry (*Rubus* spp.), and saplings (Nelson 2012, Ouachita National Forest 2010).

This study occurred within the Collaborative Forest Landscape Restoration Projects (CFLRP) on 139,903 ha in the Mark Twain National Forest (MTNF) in the Ozark Mountains in Missouri and 141,025 ha in the Ouachita National Forest (ONF) in the Ouachita Mountains in Arkansas and Oklahoma (Ouachita National Forest 2010, Mark Twain National Forest 2011). The MTNF and ONF established 151 and 101 monitoring points, respectively, for the CFLRP using a stratified random sampling design, which we then used for bird surveys. We supplemented these points by selecting an additional 100 systematic grid inventory points used by the MTNF based on management activity maps such that the total sample of 352 points (Fig. 1) covered the full range of restoration treatments in the region and would generate enough bird detections to fit models. Any point that received management treatment during the 3-year study was excluded from the analysis so that we did not have to address temporal changes in treatment or vegetation at the point level. We were able to sample 338 points in all three years and, consequently, used these points in analysis. We conducted bird surveys at the same points each year as part of the CFLRP monitoring plan to provide an average response across multiple years to the management and resulting vegetation conditions measured in 2013. Constraints on effort did not permit us to re-measure vegetation each year of the study, but we did not observe major changes in vegetation in the 2 years post-vegetation sampling. Two-hundred and fourteen points had some degree of prescribed burning or tree thinning within the past 10 years, with the objective of restoring pine woodland, while 124 points had no prescribed burning or tree thinning within the past 10 years and consisted of mature oak or oak-pine forest. The extent of management and local site features varied significantly across our points resulting in a highly heterogeneous vegetation gradient that spanned the continuum from mature, closed-canopy forest (non-restored areas) to open savanna-woodland (restored areas).

2.2. Data collection

2.2.1. Avian surveys

We surveyed abundance of 19 breeding bird species (Table 1) that were either a species of regional or range-wide concern (Central Hardwoods Joint Venture 2012, Partners in Flight 2012) or we hypothesized would show a strong response to management activities. We conducted 10-min unlimited-radius point-count surveys mid-May through early July 2013–2015. Each point was surveyed once per breeding season in each of the three years for a total of three visits. We

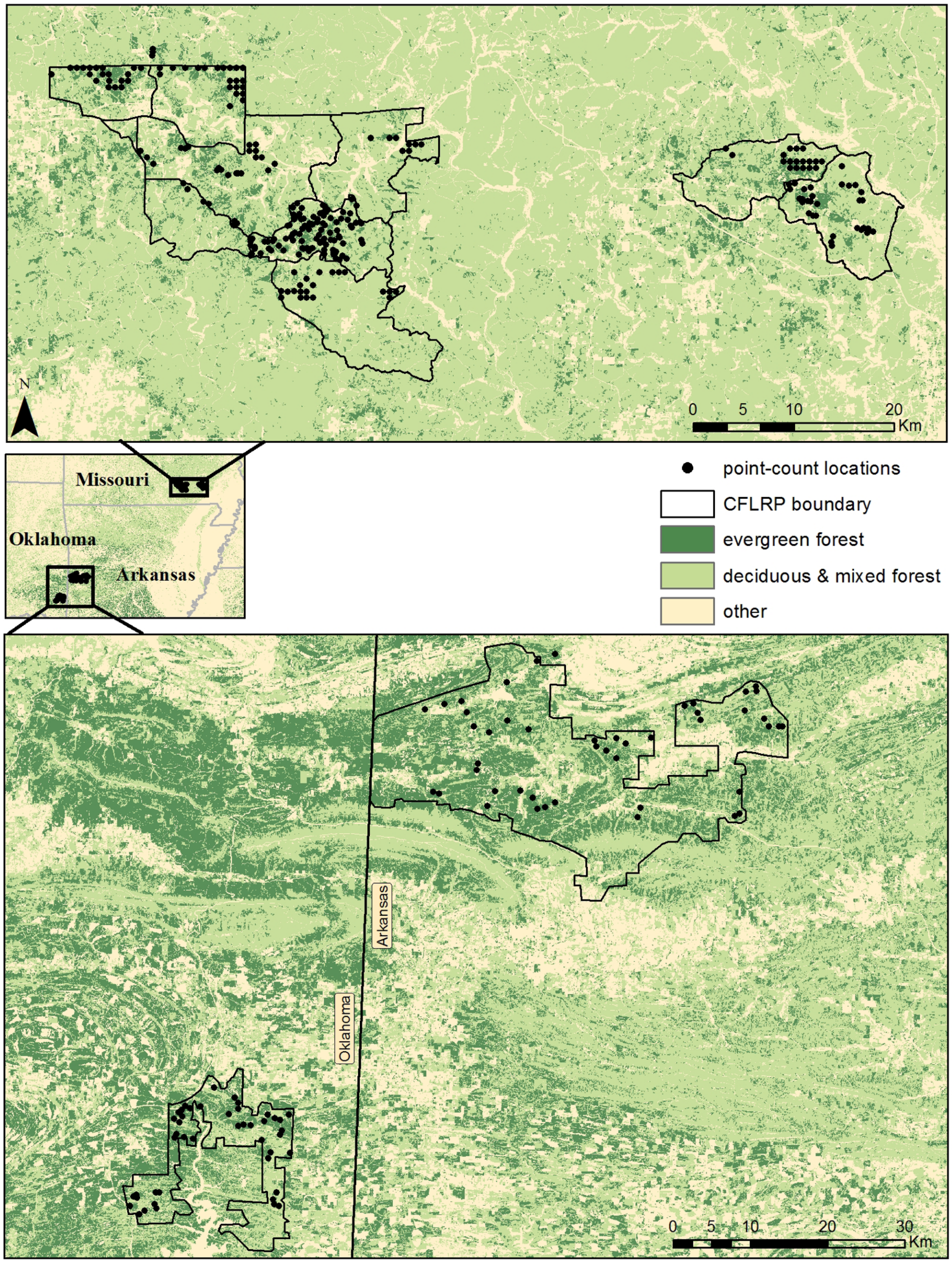

Fig. 1. Avian point-count locations (black circles) in the Collaborative Forest Landscape Restoration Projects (black boundaries) in the Mark Twain National Forest in Missouri and Ouachita National Forests in Arkansas and Oklahoma.

conducted surveys on days with minimal or no precipitation and light to moderate wind speeds starting 15 min after sunrise and concluding no later than 1000 h CDT. Observers recorded the time of initial detection, exact distance (meters) to the individual, and detection type (e.g., song, call, or visual) of each unique individual; flyover individuals were excluded. Distances were measured with Bushnell Yardage Pro laser range-finders (Bushnell, Overland Park, KS, USA) or by observer judgment if the range-finder could not be used due to topography or vegetation. All observers were trained in focal bird species identification and distance estimation prior to surveys.

2.2.2. Habitat, landscape, and management variables

We measured site-level vegetation structure at each point in the 2013 breeding season using a modified BBIRD protocol (Martin et al. 1997) after all technicians were thoroughly trained. We recorded point-level canopy cover, ground cover composition, and tree density at each point (Table 2). We measured point-level canopy cover as the average of four spherical densiometer readings taken at the point facing each cardinal direction. We visually estimated the percentage of grass/forb cover, shrub cover, leaf litter, and bare ground in four quadrants within a 5-m radius around the point and calculated the mean for each category. The sum of percentages in each quadrant was allowed to exceed 100 because the cover categories could be multi-layered. We measured diameter-at-breast height (DBH) of all trees within an 11.3-m radius with DBH ≥ 2.5 cm, and trees were recorded as deciduous, evergreen, or snag and later converted to density of saplings (2.5–12.5 cm DBH), pole timber (13–27.5 cm DBH), and saw timber (> 27.5 cm DBH). We calculated snag density based on the number of dead trees ≥ 12.5 cm DBH. We calculated deciduous and evergreen basal area by summing areas estimated from DBH values. We examined landscape composition

Table 1
Number of detections (singing males) and predicted densities (males/ha) with standard errors (SE) for focal species during point-count surveys in the Ozark-Ouachita Interior Highlands, 2013–2015 after deleting observations above the 95th percentile of detection distances. Brown-headed Nuthatch, Red-cockaded Woodpecker, and Red-headed Woodpecker cannot be accurately sexed via point counts and detections include both males and females. Species with < 25 detections were not analyzed.

Common name	Detections	Mean density (SE)
Acadian Flycatcher (*Empidonax virescens*)	267	0.15 (0.03) [MTNF] 0.01 (0.001) [ONF]
Bachman's Sparrow (*Peucaea aestivalis*)[a]	4	–
Black-and-white Warbler (*Mniotilta varia*)	142	0.19 (0.04) [MTNF] 0.07 (0.03) [ONF]
Blue-winged Warbler (*Vermivora cyanoptera*)[†a]	39	0.07 (0.05)
Brown-headed Nuthatch (*Sitta pusilla*)[* a]	25	0.36 (0.54)
Eastern Towhee (*Pipilo erythrophthalmus*)[b]	180	0.13 (0.02) [MTNF] 0.02 (0.01) [ONF]
Eastern Wood-Pewee (*Contopus virens*) [b]	718	0.29 (0.03) [MTNF] 0.08 (0.01) [ONF]
Kentucky Warbler (*Geothlypis formosa*) [a]	123	0.04 (0.01) [MTNF] 0.07 (0.02) [ONF]
Northern Bobwhite (*Colinus virginianus*) [b]	24	–
Ovenbird (*Seiurus aurocapilla*)	437	0.29 (0.05) [MTNF] 0.01 (0.01) [ONF]
Pine Warbler (*Setophaga pinus*)	1012	0.67 (0.04)
Prairie Warbler (*Setophaga discolor*) [a]	362	0.11 (0.01)
Red-cockaded Woodpecker (*Dryobaetes borealis*)[*a]	1	–
Red-headed Woodpecker (*Melanerpes erythrocephalus*) [a]	155	0.04 (0.01) [MTNF] 0.03 (0.02) [ONF]
Summer Tanager (*Piranga rubra*)	420	0.22 (0.03)
White-eyed Vireo (*Vireo griseus*)[b]	154	0.20 (0.05) [MTNF] 0.13 (0.04) [ONF]
Worm-eating Warbler (*Helmitheros vermivorum*)[a]	154	0.13 (0.02) [MTNF] 0.03 (0.01) [ONF]
Wood Thrush (*Hylocichla mustelina*)[†a]	57	0.01 (0.004)
Yellow-breasted Chat (*Icteria virens*) [b]	620	0.27 (0.04) [MTNF] 0.22 (0.05) [ONF]

† MTNF only.
* ONF only.
[a] species of regional and range-wide concern.
[b] species of regional concern.

