



# Shelterwood harvests promote high breeding bird diversity and shrubland species for less than 10 years in hardwood forests

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## ABSTRACT

We compared forest structure and breeding bird communities between shelterwood harvests (SW;  $n = 15$ ) and mature upland hardwood forests (M;  $n = 16$ ) over 17 years (Y). Both were relatively static throughout the study period in M. In contrast, heavy canopy reduction and increased light after timber harvests in SW initiated rapid increases in small tree stem densities and shrub cover driven primarily by blackberry (*Rubus* spp.) - a clonal shrub that “pioneers” recently disturbed, high-light environments. This open-canopy forest structure with low, dense vegetation was short-lived; young trees reached canopy closure within 10 years, with concomitant reductions in blackberry cover and stem density. Total abundance, species richness, and diversity of breeding birds was greater in SW than M, especially the first several years post-harvest; in Y6 these metrics were more than twice as high in SW as in M. Higher abundance, richness, and diversity in SW was driven by an influx of shrubland associates (indigo buntings (*Passerina cyanea*), chestnut-sided warblers (*Setophaga pensylvanica*), Eastern towhees (*Pipilo erythrophthalmus*)) and positive or neutral responses by most other species; only ovenbirds (*Seiurus aurocapilla*) were more abundant in M. Abundances of shrubland bird species in particular tracked temporal changes in SW forest structure but each differed slightly in their patterns of increase, peak (with 15–26 times more in SW than M), and decline. By Y10 breeding bird communities in SW resembled those in M, although total abundance, species richness, and diversity remained slightly higher in SW throughout the study period. Total abundance, species richness, diversity, and abundance of shrubland bird species were positively- and ovenbird was negatively correlated with blackberry cover, indicating that it is a suitable stand-alone predictor of post-disturbance young forest and changes in breeding bird communities as forests mature. Our results show that young hardwood forests provide habitat for shrubland bird species and promote high breeding bird diversity for <10 years.

## 1. Introduction

Forest structure, including vertical strata, low dense woody cover, tree density and basal area (BA), canopy closure, and age-class is an important driver of breeding bird community composition and diversity (MacArthur and MacArthur, 1961). Hunter et al. (2001) recognized 128 breeding bird species of the eastern US associated with disturbance-maintained vegetation conditions, including grasslands, shrublands, savanna and open woodlands, or forest gaps. In contrast, other species are associated with mature closed canopy forest or use a wide range of forest structures. Disturbance dependent songbird populations, including shrubland species, are declining faster than other bird groups

(Hunter et al., 2001). In the Central Hardwood Region, widespread heavy logging in the early 20th century has yielded to homogeneous landscapes of mature even-aged forests. This, combined with a quarter-century of reduced timber harvesting on public lands (Shifley and Thompson, 2011) and dramatically reduced frequency and extent of intentional fire that previously maintained open forests has resulted in a dearth of habitat for shrubland bird species (Greenberg et al., 2011).

Disturbances are required to create open, young forests and maintain landscapes with a mosaic of age classes and structural heterogeneity that promotes breeding bird diversity at local to regional scales (Askins, 2001; Lichstein et al., 2002; Shifley and Thompson, 2011). Research in eastern upland hardwood forests indicated that breeding bird responses

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to understory disturbances such as low-severity burns or mechanical cutting of the understory, are few and transitory (e.g., Greenberg et al., 2018, 2019). In contrast, numerous studies have illustrated the role of heavy canopy-reducing disturbances by wind (e.g., Greenberg and Lanham, 2001; Prather et al., 2003), high-severity fire (e.g., Rush et al., 2012; Greenberg et al., 2018, 2023), or regeneration harvests (e.g., Annand and Thompson, 1997; Baker and Lacki, 1997; Campbell et al., 2007; McDermott and Wood, 2009; Perry and Thill, 2013; Robinson and Robinson, 1999; Perry et al., 1999) in increasing breeding bird diversity at local and landscape scales.

Changes to forest structure following canopy-reducing disturbances are ephemeral and dynamic as vegetation progresses in maturation through the “stem initiation” to the “stem exclusion” stages of stand development (Oliver and Larson, 1996; Johnson, 2008; Loftis et al., 2011). Initially, increased light to the forest floor initiates rapid increases in woody stem density as seedlings germinate and harvested tree stumps and shrubs resprout. Habitat for shrubland birds (i.e., low, dense vegetation) correspondingly increases (Hanberry and Thompson, 2019) but declines as young tree sprouts and seedlings gain height and girth, often reaching canopy closure with concomitant reductions in light, tree stem densities, and shrub cover within <15 years (Loftis et al., 2011).

Several studies show that shrubland bird species differ in their timing of colonization, peak abundance, and retention following heavy canopy reduction in central hardwood forests (Conner and Adkisson, 1975; Schlossberg and King, 2009; Perry and Thill, 2013). These patterns likely differ somewhat geographically and across upland hardwood forest variants associated with moisture- and soils-related differences in tree growth rates, species composition, and vegetation density, but most studies report that forest structure becomes unsuitable for shrubland species within 12 years of harvest (Perry and Thill, 2013).

Most studies addressing temporal patterns of breeding bird abundances across post-disturbance stages of forest stand development necessarily relied on a chronosequence of time since harvest (e.g., Crawford et al., 1981; Thompson and Capen, 1988; Duguid et al., 2016) or multi-year intervals between surveys but did not continuously track post-harvest changes in forest structure and breeding bird communities in the same locations over a long period of time. In this study, we evaluated dynamic temporal changes in forest structure, breeding bird communities (total bird abundance, species richness, diversity, and nesting guilds), and abundance of individual species in 15 young 2-age stands created by shelterwood-with-reserves regeneration harvests and 16 mature forest stands over a 17-year period. Our objective was to examine long-term temporal dynamics of forest structure, breeding bird communities, and abundance of individual species following shelterwood harvests compared to mature forests. We hypothesized that total bird abundance, species richness, diversity, and abundance of shrubland species would be greater for several years in shelterwood harvests compared to mature forest and decrease as young forests grew to canopy closure.

## 2. Methods

### 2.1. Study area

Our study sites were located in southern Appalachian hardwood forests throughout the Pisgah and Grandfather ranger districts of the Pisgah National Forest in Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina, USA. Sites ranged in elevation from 500 to 1,200 m and were located across a wide range of topographic features such as aspect, slope position, and percent slope. Annual rainfall in the region (Asheville area, 2000–2016) ranged from approximately 85–191 cm (average 119 cm) (NOAA National Weather Service). Soils were predominantly Dystrochrepts and Hapludults (Pittillo et al., 1998). Mature forest ranged from 80 years to 100 years in age at study establishment. Forests were composed of yellow poplar (*Liriodendron tulipifera*), northern red oak (*Quercus rubra*), magnolia (*Magnolia* spp.), white

ash (*Fraxinus americanus*), beech (*Fagus grandifolia*), hemlock (*Tsuga canadensis*), and silverbell (*Halesia carolina*) on moister sites; drier sites were dominated by scarlet oak (*Q. coccinea*), chestnut oak (*Q. montana*), black oak (*Q. velutina*), blackgum (*Nyssa sylvatica*), and sourwood (*Oxydendrum arboreum*). Red maple (*Acer rubrum*), hickories (*Carya* spp.), flowering dogwood (*Cornus florida*), and white oak (*Q. alba*) were common throughout (Pittillo et al., 1998).

### 2.2. Study design

Our bird study was part of a long-term “fruit study” (established in 1999) comparing stand dynamics and fleshy fruit, samara, and nut production between mature, closed-canopy forest (M; n = 16 stands) and 2-aged stands with low basal area (BA) retention created by shelterwood-with-reserves regeneration harvests (SW; n = 15 stands) in southern Appalachian hardwood forests (Greenberg et al., 2007). We selected study sites based on availability of stands that met our age, forest type, and silvicultural treatment criteria. We attempted to locate M near SW stands to minimize variability between them attributable primarily to location or topography. Shelterwood stands resulted from harvests conducted during 1998–1999 with 15–20% BA retention of mature trees, mostly scattered oaks and hickories, to create a heterogeneous stand structure and maintain hard mast production (acorns and hickory nuts) for wildlife (T. Oprean, Pisgah National Forest, pers. comm.). Shelterwood stand sizes ranged from 3.2 ha to 10.5 ha (average 7.0 ha) and were generally the same age as M study stands when they were harvested (80–100 yr old). All regenerated stands were site-prepared within a year of harvesting. This entailed cutting all small (approximately 2.5–25 cm diameter at breast height and  $\geq 1.4$  m tall) woody stems and applying herbicide to the cut surface of tree stumps of several tree and shrub species (red maple, flowering dogwood, silverbell, sourwood, yellow poplar, sassafras (*Sassafras albidum*), black locust (*Robinia pseudoacacia*), Fraser magnolia (*M. fraseri*), blackgum, rhododendron (*Rhododendron* spp.), and mountain laurel (*Kalmia latifolia*)).

