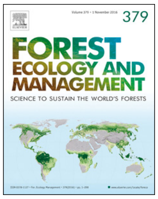
Forest Ecology and Management 424 (2018) 367–377

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Long-term avian response to fire severity, repeated burning, and mechanical fuel reduction in upland hardwood forest

Cathryn H. Greenberg[a,*], Joseph Tomcho[b], Aimee Livings-Tomcho[c], J. Drew Lanham[d], Thomas A. Waldrop[e,1], Dean Simon[f,1], Donald Hagan[d]

[a] *USDA Forest Service, Southern Research Station, Bent Creek Experimental Forest, 1577 Brevard Rd., Asheville, NC 28806, USA*
[b] *North Carolina Wildlife Resources Commission, 78 Wildlife Lane, Burnsville, NC 28714, USA*
[c] *Audubon North Carolina, P.O. Box 1544, Burnsville, NC 28714, USA*
[d] *Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634, USA*
[e] *USDA Forest Service, Southern Research Station, Clemson, SC 29634, USA*
[f] *North Carolina Wildlife Resources Commission, 8676 Will Hudson Road, Lawndale, NC 28090, USA*

ARTICLE INFO

Keywords:
Breeding birds
Fire severity
Fire surrogate
Fuel reduction
Oak woodland restoration
Prescribed fire
Repeated burns
Upland hardwood forest

ABSTRACT

Forest restoration, fuel reduction, and wildlife conservation management requires understanding if, and how repeated prescribed fire, fire severity, or mechanical methods can promote goals. We examined breeding bird response to repeated fuel reduction treatments by mechanical understory reduction (twice; Mechanical-only), prescribed burning (four times; Burn-only), or mechanical understory reduction plus burning (then three subsequent burns; Mechanical + Burn). Initial burns were hotter in Mechanical + Burn than Burn-only resulting in heavy tree mortality, canopy openness, thick shrub density, and abundant snags lasting several years. Relative density and species richness of birds increased in Mechanical + Burn within three breeding seasons of high-severity burns, and remained greater throughout subsequent burns. Increases were due to an influx of species associated with young forest conditions, with little change in most mature forest species. Repeated burning in Mechanical + Burn likely impeded forest maturation, allowing many scrub-shrub bird species to persist. Species richness in Burn-only did not differ from any treatment, but modest increases over time were apparent as structural heterogeneity increased with delayed tree mortality. Cavity-nester density was highest in Mechanical + Burn, but remained high even as snags fell to pretreatment levels. Ground-nester density was lower in Mechanical + Burn than Control and Mechanical-only, but ground-nesting species responded differently. Open woodlands were not created by any treatment due to persistent re-sprouting of top-killed trees and shrubs. We note that breeding birds appear to respond similarly to high-severity burns and silvicultural treatments with heavy canopy reduction, offering possible alternatives in managing upland hardwood forests for diverse breeding bird communities.

1. Introduction

Historically, availability of fire-maintained habitats in the Central Hardwood Region, such as savannas and oak woodlands, likely played an important role in the distribution and density of breeding bird species that require different variants of early successional or young forest conditions (Greenberg et al., 2015). Many open, fire-maintained habitats have virtually disappeared as trees encroached and grew to canopy closure after the elimination of frequent burning by Native Americans and (later) Euro-American settlers, and suppression of primarily human-caused wildfires for several decades (Greenberg et al., 2015). Populations of many disturbance-dependent bird species have declined or become locally extirpated as these open conditions have declined or disappeared (Askins, 2001).

Prescribed fire, often in conjunction with other silvicultural methods, is commonly recommended to reduce fuels, promote oak regeneration, improve wildlife habitat, and restore upland hardwood forests to an open oak woodland condition (Waldrop et al., 2016). Yet, many questions remain regarding if, and how forests can be managed to attain these goals. Further, objectives are often vaguely defined, and lack metrics to gauge their achievement. For example, 'wildlife habitat improvement' implies that all 'wildlife' will benefit from a specific

---

[*] Corresponding author.
E-mail address: kgreenberg@fs.fed.us (C.H. Greenberg).
[1] Retired.

https://doi.org/10.1016/j.foreco.2018.05.014
Received 19 January 2018; Received in revised form 20 March 2018; Accepted 6 May 2018

silvicultural disturbance (Harper et al., 2016). Yet, changes to habitat characteristics caused by fire or other disturbances might benefit some species while adversely affecting others. Critical knowledge gaps identified by forest managers include development of methods to create, maintain, or restore open woodland conditions (Waldrop et al., 2016).

By definition, disturbance-dependent birds are associated with habitats created by disturbances, but many species require specific variants, across a gradient of open structural conditions (Askins, 2001; Hunter et al., 2001; Greenberg et al., 2011, 2015). For example, field sparrows (*Spizella pusilla*) and northern bobwhite (*Colinus virginianus*) require open, grass-dominated habitats with scattered shrubs or young trees, whereas eastern meadowlarks (*Sturnella magna*) require open grasslands. Eastern towhees (*Pipilo erythrophthalmus*) and, at higher elevations chestnut-sided warblers (*Setophaga pensylvanica*), are most abundant in open, brushy, shrub- or stump sprout-dominated areas. Indigo buntings (*Passerina cyanea*) use a wide range of open conditions, as do eastern bluebirds (*Sialia sialis*) if nesting cavities are available. Thus open, shrub- and sprout-dominated young forest conditions created by high-severity disturbances are suitable for many scrub-shrub species (Askins, 2001; Rush et al., 2012), but not for those requiring open conditions with a grass-forb dominated understory. Although no disturbance-dependent species are known open oak woodland obligates (Vander Yacht et al., 2016), many could benefit from increased availability of the open woodland condition (Grundel and Pavlovic, 2007a, 2007b). Forest restoration, fuel reduction, and wildlife conservation efforts require an understanding of how repeated prescribed fire, fire severity, or mechanical methods can be applied to attain goals, and how diverse wildlife species with differing habitat requirements will respond (Driscoll et al., 2010).

We used a Before-After/Control-Impact (BACI; Smith, 2002) approach to experimentally assess how breeding birds responded to repeated fuel reduction treatments by mechanical understory reduction (Mechanical-only), dormant season prescribed burning (Burn-only), or mechanical understory reduction followed a year later by prescribed burning (Mechanical + Burn), in upland hardwood forest. Initial prescribed burns in the Mechanical + Burn treatment resulted in heavy tree mortality and abundant snags due to hotter fires fueled by cut shrubs and small trees remaining on the forest floor for a year prior (high-severity burn). In contrast, prescribed burns in the Burn-only treatment were relatively lower-intensity, and initial tree mortality was low (low-severity burn).

We reported early results after initial treatment implementation (Greenberg et al., 2007), and again after a second prescribed burn in both burn treatments (Greenberg et al., 2013). Our earlier results showed that species richness and relative density (termed density, hereafter) of total breeding birds and several species increased in the high-severity burn within three breeding seasons. Many species showed no response; a few decreased temporarily following some treatments, compared to controls (Greenberg et al., 2007). Few changes were evident after a second burn in either burn treatment, that were not already apparent within a few years of initial treatments (Greenberg et al., 2013). Since then, a third and fourth prescribed burn was conducted in both burn treatments, and a second mechanical understory reduction in the Mechanical-only treatment. Our long-term study with repeated treatment applications provided us an opportunity to examine long-term (16-year) changes in the breeding bird community in response to initial fire severity and repeated fuel reduction treatments, and also evaluate responses in the context of progress toward restoration of an open woodland community.

Based on our earlier results, we predicted (1) repeated burns in the Mechanical + Burn treatment would maintain open, shrubby young forest conditions created by the initial high-severity burns, resulting in sustained higher densities and species of breeding birds; (2) repeated burns in the Burn-only treatment would create canopy gaps as some delayed tree mortality occurred, with an associated increase in breeding bird species richness; (3) density and species richness of birds would be unaffected by repeated understory reductions in the Mechanical-only treatment where the canopy remained intact and shrub recovery was rapid; (4) density of the tree-nester guild would be unaffected by fuel reduction treatments; shrub-nester density would remain higher in Mechanical + Burn, but cavity-nester density would decrease as snag abundance declined, and; ground-nester density would temporarily decrease after each burn in both burn treatments, due to temporary decreases in leaf litter depth.

2. Methods

2.1. 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 was 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 were 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). 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 85–125 years. Predominant shrubs were mountain laurel (*Kalmia latifolia*) along ridge tops and on upper southwest-facing slopes, and rhododendron (*Rhododendron maximum*) in mesic areas. Elevation ranged from approximately 366–793 m. 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).

2.2. 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, cover type, and management history, to ensure consistency in baseline conditions among the treatments. Minimum size of experimental units (four per block) was 14-ha to accommodate 10-ha ‘core’ areas, with 20 m buffers around each. Dirt roads or fire lines 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 (Control) were randomly assigned within each of the three study blocks, for a total of 12 experimental units. Treatments were: (1) repeated mechanical felling of all shrubs and small trees ≥1.4 m tall and < 10.0 cm diameter at breast height (dbh) with a chainsaw (twice, winter of 2001–2002 and winter of 2011–2012) with cut fuels left scattered on-site (Mechanical-only); (2) repeated dormant season prescribed burns (four times, in February or March 2003, 2006, 2012, 2015) (Burn-only), and; (3) initial mechanical understory reduction (winter of 2001–2002), followed by four dormant season prescribed burns (as for Burn-only, above) (Mechanical + Burn) (Table 1).