Table 2
Descriptive statistics for vegetation and landscape characteristics and management activity at point-count locations for a study of relationships between bird density and savanna-woodland restoration in the Ozark-Ouachita Interior Highlands, 2013–2015.

Variable	Abbreviation	Mean	SD	Min	Max
Point-level canopy cover (%)	canopy	86.45	19.80	0	100
Shrub cover (%)	shrub	14.94	18.05	0.25	97
Sapling ha^{-1} (2.5–12.5 cm DBH)	sap	746.2	734.29	0	5625
Pole timber ha^{-1} (13–27.5 cm DBH)	pole	301.9	229.48	0	1425
Saw timber ha^{-1} (> 27.5 cm DBH)	saw	181.8	122.07	0	800
Evergreen basal area ha^{-1}	evergBA	13.91	14.99	0	90.08
Deciduous basal area ha^{-1}	decidBA	14.95	12.58	0	74.88
Snag basal area ha^{-1}	snag	2.63	3.35	0	20.34
Mean canopy cover (150 m radius)	canopy150	77.97	11.35	48.23	100
Mean canopy cover (1 k radius)	canopy1k	75.3	13.86	4.82	100
Burns in 10 yr	burns	1.45	1.53	0	5
Deciduous in 1 k radius (%)	decid1k	53.11	25.63	0	100
Evergreen in 1 k radius (%)	everg1k	26.85	22.13	0	100
Mixed forest in 1 k radius (%)	mixed1k	11.31	7.83	0	47.36
Forest cover in 1 k radius (%)	forest1k	91.28	10.96	18.47	100
Deciduous in 150 m radius (%)	decid150	47.95	34.77	0	100
Evergreen in 150 m radius (%)	everg150	33.74	33.27	0	100
Mixed forest in 150 m radius (%)	mixed150	10.66	12.61	0	58.4
Forest cover in 150 m radius (%)	forest150	92.35	14.48	0	100
Burned area in 1 k radius (%)	burn1k	51.82	40.50	0	100
Thinned area in 1 k radius (%)	thin1k	24.6	26.52	0	100
Burned area in 150 m radius (%)	burn150	52.56	48.23	0	100
Thinned area in 150 m radius (%)	thin150	22.91	35.27	0	100
Region (MTNF/ONF)	reg	0.7/0.3			
Thinned/not thinned	thin	0.3/0.7			

by calculating mean canopy cover and percent forest cover within a 150-m and 1-km radius around each point using the 2011 National Land Cover Dataset (NLCD; Homer et al. 2015) in ArcMap 10.1 (ESRI, Redlands, California, USA). The 150-m radius approximated the maximum distance an observer could effectively detect birds as well as an arbitrary estimate of a bird's territory size. We used the 1-km radius to capture the larger landscape surrounding a point because bird density is affected by landscape-scale forest cover (Howell et al. 2000, Thompson et al. 2002, Mabry et al. 2010, Reidy et al. 2014). We calculated percent deciduous, evergreen, and total forest cover around each point. Total forest cover was the sum of deciduous, evergreen, and mixed forest.

We obtained the management history for all points for the 10 years prior to the final year of the study from the Mark Twain and Ouachita National Forests and used ArcMap 10.1 to extract management values for each survey point. We calculated the total number of prescribed burns a point received and whether or not the point was mechanically thinned at least once in the past 10 years. We also calculated the percent area that had been burned or thinned in the past 10 years using 150-m and 1-km buffers around each point.

2.3. Data analysis

We used a model selection approach and Akaike's Information Criterion (AIC) to evaluate support for *a priori* candidate models that examined the effects of point-level vegetation, landscape composition, and management activity on the density of each of our focal species. We used the R package "unmarked" to develop two-stage, hierarchical distance-based models that simultaneously estimate detection probability and species density. Distance-based models are based on the assumptions that individuals at distance zero are always detected, individuals are detected at their initial location, and that distances to detected individuals are accurate (Buckland et al. 2001). We truncated detection distances for each species to the 95th percentile to exclude outliers (Buckland et al. 2001) and standardized all continuous variables to a mean of zero (Fiske and Chandler 2015).

We fit models using the gdistsamp function in the R package Unmarked (Fiske and Chandler 2015). Gdistsamp extends the hierarchical distance sampling model of Royle et al. (2004) that is implemented in the distsamp function to allow the analysis of multiple visits to the same point within the same season by estimating phi, the probability of being available for detection (Fiske et al. 2015). Gdistsamp also allows users to model species abundance using the negative binomial distribution in addition to the Poisson distribution found in distsamp. We initially analyzed our data as three visits to each of 338 points, but because gdistsamp is developed for multiple visits within a season, the interpretation of phi and resulting density estimate are not completely clear when the visits span multiple years. The Unmarked package does not allow for random effects; therefore, we treated the three visits to 338 points as single-visit surveys to 1014 points by stacking our data, a method for dealing with multi-year datasets in Unmarked (A. Royle, personal communication). A potential criticism of this approach is that it creates pseudoreplication and could inflate the precision and significance of results. However, standard errors for model parameters were comparable or slightly larger after stacking the data, and inflation of p-values was not a major concern because inferences were based on variables supported by AIC, which was not affected by sample size. Therefore, we report results from models fit to the stacked data because of the more direct interpretation of density (i.e. density at the time of a point visit) without the need to consider phi.

We used a multi-stage model selection approach to evaluate *a priori* candidate models for each species while limiting the number of possible variable combinations fit for each species. We modeled detection variables first followed by four categories of density variables, carrying forward the top model from each step. We first analyzed all combinations of the hazard and half-normal key distance functions with and without singular and additive combinations of our detection variables (day of year [day], minutes since sunrise [min], observer [obs], and year [year]), with the Poisson and negative-binomial distributions for the density function which resulted in 44 models. We then used the top-ranked detection model in all models evaluating density variables. In rare cases, we were unable to use the top-ranked detection model because of model convergence failure in later steps of model building and subsequently, used the next most-supported model.

Because we surveyed points in multiple years, we fit the top detection model with and without year as a density variable. We included year as a density variable in all subsequent models if the model with year was ranked higher. To avoid multicollinearity, we evaluated density variables in four categories: point-level management, point-level vegetation, landscape-level management, and landscape-level vegetation. This approach allowed us to eliminate redundancy among variables and reduce the number of candidate models fit. The point-level management variables were the total number of burns a point received in the past 10 years, whether or not a point was thinned in the past 10 years, and additive combinations of these which resulted in three models. The point-level vegetation variables examined were average canopy cover (measured by spherical densiometer), percent shrub cover, tree density by size class, deciduous and evergreen basal area, and if applicable, region (MTNF vs. ONF). We constructed 21 *a priori* models consisting of singular and additive combinations of these point-level vegetation variables and additionally considered snag basal area for two cavity-nesting species (Brown-headed Nuthatch and Red-headed Woodpecker) which resulted in 34 models. Landscape-level management variables examined the percent area that had been burned and the percent area that had been thinned in the past 10 years which resulted in two activity models each representing a landscape scale (150 m or 1 km). The landscape-level vegetation variables included mean canopy cover within a 150-m and 1-km radius, percent forest cover within a 150-m and 1-km radius, percent deciduous forest cover within a 150-m and 1-km radius, and percent evergreen forest cover within a 150-m and 1-km radius. We constructed additive combinations of these landscape vegetation variables that did not include the same feature at both scales in the same model which resulted in 20 competing models. For each focal species, we fit these sets of candidate models and brought forward the most-supported model from each category. We constructed a final set of candidate models by considering a null density model and models with all additive combinations of the most-supported model from each category resulting in 16 candidate models specific to each species.

Initial analysis did not evaluate quadratic relationships with density variables, but results from linear models suggested that quadratic forms may be more appropriate for some species. We performed *post hoc* analysis of quadratic relationships for point-level and landscape-level canopy cover, forest type cover, and management treatment if linear forms of these variables were present in a species' top-ranked model(s).

We ranked candidate models for each species using AIC and evaluated goodness-of-fit for the top-ranked model using the Freeman-Tukey test with a parametric bootstrap for 100 simulations (Fiske and Chandler 2015). We report predictions from the most-supported model or model-averaged predictions if there were competing models with ΔAIC < 2 but did not consider models that only added additional uninformative parameters to a more supported model (Arnold 2010). We predicted species density across the ranges of supported density variables while holding other variables constant at their mean or observed frequency. Because of the large number of species analyzed, the results section only reports variables whose 95% confidence intervals did not overlap zero. Other relationships that were supported by model selection but had confidence intervals overlapping zero can be found in Tables 4, 5, and Appendix A. We grouped species as positively or negatively related to management, based on the majority of supported effects, to facilitate reporting results and discussion.

