

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

Cathryn Greenberg (✉ katie.greenberg@usda.gov)

US Forest Service: US Department of Agriculture Forest Service <https://orcid.org/0000-0002-2831-0989>

Christopher E. Moorman

North Carolina State University at Raleigh: North Carolina State University

Katherine J. Elliott

US Forest Service: US Department of Agriculture Forest Service

Katherine Martin

North Carolina State University

Mark Hopey

Blue Ridge Bird Observatory

Research Article

Keywords: Breeding birds, Disturbance-dependent birds, Hardwood forest, High-severity fire, Mixed-severity fire, Pyrodiversity, Wildfire

Posted Date: May 10th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1614362/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

Abstract

Background

Recent studies showed a connection between pyrodiversity and biodiversity in the western US, but few examined bird response to fire severity in eastern hardwood forests. We measured forest structure and conducted avian point counts for five years (2016–2021; Y1-Y5) in three burned and three unburned watersheds following mixed-severity wildfires to compare breeding bird communities across a fire-severity gradient (no burn (NB), low (L), low-moderate (LM), moderate (M), moderate-high (MH), and high (H)) in the southern Appalachian region.

Results

The percentage of wildfire-killed trees increased with fire-severity category (FSC) and over time; by Y5, 74% (48% BA) were dead in H compared to 11% (3% BA) in L. Post-wildfire shrub recovery was rapid, especially in H and MH where cover exceeded all other FSCs by Y5. Total bird abundance and species richness increased with increasing fire severity (no change in NB and L) and exceeded all other FSCs in H and MH by Y5. Most (12 of 18 tested) species were unaffected by wildfire severity. Disturbance-dependent chestnut-sided warbler (*Setophaga pensylvanica*), indigo bunting (*Passerina cyanea*), and eastern towhee (*Pipilo erythrophthalmus*) increased in H within 3–4 years; white-breasted nuthatch (*Sitta carolinensis*), hooded warbler (*Setophaga citrina*), and blue-headed vireo (*Vireo solitarius*) increased in some burned FSCs and years. Shrub-nesters were more abundant in H than all other FSCs except MH and increased over time in H, MH and LM. Cavity-nesters were more abundant in H, MH and M than L or NB, but primary cavity-nesters (woodpeckers) alone were not.

Conclusions

Our results highlight the interrelated roles of fire severity and time in driving breeding bird response in central hardwood forests, illustrated by sharp contrasts in bird responses between L (no effects) and higher-severity (H and MH) burns that promoted disturbance-dependent species, but also a more gradual increase in total bird abundance and species richness in LM and M corresponding with delayed tree mortality and shrub recovery. We suggest that high-severity burns are more important than pyrodiversity *per se* in promoting bird diversity, as disturbance-dependent species were mainly associated with high-severity burns whereas no species was limited to unburned forests or lower-severity burns (L-M).

Introduction

The linkage between structural heterogeneity of vegetation in deciduous forests of the Central Hardwood Region of North America and breeding bird diversity has been a tenet of ecology for decades (McArthur and McArthur 1961; MacArthur et al. 1962). 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 and natural disturbances in increasing breeding bird diversity at local and landscape scales. Specifically, fire is an important disturbance agent in central hardwood forests of the eastern US and was historically integral in shaping forest structure and composition, and maintaining diverse communities of birds and other wildlife (Greenberg et al. 2016a; Arthur et al. 2021).

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 forest composition and structure or attaining other management outcomes. 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; Greenberg et al. 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; Arthur et al. 2021; Greenberg et al. 2021). Unlike most low-severity prescribed burns, wildfires often create a gradient of forest conditions, or spatial and temporal “pyrodiversity” (Martin and Sapsis 1992; 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; Rose and Simons 2016). 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 spatial patterns 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. Other species, including hooded warbler (*Setophaga citrina*) and cerulean warbler (*Setophaga cerulea*), use small gaps within a mature forest matrix (Hunter 2001; Shifely and Thompson 2011), whereas indigo bunting (*Passerina cyanea*), eastern towhee (*Pipilo erythrophthalmus*), and chestnut-sided warbler (*Setophaga pensylvanica*) are most abundant in recently disturbed, open-canopy forests. However, adults and juveniles of many mature forest species move into canopy gaps or young forest during the post-fledging stage (Anders et al. 1998; Vega Rivera et al. 1998; Marshall et al. 2003; King et al. 2006; Stoleson 2013) or use young forests 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 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 to 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. Our central hypothesis was that the level of disturbance created by higher severity patches of wildfire, including the resulting tree mortality, canopy openness and change in shrub cover, would result in an increase in abundance and diversity of breeding birds. Therefore, we evaluated the variation in forest structure and breeding bird communities (total bird abundance, species richness, 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. The use of fire-severity categories allowed us to examine a fire severity response threshold.

Methods

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). 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, and Arrowwood). 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 1800s. 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. Heavy rainfall (approximately 50 mm) on 28 November 2016 extinguished most of the wildfires in the region. Satellite-based Relative differenced Normalized Burn Ratio (RdNBR) (Miller and Thode 2007) burn severity categories informed by plot-level burn severity index values (see Methods) indicated that 25%-46% of burned study watersheds burned at low-moderate severity or less, 31%-37% at moderate-, 12%-17% at moderate-high-, and 5-25% at high-severity (Caldwell et al. 2020).

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-high-severity (MH), moderate-severity (M), low-moderate-severity (LM), and low-severity (L) burn conditions, 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 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 (15 H, 10 MH, 8 M, 9 LM, and 6 L), and 20 within the three unburned watersheds (6-7 plots each) for bird point counts and forest structure analyses.

Burn-severity index

We developed a composite plot-level burn severity index using measurements of forest floor depth (soil O_i and O_e + O_a horizons), char height (a measure of flame height) on each live and dead tree bole, tree mortality, BA loss, and mineral soil exposure (Caldwell et al. 2020). 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. Plot-level FSCs were defined using composite burn severity index ranges: L: ≤ 1.2 , LM: 1.3–1.9, M: 2.0–2.7, MH: 2.8–3.5, and H: > 3.5 (see Caldwell et al. 2020 for more detail).

Forest structure measurements

We assessed tree status (live or dead) annually (2017-2021) and measured percent cover of forest structure attributes including canopy, shrub (woody plants < 5 cm dbh), and leaf litter within vegetation plots most years (2017-2019 and 2021) during May-October. 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 snag density. Dead trees (and thus snags) included only those killed by wildfires or dying subsequently (i.e., no pre-wildfire snags).

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). Point count times were rotated between the two surveys to minimize time-of-day bias, and surveys were spaced earlier and later in the breeding season to avoid bias associated with differences in singing rates as the breeding season progressed. Most point counts were conducted by a single observer (M. Hopey), but three other observers conducted counts during the study. We did not estimate detectability (Allredge et al. 2008) and assumed that bird detection error was minimal and consistent among plots due to a small (25m) point count radius, one primary observer, and repeated surveys each year. Density of birds (total, nesting guilds or species) per point count was calculated by averaging across both surveys per point count per year and extrapolating to number per 10 ha. Species richness represented the total number of species detected during both visits per plot each year.

Statistical analysis

We used 1-way analysis of variance (ANOVA) to examine whether pre-wildfire live tree density and basal area (BA) differed among FSCs. Pre-wildfire live tree densities and BA were calculated as the sum of live trees + fire-killed dead trees (i.e., 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 to compare forest structure measurements among the six FSCs (NB, L, LM, M, MH, and H) and years (Y1-Y3, Y5) and tested for FSC x year interactions. Forest structure measurements included percent cover of shrubs, leaf litter, and canopy, as well as density (number/ha) and BA (m^2/ha) (not including tree growth or ingrowth) of dead trees (those dying during or after the wildfire, not including pre-wildfire snags), and the percentage of dead trees and BA relative to the total that included live trees.

We used 2-way repeated measures mixed-effects ANOVAs to compare breeding bird 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) among the six FSCs and five years (Y1-Y5) and tested for FSC x year interactions. For these analyses, we considered plot as the experimental unit, plot within watershed as a random factor, and FSC, year, and the FSC x 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 x year interaction effects on bird communities as indicators that 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 x 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 (Zar 1998) for ANOVAs to reduce heteroscedasticity.

We used stepwise multiple regression using plot as the experimental unit to explore relationships between select forest structure attributes (i.e., the percentage of dead trees and dead BA, snag density, and percent cover of shrubs, leaf litter, and canopy) and total bird abundance, species richness, abundance of birds within nesting guilds (tree-, ground, shrub and cavity-nesters), primary and secondary cavity nesters, and abundance of sufficiently common species. We limited these regressions to Y5 when post-wildfire changes to forest structure and bird responses were most pronounced, and to reduce the known confounding effects of delayed bird response to substantial forest canopy reduction (e.g., Greenberg et al. 2014, 2018; this study).

Results

Forest structure

Pre-wildfire average (\pm SE) live tree density and BA were $964 \pm 59/\text{ha}$ (range 713-1,122/ha) and 42.5 ± 2.9 (range $34 \pm 51 \text{ m}^2/\text{ha}$) across watersheds, respectively, and did not differ among FSCs assigned after the burn ($p \geq 0.58$).

Tree mortality and snag density

Initial (Y1) tree mortality in burned watersheds ranged from an average of 3% (0.1% BA) in L, to 7% (1% BA) in LM and 52% (25% BA) in H; by Y5, 11% (3% BA) of trees in L, 33% (15% BA) in LM, and 74% (48% BA) in H had died. In

comparison, 7% (3% BA) of trees in unburned watersheds died over the 5-year study period, and tree mortality rates did not differ between NB and L. The percentage of trees killed by (and dying subsequent to) wildfire differed among years and was greater in H than all other FSCs, greater in MH than NB, L, LM, and M, greater in M than NB and L, and greater in LM than L (Table 1, Fig. 1). A FSC x year interaction effect and partitioned F-tests (SLICE option) indicated that tree mortality increased over time in all FSCs except L and differed among some FSCs within all years. Within H and MH, the percentage of dead trees was lower in Y1 than Y2, Y3 and Y5, and lower in Y2 than Y5. Within LM, the percentage of dead trees was lower in Y1 than all subsequent years and lower in Y2 and Y3 than Y5. Within M, the percentage of dead trees was lower in Y1 than Y3 or Y5 and lower in Y2 and Y3 than Y5. Within NB, the percentage of dead trees was lower in Y1 and Y2 than Y3 or Y5. In Y1, the percentage of dead trees was greater in H than all other FSCs, greater in MH and M than NB, L and LM, and greater in LM than NB. In Y2, Y3 and Y5, the percentage of dead trees was greater in H than all FSCs except MH, greater in MH than NB, L, LM, and M, greater in M than NB and L, and greater in LM than NB; in Y3 and Y5 there was additionally a greater percentage of dead trees in LM than L. The percentage of tree BA killed by or dying subsequent to wildfire differed among years and was greater in H and MH than L, LM, M and NB; no significant FSC x year interaction effect was detected (Table 1, Fig. 1).