During the initial prescribed burns (March 2003), fine woody fuel loading on Mechanical + Burn, where the shrub layer was felled, was approximately double that on Control and Burn-only units. Average fire temperature measured 30 cm aboveground was much hotter in Mechanical + Burn (517 °C) than Burn-only (321 °C); temperatures varied within Burn-only and Mechanical + Burn units, but a higher proportion of Mechanical + Burn units burned at high (601–900 °C)

Table 1
Dates of all fuel reduction treatments applied to experimental units and control (Control) ($n = 3$ per treatment), Green River Game Land, Polk County, NC, 2001–2016. Treatments were: two mechanical understory reduction treatments (Mechanical-only; M); four low-intensity burns (Burn-only; B); mechanical understory reduction followed by a high-severity burn and three subsequent lower-intensity burns (Mechanical + Burn; MB), and; untreated Control (C) ($n = 3$ each).

Treatment	Dormant Season 2001–2002	Dormant Season 2002–2003	Dormant Season 2005–2006	Dormant Season 2011–2012	Dormant Season 2014–2015
Control					
Mechanical-only	M[a]			M[a]	
Burn-only		B[b]	B[b]	B[b]	B[b]
Mechanical + Burn	M[a]	B[b]	B[b]	B[b]	B[b]

[a] Mechanical understory reduction only.
[b] Prescribed burn only.

temperatures than Burn-only (39% and 11%, respectively) (Waldrop et al., 2010). The second burn (March 2006) was less intense, with flame lengths generally < 1.5 m. Average temperature was 158 °C in Burn-only and 223 °C in Mechanical + Burn, and temperatures were more uniform (≤ 300 °C across $\geq 67\%$ of each Burn-only and Mechanical + Burn unit) (Waldrop et al., 2010). Fire temperatures were not measured in the third and fourth burns, but flame lengths were generally low-intensity, with flame lengths observed to be 0.5–2 m (Waldrop et al., 2016).

2.3. Habitat sampling

We measured live tree and snag (≥ 10 cm dbh) density, live tree basal area, shrub (woody stems ≥ 1.4 m ht and < 10 cm dbh) stem density, and leaf litter depth during most years when breeding birds were sampled (Waldrop et al., 2016), including before and after all repeated treatments. Tree and snag density were measured within 10, 0.05-ha (10×50 m) plots located at 50×50 m intervals starting from a randomly selected grid-point origin within each experimental unit (Waldrop et al., 2016). Shrub stem density (including all stems within sprout clumps) was measured within 20, 1 m^2 quadrats within each vegetation plot. 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 that were spaced at 50-m intervals throughout each experimental unit. Litter depth was measured only in Burn-only and Mechanical + Burn in 2011 and 2012 (before and after the third burn) and was not measured at all in 2016. For each habitat feature measured we used the average (plots, quadrats, or transects) across each experimental unit ($n = 3$ per treatment) in our statistical analyses.

2.4. 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 in all treatment units was surveyed for 10 min during three separate visits between 15 May and 30 June during each year sampled. Bird surveys were conducted pretreatment (2001); after all initial treatments were implemented (2003, 2004, 2005); after a second (March 2006) burn in Burn-only and Mechanical + Burn (2006, 2007, 2009, 2011); after a second mechanical understory reduction in Mechanical-only, and a third burn in Burn-only and Mechanical + Burn (2012, 2014), and; after a fourth burn in Burn-only and Mechanical + Burn (2015, 2016).

Point counts were conducted within four hours of sunrise. All birds 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 progressed. Most point counts were conducted by a single observer (J. Tomcho; total three observers during the entire study period). 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, one primary observer, multiple survey points, repeated surveys within each unit, and timing of surveys across time of day and breeding season. Density of birds within experimental units 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.

2.5. Data analysis

We used repeated measures ANOVAs (PROC MIXED; SAS 9.3) in a randomized block design to examine changes in habitat features and breeding bird communities in response to the fuel reduction treatments and control over all sampled years (pretreatment and subsequent, repeated fuel reduction treatments). Breeding bird response variables analyzed were species richness and total density, density within tree-, cavity-, shrub-, or ground-nesting guilds (Hamel, 1992), and density of sufficiently common (≥ 200 total observations) species. We elected not to use occupancy modeling due to potentially large biases in occupancy estimates and their sensitivity to home range sizes, especially for breeding birds (Hayes and Monfils, 2015). Additionally, occupancy models estimate the proportion of sites occupied by commonly detected species (MacKenzie et al., 2003), but not for less common species, and cannot address possible changes in bird densities. We chose to use a more traditional approach to data analyses because we were interested in how bird communities, including presence and abundance of all species, responded to treatments.

Habitat response variables were live tree and snag density, tree basal area, shrub stem density, and leaf litter depth. We assumed that litter depth in Mechanical-only and Control was relatively constant, and therefore used 2006 litter depth measurements for the missing 2011 and 2012 values in those treatments, for a balanced design in ANOVAs. Density data ($+0.01$) were natural-log transformed to reduce heteroscedasticity, and percent cover data (for shrubs) were square-root arcsine transformed for ANOVAs.

Our primary interest was in treatment effects or treatment × year interaction effects as indicators that at least one treatment was responding differently from the others overall, or after repeated fuel reduction treatments. A non-significant treatment × year interaction indicated that that there was a consistent difference among treatments, including Controls, across years. Treatment, year, or treatment x year interaction differences were considered significant with an overall experimental α of < 0.05. Where significant treatment x year interactions were present, we identified treatments or years warranting further examination ($p < 0.05$ in tests of effect slices), and used the least square means for partitioned F-tests (SLICE option) in PROC MIXED (SAS 9.4) to examine the significance of treatment differences within identified years, and among-year differences within identified treatments. Because of the large number of years sampled and an associated higher probability of a Type I error, we used the Bonferroni correction (Bland

Table 2

Results of mixed-model ANOVA comparing treatment[1], year, and treatment x year interaction effects on select forest structural features, Green River Game Land, Polk County, NC. Treatments were: two mechanical understory reduction treatments (Mechanical-only; M); four low-intensity burns (Burn-only; B); mechanical understory reduction followed by a high-severity burn and three subsequent lower-intensity burns (Mechanical + Burn; MB), and; untreated Control (C) (n = 3 each).

Habitat variable	RM MIXED-MODEL ANOVA_RESULTS			
	P_{trt}	P_{yr}	P_{trtXyr}	Treatment diffs[1]
Live tree D	0.0022	< 0.0001	< 0.0001	C^{a} M^{a} B^{a} MB^{b}
Live Tree Basal Area	0.0327	0.0099	0.0001	C^{a} M^{a} B^{ab} MB^{b}
Snag D	0.0233	< 0.0001	0.0252	C^{a} M^{a} B^{ab} MB^{b}
Shrub stem D	0.0152	< 0.0001	< 0.0001	C^{ab} M^{a} B^{ab} MB^{b}
Leaf litter depth	< 0.0001	< 0.0001	< 0.0001	C^{a} M^{a} B^{b} MB^{c}

[1] Different letters among treatments within a row indicates significant differences among treatments.

and Altman, 1995) to adjust test statistics (slices). For treatment effects within years we used a Bonferroni-adjusted α = 0.008 (six between-treatment comparisons within years). For year effects within treatments we focused our comparisons on combinations of years immediately prior to and after each of the four repeated treatments (28 comparisons), but report all between-year effects within treatments using a Bonferroni-adjusted α = 0.002.

3. Results

3.1. Habitat

Live tree density was lower in Mechanical + Burn than in other treatments, and a significant treatment x year interaction was detected (Table 2; Fig. 1a). Within Mechanical + Burn, decreased live tree density was evident within three growing seasons of the initial high-severity burns (2005); by 2006 (after the second burn) density was significantly (29.3%) lower than pretreatment, and by 2012 (after the third burn) density was 71.3% lower than pretreatment (Table 2; Fig. 1a). Within Burn-only, live tree density was significantly reduced within three growing seasons of initial low-intensity burns (2005) (8.1% lower than pretreatment), and further significant reductions (35.7%) were evident within six growing seasons after the second burn (2011). Live tree BA differed among years and was lower in Mechanical + Burn than Control or Mechanical-only; a treatment × year effect was detected (Table 2; Fig. 1b). Within Mechanical + Burn, BA was significantly reduced (30.8% lower than pretreatment) by 2006, and further reductions were evident by 2011.

Snag density was greater in Mechanical + Burn than Control or Mechanical-only and differed among years; an interaction effect was detected (Table 2; Fig. 1c). Snag density more than doubled in Mechanical + Burn beginning the first growing season after the high-severity burn (2003), peaked within 3–4 growing seasons (222.8% more snags in 2005 than pretreatment), and subsequently decreased as snags fell; by 2014 there were no significant differences in snag densities among treatments. Within Burn-only, snag availability differed only marginally from other treatments; snag density increased 55.9% from pretreatment levels by 2006, and subsequently decreased. Within Control, snag availability decreased gradually from an average of 74/ha in 2001, to 40/ha in 2016.

