



Research Article

Avian Occupancy Response to Oak Woodland and Savanna Restoration

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ABSTRACT Oak (*Quercus* spp.) woodlands and savannas throughout the Mid-South, USA have become closed-canopy forests through succession in the absence of fire, contributing to declines in disturbance-dependent avian species. Restoration could ameliorate these trends, but effects of such management practices on avian communities of the Mid-South are poorly understood. We implemented an experiment on the Cumberland Plateau, Tennessee with treatments involving fall (Oct) or spring (Mar) fire with woodland (14 m²/ha) or savanna (7 m²/ha) residual basal area and unmanaged control stands (20 ha each). We conducted fixed-radius point counts 3 times annually (2010–2012) and analyzed trends in naïve occupancy for 41 species. For 20 species with adequate data (10 early-, 10 late-successional), we performed multiple-season, robust-design occupancy modeling and accounted for detection bias. We then used mixed-model polynomial regression to define relationships between occupancy and measures of live and dead basal area, midstory density, and herbaceous groundcover. Restoration substantially altered forest structural characteristics but did not affect the occupancy of most late-successional species. In contrast, the presence of early-successional species increased as live basal area decreased and herbaceous groundcover increased. Only 3 of 41 species (hooded warbler [*Setophaga citrina*], ovenbird [*Seiurus aurocapilla*], and worm-eating warbler [*Helminthos vermivorum*]) exhibited reduced occupancy as woodland and savanna conditions were approached. The presence of all other species, including 13 regionally and 2 continentally declining, remained constant or increased as restoration progressed. Woodland conditions of 10 m²/ha live basal area and 20% herbaceous groundcover maximized occupancy of early-successional species with little consequences for late-successional species. Proceeding further toward savanna conditions negatively affected species associated with lower strata of mature-forests but further increased the presence of some early-successional species. Midstory density and dead basal area were poor predictors of occupancy and thus may be necessary but not sufficient in promoting early-successional species. Our results suggest implementing oak woodland and savanna management in the Mid-South could benefit disturbance-dependent birds of high conservation priority with minimal negative impacts on the presence of late-successional species. © 2016 The Wildlife Society.

KEY WORDS birds, fire, oak, occupancy, overstory disturbance, restoration, savanna, woodland.

Grasslands, savannas, barrens, and shrublands are among the most critically threatened ecosystems in the United States (Noss et al. 1995), a phenomenon attributable to land conversion, low conservation attention, and altered disturbance regimes (Askins 2001). Representative of such declines, oak (*Quercus* spp.) woodlands and savannas are distinguished from oak forests by relative canopy openness (woodland: 30–80% canopy cover, savanna: 10–30%) and the presence of robust herbaceous groundcover (Nelson 2010).

Oak savannas once covered 11–13 million hectares of the Midwest, USA, but <1% of this extent remains (Nuzzo 1986) and a similar narrative extends into the Mid-South (Davis et al. 2002). Early southern Appalachian explorers described open grasslands with scattered trees, herds of bison (*Bison bison*) and elk (*Cervus canadensis*), and a ground-layer of shoulder-high broomsedge (*Andropogon* spp.) and abundant forbs (Van Lear and Waldrop 1989). Small, isolated, and degraded remnants are all that remain of this legacy in the Mid-South (DeSelm 1994, Delcourt et al. 1998).

The loss of oak woodlands and savannas has led to substantial declines in 70% of associated disturbance-dependent bird species (Hunter et al. 2001). This unfolding

Received: 10 January 2016; Accepted: 25 April 2016

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crisis includes early-successional species associated with grasslands and shrublands (Brennan and Kuvlesky 2005) and late-successional species that respond favorably to moderate disturbance (e.g., cerulean warbler [*Setophaga cerulea*]; Bakermans et al. 2012). In North America, populations of 169 disturbance-dependent species declined between 1966 and 1998, whereas populations of only 29 such species increased during the same period (Brawn et al. 2001). Oak savanna and woodland obligate species are rare, and possibly include only the red-headed woodpecker (*Melanerpes erythrocephalus*; Brawn et al. 2001). Nevertheless, substantial avian conservation value exists in the ability of such vegetation types to support a wide variety of avian species (Temple 1998, Davis et al. 2000, Grundel and Pavlovic 2007a). Oak woodland and savanna restoration could help stabilize declines in disturbance-dependent avian species (Vickery et al. 1999, Askins 2002) while mitigating negative impacts on some late-successional species.

Declines in disturbance-dependent birds can be linked to changing vegetation structure as succession proceeds in the absence of disturbance (Askins 1993). Invading woody plants decrease light infiltration, which can reduce or eliminate herbaceous groundcover (Hutchinson et al. 2005, Barrioz et al. 2013, McCord et al. 2014). Woodlands and savannas are eventually replaced by closed-canopy forests that lack structural heterogeneity in the overstory and midstory layers (Bowles and McBride 1998, Breshears 2006). Restoration uses overstory thinning and reintroduces fire to reverse this process (McPherson 1997, Nielsen et al. 2003). Avifaunal response to restoration is species-specific (Davis et al. 2000, Brawn 2006, Au et al. 2008), but in general increasing disturbance increases the presence of early-successional species. Residual woodland and savanna trees left after partial overstory removal allow late-successional avifauna to persist, though often at reduced densities (Dickson et al. 1995, Gram et al. 2003, Barrioz et al. 2013, Holoubek and Jensen 2015). Fire also can shift avian species composition (Davis et al. 2000, Greenberg et al. 2007, Grundel and Pavlovic 2007b) and creates snags important for cavity nesting species (Brawn et al. 2001, Lanham et al. 2002, Harper et al. 2016).

Nearly all direct measurement of avian response to oak woodland and savanna restoration has occurred along the western edge of the vegetation types' historical range (Minnesota: [Davis et al. 2000, Au et al. 2008]; Iowa: [Mabry et al. 2010]; Illinois: [Brawn 2006]; Missouri: [Reidy et al. 2014]; Kansas: [Holoubek and Jensen 2015]) where drier conditions and more recent fire suppression have retained some woodland and savanna structure. Comparable work in the Mid-South is nearly non-existent (Barrioz et al. 2013) and must proceed from closed-canopy forest because of the region's greater precipitation and a longer history of fire suppression. The agricultural landscape context of Midwestern research also limits its application to the large forested tracts of the Mid-South (Mabry et al. 2010). Additionally, avian species composition could shift more rapidly when overstory thinning and fire are used (Lanham et al. 2002), but few have investigated this claim (Greenberg

et al. 2007). An experimental approach conducted within the Mid-South and focused on key variables that capture the full range of forest conditions would provide strong inferences, improve our understanding of avian response, and lead to the development of more effective restoration strategies (Reidy et al. 2014).

Our objective was to monitor avian response during an oak woodland and savanna restoration experiment. Specifically, we intended to document restoration impacts on species-specific site occupancy estimates. In contrast to abundance and fecundity measures, which assess habitat quality, occupancy determination is a crucial first step in evaluating whether habitat for specific avian species exists within restored woodlands and savannas. We hypothesized avian response would include constant occupancy of late-successional species, influenced by the ability of residual canopy trees to provide habitat; and increased occupancy of early-successional species as live basal area (LBA; m²/ha) declined and dead basal area (DBA; m²/ha), midstory density (stems/ha), and herbaceous groundcover (%) increased. Our intent was to develop management recommendations based on vegetation structure variables for maximizing occupancy of specific species and overall avian community diversity.

STUDY AREA

Our research occurred at Catoosa Wildlife Management Area, a 32,374-ha property managed by the Tennessee Wildlife Resources Agency (TWRA) and located in the Cumberland Plateau and Mountains physiographic region, Tennessee, USA (DeSelm 1994). Site elevation ranged from 437 m to 521 m and soils were mesic typic Hapludults (Soil Survey Staff Natural Resources Conservation Service 2014) over weathered sandstone and conglomerate (Nicholson et al. 2005). Annual mean precipitation and temperature was 140 cm and 13°C for nearby Crossville, Tennessee, with summer (Jun–Sep) monthly means (11.3 cm, 23.0°C) dryer and warmer than winter (Dec–Mar) monthly means (11.7 cm, 4.7°C; National Climatic Data Center 2014). Forests were established in the 1920s following logging and agricultural abandonment and are currently oak-dominated, mixed pine-hardwood stands. Shortleaf pine (*Pinus echinata*) was a major overstory component prior the pine bark beetle (*Dendroctonus frontalis*) outbreak of 1999–2000. Salvage cutting began in 2002, followed by TWRA-implemented oak savanna restoration using prescribed fire. The rapid development of common prairie and savanna flora and historical accounts (i.e., pasturing cattle and frequent fires) provided evidence of past woodland and savanna occurrence at our site (Barrioz et al. 2013).

Prior to restoration treatments (2008), white (*Quercus alba*), southern red (*Q. falcata*), black (*Q. velutina*), and scarlet (*Q. coccinea*) oaks, and red maple (*Acer rubrum*), sourwood (*Oxydendrum arboreum*), and hickory (*Carya* spp.) all comprised >1.0 m²/ha of the live basal area of our research sites (36° 07' 51.71" N, 84° 87' 12.49" W). Midstories were dominated by blackgum (*Nyssa sylvatica*), downy serviceberry (*Amelanchier arborea*), red maple, sourwood, and sassafras (*Sassafras albidum*). The ground-layer contained little

herbaceous vegetation, and was dominated by blueberry (*Vaccinium spp.*), woody plant regeneration, and litter. Mean vegetation metrics in 2008 were 85% canopy cover, 17.8 m²/ha live basal area, 3.9 m²/ha dead basal area, 1,936 midstory stems/ha (woody stems >1.37 m tall, <12.7 cm DBH), and 4.4% herbaceous groundcover (Vander Yacht 2013). Pre-treatment point counts (Ralph et al. 1995) in 2008 indicated a dominance of late-successional species (Ehrlich et al. 1988): red-eyed vireo (*Vireo olivaceus*), ovenbird (*Seiurus aurocapilla*), hooded warbler (*Setophaga citrina*), scarlet tanager (*Piranga olivacea*), and black-and-white warbler (*Mniotilta varia*).

