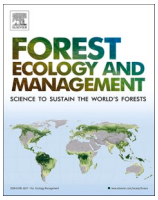
Forest Ecology and Management 529 (2023) 120715

Contents lists available at ScienceDirect

Forest Ecology and Management

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



Breeding bird abundance and species diversity greatest in high-severity wildfire patches in central hardwood forests

Cathryn H. Greenberg [a,*], Christopher E. Moorman [b], Katherine J. Elliott [c], Katherine Martin [d], Mark Hopey [e], Peter V. Caldwell [c]

[a] USDA Forest Service, Southern Research Station, Upland Hardwood Ecology and Management Research Work Unit, Asheville, NC 28806, USA
[b] Fisheries, Wildlife, and Conservation Biology Program, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA
[c] USDA Forest Service, Center for Forest Watershed Science, Coweeta Hydrologic Laboratory, Otto, NC 28763, USA
[d] Center for Geospatial Analytics, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA
[e] Blue Ridge Bird Observatory, Mars Hill, NC 28754, USA

ARTICLE INFO

Keywords:
Breeding birds
Disturbance-dependent birds
Central hardwood forest
High-severity fire
Mixed-severity fire
Wildfire

ABSTRACT

In 2016, mixed-severity wildfires in the southern Appalachians created a gradient of forest structures not typical following prescribed burns, providing a unique opportunity to study temporally dynamic conditions and breeding bird response. We measured forest structure and breeding bird communities across a fire-severity gradient in 3 burned and 3 unburned watersheds for 5 years (Y1-Y5). We categorized plots as unburned (NB), low- (L), moderate- (M), or high-severity (H) using a composite fire-severity index. Tree mortality increased with fire-severity category (FSC) and over time; by Y5, 7 % of trees in NB, 11 % in L, 38 % in M, and 71 % in H had died. Shrub recovery was rapid and most pronounced in H, exceeding other FSCs (70 % vs 21 %–44 %) by Y5. Total bird abundance, species richness, and diversity increased over time in H (by Y3) and M (by Y4); by Y5, these metrics were highest in H and twice as high in H as in NB. Low-severity wildfires had no detectable effects on birds. Abundance of 7 species was greatest in higher-severity FSCs; 11 species did not differ among FSC, although ovenbirds (*Seiurus aurocapilla*) indicated a trend of lower abundance in H. No species was limited to NB, L, or M, whereas disturbance-dependent indigo bunting (*Passerina cyanea*), chestnut-sided warbler (*Setophaga pensylvanica*), and eastern towhee (*Pipilo erythrophthalmus*) were primarily associated with H. Increased richness and diversity were associated with heavy tree mortality and subsequent shrub recovery in H, accompanied by an influx of disturbance-dependent species and positive or neutral responses by most other species. Results highlight the interrelated roles of fire severity and time in driving forest structure and breeding bird response. Breeding birds responded to high-severity burns similarly to silvicultural treatments with heavy canopy reduction documented in other studies, offering possible alternatives when managing for breeding bird diversity in hardwood forests.

1. Introduction

The linkage between structural heterogeneity of vegetation and breeding bird diversity has been a tenet of ecology for decades (MacArthur and MacArthur, 1961). Forest disturbance is a primary driver of structural heterogeneity at multiple scales (e.g., Greenberg and Collins, 2016). Low severity disturbances generally retain dense canopy structure that casts heavy shade and limits development of vegetation in the lower portions of the forest profile. As such, numerous studies have illustrated the role of forest canopy-reducing anthropogenic (e.g., McDermott and Wood, 2009; Perry and Thill 2013) and natural disturbances (e.g., Prather and Smith, 2003), including fire (e.g., Rush et al., 2012; Greenberg et al., 2018), in creating habitat for disturbance-dependent species, thereby promoting species diversity at local and landscape scales.

Fire has been used intentionally for thousands of years in central hardwood forests, first by Native Americans, then early European settlers, and more recently by forest managers who use prescribed fire under controlled conditions with goals of creating or maintaining specific vegetation composition and structure or attaining other

* Corresponding author.
E-mail address: Cathryn.greenberg@usda.gov (C.H. Greenberg).

https://doi.org/10.1016/j.foreco.2022.120715
Received 26 August 2022; Received in revised form 30 November 2022; Accepted 4 December 2022

management outcomes (see Greenberg et al., 2016a; Arthur et al., 2021). Humans still ignite most wildfires, either accidentally (e.g., unattended campfires; cigarette butts) or intentionally (i.e., arson), often under extreme drought conditions (Greenberg et al., 2016a,b; 2021). In the southern Appalachian region, lightning-ignited ("natural") wildfires are rare due to the high moisture content of vegetation and rainfall that usually accompanies lightning during summer thunderstorms (Greenberg et al. 2016a; 2021; Arthur et al. 2021). Historically and today, dormant-season fires dominated the fire regime, with fire return intervals of 5–13 years (Arthur et al. 2021). Unlike most low-severity prescribed burns, wildfires often create a gradient of forest conditions, or spatial and temporal "pyrodiversity" (e.g., Jones and Tingley, 2021), as they burn with mixed-severities across topographically diverse landscapes.

Historically, the frequent, widespread use of fire in central hardwood forests created open woodlands and even savannas and prairies that supported populations of several breeding bird species now uncommon or extirpated from the region, such as northern bobwhite (*Colinus virginianus*), golden-winged warbler (*Vermivora chrysoptera*), and red-cockaded woodpecker (*Leuconotopicus borealis*) (Greenberg et al., 2016a,b). Moreover, disturbance-dependent songbird populations in North America are declining faster than other groups of birds (Hunter et al., 2001). These declines are associated with changing cultural practices that encouraged fire suppression and dramatically reduced the frequency and extent of intentional fire that previously maintained open forests (Spetich et al., 2011; Greenberg et al., 2016b). Other factors driving bird declines include forest regrowth to mature, relatively even-aged forest patches following widespread, heavy logging in the early 20th century and abandonment of agricultural fields, combined with a quarter-century of reduced timber harvesting on public lands (Shifley and Thompson, 2011).

In central hardwood forests, bird species differ in the amount and distribution of canopy cover and associated forest conditions they require. Many species are generalists, occurring across a gradient of forest conditions, but others have a narrower range of habitat requirements. A few species, such as ovenbird (*Seiurus aurocapilla*), are closely associated with closed canopy mature forest during the breeding season. Others, such as hooded warbler (*Setophaga citrina*), use small gaps within a mature forest matrix, whereas indigo bunting (*Passerina cyanea*), eastern towhee (*Pipilo erythrophthalmus*), and chestnut-sided warbler (*Setophaga pensylvanica*) are most abundant in larger openings and in open-canopy forests (Annand and Thompson, 1997; Robinson and Robinson, 1999; Moorman and Guynn, 2001). However, adults and juveniles of many mature forest species move into canopy gaps or young forests during the post-fledging stage (e.g., Marshall et al., 2003; King et al., 2006; Stoleson, 2013) or use them as stopover locations during migration (Pagen et al., 2000; Vitz and Rodewald, 2006; Bowen et al., 2007). The variable habitat requirements among species and the increased use of more open forest conditions during the post-fledging and non-breeding periods indicate that a gradient of disturbance severities across forested landscapes could maximize availability of habitat for multiple bird species.

Earlier research in the southern Appalachians showed little effect of low-severity prescribed burns on breeding bird communities (Greenberg et al., 2014, 2018, 2019) but dramatic increases in species richness and occupancy or abundance after high-severity prescribed burns or wildfire due to an influx of species associated with open forest conditions (Klaus et al., 2010; Rush et al., 2012; Rose and Simons, 2016; Greenberg et al., 2018). Most of these study designs were necessarily limited to comparisons between burned and unburned forest (Greenberg et al., 2018) or a chronosequence of fire severities and times since burn (Klaus et al., 2010; Rush et al., 2012; Rose and Simons, 2016) but did not incorporate a gradient of burn severities created by multiple independent and virtually concurrent wildfires, or track changes in forest structure and breeding bird communities in the same locations over time.

More than 21 large-scale wildfires burned > 61,000 ha across the topographically complex southern Appalachian region of the eastern US in fall 2016 following prolonged dry conditions and multiple human-caused ignitions. These mixed-severity wildfires created a gradient of forest structural conditions that are not typical following prescribed burns (Caldwell et al., 2020), providing a unique opportunity to study temporally dynamic change in forest structure and breeding bird response across a range of fire severities in multiple burned and unburned watersheds. We hypothesized that the level of disturbance created by high-severity patches of wildfire, including heavy tree mortality with consequently greater canopy openness and shrub cover, would result in a greater abundance, species richness, and diversity of breeding birds. Therefore, we evaluated the variation in forest structure and breeding bird communities (total bird abundance, species richness, diversity, and nesting guilds) and species-specific responses to mixed-severity wildfires across fire-severity categories (FSCs), ranging from unburned to high-severity for five years post-wildfire. We chose to use fire-severity categories instead of continuous modelling (Cottingham et al., 2005) to maximize sample sizes across a range of fire-severity index values, simplify interpretation of dynamic changes in forest structure and bird responses over the 5-year study period, and better identify response thresholds.