3. Results

We surveyed 338 points in each of three years (2013–2015). Survey points spanned the vegetation gradient from open-canopy savanna to closed-canopy forest and had varying degrees of management (Table 2). We had from 1 to 1012 detections for each of the 19 focal species and were able to fit density models to 16 species with ≥ 25 detections (Table 1). There was no evidence of lack of fit for the top model of any species based on goodness-of-fit tests ($P > 0.10$). Wood Thrush had the lowest average density while Pine Warbler, Eastern Wood-Pewee, Ovenbird, and Yellow-breasted Chat had the greatest densities (Table 1). No species had an average density > 1 male/ha. All but one species (Wood Thrush) showed support for at least one detection variable; day and obs were commonly-supported detection variables but the most-supported detection model varied across species (Table 3). Density of 8 species was related to year. All species had support for relationships between density and management and vegetation variables (Table 3, 4, 5, Appendix A). A complete ranking of final models for each species can be found in the Supplemental Material.

3.1. Species positively related to restoration

Densities of 10 species (Brown-headed Nuthatch, Blue-winged Warbler, Eastern Towhee, Eastern Wood-Pewee, Kentucky Warbler, Pine Warbler, Prairie Warbler, Red-headed Woodpecker, White-eyed Vireo, and Yellow-breasted Chat) were overall positively related to fire or thinning but relationships to vegetation structure were more complex (Table 4, 5). Region was supported for 3 species; Eastern Towhee and Eastern Wood-Pewee were more abundant in MTNF than ONF while Kentucky Warbler was more abundant in ONF (Table 5, Appendix A).

3.1.1. Management effects

Fire history and tree thinning were supported for 8 and 4 species, respectively (Table 4). Densities of Brown-headed Nuthatch, Eastern Wood-Pewee, Pine Warbler (Fig. 2A), Prairie Warbler (Fig. 2A), and Red-headed Woodpecker (Fig. 2A) increased as total burns increased in the last 10 years. Similarly, Eastern Towhee (Fig. 3A), Eastern Wood-Pewee, Pine Warbler, Prairie Warbler (Fig. 3A), and Yellow-breasted

Table 3
Number of parameters (K), ΔAIC, and P-value from Freeman-Tukey goodness-of-fit test for the top-ranked density (λ) and detection (σ) model predicting species density for 16 species in the Ozark-Ouachita Highlands, 2013–2015. Multiple models presented where supported and model-averaging was performed.

Species, most-supported model(s)[a]	K	ΔAIC	P
Acadian Flycatcher			
λ(year + canopy + shrub + decidBA + evergBA + reg + burns + canopy150 + everg1k + everg1k^2) σ(min + obs)	25	0	0.505
Black-and-white Warbler			
λ(canopy + shrub + decidBA + evergBA + reg + burns + thin + canopy1k + forest150 + forest150^2) σ(day + obs)	24	0	0.505
λ(canopy + shrub + decidBA + evergBA + reg + burns + thin + canopy1k + forest150) σ(day + obs)	23	0.08	–
λ(canopy + shrub + decidBA + evergBA + reg + canopy1k + forest150 + burn150) σ(day + obs)	23	1.84	–
Blue-winged warbler			
λ(year + canopy + canopy^2 + sap + pole + saw + burn1k) σ(day)	12	0	0.446
Brown-headed Nuthatch			
λ(burns + forest1k) σ(day)	7	0	0.465
λ(burns) σ(day)	6	0.61	–
Eastern towhee			
λ(decidBA + evergBA + reg + canopy150 + decid1k + decid1k^2 + burn1k + thin1k) σ(day + obs)	22	0	0.475
Eastern Wood-Pewee			
λ(year + sap + pole + saw + reg + burn1k + thin1k) σ(day + obs)	22	0	0.634
λ(year + sap + pole + saw + reg + burn1k + burn1k^2 + thin1k) σ(day + obs)	23	1.24	–
λ(year + sap + pole + saw + reg + burns + burns^2) σ(day + obs)	22	1.4	–
λ(year + sap + pole + saw + reg + burns) σ(day + obs)	21	1.67	–
Kentucky Warbler			
λ(year + canopy + reg + thin + forest150) σ(day)	11	0	0.446
λ(year + canopy + reg + forest150) σ(day)	10	1.82	–
Ovenbird			
λ(canopy + shrub + sap + pole + saw + reg + burns + thin + canopy150 + everg150 + burn1k + burn1k^2 + thin1k) σ(obs)	26	0	0.465
Pine Warbler			
λ(year + canopy + canopy^2 + decidBA + evergBA + burns + thin + decid150 + canopy1k + burn1k + thin1k) σ(min + day)	18	0	0.693
Prairie Warbler			
λ(canopy + canopy^2 + shrub + sap + pole + saw + burns + thin + canopy150 + decid1k + burn1k + thin1k) σ(year + day)	19	0	0.515
Red-headed Woodpecker			
λ(year + sap + pole + saw + snag + reg + burns + thin + canopy150 + canopy150^2 + forest150) σ(day)	17	0	0.436
Summer tanager			
λ(year + everg1k + burn150 + thin150 + thin150^2) σ(obs)	19	0	0.465
λ(year + everg1k + burn150 + thin150) σ(obs)	18	0.36	–
λ(year + everg1k) σ(obs)	16	0.65	–
λ(year + everg1k + everg1k^2 + burn150 + thin150) σ(obs)	19	1.09	–
λ(year + burns + everg1k) σ(obs)	17	1.63	–
λ(year + burn150 + thin150) σ(obs)	17	1.74	–
White-eyed Vireo			
λ(year + canopy + decidBA + evergBA + reg + burns + burns^2 + thin + canopy1k + forest150 + burn1k + thin1k) σ(obs)	25	0	0.446
λ(year + canopy + decidBA + evergBA + reg + burns + thin + canopy1k + forest150 + burn1k + burn1k^2 + thin1k) σ(obs)	25	0.97	–
Wood Thrush			
λ(burns + thin + canopy150 + everg1k + burn1k + thin1k)	10	0	0.455
λ(burns + thin + canopy150 + everg1k)	8	1.84	–
Worm-eating Warbler			
λ(year + canopy + shrub + decidBA + evergBA + reg + burns) σ(day + obs)	22	0	0.515
Yellow-breasted chat			
λ(canopy + shrub + sap + pole + saw + reg + canopy150 + decid1k + burn1k + burn1k^2 + thin1k) σ(year + obs)	26	0	0.505

[a] Variable abbreviations defined in Table 2.

Chat (Fig. 3A) had positive relationships with the area burned in the last 10 years within 1 km. White-eyed Vireo density peaked at 1–2 burns in the last 10 years (Fig. 2A) and was positively related to area burned (Fig. 3A). Kentucky Warbler was positively related, and Pine Warbler negatively related, to thinned points (Fig. S1 in the Supplemental Material). Blue-winged Warbler and Yellow-breasted Chat densities were positively related to the area thinned within 1 km (Fig. 4A).

3.1.2. Point-level vegetation effects

Densities of Blue-winged Warbler, Kentucky Warbler, Prairie Warbler, and Yellow-breasted Chat decreased as point-level canopy cover increased, whereas Pine Warbler density increased with canopy cover to its maximum at 80% canopy closure and then declined (Table 5, Fig. 5A). Prairie Warbler density was positively related to shrub cover (Table 5, Fig. S2 in Supplemental Material). Eastern Wood-Pewee and Red-headed Woodpecker densities were negatively related to sapling density while Blue-winged Warbler and Prairie Warbler densities were negatively related to pole timber (Table 5, Fig. S3 in the Supplemental Material). Eastern Towhee, Pine Warbler, and White-eyed Vireo were negatively related to deciduous basal area (Table 5, Fig. 6A).

3.1.3. Landscape-level vegetation effects

Eastern Towhee, White-eyed Vireo, and Yellow-breasted Chat densities were negatively related to mean canopy cover within 150 m, 1 km, and 150 m, respectively (Table 5, Fig. 7A). Red-headed Woodpecker reached its greatest density at intermediate mean canopy cover within 150 m (Fig. 7A). Pine Warbler, Prairie Warbler, and Yellow-breasted Chat densities were negatively related to deciduous forest cover whereas Eastern Towhee density peaked in areas with little to moderate deciduous forest cover before decreasing (Table 5, Fig. 8A). Similarly, Kentucky Warbler and Red-headed Woodpecker densities were negatively related to total forest cover (Table 5, Fig. 8A).

3.2. Species negatively related to restoration

Densities of 5 species (Acadian Flycatcher, Black-and-white Warbler, Ovenbird, Wood Thrush, and Worm-eating Warbler) were

Table 4
Summary of effects of point- and landscape-level management variables on predicted densities of 16 species surveyed in the Ozark-Ouachita Highlands, 2013–2015. Symbols indicate positive (+), negative (−), or quadratic (◊) relationships to bird density based on the most-supported model(s); symbols in parentheses had coefficients whose 95% confidence interval overlapped zero. Blanks indicate a variable was not in the most-supported model(s).

Species	Burns	Thin	Burned 150 m	Thinned 150 m	Burned 1 km	Thinned 1 km
Species positively related to restoration						
Blue-winged Warbler					(+)	+
Brown-headed Nuthatch	+					
Eastern Towhee					+	(+)
Eastern Wood-Pewee	+				+	(−)
Kentucky Warbler		+				
Pine Warbler	+	−			+	(−)
Prairie Warbler	+	(−)			+	(+)
Red-headed Woodpecker	+	(+)				
White-eyed Vireo	◊	(+)			+	(+)
Yellow-breasted Chat					◊	+
Species negatively related to restoration						
Acadian Flycatcher	−					
Black-and-white Warbler	−	(−)	−	(−)		
Ovenbird	(−)	−			◊	(+)
Wood Thrush	−	−			−	(+)
Worm-eating Warbler	−					
Inconclusive						
Summer Tanager	(−)		(−)	(◊)		

negatively related to restoration treatment or the resulting vegetation (Table 3, 4). Acadian Flycatcher, Black-and-white Warbler, Ovenbird, and Worm-eating Warbler were less abundant in the ONF (Table 5), and we only analyzed Wood Thrush density in the MTNF because there was a single detection in ONF. Summer Tanager results were mostly inconclusive. Summer Tanager density was positively related to percent evergreen forest (Fig. 8B) but negatively related to prescribed burns, the percent area burned, and area thinned (Fig. 4B), but all relationships were weak and confidence intervals overlapped zero (Table 4, 5, Appendix A).