The density (no/ha) of trees killed by wildfire or dying subsequently differed among years and was greater in H than all other FSCs, greater in MH than NB, LM and L, and greater in M than NB (Table 1; Fig. 1). A FSC x year interaction effect and partitioned F-tests indicated that tree mortality increased over time within all FSCs except L and differed among some FSCs during all years. Within H, L and M, mortality was lower in Y1 than all subsequent years, and lower in Y2 and Y3 than Y5. Within MH, mortality was lower in Y1 than all subsequent years and lower in Y2 than Y5; within NB mortality was lower in Y1 and Y2 than Y3 and Y5. Tree mortality was higher in H than all other FSCs within all post-wildfire years. Additionally, in Y1 mortality was greater in MH than NB and L. In Y2 and Y3, mortality was greater in MH than NB, L and LM, and greater in M than NB. In Y5, mortality was greater in LM, M and MH than NB and greater in MH than L (Table 1, Fig. 1). Tree BA (m^2/ha) mortality differed among years and was greater in H and MH than L, LM, M and NB (Table 1; Fig. 1). A FSC x year interaction effect and partitioned F-tests indicated that cumulative BA mortality increased over time within LM, M, MH, and H and differed among some FSCs in all years. Within H, BA mortality was lower in Y1 than all subsequent years and lower in Y2 than Y5. Within MH, BA mortality was lower in Y1 than all subsequent years, and lower in Y2 and Y3 than Y5. Within M, BA mortality was lower in Y1, Y2 and Y3 than Y5, and within LM it was lower in Y1 and Y2 than Y5. In Y1 BA mortality was greater in H than all other FSCs. In Y2, Y3 and Y5 BA mortality was greater in H than all other FSCs except MH, and greater in MH than NB, L, LM and M; in Y5 it was also greater in M than NB (Table 1, Fig. 1).

In Y5, snag density was greater in H than NB, L and LM, greater in MH than NB or L, and greater in M than NB ($p < 0.0001$) (Fig. 2).

Shrub cover

Shrub cover immediately after wildfires (Y1) ranged from 4-10% among FSCs in burned watersheds, compared to 35% in unburned watersheds. Post-wildfire shrub recovery was rapid and most pronounced in H and MH, averaging 75% and 64% cover, respectively, by Y5 and exceeding all other FSCs (21%-44%) as top-killed trees and shrubs resprouted and *Rubus* spp. responded to the open conditions (Fig. 3). Percent shrub cover was greater in H, MH, and NB than L, LM and M and differed among years (Table 1, Fig. 3). A FSC x year interaction effect and partitioned F-tests indicated that percent shrub cover increased over time within all FSCs and differed among some FSCs during all years. Within H, percent shrub cover increased each year post-wildfire; within MH, it was lower in Y1 and Y2 than all subsequent years. Within L, LM and M, shrub cover was lower in Y1 than Y3 or Y5 and lower in Y2 than Y5. Within

NB, shrub cover was lower in Y1 and Y2 than Y3. In Y1, shrub cover was greater in NB than all burned FSCs and greater in H than L; in Y2, it was greater in H, MH, and NB than L, and greater in NB than LM or M. In Y3, shrub cover was greater in H than L, LM, M and MH, greater in M and NB than L, and greater in MH and NB than LM or M. In Y5, percent shrub cover was greater in H and MH than all other FSCs and greater in NB than L (Table 1, Fig. 3).

Leaf litter cover

Leaf litter cover was initially (Y1) reduced in all FSCs ($\leq 27\%$) compared to NB (85%) but was rapidly replenished as leaves fell from deciduous trees each fall; by Y5, leaf litter cover was $\geq 86\%$ in all FSCs except H (67%) and MH (71%) (Fig. 3). Percent leaf litter cover differed among years and was greater in NB than all other FSCs and lower in H than all FSCs except MH; a FSC x year interaction effect and partitioned F-tests indicated that leaf litter cover changed over time within all FSCs and differed among some FSCs in Y1, Y2, and Y5 (Table 1, Fig. 3). Within H, leaf litter cover was lower in Y1 and Y2 than all subsequent years; within MH, it was lower in Y1 than all subsequent years and lower in Y2 than Y3. Within L, leaf litter cover was lower in Y1 than all subsequent years and lower in Y2 than Y5. Within LM and M, leaf litter cover was lower in Y1 than all subsequent years, and within NB it was lower in Y1 and Y2 than Y3, and lower in Y3 than Y5. In Y1, leaf litter cover was greater in NB than all other FSCs. In Y2 and Y5, leaf litter cover was greater in L, LM, M and NB than H, and greater in NB than MH; in Y5, it was additionally greater in L than MH.

Canopy cover

Percent canopy cover (measured at breast height) decreased by Y2 in all burned FSCs corresponding with delayed tree mortality but remained $>90\%$ throughout the study period in all FSCs except MH (79% in Y2) and H (57% in Y2). Canopy cover slowly increased as shrub cover increased and exceeded breast height but remained lower in H (73%) and MH (87%) than other FSCs ($\geq 95\%$) by Y5 (Fig. 3). Canopy cover differed among years and was lower in H than all FSCs except MH, lower in MH than NB, L and M, and lower in M than NB. A FSC x year effect and partitioned F-tests indicated that percent canopy cover changed over time within all FSCs and differed among some FSCs within Y2, Y3 and Y5 (Table 1, Fig. 3). Within H, canopy cover was greater in Y1 and Y2 than all subsequent years; within MH, it was greater in Y1 than all subsequent years and greater in Y3 than Y5. Within L, canopy cover was greater in Y1 than Y2 or Y3. Within LM and M, canopy cover was greater in Y1 than all subsequent years. Canopy cover was lower in H than all other FSCs during all post-wildfire years except Y2 when it did not differ from MH. In Y2 and Y5, canopy cover was lower in MH than L or LM; in Y3, it was lower in MH than NB, L, LM and M.

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 and greater in MH than L (Table 2; Fig. 4). A FSC x year interaction effect and partitioned F-tests indicated that total abundance changed over time within all FSCs except NB and L and differed among FSCs in Y4 and Y5. Within H and MH, total abundance was lower in Y1 than Y3, Y4 and Y5, and lower in Y2 than Y4 and Y5. Within M, total abundance was lower in Y1, Y2 and Y3 than Y4, and in LM, abundance was lower in Y1 and Y3 than Y4 or Y5. In Y4, abundance was greater in LM, M, MH, and H than L and NB. In Y5, abundance was greater in H than NB, L or M and greater in LM and MH than NB. Stepwise multiple regression (Y5 only) indicated that total bird abundance was positively correlated with the percentage of dead trees (Table 3).

Species richness was greater in H than NB or L and differed among years (Table 2, Fig. 4). A FSC x year interaction effect and partitioned F-tests indicated that species richness changed over time in H, MH, and LM and differed

among FSCs in Y4 and Y5. Within H, species richness was lower in Y1 than Y3, Y4, and Y5 and lower in Y2 and Y3 than Y5. Within MH, richness was lower in Y1 than Y3, Y4, and Y5 and lower in Y2 than Y5. Within LM, richness was lower in Y1 than Y4 or Y5 and lower in Y3 than Y4. In Y4, species richness was greater in H than NB or L, greater in LM, M and MH than L, and greater in LM and M than NB. In Y5, richness was greater in H than NB, L, LM or M and greater in LM and MH than NB. Stepwise multiple regression indicated that species richness was positively correlated with the percentage of dead trees, and negatively correlated with percent canopy cover (Table 3).

Abundance of ground- and tree-nesters did not differ among FSCs or years and no FSC x year interaction effects were detected (Table 2, Fig. 5); stepwise multiple regression showed no correlations between ground- or tree-nesters and forest structure attributes (Table 3). Cavity-nester abundance differed among years and was greater in H, MH and M than NB or L; no FSC x year interaction effect was detected (Table 2; Fig. 5). Stepwise multiple regression showed a weak positive correlation between cavity-nester abundance and snag density (Table 3). Primary cavity-nester (woodpeckers) abundance differed among years but not among FSCs, and no FSC x year interaction effect was detected (Table 2; Fig. 6). Stepwise multiple regression showed a weak positive relationship between primary cavity-nester abundance and percent shrub cover (Table 3). Secondary cavity-nester abundance was greater in H than L and NB, greater in M and MH than NB, and greater in M than L; year or FSC x year effects were not detected (Table 2; Fig. 6). Stepwise multiple regression showed no significant relationship between secondary cavity-nester abundance and any tested forest structure variable (Table 3).

Shrub-nester abundance differed among years and was greater in H than NB, L, LM and M (Table 2; Fig. 5). A FSC x year interaction effect with partitioned F-tests indicated that shrub-nester abundance changed over time within H, MH and LM and differed among FSCs in Y4 and Y5. Within H, shrub-nester abundance was lower in Y1 and Y2 than Y3, Y4, or Y5 and lower in Y3 and Y4 than Y5. Within MH, shrub-nester abundance was lower in Y1 and Y2 than all subsequent years, and within LM, abundance was lower in Y1, Y2, and Y3 than Y5. In Y3, shrub-nester abundance was greater in H than NB or L; in Y5, it was greater in H than all other FSCs and greater in LM and MH than NB. Stepwise multiple regression indicated that shrub-nester abundance was positively correlated with the percentage of dead trees and negatively correlated with percent canopy cover (Table 3).