METHODS

Experimental Design and Data Collection

In 2008, we delineated 10, 20-ha experimental units (stands) within a 300-ha area (none >500 m apart) of a 1,500-ha oak woodland and savanna restoration effort. Boundaries were configured to maximize core area. We assigned 1 of 5 treatments to each stand using a completely randomized design with 2 replicates: fall fire and woodland residual basal area (14 m²/ha), fall fire and savanna residual basal area (7 m²/ha), spring fire and woodland residual basal area, spring fire and savanna residual basal area, and unmanaged controls. We used commercial logging to accomplish overstory reductions (winter 2008–2009). Where possible, oak, hickories, and shortleaf pine were retained and fire-intolerant species including maples (*Acer spp.*), yellow poplar (*Liriodendron tulipifera*), and sweetgum (*Liquidambar styraciflua*) were removed. We conducted fall fires 11 October 2010 prior to leaf abscission, and spring fires 22 March 2011 prior to leaf emergence.

We sampled vegetation annually (2010–2012) during the growing season at 15 plots within each stand core (50-m buffer) to reduce edge effects: 11 located along a 70 × 70-m grid with a random start point (Avery and Burkhart 2002) and 4 at point count stations. We selected vegetation variables based on the life histories of examined avian species, ease of measurement by land managers, and ability to characterize the key structural aspects of the forest to savanna continuum. To calculate LBA and DBA (m²/ha), we measured diameter at breast height (DBH) of all live and dead overstory (>12.7 cm DBH, >3.05 m tall) trees within 11.3 m of each plot location. We determined midstory density from counts of woody stems (>1.37 m tall, <12.7 cm DBH) within 7, 3-m radius sub-plots. We characterized groundcover <1.37 m at 1-m intervals along a 50-m transect using the point intercept method (Bonham 1989), and recorded the proportion containing graminoids and forbs (% herbaceous groundcover). Transects were oriented perpendicular to slope and through each plot center.

We sampled the avian community using standard point counts (Ralph et al. 1995). Within each stand core, we systematically located 50-m fixed-radius points ($n=4$) >200 m apart. Between stands, point count separation ranged from 149–279 m because of the juxtaposition of irregular stand configurations. Trained observers recorded all

avian species encountered by sight or sound during a 10-minute period. We visited each point 3 times annually (mid-May, late May, and early Jun) from 2010 to 2012 (actual date range: 14 May–19 Jun). Surveys occurred within 5 hours of sunrise, and survey times (early-, mid-, or late-morning) were varied across visits within a year to reduce daily temporal bias. We minimized observer bias by distributing effort across stands and visits within a year. Surveys did not occur when wind (>18 kph), rain, fog, or background noise may have decreased detection. We excluded flyovers (birds flying overhead but not coming from or going to the survey radius) from data. We generated 40 station-specific encounter histories (detection [1] or non-detection [0]) for each species, composed of 3 primary (year, 2010–2012) and 3 secondary (visit) sampling periods (e.g., 000 010 101). Observational point count procedures were part of a study plan approved by TWRA.

Statistical Analysis

We tested for differences in the proportion of visits where a species was present, ignoring detection bias (naïve occupancy), across controls ($n=72$), woodlands ($n=144$), and savannas ($n=144$) using a 2-tailed Fisher's exact test. Such a test is more accurate than chi-square comparisons when sample sizes are small (McDonald 2014). If the overall test was significant, we made pairwise comparisons using a Bonferroni adjustment. We analyzed count data, but we present proportions for ease of comparison. We labeled trends across treatments as positive or negative in relation to increasing disturbance. We analyzed all species present at >1% of our point count visits to evaluate impacts inclusive of all but the most uncommon species at our site.

We conducted a detailed analysis of occupancy for the 10 most frequently encountered species within each of 2 assemblages, late- and early-successional. This restriction ensured adequate data for model development while examining a range of potential avian response. Late-successional species were those associated with forests and small gaps within forests, and early-successional species were those associated with shrublands and grasslands (Ehrlich et al. 1988, Becker et al. 2011). We estimated occupancy using a multiple-season, robust-design model (MacKenzie et al. 2003). We did not estimate local colonization and extinction probabilities to avoid over-parameterization. Modeling estimated 2 parameters: the probability a site was occupied by a species (ψ), and the probability of detection given a species was present (p). Robust-design models assume constant ψ within a primary sampling period to allow for precise estimates of p and ψ . Vegetation consistency between visits within a year, the stability of singing rates during the peak breeding season (Ralph et al. 1995), and our inclusion of visit-level variation in p supported our use of this assumption. We used multinomial, maximum-likelihood to estimate ψ and p within Program MARK (White and Burnham 1999).

We modeled p and ψ using 4 a priori approaches for each parameter. We modeled p as varying by year, by visits within a year, by the additive effects of both year and visit, and as

constant. We modeled ψ as varying by year, by 20-ha stand, by the additive effects of year and stand, and as constant. Modeling accounted for potential variation in p over years and visits, whereas observer bias, meteorological conditions, background noise, and daily temporal effects on p (Alldredge et al. 2007) were addressed through survey design. Species presence determination has been shown to be unaffected by habitat structure, which could affect singing rates and therefore p , when census periods are >3 minutes (McShea and Rappole 1997).

We used Akaike's Information Criterion for small sample sizes (AIC_c) to compare models (16 total) under an information-theoretic framework (Burnham and Anderson 2002). We tested the resulting top model's goodness-of-fit using a bootstrap test (1,000 iterations) designed for ψ models by MacKenzie and Bailey (2004). When necessary, we adjusted for lack of fit (\hat{c} slightly >1) within Program MARK and used quasi-likelihood adjusted AIC_c ($QAIC_c$) for model comparisons. We summarized the relative influence of each effect (e.g., year, stand, visit) on parameters by combining weights across models involving the same levels of p and ψ variation. This evaluated whether ψ for a species was constant or dynamic across time and/or stands while incorporating potential detection bias. We concluded constant ψ during our experiment for a species when constant ψ models comprised the majority of cumulative model weight ($w_i > 0.50$). We also examined 95% confidence intervals surrounding beta estimates of competing ($\Delta QAIC_c < 2.0$) ψ models to confirm such model parameters were uninformative (CIs included 0). We did not perform subsequent analysis on species with model support for constant ψ during our experiment. We determined relationships between ψ and vegetation structure variables for species with the majority of cumulative model weight ($w_i > 0.50$) associated with year, stand, or year + stand effects.

For these species, we model-averaged ψ estimates ($n = 30$, 10 stands \times 3 years) across all candidate models to incorporate estimation and model selection error. We then determined the relationship between ψ and stand-level vegetation structure variable means using mixed-model polynomial regression in SAS 9.4 (PROC GLIMMIX, SAS Institute, Cary, NC). We used a logit transformation ($e^\beta / (1 + e^\beta)$) to handle the constrained nature of real ψ probabilities (0–1; MacKenzie et al. 2003). We included the repeated measures inherent in our experimental design by designating year as a random effect and autoregressively correlating stands over years. When we observed only small differences ($<5 \Delta AIC_c$) in fit between random effect inclusion and omission, we removed such adjustment (Littell et al. 2006). Fixed-effects were LBA, DBA, midstory density, and herbaceous groundcover. We weighted ψ estimates by their associated variances generated in Program MARK (i.e., observations with greater variance had less model weight). We included second-order polynomials because we hypothesized relationships could be quadratic in form. This resulted in comparing 8 vegetation structure variable models for each species. All data met assumptions of normality (Shapiro–Wilk $W > 0.90$) and equality of variance.

We determined the best vegetation structure ψ model, overall and within each variable, using AIC_c scores (Burnham and Anderson 2002). We selected the most parsimonious model when ΔAIC_c was <2.0 (i.e., first-order model). We back-transformed ψ to real probabilities and depicted curvilinear relationships with 95% confidence intervals. We then conducted contrast tests between pairs of maximum and minimum ψ (multiple pairs for second-order models) within the observed range of each vegetation structure variable. We concluded constant ψ over the range of a variable when these contrasts were non-significant ($\alpha = 0.05$). We report estimates of vegetation structure variables at which predicted ψ curves approached an asymptote. In reporting results, we describe ψ and vegetation structure relationships from our restoration-focused perspective (e.g., decreasing LBA, increasing herbaceous groundcover). We modeled relationships separately in expectation that species-specific habitat preferences would dictate which variable was most influential in directing ψ response; however, we recognized the potential interconnectedness of vegetation strata (e.g., greater LBA is related to less herbaceous groundcover). To address this issue, we ran correlations between all vegetation structure variables. When significant, we performed appropriate regression analysis to define relationships between vegetation variables.

RESULTS

From 2010 to 2012, we encountered 3,002 individual birds (777 in 2010, 899 in 2011, and 1,326 in 2012) representing 67 species. We documented 26 species during $<1\%$ of point count visits. Limited observations of these species indicated equal or greater presence in treatments compared to controls for all but black-billed cuckoo (*Coccyzus erythrophthalmus*). The 5 most frequently encountered species were red-eyed vireo, indigo bunting (*Passerina cyanea*), prairie warbler (*Setophaga discolor*), hooded warbler, and ovenbird (Table 1). We recorded more late- (36) than early-successional (29) species. Most early-successional species were shrubland (27) rather than grassland associates (2: field sparrow [*Spizella pusilla*] and eastern kingbird [*Tyrannus tyrannus*]). Naïve ψ increased or was constant ($P > 0.05$, Fisher's exact test) as disturbance increased for 88% (36 of 41) of analyzed species (Table 1). The 20 species selected for detailed ψ modeling represented a diverse array of niches and conservation statuses (Table 2). Naïve ψ of late-successional species selected for additional modeling was constant (4 species), declined (4 species), or increased (2 species) with increasing disturbance. All selected early-successional species increased in naïve ψ as disturbance increased (Table 1).

