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Bird response to fire severity and repeated burning in upland hardwood forest



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ABSTRACT

Prescribed burning is a common management tool for upland hardwood forests, with wildlife habitat improvement an often cited goal. Fire management for wildlife conservation requires understanding how species respond to burning at different frequencies, severities, and over time. In an earlier study, we experimentally assessed how breeding bird communities and species responded to fuel reduction treatments by mechanical understory reduction, low-severity prescribed fires, or mechanical understory reduction followed a year later by high-severity prescribed fires in upland hardwood forest. Here, we assess longer-term response to the initial mechanical treatment (M), and a second low-intensity burn in twice burned (B2) and mechanical + twice burned (MB2) treatments and controls (C). Initial (2003) higher dead fuel loadings and consequently high-severity fires in MB2 created open-canopy structure with abundant snags, resulting in much higher species richness and density of breeding birds compared to other treatments. Relative bird density and richness remained much higher in MB2 after a second burn, but few changes were evident that were not already apparent after one burn. The initial (2003) burn in B2 had cooler, low-severity fires that killed few trees. Delayed tree mortality occurred in both burn treatments after one burn, and continued in both after a second low-intensity burn. In B2, this resulted in gradual development of a “perforated,” patchy canopy structure with more snags. Abundance of total birds and most species in B2 was similar to C, but several additional species associated with open-forest conditions occurred at low levels, increasing richness in B2. In both burn treatments, burning temporarily reduced habitat suitability for ground-nesting birds. Bird communities in M were similar to C, as shrubs recovered rapidly. Results indicate that one or two relatively low-intensity burns with patches of hotter fire may result in gradual, subtle changes to canopy cover and structure that may slightly increase bird species richness over time. In contrast, a single high-intensity, high severity fire can create young forest conditions and a heterogeneous canopy structure that can be maintained by repeated burning and increase breeding bird relative abundance and richness by attracting disturbance-adapted species while retaining most other forest species.

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1. Introduction

Prescribed burning is an important land management tool for upland hardwood forests, with fuel reduction, ecosystem restoration, and wildlife habitat improvement often cited as primary goals. Research on how prescribed fire or other fuel reduction methods affect breeding bird communities in upland hardwood forests is scant, but results suggest that changes to species diversity or composition are associated with changes to forest structure

(Greenberg et al., 2007). Many bird species that require open, young-forest conditions have shown regional or continental population declines and are listed as high-priority for conservation (Warburton et al., 2011). Fire management for restoration or wildlife conservation requires an understanding of how different taxa, species, or guilds respond to burning in different forest types, at different frequencies and severities, and over time (Driscoll et al., 2010).

In pine-dominated forests of the western US, post-fire change in the relative abundance of breeding bird species and community assemblage is associated with fire severity and resulting change to forest structure such as tree density, snags, shrub cover, and leaf litter (Hejl, 1994; Smucker et al., 2005). In upland hardwood forests of the eastern US, high-severity fires are rare, and effects on

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breeding bird communities are not well known. Research indicates that single or multiple low-intensity burns with little tree mortality may have a negligible effect on most bird species, or short-term effect on some species associated with shrub or leaf litter cover (Aquilani et al., 2000; Artman et al., 2001; Greenberg et al., 2007). In contrast, high-severity fires with heavy tree mortality may create habitat for species requiring open, early successional conditions (Greenberg et al., 2011) or snags for nest cavities, while retaining many species associated with closed canopy forest, at least in the short-term (Greenberg et al., 2007).

In upland hardwood forests of the eastern US, historic fire frequency and landscape occurrence were strongly associated with population centers of Native Americans and later European settlers, who used fire to clear land, hunt, and increase forage for game or livestock (Van Lear and Harlow, 2000). Lightning-caused (non-anthropogenic) fires were historically rare (Schroeder and Buck, 1970). In the past, fire severity was likely variable, mediated by weather, fuels, and topography. Different human-caused fire regimes resulted in ecosystem structures ranging from grasslands, to shrublands or open woodlands (Guyette et al., 2006a,b; Spetich et al., 2011), and played an important role in the distribution of breeding bird species that require young forest or other open, early successional conditions (Brawn et al., 2001; Spetich et al., 2011).

Over the past several decades, fire suppression policies (Spetich et al., 2011), reduced levels of timber harvest (Shifley and Thompson, 2011), abandonment of farmland and pasture, and habitat loss to development (Greenberg et al., 2011) have led to declining populations of many eastern US bird species associated with early successional communities (Hunter et al., 2001). Fourteen eastern US disturbance-dependent species are federally listed as endangered, threatened, or special concern, whereas most species not dependent on early successional conditions show stable or increasing population trends, and none are federally listed (Warburton et al., 2011).

Today, prescribed burns in upland hardwood forests are usually conducted in winter and under restrictive fuel and weather conditions that generally result in low-intensity burns to minimize safety risks and potential damage to timber. Accordingly, changes to forest structure are often limited to reductions in shrub and leaf litter cover that are short-lived, with little overstory mortality (Waldrop et al., 2008). Increasingly, “restoration burns” are conducted across large landscapes of diverse topography and fuel loads with incomplete knowledge of how different frequencies, seasons, or severities of burns affect biotic communities.

In an earlier study of fire and fire surrogates for fuel reduction, we experimentally assessed how breeding bird communities and species in a southern Appalachian upland hardwood forest responded to fuel reduction treatments by mechanical felling of the understory, prescribed burning, or mechanical felling of the understory followed a year later by prescribed burning (Greenberg et al., 2007). Initial (2003) prescribed burns in mechanical + burn treatment areas were hotter than in the burn-only treatment areas because of cut fuels that were left in place for a year prior to burning, killing substantial numbers of overstory trees and effectively creating conditions of low-severity (burn-only) and high-severity (mechanical + burned). In this study, we use the same experimental design and study sites to assess longer-term response of breeding bird communities to a second prescribed fire in these treatments that were burned initially at high versus low severities. Our objective was to determine how fire severity and repeated dormant season burning affected breeding bird species richness and community composition. Because the initial (2002) mechanical treatment was not repeated, shrub recovery was rapid, and the overstory was unaffected, results of the mechanical-only treatment will be presented but not emphasized here.

1.1. Study area

Our study was conducted on the 5841-ha Green River Game Land (35°17'9"N, 82°19'42"W, blocks 1 and 2; 35°15'42"N, 82°17'27"W, block 3) in Polk County, North Carolina. The Game Land is in the mountainous Blue Ridge Physiographic Province of Western North Carolina. Average annual precipitation is 1638 mm and is distributed evenly throughout the year, and average annual temperature is 17.6 °C (Keenan, 1998). Soils are primarily of the Evard series (fine-loamy, oxidic, mesic, Typic Hapludults), which are very deep (>1 m) and well-drained in mountain uplands (USDA Natural Resources Conservation Service, 1998). Elevation ranges from approximately 366–793 m. The upland hardwood forest was composed mainly of oaks *Quercus* spp. and hickories *Carya* spp. Shortleaf pine (*Pinus echinata*) and Virginia pine (*P. virginiana*) were found on ridgetops, and white pine (*P. strobus*) occurred in moist coves. Forest age within experimental units ranged from about 85 to 125 years. Predominant shrubs were mountain laurel (*Kalmia latifolia*) along ridge tops and on upper southwest-facing slopes, and rhododendron (*Rhododendron maximum*) in mesic areas. Prior to our first prescribed burns in 2003, none of the sites had been thinned or burned for at least 50 years (D. Simon, personal communication).