Six of the 18 species analyzed responded differently among FSCs and (or) showed a FSC x year interaction effect; a year effect was detected for several species (Table 2; Fig. 7). Indigo bunting abundance differed among years and was greater in H than all other FSCs except MH; no FSC x year interaction effect was detected. Chestnut-sided warbler abundance differed among years and was greater in H than all other FSCs and greater in MH than NB. A FSC x year interaction effect and partitioned F-tests indicated that within H, chestnut-sided warbler abundance was lower in Y1, Y2, and Y3 than Y4 and Y5. In Y4, chestnut-sided warbler abundance was greater in H than all other FSCs and greater in MH than NB; in Y5, abundance was greater in H than all other FSCs except MH and greater in MH than NB. Eastern towhee abundance differed among years, and was greater in H than all other FSCs and greater in MH than NB. A FSC x year interaction effect and partitioned F-tests indicated that within H, eastern towhee abundance was lower in Y1 and Y2 than Y3, Y4, and Y5; within MH, abundance was lower in Y1 than Y3 and Y5, and lower in Y2 and Y4 than Y5. In Y3, eastern towhee abundance was greater in H than NB, L and LM; in Y4, it was greater in H than all other FSCs, and in Y5 it was greater in H than all other FSCs except MH, and greater in MH than NB. White-breasted nuthatch (*Sitta carolinensis*) abundance was greater in M and MH than H, LM, L and NB; no year or FSC x year interaction effects were detected. Blue-headed vireo (*Vireo solitarius*) abundance did not differ among FSCs or years, but a FSC x year interaction effect with partitioned F-tests indicated that in Y5 abundance was greater in H than NB and greater in LM than L, MH and NB. Hooded warbler abundance did not differ among FSCs, but a FSC x year interaction effect and partitioned F tests indicated that within H and MH abundance was greater in Y5 than all other

years. In Y5, hooded warbler abundance was greater in H than NB, LM and M, and greater in MH than NB, L, LM and M.

Stepwise multiple regression (Y5 only) indicated that 12 of the 18 species analyzed were significantly correlated with one or more forest structure attributes but correlations were weak ($R^2 \leq 0.15$) for all except Carolina chickadee (*Poecile carolinensis*), chestnut-sided warbler, eastern towhee, and indigo bunting ($R^2 \geq 0.28$) (Table 3). Carolina chickadee abundance was positively correlated with percentage of dead BA and percent canopy cover, and negatively correlated with snag density. Chestnut-sided warbler abundance was positively correlated with percentage of dead BA. Eastern towhee abundance was positively correlated with percentage of dead trees and percent shrub cover. Indigo bunting abundance was negatively correlated with percent canopy cover.

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 forest structures and pyrodiverse landscapes driven by initial and delayed tree mortality and shrub recovery. Spatial and temporal changes in post-wildfire breeding bird communities generally reflected fire severity and associated immediate and delayed changes in forest structure over time. The greatest contrasts were between low-severity patches where no changes were detected, and higher-severity (H and MH) patches where community-level and species' responses were rapid and more pronounced than in intermediate FSCs (LM and M); by Y5, total bird abundance and species richness were more than twice as high in H than NB. In addition, three disturbance-dependent species – indigo bunting, chestnut-sided warbler, and eastern towhee – were primarily associated with higher-severity burn patches (H and MH). No species was adversely affected by any FSC, and none were strongly associated with intermediate-severity (LM and M) FSCs. However, we documented a gradual increase in total bird abundance and species richness in intermediate-severity FSCs (LM and M) corresponding with delayed tree mortality and shrub recovery. In general, community-level responses became evident 3–4 years after wildfires in FSCs of LM or higher severity after shrub cover and tree mortality reached or exceeded about 33% with at least 13% BA mortality. Our study corroborates others in eastern (Rush et al. 2012; Rose and Simons 2016;) and western (Hutto and Patterson 2016; Tingley et al. 2016; Taillie et al. 2018) forests of North America, illustrating the interrelated roles of fire severity, time, and dynamic changes to forest structure in driving breeding bird response following disturbance.

We documented no appreciable difference (except timing of responses) in breeding bird communities or distributions of most species among FSCs of LM or greater, and little evidence of any species uniquely or strongly associated with LM or M FSCs. Exceptions were disturbance-dependent species that were strongly associated with higher-severity FSCs. In contrast, studies in the western US report that different bird species are sensitive to different combinations of fire severity and years since fire, and breeding bird assemblages within patches of contrasting burn severities differentiate over time (Hutto and Patterson 2016; Tingley et al. 2016; Taillie et al. 2018). Our study period was relatively short (5 years), highlighting the need for longer-term research on post-wildfire changes in breeding bird communities across FSCs, with potentially ongoing delayed tree mortality and stand dynamics as forests recover and mature. However, our short-term results showing delayed increases in species richness and abundance, and the occasional occurrence of disturbance-dependent species in LM or M suggested that bird communities in these intermediate burn-severity patches are more likely to converge than diverge over time if delayed tree mortality and associated shrub recovery continues to increase.

Our results corroborate several other studies showing 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 of high-severity burns (Klaus et al. 2010; Rose and Simons 2016; Rush et al. 2012; 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 an upland hardwood forest, likely as ongoing delayed tree mortality created conditions analogous to LM 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.

Although we did not detect decreased abundance of any bird species, we documented a strong, positive response to high-severity burn patches by three disturbance-dependent bird species within a few years of the wildfires. 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 heavy shrub cover. Chestnut-sided warbler and eastern towhee abundance increased 3–4 breeding seasons post-wildfire within the high-severity FSC, indicating these two species require both open conditions and dense shrub cover. Other studies also reported greater occupancy or abundance of indigo buntings, eastern towhees, and other shrub-nesting species following high-severity burns (Klaus et al. 2010; Rush et al. 2012; Rose and Simons 2016; Greenberg et al. 2018); chestnut-sided warblers generally occur at higher elevations and did not occur in most prior burn studies conducted at lower elevations than ours.

Three species not typically considered disturbance-dependent (white-breasted nuthatch, blue-headed vireo, and hooded warbler) also responded positively to wildfire. White-breasted nuthatches abundance was greater in M and MH than other FSCs. Greenberg et al. (2018) similarly reported greater abundance of white-breasted nuthatches in high-severity burns; our results suggest the species may also respond positively to intermediate-severity burns. In this study, hooded warblers increased in H and MH 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); Rush et al. (2012) reported hooded warbler avoidance of high-severity burns (Rush et al. 2012), whereas Greenberg et al. (2018) found similar densities of hooded warblers in high-severity burns and lower densities in low-severity burns compared to unburned forest. Blue-headed vireos, a midstory-nesting species, were more abundant in H than NB and more abundant in LM than NB, L or MH; this response is difficult to interpret and may not be biologically meaningful. Other studies did not indicate that blue-headed vireos respond to fire or fire severity (Klaus et al. 2010). Our results corroborate other studies indicating that disturbance-dependent species respond mainly to open forest conditions created by heavy disturbances such as high-severity wildfire (Rush et al. 2012; Greenberg et al. 2018); a few other species may also respond positively to moderate-to-high severity burns, whereas most are resilient, showing little response to substantial overstory reductions. However, unlike 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 a greater diversity of breeding bird species than high-severity burns alone embedded within an unburned matrix.

In our study, the shrub-nesting guild was more abundant in higher severity FSCs, especially 3–4 years post-wildfire, likely because of the rapid increase in shrub cover associated with new and resprouting stems and increased sunlight penetration 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 NB, 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; Greenberg et al. 2007) but not all (Greenberg et al. 2018) showing short-term declines in shrub-nester density after burns.

Tree-nesting and ground-nesting species abundances were unrelated to wildfire severity in our study. Although the tree-nesting guild's resilience to heavy canopy reduction has previously been documented (Greenberg et al. 2018), the lack of response by ground-nesting species was surprising. In contrast to our results, 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, reported responses differed among ground-nesting species and results were not consistent among studies. For example, some studies reported trends of lower worm-eating warbler (*Helmitheros vermivorum*) and black-and-white warbler (*Mniotilta varia*) abundance following burns (Aquilani et al. 2000, Greenberg et al. 2018), whereas others corroborated our results showing 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 show no (Greenberg et al. 2014, 2019) or non-definitive (Greenberg et al. 2018) responses.

Our results indicated that the cavity-nesting guild, including both primary and secondary cavity-nesters, was most abundant in higher-severity FSCs (H, MH and M) with high snag densities; abundance was positively correlated with snag density in Y5. Other studies have also reported increased cavity-nester abundance after high-severity burns, but it is unclear whether this is 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) reported 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 report 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 suggest that open conditions created by high-severity wildfire rather than snag abundance *per se* may at least partly drive cavity-nester response in central hardwood forests, and indicate that once some threshold is reached, snags may not be a limiting factor for the cavity-nesting guild.

Our cavity-nester results were likely driven by common secondary cavity-nesting species rather than primary cavity-nesters – woodpeckers that drill for insect larvae and excavate cavities in dead trees. When analyzed separately, we documented a positive response by secondary cavity-nesters to higher-severity FSCs and no correlation with any forest structure variable, but no woodpecker response, and a weak correlation between abundance and percent shrub cover. Detections of most cavity-nesting species were too few for statistical testing; only three, all secondary cavity-nesters (Carolina chickadee, eastern tufted titmouse and white-breasted nuthatch), were analyzed. Among these, only white-breasted nuthatches responded to any FSC, with increased abundance in M and MH. Our results suggest that analyses of guilds containing many species may mask the varied responses by individual species.

The breeding bird community in our study, especially the disturbance-dependent species, responded similarly to that documented following other types of natural disturbance (e.g., windthrow) and overstory reduction via timber harvest. For example, species richness and abundance of total birds and disturbance-dependent species in particular

increased after heavy canopy reduction 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 shrubland species with no adverse effects on most other species, with the exception of ovenbirds and perhaps some other ground-nesting species, resulting in increased species richness and total bird abundance or occupancy 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 (Champlain et al. 2009; Greenberg et al. 2011, Moorman et al. 2012).