Shrub stem density differed among years and was greater in Mechanical + Burn than Mechanical-only; a treatment x year interaction was detected (Table 2; Fig. 1d). Shrub stem density was dynamic within all treatments, and treatments differed within all years except 2001 (pretreatment) and 2006 (one growing season after the second burn). Within Mechanical-only, shrub stem density was significantly reduced from pretreatment levels by each mechanical understory reduction (2003 and 2012), and recovered to pretreatment levels within two or three growing seasons. Within Burn-only, shrub stem density decreased following each burn, also recovering rapidly to approximately pretreatment levels. Within Mechanical + Burn, shrub stem density was reduced by each burn, but only two of the four burns (2003 and 2012) reduced stem densities to below pretreatment levels. Recovery was rapid, with shrub stem densities far exceeding pretreatment levels within a few growing seasons of each burn (2005, 2011, 2014, 2015, 2016). For example, shrub stem densities were 537.4% greater than pretreatment just three growing seasons after the third burn (2014); immediately after the fourth burn (2015), stem densities still exceeded pretreatment levels by 279.1%.

Leaf litter depth was lower Mechanical + Burn than other treatments, and lower in Burn-only than Control or Mechanical-only; a treatment × year interaction effect was detected (Table 2; Fig. 1e). Litter depth decreased significantly following each burn in Burn-only and Mechanical + Burn, and recovered to pretreatment levels within one or two years as leaves dropped from trees each fall.

3.2. Breeding birds

We detected 7236 individuals of 56 breeding bird species during the 11 years sampled between 2001 and 2016 (Table 3). Total bird density was 47.0–149.5% greater in Mechanical + Burn than Mechanical-only, Burn-only, or Control beginning three breeding seasons after the initial high-severity burn (2005) and differed among years; no treatment × year interaction was detected (Table 3; Fig. 2a).

Species richness differed among years and was greater in Mechanical + Burn than Mechanical-only or Control; a treatment x year interaction was detected (Table 3; Fig. 2b). Species richness changed over time within Mechanical-only, Burn-only, and Mechanical + Burn, and differed among at least some treatments every year beginning three breeding seasons after initial treatments (2005). Within Mechanical-only, richness was greater after the second mechanical treatment (2012) than 2004 or 2005, but never differed from pretreatment (2001). Within Burn-only, species richness was intermittently greater than pretreatment beginning four breeding seasons after the second burn (2009, 2014, 2016). Within Mechanical + Burn, species richness was consistently and substantially (by 44.7–70.2%) greater than pretreatment beginning three breeding seasons after the initial high-severity burn (2005). Species richness was also substantially (by 41.8–119.4%) greater in Mechanical + Burn than Mechanical-only or Control most years beginning in 2005, but greater than Burn-only only in two years (2006, 2012). Species richness was greater in Burn-only than Mechanical-only and Control only in one year (2014), and richness never differed between Mechanical-only and Control (Fig. 2b).

Tree-nester density differed among years but not treatments, although trends suggested greater density in Mechanical + Burn; no treatment × year interaction was detected (Table 3; Fig. 3a). Shrub-nester density differed among years and was greater in Mechanical + Burn than other treatments; a marginal treatment × year interaction effect was detected (p = 0.0572) (Table 3; Fig. 3b). Shrub-nester density was dynamic within Mechanical-only, Burn-only, and Mechanical + Burn, and differed among some treatments each year starting immediately after initial treatments (2003). Within Mechanical-only and Burn-only, shrub-nester density differed among some years, but differences did not correspond with repeated treatments, and never differed from pretreatment levels. Within Mechanical + Burn, shrub-nester density decreased immediately following the initial, high-severity burn (2003), but increased the following year (2004) and remained greater than 2003 levels for the duration of the study and throughout three subsequent burns, with nearly twice the densities of other treatments during most years (Fig. 1b). Cavity-nester density was greater in Mechanical + Burn than other treatments, and density in Burn-only was greater than Mechanical-only; no year or treatment × year effects were detected (Table 3; Fig. 3c). Ground-nester

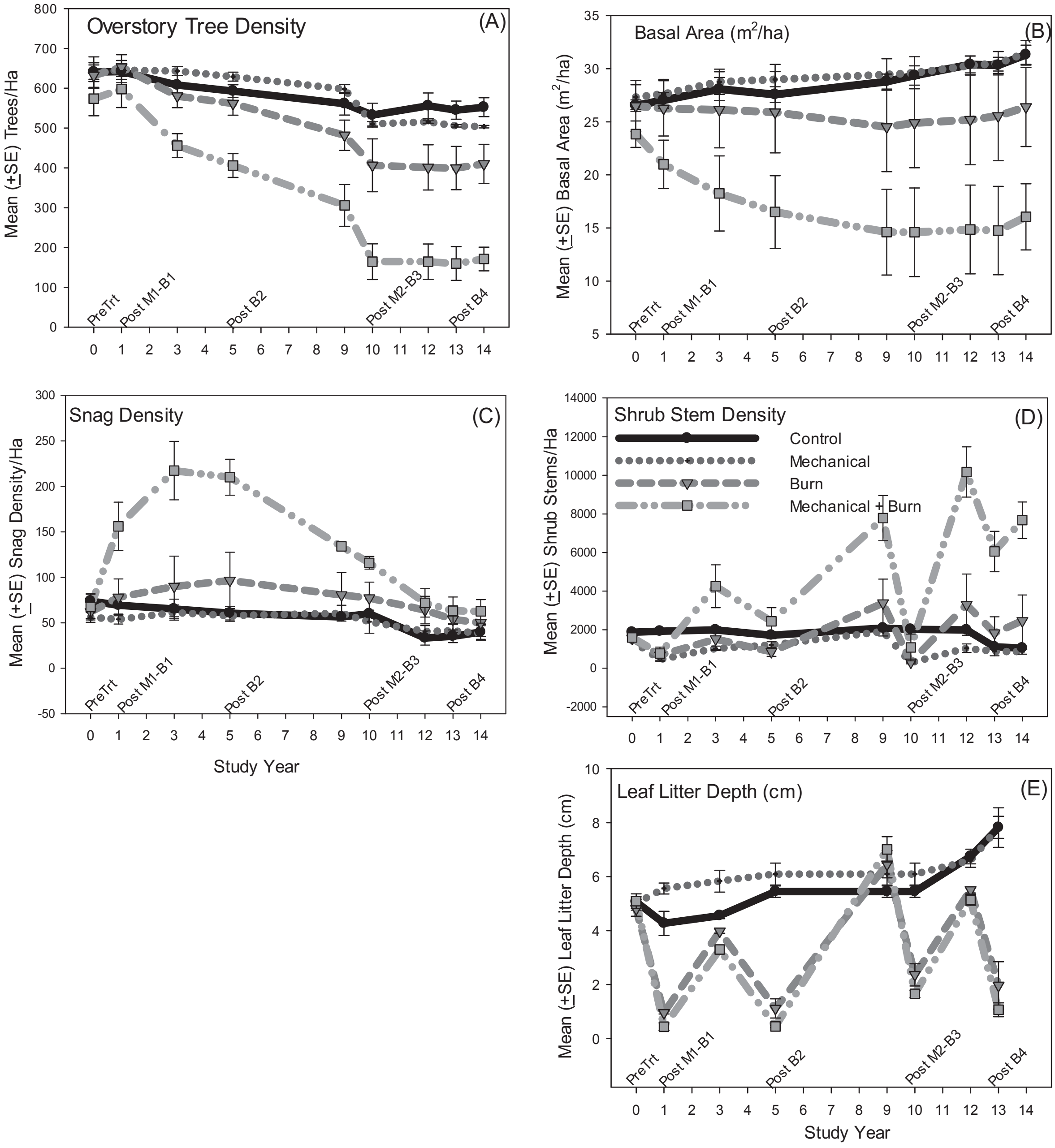


Fig. 1. Mean (± SE) (A) live tree density; (B) live tree BA; (C) snag density; (D) shrub stem density, and; (E) leaf litter depth before (2001) and after repeated application of three fuel reduction treatments, Green River Game Lands, Polk County, NC. Treatments were: two mechanical understory reduction treatments (Mechanical-only; M); four low-intensity burns (Burn-only; B); mechanical understory reduction followed by a high-severity burn and three subsequent lower-intensity burns (Mechanical + Burn; MB), and; untreated Control (C) (n = 3 each).

density differed among years, and was lower in Mechanical + Burn than Mechanical-only or Control; no treatment × year interaction effect was detected (Table 3; Fig. 3d) but trends suggested decreased density immediately after burns in both Burn-only and Mechanical + Burn, followed by increases within two breeding seasons (Fig. 3d).

Among the 16 species analyzed, densities of 11 changed in response to treatments (Table 3). Densities of many common species including red-eyed vireos (*Vireo olivaceus*), blue-headed vireos (*V. solitarius*), scarlet tanagers (*Piranga olivacea*), blue-gray gnatcatchers (*Polioptila caerulea*), and black-and-white warblers (*Mniotilta varia*) did not differ among treatments, and no treatment × year interaction effects were detected (Table 3; Fig. 4). Carolina wren density did not differ among treatments; a treatment × year effect was detected (Table 3), but differences within treatments or years did not appear to be biologically meaningful.