Occupancy Modeling

Generally, detection was best modeled as constant over years and visits (Table 2). Models holding p constant had the greatest cumulative model weight for 10 of the 20 modeled species, and were the best or competitive with the best model ($<2.0 \Delta QAIC_c$) for 12 species. This trend was not consistent across assemblages; for 7 of 10 late-successional species, constant p models received the most support, whereas for 7 of

Table 1. Individual encounters and trends in naïve occupancy (ψ) across treatments for passerine species detected at >1% of point count visits during an oak woodland and savanna restoration experiment, 2010–2012, at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA.

Species ^a	Encounters ^b	Naïve ψ by treatment (%) ^b			Fischer's exact and post hoc tests ^c				Trend ^d
		Control	Woodland	Savanna	P	C vs. W	C vs. S	W vs. S	
Late-successional									
Red-eyed vireo (<i>Vireo olivaceus</i>)	315	62.5	68.8	41.7	<0.001*	0.999	0.018*	<0.001*	–
Hooded warbler (<i>Setophaga citrina</i>)	214	59.7	46.5	31.3	<0.001*	0.250	<0.001*	0.033*	–
Ovenbird (<i>Seiurus aurocapilla</i>)	191	77.8	34.7	15.3	<0.001*	<0.001*	<0.001*	0.001*	–
Blue-gray gnatcatcher (<i>Poliophtila caerulea</i>)†	187	22.2	41.0	43.1	0.006*	0.020*	0.008*	0.999	+
Tufted titmouse (<i>Baeolophus bicolor</i>)	140	19.4	25.0	29.2	0.308				
Black-and-white warbler (<i>Mniotilta varia</i>)†	74	26.4	19.4	13.2	0.055				
Scarlet tanager (<i>Piranga olivacea</i>)	72	29.2	10.4	18.1	0.003*	0.003*	0.240	0.273	–
White-breasted nuthatch (<i>Sitta carolinensis</i>)	82	9.7	16.0	18.1	0.301				
Yellow-throated vireo (<i>Vireo flavifrons</i>)	49	5.6	12.5	15.3	0.109				
Eastern wood-pewee (<i>Contopus virens</i>)†	51	0.0	14.6	15.3	<0.001*	<0.001*	<0.001*	0.999	+
Red-bellied woodpecker (<i>Melanerpes carolinus</i>)	44	5.6	11.1	12.5	0.274				
Blue jay (<i>Cyanocitta cristata</i>)	39	13.9	8.3	6.3	0.183				
Great crested flycatcher (<i>Myiarchus crinitus</i>)†	43	2.8	9.0	15.3	0.011*	0.458	0.015*	0.445	+
Yellow-throated warbler (<i>Setophaga dominica</i>)	40	2.8	6.9	14.6	0.009*	0.999	0.026*	0.168	+
Carolina chickadee (<i>Poecile carolinensis</i>)	46	6.9	7.6	9.0	0.906				
Worm-eating warbler (<i>Helminthos vermivorum</i>)	19	18.1	0.7	0.0	<0.001*	<0.001*	<0.001*	0.999	–
Downy woodpecker (<i>Picoides pubescens</i>)	26	2.8	8.3	6.3	0.306				
Hairy woodpecker (<i>Picoides villosus</i>)	18	4.2	4.2	4.9	0.999				
Pileated woodpecker (<i>Dryocopus pileatus</i>)	12	2.8	2.8	4.2	0.808				
Black-throated-green warbler (<i>Setophaga virens</i>)	9	5.6	2.1	0.7	0.071				
Northern parula (<i>Setophaga americana</i>)	8	1.4	1.4	2.8	0.708				
Yellow-billed cuckoo (<i>Coccyzus americanus</i>)†	7	0.0	3.5	1.4	0.223				
Cedar waxwing (<i>Bombycilla cedrorum</i>)	5	1.4	1.4	1.4	0.999				
Early-successional									
Indigo bunting (<i>Passerina cyanea</i>)†	281	9.7	41.0	75.7	<0.001*	<0.001*	<0.001*	<0.001*	+
Prairie warbler (<i>Setophaga discolor</i>)†	228	4.2	33.3	58.3	<0.001*	<0.001*	<0.001*	<0.001*	+
Yellow-breasted chat (<i>Icteria virens</i>)†	157	8.3	25.0	47.2	<0.001*	0.010*	<0.001*	<0.001*	+
Eastern towhee (<i>Pipilo erythrophthalmus</i>)†	112	1.4	27.1	34.0	<0.001*	<0.001*	<0.001*	0.749	+
Red-headed woodpecker (<i>Melanerpes erythrocephalus</i>)†	89	2.8	18.1	30.6	<0.001*	0.003*	<0.001*	0.057	+
Carolina wren (<i>Thryothorus ludovicianus</i>)	56	4.2	7.6	27.1	<0.001*	0.999	<0.001*	<0.001*	+
Chipping sparrow (<i>Spizella passerina</i>)†	53	5.6	10.4	17.4	0.032	0.935	0.057	0.373	+
Field sparrow (<i>Spizella pusilla</i>)†	56	0.0	9.7	19.4	<0.001*	0.017*	<0.001*	0.087	+
Northern flicker (<i>Colaptes auratus</i>)	33	2.8	6.3	13.2	0.018*	0.999	0.043*	0.216	+
Common yellowthroat (<i>Geothlypis trichas</i>)†	38	0.0	6.9	15.3	<0.001*	0.099	<0.001*	0.114	+
Mourning dove (<i>Zenaidura macroura</i>)	38	2.8	6.9	12.5	0.043*	0.999	0.070	0.489	+
American crow (<i>Corvus brachyrhynchos</i>)	28	2.8	7.6	6.3	0.449				
Brown-headed cowbird (<i>Molothrus ater</i>)†	24	2.8	4.2	9.7	0.080				
Northern cardinal (<i>Cardinalis cardinalis</i>)	24	2.8	6.3	6.9	0.497				
White-eyed vireo (<i>Vireo griseus</i>)	24	0.0	4.9	8.3	0.023*	0.295	0.029*	0.999	+
American goldfinch (<i>Spinus tristis</i>)	22	0.0	2.1	5.6	0.067				
Ruby-throated hummingbird (<i>Archilochus colubris</i>)	6	1.4	3.5	0.0	0.068				
Eastern bluebird (<i>Sialia sialis</i>)	7	0.0	0.7	2.8	0.279				

* indicates significance ($\alpha = 0.05$).

† denotes species with significant (95% CI) regional declines from 1966 to 2012 (Sauer et al. 2014) and 2014 North American Bird Conservation Initiative Watch List species (Rosenberg et al. 2014).

^a Species presented by assemblage (Ehrlich et al. 1988) in descending order of mean naïve occupancy. Additional species (26) encountered during <1% of point count visits included great blue heron (*Ardea herodias*), Canada goose (*Branta canadensis*), Cooper's hawk (*Accipiter cooperii*), red-shouldered hawk (*Buteo lineatus*), broad-winged hawk (*Buteo platypterus*), black vulture (*Coragyps atratus*), turkey vulture (*Cathartes aura*), northern bobwhite (*Colinus virginianus*)†, wild turkey (*Meleagris gallopavo*), black-billed cuckoo (*Coccyzus erythrophthalmus*)†, barred owl (*Strix varia*), chimney swift (*Chaetura pelagica*)†, Acadian flycatcher (*Empidonax virens*)†, eastern phoebe (*Sayornis phoebe*), eastern kingbird (*Tyrannus tyrannus*)†, veery (*Catharus fuscescens*), Swainson's thrush (*Catharus ustulatus*), wood thrush (*Hylocichla mustelina*)†, American robin (*Turdus migratorius*), brown thrasher (*Toxostoma rufum*)†, gray catbird (*Dumetella carolinensis*), yellow warbler (*Setophaga petechia*)†, cerulean warbler (*Setophaga cerulea*)†, Kentucky warbler (*Geothlypis formosa*)†, summer tanager (*Piranga rubra*)†, and blue grosbeak (*Passerina caerulea*).

^b Encounters from 2010 to 2012 at 40, fixed-radius (50 m) point counts. Naïve occupancy is visits where a species was detected divided by total visits \times 100. Controls were unmanaged. Woodlands and savannas were thinned (14 m²/ha and 7 m²/ha live basal area, respectively) and burned prior to 2011.

^c Fischer's exact test on count data of presence and absence of a species by visit. Post hoc comparisons using Bonferroni α adjustment are between controls and woodlands (C vs. W), controls and savannas (C vs. S), and woodlands versus savannas (W vs. S).

^d Direction of trend in naïve ψ as related to increasing disturbance (control to woodland to savanna).

Table 2. Top detection (p) and occupancy (ψ) models with cumulative model weights for selected passerine species detected during an oak woodland and savanna restoration experiment, 2010–2012, at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA.