2. Methods

2.1. Study area

Our study was conducted in the Nantahala National Forest in the southern Appalachian Mountains of Macon County in western North Carolina, USA (latitude 35.0 to 35.4° N; longitude 82.9 to 84.3° W) (Fig. 1). The climate was characterized by warm summers and cool winters. Average annual temperature was 12.6 °C and precipitation was 1,375 mm yr − 1 (NCDC, 2020) but both vary somewhat with elevation and aspect (Laseter et al., 2012). Forests were southern mixed deciduous forest with an overstory dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), red maple (*Acer rubrum*), tulip-poplar (*Liriodendron tulipifera*), birch (*Betula* spp.), sourwood (*Oxydendrum arboreum*) and evergreen shrubs, including rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*), sometimes forming a dense understory or midstory.

We selected three watersheds that burned in the Tellico (Indian Branch and Iron Bridge watersheds) and Camp Branch fires (Camp Branch watershed), and three adjacent topographically-similar unburned watersheds (Chestnut Cove, Tellico Creek, and Arrowwood) (Fig. 1). Watershed areas ranged 42.3–378.6 ha, and elevations ranged 819–1,628 m (Caldwell et al., 2020). All study watersheds were completely forested with a history of intermittent partial timber harvests since the late 1800 s. The watershed area-weighted mean stand age in 2016 ranged from 81 to 127 years old (Caldwell et al., 2020). The Tellico Fire started on 3 November 2016 and burned 5,739 ha; the Camp Branch Fire started on 23 November 2016 and burned 1,310 ha. Both fires were the result of arson. Heavy rainfall (approximately 50 mm) on 28 November 2016 extinguished most of the wildfires in the region.

2.2. Sampling design

We established 12, 7-m radius (0.015-ha) vegetation plots (winter, 2016–2017) in each unburned watershed (NB), and 20 plots in each burned watershed (B) in a stratified randomized design to include high-severity (H), moderate-severity (M), and low-severity (L) burn conditions (section 2.3; see Caldwell et al., 2020 for details), for a total of 96 vegetation plots across six watersheds. We measured the diameter at breast height (dbh) of all live and wildfire-killed trees (≥5.0 cm dbh) and tagged all live trees in each plot. Wildfire-killed trees could generally be distinguished from pre-wildfire snags by the presence of branches with twigs and sometimes dead leaves, and little decomposition. Vegetation plots were initially established to assess wildfire effects on

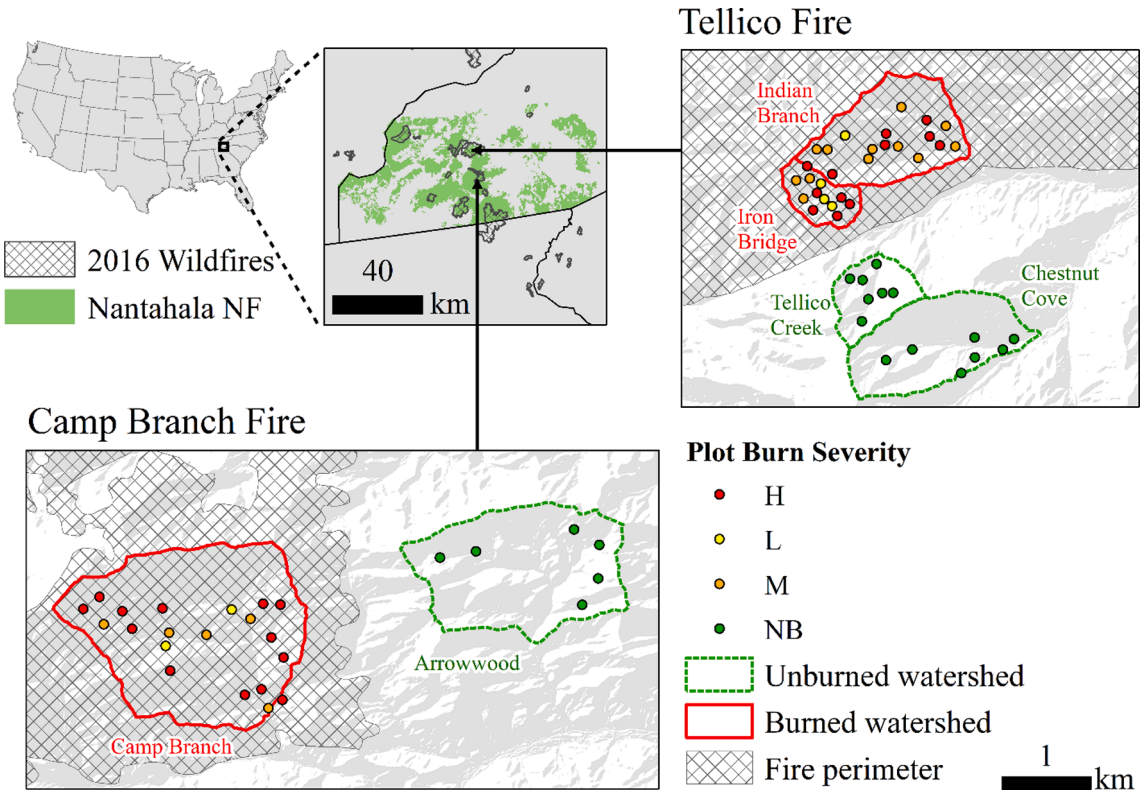


Fig. 1. Study area map including 3 burned and 3 unburned watersheds, with breeding bird point-count locations by fire-severity category (unburned, low-, moderate-, and high-severity) following the 2016 wildfires, Nantahala National Forest, Macon County, North Carolina.

vegetation and water (Caldwell et al., 2020). For this study, we discarded several plots that were too closely spaced, using only those ≥ 150 m apart to improve independence. Thus, we used 48 plots within the three burned watersheds (25H, 17 M, and 6 L), and 20 within the three unburned watersheds (6–7 plots each) for bird point counts and forest structure analyses.

2.3. Burn-severity index

We developed a composite plot-level burn severity index using measurements of forest floor depth (soil Oi and Oe + Oa horizons), char height (a measure of flame height) on each live and dead tree bole, tree mortality, basal area (BA) loss, and mineral soil exposure (see Caldwell et al., 2020 for details). Forest floor depth, tree bole char height, and mineral soil exposure were measured in January and February 2017; tree mortality was assessed in September 2017 (one growing season after the wildfires and prior to leaf fall). Char height was averaged across all trees per plot. Total BA (live and wildlife-killed) was calculated to estimate percentage of BA lost through tree mortality due to the wildfire. Forest floor depth and bare mineral soil were each averaged across 20 measurement points uniformly distributed across each plot. We assigned each of these variables (tree mortality, BA loss, char height, forest floor depth, and exposed mineral soil) a 1–5 (low to high) rating and calculated the composite burn severity index value per plot as the mean all five variables. Six plot-level FSCs were defined based on composite burn severity index ranges (Caldwell et al., 2020); our exploratory analyses indicated that breeding bird responses were most clearly explained using fewer FSCs. Therefore, for this study we defined plot-level FSCs using composite burn severity index ranges: L: ≤1.2, M: 1.3–2.7, H: ≥2.8 (see Caldwell et al. 2020 for maps and detail). Satellite-based Relative differenced Normalized Burn Ratio (RdNBR) informed by plot-level burn severity index values indicated that 20 %-42 % of burned study watersheds burned at high severity (Caldwell et al., 2020).

2.4. Forest structure measurements

We assessed tree status (live or dead) and measured percent cover of forest structure attributes including canopy, shrub (woody plants < 5 cm dbh), and leaf litter within vegetation plots three times (May-October 2017, 2018, 2021) within the 5-year study period. We used a modified Weins method (Weins, 1969; Moorman and Guynn, 2001) to quantify shrub and leaf litter cover. Presence (contacts) or absence of each variable was tallied using a 1-m vertical pole at 1-m intervals along four transects starting at plot center and extending 5-m out in each cardinal direction (20 points per plot). Percent cover of each category was calculated as the number of contacts (i.e., shrub contact anywhere along the vertical pole or litter contact beneath the pole) divided by the total number of pole readings in the plot (20). Percent canopy cover was measured at plot centers using a spherical densiometer held at breast height (ca. 1.4 m) as a crude metric of understory light and microclimate. In 2021, we additionally recorded whether dead trees were fallen or standing (≥1.8 m height) to estimate standing snag density. Dead trees (and thus snags) included only those killed by wildfires or dying subsequently (i.e., no pre-wildfire snags).