Densities of several species were greater in Mechanical + Burn and (or) Burn-only than other treatments. Eastern towhee density differed among years and was greater Mechanical + Burn than other treatments; a treatment x year interaction effect was detected (Table 3; Fig. 4). Eastern towhee density was consistently greater in Mechanical + Burn than Control beginning in three breeding seasons after initial treatments (2005) and greater than Mechanical-only most years (2005, 2007, 2014, 2015, 2016), but greater than Burn-only only in three years (2005, 2006, 2011); density did not differ among Mechanical-only, Burn-only, or Control within any sampled year. Within Mechanical-only, post-treatment eastern towhee densities never differed from pretreatment, and densities did not differ before and after either mechanical understory reduction treatment; densities increased

Table 3
Total number of individual bird detections (all years, units, and point counts) and results of mixed-model ANOVA comparing treatment[1], year, and treatment × year interaction effects on breeding bird species richness and total density (no/10 ha), and density by species[2] (if ≥ 200 observations) and nesting guilds, Green River Game Lands, Polk County, NC. Treatments were: two mechanical understory reduction treatments (Mechanical-only; M); four low-intensity burns (Burn-only; B); mechanical understory reduction followed by a high-severity burn and three subsequent lower-intensity burns (Mechanical + Burn; MB), and; untreated Control (C) (n = 3 each). All treatment units were sampled before (2001) and after repeated treatment applications during most years through 2016.

Guild/species total density species richness	RM MIXED-MODEL ANOVA_RESULTS							
	Obs	P_{trt}	P_{yr}	P_{trtXyr}	Treatment diffs[1]			
Tree-nester	2134	0.1165	0.0020	0.9709				
ACFL	33	–	–	–				
AMCR	31	–	–	–				
AMRE	7	–	–	–				
BGGN	318	0.4586	< 0.0001	0.1711				
BHCO	102	–	–	–				
BLJA	94	–	–	–				
BTNW	257	0.0406	< 0.0001	0.6157	C^{a}	M^{ab}	B^{ab}	MB^{b}
BWHA	14	–	–	–				
CEDW	94	–	–	–				
COGR	4	–	–	–				
COHA	2	–	–	–				
EAWP	212	0.0022	< 0.0001	0.1240	C^{a}	M^{ab}	B^{bc}	MB^{c}
NOPA	3	–	–	–				
PIWA	76	–	–	–				
REVI	512	0.4837	0.0435	0.0580				
SCTA	203	0.5797	0.3730	0.3866				
SSHA	2	–	–	–				
SUTA	6	–	–	–				
YBCU	5	–	–	–				
YTVI	17	–	–	–				
YTWA	59	–	–	–				
Shrub nester	2234	0.0012	< 0.0001	0.0572	C^{a}	M^{a}	B^{a}	MB^{b}
AMGO	142	–	–	–				
AMRO	10	–	–	–				
BHVI	506	0.2765	0.0234	0.5611				
BRTH	7	–	–	–				
CHSP	29	–	–	–				
EATO	378	0.0068	< 0.0001	0.0003	C^{a}	M^{a}	B^{a}	MB^{b}
HOWA	617	0.0330	< 0.0001	0.1749	C^{a}	M^{ab}	B^{b}	MB^{ab}
INBU	206	0.0022	< 0.0001	0.0029	C^{a}	M^{a}	B^{a}	MB^{b}
MODO	84	–	–	–				
NOCA	59	–	–	–				
PRAW	32	–	–	–				
RTHU	192	–	–	–				
SWWA	4	–	–	–				
WOTH	44	–	–	–				
YBCH	7	–	–	–				
Cavity nester	1795	0.0011	0.2751	0.8679	C^{ab}	M^{b}	B^{a}	MB^{c}
BADO	1	–	–	–				
CACH	265	0.0433	0.0629	0.0004	C^{ab}	M^{a}	B^{ab}	MB^{b}
CARW	222	0.0609	< 0.0001	0.0058				
CHSW	1	–	–	–				
DOWO	145	–	–	–				
EABL	88	–	–	–				
GCFL	8	–	–	–				
HAWO	29	–	–	–				
PIWO	55	–	–	–				
RBWO	58	–	–	–				
RHWO	12	–	–	–				
ETTI	452	0.0429	0.0563	0.9902	C^{ab}	M^{a}	B^{ab}	MB^{b}
WBNU	395	0.0134	0.0196	0.3187	C^{a}	M^{a}	B^{ab}	MB^{b}
YSFL	18	–	–	–				
Ground nester	923	0.0134	< 0.0001	0.1048	C^{a}	M^{a}	B^{ab}	MB^{b}
BAWW	216	0.1979	0.0003	0.4591				
KEWA	1	–	–	–				
OVEN	347	0.0322	0.0009	0.7408	C^{ab}	M^{a}	B^{ab}	MB^{b}
WEWA	345	0.0556	< 0.0001	0.2075	C^{a}	M^{ab}	B^{ab}	MB^{b}
WITU	14	–	–	–				
Other	31	–	–	–				
EAPH	31	–	–	–				
Total	7236	0.0063	< 0.0001	0.7488	C^{a}	M^{a}	B^{a}	MB^{b}
Richness	56	0.0085	< 0.0001	0.0150	C^{a}	M^{a}	B^{ab}	MB^{b}

[1] Different letters among treatments within a row indicates significant differences among treatments.

[2] ACFL = Acadian flycatcher (*Empidonax virescens*); AMCR = American crow (*Corvus brachyrhynchos*); AMGO = American goldfinch (*Carduelis tristis*); AMRE = American redstart (*Setophaga ruticilla*); AMRO = American robin (*Turdus migratorius*); BADO = barred owl (*Strix varia*); BAWW = black-and-white warbler (*Mniotilta varia*); BGGN = blue-gray gnatcatcher (*Polioptila caerulea*); BHCO = brown-headed cowbird (*Molothrus ater*); BHVI = blue-headed vireo (*Vireo solitarius*); BLJA = blue jay (*Cyanocitta cristata*); BRTH = brown thrasher (*Toxostoma rufum*); BTNW = black-throated green warbler (*Setophaga virens*); BWHA = broad-winged hawk (*Buteo platypterus*); CACH = Carolina chickadee (*Poecile carolinensis*); CARW = Carolina wren (*Thyrothorus ludovicianus*); CEDW = cedar waxwing (*Bombycilla cedrorum*); CHSP = chipping sparrow (*Spizella passerina*); CHSW = chimney swift (*Chaetura pelagica*); COGR = common grackle (*Quiscalus quiscula*); COHA = Cooper's hawk (*Accipter cooperii*); DOWO = downy woodpecker (*Picoides pubescens*); EABL = eastern bluebird (*Sialia sialis*); EAPH = eastern phoebe (*Sayomis phoebe*); EATO = eastern towhee (*Pipilo erythrophthalmus*); EAWP = eastern wood-pewee (*Contopus virens*); ETTI = eastern tufted titmouse (*Baeolophus bicolor*); FLIN = yellow-shafted flicker; GCFL = great-crested flycatcher (*Myiarchus crinitus*); HAWO = hairy woodpecker (*Picoides villosus*); HOWA = hooded warbler (*Setophaga citrina*); INBU = indigo bunging (*Passerina cyanea*); KEWA = Kentucky warbler (*Geothlypis formosa*); MODO = mourning dove (*Zenaida macroura*); NOCA = northern cardinal (*Cardinalis cardinalis*); NOPA = Northern parula (*Setophaga americana*); OVEN = ovenbird (*Seiurus aurocapillus*); PIWA = pine warbler (*Setophaga pinus*); PIWO = pileated woodpecker (*Drycopus pileatus*); PRAW = prairie warbler (*Setophaga discolor*); RBWO = red-bellied woodpecker (*Melanerpes carolinus*); REVI = red-eyed vireo (*Vireo olivaceus*); RHWO = red-headed woodpecker (*Melanerpes erythrocephalus*); RTHU = ruby-throated hummingbird (*Archilochus colubris*); SCTA = scarlet tanager (*Piranga olivacea*); SSHA = sharp-shinned hawk (*Accipiter striatus*); SUTA = summer tanager (*Piranga rubra*); SWWA = Swainson's warbler (*Limnothlypis swainsonii*); WBNU = white-breasted nuthatch (*Sitta carolinensis*); WEWA = worm-eating warbler (*Helmitheros vermivorus*); WITU = wild turkey (*Meleagris gallopavo*); WOTH = woodthrush (*Hylocichla mustelina*); YBCH = yellow-breasted chat (*Icteria virens*); YBCU = yellow-billed cuckoo (*Coccyzus americanus*); YSFL = yellow-shafted flicker (*Colaptes auratus*); YTVI = yellow-throated vireo (*Vireo flavifrons*); YTWA = yellow-throated warbler (*Setophaga dominica*).

beginning six breeding seasons after the first mechanical treatment compared to 2003. Within Burn-only, eastern towhee density was lower immediately after the first two burns (2003, 2006) than several subsequent years (2007, 2009, 2012, 2014, 2016), but did not differ from pretreatment in any year. Within Mechanical + Burn, eastern towhee density increased within three breeding seasons (2005) after initial high-severity burns and remained higher for the duration of the study. Indigo bunting density differed among years and was greater in Mechanical + Burn than Mechanical-only, Burn-only, or Control; a treatment × year interaction effect was detected (Table 3; Fig. 4). Indigo bunting density was consistently greater in Mechanical + Burn than other treatments in all years except 2003 (immediately after high-severity burns); density did not differ between Mechanical-only and Control in any year (Fig. 4). Within Burn-only, indigo bunting density was greater than pretreatment or immediately after initial burns only twice (2007, 2009). Within Mechanical + Burn, indigo bunting density increased beginning two breeding seasons (2004) after initial high-severity burns, and remained greater thereafter. Eastern wood-pewee