### 2.3. Breeding bird surveys

We established 200 × 50 m (1 ha) strip transects through the center of all 31 treatment (SW and M) units. We could not control for edge effects in all units due to constraints of stand size or irregular shape but most strip transects were  $\geq 25$  m from edges. We conducted bird surveys once during the breeding season (4 May – 13 July) for 17 years (2000–2009, 2011, 2013, 2016; Y1–Y10, Y12, Y14, Y17, respectively) starting about a year post-harvest by slowly (about 15 min per transect) walking transect centerlines between sunrise and four hours after sunrise and recording all individual birds seen or heard within 25 m on either side. Flyovers were not included in data analyses. A few transects were not surveyed in some years (2 in Y1, 1 in Y2, 6 in Y3, 2 in Y6) for logistical reasons. We standardized our sampling design to minimize potential detection bias (Thompson and La Sorte, 2008). Most bird surveys were conducted by a single, highly experienced observer (J. Tomcho); three other highly experienced observers also conducted surveys during the study. Additionally, we used a short (25-m) fixed detection distance from transect centerline, ensured that surveys in SW and M were distributed evenly throughout the study period, and avoided surveys during moderate-high winds or precipitation. Because most bird detections were aural, differences in detectability between treatments due to vegetation structure were further minimized. Relative abundance (number/10 ha) for each treatment unit was calculated by summing all individuals (by nesting guild, species, or total) detected within the 1 ha transect and multiplying by 10. Species richness represented the total number of species detected within transects each unit and year. Species diversity was calculated using the Shannon diversity index (Shannon, 1948).

## 2.4. Forest structure

We periodically quantified forest structure within a 20 × 50 m (0.1 ha) plot randomly placed within each study stand. In Y5, Y10, Y14 and Y17, tree stems of individuals ≥ 0.5 m height were tallied by species in four size classes: Class 1 = stem < 2.54 cm; Class 2 = 2.54–7.5 cm diameter at breast height (dbh); Class 3 = 7.6–12.6 cm dbh; Class 4 = ≥ 12.7 cm dbh. “Individual” tree stems were defined as single stems or the largest-diameter stem within a cluster of stump sprouts. Stump sprouts were also tallied by size class for ≤ 30 randomly selected subset of individuals per species within each plot. The total number of sprout count subsamples per species within plots was often low (especially after they were subdivided into 4 size classes) so we pooled them across M and (separately) SW plots for each year and applied the average number of stump sprouts (by species and size class) to the number of individuals (by species and size class) to each treatment, respectively. Thus, total stem counts (individuals + stump sprouts) used in data analyses were crude estimates. Dbh of trees ≥ 12.7 cm was measured in Y5, Y14, and Y17 and used to calculate BA; BA for Y10 was interpolated based on tree growth Y5–Y14.

We visually estimated percent cover of all clonal shrub species in 20, 2 × 5 m (total 0.02 ha) subplots located along each side of a 50 m centerline through each vegetation plot and averaged for a plot-level estimate (Y5, Y10, Y14, and Y17). As part of the larger fruit study, blackberry (*Rubus* spp.; a fleshy fruit-producing shrub) was additionally measured during all bird survey years except Y12. In Y8 and Y17 we estimated the height of the dominant canopy (mature trees in M; post-harvest “new growth” in SW) by averaging crown heights of 3 trees per plot – one at each of 3 points along the centerline of each vegetation plot. We used a spherical densiometer to estimate percent canopy cover in Y5, Y10, Y14, and Y17 at each of five subplots established at a randomly chosen distance along and perpendicular (≤ 25 m out) to each bird transect in a subset of study stands (n = 6 per treatment); values were averaged over all five subplots for a stand-level estimate of canopy cover.

## 2.5. Data analysis

We used repeated measures ANOVAs (PROC MIXED; SAS 9.3) in a randomized block design to compare forest structure features and breeding bird communities in M and SW treatments over 17 years following harvests in SW. Forest structure variables were tree stem density by size class, BA of trees ≥ 12.7 cm dbh, percent cover of total and dominant (average ≥ 3% cover in M or SW) genera of clonal shrubs (rhododendron (*R. maximum*), huckleberry (predominantly *Gaylussacia ursina*; also *G. baccata*), blackberry (predominantly *R. allegheniensis*; also *R. phoenicolasius* and *R. odoratus*) and mountain laurel), height of the dominant tree canopy, and percent canopy cover.

Preliminary inspection of shrub data indicated that blackberry – a clonal shrub that “pioneers” recently disturbed, high-light environments – occurred nearly exclusively in SW, and its percent cover was highly dynamic over time relative to the other three dominant clonal species; thus, it was the primary driver of temporal changes in total clonal shrub cover in SW. Exploratory Spearman’s correlations further indicated that blackberry cover was significantly ( $p < 0.0001$ ) positively correlated with the density of Class 1 tree stems ( $r = 0.67$ ) – another key indicator of early post-disturbance forest stand development, and negatively correlated with the density ( $r = -0.70$ ) and BA ( $r = -0.73$ ) of Class 4 stems – both indicators of later stages of stand development (Loftis et al., 2011). These preliminary results suggested that temporal changes in blackberry cover were a potential suitable indicator of temporal changes in other forest structural features following SW harvests (e.g., Loftis et al., 2011), and therefore a possible stand-alone predictor of breeding bird responses. Because we measured blackberry (as a fleshy fruit-producing species included in our “fruit” study) cover in all years of the bird surveys (except Y12) we conducted ANOVA to more closely

examine treatment differences and temporal dynamics of blackberry cover in SW, and Spearman’s correlations to examine possible relationships between percent cover of blackberry alone and breeding bird response variables.

Breeding bird response variables were total abundance, species richness, diversity, abundance within nesting guilds (Hamel, 1992), and abundance of sufficiently common (≥ 40 total observations) species. We used naïve estimates of relative bird abundance (Thompson and La Sorte, 2008) because our data were not collected in an occupancy framework allowing estimates of detectability (e.g., lack of repeated surveys or distance data) (Royle, 2004; Dail and Madsen, 2011). However, both generalized linear mixed models (GLMMs) and N-mixture models generally show the same patterns (Goldstein and de Valpine, 2022). Further, our more traditional approach to data analyses allowed us to examine how bird communities, including both presence and relative abundance of species, responded to shelterwood harvests and mature forests over time as young forests matured in SW. Forest structure and breeding bird data were ln transformed for ANOVAs as needed to reduce heteroscedasticity.

Our primary interest was in treatment effects, or treatment × year interaction effects as indicators that forest structure and bird communities were responding differently within SW or M. A non-significant treatment year interaction indicated that there was a consistent difference between SW and M across years. Treatment, year, or treatment × year interaction differences were considered significant with an overall experimental  $\alpha$  of < 0.05. Where significant treatment × year interactions were present, we identified treatments or years warranting further examination ( $p < 0.05$  in tests of effect slices) and used the least square means for partitioned F-tests (SLICE option) in PROC MIXED (SAS 9.4) to examine the significance of treatment differences within identified years.