2.5. Breeding bird surveys

We conducted two, 10-minute point counts within four hours of sunrise during the breeding season (May 19-July 5) for five years (2017–2021; Y1-Y5, respectively) starting the first breeding season post-wildfire. We located points at vegetation plot centers, and recorded all birds seen or heard within a 25-m radius (excluding flyovers). We standardized our sampling design to minimize potential detection bias (Thompson and La Sorte, 2008). Most point counts were conducted by a single, highly experienced observer (M. Hopey); two other highly experienced observers also conducted counts during the study. Additionally, we avoided surveys during moderate-high winds or precipitation, rotated the two surveys per season over time-of-day, and spaced

them earlier and later in the breeding season to account for possible differences in singing rates as the morning or breeding season progressed. Our small (25-m radius) plot size minimized the possibility for differences in bird detectability among FSCs due to vegetation structure, especially because most detections across all FSCs were aural. We elected to use naïve estimates of relative bird abundance (Thompson and La Sorte, 2008) rather than those derived from *N*-mixture models, as naïve estimates are generally less biased when detection probability is ≥ 0.65 and *N*-mixture models are highly sensitive to assumption violations associated with closed populations (Royle, 2004; Dail and Madsen, 2011; Fogarty and Fleishman, 2021; Goldstein and de Valpine, 2022) and unmodeled heterogeneity in count data within a sample unit (Duarte et al., 2018). Further, both generalized linear mixed models (GLMMs) and N-mixture models generally show the same patterns (Goldstein and de Valpine, 2022). We calculated relative abundance of birds (total, nesting guilds or species) per point count by averaging across both surveys per point count per year and extrapolating to the number detected per 10 ha. Species richness represented the total number of species detected during both visits per plot each year. Species diversity was calculated using the Shannon diversity index (Shannon, 1948).

2.6. Statistical analysis

We used 1-way analysis of variance (ANOVA) to examine whether pre-wildfire live tree density and BA differed among FSCs. Pre-wildfire live tree densities and BA were calculated as the sum of live trees + fire-killed dead trees (e.g., not including pre-wildfire snags) measured in bird plots four months post-wildfire (March 2017). We also used 1-way ANOVA to compare snag density among FSCs in Y5. We used 2-way repeated measures mixed-effects ANOVAs with compound symmetry covariance structure to compare forest structure measurements and breeding bird communities among the four FSCs (NB, L, M, and H) and years (Y1,Y2, and Y5 for forest structure; Y1-Y5 for birds) and tested for FSC × year interactions. Forest structure measurements included percent cover of shrubs, leaf litter, and canopy, as well as the percent BA of trees that died during or after the wildfire (not including pre-wildfire snags) based on total pre-burn live trees. Breeding bird variables included species richness and relative abundance (termed abundance) of total birds, birds within tree-, cavity-, shrub- (including midstory), or ground-nesting guilds (Hamel, 1992), primary (woodpeckers) and secondary cavity-nesters, and common species (if ≥ 30 observations during the study period). For these analyses, we considered plot as the experimental unit, plot within watershed as a random factor, and FSC, year, and the FSC × year interaction as fixed effects. We performed all post hoc tests using least squares means tests. Our primary interest was the effect of FSC or FSC × year interaction effects as indicators that forest structure or bird community composition differed within or among FSCs over time. A non-significant interaction effect indicated a consistent difference among FSCs across years. FSC, year, or FSC × year interaction differences were considered significant with an overall experimental α of ≤ 0.05. When significant interaction effects were present, we used the least square means for partitioned F-tests (SLICE option) in PROC MIXED (SAS 9.4) to examine the significance of FSC differences within identified years, and among-year differences within identified FSCs. Percentage data were arcsine square-root transformed for ANOVAs to reduce heteroscedasticity.

3. Results

3.1. Forest structure

Pre-wildfire live tree density (±SE) and BA were 930.4 ± 44.6/ha and 41.5 ± 2.0 m^2/ha across watersheds, respectively, and did not differ among FSCs assigned post-wildfire ($p \geq 0.36$). Initial (Y1) tree mortality in burned watersheds ranged from 3 % (0.1 % BA) in L, to 12 % (2 % BA) in M and 44 % (19 % BA) in H; by Y5, 11 % (3 % BA) of trees in L, 38 % (14 % BA) in LM, and 71 % (44 % BA) in H had died. In comparison, 7 % (3 % BA) of trees in unburned watersheds died over the 5-year study period. Percentage mortality increased over time and was greater in H than all other FSCs and greater in M than L (Fig. 2). A FSC × year interaction effect and partitioned F-tests indicated that percentage tree mortality increased over time in all FSCs except L and differed among some FSCs within all years. Within H and M, the percentage of dead trees increased each year; within L, the percentage of dead trees was lower in Y1 than Y5, and within NB, it was lower in Y1 and Y2 than Y5. In Y1, Y2 and Y5, the percentage of dead trees was greater in H than all other FSCs and greater in M than L or NB. The percentage of tree BA killed by or dying subsequent to wildfire increased over time; percentage BA mortality was greater in H than all other FSCs and greater in M than NB (Fig. 2). A FSC × year interaction effect and partitioned F-tests (SLICE option) indicated that percentage BA mortality within H increased each year; within M and NB, BA mortality was lower in Y1 and Y2 than Y5. In Y5, standing snag density was greater in H than all other FSCs and greater in M than L and NB ($p < 0.0001$) (Fig. 2).

Shrub cover was initially (Y1) reduced in all burned FSCs (4–8 %) compared to NB (35 %). Post-wildfire shrub recovery was rapid and most pronounced in H, averaging 70 % cover by Y5 and exceeding all other FSCs (21 %-44 %) (Fig. 2). Percent shrub cover increased over time, and was greater in H than L and M, and greater in NB than L (Fig. 2). A FSC × year interaction effect and partitioned F-tests indicated that percent shrub cover increased over time within all burned FSCs and differed among some FSCs during all years. Percent shrub cover increased each year post-wildfire within H and M; within L, it was lower in Y1 and Y2 than Y5. In Y1, shrub cover was greater in NB than all burned FSCs; in Y2, it was greater in NB than L or M (Fig. 2). In Y5, shrub cover was greater in H than all other FSCs and lower in L than NB.

Leaf litter cover was initially (Y1) reduced in all FSCs (≤27 %) compared to NB (85 %) but rapidly replenished as leaves fell from deciduous trees each fall; by Y5, leaf litter cover was ≥ 87 % in all FSCs except H (68 %) (Fig. 2). Percent leaf litter cover increased over time and was lower in H and greater in NB than other FSCs. A FSC × year interaction effect and partitioned F-tests indicated that leaf litter cover increased over time within all burned FSCs and differed among some FSCs each year (Fig. 2). Litter cover increased each year within H, M and L. In Y1, litter cover was lower in all burned FSCs than NB; in Y2 it was lower in H than all other FSCs and lower in M than NB, and in Y5 it was lower in H than all other FSCS.

Percent canopy cover (measured at breast height) decreased by Y2 with delayed tree mortality but remained ≥ 91 % in all FSCs except H throughout the study period. Changes were most notable in H where canopy cover decreased to 66 % by Y2 and increased to 78 % by Y5 as shrub cover increased and exceeded breast height. Percent canopy cover differed among years and was lower in H than all other FSCs. A FSC × year effect and partitioned F-tests indicated that percent canopy cover changed over time within H, M and NB, and differed among some FSCs within Y2 and Y5 (Fig. 2). Within H, M and NB, canopy cover was greater in Y1 than Y2; in H, canopy cover increased between Y2 and Y5. In Y2 and Y5, canopy cover was lower in H than all other FSCs.

3.2. Breeding birds

We detected 47 species of breeding birds within the 25-m radius point counts over the 5-year study period. Total breeding bird abundance differed among years and was greater in H than NB or L (Table 1; Fig. 3). A FSC × year interaction effect and partitioned F-tests indicated that total abundance changed over time within H and M and differed among FSCs in Y3, Y4 and Y5. Within H, total abundance was lower in Y1 and Y2 than all subsequent years. Within M, abundance was lower in Y1 than Y4 and Y5, lower in Y2 than Y3, and lower in Y3 than Y4 and Y5. In Y3, abundance was greater in H than all other FSCs. In Y4, total abundance was greater in M and H than NB and L, and in Y5 it was