3.2.1. *Management effects*

Densities of Acadian Flycatcher (Fig. 2B), Black-and-white Warbler (Fig. 2B), Wood Thrush, and Worm-eating Warbler (Fig. 2B) were negatively related to the number of prescribed burns in the last 10 years (Table 4). Black-and-white Warbler and Wood Thrush densities were negatively related to the area burned within 150 m and 1 km, respectively (Table 4, Fig. 3B). Ovenbird density had a quadratic relationship with percent area burned within 1 km but was overall negatively related to area burned (Table 4, Fig. 3B). Ovenbird and Wood Thrush densities were both lower at points that had been thinned within the past 10 years (Table 4, Fig. S1 in the Supplemental Material).

Table 5
Summary of effects of point- and landscape-level vegetation variables on predicted densities of 16 species surveyed in the Ozark-Ouachita Highlands, 2013–2015. Symbols indicate positive (+), negative (−), or quadratic (◊) relationships to bird density based on the most-supported model(s); symbols in parentheses had coefficients whose 95% confidence interval overlapped zero. Blanks indicate a variable was not in the most-supported model(s).

Species	Region*	Point-level canopy	Shrub cover	Sapling density	Pole density	Saw density	DecidBA	EvergBA	Mean canopy	Decid forest	Everg forest	Forest cover
Species positively related to restoration												
Blue-winged Warbler		−		(+)	−	(+)						
Brown-headed Nuthatch												(−)[b]
Eastern Towhee	−						−	(−)	−[a]	◊[b]		
Eastern Wood-Pewee	−			−	(−)	(+)						
Kentucky Warbler	+	−										−[a]
Pine Warbler		◊					−	(+)	(+)[b]	−[a]		
Prairie Warbler		◊	+	(+)	−	(+)			(−)[a]	−[b]		
Red-headed Woodpecker	(−)			−	(+)	(−)	(+)[c]		◊[a]			−[a]
White-eyed Vireo	(−)	(−)					−	(−)	−[b]			(−)[a]
Yellow-breasted Chat	(−)	−	(+)	(−)	(−)	(−)			−[a]	−[b]		
Species negatively related to restoration												
Acadian Flycatcher	−	(−)	(−)				+	(+)	+[a]		◊[b]	
Black-and-white Warbler	−	+	(+)				−	(−)	(−)[b]			−[a]
Ovenbird	−	+	+	+	(−)	(+)			+[a]		+[a]	
Wood Thrush									(+)[a]		−[b]	
Worm-eating Warbler	−	+	+				(+)	(−)				
Inconclusive												
Summer Tanager											(+)[b]	

* Species density was lower (−) or higher (+) in ONF.
[a] 150-m radius.
[b] 1-km radius.
[c] Only snag basal area evaluated.

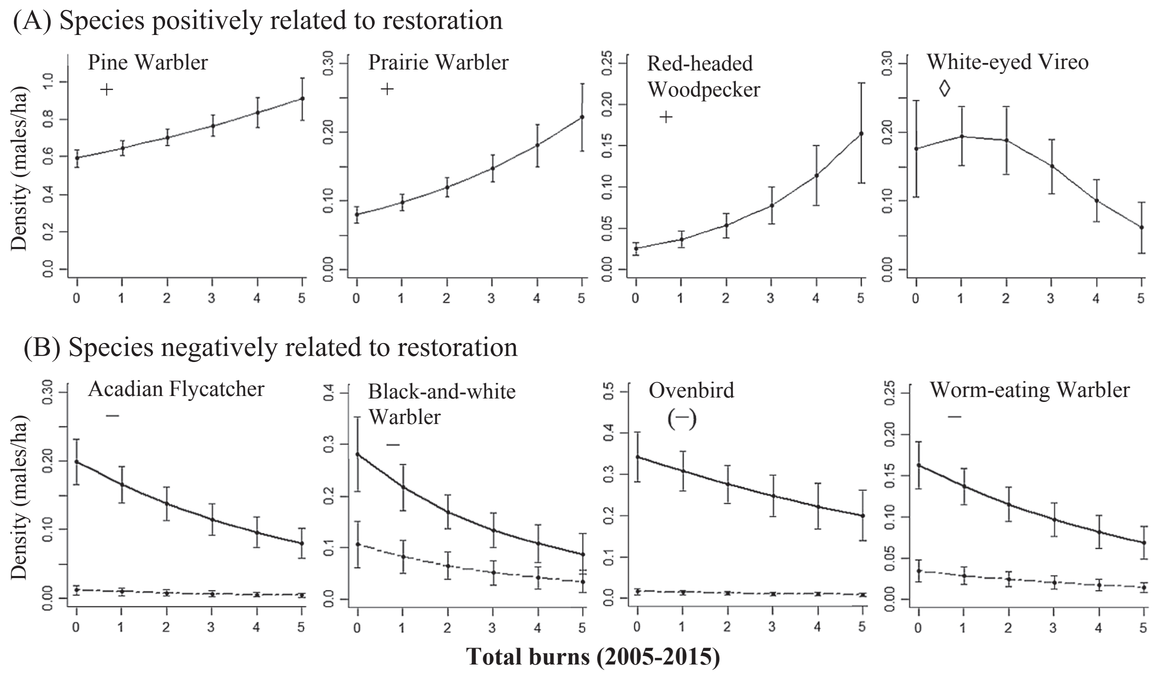

Fig. 2. Predicted species density and standard error in relation to total number of prescribed burns from 2005 to 2015 in the Ozark-Ouachita Highlands, May-July 2013–2015. Symbols indicate positive (+), negative (−), or quadratic (◊) relationships to bird density; symbols in parentheses were coefficients whose 95% confidence interval overlapped zero as summarized in Table 4. Solid and dotted lines represent MTNF and ONF, respectively, when region was supported.

3.2.2. Point-level vegetation effects

Black-and-white Warbler, Ovenbird, and Worm-eating Warbler were positively related to point-level canopy cover (Table 5, Fig. 5B), but Ovenbird and Worm-eating Warbler densities were also positively related to shrub cover (Table 5, Fig. S2 in the Supplemental Material). Ovenbird density was positively related to sapling density (Table 5, Fig. S3 in the Supplemental Material). Acadian Flycatchers were more abundant in areas with higher deciduous basal area whereas Black-and-white Warbler density decreased with increasing deciduous basal area (Table 5, Fig. 6B).

3.2.3. Landscape-level vegetation effects

Acadian Flycatcher and Ovenbird densities were positively related to mean canopy cover within 150 m (Table 5, Fig. 7B). Acadian Flycatcher density had a quadratic relationship with percent evergreen forest within 1 km with highest densities at 0% evergreen forest

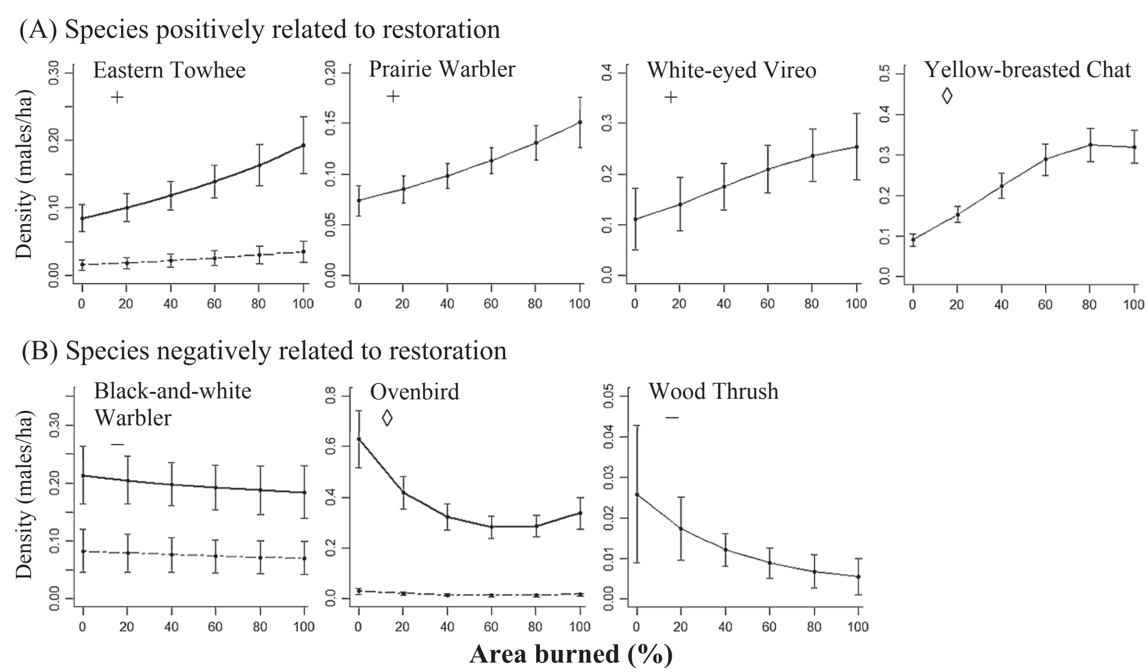

Fig. 3. Predicted species density with standard error in relation to percent area burned from 2005 to 2015 in the Ozark-Ouachita Highlands, May-July 2013–2015. Symbols indicate positive (+), negative (−), or quadratic (◊) relationships to bird density as summarized in Table 4. Solid and dotted lines represent MTNF and ONF, respectively, when region was supported.