## 3. Results

### 3.1. Forest structure

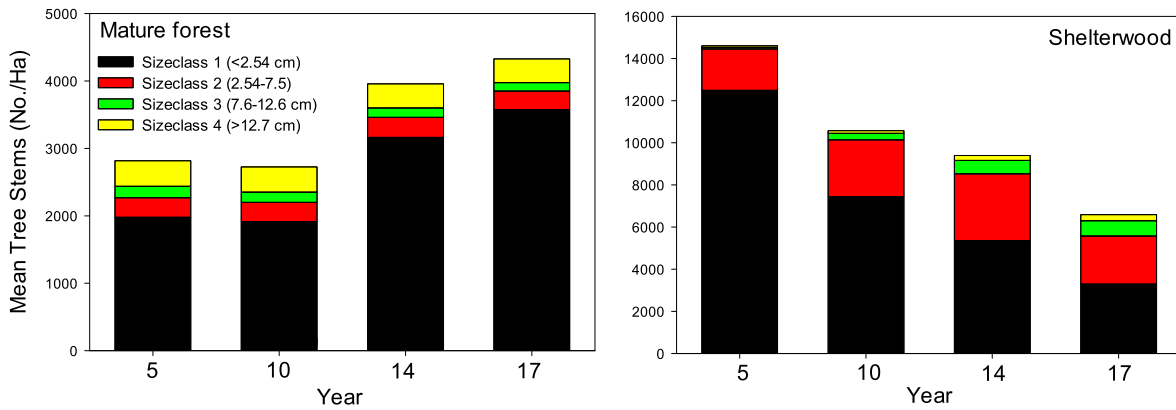
Total (all size classes; ≥ 0.5 m ht including individuals and stump sprouts) tree stem density (measured Y5, Y10, Y14, Y17) was greater in SW than M and greater in Y5 than Y10 and Y17, and in Y14 than Y17; a treatment × year interaction effect was detected (Table 1; Fig. 1). Tests

**Table 1**

Results of repeated measures mixed-model ANOVAs comparing forest structural features between mature forest and shelterwood harvest treatments, years, and treatment × year interaction effects, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. Variables include percent cover of four dominant clonal shrub genera and total clonal shrubs, density of total tree stems (≥ 0.5 m ht) in 4 size classes (Class 1 = stem < 2.54 cm diameter; Class 2 = 2.54–7.5 cm dbh; Class 3 = 7.6–12.6 cm dbh; Class 4 ≥ 12.7 cm dbh), BA of trees ≥ 12.7 cm dbh, and canopy cover<sup>1</sup> (5, 10, 14 and 17 years post-harvest), and canopy height (8 and 17 years post-harvest). Tree stem and BA data were ln transformed for analysis.

Forest Structural Feature	P <sub>trt</sub>	P <sub>yr</sub>	P <sub>trt x yr</sub>
Total clonal shrubs (% cover)	0.7612	<0.0001	<0.0001
Huckleberry (% cover)	0.5301	0.0004	0.0673
Mountain laurel (% cover)	<0.0001	0.1936	0.0654
Rhododendron (% cover)	0.3249	0.0044	0.1029
Blackberry (% cover)	<0.0001	<0.0001	<0.0001
Total tree stem density (no./ha)	<0.0001	0.0015	<0.0001
Class 1 tree stem density (no./ha)	0.0006	<0.0001	<0.0001
Class 2 tree stem density (no./ha)	<0.0001	0.0057	0.0267
Class 3 tree stem density (no./ha)	0.0059	<0.0001	<0.0001
Class 4 tree density (no./ha)	<0.0001	<0.0001	<0.0001
Class 4 tree BA/ha	<0.0001	<0.0001	<0.0001
Canopy cover (%)	0.0236	0.0001	0.0005
Canopy Height (m)	<0.0001	<0.0001	0.0049

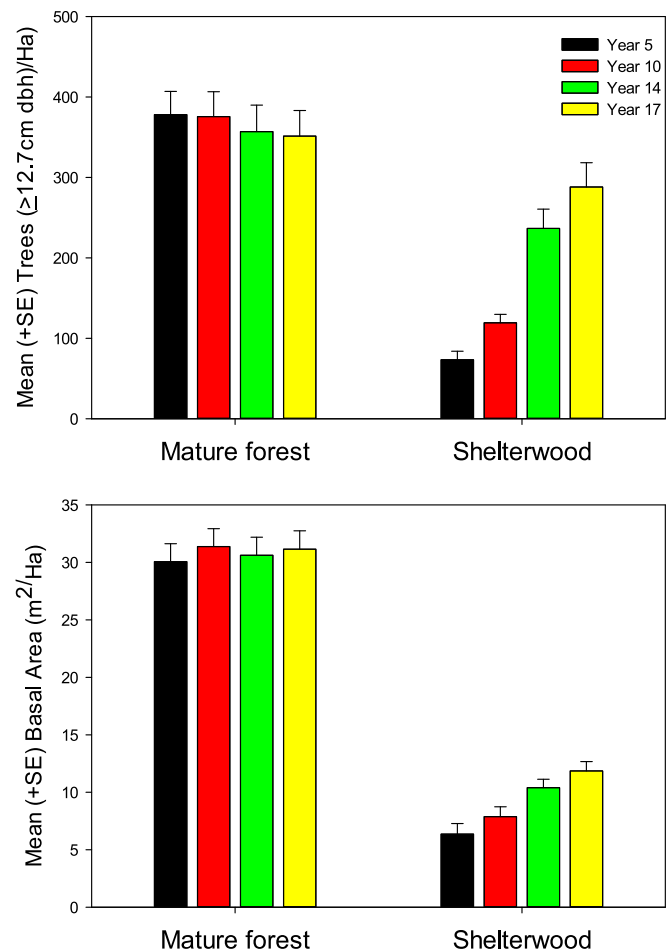
<sup>1</sup> measured along bird transects in a subset of treatment units (n = 6 each, M and SW).



**Fig. 1.** Density of tree stems ( $\geq 0.5$  m ht) in 4 size-classes (Class 1 = stem < 2.54 cm diameter; Class 2 = 2.54–7.5 cm dbh; Class 3 = 7.6–12.6 cm dbh; Class 4  $\geq 12.7$  cm dbh), in mature forest ( $n = 16$ ) and shelterwood harvests (harvested ca. 1999;  $n = 15$ ) 5, 10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

of effect slices indicated that total density was lower in M than SW all years; within M it was lower in Y5 than Y14 and Y17, and within SW density decreased each year except Y5 to Y10. Density of Class 1 stems was lower in M than SW, greater in Y5 than all subsequent years and greater in Y14 than Y17; a treatment  $\times$  year interaction effect was detected. Within M, Class 1 stem density was lower in Y5 and Y10 than Y14 and Y17; within SW, it was greatest in Y5 and decreased each subsequent year. In Y5, Y10, and Y14, Class 1 stem density was lower in M than SW. Density of Class 2 stems was lower in M than SW, lower in Y5 than Y14, and greater in Y14 than Y17; a treatment  $\times$  year interaction effect was detected. Within SW, Class 2 stem density was lower in Y5 than Y10 and Y14 and greater in Y14 than Y17. Within all years, Class 2 stem density was lower in M than SW. Density of Class 3 stems was lower in M than SW, lower in Y5 than all subsequent years, and lower in Y10 than Y17; a treatment  $\times$  year interaction effect was detected. Within SW, Class 3 stem density increased each year except Y14 to Y17; in Y5, it was greater in M than SW, but lower in M than SW in all subsequent years. Density of Class 4 stems was greater in M than SW and increased each year except Y14 to Y17; a treatment  $\times$  year interaction effect was detected (Table 1; Figs. 1, 2). Within SW, Class 4 stem density increased each year except Y14 to Y17. Class 4 stem density was greater in M than SW in Y5, Y10, and Y14. Tree (Class 4;  $\geq 12.7$  cm dbh) BA was greater in M than SW, lower in Y5 than all subsequent years, and lower in Y10 than Y17; a treatment  $\times$  year interaction effect was detected (Table 1; Fig. 2). BA was greater in M than SW in all years; within SW, it was lower in Y5 and Y10 than Y14 and Y17.