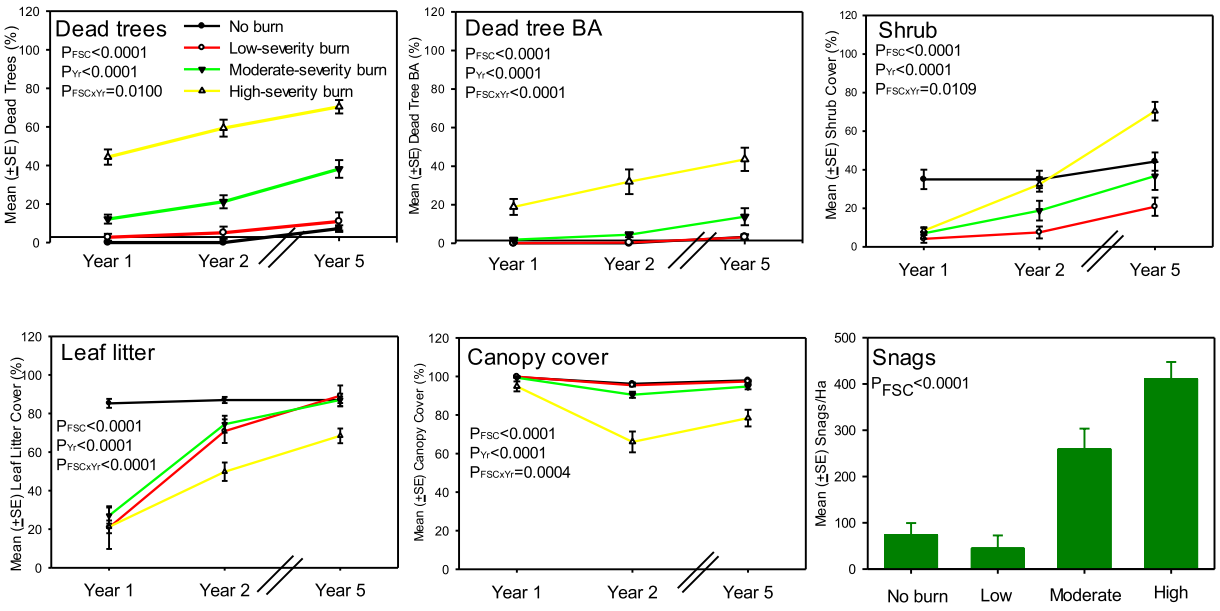


Fig. 2. Mean (±SE) cumulative percentage of dead trees and dead tree BA, mean percent cover of shrubs, leaf litter, and canopy at breast height in four fire-severity categories 1, 2, and 5 years following 2016 wildfires, and; density (no./ha) of snags (≥1.8 m height) 5 years post-wildfire, Nantahala National Forest, Macon County, North Carolina. Dead trees and snags include only those killed by the wildfire or dying subsequently (e.g., not pre-wildfire snags).

greater in H than all other FSCs and greater in M than NB.

Species richness differed among years and was greater in H than NB or L (Table 1, Fig. 3). A FSC × year interaction effect and partitioned F-tests indicated that species richness changed over time in H and M and differed among FSCs in Y4 and Y5. Within H, species richness increased every year post-wildfire. Within M, species richness was lower in Y1-Y3 than Y4. Within Y4, richness in H and M was greater than NB and L; in Y5, it was greater in H than all other FSCs.

Species diversity differed among years and was greater in H than NB or L (Table 1, Fig. 3). A FSC × year interaction effect and partitioned F-tests indicated that diversity changed over time in M and H and differed among FSCs in Y4 and Y5. Within H, diversity was lower in Y1 than all subsequent years, and lower in Y2 and Y3 than Y5. Within M, diversity was lower in Y1-Y3 than Y4. Within Y4, diversity was greater in H and M than L and NB; within Y5, it was greater in H and M than NB, and lower in M than H.

Abundance of tree-nesters did not differ among FSCs or years and no FSC × year interaction was detected (Table 1, Fig. 4). Ground-nester abundance was marginally ($p = 0.06$) lower in L than all other FSCs, including NB. Cavity-nester abundance was greater in H and M than L and NB; year and FSC × year interaction effects were not detected (Table 1; Fig. 4). Primary cavity-nester (woodpeckers) abundance did not differ among FSCs or years and no FSC × year interaction was detected (Table 1; Fig. 4). Secondary cavity-nester abundance was greater in H and M than L and NB; year or FSC × year interaction effects were not detected (Table 1; Fig. 4). Shrub-nester abundance differed among years and was greater in H than M and NB (Table 1; Fig. 4). A FSC × year interaction effect with partitioned F-tests indicated that shrub-nester abundance changed over time within H and M and differed among FSCs in Y3, Y4 and Y5. Within H, shrub-nester abundance was lower in Y1 and Y2 than all subsequent years, and lower in Y3 and Y4 than Y5. Within M, abundance was lower in Y1 and Y2 than Y5, and lower in Y3 than Y4 and Y5. In Y3, shrub-nester abundance was greater in H than NB or M; in Y4 it was greater in H than NB, and in Y5 it was greater in H than all other FSCs and greater in M than NB.

Seven of the 18 species analyzed showed significantly different responses among FSCs and (or) showed a FSC × year interaction effect; a year effect was detected for several species (Table 1; Fig. 5). Indigo bunting abundance differed among years and was greater in H than all other FSCs; no FSC × year interaction effect was detected. Chestnut-sided warbler abundance was greater in H than all other FSCs (Fig. 5). A FSC × year interaction effect and partitioned F-tests indicated that chestnut-sided warbler abundance changed over time within H and differed among FSCs within Y4 and Y5. Within H, chestnut-sided warbler abundance was lower in Y1 than Y3-Y5, and lower in Y2 and Y3 than Y4 and Y5. In Y4 and Y5, chestnut-sided warbler abundance was greater in H than all other FSCs. Eastern towhee abundance differed among years and was greater in H than all other FSCs (Fig. 5). A FSC × year interaction effect and partitioned F-tests indicated that eastern towhee abundance changed over time within H and differed among FSCs in Y3, Y4 and Y5. Within H, eastern towhee abundance was lower in Y1 than Y3, Y4, and Y5. In Y3 and Y5, eastern towhee abundance was greater in H than all other FSCs; in Y4, it was greater in H than L and NB. Hooded warbler abundance differed among years but not among FSCs; a FSC × year interaction effect and partitioned F-tests indicated that hooded warbler abundance changed over time within H and M and differed among FSCs in Y5 (Fig. 5). Within H, abundance was greater in Y5 than all other years, and within M abundance was lower in Y1-Y3 than Y4. In Y5, hooded warbler abundance was greater in H than all other FSCs. White-breasted nuthatch (*Sitta carolinensis*) abundance was greater in H and M than NB (Fig. 5), Carolina chickadee (*Poecile carolinensis*) abundance was greater in M than NB (Fig. 5), and black-and-white warbler (*Mniotilta varia*) abundance was greater in H than L and NB (Fig. 5); no year or FSC × year interaction effects were detected for these species. Abundance of the remaining 11 species tested did not differ among FSCs (Table 1), although black-throated blue warbler (*Setophaga caerulescens*) abundance was marginally ($p < 0.10$) greater in L than all other FSCs, and ovenbird abundance was marginally greater M and NB than H (Fig. 5).

4. Discussion

Our study design incorporated a gradient of burn severities created at the same time by multiple, independent wildfires, allowing us to examine how burn severity affected forest structure and breeding bird communities in the same places over time. Mixed-severity wildfires created a gradient of vegetation structures driven by initial and delayed tree mortality and shrub recovery. Spatial and temporal changes in post-

Table 1
Total number of individual detections (all years and point counts) and results of mixed-model ANOVAs comparing breeding bird species richness, diversity (H'), and abundance (number/10 ha) of total birds, nesting guilds (including primary and secondary cavity-nesters), and common (≥30 detections) species among four fire-severity categories (FSCs), years (2017–2021), and interaction effects following 2016 wildfires, Nantahala National Forest, Macon County, NC.