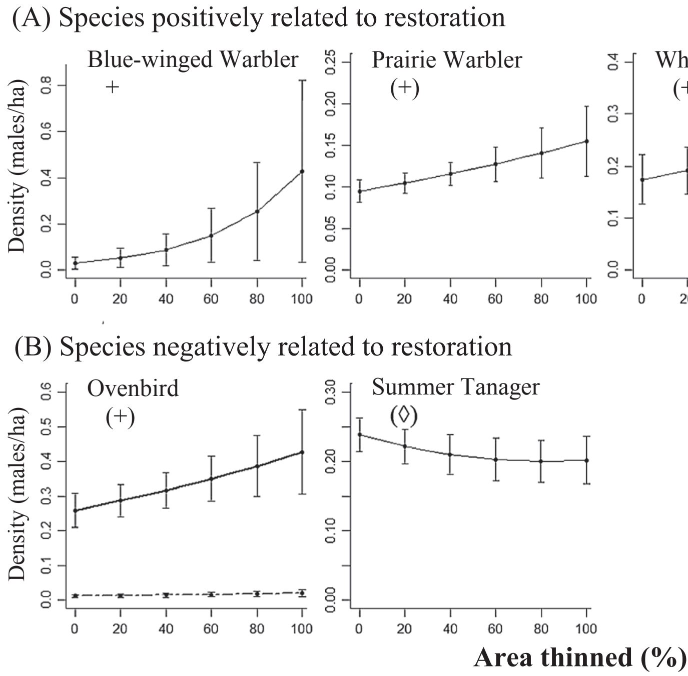

Fig. 4. Predicted species density with standard error in relation to percent area thinned from 2005 to 2015 in the Ozark-Ouachita Highlands, May-July 2013–2015. Symbols indicate positive (+), negative (−), or quadratic (◊) relationships to bird density; symbols in parentheses were coefficients whose 95% confidence interval overlapped zero as summarized in Table 4. Solid and dotted lines represent MTNF and ONF, respectively, when region was supported.

(Table 5). Ovenbird density was positively related, and Wood Thrush negatively related, to evergreen forest cover within 150 m and 1 km, respectively (Table 5, Fig. 8B). Black-and-white Warbler density was negatively related to total forest cover within 150 m (Table 5, Fig. 8B).

4. Discussion

We examined the effects of pine woodland restoration on a diverse suite of breeding birds by estimating species density in relation to a range of management and vegetation conditions at multiple scales. As predicted, densities of early-successional, disturbance-dependent, and generalist species were positively related to restoration activity and the resulting vegetation while mature-forest species were negatively related to these attributes. Ten species had positive relationships directly with management treatment and also showed greater densities in areas with little to moderate canopy cover, decreased tree density, and less forest

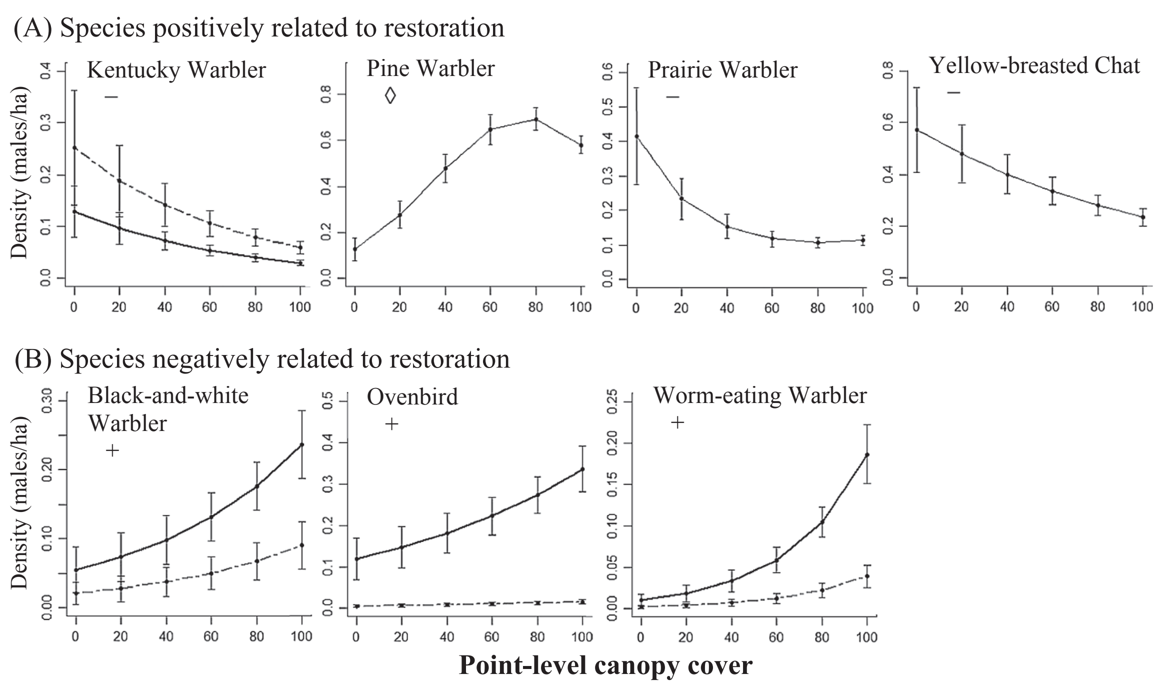

Fig. 5. Predicted species density with standard error in relation to point-level canopy cover in the Ozark-Ouachita Highlands, May-July 2013–2015. Symbols indicate positive (+), negative (−), or quadratic (◊) relationships to bird density as summarized in Table 5. Solid and dotted lines represent MTNF and ONF, respectively, when region was supported.

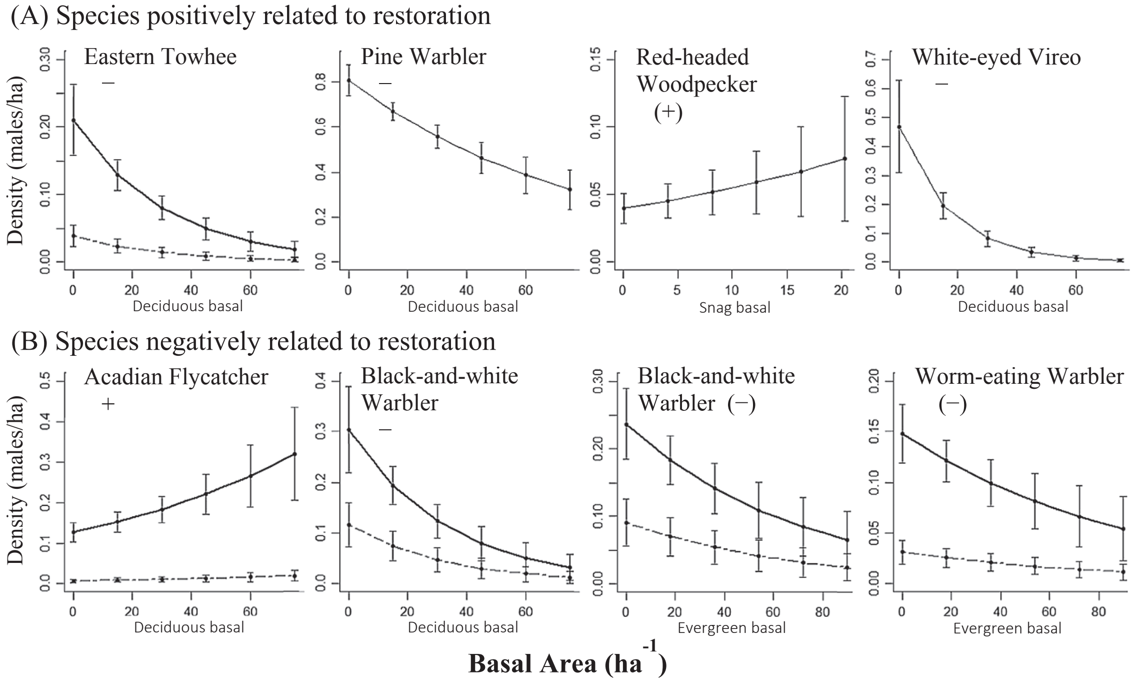

Fig. 6. Predicted species density with standard error in relation to deciduous or evergreen basal area in the Ozark-Ouachita Highlands, May-July 2013–2015. Symbols indicate positive (+) or negative (−) relationships to bird density; symbols in parentheses were coefficients whose 95% confidence interval overlapped zero as summarized in Table 5. Solid and dotted lines represent MTNF and ONF, respectively, when region was supported.

cover. Only five species were negatively related to restoration; these species avoided large tracts of evergreen forest and preferred areas with closed canopy and increased basal area. Early-successional species forage and nest in thick ground cover and benefitted from the creation of open canopies and lush understory. Generalist species such as Eastern Wood-Pewees utilized the same area without impacting the success of early-successional species, an important factor given that grassland and shrubland species are experiencing some of the worst declines in North American landbirds (Brawn et al. 2001, Hunter et al. 2001, Brennan and Kuvlesky 2005, Sauer and Link 2011). Mature-forest species did not generally respond positively to restoration, but Black-and-white Warbler, Ovenbird, and Worm-eating Warbler had some contradictory relationships that could indicate some tolerance for savanna-woodland restoration.