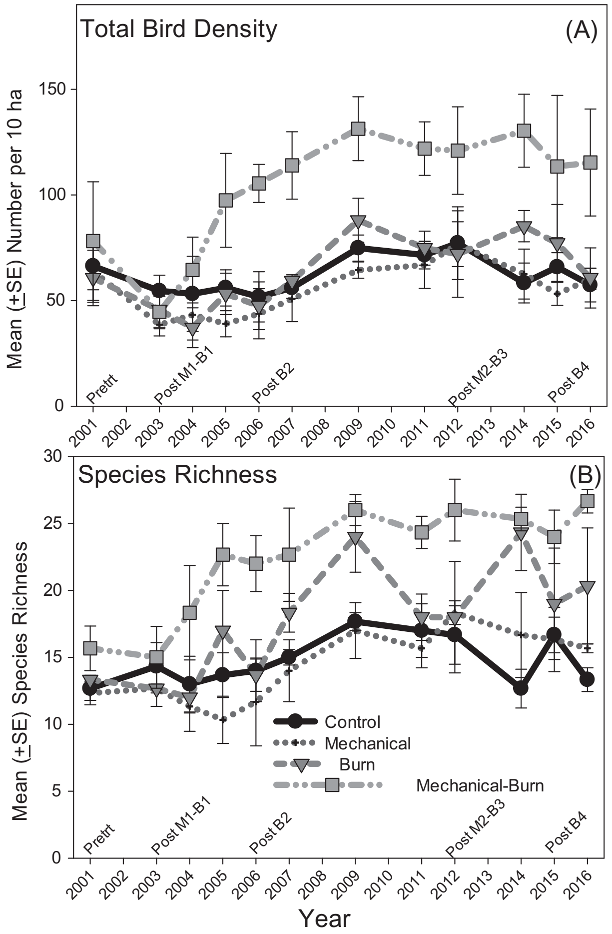


Fig. 2. Mean (± SE) total (A) density, and (B) species richness of breeding birds before (2001) and after repeated application of three fuel reduction treatments. Treatments were: two mechanical understory reduction treatments (Mechanical-only; M); four low-intensity burns (Burn-only; B); mechanical understory reduction followed by a high-severity burn and three subsequent lower-intensity burns (Mechanical + Burn; MB), and; untreated Control (C) (n = 3 each).

(*Contopus virens*) density was greater in Mechanical + Burn than Mechanical-only or Control, and greater in Burn-only than Control; no treatment × year interaction effect was detected (Table 3; Fig. 4). White-breasted nuthatch (*Sitta carolinensis*) and eastern tufted titmice (*Baelolophus bicolor*) densities were greater in Mechanical + Burn than Mechanical-only; no treatment × year interaction effects were detected (Table 3). Carolina chickadee density was greater in Mechanical + Burn than Mechanical-only; a treatment × year effect was detected (Table 3), but differences within treatments or years did not appear to be biologically meaningful.

Densities of four tested species were lower in Mechanical + Burn or Burn-only than Mechanical-only or Control, with no treatment × year interaction effects detected. Black-throated green warbler (*S. virens*) and (marginally) worm-eating warbler (*Helmitheros vermivorus*) ($p = 0.0556$) densities were lower in Mechanical + Burn than Control (Table 3; Fig. 4). Ovenbird (*Seiurus aurocapillus*) density was lower in Mechanical + Burn than Mechanical-only, and hooded warbler (*S. citrina*) density was lower in Burn-only than Control (Table 3; Fig. 4).

4. Discussion

4.1. Habitat

Initial high-severity burns in Mechanical + Burn caused heavy tree mortality within three growing seasons, creating an open canopy and abundant snags that fell to pretreatment levels within a decade. Despite some reduction in shrub stem density after each subsequent low-intensity burn in Mechanical + Burn, recovery was rapid and far exceeded pretreatment levels as top-killed trees and shrubs resprouted and *Rubus* spp. responded to the open conditions. In contrast, initial and subsequent burns in Burn-only were relatively low-intensity, resulting in delayed tree mortality at much lower levels than Mechanical + Burn; shrub stem density recovered rapidly after burns, but did not exceed pretreatment levels. Tree mortality in Burn-only was concentrated in smaller trees, but 'hotspots' also killed some larger trees, eventually creating gaps that attracted some open-forest bird species (Hunter et al., 2001). Our study was not designed to test whether ongoing post-burn tree mortality in Burn-only was initiated by the initial, low-intensity burn (Keyser et al., 2018) or (and) perpetuated by subsequent low-intensity burns. However, patterns of decreasing live-tree density suggest that each repeated burn initiated additional, delayed tree mortality. Leaf litter depth decreased in both Burn-only and Mechanical + Burn after each repeated burn, but recovered quickly as leaves dropped from deciduous trees the following autumn. Shrub recovery to pretreatment levels was rapid following each understory reduction in Mechanical-only.

Despite an open canopy structure and increased sunlight in Mechanical + Burn, herbaceous plant cover increased only modestly (peaking at 13%), and grass cover was negligible (peaking at 3% cover, with no differences among treatments) (Waldrop et al., 2016). Thick shrub cover, and (or) absence of a seedbank, likely prevented proliferation of grasses and forbs (Waldrop et al., 2016). Restoration to an open oak woodland condition was not achieved by multiple applications of any treatment (Waldrop et al., 2016).

4.2. Breeding birds

The initial high-severity burn in Mechanical + Burn caused profound changes in forest structure that enhanced suitability for many breeding bird species, and those associated with open, young forest conditions in particular. Breeding bird density increased in Mechanical + Burn by up to 68%, and species richness increased by up to 70.2% within three breeding seasons after initial high-severity burns, and remained consistently higher than other treatments without any apparent additive effects of three subsequent burns. In contrast, density of breeding birds was unaffected by initial or repeated low-intensity burns in Burn-only, where changes to forest structure were gradual and subtle. Species richness in Burn-only did not significantly differ from any treatment (including Mechanical + Burn), but a trend of modest increases over time was apparent, with 2.5–82% more species than pretreatment levels beginning in 2005. Other studies indicate that breeding bird response is negligible or transient after single (Aquilani et al., 2000; Greenberg et al., 2007; Klaus et al., 2010; Greenberg et al., 2014) or repeated (Artman et al., 2001) low-intensity dormant season burns. However, our longer-term results suggest that repeated, low-intensity burns may eventually lead to greater species richness as trees gradually die and structural heterogeneity increases. In our study, understory reduction beneath an intact canopy in Mechanical-only had no detectable effect on total bird density; species richness varied somewhat, but changes appeared unrelated to treatment applications and never differed from pretreatment or Control. Our results indicate that canopy openness, in combination with high shrub stem density, is an important driver of breeding bird density and species richness in upland hardwood forest.

Increased species richness in Mechanical + Burn was primarily due to an influx of species associated with young, open forest and edge conditions such as eastern bluebirds, indigo buntings, eastern towhees, brown thrashers (*Toxostoma rufum*), chipping sparrows (*Spizella passerina*), American goldfinches (*Carduelis tristis*), mourning doves (*Zenaida macroura*), red-headed woodpeckers (*Melanerpes*