Group	Obs	P_{FSC}	P_{yr}	$P_{FSC \times yr}$
Ground-nest	432	0.0624	0.5408	0.9207
Black-and-white warbler (*Mniotilta vario*)	138	0.0296	0.0211	0.9841
Canada warbler (*Cardellina canadensis*)	53	0.9382	0.0126	0.8841
Ovenbird (*Seiurus aurocapillus*)	123	0.0585	0.5620	0.6484
Slate-colored junco (*Junco hyemalis*)	46	0.1661	0.3842	0.7143
Veery (*Catharus fuscescens*)	15	———	———	———
Worm-eating warbler (*Helmitheros vermivorus*)	55	0.1017	0.5358	0.6098
Winter wren (*Troglodytes hiemalis*)	2	———	———	———
Cavity-nest	240	0.0044	0.0829	0.2545
Primary	54	0.3298	0.2242	0.5076
Downy woodpecker (*Picoides pubescens*)	20	———	———	———
Hairy woodpecker (*Picoides villosus*)	13	———	———	———
Northern flicker (*Colaptes auratus*)	5	———	———	———
Pileated woodpecker (*Drycopus pileatus*)	12	———	———	———
Red-bellied woodpecker (*Melanerpes carolinus*)	1	———	———	———
Red-headed woodpecker (*Melanerpes erythrocephalus*)	1	———	———	———
Yellow-bellied sapsucker (*Sphyrapicus varius*)	2	———	———	———
Secondary	186	0.0035	0.3215	0.5047
Brown creeper (*Certhia americana*)	10	———	———	———
Carolina chickadee (*Poecile carolinensis*)	68	0.0351	0.6151	0.8863
Carolina wren (*Thyrothorus ludovicianus*)	17	———	———	———
Eastern bluebird (*Sialia sialis*)	2	———	———	———
Eastern tufted titmouse (*Baeolophus bicolor*)	38	0.7362	0.3515	0.9150
White-breasted nuthatch (*Sitta carolinensis*)	51	0.0201	0.1816	0.5764
Shrub-nest	599	0.0038	0.0010	0.0020
American goldfinch (*Carduelis tristis*)	6	———	———	———
American robin (*Turdus migratorius*)	3	———	———	———
Blue-headed vireo (*Vireo solitarius*)	120	0.3072	0.3481	0.2301
Brown thrasher (*Toxostoma rufum*)	2	———	———	———
Black-throated-blue warbler (*Setophaga caerulescens*)	200	0.0603	0.0202	0.4450
Chestnut-sided warbler (*Setophaga pensylvanica*)	33	0.0009	0.0657	0.0043
Eastern towhee (*Pipilo erythrophthalmus*)	75	<0.0001	0.0206	0.0039
Gray catbird (*Dumatella carolinensis*)	2	———	———	———
Hooded warbler (*Setophaga citrina*)	81	0.4463	0.0134	0.0004
Indigo bunting (*Passerina cyanea*)	33	0.0014	0.6998	0.7373
Mourning dove (*Zenaida macroura*)	2	———	———	———
Ruby-throated hummingbird (*Archilochus colubris*)	13	———	———	———
Woodthrush (*Hylocichla mustelina*)	29	———	———	———
Tree-nest	362	0.2778	0.8669	0.3426
Acadian flycatcher (*Empidonax virescens*)	2	———	———	———
American crow (*Corvus brachyrhynchos*)	2	———	———	———
Blackburnian warbler (*Setophaga fusca*)	9	———	———	———
Blue jay (*Cyannocitta cristata*)	28	———	———	———
Black-throated green warbler (*Setophaga virens*)	49	0.8676	0.4173	0.6977
Cedar waxwing (*Bombycilla cedrorum*)	3	———	———	———
Eastern wood-pewee (*Contopus virens*)	23	———	———	———
Northern parula (*Setophaga americana*)	64	0.9242	0.3488	0.4163
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	13	———	———	———
Red-eyed vireo (*Vireo olivaceus*)	115	0.7677	0.0599	0.8525
Scarlet tanager (*Piranga olivacea*)	47	0.6125	0.4478	0.1146
Yellow-throated vireo (*Vireo flavifrons*)	2	———	———	———
Yellow-throated warbler (*Setophaga dominica*)	5	———	———	———
Other	9	———	———	———
Eastern phoebe (*Sayomis phoebe*)	6	———	———	———
Unknown	3	———	———	———
Total Abundance	1642	0.0054	0.0073	0.0009
Richness	———	0.0108	0.0024	0.0407
Diversity	———	0.0183	0.111	0.0060

wildfire breeding bird communities generally reflected fire severity and associated immediate and delayed changes in vegetation structure over time. The greatest contrasts were between low-severity patches, where tree mortality did not differ from that in unburned patches, and high-severity patches where tree mortality and shrub cover exceeded 70 % by Y5. Breeding bird community-level and species' responses were negligible in L but rapid and pronounced in H; by Y5, total bird abundance, species richness, and diversity were twice as high in H as NB. Community level (total abundance, species richness, and diversity) breeding bird responses were also evident in M but occurred more slowly (by Y4) than in H (by Y3). Three disturbance-dependent species – indigo bunting, chestnut-sided warbler, and eastern towhee – were primarily associated with high-severity burn patches, whereas abundance of most species did not differ among FSCs. These results indicate that an influx of disturbance-dependent birds, and positive responses by several other species, increased total abundance, species richness, and diversity of breeding birds in high-severity wildfire patches.

Our results corroborate several other studies that showed negligible or transient effects of low-severity burns (Aquilani et al., 2000; Artman et al., 2001; Klaus et al., 2010; Greenberg et al., 2014, 2018, 2019) on breeding birds, but dramatic increases in total bird abundance, species richness, and abundance of some species within a few breeding seasons

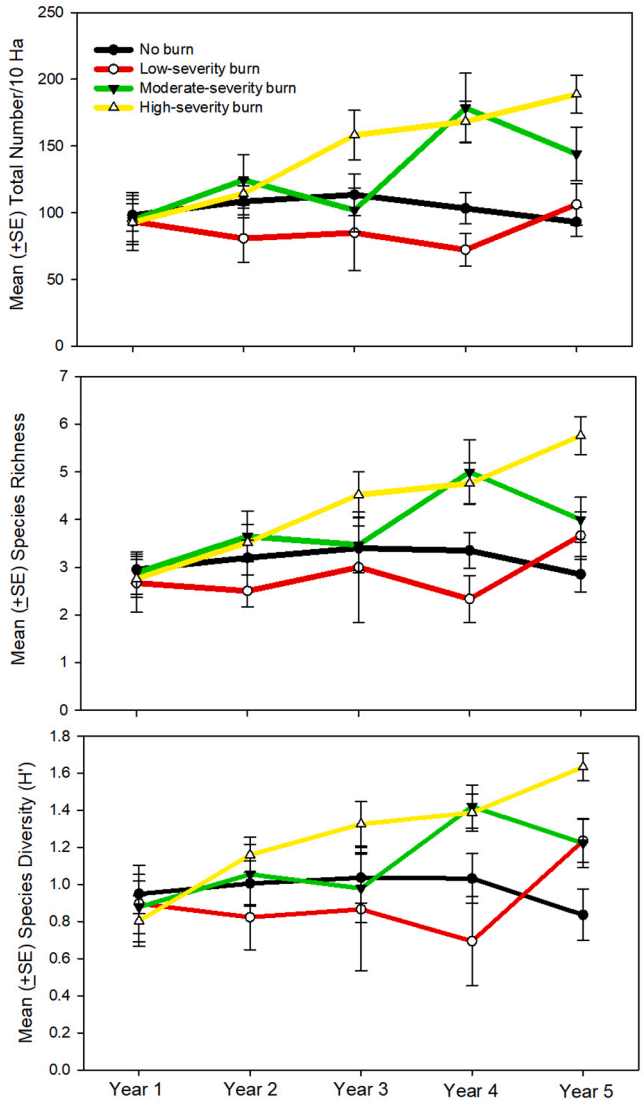


Fig. 3. Mean (±SE) total number of birds/10 ha, species richness, and species diversity (H') 1–5 years post-wildfire in four fire-severity categories following 2016 wildfires, Nantahala National Forest, Macon County, North Carolina.

of high-severity burns (Klaus et al., 2010; Rush et al., 2012; Rose and Simons, 2016; Greenberg et al., 2018). Greenberg et al. (2018) reported a non-significant trend of increasing species richness after four repeated low-severity prescribed burns over a 16-year study period in upland hardwood forests, likely as ongoing delayed tree mortality approached levels analogous to moderate-severity burns in our study. Many of these studies addressed prescribed burns; ours further illustrates that, like prescribed fire, low-severity wildfire does not promote avian community diversity or disturbance-dependent species.

Abundance of the shrub-nesting guild increased over time in moderate- and high-severity wildfire patches, corresponding with rapid increases in shrub cover as top-killed trees and shrubs resprouted and blackberry (*Rubus* spp.) responded to the open conditions following heavy overstory mortality. Several studies also reported increased shrub-nester abundance within a few years of high-severity burns (Greenberg et al., 2018). Interestingly, we did not detect any initial post-wildfire decrease in shrub-nester abundance in any FSC relative to unburned patches, despite substantial reductions in shrub cover immediately following the wildfires. Results of other studies are equivocal, with some (Aquilani et al., 2000; Artman et al., 2001) but not all (Greenberg et al. 2018) showing short-term declines in shrub-nester density after burns.

We documented a strong, positive response to high-severity burn patches by several shrub-nesting bird species, but post-fire increases varied temporally among species. Indigo buntings rapidly colonized higher-severity FSCs and abundance did not detectably increase thereafter, indicating the species is able to quickly pioneer heavily disturbed sites with or without extensive shrub cover (Moorman and Guynn, 2001). Chestnut-sided warbler and eastern towhee abundance increased in H within 3 breeding seasons post-wildfire, as shrub cover became increasingly dense. Other studies also reported greater occupancy or abundance of indigo buntings, chestnut-sided warblers (at higher elevations), and eastern towhees within a few years of high-severity wildfires (Klaus et al., 2010; Rush et al., 2012; Rose and Simons, 2016; Greenberg et al., 2018). Hooded warblers – generally considered to be small-gap specialists (Annand and Thompson, 1997; Robinson and Robinson, 1999) – increased in high- and moderate-severity wildfire patches and abundance was greatest in high-severity patches five years post-wildfire. Results of other studies show inconsistent hooded warbler responses ranging from none (Aquilani et al., 2000), to decreased (Artman et al., 2001; Rose and Simons, 2016), to increased abundance after low-severity burns (Rush et al., 2012).