Species ^a	Model ^b	w_i	K	Cumulative p model weights ^c				Cumulative ψ model weights ^c				\bar{p} (SE) ^d	$\bar{\psi}$ (SE) ^d
				(.)	Year	Visit	Y+V	(.)	Year	Stand	Y+S		
Late-successional													
Tufted titmouse	$p(\text{visit}) \psi(.)$	0.39	4	0.14	0.14	0.54*	0.18	0.78*	0.22	0.00	0.00	0.27 (0.07)	0.94 (0.13)
Blue-gray gnatcatcher	$p(.) \psi(.)$	0.33	2	0.43*	0.10	0.39	0.08	0.79*	0.21	0.00	0.00	0.41 (0.07)	0.93 (0.09)
Red-eyed vireo	$p(.) \psi(.)$	0.47	2	0.68*	0.11	0.18	0.03	0.71*	0.13	0.12	0.03	0.61 (0.05)	0.91 (0.06)
Black-and-white warbler	$p(\text{year+visit}) \psi(.)$	0.48	6	0.00	0.01	0.45	0.54*	0.74*	0.25	0.00	0.01	0.21 (0.08)	0.85 (0.20)
White-breasted nuthatch	$p(.) \psi(.)$	0.32	2	0.67*	0.23	0.08	0.03	0.55*	0.40	0.00	0.05	0.19 (0.05)	0.79 (0.19)
Hooded warbler	$p(.) \psi(\text{year+stand})$	0.40	13	0.79*	0.07	0.13	0.01	0.02	0.02	0.46	0.49*	0.60 (0.04)	0.71 (0.13)
Scarlet tanager	$p(.) \psi(.)$	0.32	2	0.53*	0.11	0.30	0.06	0.62*	0.16	0.14	0.09	0.27 (0.07)	0.62 (0.15)
Ovenbird	$p(.) \psi(\text{year+stand})$	0.79	13	0.79*	0.07	0.12	0.01	0.00	0.00	0.00	1.00*	0.59 (0.06)	0.60 (0.17)
Eastern wood-pewee	$p(.) \psi(\text{year+stand})$	0.62	13	0.62*	0.30	0.06	0.03	0.00	0.00	0.30	0.70*	0.23 (0.07)	0.53 (0.18)
Yellow-throated vireo	$p(\text{year+visit}) \psi(.)$	0.50	6	0.05	0.28	0.09	0.58*	0.75*	0.23	0.00	0.01	0.26 (0.11)	0.49 (0.10)
Early-successional													
Indigo bunting	$p(\text{year}) \psi(\text{stand})$	0.69	13	0.16	0.77*	0.01	0.06	0.03	0.00	0.90*	0.07	0.65 (0.08)	0.73 (0.14)
Red-headed woodpecker	$p(\text{year}) \psi(\text{year+stand})$	0.42	15	0.16	0.51*	0.09	0.24	0.00	0.00	0.29	0.71*	0.32 (0.08)	0.66 (0.17)
Prairie warbler	$p(\text{year}) \psi(\text{year+stand})$	0.52	15	0.00	0.54*	0.00	0.46	0.00	0.00	0.03	0.97*	0.55 (0.09)	0.65 (0.16)
Yellow-breasted chat	$p(\text{year}) \psi(\text{year+stand})$	0.45	15	0.16	0.50*	0.08	0.25	0.01	0.01	0.06	0.92*	0.49 (0.11)	0.59 (0.18)
Eastern towhee	$p(.) \psi(\text{year+stand})$	0.32	13	0.32*	0.28	0.23	0.17	0.00	0.00	0.01	0.99*	0.42 (0.10)	0.58 (0.18)
Mourning dove	$p(\text{year}) \psi(.)$	0.43	4	0.27	0.60*	0.04	0.09	0.52*	0.33	0.10	0.05	0.15 (0.09)	0.57 (0.26)
Carolina wren	$p(.) \psi(\text{stand})$	0.61	11	0.69*	0.11	0.18	0.03	0.02	0.00	0.88*	0.09	0.30 (0.07)	0.48 (0.19)
Field sparrow	$p(\text{year}) \psi(.)$	0.32	4	0.38	0.47*	0.07	0.09	0.38	0.38*	0.08	0.16	0.29 (0.18)	0.47 (0.14)
Chipping sparrow	$p(\text{year}) \psi(.)$	0.58	4	0.14	0.76*	0.01	0.08	0.65*	0.22	0.01	0.12	0.29 (0.11)	0.46 (0.10)
Common yellow throat	$p(\text{year}) \psi(.)$	0.29	4	0.47*	0.34	0.11	0.08	0.69*	0.26	0.01	0.04	0.22 (0.11)	0.40 (0.16)

*indicates the highest cumulative weight.

^a Species in descending order of mean occupancy by assemblage group.

^b w_i is model weight and K is number of model parameters. Models adjusted by calculated variance inflation factors (mean $\hat{c} = 1.23$) from bootstrap goodness-of-fit tests (1,000 iterations) on the top model for each species. Comparisons of Quasi-likelihood Akaike's Information Criterion selected top models.

^c Cumulative model weights are the sum for each way in which p and ψ were allowed to vary including constant (.), by year, by visit, by 20-ha experimental unit, or additive effects of year and visit (Y+V) or year and stand (Y+S).

^d Model averaging conducted across all 16 candidate models for p and ψ estimates.

10 early-successional species, $p(\text{year})$ models received the most support. Detection was best modeled for the remaining 3 late-successional species as varying by visit or by year and visit, and detection for the remaining 3 early-successional species was best modeled as constant over years and visits. Mean model-averaged p was similar for late-successional (0.36 ± 0.07 SE) and early-successional (0.37 ± 0.10 SE) species (Table 2).

Occupancy was constant over the experiment's duration for half of the 20 species (Table 2). Confidence intervals (95%) of beta estimates included 0 for any models competitive ($<2.0 \Delta\text{QAIC}_c$) with the top constant ψ model. Based on this evidence, we concluded constant ψ across years and stands for 7 late-successional species (tufted titmouse [*Baeolophus bicolor*], blue-gray gnatcatcher [*Poliophtila caerulea*], red-eyed vireo, black-and-white warbler, white-breasted nuthatch [*Sitta carolinensis*], scarlet tanager, yellow-throated vireo [*Vireo flavifrons*]) and 3 early-successional species (mourning dove [*Zenaida macroura*], chipping sparrow [*Spizella passerina*], common yellowthroat [*Geothlypis trichas*]). This included 5 species with significant trends in naïve occupancy across restoration treatments (Table 1). We believe incorporating detection increased ψ accuracy for these species.

We concluded dynamic ψ for 3 late- (hooded warbler, ovenbird, eastern wood-pewee [*Contopus virens*]) and 7 early- (indigo bunting, red-headed woodpecker, prairie warbler, yellow-breasted chat [*Icteria virens*], eastern towhee [*Pipilo*

erythrophthalmus], Carolina wren [*Thryothorus ludovicianus*], field sparrow) successional species. The top model for field sparrow was constant ψ , but a $\psi(\text{year})$ model with a non-zero beta estimate (95% CI) was competitive ($\Delta\text{QAIC}_c = 0.44$) and cumulative model weight of models involving year was greater than constant ψ models. Model-averaged ψ ranged from 0.40 ± 0.16 SE (common yellowthroat) to 0.94 ± 0.13 SE (tufted titmouse). Mean ψ for late-successional species in controls (0.74 ± 0.11 SE) was more than double the same figure for early-successional species (0.28 ± 0.16 SE). The ψ of late-successional species was typically constant across treatments, whereas early-successional species generally increased in ψ as residual basal area of treatments decreased. Late-successional species' presence remained relatively constant over time, except for declines in ovenbird and increases in eastern wood-pewee. Early-successional species generally increased in ψ over time.

Occupancy and Vegetation Relationships

We observed a wide range and a diversity of trends over time for each vegetation structure variable. Across stands, LBA ranged from 1.5 (± 0.4 SE) to 23.4 (± 1.4 SE) m^2/ha and DBA ranged from 1.3 (± 0.4 SE) to 6.2 (± 1.4 SE) m^2/ha , and both of these overstory measures remained generally constant (± 1 SE) over time. Midstory density ranged from 94 (± 32 SE) to 7,629 (± 721 SE) stems/ha, and was constant over time within controls (4,228 stems/ha ± 535

SE). Within treatments, midstory density was consistently and substantially reduced following fire (2011), and returned to 2010 levels by 2012. Herbaceous groundcover ranged from 1.5% (± 0.6 SE) to 69.9% (± 7.5 SE), was low in controls ($3.3\% \pm 1.0$ SE), intermediate in woodland treatments ($15.5\% \pm 3.5$ SE), and $>30\%$ in savanna treatments ($35.7\% \pm 5.4$ SE). Over time, herbaceous groundcover increased substantially in treatments by the second year post-fire (2012). Only LBA and herbaceous groundcover were correlated ($r = -0.76$, $P < 0.01$). As LBA decreased, herbaceous groundcover increased exponentially (herbaceous

groundcover = $77.66 \times 0.86^{\text{LBA}}$, $F = 57.7$, $P < 0.01$). This model explained 67% of the variation in herbaceous groundcover.

Models incorporating LBA were the top model by AIC_c ranking and had the greatest cumulative model weight in comparison to other variables for 5 of the 10 analyzed species (Table 3). Additionally, a first-order LBA model was competitive ($\Delta\text{AIC}_c = 0.74$) with the top model for ovenbird. The ψ of all 10 analyzed species changed ($P < 0.05$) over the observed range of LBA (Table 4). Two late-successional species decreased in ψ as LBA

Table 3. Top ranking mixed-effect polynomial regression models of the relationship between each vegetation structural variable and occupancy (ψ) of passerine species during an oak woodland and savanna restoration experiment, 2010–2012, at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA.