2. Methods and materials

2.1. Study design

Our experimental design was a randomized block design with repeated measures over years. We selected three study areas (blocks) within the Game Land. Perennial streams border and (or) traverse all three replicate blocks. Blocks were selected based on size (on the basis of their capacity to accommodate four experimental units each), forest age, type, and management history, to ensure consistency in baseline conditions among the treatments. Treatment units included all prevailing combinations of elevation, aspect, and slope. Minimum size of experimental units (four within each block) was 14-ha to accommodate 10-ha “core” areas, with 20 m buffers around each. Dirt roads or firebreaks separated some of the experimental units but did not traverse any, and wooded trails traversed some experimental units.

Three fuel reduction treatments and an untreated control (C) were randomly assigned within each of the three study blocks, for a total of 12 experimental units. Treatments were: (1) twice-burned (March 2003 and March 2006) (B2), (2) mechanical felling of all shrubs and small trees >1.8 m tall and <10.0 cm in diameter at breast height (dbh) with a chainsaw (2002 only) (M), and (3) mechanical cutting of the understory in 2002 as described, followed by two burns (March 2003 and 2006) (MB2). Cut fuels were left scattered onsite resulting in little or no vertical structure initially, with subsequent recovery in M. In 2003 (first burn), burn treatments in two blocks were ignited by helicopter using a plastic sphere dispenser and a spot fire technique. For logistical and safety reasons, the other block was ignited by hand crews using spot fire and strip-headfire techniques, with ignition points determined in similar fashion to those used by the helicopter ignition (Waldrop et al., 2008, 2010). In 2006 (second burn), burn treatments in all blocks were ignited by hand. Fire temperature was measured in both burn treatments with thermocouples placed 30 cm above-ground at grid points spaced at 50-m intervals throughout experimental units.

2.2. Forest structure sampling

We measured tree and snag basal area (BA) and density, percent cover of low and tall shrubs, and leaf litter depth in each experi-

mental unit to examine changes in select features of forest structure resulting from the fuel reduction treatments 2 years after one prescribed burn (2005) (Greenberg et al., 2007), and again in 2006 and 2011 after the second prescribed burn. Tree and snag (≥ 10 cm dbh) density, and percent cover of tall (≥ 1.4 m ht) shrubs was measured within 10, 0.05-ha (10×50 m) plots located at grid points (50×50), starting from a randomly selected grid-point origin. Percent cover of low (< 1.4 m ht) shrubs was estimated in 20, 1-m² quadrats placed systematically within each of the 10 larger plots. We minimized error in visual estimates of percent cover by using the same observers during all years. Leaf litter depth was measured using a meter stick at three locations along each of three randomly oriented, 15-m transects originating at grid points. We used the average of all measurements (plots, quadrats, or transects) for each experimental unit ($n = 3$ replicates per treatment or control) in our statistical analyses.

2.3. Bird sampling

We surveyed breeding bird communities using three, 50-m radius (0.785-ha area) point counts spaced 200 m apart in each experimental unit (Ralph et al., 1993). Each point was surveyed for 10 min during three separate visits between 15 May and 30 June during 2001–2005 to study effects of the fuel reduction treatments after one prescribed burn (Greenberg et al., 2007), and in 2006, 2007, 2009, and 2011 to study the longer-term effects of fuel reduction treatments that included a second prescribed fire in both burn treatments (the focus of this paper). During the study period, a single observer (J. Tomcho) conducted all surveys to reduce bias associated with different observers. Point counts were conducted within four hours of sunrise. All birds that were seen or heard within a 50-m radius were recorded. Point count times were rotated among the three visits to each experimental unit to avoid time-of-day bias. Each unit was surveyed early-, mid-, and late-season within the 6-week survey period to avoid bias associated differences in singing rates as breeding season progresses. We did not estimate detectability of different bird species (Alldredge et al., 2008), and assumed that bird detection error was minimal and consistent among units due to a small (50-m) point count radius, surveys conducted by a single observer, multiple survey points and repeated surveys within each unit, and timing of surveys across time of day and breeding season. Relative density of birds for each experimental unit was calculated by averaging across the three surveys and three point counts (9 observation periods per unit) for each year, and extrapolating the average number per point count to number per 10 ha. Species richness represented the total number of species detected during all three visits and point counts in each experimental unit each year.

2.4. Data analysis

We used repeated measures analysis in a randomized block design to compare the fuel reduction treatments and control over the years from 2005 (2 years after a single burn in both burn treatments) to 2011 (post-treatment years 2006, 2007, 2009, 2011), after a second burn in B2 and MB2). Response variables analyzed were bird species richness and total density, density of birds within tree-, shrub-, cavity-, or ground-nesting guilds (Hamel, 1992), and density of common bird species. There was concern that analysis for each individual species may violate the normality assumption required for the repeated measures analysis because many individual species were detected on the three plots and three observation times for a given block, treatment and year, resulting in many zero observations. To determine whether individual species were sufficiently common for inclusion in statistical analyses, we checked density data for conforming approximately to the normal distribu-

tion by inspecting the residuals. We were quite liberal and included a species in the analysis if the skewness of the residuals was between -2 and 2 and kurtosis of residuals was less than 5 . We also determined that all cells in a stem and leaf plot had $< 50\%$ of the observations to assure that there were not too many residuals at zero. Thus, although many species did not pass a typical normality test, we feel they were sufficiently normal to perform a valid analysis. Density data ($+0.01$) were natural-log transformed for ANOVAs.

Percent cover data (for shrubs) were square-root arcsine transformed for ANOVA. We interpreted either a significant treatment effect and (or) treatment by year interaction effect as evidence of a treatment effect. All repeated measures analyses were performed using PROC MIXED (SAS 9.1). All significant repeated measures analyses were followed by Tukey's multiple comparisons at the 0.05 significance level on the least square means to determine differences between treatments and years.

3. Results

3.1. Fire behavior

During the first prescribed burns (March, 2003), flame lengths of 1–2 m occurred throughout all burn units, but flame lengths reached up to 5 m in localized spots within blocks, where topography or intersecting flame fronts contributed to erratic fire behavior (Waldrop et al., 2010). In 2003, loading of dead fine woody fuels on mechanical + burn sites, where the shrub layer was felled, was approximately double that on control and mechanical-only sites. In the 2003 burns, temperature at 30 cm aboveground averaged 312 °C in the burn-only treatment, but patches (6–22% of each burn unit) burned at temperatures > 600 °C. In the mechanical + burn treatment, temperatures at 30 cm aboveground averaged 517 °C, and 22–49% of each unit burned at temperatures > 600 °C. The second burn (March, 2006) was less intense, with flame lengths generally < 1.5 m. In 2006, measured temperatures 30 cm aboveground were generally < 158 °C on B2 sites and 223 °C in MB2 sites, with $< 3\%$ of any burn unit exceeding 600 °C. A detailed description of fire behavior in this study is given by Waldrop et al. (2010).