Several prior studies reported short-term declines in the ground-nesting guild or individual ground-nesting species after burns, likely corresponding with short-term reductions in leaf litter and/or shrub cover (Greenberg et al., 2018). However, results for ground-nesting species are not consistent among studies. For example, some studies reported trends of lower worm-eating warbler and black-and-white warbler abundance following burns (Aquilani et al., 2000, Greenberg et al., 2018), whereas others showed no response (Artman et al., 2001; Rush et al., 2012; Rose and Simons, 2016). Similarly, several studies reported ovenbird declines after burns (Aquilani et al., 2000; Artman et al., 2001; Klaus et al., 2010; Rush et al., 2012; Rose and Simons, 2016), whereas others showed no (Greenberg et al., 2014, 2019) or non-definitive (Greenberg et al., 2018) responses. In our study, abundance of birds within the ground-nesting guild was marginally lower in L than all other FSCs, including NB; this result may not be biologically meaningful, as responses tied to leaf litter reduction would likely have occurred in all burned FSCs, especially H. Although we detected marginally fewer ovenbirds in H than in M and NB, we detected more black-and-white warblers in H than L or NB, which demonstrates the inconsistency of the ground-nesting bird response.

The cavity-nesting guild was most abundant in moderate- and high-severity burned patches, where snag densities were also the greatest. This response was mainly driven by secondary cavity nesters; primary cavity nester (woodpecker) abundance did not differ among FSCs. However, we note that the number of total primary cavity-nesters detected was much lower than the number of secondary cavity-nesters, likely resulting in greater variability that could have affected significance. Detections of most cavity-nesting species and all primary-cavity nesters were too few for statistical testing. Other studies have also reported increased cavity-nester abundance after high-severity burns, but it is unclear whether this was due to a pulse in snag availability, the concomitant creation of open-canopy conditions and associated changes to forest structure, or both. Kilgo and Vukovich (2014) documented an increase in cavity-nesting red-headed woodpeckers (*Melanerpes erythrocephalus*) on experimentally-created high-snag-density plots but did not account for associated changes in forest canopy cover. Greenberg et al. (2018) reported an increase in cavity nesters after high-severity burns with heavy tree mortality, but abundance remained high even as snags fell to pretreatment levels over the 16-year study period. Similarly, Rush et al. (2012) noted that cavity-nesting species did not increase within six years after high-severity wildfire that created abundant snags. In contrast, several studies in the western US reported a strong response by cavity nesters – mainly some woodpecker species – after wildfire (e.g., Hutto and Patterson, 2016; Tingley et al., 2016; Taillie et al., 2018). Our findings indicate that open

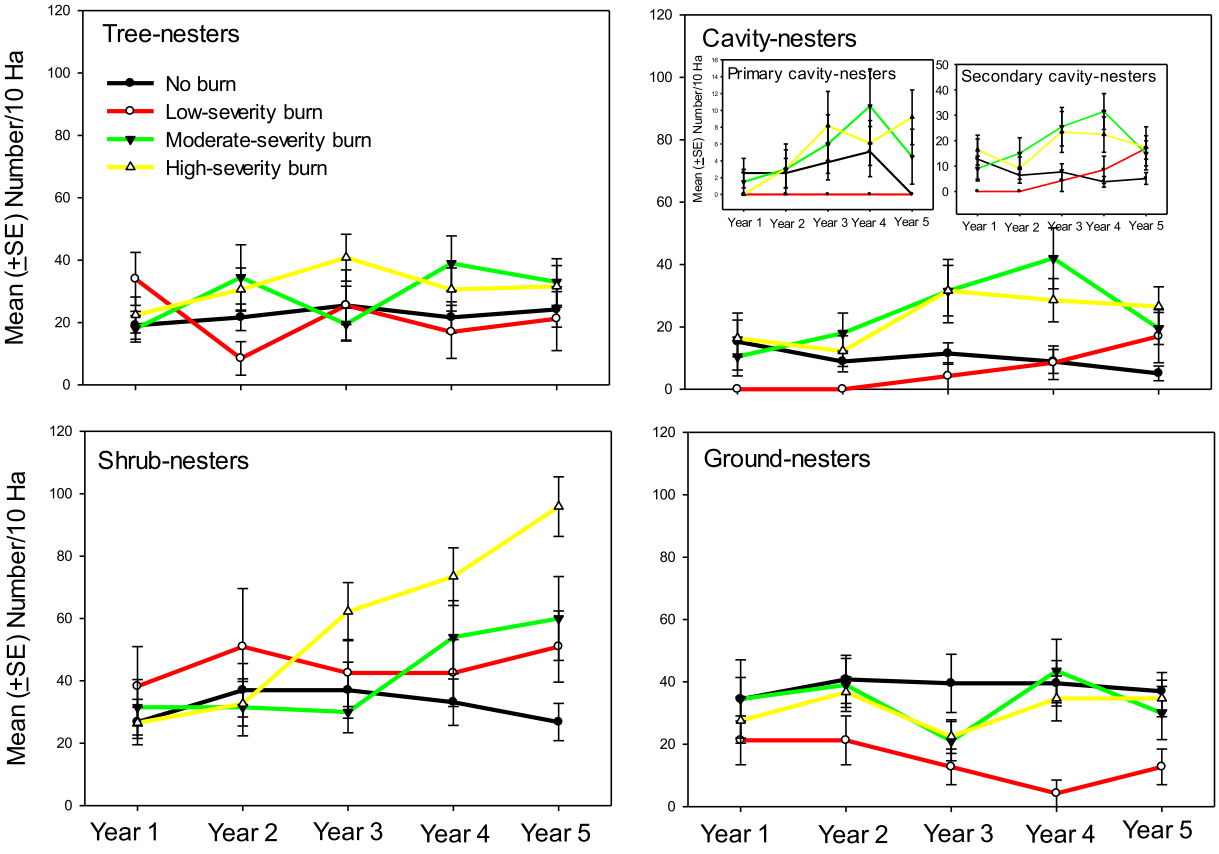


Fig. 4. Mean (±SE) number of birds/10 ha in four nesting guilds (cavity- (including primary and secondary cavity-nesters), shrub-, ground-, and tree-nesters) 1–5 years post-wildfire in four fire-severity categories following 2016 wildfires, Nantahala National Forest, Macon County, North Carolina.

conditions created by high-severity wildfire rather than snag abundance *per se* may at least partly drive cavity-nester response in central hardwood forests.

Our study corroborates others in central hardwood forests (Rush et al., 2012; Rose and Simons, 2016; Greenberg et al., 2018) and western US forests illustrating the interrelated roles of fire severity, time, and dynamic changes to forest structure in driving breeding bird community and species-specific responses. Research in several western forest types showed that post-fire bird responses are influenced by an interaction between fire severity and years since fire (Smucker et al., 2005; Kotliar et al., 2007; Stephens et al., 2015, Hutto and Patterson, 2016; Tingley et al., 2016; Taillie et al., 2018), and breeding bird assemblages within patches of contrasting burn severities differentiate over time (Tingley et al., 2016). We documented a strong, temporally dynamic association between disturbance-dependent species and high-severity burn patches, but no evidence that any species was uniquely associated with unburned or low- or moderate-severity burned patches. Additionally, the delayed increases in species richness and occasional occurrence of disturbance-dependent species in M suggested that bird communities in moderate burn-severity patches are more likely to converge with high-severity patches than diverge over time if delayed tree mortality and associated shrub cover continue to increase. In the absence of repeated disturbances, breeding bird communities in both H and M will converge with those in NB and L as forests mature and become unsuitable for disturbance-dependent species. In contrast with results of studies in western ecosystems (Hutto and Patterson, 2016; Tingley et al., 2016; Taillie et al., 2018), we documented little evidence to suggest that a mosaic of burn severities would result in higher species richness, diversity, or abundance of breeding bird species than high-severity burns alone embedded within an unburned matrix.

The breeding bird community in our study, especially the disturbance-dependent species, responded similarly to that documented following other types of natural or silvicultural disturbances with heavy overstory reduction. For example, species richness and abundance of total birds and disturbance-dependent species in particular increased after heavy overstory windthrow by microbursts (Greenberg and Lanham, 2001) and tornados (Newbold, 1996; Prather and Smith, 2003). Although results may vary with patch size and residual canopy retention, several studies reported similar bird responses following timber harvests such as shelterwood and group selection regeneration harvests (e.g., Annand and Thompson, 1997; Rodewald and Smith, 1998; Moorman and Guynn, 2001; Augenfeld et al., 2008; McDermott and Wood, 2009; Newell and Rodewald, 2012; Perry and Thill, 2013) or woodland and savanna restoration treatments (Vander Yacht et al., 2016). Like high-severity wildfire, these silvicultural practices positively affected abundance or occupancy of disturbance-dependent species with no adverse effects on most other species, resulting in increased species richness and total bird abundance within a few years after the disturbance. Higher-severity burns generally create an abundance of snags compared to regeneration harvest practices, at least in the short-term. However, both generally retain some live-tree canopy within (e.g., shelterwoods) or near (e.g., group selections) the affected forest and create a pulse of resources attractive to birds such as dense shrub cover, high densities of flying/foliar insects, and an abundance of fleshy fruits for several years after disturbance (Greenberg et al., 2011, Moorman et al., 2012).