Total clonal shrub cover (tested Y5, Y10, Y14, Y17) did not differ between M and SW and was greater in Y5 than all subsequent years; a treatment  $\times$  year interaction effect was detected (Table 1; Fig. 3). Tests of effect slices indicated that within SW, total cover was greater in Y5 than all subsequent years. Dominant clonal shrub species differed in their responses to SW (Table 1; Fig. 3). Huckleberry cover did not differ between M and SW but was greater in Y5 than all subsequent years and greater in Y14 than Y17; no treatment  $\times$  year interaction effect was detected. Mountain laurel cover was greater in M than SW but did not differ among years, and no treatment  $\times$  year interaction effect was detected. Rhododendron cover did not differ between treatments but was lower in Y5 than Y14 and Y17, and lower in Y10 than Y17; no treatment  $\times$  year interaction effect was detected. Blackberry cover was greater in SW than M and greater in Y5 than all subsequent years; a treatment  $\times$  year interaction effect was detected. Within SW, blackberry cover was greater in Y5 than all subsequent years; in Y5 it was greater in SW than M. Closer examination of temporal change in blackberry cover (measured Y1-Y10, Y14, Y17) (ANOVA  $p_{Trt}$ ,  $p_{Yr}$ ,  $p_{Trt \times Yr}$  all < 0.0001) showed that within SW, cover increased most years post-harvest to a peak in Y5 and Y6, then decreased rapidly to low levels by Y8 and



**Fig. 2.** Mean (+SE) density and BA of trees ( $\geq 12.7$  cm dbh) in mature forest ( $n = 16$ ) and shelterwood harvests ( $n = 15$ ; harvested ca. 1999) 5, 10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

thereafter; in Y1-Y7, cover was greater in SW than M (Fig. 4).

Tree canopy height (measured Y8 and Y17) was greater in M than SW, and lower in Y8 than Y17 (Table 1; Fig. 5). Tests of effect slices indicated that tree height was greater in M than SW in Y8 and Y17 and increased in SW from Y8 to Y17. Canopy cover was greater in M than SW and lower in Y5 than all subsequent tested years; a treatment  $\times$  year



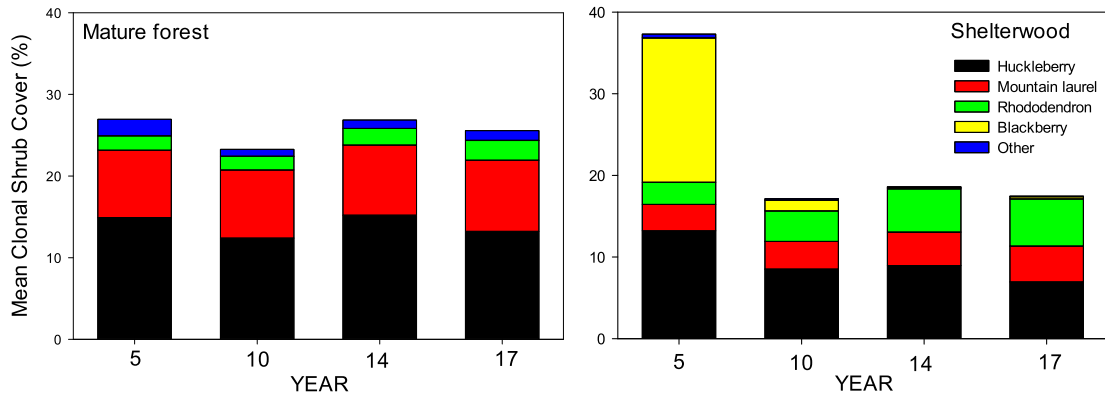


Fig. 3. Percent cover of the four dominant clonal shrub genera and total shrubs in mature forest (n = 16) and shelterwood harvests (n = 15; harvested ca. 1999) 5, 10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

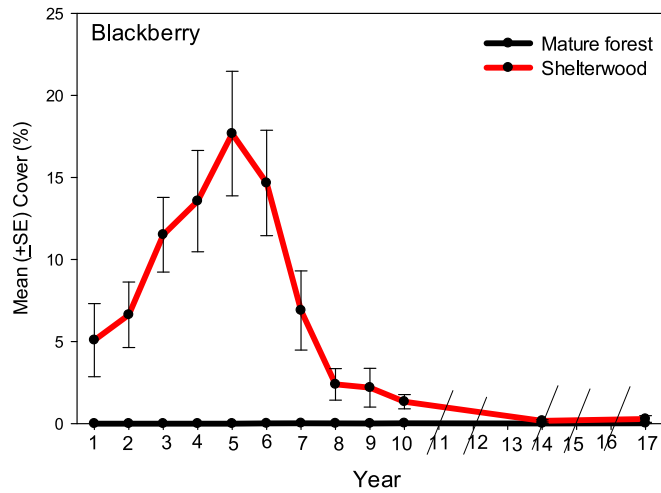


Fig. 4. Percent cover of blackberry (*Rubus* spp.) in mature forest (n = 16) and shelterwood harvests (n = 15; harvested ca. 1999), 1–10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

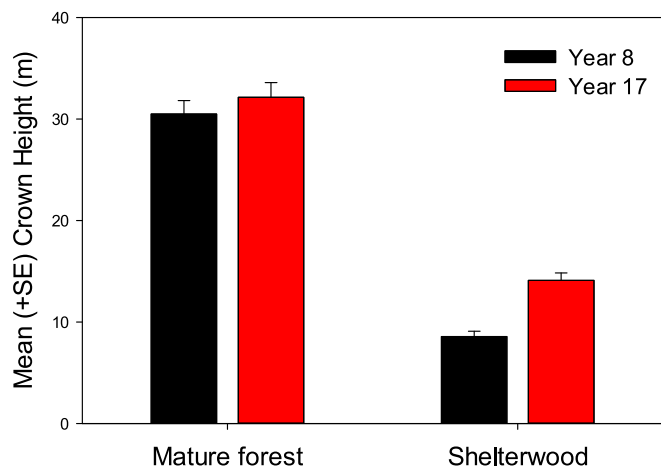


Fig. 5. Mean (+SE) main canopy height in mature forest (n = 16) and shelterwood harvests (n = 15; harvested ca. 1999) 8 and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

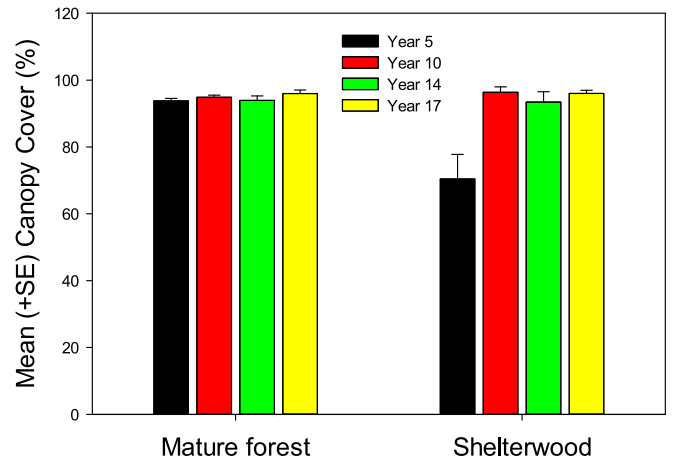


Fig. 6. Mean (+SE) canopy cover (%) estimated along bird transects using a spherical densiometer in mature forest (n = 6) and shelterwood harvests (n = 6; harvested ca. 1999) 5, 10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

interaction effect was detected (Table 1; Fig. 6). Within SW, canopy cover was lower in Y5 than all subsequent years; within Y5, it was greater in M than SW.

### 3.2. Breeding birds

We detected 2,016 individuals of 58 breeding bird species within transects across all sampled years. Total abundance, species richness, and diversity (Table 2, Fig. 7) were greater in SW than M and differed among years; no treatment × year interaction effects were detected. Total bird abundance, species richness, and diversity all showed a moderate to strong, positive correlation with blackberry cover (Table 2).

Among the 16 species analyzed, four showed both treatment and treatment × year interaction effects (Table 2, Fig. 8). Indigo buntings (*Passerina cyanea*), chestnut-sided warblers (*Setophaga pensylvanica*), Eastern towhees (*Pipilo erythrophthalmus*), and Carolina wrens (*Thryothorus ludovicianus*) were more abundant in SW than M, and abundance within SW was dynamic over time. Tests of effect slices indicated that indigo buntings were more abundant in SW than M during Y1–Y7 and Y12. Within SW, abundance was greatest in Y1 and Y2 and decreased nearly every year through Y6; abundance thereafter was low and variable among years. Indigo bunting abundance was strongly, positively correlated with blackberry cover (Table 3). Chestnut-sided warblers were more abundant in SW than M during all years Y1–Y9 except Y8.