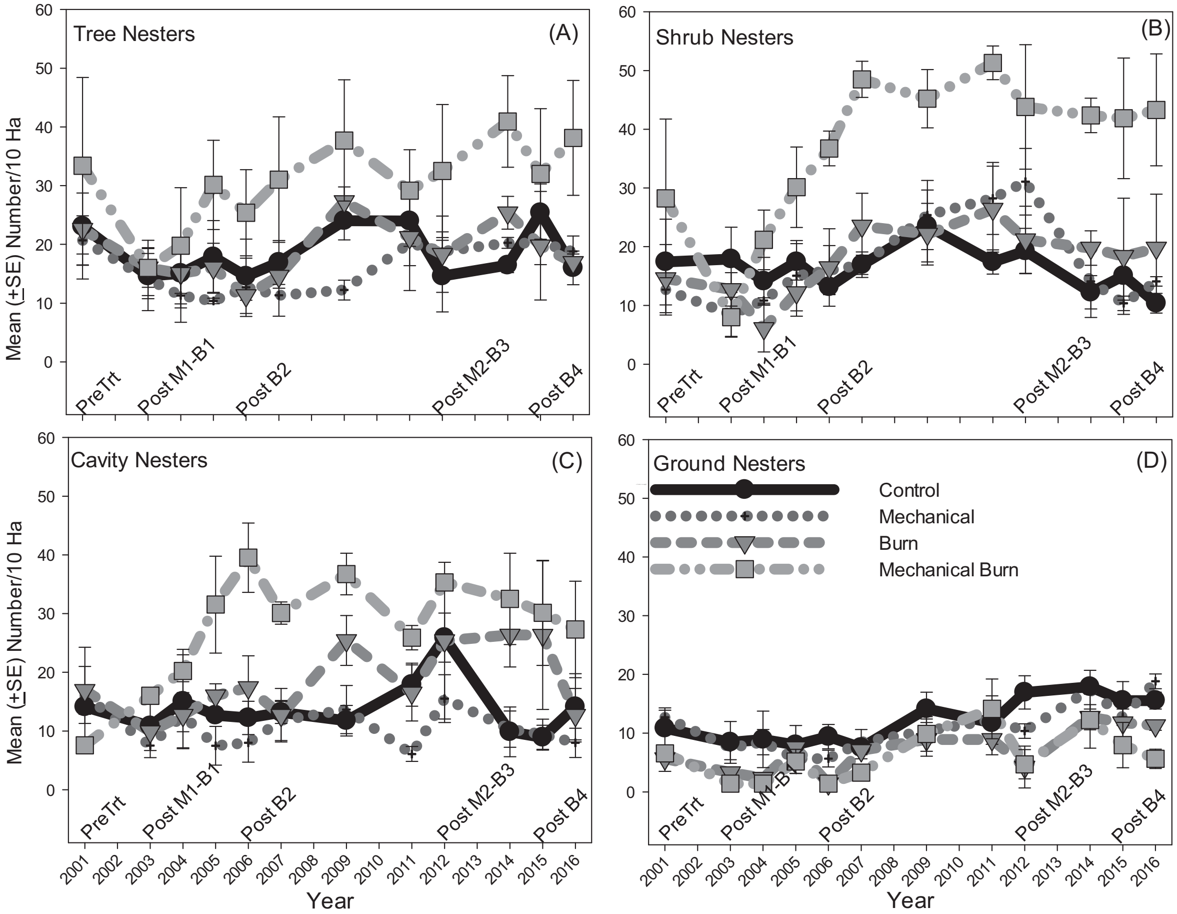


Fig. 3. Mean (± SE) total density of breeding birds in (A) tree-, (B) shrub-, (C) cavity-, and (D) ground-nesting guilds before (2001) and after repeated application of three fuel reduction treatments, Green River Game Lands, Polk County, NC. Treatments were: two mechanical understory reduction treatments (Mechanical-only; M); four low-intensity burns (Burn-only; B); mechanical understory reduction followed by a high-severity burn and three subsequent lower-intensity burns (Mechanical + Burn; MB), and; untreated Control (C) (n = 3 each).

erythrocephalus), pine warblers (*S. pinus*), and prairie warblers (*S. discolor*) starting within three breeding seasons of the initial, high-severity burn, with little change in the occurrence of most other species. Additionally, densities of several species associated with mature, closed canopy or interior forest conditions, such as scarlet tanagers, blue-gray gnatcatchers, blue-headed vireos, red-eyed vireos, and black-and-white warblers (Kendeigh, 1982) remained high in Mechanical + Burn throughout the 16-year study period. The presence of some overstory trees apparently provided adequate structure for canopy-associated birds, and (or) thick cover provided by heavy sprouting of top-killed trees and shrubs offered optimal foraging opportunity for post-fledgling bird species that are otherwise associated with mature forest (Whitehead, 2003; Marshall et al., 2003).

Other studies indicate that fire severity, time since burn, or both influence patterns of bird species occurrence in hardwood ecosystems (Klaus et al., 2010; Rose and Simons, 2016; Grundel and Pavlovic, 2007a, 2007b). Klaus et al. (2010) reported higher species richness in medium- and high-severity burns than low-severity burns or unburned southern Appalachian hardwood forest. Their study, which included higher elevations than ours, also showed a positive response to high-severity burns by many of the same young, open forest-associated species seen in our study, in addition to higher-elevation species such as chestnut-sided warblers and (once) golden-winged warblers (*Vermivora chrysoptera*). Based on their results showing increased bird diversity 3–6 years after a high-severity burn, Klaus et al. (2010) suggested that subsequent frequent, repeated burning could lead to decreased bird diversity by inhibiting 'habitat regeneration.' We also found a delayed increase in density and species richness of breeding birds after high-severity burning, but our results suggest that repeated burning at 3–6 year intervals after initial high-severity burns may help to maintain high bird species richness and density by impeding forest regrowth to canopy closure, and maintaining open forest conditions.

Some nesting guilds responded to treatments, but responses did not always correspond as expected to changes in forest structure. Further, some species within guilds responded differently to treatments. Tree-nester density did not differ among treatments, although an overall trend of higher density in Mechanical + Burn was apparent despite heavy tree mortality. Many tree-nesting species showed no response to treatments. Black-throated green warbler density was lower in Mechanical + Burn than Control. In contrast, densities of eastern wood-pewees increased in Mechanical + Burn after the high-severity burn and remained high throughout subsequent burns. Densities increased to a lesser extent (compared to Control) and over a longer period in Burn-only, suggesting that reduced canopy cover, or increased structural heterogeneity created by burning increased habitat suitability despite reductions in tree density. Additionally, increased visibility and (or) density of flying insects (Campbell et al., 2007, 2018) after burning could enhance foraging opportunity, or visibility for insect salliers such as eastern wood-pewees. Other studies also reported a positive response by eastern wood-pewees to prescribed burns (Artman et al., 2001) and high-severity burns in the southern Appalachians (Klaus et al., 2010; Rose and Simons, 2016).

Shrub-nester density increased in Mechanical + Burn within three breeding seasons after initial high-severity burns, and remained higher

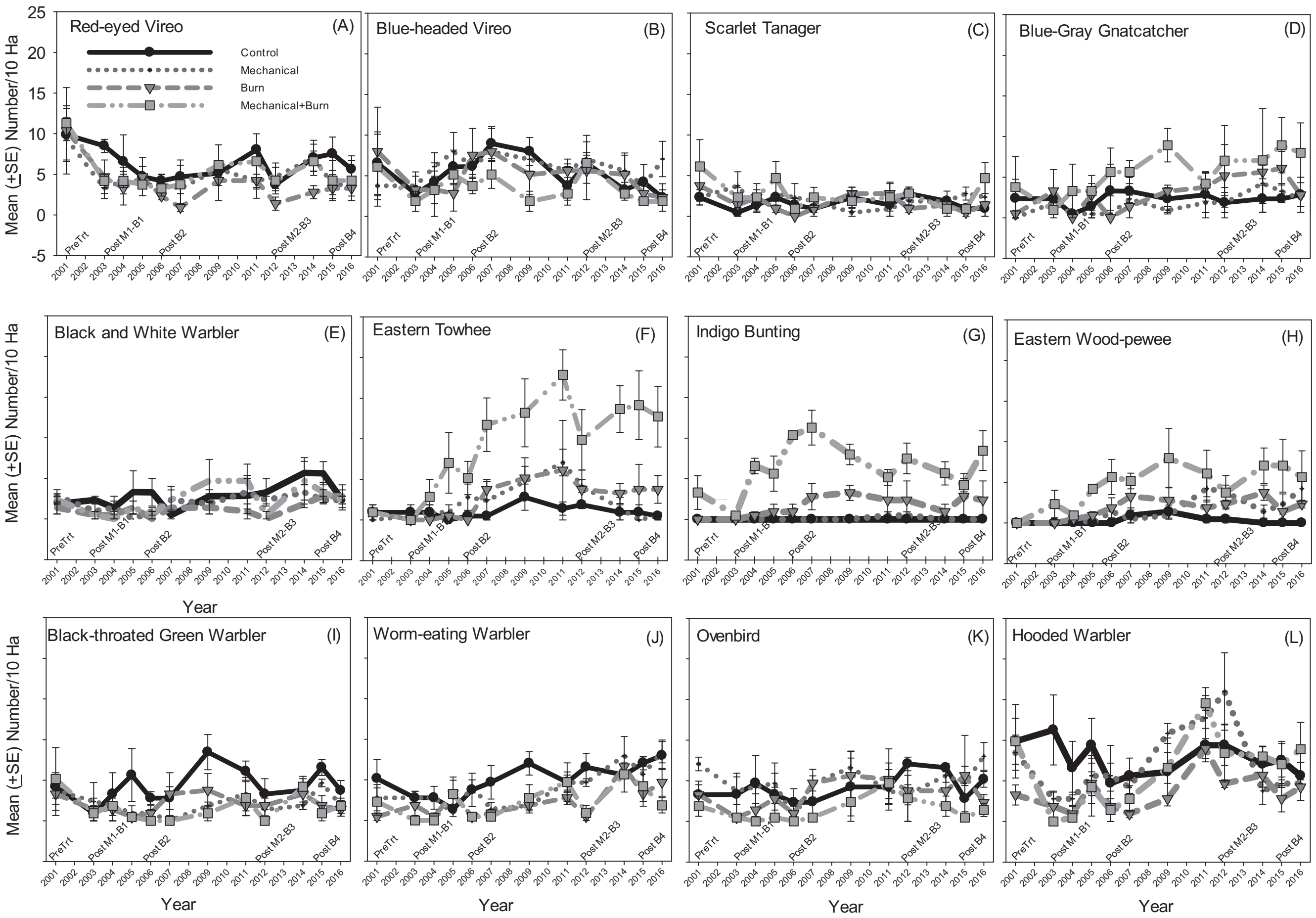


Fig. 4. Mean (± SE) total density of (A) red-eyed vireo; (B) blue-headed vireo; (C) scarlet tanager; (D) blue-gray gnatcatcher; (E) eastern towhees; (F) indigo buntings; (G) eastern wood-pewee; (H) black-throated green warbler; (I) worm-eating warbler; (J) ovenbird; (K) black-and-white warbler, and; (L) hooded warbler before (2001) and after repeated application of three fuel reduction treatments, Green River Game Lands, Polk County, NC Treatments were: two mechanical understory reduction treatments (Mechanical-only; M); four low-intensity burns (Burn-only; B); mechanical understory reduction followed by a high-severity burn and three subsequent lower-intensity burns (Mechanical + Burn; MB), and; untreated Control (C) (n = 3 each).

throughout the study duration despite substantial reduction in shrub stem density immediately following each repeated burn. Thick shrub cover occurring within a few years of high-severity burns, and rapid shrub recovery after subsequent burns likely contributed to high shrub-nester densities (Rush et al., 2012). We did not detect substantial changes in density of total shrub-nesters in Mechanical-only or Burn-only, where shrub stem densities never exceeded pretreatment levels. Surprisingly, density trends within those treatments did not closely correspond with reduced shrub density after repeated mechanical understory reductions or burns. In contrast, some studies report short-term declines in density of shrub-nesters after understory reduction treatments (Rodewald and Smith, 1998).