Longer-term research is needed to determine how breeding bird communities or species would respond in the absence of further disturbances as forests recover and mature over time. Similarly, long-term research is needed to better elucidate how habitat for shrubland birds could be created or prolonged by forest management actions after wildfires. For example, could repeated prescribed burning in high-severity wildfire patches inhibit forest growth and recovery, thereby maintaining the canopy openness and dense shrub cover needed by

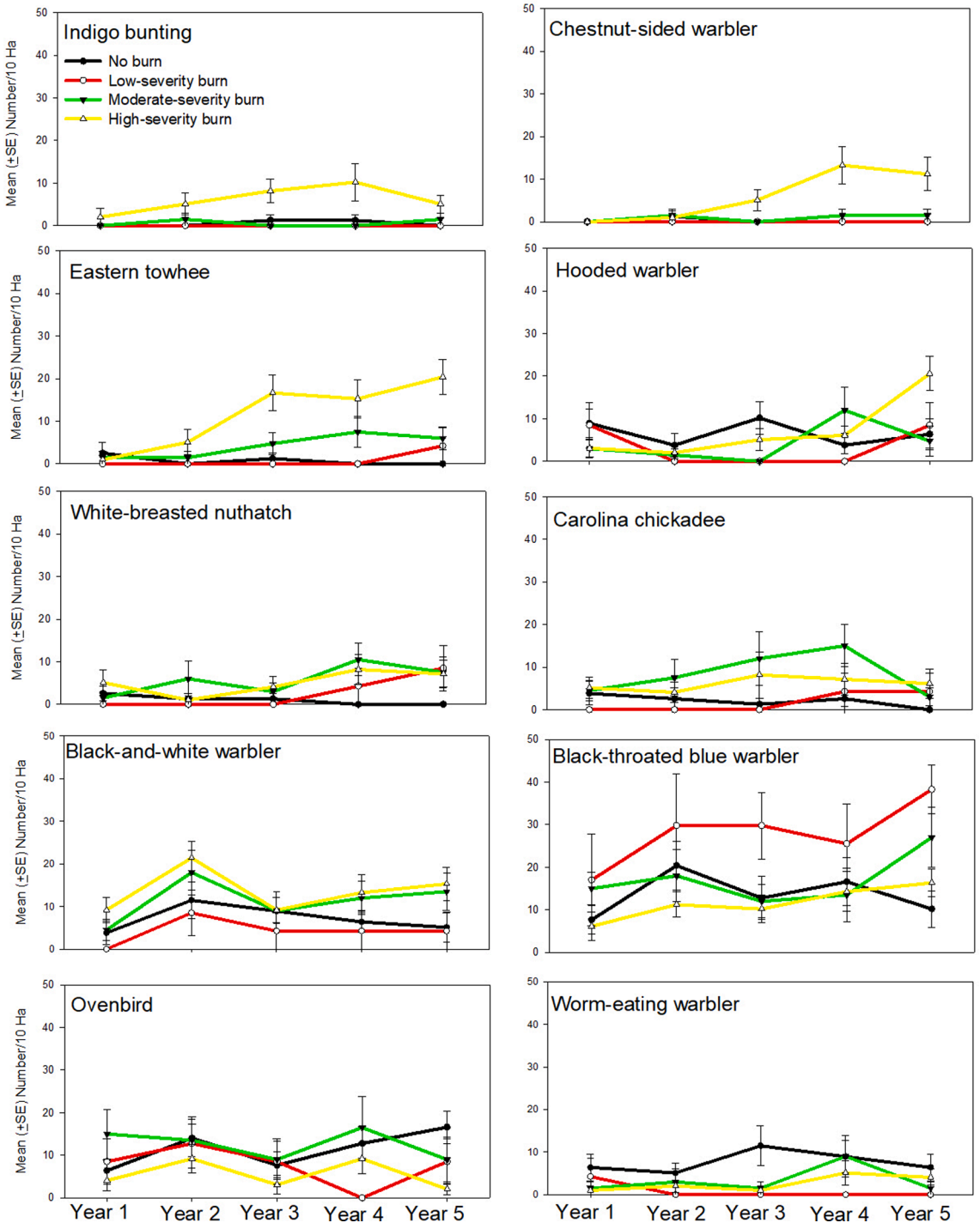


Fig. 5. Mean (±SE) total number of birds/10 ha for all species showing significant ($p < 0.05$) or marginally significant ($p < 0.10$) treatment and (or) treatment × year interaction (see Table 1), 1–5 years post-wildfire in four fire-severity categories following 2016 wildfires, Nantahala National Forest, Macon County, North Carolina.

shrubland birds? Could ongoing burn-related delayed tree mortality, or repeated prescribed burns in moderate-severity wildfire patches eventually result in sufficient canopy reduction to create habitat for shrubland bird species?

5. Conclusions

High-severity burn patches, with substantial tree mortality and a resulting increase in shrub cover, were a key driver in promoting greater breeding bird species richness, total bird abundance, and abundance of disturbance-dependent species, with positive or neutral effects for most other species. In contrast, low-severity wildfire patches with negligible tree mortality did not increase abundance of any species relative to unburned forest. Moderate-severity burns also resulted in increased bird species richness and total bird abundance, but the finer-scale heterogeneity created by initial and delayed tree mortality in these FSCs were insufficient to create the open conditions and dense shrub cover required by species associated with shrubland and young forest. In general, increased bird abundance and species richness became evident in moderate-severity burns as shrub cover and tree mortality exceeded

about 30 % (14 % BA mortality).

Historically and today, "natural", or lightning-ignited wildfires, were uncommon in central hardwood forests. However, humans have managed forests with fire for thousands of years for multiple objectives, likely creating habitat for diverse bird communities (Greenberg et al., 2016a, 2016b, 2021). Forecasts of longer, more frequent droughts associated with climate change, together with mainly human-caused ignitions, will likely increase future wildfire frequency in eastern hardwood forests (Vose et al., 2021), highlighting the importance of understanding wildfire impacts on breeding bird and other wildlife communities. Canopy reduction by other disturbances – both natural (e.g., windthrow) or silvicultural (e.g., timber harvest) – elicits changes in breeding bird community composition similar those seen after high-severity wildfire. Hence, we suggest that silvicultural methods can be used in central hardwood forests to increase breeding bird abundance and richness and create habitat for shrubland bird species without adverse effects on most other bird species and without the risks and loss of timber revenue associated with high-severity wildfire.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

Vegetation plots were established with support from the USDA Forest Service Coweeta Hydrologic Laboratory, Southern Research Station, Nantahala Ranger District, Southern Region 8, and the Water Resources Program Washington Office as well as the National Science Foundation (NSF) Long-Term Ecological Research (LTER) program (award #DEB-0823293), the USDA Institute of Food and Agriculture, Agricultural and Food Research Initiative Competitive Program, Agro-ecosystem Management (award #2017-67019-26544), and The Nature Conservancy. Jim Vose assisted with conception and experimental designing and procuring funding for plot establishment. Data collection for the bird study was made possible with funding from the USFS North Carolina Supervisor's Office, with special thanks to Sheryl Bryan. USFS Mike Wilkins and Bryan Killian provided logistical support. Joel Scott, Edd Watson, Donovan Stone, Logan Kallum, Justice McCormick, Thomas DellaRocco, and Molly Suminski collected vegetation and habitat data. Joe Tomcho and Kathryn Gunther assisted with bird surveys. Frank Roesch, Stanley Zarnoch and Krishna Pacifici provided statistical guidance. Any opinions, findings, conclusions ore recommendations expressed in the material are the authors and do not necessarily reflect the views of the USDA.

References

Annand, E.M., Thompson III, F.R., 1997. Forest bird 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.

Arthur, M.A., Varner, J.M., Lafon, C.W., Alexander, H.D., Dey, D.C., Harper, C.A., Horn, S.P., Hutchinson, T.F., Keyser, T.L., Lashley, M.A., Moorman, C.E., Schweitzer, C.J., 2021. In: C.H. Greenberg, Collins, B.S. (Eds.), Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems. Springer, Managing Forest Ecosystems 39, pp. 105-147.

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.

Augenfeld, K.H., Franklin, S.C., Snyder, D.H., 2008. Breeding bird communities of upland hardwood forest 12 years after shelterwood logging. For. Ecol. Manage. 255, 1271–1282.

Bowen, L.T., Moorman, C.E., Kilgo, J.C., 2007. Seasonal bird use of canopy gaps in a bottomland forest. Wilson J. Ornithol. 119, 77–88.

Caldwell, P.V., Elliott, K.J., Liu, N., Vose, J.M., Zietlow, D.R., Knoepp, J.D., 2020. Watershed-scale vegetation, water quantity, and water quality responses to wildfire in the southern Appalachian mountain region. United States. Hydrol. Proc. 34 (26), 5188–5209.

Cottingham, K.L., Lennon, J.T., Brown, B.L., 2005. Knowing when to draw the line: designing more informative ecological experiments. Front. Ecol. Envir. 3 (3), 145–152.

Dail, D., Madsen, L., 2011. Models for estimating abundance from repeated counts of an open metapopulation. Biometrics 67, 577–587.