**Table 2**

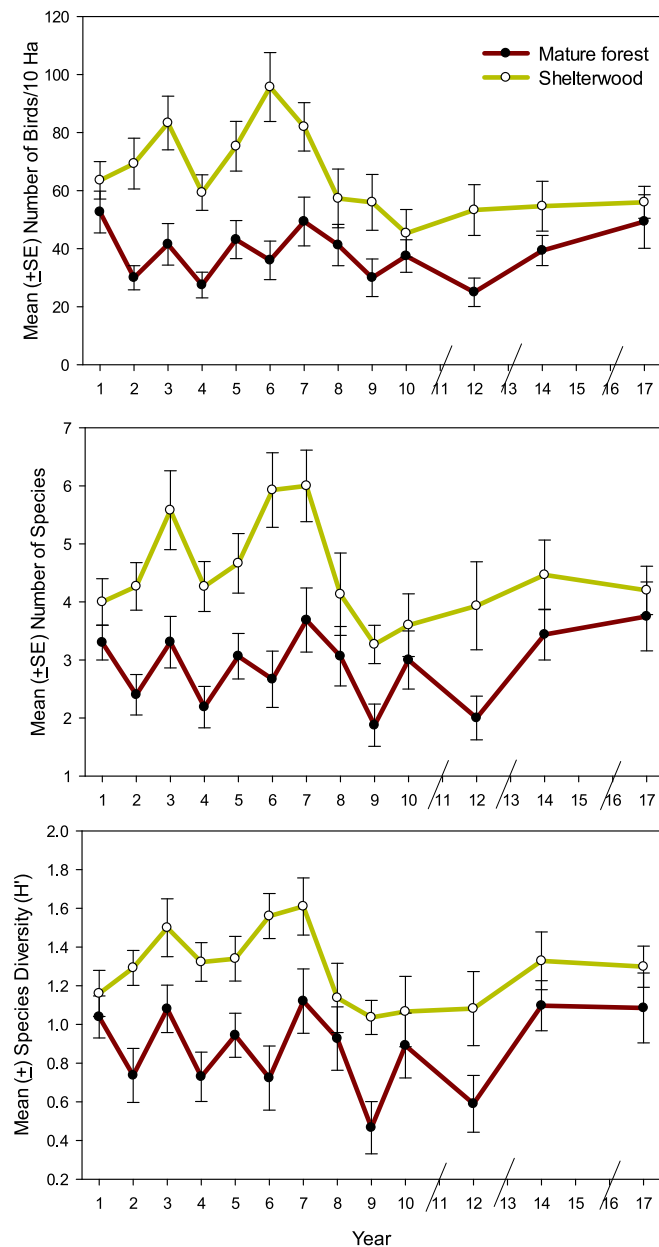
Total number of individual detections (all years and transects) and results of repeated measures mixed-model ANOVAs comparing breeding bird total abundance, species richness, diversity, nesting guilds, and common ( $\geq 40$  detections total) species between mature forest and shelterwood harvest treatments, years (2000–2016; surveyed 1–10, 12, 14, 17 years post-harvest), and treatment  $\times$  year interaction effects, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. Data were  $\ln$  transformed for analysis.

Group	Obs	P <sub>trt</sub>	P <sub>yr</sub>	P <sub>trt x yr</sub>
<b>Ground-nesters</b>	332	0.0433	0.0017	0.4523
Black-and-white warbler ( <i>Mniotilta varia</i> )	78	0.4185	<0.0001	0.1380
Canada warbler ( <i>Cardellina canadensis</i> )	5	–	–	–
Eastern wild turkey ( <i>Meleagris gallopavo</i> )	4	–	–	–
Kentucky warbler ( <i>Geothlypis formosa</i> )	1	–	–	–
Louisiana waterthrush ( <i>Parkesia motacilla</i> )	3	–	–	–
Ovenbird ( <i>Seiurus aurocapilla</i> )	104	0.0005	0.0585	0.4704
Ruffed grouse ( <i>Bonasa umbellus</i> )	10	–	–	–
Slate-colored junco ( <i>Junco hyemalis</i> )	34	–	–	–
Veery ( <i>Catharus fuscescens</i> )	6	–	–	–
Whip-poor-will ( <i>Antrostomus vociferus</i> )	1	–	–	–
Winter wren ( <i>Troglodytes hiemalis</i> )	1	–	–	–
Worm-eating warbler ( <i>Helmithos vermivorus</i> )	85	0.9943	0.0519	0.5933
<b>Cavity-nesters</b>	289	0.0292	0.6310	0.6006
<b>Primary cavity-nesters</b>	54	0.7853	0.0697	0.5709
Downy woodpecker ( <i>Picoides pubescens</i> )	22	–	–	–
Hairy woodpecker ( <i>Picoides villosus</i> )	9	–	–	–
Northern flicker ( <i>Colaptes auratus</i> )	2	–	–	–
Pileated woodpecker ( <i>Drycopus pileatus</i> )	14	–	–	–
Red-bellied woodpecker ( <i>Melanerpes carolinus</i> )	4	–	–	–
Yellow-bellied sapsucker ( <i>Sphyrapicus varius</i> )	3	–	–	–
<b>Secondary cavity nesters</b>	235	0.0007	0.3499	0.6872
Brown creeper ( <i>Certhea americana</i> )	1	–	–	–
Carolina chickadee ( <i>Poecile carolinensis</i> )	81	0.0199	0.4236	0.7012
Carolina wren ( <i>Thyrothrus ludovicianus</i> )	41	0.0015	0.0105	0.0003
Tufted titmouse ( <i>Baeolophus bicolor</i> )	68	0.1959	0.0547	0.0255
Great-crested flycatcher ( <i>Myiarchus crinitus</i> )	2	–	–	–
White-breasted nuthatch ( <i>Sitta carolinensis</i> )	42	0.9340	0.3144	0.6835
<b>Shrub-nesters</b>	854	<0.0001	0.0138	0.0100
American goldfinch ( <i>Carduelis tristis</i> )	14	–	–	–
American robin ( <i>Turdus migratorius</i> )	3	–	–	–
Black-throated blue warbler ( <i>Setophaga caerulescens</i> )	83	0.1698	0.9118	0.0226
Blue-headed vireo ( <i>Vireo solitarius</i> )	54	0.2638	0.8487	0.6239
Brown thrasher ( <i>Toxostoma rufum</i> )	1	–	–	–
Chestnut-sided warbler ( <i>Setophaga pensylvanica</i> )	118	<0.0001	<0.0001	<0.0001
Eastern towhee ( <i>Pipilo erythrophthalmus</i> )	212	<0.0001	0.0002	<0.0001
Hooded warbler ( <i>Setophaga citrina</i> )	121	0.0439	0.0044	0.3323
Indigo bunting ( <i>Passerina cyanea</i> )	139	<0.0001	<0.0001	<0.0001
Mourning dove ( <i>Zenaidura macroura</i> )	8	–	–	–
Northern cardinal ( <i>Cardinalis cardinalis</i> )	39	–	–	–
Prairie warbler ( <i>Setophaga discolor</i> )	2	–	–	–
Ruby-throated hummingbird ( <i>Archilochus colubris</i> )	28	–	–	–
Swainson's warbler ( <i>Limothlypis swainsonii</i> )	15	–	–	–
Wood thrush ( <i>Hylocichla mustelina</i> )	16	–	–	–
Yellow-breasted chat ( <i>Icteria virens</i> )	1	–	–	–