Conclusions

Our results indicated that high or moderately high-severity burn patches with heavy tree mortality promote breeding bird species richness, total bird abundance, and abundance of disturbance-dependent species within three years, with positive or undetected effects for other species in central hardwood forests. In contrast, low-severity wildfire patches with negligible tree mortality do not promote breeding bird diversity or abundance of any species relative to unburned forest. Low-moderate and 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 recently disturbed young forest, at least in the short-term. In general, increased bird abundance and species richness became evident 3–4 years after wildfires in FSCs of LM or higher after shrub cover and tree mortality reached or exceeded about 33% with at least 13% BA mortality. Longer-term research is needed to determine whether ongoing tree mortality or repeated burning in LM or M would eventually result in habitat for disturbance-dependent bird species, and how communities or species would respond in the absence of further disturbance as forests recover and mature over time.

Whereas pyrodiversity – variable levels of initial and delayed tree mortality and associated increases in shrub cover over time – created by mixed-severity wildfires promoted bird abundance and species richness of birds in general, our results indicated that the high-severity burns with heavy tree mortality were the key driver of positive breeding bird responses to wildfire in central hardwood forests. Historically, “natural”, or lightning-ignited wildfires, were uncommon in central hardwood forests, but humans managed forests with fire for thousands of years for multiple objectives, likely including habitat creation for game species or other wildlife (Greenberg et al. 2016a, 2016b, 2021). Forecasts of longer, more frequent droughts associated with climate change will likely increase future wildfire frequency in the southeast (Vose et al. 2021), highlighting the importance of understanding their impacts on breeding bird and other wildlife communities.

Many studies show that canopy reduction by other disturbances – both natural (e.g., windthrow) or silvicultural (e.g., timber harvest) - elicit changes in breeding bird community composition similar those seen after high-severity wildfire. Hence, we suggest that silvicultural means can be used in central hardwood forests to achieve management and restoration goals of increasing breeding bird abundance, richness, and habitat for disturbance-dependent

species without adverse effects on most other bird species and without the risks and loss of timber revenue associated with high-severity wildfire.

Declarations

Funding and 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 and Krishna Pacifici provided statistical guidance. Pete Caldwell provided assistance with locating vegetation data files. Any opinions, findings, conclusions or recommendations expressed in the material are the authors and do not necessarily reflect the views of the USDA.

Authors' contributions

KJE provided the overall study design and obtained funding to install vegetation plots and initial tree data gathering. KM subsequently oversaw implementation of the vegetation portion of the study. CHG and CEM obtained funding designed protocols for bird and habitat structure data gathering. MEH performed and oversaw field data collection. CHG analyzed data and led manuscript preparation and CEM, KM, KJE, and MEH provided editorial assistance. All authors read and approved the final manuscript.

Availability of data and materials

Available from the corresponding author upon request

Ethics approval and consent to participate

Not applicable as no live vertebrates were handled for this research

Consent for publication

Not applicable

Competing interests

The authors declare no competing interests

References

1. Alldredge, M. W., K. Pacifici, T. R. Simons, and K. H. Pollock. 2008. A novel field evaluation of the effectiveness of distance and independent observer sampling to estimate aural avian detection probabilities. *Journal of Applied Ecology* 45: 1349–1356.
2. Anders, A. D., J. Faaborg, and F. R. Thompson III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile wood thrushes. *The Auk* 115: 349–358.
3. Annand, E. M., and F. R. Thompson III. 1997. Forest bird response to regeneration practices in central hardwood forests. *The Journal of Wildlife Management* 61: 159–171.
4. Aquilani, S. M., D. C. LeBlanc, and T. E. Morrell. 2000. Effects of prescribed surface fires on ground- and shrub-nesting neotropical migratory birds in a mature Indiana oak forest, USA. *Natural Areas Journal* 20: 317–324.
5. Artman, V. L., E. K. Sutherland, and D. F. Downhower. 2001. Prescribed burning to restore mixed-oak communities in southern Ohio: Effects on breeding-bird populations. *Conservation Biology* 15: 1423–1434.
6. Arthur, M. A., J. M. Varner, C. W. Lafon, H. D. Alexander, D. C. Dey, C. A. Harper, S. P. Horn, T. F. Hutchinson, T. L. Keyser, M. A. Lashley, C. E. Moorman, and C. J. Schweitzer. 2021. Fire Ecology and Management in Eastern Broadleaf and Appalachian Forests. In *Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems*, eds. C. H. Greenberg, and B. Collins, 105–147. Cham: Springer.
7. Augenfeld, K. H., S. C. Franklin, and D. H. Snyder. 2008. Breeding bird communities of upland hardwood forest 12 years after shelterwood logging. *Forest Ecology and Management* 255: 1271–1282.
8. Bowen, L. T., C. E. Moorman, and J. C. Kilgo. 2007. Seasonal bird use of canopy gaps in a bottomland forest. *Wilson Journal of Ornithology* 119: 77–88.
9. Caldwell, P. V., K. J. Elliott, N. Liu, J. M. Vose, D. R. Zietlow, and J. D. Knoepp. 2020. Watershed-scale vegetation, water quantity, and water quality responses to wildfire in the southern Appalachian mountain region, United States. *Hydrological Processes* 34 (26): 5188–5209.
10. Champlin, T. B., J. C. Kilgo, and C. E. Moorman. 2009. Food abundance does not determine bird use of early-successional habitat. *Ecology* 90: 1586–1594.
11. Greenberg, C. H., and D. J. Lanham. 2001. Breeding bird assemblages of hurricane-created gaps and adjacent closed canopy forest in the southern Appalachians. *Forest Ecology and Management* 153: 251–260.
12. Greenberg, C. H., A. L. Tomcho, J. D. Lanham, T. A. Waldrop, J. Tomcho, R. J. Phillips, and D. Simon. 2007. Short-term effects of fire and other fuel reduction treatments on breeding birds in a southern Appalachian upland hardwood forest. *The Journal of Wildlife Management* 71 (6): 1906–1916.
13. Greenberg, C. H., R. W. Perry, C. A. Harper, D. J. Levey, and J. M. McCord. 2011. The role of recently disturbed upland hardwood forest as high quality food patches. In *Sustaining Young Forest Communities*, ed. CH Greenberg Collins B, 121–141. Dordrecht: Springer.
14. Greenberg, C. H., J. Tomcho, A. Livings-Tomcho, J. D. Lanham, T. A. Waldrop, D. Simon, and D. Hagan. 2018. Long-term avian response to fire severity, repeated burning, and mechanical fuel reduction in upland hardwood forest. *Forest Ecology and Management* 424: 367–377.
15. Greenberg, C. H., K. E. Franzreb, T. L. Keyser, S. J. Zarnoch, D. M. Simon, and G. S. Warburton. 2014. Short-term response of breeding birds to oak regeneration treatments in upland hardwood forest. *Natural Areas Journal* 34: 409–422.
16. Greenberg, C. H., K. Weeks, and G. S. Warburton. 2016b. The historic role of humans and other keystone species in shaping central hardwood forests for disturbance-dependent wildlife. In *Natural disturbances and historic range of variation*, eds. C. H. Greenberg, and B. Collins, 319–354. Cham: Springer.

17. Greenberg, C. H., T. L. Keyser, W. H. McNab, and P. Scott. 2019. Breeding bird response to season of burn in an upland hardwood forest. *Forest Ecology and Management* 449: 117442.
18. Greenberg, C. H., B. S. Collins, W. H. McNab, D. K. Miller, and G. R. Wein. 2016a. Introduction to natural disturbances and historic range of variation: Type, frequency, severity, and post-disturbance structure in central hardwood forests. In *Natural disturbances and historic range of variation*, eds. C. H. Greenberg, and B. Collins, 1–32. Cham: Springer.
19. Greenberg, C. H., B. S. Collins, S. Goodrick, M. C. Stambaugh, and G. R. Wein. 2021. Introduction to fire ecology across USA forested ecosystems: Past, present, and future. In *Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems*, eds. C. H. Greenberg, and B. Collins, 1–30. Cham: Springer.
20. Hamel, P. B. 1992. *The Land Manager's Guide to the Birds of the South*. Chapel Hill, NC: The Nature Conservancy, Southeastern Region.
21. Hunter, W. C., D. A. Buehler, R. A. Canterbury, J. L. Confer, and P. B. Hamel. 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin* 29: 440–455.
22. Hutto, R. L., and D. A. Patterson. 2016. Positive effects of fire on birds may appear only under narrow combinations of fire severity and time-since-fire. *International Journal of Wildland Fire* 25 (10): 1074–1085.
23. Jones, G. M., and M. W. Tingley. 2021. Pyrodiversity and biodiversity: a history, synthesis, and outlook. *Diversity and Distributions*. DOI:10.1111/ddi.13280.
24. Kilgo, J. C., and M. A. Vukovich. 2014. Can snag creation benefit a primary cavity nester: response to an experimental pulse in snag abundance. *Biological Conservation* 171: 21–28.
25. King, D. I., R. M. DeGraaf, and M. L. Smith, J. Buonaccorsi. 2006. Habitat selection and
26. habitat-specific survival of fledgling ovenbirds. *Journal of Zoology* 269:414–421.
27. Klaus, N. A., S. A. Rush, T. S. Keyes, J. Petrick, and R. J. Cooper. 2010. Short-term effects of fire on breeding birds in southern Appalachian upland forests. *The Wilson Journal of Ornithology* 122: 518–531.
28. Laseter, S. H., C. R. Ford, J. M. Vose, and L. W. Swift. 2012. Long-term temperature and precipitation trends at the Coweeta hydrologic laboratory, Otto, North Carolina, USA. *Hydrology Research* 43 (6): 890–901. <https://doi.org/10.2166/Nh.2012.067>.
29. MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42 (3): 594–598.
30. MacArthur, R. H., J. W. MacArthur, and J. Preer. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. *The American Naturalist* 96 (888): 167–174.
31. Marshall, M. R., J. A. DeCecco, A. B. Williams, G. A. Gale, and R. J. Cooper. 2003. Use of regenerating clearcuts by late-successional bird species and their young during the post-fledging period. *Forest Ecology and Management* 183: 127–135.
32. Martin, R. E., and D. B. Sapsis. 1992. Fires as agents of biodiversity: pyrodiversity promotes biodiversity. In: *Proceedings of the Conference on Biodiversity of Northwest California Ecosystems*. Cooperative Extension, University of California, Berkeley, CA, pp. 150–157.
33. McDermott, M. E., and P. B. Wood. 2009. Short- and long-term implications of clearcut and two-age silviculture for conservation of breeding forest birds in the central Appalachians, USA. *Biological Conservation* 142: 212–220.
34. Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta normalized burn ratio (dNBR). *Remote Sensing of Environment* 109(1):66–80. <https://doi.org/10.1016/j.rse.2006.12.006>.