Duarte, A., Adams, M.J., Peterson, J.T., 2018. Fitting N-mixture models to count data with unmodeled heterogeneity: Bias, diagnostics, and alternative approaches. Ecol. Model. 374, 51–59.

Fogarty, F.A., Fleishman, E., 2021. Bias in estimated breeding-bird abundance from closure-assumption violations. Ecol. Indic. 131, 108170.

Goldstein, B.R., de Valpine, P., 2022. Comparing N-mixture models and GLMMs for relative abundance estimation in a citizen science dataset. Sci. Rep. 12, 1–12.

Greenberg, C.H., Perry, R.W., Harper, C.A., Levey, D.J., McCord, J.M., 2011. The role of recently disturbed upland hardwood forest as high quality food patches. In: C.H. Greenberg, Collins, B.S., Thompson, F.R., III (Eds.), Sustaining Young Forest Communities: Ecology and Management of Early Successional Habitats in the Central Hardwood Region, USA. Springer, Managing Forest Ecosystems 21, pp. 121-141.

Greenberg, C.H., Collins, B.S., McNab, W.H., Miller, D.K., Wein, G.R., 2016a. Introduction to natural disturbances and historic range of variation: Type, frequency, severity, and post-disturbance structure in central hardwood forests. In: C.H. Greenberg, Collins, B.S. (Eds.), Natural disturbances and historic range of variation. Springer, Managing Forest Ecosystems 32, pp. 1-32.

Greenberg, C.H., Weeks, K., Warburton, G.S., 2016b. The historic role of humans and other keystone species in shaping central hardwood forests for disturbance-dependent wildlife. In: C.H. Greenberg, Collins, B.S. (Eds.), Natural disturbances and historic range of variation. Springer, Managing Forest Ecosystems 32, pp. 319-354.

Greenberg, C.H., Collins, B.S., Goodrick, S., Stambaugh, M.C., Wein, G.R., 2021. Introduction to fire ecology across USA forested ecosystems: Past, present, and future. In: C.H. Greenberg, Collins, B.S. (Eds.), Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems. Springer, Managing Forest Ecosystems 39, pp. 1-30.

Greenberg, C.H., Lanham, D.J., 2001. Breeding bird assemblages of hurricane-created gaps and adjacent closed canopy forest in the southern Appalachians. For. Ecol. Manage. 153, 251–260.

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., Tomcho, J., Livings-Tomcho, A., Lanham, J.D., Waldrop, T.A., Simon, D., Hagan, D., 2018. Long-term avian response to fire severity, repeated burning, and mechanical fuel reduction in upland hardwood forest. For. Ecol. Manage. 424, 367–377.

Greenberg, C.H., Keyser, T.L., McNab, W.H., Scott, P., 2019. Breeding bird response to season of burn in an upland hardwood forest. For. Ecol. Manage. 449, 117442.

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

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.

Hutto, R.L., Patterson, D.A., 2016. Positive effects of fire on birds may appear only under narrow combinations of fire severity and time-since-fire. Int. J. Wildl. Fire 25(10): 1074-1085.

Jones, G.M., Tingley, M.W., 2021. Pyrodiversity and biodiversity: a history, synthesis, and outlook. Div. Distrib. DOI: 10.1111/ddi.13280.

Kilgo, J.C., Vukovich, M.A., 2014. Can snag creation benefit a primary cavity nester: response to an experimental pulse in snag abundance. Biol. Conserv. 171, 21–28.

King, D.I., DeGraaf, R.M., Smith, M.L., Buonaccorsi, J., 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds. J. Zool. 269, 414–421.

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. Ornithol. 122, 518–531.

Kotliar, N.B., Kennedy, P.L., Ferree, K., 2007. Avifaunal responses to fire in southwestern montane forests along a burn severity gradient. Ecol. Applic. 17 (2), 491–507.

Laseter, S.H., Ford, C.R., Vose, J.M., Swift, L.W., 2012. Long-term temperature and precipitation trends at the Coweeta hydrologic laboratory, Otto, North Carolina. USA. Hydrol. Res. 43 (6), 890–901. https://doi.org/10.2166/Nh.2012.067.

MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. Ecology 42 (3), 594–598.

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.

McDermott, M.E., Wood, P.B., 2009. Short- and long-term implications of clearcut and two-age silviculture for conservation of breeding forest birds in the central Appalachians. USA. Biol. Conserv. 142, 212–220.

Moorman, C.E., Bowen, L.T., Kilgo, J.C., Hanula, J.L., Horn, S., Ulyshen, M.D., 2012. Arthropod abundance and seasonal bird use of bottomland forest harvest gaps. Wilson J. Ornithol. 124, 31–39.

Moorman, C.E., Guynn, D.C., 2001. Effects of group-selection opening size on breeding bird habitat use in a bottomland forest. Ecol. Appl. 11, 1680–1691.
NCDC, 2020. 1981–2010 Climate Normals, Franklin NC. Retrieved April 30, 2020 from. www.ncdc.noaa.gov/cdo-web/datatools/normals.
Newbold, C.D., 1996. The effects of tornado and clearcut disturbances on breeding birds in a Tennessee oak-hickory (*Quercus-Carya spp.*) forest. University of Tennessee, Knoxville. Master's thesis.
Newell, F.L., Rodewald, A.D., 2012. Management for oak regeneration: Short-term effects on the bird community and suitability of shelterwood harvests for canopy songbirds. J. Wildl. Manage. 76, 683–1663.
Pagen, R.W., Thompson III, F.R., Burhans, D.E., 2000. Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. Condor 102, 738–747.
Perry, R.W., Thill, R.E., 2013. Long-term responses of disturbance-associated birds after different timber harvests. For. Ecol. Manage. 307, 274–283.
Prather, J.W., Smith, K.G., 2003. Effects of tornado damage on forest bird populations in the Arkansas Ozarks. Southwest. Nat. 48, 292–297.
Robinson, W.D., Robinson, S.K., 1999. Effects of selective logging on forest bird populations in a fragmented landscape. Conserv. Biol. 13, 58–66.
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.
Rose, E.T., Simons, T.R., 2016. Avian response to fire in pine-oak forests of Great Smoky Mountains National Park following decades of fire suppression. Condor 118, 179–193.
Royle, J.A., 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60, 108–115.
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.
Shannon, C.E., 1948. A mathematical theory of communication. Bell System Tech. J. 27, 379–423.
Shifley, S.R., Thompson III, F.R., 2011. Spatial and temporal patterns in the amount of young forests and implications for biodiversity. In: C.H. Greenberg, Collins, B.S., Thompson, F.R., III (Eds.), Sustaining Young Forest Communities: Ecology and Management of Early Successional Habitats in the Central Hardwood Region, USA. Springer, Managing Forest Ecosystems 21, pp. 73-95.
Smucker, K.M., Hutto, R.L., Steele, B.M., 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecol. Applic. 15 (5), 1535–1549.
Spetich, M.A., Perry, R.W., Harper, C.A., Clark, S.L., 2011. Fire in eastern hardwood forests through 14,000 years. In: C.H. Greenberg, Collins, B.S., Thompson, F.R., III (Eds.), Sustaining Young Forest Communities: Ecology and Management of Early Successional Habitats in the Central Hardwood Region, USA. Springer, Managing Forest Ecosystems 21, pp. 41-58.
Stephens, J.L., Ausprey, I.J., Seavy, N.E., Alexander, J.D., 2015. Fire severity affects mixed broadleaf–conifer forest bird communities: Results for 9 years following fire. Condor: Ornithol. Applic. 117 (3), 430–446.
Stoleson, S.H., 2013. Condition varies with habitat choice in postbreeding forest birds. Auk 130 (3), 417–428.
Taillie, P.J., Burnett, R.D., Roberts, L.J., Campos, B.R., Peterson, M.N., Moorman, C.E., 2018. Interacting and non-linear avian responses to mixed-severity wildfire and time since fire. Ecosphere 9, e02291.
Thompson III, F.R., La Sorte, F.A., 2008. Comparison of methods for estimating bird abundance and trends from historical count data. J. Wildl. Manage. 72 (8), 1674–1682.
Tingley, M.W., Ruiz-Gutiérrez, V., Wilkerson, R.L., Howell, C.A., Siegel, R.B., 2016. Pyrodiversity promotes avian diversity over the decade following forest fire. Proc. Royal Soc. B: Biol. Sci. 283 (1840), 20161703.
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.
Vitz, A.C., Rodewald, A.D., 2006. Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. Biol. Conserv. 127, 477–486.
Vose, J.M., Peterson, D.L., Fettig, C.J., Halofsky, J.E., Hiers, J.K., Keane, R.E., Loehman, R., Stambaugh, M.C., 2021. Fire and forests in the 21st century: Managing resilience under changing climates and fire regimes in USA Forests. In: C.H. Greenberg, Collins, B.S. (Eds.), Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems. Springer, Managing Forest Ecosystems 39, pp. 465-502.
Wiens, J.A., 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. 8, 1–93.