3.2. Forest structure

Several forest structural features differed among the three fuel reduction treatments and control. Live tree BA was lower in MB2 than in M or C but did not differ from B2; a year effect was detected, and a treatment by year interaction indicates that live tree BA decreased over time in MB2 after a second burn (Table 1). Live tree density was lowest in MB2 compared to the other treatments and C. More trees were alive in 2006 than in 2011, and a treatment by year effect indicated that live tree density declined in the B2 and MB2 treatments after a second burn (Table 1). Snag BA was greater in MB2 than M but did not differ among the other treatments or C. Snag BA was higher in 2006 than in 2011, and a treatment by year interaction effect indicated that snag BA declined most rapidly in MB2 (Table 1). Snag density was highest in MB2 compared to the other treatments or C, and density was higher in 2006 than in 2011; a treatment by year interaction effect indicated that snag density decreased in MB2 within a few years of the second burn (Table 1). Leaf litter depth was reduced in B2 and MB2 following the second prescribed burn (2006) but was similar to M or C by 2011 (5 years post-burn) (Table 1). Percent cover of low shrubs did not differ among treatments, but was lower in 2006 than in 2011; a treatment by year interaction indicated that recovery of low shrubs was greatest in MB2 (Table 1). Percent cover of tall

Table 1

Mean (\pm SE)^a live tree basal area (BA) and density, snag BA and density, leaf litter depth, and percent cover of low and tall shrubs in three fuel reduction treatments: twice burned (B2), mechanical understory reduction (M), mechanical + twice burned (MB2), and controls (C) ($n = 3$ each) 1 year before a second burn in B2 and MB2 treatments (2005), immediately after a second burn in B2 and MB2 treatments (2006), and 5 years after the second burn (2011), at Green River Game Land, Polk County, NC. P -values are results of repeated measures ANOVA comparing treatment, years, and treatment by year effects.

Habitat variable	Year	Treatment ^b				RM ANOVA		
		C $\bar{x} \pm$ SE	M $\bar{x} \pm$ SE	B2 $\bar{x} \pm$ SE	MB2 $\bar{x} \pm$ SE	P_{trt} df = 3, 6	P_{yr} df = 2, 16	$P_{\text{trt} \times \text{Yr}}$ df = 6, 16
Live Tree BA (m ² /ha)	2005	26.1 \pm 1.1A	28.8 \pm 1.2A	26.2 \pm 3.6AB	18.2 \pm 3.5B	0.0322	0.0031	<0.0001
	2006	27.6 \pm 0.7	29.0 \pm 1.4	25.9 \pm 3.8	16.6 \pm 3.4			
	2011	28.8 \pm 0.7	29.7 \pm 1.3	24.6 \pm 4.2	14.6 \pm 4.1			
Live Tree Density (ha)	2005	552.0 \pm 12.5A	594.0 \pm 9.5A	505 \pm 3 33.3A	277.3 \pm 60.2B	0.0012	<0.0001	0.0106
	2006	547 \pm 16.7	585 \pm 6.8	484 \pm 51.3	236.7 \pm 55.2			
	2011	506.0 \pm 26.6	539.3 \pm 5.2	402.0 \pm 56.9	169.3 \pm 47.0			
Snag BA (m ² /ha)	2005	3.2 \pm 1.0AB	2.1 \pm 0.3A	3.4 \pm 1.2AB	7.5 \pm 1.6B	0.0466	0.0057	0.0539
	2006	3.0 \pm 0.5	2.0 \pm 0.3	3.1 \pm 1.3	6.9 \pm 1.4			
	2011	2.3 \pm 0.4	2.2 \pm 0.4	2.8 \pm 1.2	5.0 \pm 1.1			
Snag Density (ha)	2005	56.7 \pm 14.1A	60.7 \pm 6.7A	90.0 \pm 33.3A	212.0 \pm 29.0B	0.0025	0.0029	0.0046
	2006	60.7 \pm 7.4	58.0 \pm 6.1	96.7 \pm 30.9	210.0 \pm 19.7			
	2011	55.3 \pm 2.4	58.0 \pm 7.6	80.0 \pm 24.7	133.3 \pm 3.7			
Leaf Litter Depth (mm)	2005	46.2 \pm 1.8A	59.0 \pm 3.8A	39.3 \pm 0.4B	32.7 \pm 1.2B	<0.0001	<0.0001	<0.0001
	2006	54.3 \pm 2.0	62.6 \pm 4.8	11.3 \pm 3.6	4.8 \pm 0.6			
	2011	68.7 \pm 3.1	76.7 \pm 5.3	65.8 \pm 2.6	65.7 \pm 1.7			
Low Shrub (<1.4 m ht) % Cover	2005	9.6 \pm 1.3	15.6 \pm 2.7	8.6 \pm 2.5	18.9 \pm 5.6	0.0990	<0.0001	0.0014
	2006	9.5 \pm 3.8	18.6 \pm 2.2	6.7 \pm 1.8	12.5 \pm 2.6			
	2011	14.1 \pm 2.3	22.2 \pm 2.8	14.9 \pm 3.5	26.2 \pm 3.8			
Tall Shrub (\geq 1.4 m ht) % Cover	2005	17.8 \pm 4.3A	2.6 \pm 2.4AB	4.1 \pm 2.4B	1.3 \pm 0.6B	0.0139	0.0242	0.0228
	2006	14.2 \pm 3.8	4.4 \pm 1.4	3.6 \pm 2.2	0.5 \pm 0.3			
	2011	11.2 \pm 1.7	8.4 \pm 1.9	4.7 \pm 0.9	6.8 \pm 4.4			

^a Means and SE's are from raw data and do not represent lsmeans output from the statistical model.

^b Different letters among treatments within a row indicates significant differences among treatments.

shrubs was lowest in B2 and MB2, and greatest in C (cover in M did not differ from other treatments); cover was greater in 2011 than in 2006, and a treatment by year interaction was detected (Table 1).

3.3. Breeding birds

We detected 49 breeding bird species over the 4 years sampled following a second prescribed burn (2006, 2007, 2009, and 2011). After the second burn in B2 and MB2 (post-treatment), total relative bird density was greater in MB2 than other treatments and varied among years, but no treatment by year interaction effect was detected (Table 2; Fig. 1a). Post-treatment species richness was highest in MB2 compared to M or C; richness in B2 did not differ from any treatment or C (Table 2; Fig. 1b). Richness differed among years; no treatment by year interaction effect was detected.

Relative abundance of tree-nesters was marginally higher in MB2 than M but did not differ among other treatments or C; abundance differed among years, but no treatment by year interaction was detected (Table 2; Fig. 2a). Shrub-nesters also were marginally more abundant in MB2 than in other treatments; abundance differed among years, but no treatment by year interaction was detected (Table 2; Fig. 2b). Relative abundance of cavity-nesters was greater in MB2 than in the other treatments and lower in M than in B2 but did not differ among years, and we did not detect a treatment by year interaction (Table 2; Fig. 2c). Ground-nester abundance did not differ among treatments but did differ among years; a marginal treatment by year interaction suggested that, after a second burn, change in abundance was most dynamic in both burn treatments (Table 2; Fig. 2d).