Pine savanna-woodland is restored by using a combination of thinning, which opens the canopy and shifts the composition from

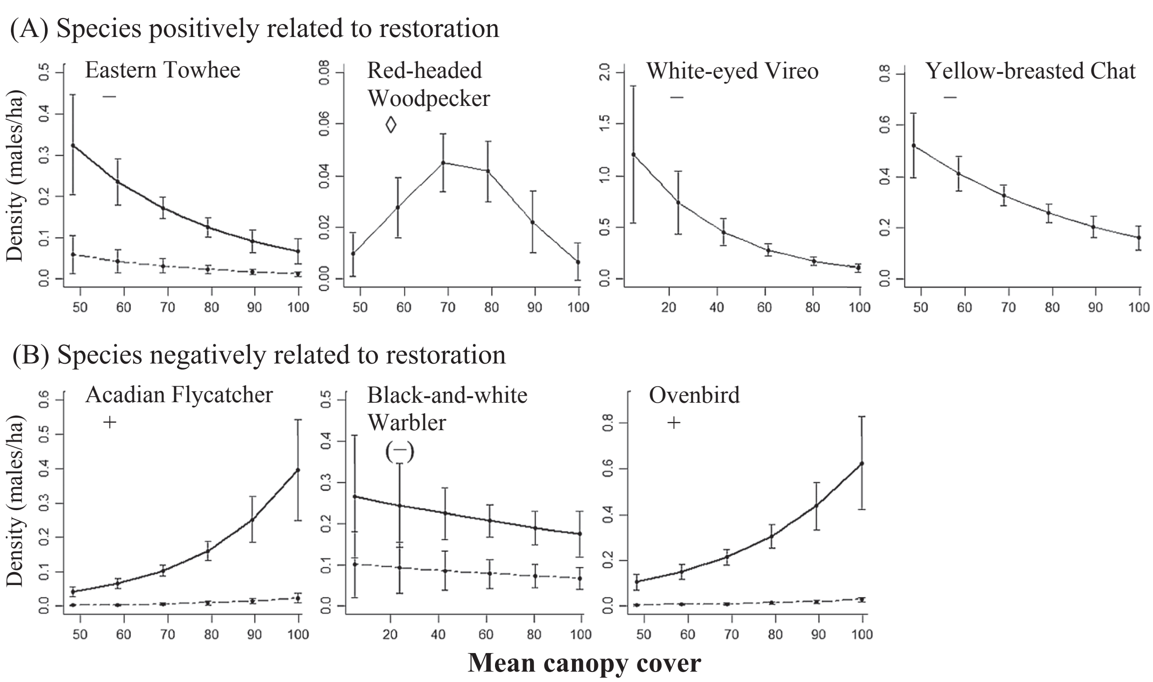

Fig. 7. Predicted species density with standard error in relation to mean canopy cover in the Ozark-Ouachita Highlands, May-July 2013–2015. Symbols indicate positive (+), negative (−), or quadratic (◊) relationships to bird density; symbols in parentheses were coefficients whose 95% confidence interval overlapped zero as summarized in Table 5. Solid and dotted lines represent MTNF and ONF, respectively, when region was supported.

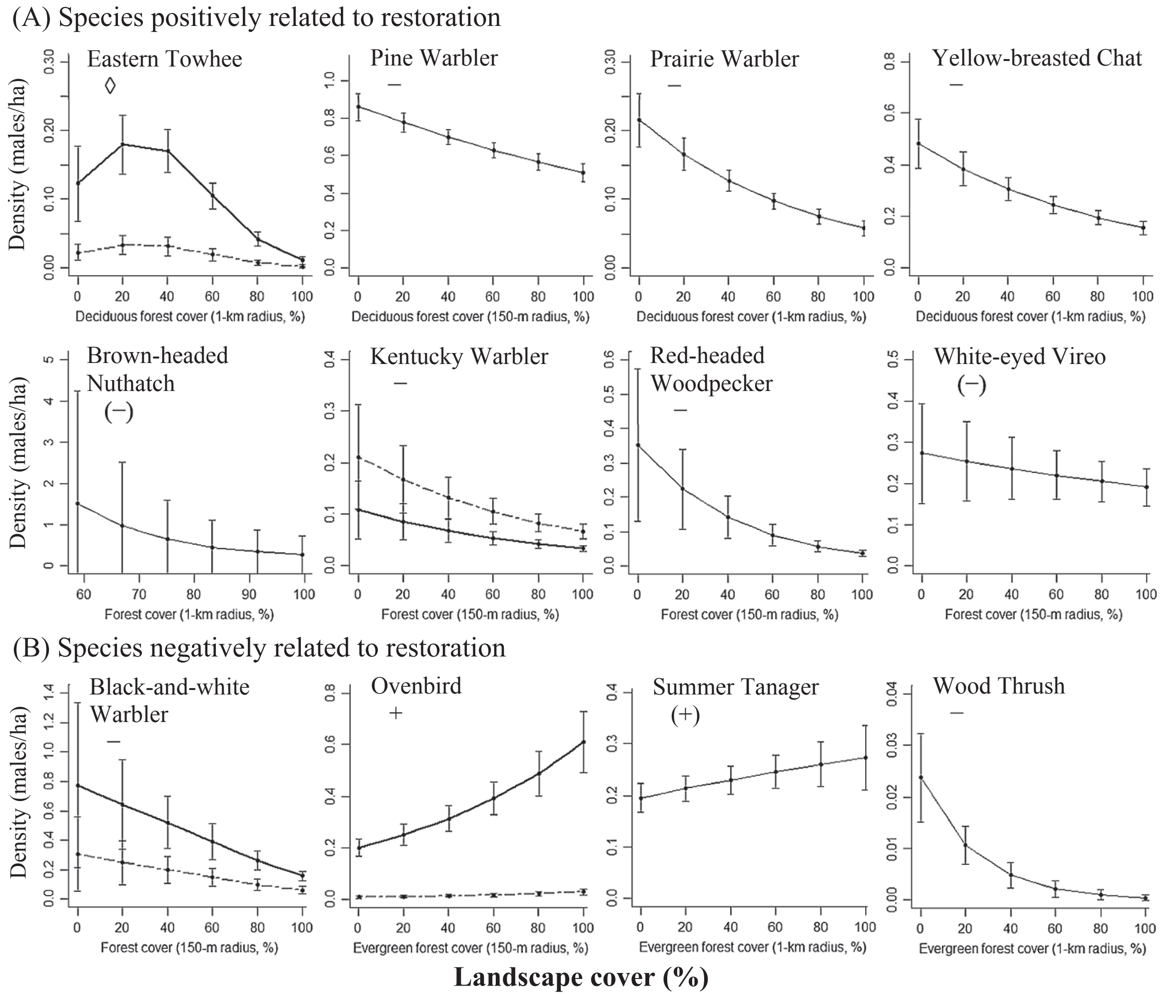

Fig. 8. Predicted species density with standard error in relation to percent landscape cover in the Ozark-Ouachita Highlands, May-July 2013–2015. Symbols indicate positive (+), negative (−), or quadratic (◊) relationships to bird density; symbols in parentheses were coefficients whose 95% confidence interval overlapped zero as summarized in Table 5. Solid and dotted lines represent MTNF and ONF, respectively, when region was supported.

hardwood to pine, and prescribed fire to stop the growth of deciduous sprouts or saplings that would succeed to dense midstory and eventually closed forest. Both treatments accomplish separate objectives, but the combination of thinning and fire is usually required to restore savanna-woodland from the mature forest that still dominates the region (Peterson and Reich 2001, Lanham et al. 2002, Brudvig and Asjornsen 2009, Dey et al. 2017). Tree thinning, strategically followed by a regimen of low-intensity prescribed burns, creates conditions suitable for multiple bird guilds by leaving large, widely-spaced trees for canopy-nesting species while allowing the development of grasses and shrubs for ground- or shrub-nesting species. Selectively removing trees helps reach savanna-woodland conditions faster, but prescribed fire is a crucial step in maintaining the open midstory. Pine woodland is well-adapted to frequent low-intensity fires because shortleaf pine saplings are fire-tolerant while many hardwood species are not (Guyette et al. 2007). Frequent burns (2–4 burns/decade) prevent dense sapling layers and canopy ingrowth by stopping or delaying growth of hardwood species (Peterson and Reich 2001) and allow herbaceous or woody cover to thrive (Barrioz et al. 2013). The seasonal timing of and time between burns are also important drivers of vegetation and wildlife response (Sparks et al. 1999, Barrioz et al. 2013, Vander Yacht et al. 2017) but not ones we examined in this study.

Management was an important driver of species density in this and similar studies (Thompson et al. 1992, Clawson et al. 2002, Gram et al. 2003, Wallendorf et al. 2007, Reidy et al. 2014). With the exception of Summer Tanager, all of our focal species were affected by at least one management variable. Only six species were directly related to thinning activity but 13 of 16 species were related to some aspect of canopy cover, tree density, or basal area, all of which are affected by thinning. Mechanical thinning selectively removes some overstory trees which opens the canopy and allows the understory to flourish as increased sunlight reaches the ground (Scholes and Archer 1997, Brudvig and Asbjomsen 2009, Barrioz et al. 2013). Studies relating bird response directly to thinning treatment are rare (Barrioz et al. 2013) because most studies use measures of tree density, basal area, stocking, or ground cover to indirectly evaluate thinning effects (Kendrick et al. 2013, Reidy et al. 2014, Holoubek and Jensen 2015, Vander Yacht et al. 2016). Fewer species may have been directly related to thinning treatment as thinning could have occurred prior to the 10-year period we examined or because thinning was limited or low-intensity in the study area. On average, twice as much area was burned as was thinned, and most areas that were thinned still had moderate canopy closure (Table 2). The range of canopy cover within a 1-km radius was wide (5–100%), but average canopy closure was still 78%, reflecting a landscape that is still mostly woodland or forest with only small areas of savanna. Relating bird abundances to direct measures of tree density is likely a better approach than a simple measure of whether a stand was thinned or not and can more accurately reflect the intensity of thinning activity.