35. Moorman, C. E., L. T. Bowen, J. C. Kilgo, J. L. Hanula, S. Horn, and M. D. Ulyshen. 2012. Arthropod abundance and seasonal bird use of bottomland forest harvest gaps. *The Wilson Journal of Ornithology* 124: 31–39.
36. Moorman, C. E., and D. C. Guynn. 2001. Effects of group-selection opening size on breeding bird habitat use in a bottomland forest. *Ecological Applications* 11: 1680–1691.
37. Newbold, C. D. 1996. The effects of tornado and clearcut disturbances on breeding birds in a Tennessee oak-hickory (*Quercus-Carya spp.*) forest. Master's thesis, University of Tennessee, Knoxville.
38. Newell, F. L., and A. D. Rodewald. 2012. Management for oak regeneration: Short-term effects on the bird community and suitability of shelterwood harvests for canopy songbirds. *The Journal of Wildlife Management* 76: 683–663.
39. NCDC. 2020. 1981–2010 Climate Normals, Franklin NC. Retrieved April 30, 2020 from .
40. Pagen, R. W., F. R. Thompson III, and D. E. Burhans. 2000. Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. *Condor* 102: 738–747.
41. Perry, R. W., and R. E. Thill. 2013. Long-term responses of disturbance-associated birds after different timber harvests. *Forest Ecology and Management* 307: 274–283.
42. Prather, J. W., and K. G. Smith. 2003. Effects of tornado damage on forest bird populations in the Arkansas Ozarks. *The Southwestern Naturalist* 48: 292–297.
43. Rodewald, P. G., and K. G. Smith. 1998. Short-term effects of understory and overstory management on breeding birds in Arkansas oak-hickory forests. *The Journal of Wildlife Management* 62: 1411–1417.
44. Rose, E. T., and T. R. Simons. 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.
45. Rush, S., N. Klaus, T. Keys, J. Petrick, and R. Cooper. 2012. Fire severity has mixed benefits to breeding bird species in the southern Appalachians. *Forest Ecology and Management* 263: 94–100.
46. Shifley, S. R., and F. R. Thompson III. 2011. Spatial and temporal patterns in the amount of young forests and implications for biodiversity. In *Sustaining Young Forest Communities*, eds. C. H. Greenberg, and B. Collins, 73–95. Dordrecht: Springer.
47. Spetich, M. A., R. W. Perry, C. A. Harper, and S. L. Clark. 2011. Fire in eastern hardwood forests through 14,000 years. In *Sustaining Young Forest Communities*, eds. C. H. Greenberg, B. Collins, and F. R. Thompson III, 41–58. Dordrecht: Springer.
48. Stoleson, S. H. 2013. Condition varies with habitat choice in postbreeding forest birds. *The Auk* 130 (3): 417–428.
49. Taillie, P. J., R. D. Burnett, L. J. Roberts, B. R. Campos, M. N. Peterson, and C. E. Moorman. 2018. Interacting and non-linear avian responses to mixed-severity wildfire and time since fire. *Ecosphere* 9: e02291.
50. Tingley, M. W., V. Ruiz-Gutiérrez, R. L. Wilkerson, C. A. Howell, and R. B. Siegel. 2016. Pyrodiversity promotes avian diversity over the decade following forest fire. *Proceedings of the Royal Society B: Biological Sciences* 283(1840):20161703.
51. Vander Yacht, A. L., P. D. Keyser, D. A. Buehler, C. A. Harper, D. S. Buckley, and R. D. Applegate. 2016. Avian occupancy response to oak woodland and savanna restoration. *The Journal of Wildlife Management* 80: 1091–1105.
52. Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood thrush postfledging movements and habitat use in northern Virginia. *Condor* 100: 69–78.

53. Vitz, A. C., and A. D. Rodewald. 2006. Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. *Biological Conservation* 127: 477–486.
54. Vose, J. M., D. L. Peterson, C. J. Fettig, J. E. Halofsky, J. K. Hiers, R. E. Keane, R. Loehman, and M. C. Stambaugh. 2021. Fire and forests in the 21st century: Managing resilience under changing climates and fire regimes in USA Forests. In *Fire Ecology and Management*, eds. C. H. Greenberg, and B. Collins, 465–502. Cham: Past, Present, and Future of US Forested Ecosystems Springer.
55. Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithological Monographs* 8: 1–93.
56. Zar, J. H. 1998. *Biostatistical Analysis*. Fourth edition. Englewood Cliffs, New Jersey: Prentice Hall.

Tables

Table 1. Results of mixed-model ANOVAs comparing select forest structure characteristics, years (2017-2021), and interaction effects among six fire-severity categories (FSCs) following 2016 wildfires, Nantahala National Forest, Macon County, NC.

Characteristic	P _{FSC}	P _{yr}	P _{FSCyr}
Percentage dead trees (%)	<0.0001	<0.0001	0.0245
Percentage dead BA (m ² /ha)	<0.0001	<0.0001	0.0583
Dead tree density (No/ha)	<0.0001	<0.0001	0.0002
Dead tree BA (m ² /ha)	<0.0001	<0.0001	<0.0001
Shrub cover (%)	0.0008	<0.0001	<0.0001
Leaf litter (%)	<0.0001	<0.0001	<0.0001
Canopy cover (%)	<0.0001	<0.0001	0.0005

Table 2. Total number of individual detections (all years and point counts) and results of mixed-model ANOVAs comparing breeding bird species richness per plot, abundance (number/10 ha) of total birds, nesting guilds, and common (≥ 30 detections) species¹ among six 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 x yr}
Ground-nest	432	0.1680	0.3080	0.5472
BAWW	138	0.1098	0.0043	0.2157
CAWA	53	0.6873	0.0084	0.8500
OVEN	123	0.1462	0.3671	0.1758
SCJU	46	0.2650	0.1661	0.7933
VEER	15	—	—	—
WEWA	55	0.2946	0.2109	0.7470
WIWR	2	—	—	—
Cavity-nest	240	0.0050	0.0056	0.2277
Primary	54	0.2318	0.0383	0.8118
DOWO	20	—	—	—
HAWO	13	—	—	—
NOFL	5	—	—	—
PIWO	12	—	—	—
RBWO	1	—	—	—
RHWO	1	—	—	—
YBSA	2	—	—	—
Secondary	186	0.0087	0.0775	0.2750
BRCR	10	—	—	—
CACH	68	0.0974	0.3224	0.9617
CARW	17	—	—	—
EABL	2	—	—	—
ETTI	38	0.5842	0.2785	0.8499
WBNU	51	0.0010	0.0516	0.1679
Shrub-nest	599	0.0071	<0.0001	0.0024
AMGO	6	—	—	—
AMRO	3	—	—	—
BHVI	120	0.5563	0.2964	0.0496
BRTH	2	—	—	—
BTBW	200	0.1932	0.0185	0.5661
CSWA	33	0.0021	0.0206	0.0190

EATO	75	<0.0001	0.0005	0.0119
GRCA	2	—	—	—
HOWA	81	0.6414	0.0010	0.0113
INBU	33	0.0019	0.4664	0.7718
MODO	2	—	—	—
RTHU	13	—	—	—
Tree-nest	362	0.4541	0.6351	0.7386
ACFL	2	—	—	—
AMCR	2	—	—	—
BLBW	9	—	—	—
BLJA	28	—	—	—
BTNW	49	0.8542	0.1652	0.8797
CEDW	3	—	—	—
EAWP	23	—	—	—
NOPA	64	0.8295	0.2002	0.3626
RBGR	13	—	—	—
REVI	115	0.9005	0.0111	0.8626
SCTA	47	0.5848	0.5142	0.3339
YTVI	2	—	—	—
YTWA	5	—	—	—
Other	9	—	—	—
EAPH	6	—	—	—
UNKN	3	—	—	—
Total	1642	0.0212	<0.0001	0.0062
Richness	—	0.0444	<0.0001	0.0464

¹ACFL=Acadian flycatcher (*Empidonax vireescens*); AMCR=American crow (*Corvus brachyrhynchos*); AMGO=American goldfinch (*Carduelis tristis*); AMRO=American robin (*Turdus migratorius*); BAWW=black-and-white warbler (*Mniotilta vario*); BHVI=blue-headed vireo (*Vireo solitarius*); BLBW=blackburnian warbler (*Setophaga fusca*); BLJA=blue jay (*Cyanocitta cristata*); BRGR=brown creeper (*Certhia americana*); BRTH=brown thrasher (*Toxostoma rufum*); BTBW=black-throated blue warbler (*Setophaga caerulescens*); BTNW=black-throated green warbler (*Setophaga virens*); BAWW=black-and-white warbler (*Mniotilta varia*); CACH=Carolina chickadee (*Poecile carolinensis*); CARW=Carolina wren (*Thyrothorus ludovicianus*); CAWA=Canada warbler (*Cardellina canadensis*); CEDW=cedar waxwing (*Bombcilla cedrorum*); CSWA=chestnut-sided warbler (*Setophaga pensylvanica*); DOWO=downy woodpecker (*Picoides pubescens*); EABL=eastern bluebird (*Sialia sialis*);

EAPH=eastern phoebe (*Sayornis phoebe*); EATO=eastern towhee (*Pipilo erythrophthalmus*); EAWP=eastern woodpecker (*Contopus virens*); ETTI=tufted titmouse (*Baeolophus bicolor*); GRCA=gray catbird (*Dumetella carolinensis*); HAWO=hairy woodpecker (*Picoides villosus*); HOWA=hooded warbler (*Setophaga citrina*); INBU=indigo bunting (*Passerina cyanea*); MODO=mourning dove (*Zenaidura macroura*); NOFL=northern flicker (*Colaptes auratus*); NOPA=Northern parula (*Setophaga americana*); OVEN=ovenbird (*Seiurus aurocapillus*); PIWO=pileated woodpecker (*Drycopus pileatus*); RBWO=red-bellied woodpecker (*Melanerpes carolinus*); REVI=red-eyed vireo (*Vireo olivaceus*); RBGR=rose-breasted grosbeak (*Pheucticus ludovicianus*); RHWO=red-headed woodpecker (*Melanerpes erythrocephalus*); RTHU=ruby-throated hummingbird (*Archilochus colubris*); SCJU=slate-colored junco (*Junco hyemalis*); SCTA=scarlet tanager (*Piranga olivacea*); VEER=veery (*Catharus fuscescens*); WBNU=white-breasted nuthatch (*Sitta carolinensis*); WEWA=worm-eating warbler (*Helmitheros vermivorus*); WIWR=winter wren (*Troglodytes hiemalis*); WOTH=woodthrush (*Hylocichla mustelina*); YBSA=yellow-bellied sapsucker (*Sphyrapicus varius*); YTVI=yellow-throated vireo (*Vireo flavifrons*); YTWA=yellow-throated warbler (*Setophaga dominica*).