Among the common shrub-nesting species tested, eastern towhees and indigo bunting densities increased in Mechanical + Burn within three breeding seasons after initial high-severity burns and remained higher throughout three subsequent burns. Other studies reported greater occupancy or numbers of indigo buntings, eastern towhees, and several other disturbance-dependent species in burned hardwood forests with ≤14 m^2 basal area (Vander Yacht et al., 2016), or in high-severity burns having thick shrub cover (Klaus et al., 2010). In our study, hooded warbler densities were lower in Burn-only than Control, but densities in Mechanical + Burn did not differ from other treatments despite the presence of much higher shrub stem densities during most years. Our short-term results indicated that hooded warbler density decreased temporarily immediately following all three initial fuel reduction treatments (Greenberg et al., 2007). This pattern was apparent, but not significant in our longer-term results reported here. Results of other studies are equivocal, showing no response (Aquilani et al., 2000), decreased (Artman et al., 2001), or increased (Rush et al., 2012) hooded warbler density after low-severity burns. Vander Yacht et al. (2016) reported reduced hooded warbler occupancy as treatment stands approached woodland and savanna conditions with low basal area and increased cover of grasses and forbs.

Cavity-nester density was greater in Mechanical + Burn, where snag density was high following the initial high-severity burns, compared to other treatments. Surprisingly, cavity-nester density remained high even as snag density decreased substantially over time, suggesting that cavity-nesters responded more to the open conditions created by heavy tree mortality than to high snag availability *per se*. Vander Yacht et al. (2016) reported that snag abundance was a poor predictor of breeding bird occupancy in oak woodland and savanna restoration treatments in Tennessee. Similarly, Rush et al. (2012) did not find any correspondence between cavity-nesting species and high snag densities in high-severity burns in the southeastern southern Appalachians. These results suggest that snags may not be a limiting factor for the cavity-nesting guild in upland hardwood forest. Among the common cavity-nesting species tested, white-breasted nuthatch density was generally highest in Mechanical + Burn. Others, including eastern tufted titmouse, Carolina chickadees, and Carolina wrens showed treatment differences, but their densities did not differ between any treatment and Control, and response trends in relation to treatments were unclear.

Ground-nester density was lower in Mechanical + Burn than

Mechanical or Control, but did not differ from Burn-only. A clear, non-significant trend of short-term decreases in ground-nester density after burns was evident, and corresponded with temporary post-burn decreases in the leaf litter nesting substrate, followed by recovery as leaves dropped from deciduous trees each autumn. Despite a clear response at the guild-level, responses differed among the individual ground-nesting species tested. Our earlier (Greenberg et al., 2007, 2013) and long-term results reported here indicated that black-and-white warbler density did not differ among treatments, although a pattern of short-term decreased density after burning was apparent. Results of other studies are equivocal; some showed little effect of low- or high-severity burns on black-and-white warblers (Artman et al., 2001; Rush et al., 2012), whereas others reported decreased density after burning (Aquilani et al., 2000). Similarly, our earlier (Greenberg et al., 2007, 2013) and long-term results reported here did not show a definitive response by ovenbirds; density was lower in Mechanical + Burn than Mechanical-only, but did not differ from Burn-only or Control. Further, ovenbirds did not show an immediate, clear response to each burn. Several other studies report ovenbird declines after prescribed burns (Aquilani et al., 2000; Artman et al., 2001), high-severity burns (Rush et al., 2012), burns in conjunction with basal area reductions (Vander Yacht et al., 2016), or other canopy-reducing disturbances that such as timber harvests (Rodewald and Smith, 1998; Greenberg et al., 2014), at least in the short-term. In contrast, Greenberg et al. (2014) reported that ovenbird densities did not change after a low-intensity prescribed burn in the southern Appalachians. Our earlier results indicated that worm-eating warbler density was lower in Mechanical + Burn than Mechanical-only or Control (Greenberg et al., 2007); our long-term results reported here also indicated that they were marginally less abundant in Mechanical + Burn than Control, but did not differ from Burn-only or Mechanical-only. A trend of short-term decreases in worm-eating warbler density after burns in Mechanical + Burn and Burn-only was evident, but not statistically significant. Several studies show a negative effect of prescribed burning (Artman et al., 2001), or burns in conjunction with basal area reduction, on worm-eating warblers (Vander Yacht et al., 2016), at least in the short-term. Different responses among species highlight the importance of considering multiple species when managing forests with fire or other silvicultural methods for bird conservation.

Our results suggest that high-severity fire creates an open, young forest structure that is important for many bird species of conservation concern in the Central Hardwood Region. However, we note that breeding birds appear to respond similarly to high-severity burns (Klaus et al, 2010; Rush et al., 2012; Rose and Simons, 2016; this study) and other silvicultural treatments with heavy canopy reduction, such as shelterwood harvests (e.g., Annand and Thompson, 1997; Rodewald and Smith, 1998; Whitehead, 2003; Greenberg et al., 2014; Kendrick et al., 2015; Vander Yacht et al., 2017). Both disturbance types create a similar, open canopy structure with thick shrub cover; greater snag density in high-severity burns is an important difference, but our results indicate that snags fall within a decade with no detectable effect on cavity-nesters or other breeding birds. Without repeated disturbances such as burning or mechanical shrub reduction, both high-severity burns and shelterwood harvests in upland hardwood forests will likely grow to canopy closure within about 10 years (Loftis et al., 2011). Thus, a 'sustained yield' of new high-severity burns or timber harvests (Shifley and Thompson, 2011), or else repeated disturbances in existing open-canopy young forest is needed to sustain availability of this forest structure for many species of conservation concern. We suggest that fire and other silvicultural methods may offer alternatives in managing upland hardwood forests for conserving diverse breeding bird communities.

5. Conclusions

Our results show that high-severity fire in Mechanical + Burn created an open canopy condition, abundant snags lasting for several years, and thick shrub cover, resulting in high density and species richness of breeding birds by providing suitable habitat for species associated with young forest conditions while retaining most associated with mature forest. Subsequent, lower-intensity prescribed burns in Mechanical + Burn maintained the open-forest structure and associated breeding bird community by impeding forest maturation, but did not provide additive effects on breeding bird communities. In contrast, four repeated low-intensity burns (Burn-only) resulted in delayed mortality of mainly smaller trees, or a few larger trees in 'hot spots,' leading to increased structural heterogeneity over time. The gradual and subtle changes to forest structure in Burn-only were likely promoted by repeated burning that led to modest, ongoing tree mortality. The increasingly 'perforated' overstory in Burn-only did not affect breeding bird density, but species richness became increasingly variable, albeit not significantly, over time. Repeated (twice) mechanical understory reduction alone (Mechanical-only) had little effect on density or species richness of birds. Cavity-nester density was highest in Mechanical + Burn, but remained high even as snags fell to pretreatment levels, suggesting that snags may not be a limiting factor for the cavity-nesting guild in upland hardwood forest. Ground-nester density was lower in Mechanical + Burn than Control and Mechanical-only, but ground-nesting species responded differently. Repeated burning in either burn treatment did not create open woodlands due to persistent re-sprouting of top-killed trees and shrubs, and negligible increases in grasses and forbs. Bird species associated with grass-forb dominated understories, such as northern bobwhite, were absent from all treatments. Our results indicate that breeding bird species richness is closely associated with canopy openness and structural heterogeneity, rather than changes to shrub cover under an intact canopy, and highlights the role of fire in creating 'habitat variability' (Hiers et al., 2016) that provides suitable conditions for species with varying habitat requirements. We suggest that other silvicultural methods that substantially reduce canopy cover, such as shelterwood regeneration harvests, can create open, young forest conditions similar to those following high-severity burns, and may offer alternatives in managing upland hardwood forests for conserving diverse breeding bird communities.

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgements

This research was supported by the Joint Fire Science Program, grant no. 13-1-04-44. Original funding to establish the study site was from the USDA Forest Service through the National Fire Plan. We thank the North Carolina Wildlife Resources Commission for their field support, for permitting this study to be conducted on state Game Lands, and for conducting all fuel reduction treatments. Special thanks to Stan Zarnoch for providing statistical guidance.

References

Annand, E.M., Thompson, F.R.I.I.I., 1997. Forest birds response to regeneration practices in central hardwood forests. J. Wildl. Manage. 61, 159–171.

Aquilani, S.M., LeBlanc, D.C., Morrell, T.E., 2000. Effects of prescribed surface fires on ground- and shrub-nesting neotropical migratory birds in a mature Indiana oak forest. USA. Nat. Areas J. 20, 317–324.