Species ^a	Model ^b	Model ranking ^c					Cumulative model weights ^c			
		AIC _c	ΔAIC_c	w_i	Deviance	K	w_i LBA	w_i DBA	w_i MDEN	w_i HCOV
Late-successional										
Hooded warbler	$\psi(\text{LBA})$	102.4	0.00	0.53	95.43	2	0.68*	0.02	0.05	0.25
	$\psi(\text{HCOV})$	105.8	3.49	0.09	98.92	2				
	$\psi(\text{MDEN})$	107.7	5.31	0.04	100.74	2				
	$\psi(\text{DBA})$	109.0	6.68	0.02	102.11	2				
Ovenbird	$\psi(\text{HCOV})$	166.1	0.28	0.31	159.16	2	0.33	0.00	0.00	0.66*
	$\psi(\text{LBA})$	166.5	0.74	0.24	159.61	2				
	$\psi(\text{MDEN} + \text{MDEN}^2)$	174.8	8.97	0.00	165.17	3				
	$\psi(\text{DBA})$	180.4	14.63	0.00	173.51	2				
Eastern wood-pewee	$\psi(\text{LBA} + \text{LBA}^2)$	215.2	0.00	0.43	205.95	3	0.59*	0.00	0.00	0.40
	$\psi(\text{HCOV} + \text{HCOV}^2)$	215.5	0.28	0.38	205.86	3				
	$\psi(\text{DBA})$	225.9	10.73	0.00	218.99	2				
	$\psi(\text{MDEN})$	227.1	11.92	0.00	220.17	2				
Early-successional										
Indigo bunting	$\psi(\text{LBA})$	93.2	0.00	0.77	86.31	2	1.00*	0.00	0.00	0.00
	$\psi(\text{HCOV} + \text{HCOV}^2)$	111.4	18.13	0.00	101.76	3				
	$\psi(\text{DBA})$	137.2	43.95	0.00	130.26	2				
	$\psi(\text{MDEN})$	138.2	44.98	0.00	131.28	2				
Red-headed woodpecker	$\psi(\text{LBA} + \text{LBA}^2)$	122.6	0.00	0.85	113.01	3	1.00*	0.00	0.00	0.00
	$\psi(\text{HCOV})$	140.6	17.97	0.00	133.66	2				
	$\psi(\text{MDEN})$	143.3	20.65	0.00	136.34	2				
	$\psi(\text{DBA})$	143.3	20.73	0.00	136.42	2				
Prairie warbler	$\psi(\text{HCOV} + \text{HCOV}^2)$	137.6	0.00	0.98	128.00	3	0.00	0.00	0.00	1.00*
	$\psi(\text{LBA})$	150.6	13.04	0.00	143.71	2				
	$\psi(\text{MDEN})$	172.0	34.43	0.00	165.11	2				
	$\psi(\text{DBA})$	173.4	35.84	0.00	166.52	2				
Yellow-breasted chat	$\psi(\text{HCOV} + \text{HCOV}^2)$	127.6	0.00	0.91	118.04	3	0.01	0.00	0.00	0.99*
	$\psi(\text{LBA})$	138.6	10.99	0.00	131.71	2				
	$\psi(\text{MDEN})$	145.7	18.09	0.00	138.81	2				
	$\psi(\text{DBA})$	146.4	18.79	0.00	139.50	2				
Eastern towhee	$\psi(\text{HCOV} + \text{HCOV}^2)$	186.9	0.00	0.84	177.26	3	0.16	0.00	0.00	0.84*
	$\psi(\text{LBA} + \text{LBA}^2)$	190.8	3.90	0.12	181.16	3				
	$\psi(\text{DBA})$	225.2	38.33	0.00	218.27	2				
	$\psi(\text{MDEN})$	228.0	41.11	0.00	221.05	2				
Carolina wren	$\psi(\text{LBA})$	123.6	0.00	0.74	116.67	2	1.00*	0.00	0.00	0.00
	$\psi(\text{HCOV})$	135.2	11.61	0.00	128.28	2				
	$\psi(\text{DBA})$	144.5	20.87	0.00	137.54	2				
	$\psi(\text{MDEN})$	147.4	23.82	0.00	140.49	2				
Field sparrow	$\psi(\text{HCOV})$	41.4	0.00	0.69	34.50	2	0.00	0.00	0.00	1.00*
	$\psi(\text{LBA})$	53.8	12.4	0.00	46.90	2				
	$\psi(\text{MDEN})$	55.6	14.19	0.00	48.69	2				
	$\psi(\text{DBA})$	57.7	16.24	0.00	50.73	2				

* identifies the greatest cumulative model weight.

^a Species in descending order of mean occupancy by assemblage group. Only species with non-constant occupancy during our experiment are presented.

^b Eight occupancy models for each species include first- and second-order live basal area (LBA), dead basal area (DBA), midstory density (MDEN), and herbaceous groundcover (HCOV) fixed-effects. Data consisted of 30 occupancy estimates (10 stands \times 3 yr) paired with stand-level vegetation structure measurements.

^c w_i is model weight and K is the number of parameters.

decreased (Tables 3 and 4; Fig. 1). Hooded warbler ψ decreased (-0.47ψ) in near linear fashion as LBA decreased. Ovenbird presence was nearly certain at $>15\text{ m}^2/\text{ha}$ LBA, declined rapidly as LBA decreased, and reached near absence below $5\text{ m}^2/\text{ha}$ LBA. Eastern wood-pewee data best supported a second-order LBA ψ model (Table 3); ψ increased as LBA declined below $15\text{ m}^2/\text{ha}$, reached a maximum at $7.4\text{ m}^2/\text{ha}$, and then declined as LBA continued to decrease (Table 4 and Fig. 1). The difference between minimum and maximum ψ was significant (Table 4), but we found no detectable difference between maximum and intercept ψ estimates ($t_{18} = 0.84$, $P = 0.41$).

For all early-successional species with evidence for dynamic ψ during our experiment, presence increased as LBA decreased (Tables 3 and 4; Fig. 1). The top LBA ψ model for 5 early-successional species was first-order (Tables 3 and 4; Fig. 1). The presence of indigo bunting, prairie warbler, and yellow-breasted chat increased rapidly as LBA declined until maximized at $10\text{ m}^2/\text{ha}$ LBA. Carolina wren followed this trend, but ψ was not maximized until LBA was reduced to $5\text{ m}^2/\text{ha}$. Field sparrow continued to increase linearly as LBA declined. Data for the remaining early-successional species (red-headed woodpecker, eastern towhee) best supported a second-order trend between LBA and ψ . These species increased in presence rapidly as LBA declined, reached a maximum (at $7.2\text{ m}^2/\text{ha}$ for red-headed woodpecker and $2.7\text{ m}^2/\text{ha}$ for eastern towhee), and then declined

as LBA continued to decrease (Table 4 and Fig. 1). Although the difference between minimum and maximum ψ estimates within these curves was significant (Table 4), differences between the maximum and y-intercept ψ estimates were not significant (red-headed woodpecker: $t_{18} = 0.94$, $P = 0.35$; eastern towhee: $t_{18} = 0.40$, $P = 0.69$).

We found little support for relationships between ψ and DBA or midstory density. Cumulative model weights for models including these variables were never >0.05 , and such models never ranked higher than LBA or herbaceous groundcover models (Table 3). Ovenbird was the only species with a DBA or midstory density model that predicted significant changes in ψ over the observed range of each variable (Table 4 and Fig. 2). Ovenbird ψ declined after DBA increased above $3\text{ m}^2/\text{ha}$. The ψ of ovenbird peaked at a mid-range of midstory density ($3,153\text{ stems}/\text{ha}$) and both the difference between the y-intercept and maximum ψ ($t_{18} = 3.02$, $P = 0.01$) and the difference between the maximum and minimum ψ (Table 4) were significant.

Models incorporating herbaceous groundcover were the top model by AIC_c ranking and had the greatest cumulative model weight in comparison to other variables for 5 of 10 species (Table 3). A second-order herbaceous groundcover model was competitive ($\Delta AIC_c = 0.28$) with the top model for eastern wood-pewee. Models incorporating herbaceous groundcover failed to predict significant ($\alpha < 0.05$) changes in ψ over the observed range of herbaceous groundcover for

Table 4. Mixed-effect polynomial regression models predicting significant ($\alpha = 0.05$) change in passerine species occupancy (ψ) over observed ranges in vegetation structure variables during an oak woodland and savanna restoration experiment, 2010–2012, at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA.