**Table 2 (continued)**

Group	Obs	P <sub>trt</sub>	P <sub>yr</sub>	P <sub>trt x yr</sub>
<b>Tree-nesters</b>	480	0.0549	0.0103	0.0071
Acadian flycatcher ( <i>Empidonax vireescens</i> )	31	–	–	–
American crow ( <i>Corvus brachyrhynchos</i> )	5	–	–	–
American redstart ( <i>Setophaga ruticilla</i> )	10	–	–	–
Black-throated green warbler ( <i>Setophaga virens</i> )	99	0.1742	0.0154	0.0633
Blackburnian warbler ( <i>Setophaga fusca</i> )	18	–	–	–
Blue-gray gnatcatcher ( <i>Ptilioptila caerulea</i> )	51	0.0025	0.0765	0.3989
Blue jay ( <i>Cyanositta cristata</i> )	15	–	–	–
Brown-headed cowbird ( <i>Molothrus ater</i> )	3	–	–	–
Cedar waxwing ( <i>Bombycilla cedrorum</i> )	15	–	–	–
Common grackle ( <i>Quiscalus quiscula</i> )	1	–	–	–
Eastern wood-peewee ( <i>Contopus virens</i> )	20	–	–	–
Northern parula ( <i>Parula americana</i> )	33	–	–	–
Pine warbler ( <i>Setophaga pinus</i> )	1	–	–	–
Red-breasted grosbeak ( <i>Pheucticus ludovicianus</i> )	13	–	–	–
Red-eyed vireo ( <i>Vireo olivaceus</i> )	132	0.3235	0.0716	0.0516
Scarlet tanager ( <i>Piranga olivacea</i> )	32	–	–	–
Yellow-billed cuckoo ( <i>Coccyzus americanus</i> )	1	–	–	–
<b>Other</b>	4	–	–	–
Eastern phoebe ( <i>Sayornis phoebe</i> )	1	–	–	–
<b>Unknown</b>	57	–	–	–
<b>Total birds</b>	2016	0.0004	0.0099	0.2144
<b>Species richness</b>	59	0.0008	0.0012	0.2491
<b>Species diversity (H')</b>	—	0.0006	<0.0001	0.2301

Within SW, abundance peaked in Y5-Y6 and decreased most years thereafter; by Y10 and subsequently, abundance in SW did not differ from M. Chestnut-sided warbler abundance was strongly, positively correlated with blackberry cover (Table 3). Eastern towhees were more abundant in SW than M during Y1-Y9 except Y4. Within SW, Eastern towhee abundance peaked Y5-Y7, then decreased through Y10, remaining low for all subsequent years. Eastern towhee abundance was strongly, positively correlated with blackberry cover (Table 3). Carolina wrens were more abundant in SW than M during Y1-Y4 and Y7. Within SW, abundance was greater in Y1-Y4, Y7, and Y9 than other years. Carolina wren abundance was moderately, positively correlated with blackberry cover (Table 3). Abundance of blue-gray gnatcatchers (*Ptilioptila caerulea*), Carolina chickadees (*Poecile carolinensis*), and hooded warblers (*Setophaga citrina*) was greater in SW than M and was weakly, positively correlated with blackberry cover (Table 3). In contrast, ovenbird (*Seiurus aurocapilla*) abundance was greater in M than SW and was moderately, negatively correlated with blackberry cover (Table 3). Two species showed only treatment  $\times$  year interaction effects. Abundance of black-throated-blue warblers (*Setophaga caerulescens*) was greater in M than SW in Y1, Y3, and Y8 and was weakly, negatively correlated with blackberry cover. Tufted titmice (*Baeolophus bicolor*) were more abundant in SW than M in Y12 and Y17. Within SW, they were less abundant in Y1 and Y4 than Y12 and Y17, and less abundant in Y2, Y3, and Y5-Y14 than in Y17. Tufted titmice abundance was not correlated with blackberry cover. Abundance of black-and-white warblers (*Mniotilta varia*), worm-eating warblers (*Helmithos vermivorus*), white-breasted nuthatches (*Sitta carolinensis*), blue-headed vireos (*Vireo solitarius*), and red-eyed vireos (*V. olivaceus*) showed no treatment or treatment  $\times$  year interaction effects, and was not correlated with blackberry cover (Table 3); black-throated green warbler (*S. virens*) abundance also showed no treatment or treatment  $\times$  year interaction effects but was weakly negatively correlated with blackberry cover



**Fig. 7.** Mean ( $\pm$ SE) total number of breeding birds/10 ha, species richness, and species diversity in mature forest ( $n = 16$ ) and shelterwood harvests ( $n = 15$ ; harvested ca. 1999) 2000–2016 (1–10, 12, 14, and 17 years post-harvest), Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

(Table 3).

Among nesting guilds, ground-nesters were more abundant in M than SW and abundance differed among years; no treatment  $\times$  year interaction effect was detected (Table 2; Fig. 9), and abundance was weakly, negatively correlated with blackberry cover (Table 3). Cavity-nesters overall were more abundant in SW than M; no year or treatment  $\times$  year interaction effect was detected, and abundance was weakly, positively correlated with blackberry cover. Within the cavity-nesting guild, primary cavity-nester (woodpecker) abundance did not differ between M and SW or among years; no treatment  $\times$  year interaction effect was detected. In contrast, secondary cavity-nester abundance was greater in SW than M; no year or treatment  $\times$  year interaction effect was detected. Shrub-nesters were more abundant in SW than M and differed among years; a treatment  $\times$  year interaction effect was detected. Tests of effects slices indicated that shrub-nesters were more abundant in SW than M

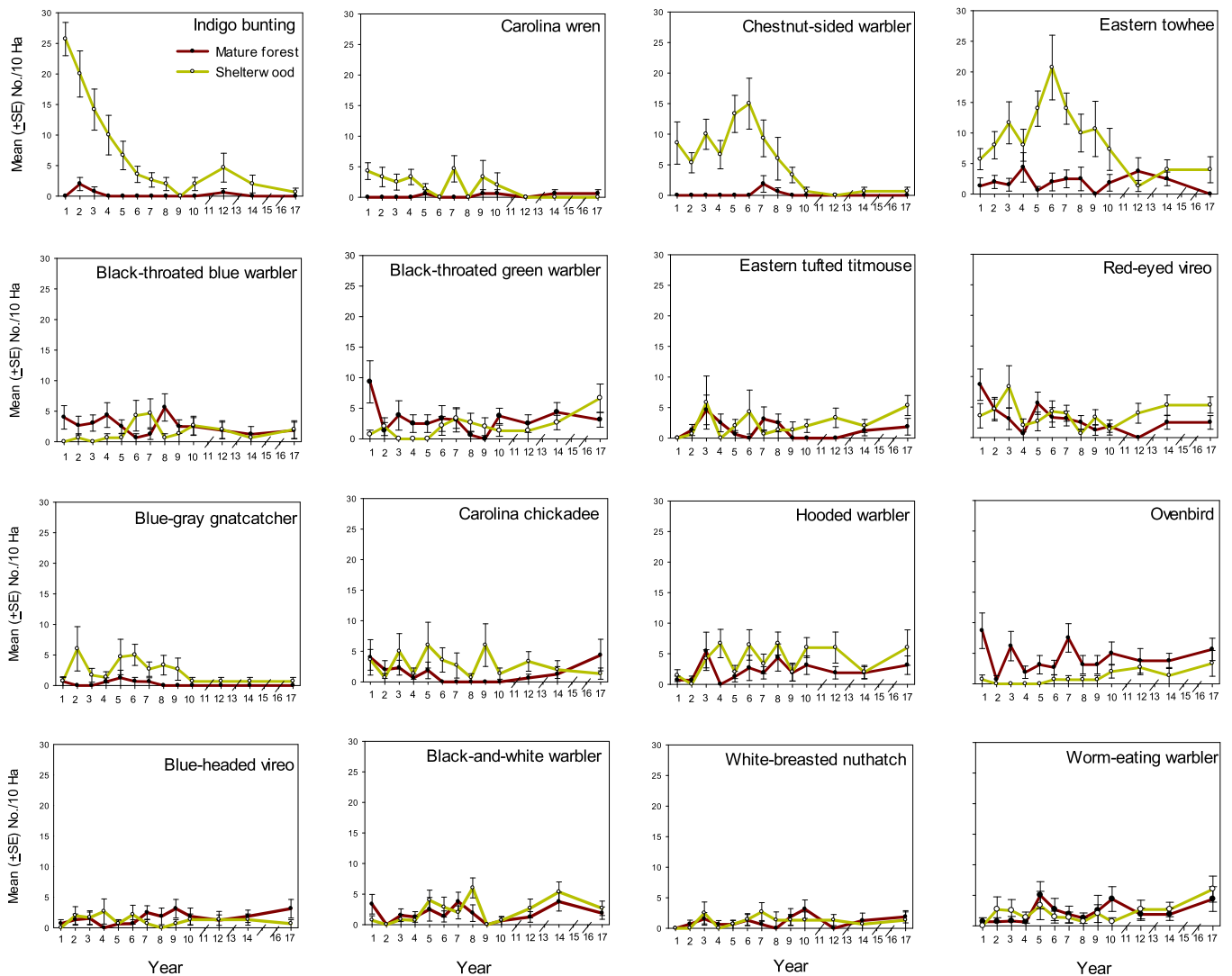
from Y1–Y10. Within SW, abundance was greater Y1–Y3, Y5, and Y7 than Y10–Y17, greater in Y4 and Y8 than Y12–Y17, and greater in Y6 than Y9–Y17. Shrub-nester abundance was strongly, positively correlated with blackberry cover (Table 3). Abundance of tree-nesters did not differ between M and SW and differed among years; a treatment  $\times$  year interaction effect was detected. Abundances varied among years within both M and SW but no distinct trends were apparent in either treatment; tree-nester abundance was greater in SW than M in Y2, Y9, and Y12 but lower in Y10. Tree-nester abundance was weakly, positively correlated with blackberry cover (Table 3).