Thinning, or the stand structure it created, was an important driver of increased densities of multiple early-successional species including Blue-winged Warbler, Kentucky Warbler, Prairie Warbler (Fig. 4A), White-eyed Vireo (Fig. 4A), and Yellow-breasted Chat. Experimental studies conducted in the Missouri Ozarks found significant, positive responses to thinning from these same species (Clawson et al. 2002, Gram et al. 2003, Kendrick et al. 2015) while certain interior-forest species are not affected or even increase in abundance in forests that have harvested areas (Thompson et al. 1992). Only three species (Pine Warbler, Ovenbird, and Wood Thrush) were negatively related to thinning. As predicted, Ovenbird and Wood Thrush avoided points that had been thinned as these are both species that prefer mid- to late-successional forest to breed (Evans et al. 2011, Porneluzi et al. 2011). Pine Warbler density, while lower at thinned points (Fig. S1 in the Supplemental Material), was still one of the most abundant species and overall positively related to restoration, likely because it requires pine trees for nesting sites. Measures of vegetation structure provided additional evidence that mechanical thinning is benefitting a multitude of species. Most early-successional species were more abundant in areas with less canopy cover, decreased tree density, and less deciduous basal area reflecting their need for open canopies and dense understories for nesting. Additionally, Eastern Wood-Pewee and Red-headed Woodpecker densities were negatively related to sapling density. Eastern Wood-Pewees, a generalist species, and Red-headed Woodpeckers, a disturbance-dependent species, are primarily aerial foragers that sally from perches to catch insects in the air (Frei et al. 2017, Watt et al. 2017). Their negative relationship with sapling density, in addition to Eastern Wood-Pewee's positive trend with saw timber density (Fig. S3 in the Supplemental Material), could be an indication that they prefer open woodlands with large trees for perches, and nest sites, with open midstories to more easily catch prey (Brawn 2006, Vander Yacht et al. 2016).

Fire activity affected many species and can be a cost-effective method to reduce understory and midstory density over large areas and has the added potential of creating canopy gaps. Eight species were positively related, and all five mature-forest species negatively related, to prescribed fire likely because fire has direct and immediate effects on the understory. Mature-forest species that nest directly on the ground in leaf litter (Black-and-white Warbler, Ovenbird, Worm-eating Warbler) or in midstory trees (Acadian Flycatcher, Wood Thrush) will avoid areas with recent or frequent fire because their required nesting substrate is absent (Reidy et al. 2014). Fire is a key component in maintaining the dense understory of savanna-woodland; as such, most early-successional species responded positively to prescribed fire. Other disturbance-dependent species, such as Brown-headed Nuthatches and Red-headed Woodpeckers, were also found in areas with higher fire frequency likely because of increased snag density (Holden et al. 2016, Perry et al. 2017), a critical component for these cavity-nesting species (Vierling and Lentile 2006, King et al. 2007).

Contrary to our predictions, very few early-successional species responded to our measure of shrub cover whereas two mature-forest species had positive responses to shrub cover, a result similar to Reidy et al. (2014). This was surprising given how many of our species forage and nest in dense understory with high shrub density (Fink et al. 2006, Nolan Jr et al. 2014). Since fire has significant impacts on understory structure, it's possible that fire activity was a stronger predictor of species density than our measure of shrub cover. Additionally, early-successional species were more abundant in areas with lower tree densities and decreased canopy cover, which were also the sites that generally had more shrub cover.

Bird response to landscape cover was generally split between species that responded positively or negatively to restoration management. Birds that responded positively to management often had negative relationships to landscape canopy cover, percent deciduous forest, or percent total forest. This likely reflected preferences for actively managed areas with lower canopy cover and more evergreen than deciduous forest, or more open landscapes since many of these species also use successional habitats. Three of five mature-forest species that responded negatively to management had positive relationships to landscape canopy (Acadian Flycatcher, Ovenbird, Wood Thrush), providing further evidence of a negative response to restoration. Acadian Flycatcher and Wood Thrush had a quadratic and negative response, respectively, and Ovenbird and Summer Tanager a positive response, to percent evergreen forest. We suggest these relationships reflect species preference for primarily deciduous or mixed deciduous-evergreen forest at a landscape scale. Interestingly, although Ovenbirds were overall negatively related to management, they increased density with percent evergreen forest (150-m radius, Fig. 8B) as well as shrub cover (Fig. S2 in Supplemental Material) and area thinned (Fig. 4B), although the confidence intervals overlapped zero for thinning. This mixed response could be because Ovenbird fledglings, as well as recently-fledged Wood Thrush and Worm-eating Warblers, typically move from nesting habitat in closed-canopy forest to areas with dense vegetation such as clearcuts or canopy gaps (Anders et al. 1998, Vitz and Rodewald 2011, Streby and Anderson 2012, Burke 2013, Jenkins et al. 2016). We suggest that some mature-forest species may tolerate low levels of disturbance in the landscape and benefit from woodland restoration as post-fledgling habitat is created.

Summer Tanager had the most model selection uncertainty (Table 3), and variables that were supported did not greatly affect density (Fig. 4B & 8B, Appendix A). This is likely because Summer Tanagers are woodland and forest generalists and were abundant across the landscape, having one of the greater densities in this study. Previous research in Missouri suggested they were positively affected by woodland restoration with densities negatively related to tree density, positively related to fire, and highest at intermediate levels of forest cover (Reidy et al. 2014).

5. Conclusions

We show that the restoration of pine savanna and woodland has the potential to significantly impact avian communities in the central US by creating suitable habitat for multiple guilds. Restoration provided conditions that supported high densities of disturbance-dependent and early-successional species, many of which are species of conservation concern experiencing sharp population declines throughout their range. Land managers often use specific vegetation measurements such as canopy cover or tree density to assess restoration progress (Anderson 1998), but our results and others have shown that relationships between bird density and vegetation and landscape cover can be complex (Barrioz et al. 2013, Reidy et al. 2014). Estimating species density is a valuable tool in gauging restoration success, but species presence does not necessarily reflect habitat quality (Van Horne 1983, Bock and Jones 2004, Fink et al. 2006, Johnson 2007). In a companion study, we determined that nesting success of disturbance-dependent species (Eastern Towhee, Prairie Warbler, Yellow-breasted Chat) and canopy-nesting species (Eastern Wood-Pewee, Pine Warbler, Summer Tanager) was also positively related to pine woodland restoration, providing additional evidence that management is creating high-quality breeding habitat (Roach et al. 2018).

Although canopy cover ranged from 0 to 100%, average landscape-level canopy closure was still > 70% because few count surveys were located in overly open areas and the landscape was still dominated by closed woodland and forest. We detected few Bachman's Sparrow, Blue-winged Warbler, and Northern Bobwhite because these species require savanna and open woodlands, which were likely too rare in the survey area to support moderate or even minimal populations. If managers wish to increase abundance of these and similar species, reducing canopy cover and tree density below that observed in this study, on average, may be necessary along with applying these strategies over enough area to support regional populations. Only five species were negatively related to restoration and were generally explained by their dependence on leaf litter or midstory trees for nesting or foraging.

These species are abundant in mature forests not being managed to restore pine woodland, which still dominate the region. Most recently-restored sites still had a woody-dominated understory, and continued prescribed burning will be required to halt the advancement of hardwood saplings and continue the shift to more grasses and forbs that are characteristic of open woodland and savanna. We provided strong evidence for relationships of pine woodland restoration with species density during the breeding season, but future work that examines longer-term effects of restoration and vegetation change as well as other aspects of species demographics such as post-fledging survival and habitat will provide additional insight into how restoration affects populations.

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Appendix A

See Table A1.

Table A1
Coefficients, standard errors (SE), and 95% confidence limits (LCL, UCL) for variables in species density models with informative parameters and ΔAIC < 2 in managed woodlands in the Ozark-Ouachita Highlands, May-July 2013-2015.

Species, variable[a]	Coefficient	SE	LCL	UCL
Acadian Flycatcher				
canopy	−0.104	0.111	−0.321	0.114
shrub	−0.153	0.130	−0.408	0.102
decid basal	0.156	0.072	0.015	0.297
everg basal	0.043	0.078	−0.110	0.195
region	−2.809	0.586	−3.957	−1.661
burns	−0.279	0.080	−0.436	−0.122
canopy150	0.496	0.142	0.219	0.774
everg1k	−0.552	0.100	−0.749	−0.356
everg1k^2	0.244	0.065	0.117	0.370
Black-and-white Warbler (1)				
canopy	0.285	0.130	0.031	0.539
shrub	0.159	0.104	−0.045	0.362
decid basal	−0.383	0.162	−0.701	−0.065
everg basal	−0.220	0.120	−0.455	0.016
region	−1.058	0.408	−1.857	−0.258
burns	−0.453	0.098	−0.645	−0.261
thin	−0.093	0.218	−0.520	0.335
canopy1k	−0.063	0.115	−0.288	0.163
forest150	−0.496	0.175	−0.838	−0.154
forest150^2	−0.060	0.043	−0.144	0.025
Black-and-white Warbler (2)				
canopy	0.296	0.129	0.043	0.549
shrub	0.194	0.099	−0.001	0.388
decid basal	−0.373	0.162	−0.690	−0.056
everg basal	−0.206	0.120	−0.441	0.029
region	−0.927	0.396	−1.703	−0.152
burns	−0.444	0.099	−0.637	−0.250
thin	−0.087	0.218	−0.515	0.342
canopy1k	−0.068	0.114	−0.293	0.156
forest150	−0.272	0.078	−0.425	−0.119
Black-and-white Warbler (3)				
canopy	0.287	0.129	0.034	0.539
shrub	0.192	0.101	−0.005	0.389
decid basal	−0.366	0.160	−0.681	−0.052
everg basal	−0.222	0.120	−0.457	0.013
region	−0.807	0.400	−1.591	−0.024
canopy1k	−0.043	0.117	−0.273	0.187
forest150	−0.255	0.078	−0.408	−0.101
burn150	−0.444	0.100	−0.640	−0.249
thin150	−0.018	0.092	−0.199	0.163
canopy1k	−0.043	0.117	−0.273	0.186
forest150	−0.254	0.078	−0.407	−0.101
burn150	−0.444	0.099	−0.639	−0.248
thin150	−0.018	0.092	−0.199	0.163
Blue-winged Warbler				
canopy	0.409	0.380	−0.336	1.154
canopy^2	0.281	0.113	0.060	0.501
sap	0.392	0.220	−0.039	0.823
pole	−0.733	0.281	−1.283	−0.182
saw	0.113	0.217	−0.312	0.537