Species ^a	Model ^b	ψ		Second-order β (SE) ^b	Min. ψ (95% CI) ^c	Max. ψ (95% CI) ^c	t^c	$Pr > t^c$
		Intercept (SE) ^b	First-order β (SE) ^b					
Late-successional								
Hooded warbler	$\psi(\text{LBA})$	0.43 (0.10)	9.9E-2 (3.5E-2)		0.43 (0.25–0.63)*	0.90 (0.74–0.96)	2.9	0.008
Ovenbird	$\psi(\text{HCOV})$	1.00 (0.00)	-1.9E-1 (3.5E-2)		0.00 (0.00–0.02)	1.00 (0.98–1.00)*	5.5	<0.001
	$\psi(\text{LBA})$	0.01 (0.01)	5.1E-1 (9.4E-2)		0.01 (0.00–0.14)*	1.00 (1.00–1.00)	5.4	<0.001
	$\psi(\text{MDEN}+\text{MDEN}^2)$	0.28 (0.32)	4.0E-3 (1.1E-3)	-6.3E-7 (1.6E-7)	0.00 (0.00–0.09)	0.99 (0.96–1.00)	4.3	<0.001
	$\psi(\text{DBA})$	1.00 (0.00)	-1.8 (6.7E-1)		0.01 (0.00–0.67)	1.00 (0.95–1.00)*	2.7	0.013
Eastern wood-pewee	$\psi(\text{LBA}+\text{LBA}^2)$	0.05 (0.26)	1.4 (1.1)	-9.3E-2 (4.3E-2)	0.00 (0.00–0.00)	0.88 (0.15–1.00)	3.8	<0.001
	$\psi(\text{HCOV}+\text{HCOV}^2)$	0.00 (0.00)	9.2E-1 (2.4E-1)	-1.1E-2 (3.8E-3)	0.00 (0.00–0.00)*	0.99 (0.58–1.00)	4.3	<0.001
Early-successional								
Indigo bunting	$\psi(\text{LBA})$	1.00 (0.00)	-3.2E-1 (3.1E-2)		0.10 (0.04–0.23)	1.00 (0.99–1.00)*	10.2	<0.001
	$\psi(\text{HCOV}+\text{HCOV}^2)$	0.33 (0.12)	2.3E-1 (3.7E-2)	-2.4E-3 (5.2E-4)	0.33 (0.14–0.59)*	0.99 (0.98–1.00)	7.1	<0.001
Red-headed woodpecker	$\psi(\text{LBA}+\text{LBA}^2)$	0.68 (0.29)	3.4E-1 (2.3E-1)	-2.4E-2 (9.2E-3)	0.00 (0.00–0.06)	0.87 (0.78–0.93)	5.1	<0.001
Prairie warbler	$\psi(\text{HCOV}+\text{HCOV}^2)$	0.05 (0.03)	3.4E-1 (5.7E-2)	-3.0E-3 (8.1E-4)	0.05 (0.01–0.18)*	1.00 (0.99–1.00)	8.8	<0.001
	$\psi(\text{LBA})$	1.00 (0.00)	-4.5E-1 (7.6E-2)		0.02 (0.00–0.13)	1.00 (0.99–1.00)*	5.9	<0.001
Yellow-breasted chat	$\psi(\text{HCOV}+\text{HCOV}^2)$	0.18 (0.09)	2.1E-1 (4.8E-2)	-2.0E-3 (7.0E-4)	0.18 (0.05–0.44)*	0.98 (0.94–0.99)	5.8	<0.001
	$\psi(\text{LBA})$	0.99 (0.01)	-2.2E-1 (7.0E-2)		0.20 (0.03–0.66)	0.99 (0.91–1.00)*	3.2	0.004
Eastern towhee	$\psi(\text{HCOV}+\text{HCOV}^2)$	0.00 (0.00)	7.7E-1 (9.3E-2)	-9.0E-3 (1.5E-3)	0.00 (0.00–0.00)*	1.00 (0.99–1.00)	10.0	<0.001
	$\psi(\text{LBA}+\text{LBA}^2)$	0.98 (0.04)	2.9E-1 (5.1E-1)	-4.9E-2 (2.2E-2)	0.00 (0.00–0.00)	0.99 (0.79–1.00)*	8.3	<0.001
Carolina wren	$\psi(\text{LBA})$	0.98 (0.01)	-2.9E-1 (4.7E-2)		0.03 (0.00–0.13)	0.98 (0.93–0.99)*	6.1	<0.001
	$\psi(\text{HCOV})$	0.31 (0.11)	5.9E-2 (1.5E-2)		0.31 (0.14–0.56)*	0.97 (0.86–0.99)	3.9	<0.001
Field sparrow	$\psi(\text{HCOV})$	0.34 (0.02)	2.1E-2 (4.5E-3)		0.34 (0.29–0.39)*	0.69 (0.57–0.78)	4.7	<0.001
	$\psi(\text{LBA})$	0.52 (0.05)	-3.1E-2 (1.5E-2)		0.33 (0.25–0.44)	0.52 (0.42–0.62)*	2.1	0.047

*denotes y-intercepts within listed maximums and minimums.

^a Species in descending order of mean occupancy by assemblage group. Includes only species with non-constant occupancy during our experiment.

^b Model fixed-effects were live basal area (LBA), dead basal area (DBA), midstory density (MDEN), and herbaceous groundcover (HCOV). Data consisted of 30 occupancy estimates (10 stands \times 3 yr) paired with stand-level vegetation structure measurements. Slope estimates based on logit scale relationships, with ψ estimates back-transformed.

^c Calculated t and P values from contrast tests of the difference between maximum and minimum ψ ($df = 19$ for first-order and 18 for second-order models).

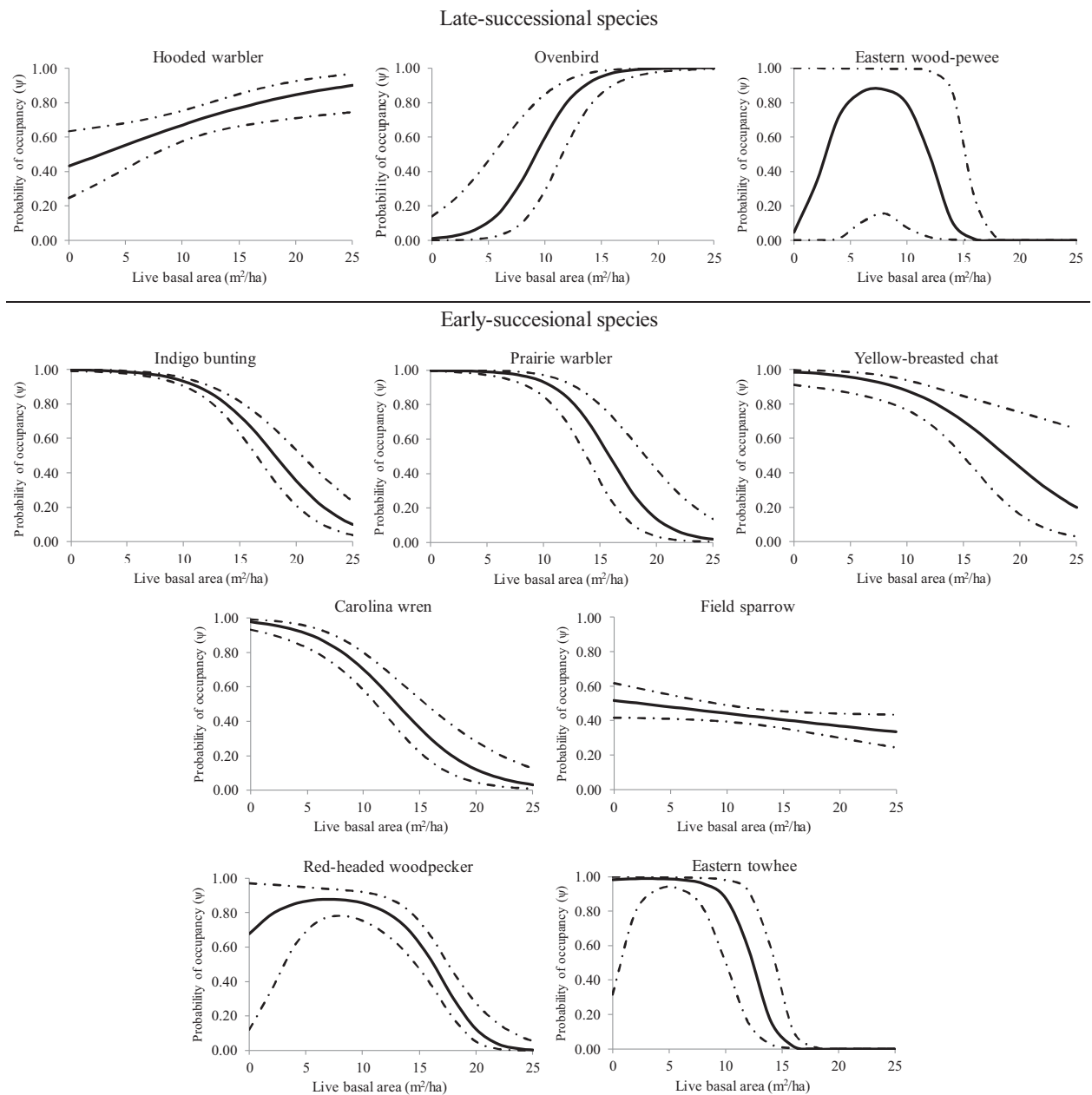


Figure 1. Mixed-effect polynomial regression prediction plots and 95% confidence intervals for the probability of occupancy as a function of live basal area (LBA, m²/ha) for selected passerine species during an oak woodland and savanna restoration experiment, 2010–2012, at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA. Only models predicting a significant ($\alpha = 0.05$) change in occupancy over the observed range in LBA are presented.

only 2 species (hooded warbler, red-headed woodpecker; Table 4). Ovenbird data best supported a first-order herbaceous groundcover ψ model (Tables 3 and 4); ψ declined sharply from 1 after herbaceous groundcover increased above 20%, reaching a minimum near 0 after an increase to 50% (Fig. 3). Eastern wood-pewee ψ increased sharply from 0 after herbaceous groundcover increased to 15%, reached a maximum near 1 at 41%, and then declined (second-order model). The difference between the minimum ψ at the y-intercept and the maximum ψ was significant (Table 4), but the difference between the maximum ψ and minimum ψ at the maximum observed herbaceous groundcover was not significant ($t_{18} = 1.63$, $P = 0.12$).