Among the 36 species that met our criteria for analysis, 10 showed a significant treatment response, and three showed a treatment by year interaction ($P < 0.05$) (Table 2). Following a second burn in B2 and MB2 treatments eastern bluebirds (*Sialia sialis*),

eastern towhees (*Pipilo erythrophthalmus*), indigo buntings (*Passerina cyanea*), pine warblers (*Setophaga pinus*), Carolina wrens (*Thyrothorus ludovicianus*), and mourning doves (*Zenaidura macroura*) showed greater relative abundance in MB2; American goldfinch (*Carduelis tristis*), and eastern wood-pewees (*Contopus virens*) were more abundant in both MB2 and B2 than C or M (Table 2). Indigo buntings increased for a short period in MB2 after the second burn, and increased the year following the second burn in B2, as indicated by treatment by year interactions. Brown thrashers (*Toxostoma rufum*) and chipping sparrows (*Spizella passerina*) also occurred only in both burn treatments but were not sufficiently common to compare statistically, or did not show a significant difference among treatments. Relative abundance of white-breasted nuthatches (*Sitta carolinensis*) was greater in MB2 than M. Ovenbird (*Seiurus aurocapillus*) relative abundance was marginally lower in MB2 than in B2 or M, but did not differ from C. Relative abundance of Carolina chickadees (*Poecile carolinensis*) was lower in M than in the other treatments or C. Relative abundance of several species differed among years, but no trend in abundance among years was apparent. Blue-gray gnatcatchers (*Poliptila caerulea*), and blue-headed vireos (*Vireo solitarius*) showed treatment by year interaction effects, but no clear trend was apparent (Table 2).

4. Discussion

4.1. Forest structure

Prescribed burning in the initial (2003) MB2 treatment was hotter than in B2 because of cut fuels that were left in place for a year prior to burning, resulting in high-severity burns with heavy tree mortality. Thus, prior to the second burn, average live tree density was already 45% lower, and BA 31% lower in MB2 than in B2 (Greenberg et al., 2007; Waldrop et al., 2008). The second pre-

Table 2
Mean (\pm SE) densities (no/10 ha) of individuals within each species and nesting guild (tree, shrub, cavity, and ground), total, and species richness of breeding birds^a in three fuel reduction treatments: twice burned (B2), mechanical understory reduction (M), mechanical + twice burned (MB2), and controls (C) ($n = 3$ each), Green River Game Land, Polk County, NC. Means (\pm SE) are presented for 2005 (before a second burn in B2 and MB2; first line), and post-treatment (after a second burn in B2 and MB2; second line) (average of 2006, 2007, 2009, and 2011). P -values are results of a repeated measures mixed-model ANOVA comparing treatment, years, and treatment by year effects^{b,c} (2005, 2006, 2007, 2009, 2011).