Table 3. Stepwise multiple regression results for breeding bird response (species richness, total abundance (no/10 ha), abundance within nesting guilds (tree, ground, shrub and cavity), primary (woodpeckers) and secondary cavity-nesters, and common (≥ 30 detections) species) and forest structural attributes (percentage of dead trees and dead BA, snag density, percent cover of shrubs, leaf litter, and canopy at breast height five years after the 2016 wildfires (Y5), Nantahala National Forest, Macon County, North Carolina. See Table 2 footnotes for bird species codes.

Group	R ²	F-val	RMSE	p-val	%Dead Trees	%Dead BA	Snag Density (no/ha)	%Shrub Cover	%Leaf Litter Cover	%Canopy Cover
BAWW	0.07	4.90	17.37	0.0303	—	—	+ 0.0303	—	—	—
BHVI	0.08	5.29	16.96	0.0247	—	—	—	—	—	-0.0247
BTBW	NS	—	—	—	—	—	—	—	—	—
BTNW	NS	—	—	—	—	—	—	—	—	—
CACH	0.28	8.34	10.09	<0.0001	—	+ <0.0001	- 0.0395	—	—	+ 0.0212
CAWA	0.09	6.69	11.99	0.0119	—	—	—	—	- 0.0019	—
CSWA	0.32	30.39	11.03	<0.0001	—	+ <0.0001	—	—	—	—
EATO	0.35	17.27	13.51	<0.0001	+ 0.0010	—	—	+ 0.0485	—	—
ETTI	NS	—	—	—	—	—	—	—	—	—
HOWA	0.15	11.03	17.21	0.0015	+ 0.0015	—	—	—	—	—
INBU	0.29	26.69	6.22	<0.0001	—	—	—	—	—	- <0.0001
NOPA	NS	—	—	—	—	—	—	—	—	—
OVEN	0.14	10.71	15.26	0.0017	—	—	—	—	+ 0.0017	—
REVI	NS	—	—	—	—	—	—	—	—	—
SCJU	NS	—	—	—	—	—	—	—	—	—
SCTA	NS	—	—	—	—	—	—	—	—	—
WBNU	0.08	5.82	12.30	0.0187	—	—	+ 0.0187	—	—	—
WEWA	NS	—	—	—	—	—	—	—	—	—
Tr Gld	NS	—	—	—	—	—	—	—	—	—
Grd Gld	NS	—	—	—	—	—	—	—	—	—
Cav Gld	0.13	9.67	23.31	0.0028	—	—	+ 0.0028	—	—	—
1°	0.13	9.94	11.73	0.0025	—	—	—	+ 0.0025	—	—
2°	NS	—	—	—	—	—	—	—	—	—
Shr Gld	0.41	22.59	39.98	<0.0001	+ 0.0033	—	—	- 0.0248	—	—

TOT	0.34	34.18	63.08	<0.0001	-	<0.0001	—	—	—	—	—
RICH	0.38	19.38	7.67	<0.0001	+	0.0056	—	—	—	—	- 0.0405

Figures

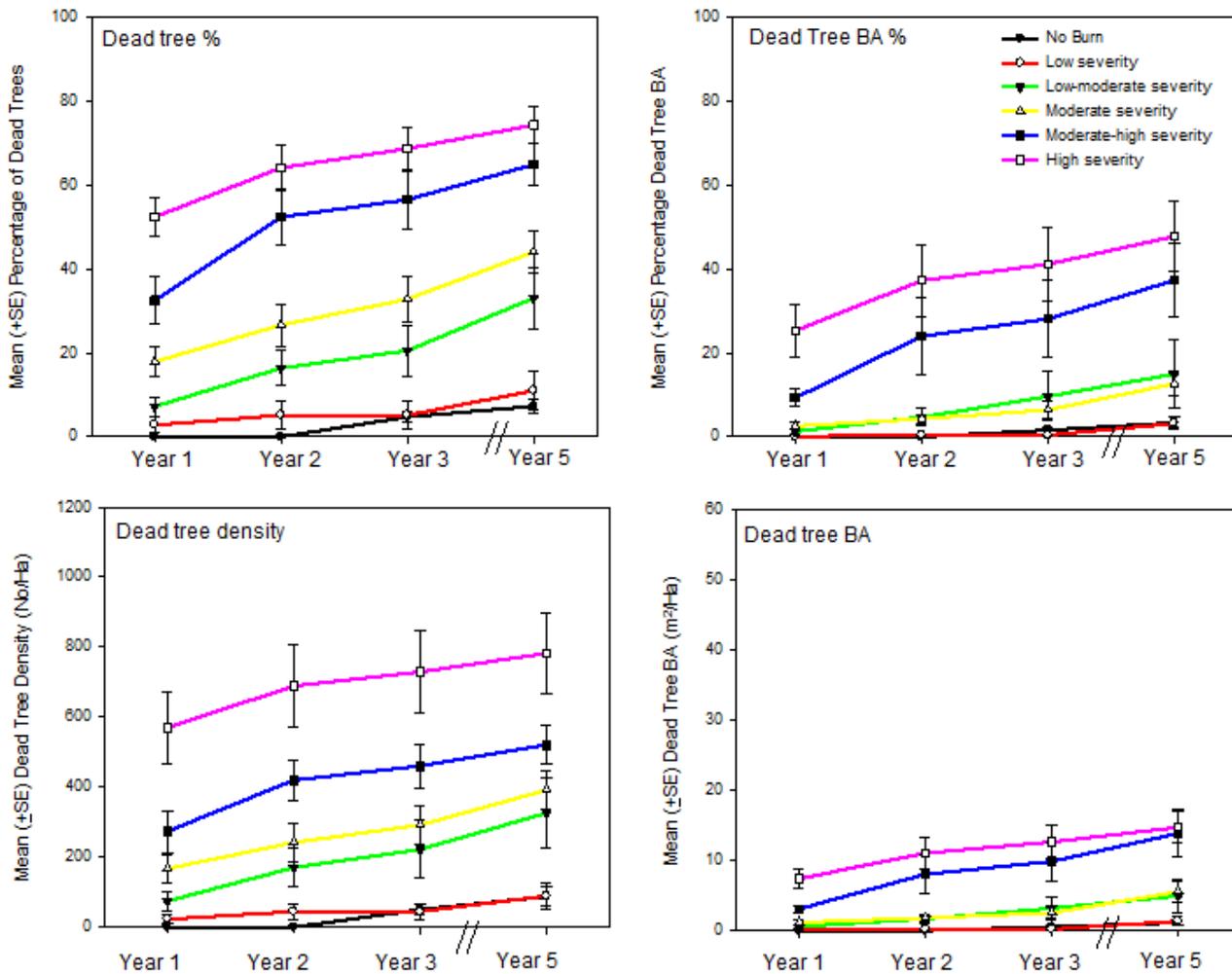


Figure 1

Mean (+SE) percentage of dead trees, percentage of dead tree BA, dead tree density (no/ha), and dead tree BA (m²/ha) in six fire-severity categories 1, 2, 3 and 5 years (Y1- Y3 and Y5) following the 2016 wildfires, Nantahala National Forest, Macon County, North Carolina. Dead trees include only those killed by the wildfire or dying subsequently (e.g., not pre-wildfire snags).

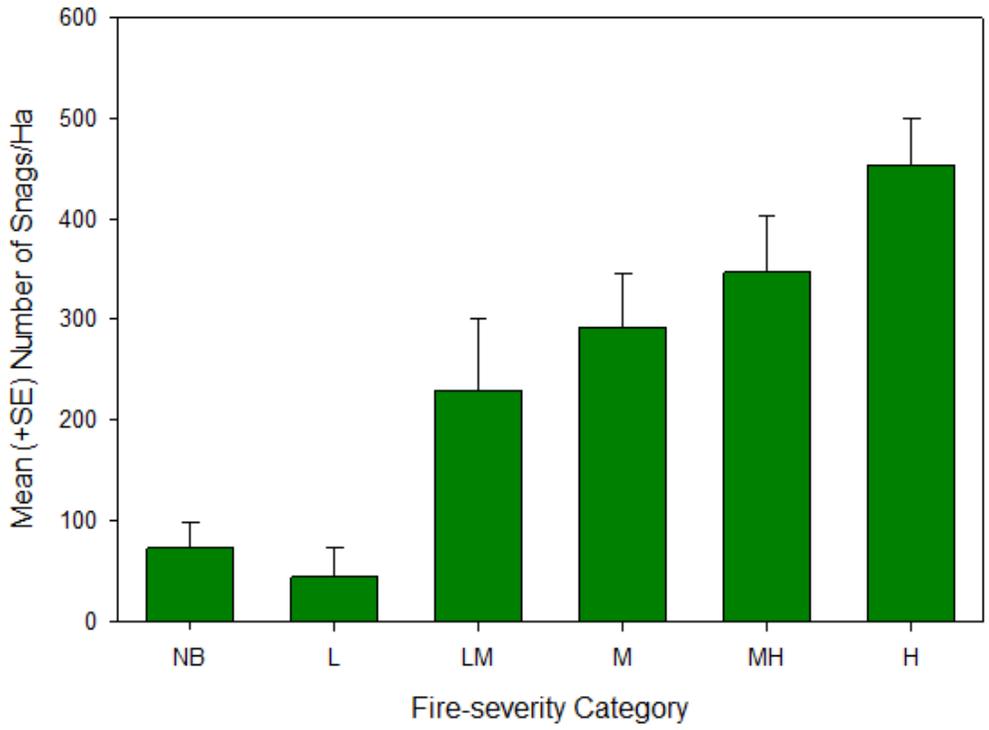


Figure 2

Mean (+SE) density of snags (>1.8m height) in six fire-severity categories 1 and 5 years post-wildfire (Y1 and Y5) following the 2016 wildfires, Nantahala National Forest, Macon County, North Carolina.