Early-successional ψ increased as herbaceous groundcover increased (Fig. 3). Data best supported second-order herbaceous groundcover models for indigo bunting, prairie warbler, yellow-breasted chat, and eastern towhee (Table 3). The rate of increase in ψ for these species was initially rapid but declined dramatically after herbaceous groundcover reached 20%. Maximum ψ for these 4 species occurred at 47% (indigo bunting), 58% (prairie warbler), 51% (yellow-breasted chat), and 43% (eastern towhee) herbaceous groundcover. Differences between these maximum ψ estimates and ψ at the maximum observed herbaceous groundcover was not significant for indigo bunting ($t_{18} = 1.93$, $P = 0.07$), prairie warbler ($t_{18} = 0.69$,

Late-successional species

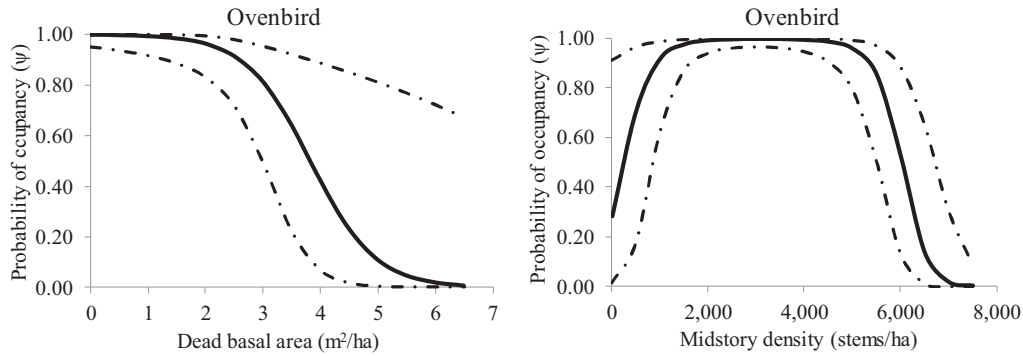
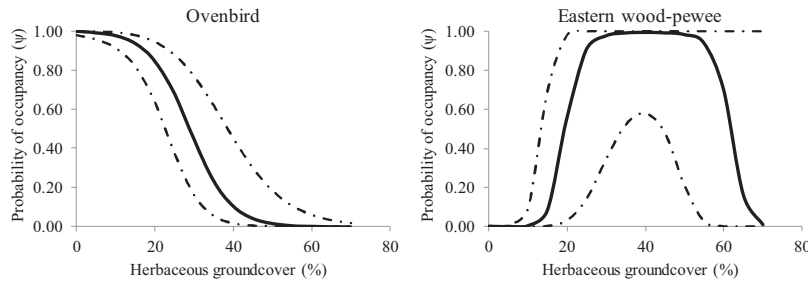


Figure 2. Mixed-effect polynomial regression prediction plots and 95% confidence intervals for the probability of occupancy as a function of dead basal area (DBA, m²/ha) and midstory density (stems/ha) for ovenbirds during an oak woodland and savanna restoration experiment, 2010–2012, at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA. Only models predicting a significant ($\alpha = 0.05$) change in occupancy over the observed range in DBA or midstory density are presented.

Late-successional species



Early-successional species

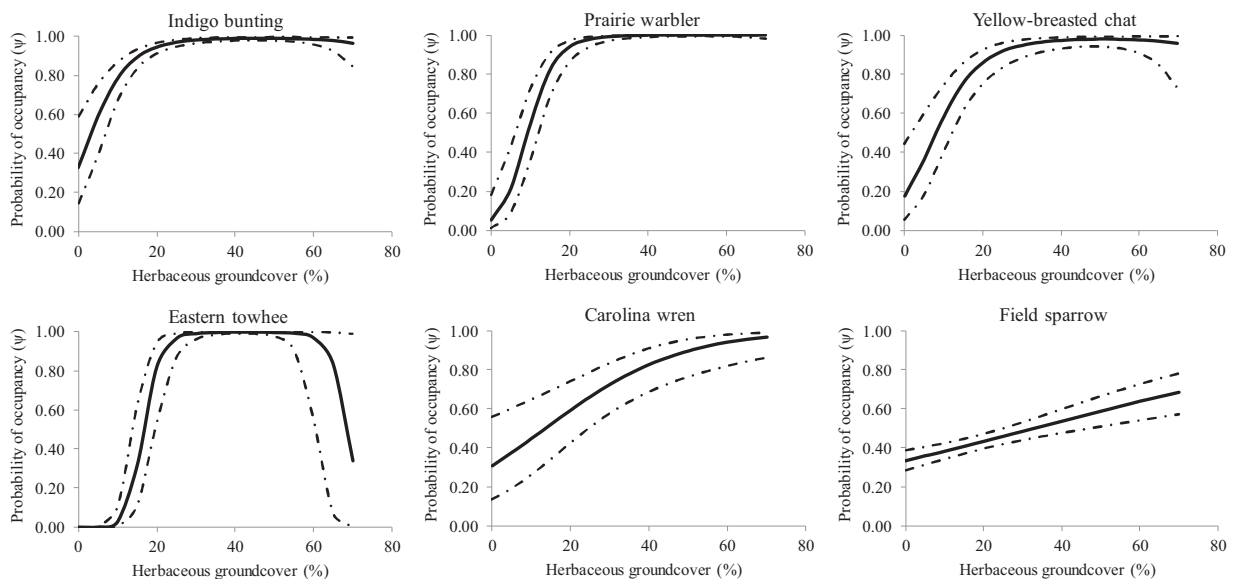


Figure 3. Mixed-effect polynomial regression prediction plots and 95% confidence intervals for the probability of occupancy as a function of herbaceous groundcover (%) for selected passerine species during an oak woodland and savanna restoration experiment, 2010–2012, at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA. Only models predicting a significant ($\alpha = 0.05$) change in occupancy over the observed range in herbaceous groundcover are presented.

$P = 0.49$), or yellow-breasted chat ($t_{18} = 0.90$, $P = 0.38$), but was significant for eastern towhee ($t_{18} = 2.81$, $P = 0.01$). Differences between minimum ψ (occurring as y-intercepts) and maximum ψ was significant for all 4 species (Table 4). Data best supported first-order herbaceous groundcover models for Carolina wren and field sparrow, with ψ increasing linearly across the entire observed range of herbaceous groundcover.

DISCUSSION

Oak woodland and savanna restoration substantially altered forest structural characteristics but only produced changes in ψ for half of the analyzed species. This was true for both naïve (21 of 41) and detection-inclusive (10 of 20) ψ analyses. Most species with constant ψ were late-successional, supporting our hypothesis that the presence of these species would be maintained during restoration. Moreover, 4 late-successional species actually increased in ψ as disturbance increased: blue-gray gnatcatcher, eastern wood-pewee, great crested flycatcher (*Myiarchus crinitus*), and yellow-throated warbler (*Setophaga dominica*). Many early-successional species increased in ψ as LBA declined and herbaceous groundcover increased, supporting our second hypothesis that restoration would benefit these species. Only 3 species had negative trends in ψ during restoration (hooded warbler, ovenbird, worm-eating warbler [*Helminthos vermivorum*]), and each of these were stable or increasing within our region from 1966 to 2012 (Sauer et al. 2014). Declines in naïve ψ with increasing disturbance occurred for 5 species, but 2 exhibited constant ψ after incorporating detection probability: red-eyed vireo and scarlet tanager. Negative trends in ψ as vegetation approached woodland and savanna conditions occurred in only 5 of the 160 explored relationships (8 models \times 20 species) and involved just 2 late-successional species: hooded warbler and ovenbird. The presence of all other species, including 13 regionally (Sauer et al. 2014) and 2 continentally (Rosenberg et al. 2014) declining species, remained constant or increased as woodland and savanna conditions were approached.

Such results reveal how well adapted the avian community of eastern oak forests is to disturbance, and demonstrates how promoting woodland and savanna conditions can retain late-successional species while increasing the presence of disturbance-dependent birds of conservation concern. Eleven of the 16 species increasing in naïve ψ as disturbance increased were declining within our region (Sauer et al. 2014). Seven of 8 species with increasing ψ as woodland and savanna conditions were approached were also declining regionally or identified on the North American Bird Conservation Initiative 2014 Watch List (Rosenberg et al. 2014). Midwestern restoration has similarly increased early-successional species while retaining late-successional species' presence (Davis et al. 2000, Brawn 2006, Au et al. 2008, Reidy et al. 2014, Holoubek and Jensen 2015). Oak woodland and savanna restoration is critically important for obligate species like the red-headed woodpecker (Brawn 2006, Grundel and Pavlovic 2007b), but our results and those from other studies demonstrate broader avian conservation

implications. The structural diversity of oak woodlands and savannas, and associated range of niches, can provide habitat for many avian species across the continuum from prairie to forest (Temple 1998, Grundel and Pavlovic 2007a).

In agreement with past research (Annand and Thompson 1997, Brawn 2006, Reidy et al. 2014), we found late-successional species' ψ generally non-responsive to changes in LBA, whereas most early-successional species' ψ increased as LBA decreased. This conveys the importance of overstory reduction in increasing early-successional species' presence and the ability of late-successional species to persist when canopy disturbance occurs. Three species that use the lower strata of closed-canopy forests declined in ψ as LBA decreased; hooded and worm-eating warblers prefer patches of dense midstory under a closed canopy (Ehrlich et al. 1988, Bakermans et al. 2012) and ovenbirds require leaf litter for nesting and foraging (Ehrlich et al. 1988). Remnant overstory trees may meet the habitat requirements of upper-canopy species, but those associated with lower strata conditions typical of mature-forests will respond negatively to overstory reductions (Artman et al. 2001, Brawn 2006, Comer et al. 2010). In contrast, some late-successional species may be disturbance-dependent and respond positively to moderate canopy disturbance (Hunter et al. 2001, Holoubek and Jensen 2015). We observed this for blue-gray gnatcatcher, eastern wood-pewee, great crested flycatcher, and yellow-throated warbler.