Guild/species	Relative density (no/10 ha)				RM ANOVA		
	C	M	B2	MB2	P_{trt} df = 3,6	P_{yr} df = 4,32	$P_{\text{trt} \times \text{yr}}$ df = 12,32
Total density	$\bar{x} \pm \text{SE}$	$\bar{x} \pm \text{SE}$	$\bar{x} \pm \text{SE}$	$\bar{x} \pm \text{SE}$			
Tree-nester	16.4 \pm 6.2 18.5 \pm 2.2	8.9 \pm 0.5 12.1 \pm 1.7	15.0 \pm 3.8 17.3 \pm 2.2	31.9 \pm 10.2 30.5 \pm 4.0	0.0613	0.0054	0.8587
Acadian flycatcher	0.0 \pm 0.0	0.0 \pm 0.0	0.5 \pm 0.5	0.0 \pm 0.0			
<i>Empidonax virens</i>	0.1 \pm 0.1	0.0 \pm 0.0	1.2 \pm 0.6	0.1 \pm 0.1	0.5323	0.3070	0.5441
American crow	0.0 \pm 0.0	0.0 \pm 0.0	0.5 \pm 0.5	0.0 \pm 0.0			
<i>Corvus brachyrhynchos</i>	0.1 \pm 0.1	0.5 \pm 0.5	0.6 \pm 0.3	0.1 \pm 0.1	–	–	–
American redstart	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.5 \pm 0.5			
<i>Setophaga ruticilla</i>	0.0 \pm 0.0	0.1 \pm 0.1	0.0 \pm 0.0	0.2 \pm 0.2	–	–	–
Blue-gray gnatcatcher	1.4 \pm 1.4	0.5 \pm 0.5	2.8 \pm 1.4	3.3 \pm 1.9			
<i>Poliophtila caerulea</i>	2.9 \pm 1.1A	1.4 \pm 0.4A	2.1 \pm 0.7A	6.1 \pm 1.0B	0.2020	0.0127	0.0273
Brown-headed cowbird	0.5 \pm 0.5	0.0 \pm 0.0	0.9 \pm 0.9	4.2 \pm 4.2			
<i>Molothrus ater</i>	0.7 \pm 0.4	0.2 \pm 0.2	1.2 \pm 0.4	2.2 \pm 0.7	0.2015	0.0672	0.4106
Blue jay	1.9 \pm 1.2	0.5 \pm 0.5	1.9 \pm 1.2	0.9 \pm 0.5			
<i>Cyanocitta cristata</i>	1.1 \pm 0.4A	0.4 \pm 0.4B	0.8 \pm 0.3A	0.5 \pm 0.2AB	0.6061	0.0978	0.2774
Black-throated green warbler	5.6 \pm 3.3	0.9 \pm 0.9	0.5 \pm 0.5	0.5 \pm 0.5			
<i>Setophaga virens</i>	5.0 \pm 1.0A	1.5 \pm 0.6B	2.5 \pm 0.9B	0.9 \pm 0.6B	0.0695	0.0141	0.7141
Broad-winged hawk	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0			
<i>Buteo platypterus</i>	0.1 \pm 0.1	0.0 \pm 0.0	0.1 \pm 0.1	0.1 \pm 0.1	–	–	–
Cedar waxwing	0.0 \pm 0.0	0.0 \pm 0.0	0.5 \pm 0.5	4.2 \pm 2.9			
<i>Bombycilla cedrorum</i>	0.2 \pm 0.2	0.0 \pm 0.0	0.7 \pm 0.4	3.6 \pm 1.1	0.0749	0.2788	0.4943
Coopers hawk	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0			
<i>Accipiter cooperii</i>	0.0 \pm 0.0	0.1 \pm 0.1	0.1 \pm 0.1	0.0 \pm 0.0	–	–	–
Eastern wood-pewee	0.0 \pm 0.0	0.0 \pm 0.0	0.9 \pm 0.5	4.2 \pm 0.0			
<i>Contopus virens</i>	0.7 \pm 0.3A	1.8 \pm 0.6A	2.5 \pm 0.6AB	6.2 \pm 1.2B	0.0153	0.1268	0.4636
Northern parula	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.5 \pm 0.5			
<i>Setophaga americana</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.1 \pm 0.1	–	–	–
Pine warbler	0.0 \pm 0.0	0.5 \pm 0.5	0.0 \pm 0.0	1.9 \pm 0.9			
<i>Setophaga pinus</i>	0.2 \pm 0.2A	0.2 \pm 0.2A	0.4 \pm 0.2A	1.5 \pm 0.5B	0.0491	0.1283	0.1588
Red-eyed vireo	4.7 \pm 2.4	3.7 \pm 0.5	4.7 \pm 1.3	3.7 \pm 0.5			
<i>Vireo olivaceus</i>	5.5 \pm 0.7	4.2 \pm 0.6	2.9 \pm 0.8	4.9 \pm 1.1	0.5885	0.5524	0.7460
Scarlet tanager	2.3 \pm 0.5	2.8 \pm 1.6	0.9 \pm 0.5	4.7 \pm 2.1			
<i>Piranga olivacea</i>	1.5 \pm 0.5	1.4 \pm 0.5	1.6 \pm 0.5	1.9 \pm 0.6	0.8559	0.3960	0.2994
Summer tanager	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	1.9 \pm 0.9			
<i>Piranga rubra</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.2 \pm 0.2	–	–	–
Yellow-billed cuckoo	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0			
<i>Coccyzus americanus</i>	0.1 \pm 0.1	0.0 \pm 0.0	0.0 \pm 0.0	0.1 \pm 0.1	–	–	–
Yellow-throated vireo	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0			
<i>Vireo flavifrons</i>	0.1 \pm 0.1	0.0 \pm 0.0	0.1 \pm 0.1	0.7 \pm 0.5	0.1462	0.3029	0.8977
Yellow-throated warbler	0.0 \pm 0.0	0.0 \pm 0.0	0.9 \pm 0.5	1.4 \pm 0.8			
<i>Setophaga dominica</i>	0.0 \pm 0.0	0.2 \pm 0.2	0.6 \pm 0.3	0.8 \pm 0.3	0.1938	0.1130	0.1929
Shrub nester	18.8 \pm 3.1 19.0 \pm 2.1	16.4 \pm 6.2 23.6 \pm 2.6	13.1 \pm 5.2 23.2 \pm 3.0	28.1 \pm 3.6 45.6 \pm 2.3	0.0693	0.0001	0.2345
American goldfinch	0.0 \pm 0.0	0.5 \pm 0.5	0.9 \pm 0.9	1.9 \pm 0.9			
<i>Carduelis tristis</i>	0.4 \pm 0.2A	0.5 \pm 0.2A	1.4 \pm 0.5AB	3.4 \pm 0.8B	0.0092	0.3935	0.3181
American robin	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0			
<i>Turdus migratorius</i>	0.0 \pm 0.0	0.1 \pm 0.1	0.0 \pm 0.0	0.4 \pm 0.3	–	–	–
Blue-headed vireo	6.1 \pm 2.1	8.0 \pm 2.4	2.8 \pm 2.2	5.2 \pm 1.3			
<i>Vireo solitarius</i>	6.7 \pm 1.0	6.7 \pm 0.6	6.6 \pm 1.2	3.4 \pm 0.6	0.3660	0.1197	0.0304
Brown thrasher	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0			
<i>Toxostoma rufum</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.1 \pm 0.1	0.4 \pm 0.3	–	–	–
Chipping sparrow	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.9 \pm 0.9			
<i>Spizella passerina</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.1 \pm 0.1	0.8 \pm 0.4	0.2547	0.0996	0.4221
Eastern towhee	0.0 \pm 0.0	0.9 \pm 0.9	0.5 \pm 0.5	7.0 \pm 3.7			
<i>Pipilo erythrophthalmus</i>	1.3 \pm 0.5A	4.2 \pm 1.0A	3.8 \pm 1.6A	12.0 \pm 1.9B	0.0101	0.0002	0.1223
Hooded warbler	9.4 \pm 3.3	5.6 \pm 2.5	4.7 \pm 2.5	4.2 \pm 3.6			
<i>Setophaga citrina</i>	6.5 \pm 1.3	8.4 \pm 1.6	3.6 \pm 1.1	6.3 \pm 1.7	0.2974	0.0018	0.7979
Indigo bunting	0.0 \pm 0.0	0.0 \pm 0.0	0.9 \pm 0.9	5.6 \pm 2.2			
<i>Passerina cyanea</i>	0.0 \pm 0.0A	0.1 \pm 0.1A	2.3 \pm 0.7A	8.7 \pm 0.9B	0.0016	0.1265	0.0363
Mourning dove	0.5 \pm 0.5	0.0 \pm 0.0	0.0 \pm 0.0	0.5 \pm 0.5			
<i>Zenaidura macroura</i>	0.8 \pm 0.5A	0.9 \pm 0.4A	0.5 \pm 0.3A	4.6 \pm 1.0B	0.0051	0.0558	0.2077
Northern cardinal	0.5 \pm 0.5	0.0 \pm 0.0	0.9 \pm 0.9	0.0 \pm 0.0			
<i>Cardinalis cardinalis</i>	0.6 \pm 0.4	0.1 \pm 0.1	1.3 \pm 0.4	1.6 \pm 0.6	0.1951	0.2337	0.9303
Prairie warbler	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0			
<i>Setophaga discolor</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.6 \pm 0.4	1.3 \pm 0.6	0.2715	0.0608	0.4314
Ruby-throated hummingbird	1.9 \pm 0.5	1.4 \pm 0.8	1.9 \pm 0.5	2.8 \pm 1.4			
<i>Archilochus colubris</i>	2.0 \pm 0.5	2.3 \pm 0.6	2.3 \pm 0.7	2.7 \pm 0.9	0.9688	0.8556	0.9265

Table 2 (continued)