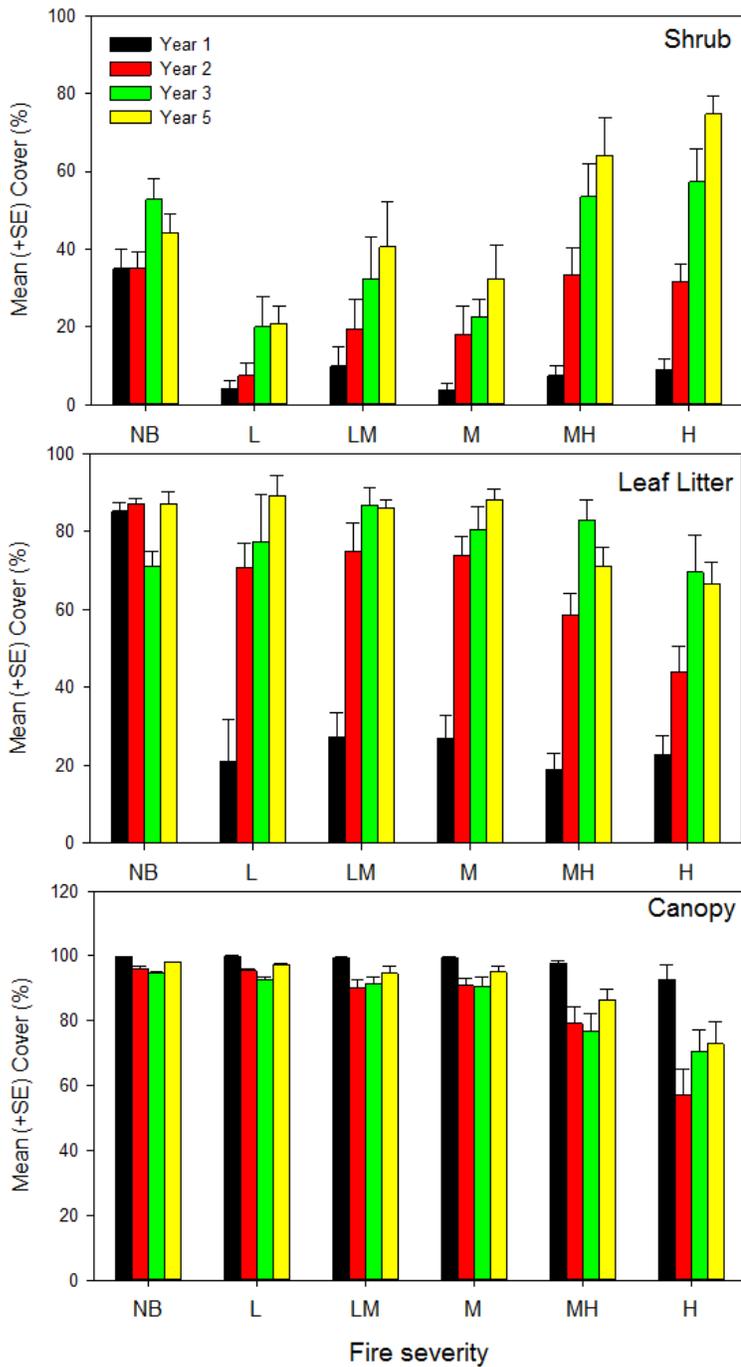


Figure 3

Mean (+SE) percent cover of shrubs, leaf litter, and canopy at breast height in six fire-severity categories 1-5 years post-wildfire (Y1-Y3 and Y5) following the 2016 wildfires, Nantahala National Forest, Macon County, North Carolina.

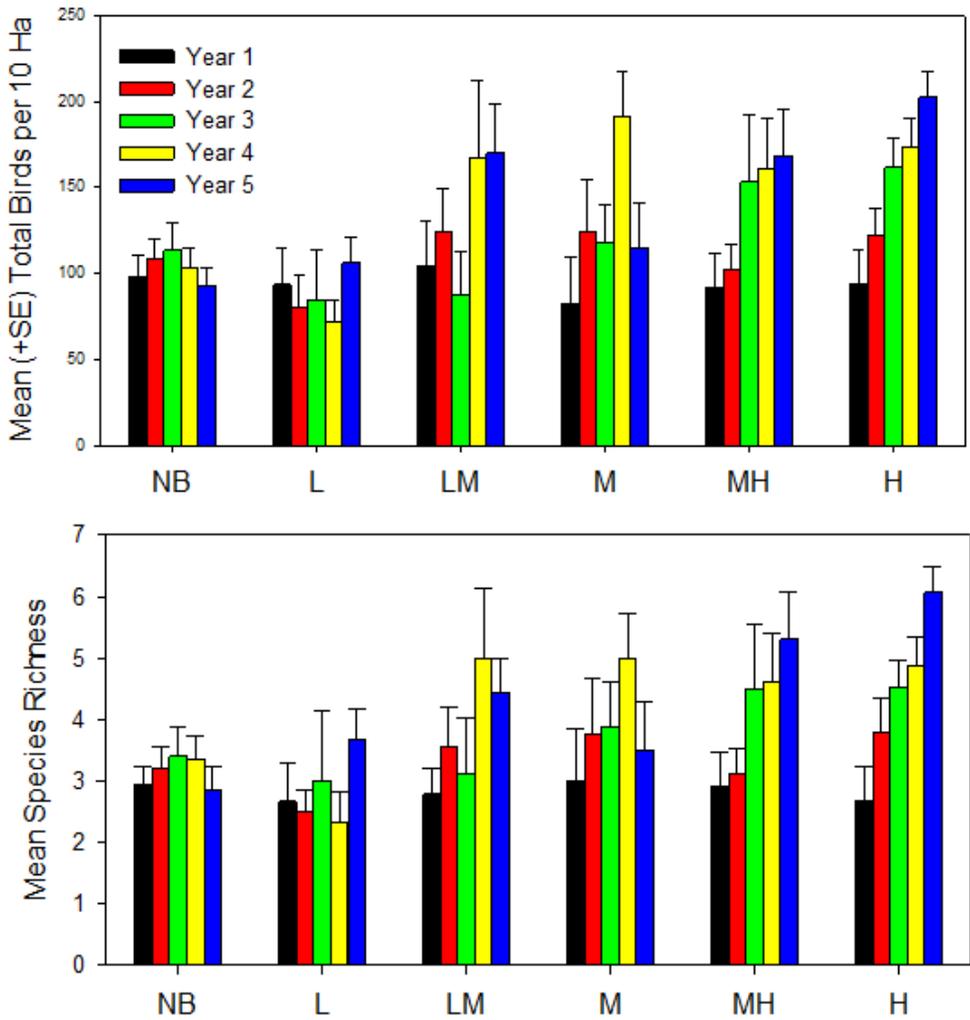


Figure 4

Mean (\pm SE) total number of birds/10 ha and species richness 1-5 years post-wildfire (Y1- Y5) in six fire-severity categories following the 2016 wildfires, Nantahala National Forest, Macon County, North Carolina.