#### 4. Discussion

Our 17-year study allowed us to compare dynamic changes in forest structure and breeding bird communities between mature- and young forests over time. In our study, forest structure and breeding bird communities in M were relatively static throughout the study period. In contrast, changes in breeding bird communities generally corresponded with the “stem initiation” and “stem exclusion” stages of forest stand development in SW following regeneration harvests with heavy overstorey removal (Oliver and Larson, 1996; Johnson, 2008; Loftis et al., 2011). Heavily reduced canopy cover and increased light after timber harvests in SW initiated rapid increases in small tree stem densities as harvested stumps resprouted and new seedlings germinated; total clonal shrub cover also increased in SW, driven primarily by blackberry responding to the recently disturbed, high-light environment. This open-canopy forest structure with low, dense vegetation was short-lived. Young, competitive trees in SW grew rapidly in girth and height, shading out and killing many of their cohorts with concomitant reductions in both small tree stem density and percent cover of blackberry within 10 years of harvest. Total abundance, species richness, and diversity of breeding birds was greater in SW than M, especially the first several years post-harvest; in Y6 these metrics were more than twice as high in SW as in M. Shrubland species and some nesting guilds also generally tracked these changes in SW forest structure, showing a strong positive response during the first several years post-harvest, followed by declines to levels similar to those in M within 10 years.

Our results indicated that an influx of shrubland birds and positive or neutral responses by most other species were the primary drivers of higher total abundance and species richness for several years following SW harvests. Shrubland associates, including indigo buntings, chestnut-sided warblers, and Eastern towhees occurred exclusively or primarily in SW, where abundances in Y1–Y7 ranged from 3 to 26 times greater than in M. Several non-shrubland species were also more abundant in SW than M although the magnitude of differences between the treatments was smaller than for shrubland associates. Abundance of Carolina wrens was consistently greater in SW than M for about 4 years post-harvest and were likely responding to slash piles resulting from timber harvests (e.g., Conner and Adkisson, 1975; pers. obs.) in SW rather than forest structure per se. Additionally, blue-gray gnatcatchers, Carolina chickadees, and hooded warblers showed greater abundance in SW than M throughout the 17-year study period; black-throated-blue warblers and tufted titmice were more abundant in SW than M in some years, and six species typically considered mature forest associates (black-and-white warbler, worm-eating warbler, white-breasted nuthatch, blue-headed vireo, red-eyed vireo, black-throated green warbler) showed no difference in abundances between SW and M for the duration of our study.

Other studies also show that both shrubland and most mature forest associated bird species are abundant following heavy canopy disturbances where some mature trees remain such as shelterwood harvests (Annand and Thompson, 1997; Baker and Lacki, 1997; Rodewald and Smith, 1998; Augenfeld et al., 2008; McDermott and Wood, 2009; Newell and Rodewald, 2012; Perry and Thill, 2013; Perry et al., 1999; Greenberg et al., 2014; Duguid et al., 2016; Kellner et al., 2016), wind disturbance (Greenberg and Lanham, 2001; Newbold, 1996; Prather et al., 2003), and high-severity wildfire (e.g., Greenberg et al., 2023). All



**Fig. 8.** Mean ( $\pm$ SE) abundance of 16 breeding bird species in mature forest ( $n = 16$ ) and shelterwood harvests ( $n = 15$ ; harvested ca. 1999) 2000–2016 (1–10, 12, 14, and 17 years post-harvest), Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

of these disturbances generally retain some live-tree canopy within or near the affected forest and create a pulse of resources attractive to birds such as low, dense woody cover, high densities of flying/foliar insects likely attracted to young foliage and flowers (Whitehead, 2003), and an abundance of fleshy fruits for several years after disturbance (e.g., Greenberg et al., 2011). Adults and juveniles of many mature forest species are shown to move into canopy gaps or young forests during the post-fledging stage (e.g., Marshall et al., 2003; Whitehead, 2003; King et al., 2006; Stoleson, 2013).

Our long-term, continuous data allowed us to illustrate different response patterns by several individual species – especially shrubland species - showing that their abundances increased, peaked, and declined at slightly different rates as young forests approached canopy closure. For example, average abundance of indigo buntings in SW peaked in Y1 at 26/10 ha (compared to none in M) but decreased each year through Y6; abundance in SW did not differ from M for most years thereafter. Chestnut-sided warblers were much more abundant in SW than M for about 9 years post-harvest (Y1–Y9), peaking around Y6 (15/10 ha in SW; none in M) and declining thereafter. Eastern towhees showed a similar trend, with much greater abundance in SW than M for about 9 years post-harvest (Y1–Y9), peaking Y5–Y7 (14–21/10 ha in SW; 1–3/10 ha in M) and declining thereafter. Other studies show similar patterns of abundance and decline by these shrubland species (e.g., Perry and Thill,

2013; Duguid et al., 2016). In a meta-analysis, Schlossberg and King (2009) reported that many shrubland birds specialize along a narrow window of time in post-disturbance stand development, highlighting that the suitability of regenerating forest for shrubland birds differs among species and across time. We additionally suggest that the temporal window of optimal post-disturbance habitat suitability for various shrubland species may differ across geographies, topographic positions, and forest compositions as they affect rates of stand development (Loftis et al., 2011).

Some other studies show that “bird succession” mirrors young forest stand development, with an initial high abundance of shrubland species yielding to species typically associated with mature, closed canopy forest as stands approach canopy closure (e.g., Crawford et al., 1981); results of others are equivocal, corroborating our results (e.g., Duguid et al., 2016; Perry et al., 1999). Although we found clear negative associations between stand development and shrubland species in SW, we saw little evidence that “mature forest species” increased in SW over our 17 year study period. In our study ovenbirds were the only species that was more abundant in M than SW; a non-significant trend suggested that abundance in SW started to increase around Y10. Many other studies also suggest that ovenbirds are negatively affected by timber harvests with heavy canopy removal (e.g., Duguid et al., 2016; Perry et al., 1999). We suggest that many species traditionally considered to be mature



**Table 3**

Spearman's Rank Correlations of percent blackberry cover with breeding bird species total abundance (no./10 ha), species richness, diversity, abundance within nesting guilds, and abundance of common species (2000–2016; surveyed 1–10, 14, 17 years post-harvest), Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