Guild/species	Relative density (no/10 ha)				RM ANOVA		
	C	M	B2	MB2	P_{trt} df = 3, 6	P_{yr} df = 4, 32	$P_{\text{trt} \times \text{yr}}$ df = 12, 32
Total density							
Species richness	$\bar{x} \pm \text{SE}$	$\bar{x} \pm \text{SE}$	$\bar{x} \pm \text{SE}$	$\bar{x} \pm \text{SE}$			
Swainson's warbler	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0			
<i>Limnothlypis swainsonii</i>	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	–	–	–
Wood thrush	0.5 ± 0.5	0.0 ± 0.0	0.5 ± 0.5	0.0 ± 0.0			
<i>Hylocichla mustelina</i>	0.7 ± 0.3	0.2 ± 0.2	0.6 ± 0.5	0.0 ± 0.0	0.1898	0.5168	0.9266
Cavity nester	12.2 ± 0.9	7.5 ± 3.3	15.9 ± 2.0	31.5 ± 8.3			
	13.6 ± 1.4A	9.7 ± 1.6B	17.8 ± 2.5A	32.7 ± 2.3C	0.0011	0.4162	0.4431
Carolina chickadee	1.9 ± 1.9	0.9 ± 0.9	1.4 ± 0.8	2.8 ± 2.8			
<i>Poecile carolinensis</i>	2.1 ± 0.5A	0.1 ± 0.1B	2.8 ± 0.8A	4.2 ± 0.6A	0.0113	0.4497	0.2786
Carolina wren	0.5 ± 0.5	0.0 ± 0.0	2.3 ± 1.7	5.2 ± 2.5			
<i>Thryothorus ludovicianus</i>	1.9 ± 0.6A	3.5 ± 0.7A	2.2 ± 0.5A	5.6 ± 0.9B	0.0106	0.1308	0.0900
Downy woodpecker	2.8 ± 0.8	0.5 ± 0.5	0.5 ± 0.5	1.9 ± 1.2			
<i>Picoides pubescens</i>	0.8 ± 0.4AB	0.7 ± 0.4A	1.9 ± 0.6AB	2.8 ± 0.6B	0.2008	0.5419	0.3035
Eastern bluebird	0.0 ± 0.0	0.0 ± 0.0	0.9 ± 0.9	2.3 ± 1.7			
<i>Sialia sialis</i>	0.1 ± 0.1A	0.0 ± 0.0A	1.2 ± 0.6A	4.6 ± 0.9B	0.0039	0.0243	0.3272
Eastern tufted titmouse	3.3 ± 0.5	2.3 ± 0.5	5.6 ± 1.6	6.6 ± 3.1			
<i>Baeolophus bicolor</i>	3.6 ± 0.6	2.5 ± 0.5	3.9 ± 0.8	6.0 ± 1.1	0.2182	0.1165	0.9157
Northern flicker	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.9 ± 0.5			
<i>Colaptes auratus</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.2	–	–	–
Great-crested flycatcher	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.5	0.5 ± 0.5			
<i>Myiarchus crinitus</i>	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	–	–	–
Hairy woodpecker	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.5	0.0 ± 0.0			
<i>Picoides villosus</i>	0.4 ± 0.3	0.1 ± 0.1	0.4 ± 0.2	0.1 ± 0.1	0.5622	0.0480	0.8392
Pileated woodpecker	0.0 ± 0.0	0.5 ± 0.5	0.0 ± 0.0	1.4 ± 1.4			
<i>Drycopus pileatus</i>	1.1 ± 0.5	0.4 ± 0.3	0.2 ± 0.2	0.7 ± 0.3	0.1901	0.2085	0.7408
Red-bellied woodpecker	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.5			
<i>Melanerpes carolinus</i>	0.7 ± 0.3	0.4 ± 0.2	0.8 ± 0.4	0.9 ± 0.5	0.7572	0.3290	0.5570
White-breasted nuthatch	3.8 ± 1.7	3.3 ± 2.6	4.2 ± 0.8	9.4 ± 1.2			
<i>Sitta carolinensis</i>	2.8 ± 0.8AB	2.1 ± 0.6B	4.3 ± 0.8AB	7.2 ± 1.2A	0.0092	0.3568	0.7719
Ground nester	8.0 ± 3.3	5.6 ± 2.5	7.5 ± 1.3	5.1 ± 2.0			
	10.7 ± 1.2	9.1 ± 1.3	6.6 ± 1.3	7.2 ± 2.0	0.1370	<0.0001	0.0638
Black-and-white warbler	3.3 ± 2.6	0.0 ± 0.0	1.4 ± 0.8	1.4 ± 0.8			
<i>Mniotilta varia</i>	2.3 ± 0.7	2.1 ± 0.7	0.9 ± 0.3	3.1 ± 0.9	0.5133	0.1193	0.2141
Ovenbird	3.3 ± 2.6	4.7 ± 2.5	2.8 ± 1.4	0.5 ± 0.5			
<i>Seiurus aurocapillus</i>	3.3 ± 1.1	3.9 ± 0.9	4.1 ± 1.2	1.9 ± 0.9	0.0776	0.0034	0.0518
Worm-eating warbler	1.4 ± 0.0	0.9 ± 0.5	3.3 ± 2.1	3.3 ± 1.7			
<i>Helmitheros vermivorus</i>	5.1 ± 0.8	3.0 ± 0.6	1.5 ± 0.4	2.1 ± 0.8	0.2587	0.1041	0.5653
Wild turkey	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0			
<i>Meleagris gallopavo</i>	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	–	–	–
Other							
Eastern phoebe	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0			
<i>Sayornis phoebe</i>	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.2	0.8 ± 0.3	0.2553	0.1858	0.5819
Total	56.0 ± 8.7	39.3 ± 6.2	53.3 ± 9.8	97.3 ± 22.2			
	63.5 ± 4.5A	56.4 ± 5.1A	67.4 ± 6.0A	118.3 ± 6.4B	0.0068	<0.0001	0.8141
Richness	13.7 ± 1.7	10.3 ± 1.8	17.0 ± 3.0	22.7 ± 2.3			
	15.9 ± 0.8A	14.6 ± 1.2A	18.5 ± 1.4AB	23.8 ± 1.0B	0.0131	<0.0001	0.2511

^a Means and SE's are from raw data and do not represent lsmeans output from the statistical model.

^b Different letters among treatments within a row (second line) indicates significant differences among treatments.

^c ANOVA performed only if a species was sufficiently common as described in Section 2.

scribed burn in both burn treatments was relatively low-intensity. Accordingly, immediate changes to forest structure following the second burns were relatively minor and short-lived in both B2 and MB2 compared to changes in MB2 following the initial burn in 2003 (Greenberg et al., 2007). Our results indicate that a single high-intensity burn has a much larger immediate influence on tree mortality and associated changes to forest structure than single or repeated low-intensity burns, at least in the short-term.

Delayed mortality of overstory trees occurred after the initial prescribed burns in 2003 in both burn treatments, and continued for several years after the second burn in 2006. Within 5 years of the second burn, live tree density was 20% lower in B2 than in controls. Our results differ from Artman et al. (2001), who reported that low-intensity burning did not affect the density of live trees or snags. In contrast, live tree density in MB2 was (on average) 67% lower than controls and 58% lower than B2 within 5 years of the second burn. Our data indicate that even relatively low-inten-

sity fire can affect tree mortality and have subtle effects on forest structure gradually over time, whereas higher-intensity fire has a much greater and more immediate influence on tree mortality and forest structure.

In our study a second, low-intensity prescribed fire did not increase snag availability despite some additional tree mortality, because older snags created by the initial burn fell. This was most pronounced in the MB2 treatment where initial (2003) fires were hotter and created more snags (Greenberg et al., 2007; Waldrop et al., 2010). Within 2 years of the initial prescribed burn, average snag density was already over twice as high in MB2 (212/ha) than B2 (90/ha). Snag loss between 2005 (2 years after the first burn) and 2011 (5 years after the second burn) was much greater in MB2 (average 37%) than B2 (11%), likely because of greater snag exposure in MB2. Because both the B2 and MB2 treatments were burned twice, our study could not address whether continuing tree mortality in the burn treatments (relative to unburned M or C) was