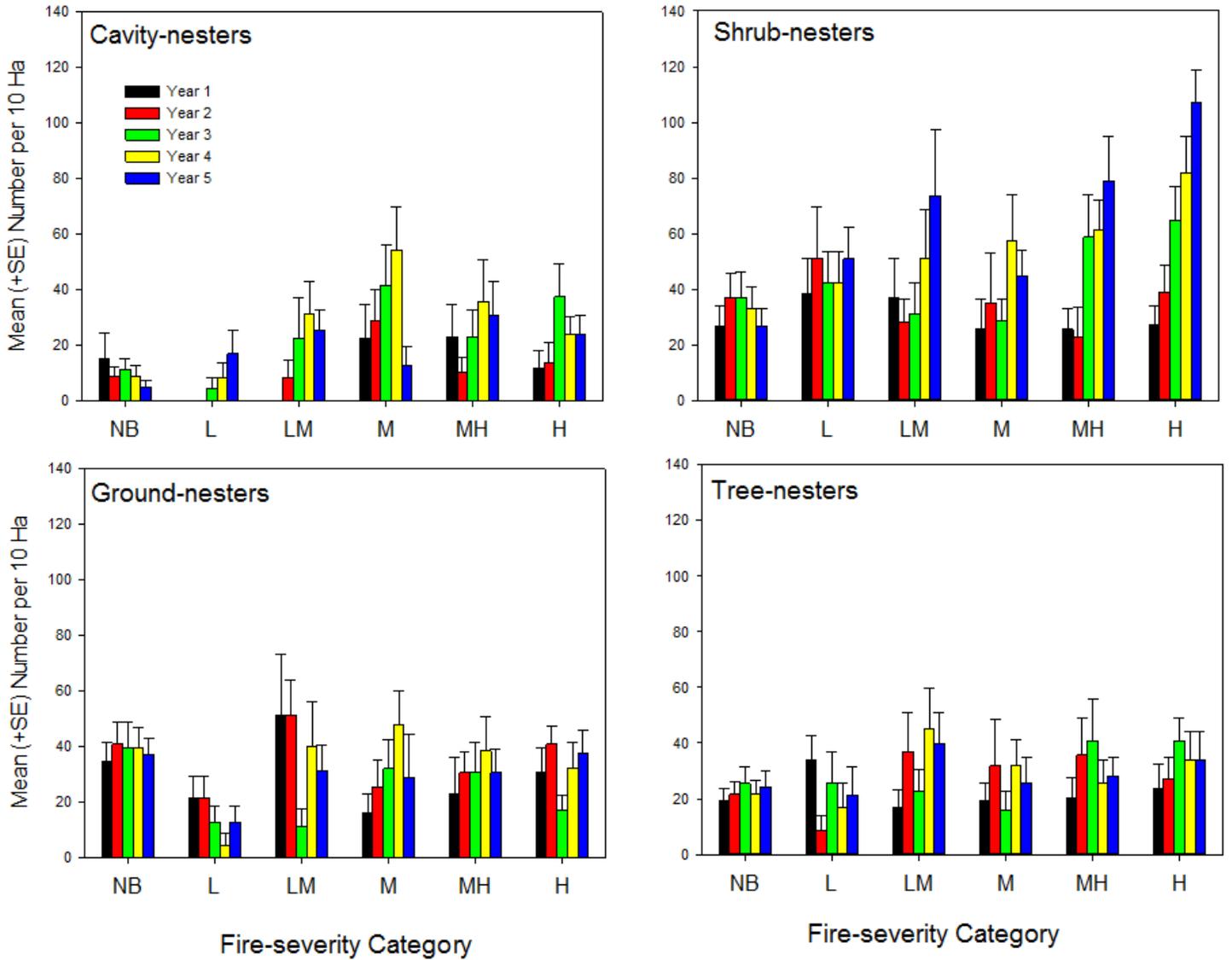


Figure 5

Mean (\pm SE) number of birds/10 ha in four nesting guilds (cavity-, shrub-, ground-, and tree-nesters) 1-5 years post-burn (Y1- Y5) in six fire-severity categories following the 2016 wildfires, Nantahala National Forest, Macon County, North Carolina.

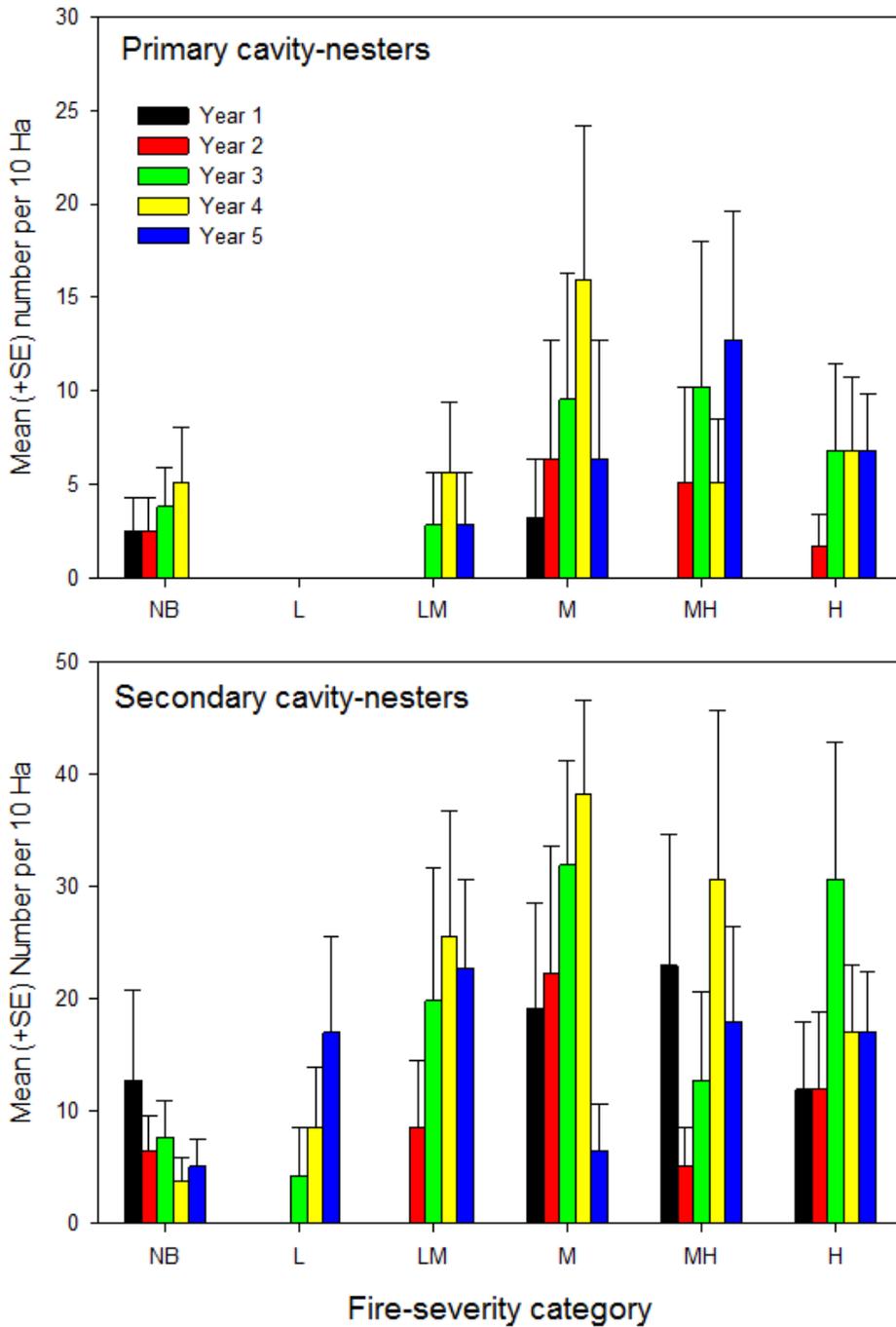


Figure 6

Mean (\pm SE) number of primary- (woodpeckers) and secondary cavity-nesters/10 ha, 1-5 years post-wildfire (Y1- Y5) in six fire-severity categories following the 2016 wildfires, Nantahala National Forest, Macon County, North Carolina.

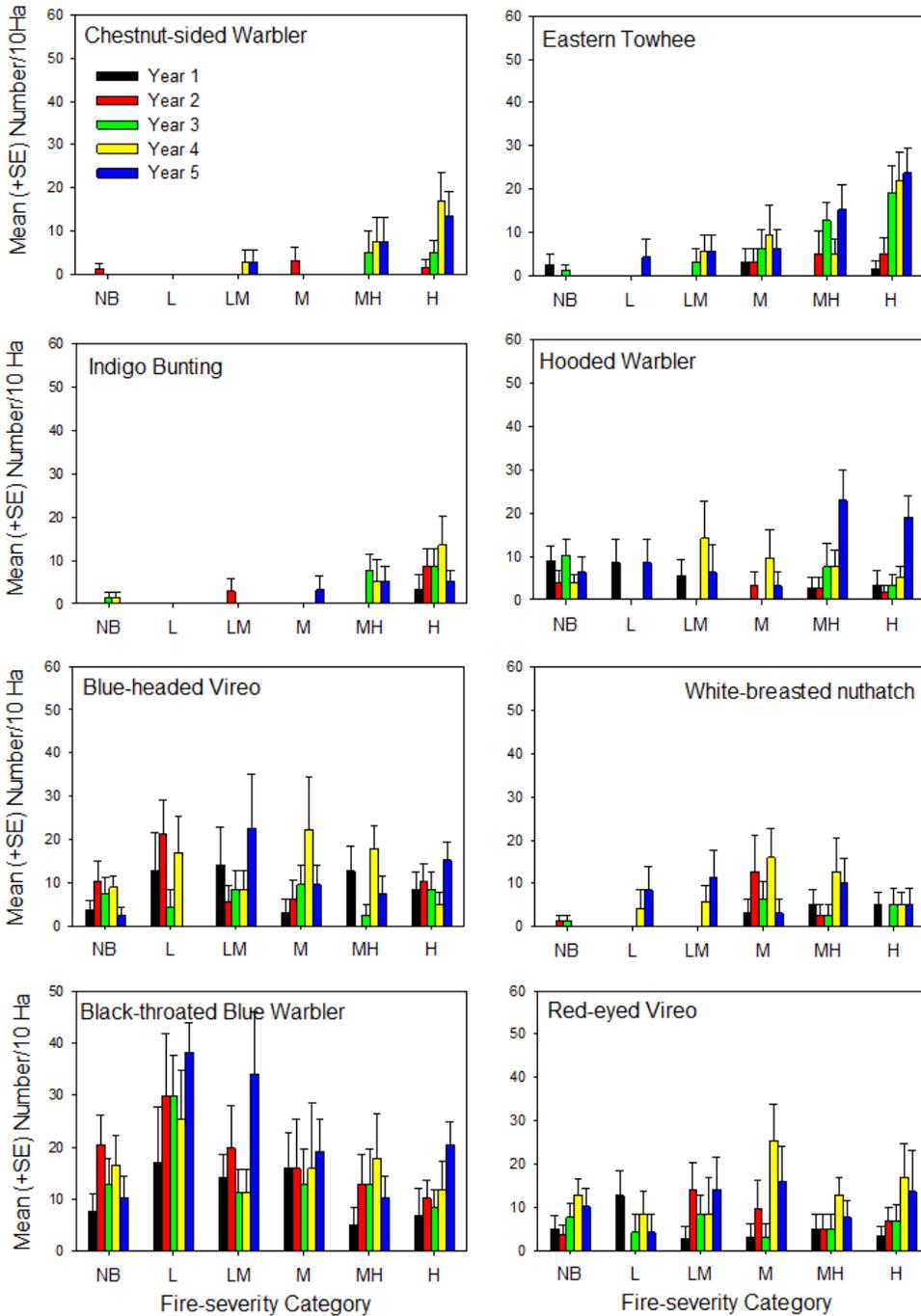


Figure 7

Mean (+SE) total number of birds/10 ha for the six species showing significant treatment and (or) treatment x year interaction effects and three common species showing no significant response (bottom row), 1-5 years post-wildfire (Y1- Y5) in six fire-severity categories following the 2016 wildfires, Nantahala National Forest, Macon County, North Carolina.