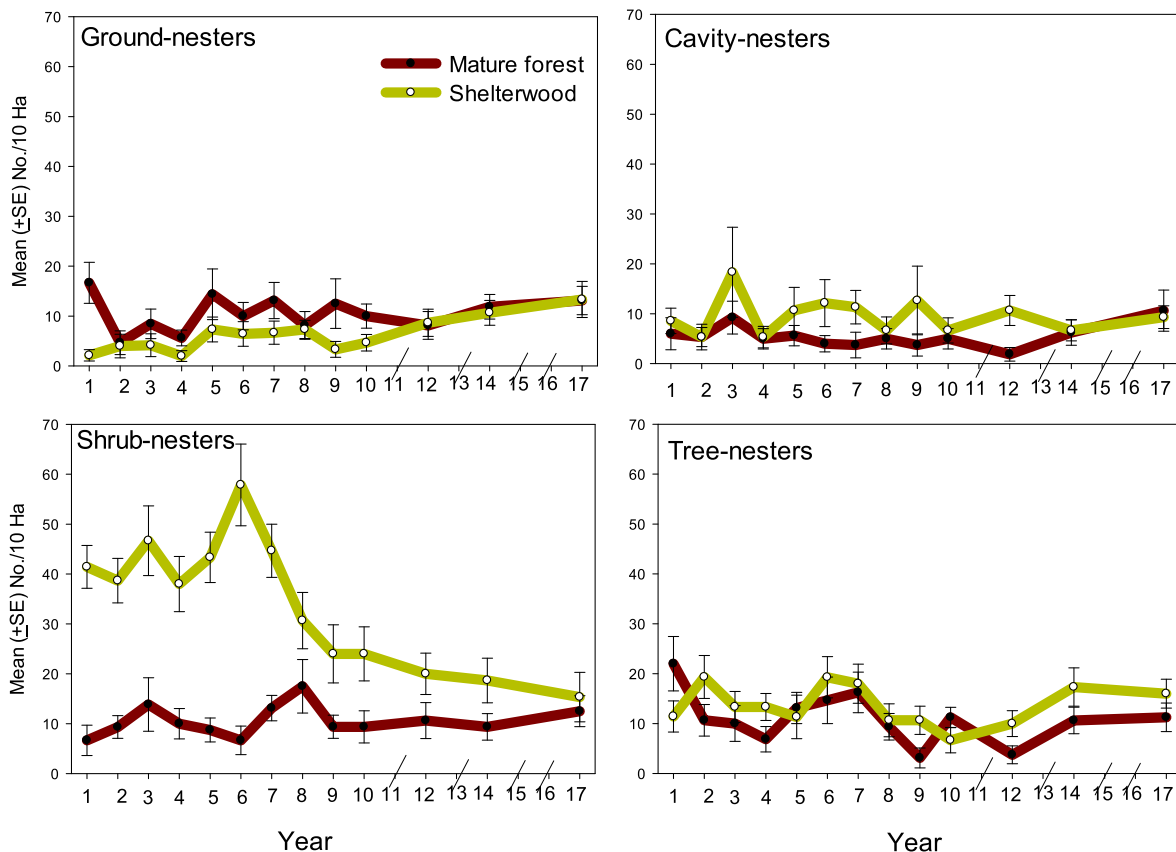
Group	r-value	p-value
<b>Ground-nesters</b>	-0.19	0.0002
Black-and-white warbler	-	0.4808
Ovenbird	-0.32	<0.0001
Worm-eating warbler	-	0.4411
<b>Shrub-nesters</b>	0.62	<0.0001
Black-throated blue warbler	-0.11	0.0413
Blue-headed vireo	-	0.4269
Chestnut-sided warbler	0.58	<0.0001
Eastern towhee	0.47	<0.0001
Hooded warbler	0.16	0.0022
Indigo Bunting	0.52	<0.0001
<b>Cavity-nesters</b>	0.12	0.0215
Carolina chickadee	0.14	0.0083
Carolina wren	0.29	<0.0001
Tufted titmouse	-	0.4261
White-breasted nuthatch	-	0.8710
<b>Tree-nesters</b>	0.13	0.0128
Black-throated green warbler	-0.12	0.0214
Blue-gray gnatcatcher	0.27	<0.0001
Red-eyed vireo	-	0.5646
<b>Total birds</b>	0.44	<0.0001
<b>Species richness</b>	0.39	<0.0001
<b>Species diversity (H')</b>	0.36	<0.0001

forest obligates are in fact resilient to disturbances (Perry et al., 1999), evidenced by similar (or greater) abundances in mature forest as in young forest through 17 years of stand development.

Our nesting guild-level responses were similar to those reported by

others after heavy canopy reductions (e.g., Greenberg et al., 2014, 2018, 2023) but were likely driven by a subset of species within those guilds. For example, our result showing fewer ground-nesters in SW than M was clearly driven by ovenbird response alone; abundance of other tested ground-nesting species (black-and-white warbler and worm-eating warbler) did not differ between the treatments. Similarly, a greater overall abundance of cavity-nesters in SW than M was driven by secondary cavity-nesters, and Carolina chickadees and Carolina wrens in particular. A much greater abundance of shrub-nesters in SW than M was driven mainly by marked increases in shrubland shrub-nesting species (indigo buntings, chestnut-sided warbler, Eastern towhee); most other tested shrub-nesting species (blue-headed vireo, black-throated blue warbler) showed no response to treatments. Similarly, one tree-nesting species (blue-gray gnatcatcher) was more abundant in SW than M but the two other tested species (black-throated green warbler and red-eyed vireo) showed no treatment response. Thus, we suggest that species-level responses are more informative than nesting guild-level responses in explaining changes in breeding bird communities following SW harvests.

Blackberry commonly becomes a prolific shrub within 2–3 years of heavy overstory reduction in eastern hardwood forests (Donoso and Nyland, 2006). In our study temporal change in blackberry cover closely tracked other changes in forest structure corresponding with stand development following harvests in SW (Loftis et al., 2011). Blackberry quickly “pioneered” SW stands in response to the recently disturbed, high-light environments and increased rapidly, peaking in Y5-Y6, then declining rapidly to negligible levels by Y8 as young trees gained girth and height, casting heavy shade. Blackberry cover and bird response variables including total abundance, species richness, diversity, shrub-nesters, and shrubland species showed similar post-disturbance response patterns in SW and were moderately to strongly correlated;



**Fig. 9.** Mean (±SE) abundance of breeding birds within four nesting guilds in mature forest (n = 16) and shelterwood harvests (n = 15; harvested ca. 1999) 2000–2016 (1–10, 12, 14, and 17 years post-harvest), Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

ovenbirds were negatively correlated with blackberry cover. Our results indicate that blackberry cover was an indicator of open, young forest stand structure and therefore a suitable stand-alone predictor of post-disturbance changes in breeding bird communities.

## 5. Conclusions

Our study corroborated others showing that heavy overstory removal by shelterwood regeneration harvests promoted higher abundance, species richness, and diversity of breeding birds. Three shrubland species (indigo bunting, chestnut-sided warbler, Eastern towhee) showed dramatic increases in abundance within 1–2 years of harvests as the understory vegetation responded to the high light environment with prolific increases in tree stem density and clonal shrub cover, driven by blackberry. Each shrubland bird species showed slightly different patterns of increase, peak, and decline but abundance of all three decreased to similar levels as in mature forest within 6–9 years. Their patterns of abundance closely tracked changes in vegetation structure associated with stand development as young, competitive trees gained height and girth, shading out and killing many of their cohorts with concomitant reductions in tree stem density and blackberry cover within 10 years. Several other bird species showed positive or neutral responses to SW; only ovenbirds responded negatively to SW. Our results further indicated that blackberry cover was an indicator of open, young forest stand structure (e.g., high density of small tree stems) and therefore a suitable stand-alone predictor of post-disturbance changes in breeding bird communities including species richness and the abundance of total birds, shrub-nesters, shrubland species, and ovenbirds. Our study indicates that shrubland species require young, recently disturbed forests, whereas most breeding bird species are not negatively affected by heavy overstory reduction. However, other studies indicate that species may respond differently to varying levels of canopy retention and (or) size of openings (e.g., Annand and Thompson, 1997; Costello et al., 2000; Moorman and Guynn, 2001; Perry and Thill, 2013). Thus, a gradient of disturbances and overstory tree retention could potentially maximize habitat availability for multiple species at a landscape level (Annand and Thompson, 1997). We suggest that forest managers develop timber harvest rotations that provide a sustained availability of young (<10 year old) forests to promote diverse breeding bird communities and shrubland species (Shifley and Thompson, 2011).

## Author contributions

Cathryn H. Greenberg designed and directed the overall study, co-directed the bird study, analyzed the data, created figures, and wrote the majority of the manuscript. J. Drew Lanham was M. Whitehead's major advisor for her PhD, co-directed the bird study and reviewed the manuscript. Maria Whitehead initiated the bird study as her PhD research (completed 2003), conducted the majority of bird surveys 2000–2003, and reviewed the manuscript. Joseph Tomcho conducted the majority of bird surveys 2004–2017, provided insights, and reviewed the manuscript.

## 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.

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