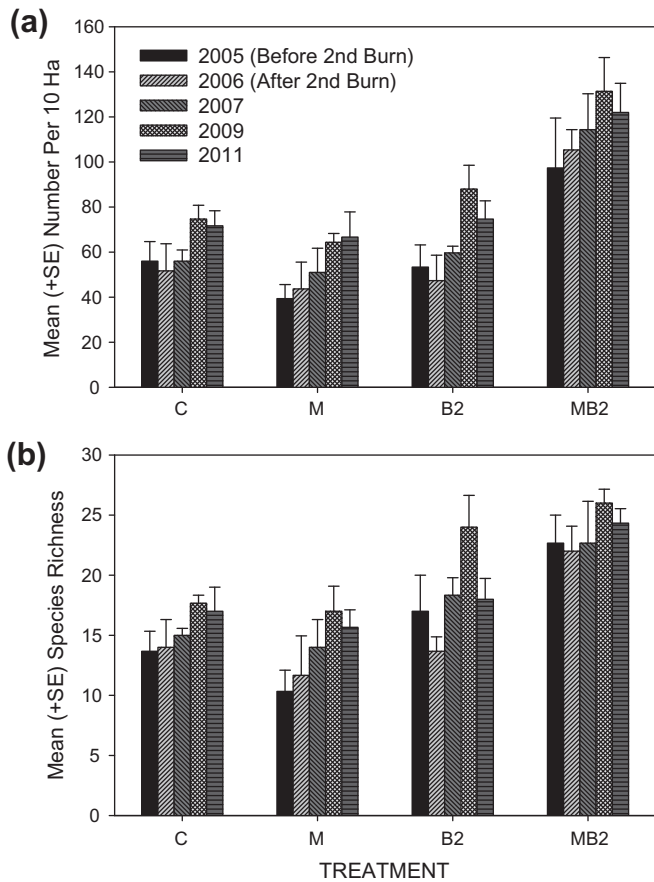


Fig. 1. Mean (+SE) total density and species richness of breeding birds in 3 fuel reduction treatments: prescribe burned twice (B2), mechanical understory reduction (M), mechanical + burned twice (MB2), and controls (C) ($n=3$ each), Green River Game Land, Polk County, NC. Data for 2005 are 2 years after the first prescribed burn but prior to the second burn. Data for 2006, 2007, 2009, and 2011 are after the second burn (conducted March, 2006) in the two burn treatments.

caused by second order effects of the first burn, first-order effects of the second burn, or other natural causes of mortality.

We found that single (Greenberg et al., 2007) and multiple prescribed burns temporarily reduced shrub cover and leaf litter depth (Waldrop et al., 2010; this study) and confirm results of other studies in upland hardwood forests (Aquilani et al., 2000; Artman et al., 2001). Initial fuel reduction treatments reduced shrub cover in all treatments relative to controls, but were most effective in both mechanical treatments because burning alone did not effectively remove rhododendrons growing in moist areas (Waldrop et al., 2008). We found that a second prescribed burn again reduced shrub cover in both burn treatments, whereas shrubs continued to recover in the M treatment, reaching approximately 50% of their original cover by 2006 (Waldrop et al., 2008). Our results indicated that shrubs in upland hardwood forest recover rapidly after mechanical thinning, and after one or two prescribed burns at different intensities. Both M and MB2 increased cover of sprouting shrubs with approximately twice as much in M and MB2 as C or B2. However, shrub height may be retarded for several years. Similarly, in our study leaf litter depth was reduced in both burn treatments after a second burn, but recovered quickly as leaves fell from trees in autumn.

4.2. Breeding birds

Initial (2003) high-intensity fires in our MB2 treatment resulted in high tree mortality, creating an open-canopy structure with an

abundance of snags lasting for several years. These high-severity conditions resulted in much higher species richness and relative abundance of breeding birds compared to lower-severity burns (B2) or mechanical understory (M) fuel reduction treatments that did not substantially change forest canopy cover (Greenberg et al., 2007). Our results indicated that relative abundance and species richness of breeding birds remained much higher in MB2 than the other treatments after a second burn (2006), but the second burn did not result in substantial additional changes that were not already apparent within 2 years of a single prescribed burn (see Greenberg et al., 2007).

Higher bird species richness and relative abundance in MB2 treatment was due to a higher occurrence and (or) abundance of species associated with young, open forest and edge conditions such as eastern bluebirds, indigo buntings, eastern towhees, brown thrashers, chipping sparrows, American goldfinches, mourning doves, and pine warblers, in addition to most other species that also occurred in the other treatments and control. However, these open-forest species also were most abundant or occurred solely in the MB2 treatment after a single, high-severity burn (Greenberg et al., 2007), indicating a second low-intensity burn at a short interval (3 years in our study) does not change habitat suitability more than a single burn, if that initial burn was hot enough to kill trees and substantially open the forest canopy. However, repeated burning after a high-severity burn will help to maintain the open forest conditions necessary to sustain higher bird species richness and diversity, if done with sufficient frequency to delay forest regrowth to canopy closure.

Delayed tree mortality occurred after both initial low- and high-severity burns, and continued after a second low-intensity burn. Variable burn temperatures and delayed tree mortality with an abundance of snags created by the first and second lower-intensity burns (B2) clearly contributed to a gradual development of a complex, “perforated” canopy structure or other habitat features suitable for some open-forest bird species in B2 compared to unburned treatments. Although relative abundance of total birds and most species in these low-severity burns was similar to unburned treatments, several of the same open-forest species occurring in MB2 also occurred less commonly in B2, and species richness was also higher in B2 than in M or C. The complex canopy structure created over time by delayed tree mortality could potentially provide suitable habitat for cerulean warblers (*Setophaga cerulean*) (Boves, 2011) or other species associated with small forest openings (Hunter et al., 2001). Although we could not assess whether a second burn contributed additionally to the delayed tree mortality initiated by a single burn, our results indicate that repeated, relatively low-intensity burning with patches of higher intensity fire, can affect a gradual change in forest structure that may, over time, attract breeding bird species associated with young forest conditions.

In our study, abundance of most species did not decline following the three fuel reduction treatments, even after the second burn. Other studies in hardwood forests also have found that densities of many species are not detectably changed following low-intensity prescribed burns (Aquilani et al., 2000; Artman et al., 2001) or other silvicultural treatments with a moderate to high level of canopy retention (Moorman and Guynn, 2001; Newell and Rodewald, 2012).

Among nesting guilds, only cavity nesters were more abundant in MB2 than the other treatments or controls, likely due to an abundance of snags. In contrast, abundance of total ground-nesting birds declined in both burn treatments for one breeding season following a second prescribed burn. However, we did not detect a response by individual ground-nesting species with the possible exception of ovenbirds. After the initial (2003) burns in the same study sites, we observed short-term declines in abundance of