(continued on next page)

Table A1 (*continued*)

Species, variable[a]	Coefficient	SE	LCL	UCL
burn1k	0.066	0.295	−0.512	0.644
thin1k	0.738	0.234	0.279	1.196
Brown-headed Nuthatch (1)				
burns	0.718	0.351	0.029	1.406
forest1k	−0.484	0.301	−1.074	0.105
Brown-headed Nuthatch (2)				
burns	0.648	0.350	−0.038	1.335
Eastern Towhee				
decid basal	−0.406	0.130	−0.661	−0.151
everg basal	−0.089	0.096	−0.276	0.099
region	−1.692	0.500	−2.671	−0.712
canopy150	−0.350	0.171	−0.685	−0.015
decid1k	−0.709	0.128	−0.959	−0.458
decid1k^2	−0.355	0.113	−0.576	−0.135
burn1k	0.331	0.117	0.102	0.560
thin1k	0.015	0.107	−0.196	0.225
Eastern Wood-Pewee (1)				
sap	−0.126	0.056	−0.235	−0.016
pole	−0.060	0.046	−0.151	0.030
saw	0.071	0.041	−0.010	0.151
region	−1.338	0.152	−1.635	−1.041
burn1k	0.176	0.051	0.077	0.276
thin1k	−0.042	0.048	−0.135	0.051
Eastern Wood-Pewee (2)				
sap	−0.126	0.056	−0.235	−0.016
pole	−0.061	0.046	−0.152	0.030
saw	0.072	0.041	−0.008	0.152
region	−1.324	0.153	−1.623	−1.025
burn1k	0.180	0.051	0.080	0.279
burn1k^2	0.056	0.064	−0.071	0.182
thin1k	−0.040	0.048	−0.134	0.054
Eastern Wood-Pewee (3)				
sap	−0.130	0.054	−0.236	−0.023
pole	−0.059	0.046	−0.149	0.030
saw	0.069	0.041	−0.011	0.150
region	−1.271	0.144	−1.554	−0.989
burns	0.173	0.052	0.070	0.275
burns^2	−0.075	0.050	−0.173	0.023
Eastern Wood-Pewee (4)				
sap	−0.147	0.053	−0.251	−0.043
pole	−0.049	0.045	−0.138	0.040
saw	0.058	0.040	−0.021	0.137
region	−1.235	0.142	−1.514	−0.956
burns	0.120	0.039	0.044	0.195
Kentucky Warbler (1)				
canopy	−0.274	0.085	−0.441	−0.108
region	0.705	0.224	0.265	1.145
thin	0.450	0.227	0.005	0.894
forest150	−0.160	0.074	−0.306	−0.014
Kentucky Warbler (2)				
canopy	−0.318	0.082	−0.478	−0.158
region	0.596	0.217	0.170	1.021
forest150	−0.189	0.074	−0.334	−0.045
Ovenbird				
canopy	0.206	0.087	0.035	0.376
shrub	0.286	0.069	0.151	0.421
sap	0.121	0.052	0.020	0.223
pole	−0.101	0.059	−0.216	0.014
saw	0.043	0.057	−0.067	0.154
region	−3.061	0.384	−3.814	−2.308
burns	−0.165	0.105	−0.371	0.040
thin	−0.442	0.182	−0.798	−0.085
canopy150	0.394	0.125	0.148	0.639
everg150	0.370	0.056	0.260	0.479
burn1k	−0.228	0.117	−0.457	0.001
burn1k^2	0.292	0.101	0.093	0.490
thin1k	0.134	0.091	−0.045	0.313
Pine Warbler				
canopy	−0.134	0.075	−0.281	0.014
canopy^2	−0.119	0.030	−0.178	−0.059
decid basal	−0.154	0.055	−0.262	−0.046
everg basal	0.015	0.038	−0.060	0.090
burns	0.131	0.049	0.035	0.227
thin	−0.302	0.100	−0.497	−0.106
canopy1k	0.029	0.046	−0.062	0.120

(*continued on next page*)

Table A1 (*continued*)

Species, variable[a]	Coefficient	SE	LCL	UCL
decid150	−0.182	0.047	−0.274	−0.090
burn1k	0.121	0.058	0.007	0.235
thin1k	−0.005	0.050	−0.103	0.092
Prairie Warbler				
canopy	0.030	0.133	−0.231	0.291
canopy^2	0.078	0.035	0.010	0.147
shrub	0.143	0.060	0.026	0.259
sap	0.043	0.090	−0.134	0.219
pole	−0.155	0.077	−0.306	−0.004
saw	0.051	0.069	−0.085	0.186
burns	0.313	0.089	0.139	0.487
thin	−0.027	0.170	−0.360	0.306
canopy150	−0.145	0.093	−0.327	0.037
decid1k	−0.338	0.075	−0.484	−0.192
burn1k	0.291	0.114	0.069	0.514
thin1k	0.130	0.089	−0.044	0.305
Red-headed Woodpecker				
sap	−0.367	0.180	−0.719	−0.015
pole	0.072	0.121	−0.165	0.308
saw	−0.015	0.114	−0.239	0.209
snag basal	0.108	0.101	−0.091	0.307
region	−0.358	0.712	−1.752	1.037
burns	0.576	0.115	0.351	0.801
thin	0.108	0.248	−0.379	0.594
canopy150	−0.320	0.288	−0.884	0.244
canopy150^2	−0.341	0.158	−0.652	−0.031
forest150	−0.329	0.085	−0.495	−0.162
Summer Tanager (1)				
everg1k	0.087	0.049	−0.009	0.182
burn150	−0.032	0.052	−0.133	0.069
thin150	−0.260	0.122	−0.499	−0.020
thin150^2	0.131	0.086	−0.038	0.300
Summer Tanager (2)				
everg1k	0.090	0.048	−0.005	0.185
burn150	−0.033	0.052	−0.134	0.068
thin150	−0.096	0.056	−0.205	0.013
Summer Tanager (3)				
everg1k	0.091	0.048	−0.002	0.185
Summer Tanager (4)				
everg1k	0.138	0.065	0.010	0.266
everg1k^2	−0.048	0.043	−0.133	0.037
burn150	−0.037	0.052	−0.138	0.064
thin150	−0.096	0.056	−0.205	0.013
Summer Tanager (5)				
everg1k	0.099	0.048	0.004	0.194
burns	−0.053	0.053	−0.158	0.051
Summer Tanager (6)				
burn150	−0.015	0.051	−0.115	0.085
thin150	−0.108	0.056	−0.217	0.002
White-eyed Vireo (1)				
canopy	−0.007	0.102	−0.207	0.193
decid basal	−0.749	0.195	−1.131	−0.367
everg basal	−0.140	0.122	−0.379	0.099
region	−0.400	0.380	−1.145	0.345
burns	0.110	0.190	−0.262	0.483
burns^2	−0.349	0.152	−0.647	−0.050
thin	0.014	0.236	−0.449	0.477
canopy1k	−0.372	0.112	−0.592	−0.153
forest150	−0.049	0.059	−0.165	0.067
burn1k	0.253	0.173	−0.087	0.593
thin1k	0.125	0.119	−0.109	0.358
White-eyed Vireo (2)				
canopy	−0.067	0.098	−0.258	0.125
decid basal	−0.707	0.195	−1.089	−0.325
everg basal	−0.131	0.121	−0.368	0.105
region	−0.395	0.376	−1.133	0.342
burns	−0.285	0.119	−0.518	−0.053
thin	−0.003	0.232	−0.458	0.452
canopy1k	−0.332	0.112	−0.550	−0.113
forest150	−0.057	0.060	−0.175	0.062
burn1k	0.532	0.158	0.223	0.841
burn1k^2	−0.315	0.148	−0.606	−0.024
thin1k	0.119	0.119	−0.114	0.352

(*continued on next page*)

Table A1 (*continued*)

Species, variable[a]	Coefficient	SE	LCL	UCL
Wood Thrush (1)				
burns	0.015	0.409	−0.787	0.817
thin	−1.561	0.704	−2.941	−0.181
canopy150	0.040	0.192	−0.336	0.417
everg1k	−0.739	0.250	−1.229	−0.248
burn1k	−0.978	0.445	−1.849	−0.106
thin1k	0.124	0.307	−0.478	0.725
Wood Thrush (2)				
burns	−0.752	0.263	−1.269	−0.236
thin	−1.917	0.642	−3.174	−0.659
canopy150	−0.079	0.182	−0.436	0.277
everg1k	−0.728	0.247	−1.211	−0.244
Worm-eating Warbler				
canopy	0.570	0.148	0.281	0.860
shrub	0.431	0.105	0.225	0.637
decid basal	0.033	0.121	−0.204	0.270
everg basal	−0.167	0.109	−0.381	0.047
region	−1.552	0.375	−2.287	−0.818
burns	−0.263	0.094	−0.448	−0.079
Yellow-breasted Chat				
canopy	−0.177	0.058	−0.290	−0.064
shrub	0.050	0.055	−0.058	0.158
sap	−0.105	0.078	−0.257	0.047
pole	−0.010	0.059	−0.126	0.106
saw	−0.057	0.058	−0.172	0.058
region	−0.179	0.256	−0.681	0.323
canopy150	−0.259	0.104	−0.462	−0.056
decid1k	−0.290	0.061	−0.409	−0.172
burn1k	0.487	0.072	0.347	0.628
$burn1k^2$	−0.275	0.086	−0.445	−0.106
thin1k	0.140	0.060	0.023	0.257

[a] Covariate abbreviations defined in Table 2.

Appendix B. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.12.057.

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