Nearly all early-successional species that increased in ψ as LBA declined were midstory or ground feeders. Such species likely were responding to effects of canopy reduction on lower strata (e.g., promotion of vigorous midstory growth or increasing herbaceous groundcover; Barrioz et al. 2013, McCord et al. 2014). All of these species also exhibited a positive relationship between ψ and herbaceous groundcover. Further, herbaceous groundcover ψ models had narrower confidence intervals than LBA ψ models, suggesting greater sensitivity to understory vegetation. Live basal area was an effective predictor of large changes in ψ for many species, but using substrate preferences of species will allow such relationships to better predict management impacts. In contrast, red-headed woodpeckers sally for prey in an open-canopy structure (Brawn 2006, Grundel and Pavlovic 2007b), and our results indicated a peak in ψ at 7.2 m²/ha LBA for this species. This overstory density is consistent with savanna conditions and demonstrates an association with sparse canopies.

Dead basal area was a poor predictor of avian ψ in our study. The single observed relationship involved the decreasing presence of ovenbird, a species typically not associated with snags (Ehrlich et al. 1988), as DBA increased. Sites exposed to greater fire intensity, as indicated by the presence of snags, could be areas where leaf-litter consumption by fire was greater. Areas with high DBA were typically lower in LBA, probably decreasing leaf fall and increasing ground-level light infiltration, negatively altering ovenbird feeding substrates. The lack of relationships could have resulted from the widespread availability of snags. Harper et al. (2016) reported no temporal difference in snag availability

between unmanaged controls and stands managed with frequent, low-intensity fire following canopy reduction. We conducted a post hoc analysis of variance (ANOVA) using PROC MIXED (SAS 9.4) and similarly found no treatment ($F_{4,5} = 1.16$, $P = 0.43$), year ($F_{2,10} = 2.63$, $P = 0.12$), or interaction ($F_{8,10} = 0.60$, $P = 0.76$) effects on DBA, which averaged $2.90 \pm 0.16 \text{ m}^2/\text{ha}$. The constant or increasing naïve ψ of all species that associate with snags (i.e., woodpeckers [*Picidae* spp.], white breasted nuthatch; Ehrlich et al. 1988) across restoration treatments provides further evidence that snags were not limiting.

Many declining late-successional species in the eastern United States require well-developed midstory structure occurring under partially intact canopies (Hunter et al. 2001). Closed-canopy forests limit the development of such conditions, but overstory disturbance and fire can promote them (Annand and Thompson 1997, Grundel and Pavlovic 2007b). In contrast, some species prefer areas of thick, woody vegetation under open canopies (Ehrlich et al. 1988). Initially, we assumed the general lack of ψ and midstory density relationships resulted from the failure of stand-level means to capture the high variability in midstory density across spatial and temporal scales; however, within stand variation in midstory density was less than or at least comparable to other variables as indicated by stand-level coefficients of variation (midstory density: 0.62 ± 0.05 , LBA: 0.58 ± 0.04 , DBA: 1.08 ± 0.04 , herbaceous groundcover: 0.90 ± 0.06). Furthermore, midstory density was unrelated to variation in LBA ($r = -0.01$, $P = 0.98$), which we attribute to the ubiquitous presence of red maple across a wide range of canopy cover. This may explain why midstory density was a poor predictor of ψ for all but the ovenbird within our study. We conclude adequate levels of midstory density may be necessary for some species but are not sufficient alone in promoting their presence. For ovenbird, we observed increases in ψ at elevated LBA with the reduced presence of the species when midstory density was sparse (<1,500 stems/ha) or particularly dense (>5,000 stems/ha), suggesting a reliance on enough disturbance to maintain intermediate ranges of midstory density within closed canopy forests.

Herbaceous groundcover accurately predicted large changes in ψ for many species. Only ovenbird declined as herbaceous groundcover increased. Eastern wood-pewee responded positively to increasing herbaceous groundcover to a point (41%), suggesting a threshold of disturbance-dependence for this late-successional species. Many early-successional species increased in ψ as herbaceous groundcover increased, but only field sparrow is traditionally associated with grass and forb groundcover. The remaining species were shrubland associates (Ehrlich et al. 1988). Dense woody undergrowth was common, but our results suggest such structure only attracted these species when pockets of herbaceous groundcover (~20%) also were present. Despite ≥ 20 years of repeated fires, Au et al. (2008) reported the avian community of oak woodlands remained distinct from remnant oak savannas through a lack of omnivorous and ground-foraging species. They suggested

additional chemical or mechanical interventions were needed to shift woodland groundcover away from woody dominance and towards increased herbaceous groundcover to attract these missing species. Our results support increasing herbaceous groundcover, facilitated by canopy disturbance and fire, as an influencing force behind increasing the presence of many avian species. The near disappearance of ovenbird and the declining presence of eastern towhee as herbaceous groundcover increased >50% suggests a second threshold above which further changes in the avian community could occur (i.e., disappearing forest, declining shrubland, and increasing grassland species).

Elevated levels of midstory density, relatively low herbaceous groundcover, and prevalence of shrubland avian species accurately reflect the early stage of restoration at our site. Frequent fire is a requisite of oak woodland and savanna establishment and maintenance (McPherson 1997, Peterson and Reich 2001). Additional fire should further decrease midstory density and increase herbaceous groundcover (Waldrop and Lloyd 1991, Hutchinson et al. 2005), potentially promoting avian species associated with more open areas (Reidy et al. 2014). Growing-season fire generally results in greater woody plant mortality and increased herbaceous cover, especially if implemented during the latter portion of the growing season (Gruchy et al. 2009, Knapp et al. 2009, Harper et al. 2016). Accelerating vegetation change in this way could equally accelerate avian community shifts. After 1 fire, we did not expect large differences in vegetation or avian response across our seasonal variation in fire. Although we could not rule out a delayed avian response to canopy disturbance, we did find evidence suggesting our single fire affected avian ψ . Negligible changes in LBA during our study and significant post-fire increases in herbaceous groundcover (Vander Yacht 2013), a key driver of avian ψ trends, supported this conclusion. Additionally, canopy reductions occurred in 2008, whereas fire application and its effects occurred during the experiment. Data for 8 of 10 species with non-constant ψ supported models incorporating variation over time, suggesting ψ changes were influenced by fire in addition to initial thinning effects.

We reiterate that ψ is not synonymous with abundance. We observed stable ψ for many species, but stable abundance was unlikely. Likewise, ψ reveals little insight into population demographics. Fecundity measures are required to evaluate population status as a sink or source. Similar research has reported the retained presence of late-successional species at reduced abundance but also improvements in nesting success related to increases in canopy openness (Brawn 2006, Bakermans et al. 2012). Our encounters with brown-headed cowbirds (*Molothrus ater*), one factor affecting fecundity, were limited but did increase over time (6 in 2010, 2 in 2011, and 16 in 2012). Other studies have reported limited influence of oak woodland and savanna restoration techniques on brown-headed cowbird abundance and nest parasitism rates (Artman et al. 2001, Brawn 2006). Such effects could be more substantial where restoration occurs within a more suburban or agriculturally dominated landscape (Lanham et al. 2002). We provide a foundation

from which future work, focusing on abundance and nesting effects, can build toward a more comprehensive understanding of the contributions of oak woodland and savanna restoration to breeding bird conservation in the Mid-South.

Our restoration stands (20 ha) exceeded home range and minimum patch size for many encountered species (Lehnen and Rodewald 2009b, Shake et al. 2012) and reflected the operational scale typical of our region; however, our results were likely influenced by their occurrence within a larger (1,500 ha) restoration effort. Oak woodland and savanna restoration should occur at similarly large scales, or as clusters of smaller patches within 1 km, to maintain viable populations of attracted avian species (Lehnen and Rodewald 2009a). Avian response to restoration is also dependent on the surrounding landscape. Conducting restoration within open landscapes or at the interface of open and forested lands results in greater avian community benefits in comparison to restoration occurring within large tracts of intact forest (Mabry et al. 2010, Reidy et al. 2014). Within the Mid-South, selecting suitable restoration sites should prove feasible considering oak forests cover >8.5 million hectares of Tennessee and Kentucky alone (Oswalt 2012a,b). Timber revenue, enhanced wildlife habitat, and increased aesthetics should appeal to private and public stakeholders, providing ample opportunity for including oak woodland and savanna restoration within future management plans across the region.

MANAGEMENT IMPLICATIONS

We documented the attraction of disturbance-dependent birds of high conservation priority and retention of many late-successional species during oak woodland and savanna restoration in the Mid-South. To achieve similar results across oak forests of the region, we recommend overstory reduction and prescribed fire. Our results indicate a woodland restoration target of 10 m²/ha LBA and 20% herbaceous groundcover will maximize the presence of shrubland birds without major negative occupancy consequences for late-successional avifauna. Savanna restoration involving greater reductions in LBA further increased early-successional occupancy but negatively affected the presence of lower-strata associated forest birds. Managers should consider both overall avian community effects and the relative conservation priorities of individual species. Realizing the full avian-habitat potential of oak woodlands and savannas will require greater shifts in groundcover dominance, away from woody plants and towards grasses and forbs, using recurring prescribed fire. The observed importance of herbaceous groundcover in directing avian ψ response indicates its value to restoration planning and evaluation. Implementing oak woodland and savanna restoration either at large scales (1,500 ha), along the interface of open and forested land, or as clusters of smaller patches will recognize the landscape dependence of avian response.

ACKNOWLEDGMENTS

We thank the University of Tennessee—Department of Forestry, Wildlife, and Fisheries, National Wild Turkey

Federation, and Tennessee Wildlife Resources Agency for financial support and management implementation contributions to this project. We acknowledge statistical support provided by A. M. Saxton (University of Tennessee). We specifically thank TWRA staff members M. Lipner, C. Kilmer, and C. Coffey (retired). We thank S. A. Barrioz for contributions to the foundations of this research. We finally acknowledge numerous field technicians for assistance with data collection: J. Clark, S. Snow, M. Critean, F. Nebenburgh, J. Trussa, A. Lambert, D. Stamey, and W. Underwood.

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Associate Editor: Michael Morrison.