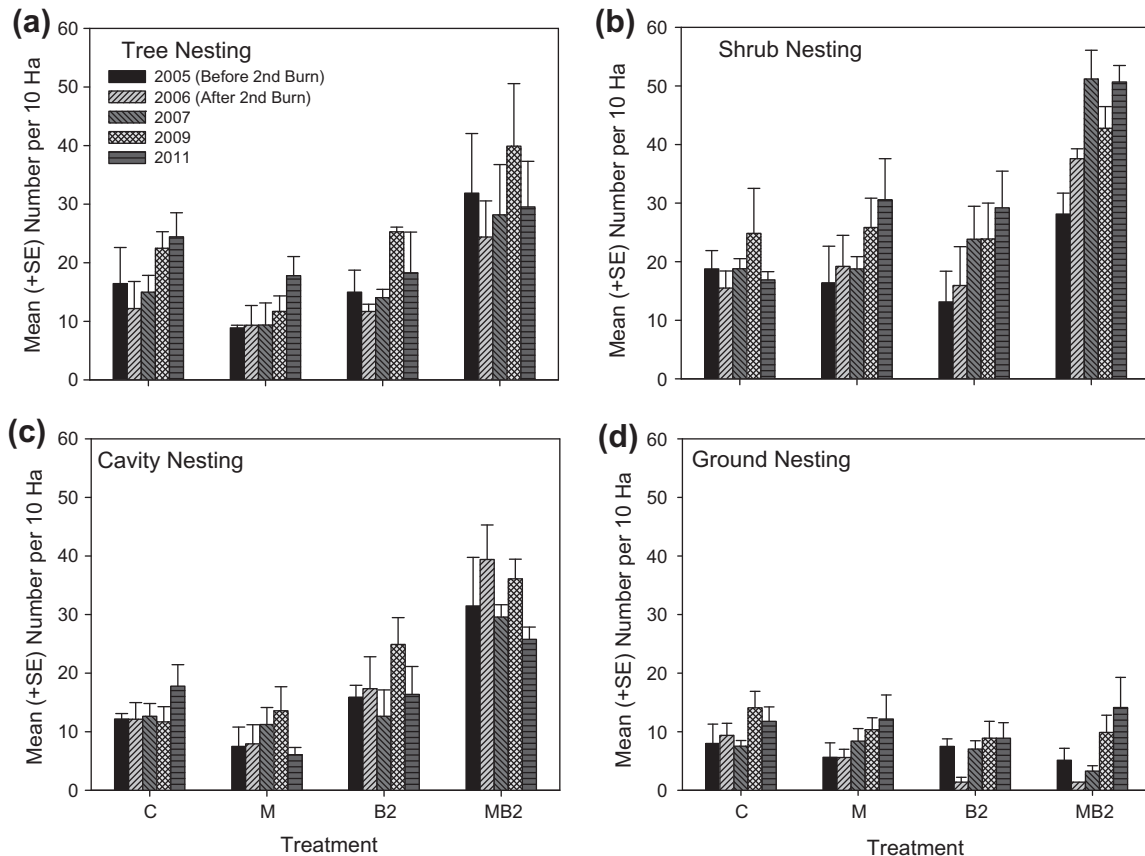


Fig. 2. Mean (+SE) total density of breeding birds in tree, cavity, shrub, and ground nesting guilds in 3 fuel reduction treatments: prescribe burned twice (B2), mechanical understory reduction (M), mechanical + burned twice (MB2), and controls (C) ($n = 3$ each), Green River Game Land, Polk County, NC. Data for 2005 are 2 years after the first prescribed burn but prior to the second burn. Data for 2006, 2007, 2009, and 2011 are after the second burn (conducted March, 2006) in the two burn treatments.

two ground-nesting species, black-and-white warblers (*Mniotilta varia*) and worm-eating warblers (*Helmitheros vermivorus*), in both burn treatments, and hooded warblers (*Setophaga citrina*) in all three fuel reduction treatments (Greenberg et al., 2007).

Other studies also showed declines in some ground- or shrub-nesting species after burning. In an Indiana upland hardwood forest, ground-nesting ovenbirds and black-and-white warblers declined, but others, including Kentucky warblers (*Geothlypis formosa*), worm-eating warblers, and shrub-nesting hooded warblers did not (Aquilani et al., 2000). In Ohio, single or repeated low-intensity prescribed burns in upland hardwood forests resulted in fewer ground and shrub-nesting birds including ovenbirds, worm-eating warblers, hooded warblers, and northern cardinals (*Cardinalis cardinalis*) (Artman et al., 2001). Differences in individual ground- or shrub-nesting species response among studies are likely due to low or no treatment replication, too few detections, and differences in patchiness of burns and shrub recovery over time. Decreased abundance of ground- or shrub-nesting birds after burns is likely due to temporary reductions in shrubs and leaf litter. Many birds forage within burned sites despite a paucity of suitable nesting substrate (Artman et al., 2001; Woinarski, 1990), making it difficult to assess how burning affects different components of habitat suitability.

In our study, relative abundance of eastern wood-pewees was greatest in the MB2 treatment, but was also high in the B2 treatment, suggesting an association of this species with burned upland hardwood forests. Abundance of eastern wood-pewees was greater in our MB2 treatment after initial burns in 2003, as well (Greenberg et al., 2007). Artman et al. (2001) also reported that eastern wood-pewees increased after several burns in an Ohio forest. Open

understory conditions created by low- or high-intensity prescribed burning may create optimal foraging conditions for this flycatcher species by improving visibility and (or) abundance of flying insects (Campbell et al., 2007).

Studies in pine forests of the western US suggest that fire severity and associated changes in forest structure, is an important driver of changes in the composition of breeding bird communities (Hejl, 1994; Smucker et al., 2005). Prescribed fire in upland hardwood forests of the eastern US are usually conducted in winter and under restrictive fuel and weather conditions that generally result in low-intensity, low-severity burns. The few studies that have examined breeding bird response to these low-severity prescribed burns in upland hardwood forests, where the overstory is unaffected, have found that changes to breeding bird communities are minor and transitory. We also found that that one (Greenberg et al., 2007) or two relatively low-intensity, low-severity prescribed fires results in few detectable changes in abundance of most breeding bird species in the short-term. However, gradual changes in canopy structure through delayed tree mortality may lead to greater species richness of breeding birds over time, as some open-forest species are attracted to more open conditions. In contrast, high-severity prescribed burns causing heavy tree mortality result in rapid increases in bird density and species richness by creating open, young forest conditions that attract species associated with open, young forest conditions while retaining many that occur in mature, closed canopy forest. Subsequent, relatively frequent (in this case, up to 5 years) low-intensity burning in an existing high-severity burn can maintain open, young forest conditions by retarding forest regrowth and reducing shrub cover, but alone may do little to change forest structure or breeding bird com-

munity composition. Our study did not address indicators of population increases such as nest success, and thus provides only preliminary evidence that high-intensity prescribed burning can be used to create a forest structure suitable for both disturbance-adapted bird species and many mature forest species during breeding season.

5. Conclusions

Our results indicate that hot fires resulting in heavy overstory tree mortality, and repeated burning can create and maintain open, young forest conditions with a heterogeneous canopy structure and increase abundance and species richness of breeding birds, including many successional-scrub species that are listed as high-priority for conservation. Mechanical understory felling a year prior to burning can provide dry fuel for higher-intensity fires that rapidly create open-forest conditions. Prescribed burning in upland hardwood forests is commonly low-intensity, conducted under highly restrictive weather and fuel parameters to minimize safety risks and potential damage to timber. Accordingly, changes to forest structure are often limited to reductions in shrub and leaf litter cover that are short-lived; overstory mortality or longer-lasting effects on forest structure are few and changes to breeding bird communities are also minimal. Similarly, effects of one-time mechanical understory reduction on breeding birds are few and short-lived, as shrubs recover rapidly. However, our study suggests that repeated, relatively low-intensity burns with patches of hotter fire may result in gradual, subtle changes to canopy cover and structure that may lead to increased bird species richness over time. Fire management for conservation of high-priority breeding bird species associated with open-canopy, young forest conditions requires substantial canopy tree mortality, and must be balanced with timber management goals.

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