Alldredge, M.W., Pacifici, K., Simons, T.R., Pollock, K.H., 2008. A novel field evaluation of the effectiveness of distance and independent observer sampling to estimate aural avian detection probabilities. J. Appl. Ecol. 45, 1349–1356.

Artman, V.L., Sutherland, E.K., Downhower, D.F., 2001. Prescribed burning to restore mixed-oak communities in southern Ohio: effects on breeding-bird populations. Conserv. Biol. 15, 1423–1434.

Askins, R.A., 2001. Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats. Wildl. Soc. Bull. 29, 407–412.

Bland, J.M., Altman, D.G., 1995. Multiple significance tests: the Bonferroni method. Brit. Med. J. 310, 170.

Campbell, J.W., Hanula, J.L., Waldrop, T.A., 2007. Effects of prescribed fire and fire surrogates on floral visiting insects of the Blue Ridge Province in North Carolina. Biol. Conserv. 134, 393–404.

Campbell, J.W., Viguiera, P., Viguiera, C.C., Greenberg, C.H., 2018. The effect of repeated forest management practices on bees, wasps, and other pollinators within the understory and midstory of a temperate forest in North Carolina. For. Sci. Published online April, 2018. 10.1093/forsci/fxx008.

Driscoll, D.A., Lendenmayer, D., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J., Clarke, M.F., Dexter, N., Fensham, R., Friend, G., Gill, M., James, S., Kay, G., Keith, D.A., MacGregor, C., Russell-Smith, J., Salt, D., Watson, J.E.M., Williams, R.J., York, A., 2010. Fire management for biodiversity conservation: key research questions and our capacity to answer them. Biol. Conserv. 143, 1928–1939.

Greenberg, C.H., Livings-Tomcho, A., Lanham, J.D., Waldrop, T.A., Tomcho, J., Phillips, R.J., Simon, D., 2007. Short-term effects of fire and other fuel reduction treatments on breeding birds in a Southern Appalachian hardwood forest. J. Wildl. Manage. 71, 1906–1916.

Greenberg, C.H., Collins, B., Thompson, F.R. III, McNab, H.R., 2011. What are early successional habitats, how can they be sustained, and why are they important? In: Greenberg, C.H., Collins, B., Thompson, F.R. III (Eds.), Sustaining Young Forest Communities: Ecology and Management of Early Successional Habitats in the Central Hardwood Region, USA. Managing Forest Ecosystems, vol. 21, pp. 191–208.

Greenberg, C.H., Waldrop, T.A., Tomcho, J., Phillips, R.J., Simon, D., 2013. Bird response to fire severity and repeated burning in upland hardwood forest. For. Ecol. Manage. 304, 80–88.

Greenberg, C.H., Franzreb, K.E., Keyser, T.L., Zarnoch, S.J., Simon, D.M., Warburton, G.S., 2014. Short-term response of breeding birds to oak regeneration treatments in upland hardwood forest. Nat. Areas J. 34, 409–422.

Greenberg, C.H., Weeks, K., Warburton, G.S., 2015. The historic role of humans and other keystone species I shaping central hardwood forests for disturbance-dependent wildlife. In: Greenberg, C.H., Collins, B.S. (Eds.), Natural Disturbances and Historic Range of Variation: Type, Frequency, Severity, and Post-Disturbance Structure in Central Hardwood Forests, USA. Managing Forest Ecosystem Series, vol. 32. Springer, USA, pp. 319–354.

Grundel, R., Pavlovic, N.B., 2007a. Distinctiveness, use, and value of Midwestern oak savannas and woodlands as avian habitats. Auk 124, 969–985.

Grundel, R., Pavlovic, N.B., 2007b. Response of bird species densities to habitat structure and fire history along a Midwestern open-forest gradient. The Condor 109, 734–749.

Hamel, P.B., 1992. The Land Manager's Guide to the Birds of the South. The Nature Conservancy, Southeastern Region, Chapel Hill, NC.

Harper, C.A., Ford, W.M., Lashley, M.A., Moorman, C.E., Stambaugh, M.C., 2016. Fire effects on wildlife in the central hardwoods and Appalachian regions, USA. Fire Ecol. 12, 127–159.

Hayes, D.B., Monfils, M.J., 2015. Occupancy modeling of bird point counts: Implications of mobile animals. J. Wildl. Manage. 79, 1361–1368.

Hiers, K.J., Jackson, S.T., Hobbs, R.J., Burnhardt, E.S., Valentine, L.E., 2016. The precision problem in conservation and restoration. Trends Ecol. Evol. 31, 820–830.

Hunter, W.C., Buehler, D.A., Canterbury, R.A., Confer, J.L., Hamel, P.B., 2001. Conservation of disturbance-dependent birds in eastern North America. Wildl. Soc. Bull. 29, 440–455.

Keenan, S.C., 1998. Soil survey of Polk County, North Carolina. USDA Natural Resources Conservation Service, Washington, DC, USA.

Kendeigh, S.C., 1982. Bird Populations in East-Central Illinois: Fluctuations, Variations, and Development over a Half-Century. Ill. Biol. Monogr. vol. 52.

Kendrick, S.W., Porneluzi, P.A., Thompson III, F.R., Morris, D.L., Haslerig, J.M., Faaborg, J., 2015. Stand-level bird response to experimental forest management in the Missouri Ozarks. J. Wildl. Manage. 79, 50–59.

Keyser, T.L., McDaniel, V.L., Klein, R.N., Drees, D.G., Burton, J.A., Forder, M.M., 2018. Short-term stem mortality of 10 deciduous broad-leaved species following prescribed burning in upland forests of the Southern US. Int. J. Wild. Fire 2017, 42–51.

Klaus, N.A., Rush, S.A., Keyes, T.S., Petrick, J., Cooper, R.J., 2010. Short-term effects of fire on breeding birds in southern Appalachian upland forests. Wilson J. Ornith. 122, 518–531.

Loftis, D.L., Schweitzer, C.J., Keyser, T.L., 2011. Structure and species composition of upland hardwood communities after regeneration treatments across environmental gradients. In: Greenberg, C.H., Collins, B., Thompson, F.R. III (Eds.), Sustaining Young Forest Communities: Ecology and Management of Early Successional Habitats in the Central Hardwood Region, USA. Managing Forest Ecosystems, vol. 21, pp. 59–71.

Marshall, M.R., DeCecco, J.A., Williams, A.B., Gale, G.A., Cooper, R.J., 2003. Use of regenerating clearcuts by late-successional bird species and their young during the post-fledging period. For. Ecol. Manage. 183, 127–135.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84, 2200–2207.

Rodewald, P.G., Smith, K.G., 1998. Short-term effects of understory and overstory management on breeding birds in Arkansas oak-hickory forests. J. Wildl. Manage. 62, 1411–1417.

Ralph, J.C., Guepel, G.R., Pyle, P., Martin, T.E., DeSante, D.F., 1993. Handbook for Field Methods for Monitoring Landbirds. USDA Forest Service Gen. Tech. Rep. GTR-PSW-144.

Rose, T.T., Simons, T.R., 2016. Avian response to fire in pine-oak forests of Great Smoky Mountains National Park following decades of fire suppression. The Condor 118, 179–193.

Rush, S., Klaus, N., Keys, T., Petrick, J., Cooper, R., 2012. Fire severity has mixed benefits to breeding bird species in the southern Appalachians. For. Ecol. Manage. 263, 94–100.

Shifley, S.R., Thompson, F.R. III., 2011 Spatial and temporal patterns in the amount of young forests and implications for biodiversity. In: Greenberg, C.H., Collins, B., Thompson, F.R. III (Eds.), Sustaining Young Forest Communities: Ecology and Management of Early Successional Habitats in the Central Hardwood Region, USA. Managing Forest Ecosystems, vol. 21, pp. 73–95.

Smith, E., 2002. BACI design. In: El-Shaarawi, A.H., Piegorsch, W.W. (Eds.), Encyclopedia of Environmetrics, vol. 1. John Wiley & Sons, Ltd, Chichester, pp. 41–148.

USDA Natural Resources Conservation Service, 1998. Soil Survey of Polk County, North Carolina. US Government Printing Office: 1998-432-697/60527/NCRS.

Vander Yacht, A.L., Keyser, P.D., Buehler, D.A., Harper, C.A., Buckley, D.S., Applegate, R.D., 2016. Avian occupancy response to oak woodland and savanna restoration. J. Wildl. Manage. 80, 1091–1105.

Vander Yacht, A.L., Barrioz, S.A., Keyser, P.D., Harper, C.A., Buckley, D.S., Buehler, D.A., Applegate, R.D., 2017. Vegetation response to overstory disturbance and season of burn during oak woodland and savanna restoration in Tennessee. For. Ecol. Manage. 390, 187–202.

Waldrop, T.A., Phillips, R.A., Simon, D.A., 2010. Fuels and predicted fire behavior in the southern Appalachian mountains after fire and fire surrogate treatments. For. Sci. 56, 32–45.

Waldrop, T.A., Hagan, D.L., Simon, D.A., 2016. Repeated application of fuel reduction treatments in the southern Appalachian mountains, USA: Implications for achieving management goals. Fire Ecol. 12, 1–20.

Whitehead M.A., 2003. Seasonal Variation in Food Resource Availability and Avian Communities in 4 Habitat Types in the Southern Appalachian Mountains. (Dissertation), Clemson University, SC.