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Seasonal bird communities in Shelterwood harvests and unmanaged mature forest

Cathryn H. Greenberg[a], **Margaret Woodbridge**[a], **Maria Whitehead**[b], **J. Drew Lanham**[c], **Charles Kwit**[d], **and Joseph Tomcho**[e]

[a]USDA Forest Service, Southern Research Station, Upland Hardwood Ecology and Management Research Work Unit, Asheville, NC 28806, USA; [b]Clemson University Dept. of Forestry and Environmental Conservation, 180 North Caldwell Street, Brevard, NC 28712, USA; [c]Clemson University Dept. of Forestry and Environmental Conservation, 115 Lehotsky Hall, Clemson, SC 29634, USA; [d]University of Tennessee, Knoxville, School of Natural Resources, 401 Agriculture and Natural Resources Building, Knoxville, TN 37996, USA; [e]North Carolina Wildlife Resources Commission, 78 Wildlife Lane, Burnsville, NC 28714, USA

Corresponding author: **Cathryn H. Greenberg** (email: Cathryn.greenberg@usda.gov)

Abstract

Effective bird conservation planning requires consideration of year-round habitat requirements. We evaluated how bird communities differed across seasons, and between young shelterwood (SW) and unmanaged mature (M) hardwood forests over 8 years. We detected 3952 individuals of 82 bird species within transects. Total abundance, richness, and diversity were highest in summer and lowest in winter. Richness was greater in SW than M during all seasons; abundance and diversity were greater in SW during summer, fall, and spring. Community composition differed between SW and M during all seasons except winter. Within seasons, abundance of most analyzed species was greater in SW than M or similar between the treatments. In SW young forest habitat suitability for most species (except indigo buntings) persisted for at least 8 years. Residency guilds and some species showed greater habitat selectivity in some seasons (heavier use of SW) than others (similar use of both SW and M). Our study illustrates the important role of young forests in promoting bird diversity year-round. However, knowledge gaps remain regarding bird use of all forest age-classes during all seasons, and how long dynamically changing young forests support more birds and bird species than mature forest during non-breeding seasons.

Key words: forest structure, mature forest, migratory birds, seasonal bird communities, shelterwood harvest, stand development

Introduction

North American bird populations have declined precipitously over the past five decades, with migratory species, including those overwintering in temperate regions and South America, being particular hard-hit (Rosenberg et al. 2019). In the eastern US, forest birds have declined by nearly 30% since 1970 (NABCI 2022). Habitat loss and global climate change are major contributors to population declines and extinctions worldwide (La Sorte et al. 2017). Migratory birds may be especially vulnerable to these threats as they rely on habitats across multiple geographic regions throughout the annual cycle. Annual survival of adult and juvenile birds is a key driver of population dynamics (e.g., Germain et al. 2018). Bird mortality is often highest during winter (Jannson et al. 1981; Rogers et al. 1991), and winter conditions such as food availability can affect bird productivity the following breeding season (Robb et al. 2008), highlighting the importance of suitable winter habitats for year-round and winter residents. Similarly, long-distance migration is associated with high risk of mortality and is likely an important driver of migratory bird populations (Hutto 2000; Moore et al. 2005). Stopover sites can ideally provide both cover from predators and abundant food to meet high energy demands (Moore et al. 2005) and may be critical to promoting survival during long-distance migrations. Forest management for breeding bird habitats is critical, yet effective conservation planning requires consideration of habitat requirements throughout the annual cycle, including over-wintering birds, permanent residents, and non-resident migratory birds *en route* to their wintering or breeding grounds during fall and spring migrations (Moore et al. 2005).

Young hardwood forests within the Central Hardwoods Region play an important role in promoting the abundance and diversity of birds during the breeding season. Multiple studies show higher breeding bird diversity after heavy forest canopy reduction by natural or anthropogenic disturbances ranging from high-severity wildfire (e.g., Greenberg et al. 2023*a*) or wind (e.g., Greenberg and Lanham 2001; Prather and Smith 2003), to artificially-created canopy gaps (Bowen et al. 2007) and shelterwood- and other regeneration harvest methods (e.g., Annand and Thompson 1997; McDermott and Wood 2009; Newell and Rodewald 2012; Perry and Thill 2013;

Duguid et al. 2016; Greenberg et al. 2023*b*). This is largely due to an influx of shrubland species to recently disturbed forests, combined with a positive or neutral response by most mature forest species (Greenberg et al. 2023*b*). Similar results are evident for the relatively few studies conducted outside of the breeding season, with heavier use of gaps, edge, and other young forests during migration (Blake and Hoppes 1986; Martin and Karr 1986; Kilgo et al. 1999; Rodewald and Brittingham 2002; Bowen et al. 2007) and the post-breeding period, when adults and post-fledgling juveniles of many mature forest species are shown to move into canopy gaps or young forests (e.g., Whitehead 2003; Bowen et al. 2007).

Heavy forest canopy reduction initiates rapid increases in woody stem density as tree seedlings germinate and harvested stumps and shrubs resprout in response to increased light to the forest floor. This creates 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 (Blake and Hoppes 1986; Whitehead 2003), and an abundance of fleshy fruits for several years after disturbance primarily during late spring through fall (e.g., Greenberg et al. 2011). However, 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 (e.g., Loftis et al. 2011). Young tree sprouts and seedlings rapidly gain height and girth, often reaching canopy closure with concomitant reductions in light, tree stem densities, and shrub cover within less than 15 years (Loftis et al. 2011). Most studies report that breeding habitat for shrubland species becomes unsuitable within 9–12 years of harvest (Perry and Thill 2013; Perry et al. 2018; Greenberg et al. 2023*b*). However, most bird-habitat studies are conducted during the breeding season, and thus may not capture the range of forest conditions selected by different species across the annual cycle.

Disproportionate use of some habitats relative to availability (e.g., Moore et al. 1990; Bowen et al. 2007), species-specific habitat use (Morrison et al. 1986), differential use of the same habitats across seasons (Blake and Hoppes 1986; Martin and Karr 1986), and a positive association between habitat use and food availability or dietary preferences (Blake and Hoppes 1986; Martin and Karr 1986; Moore et al. 2005) all suggest that birds actively select among locally available habitats as stopover sites during migration (Moore et al. 2005) and in winter (Morrison et al. 1986) just as they do during and across the breeding season. Similarly, suitable habitats for migratory species during the breeding season do not necessarily correspond with those used during migration, or even between spring and fall migration periods (Hutto 2000; Petit 2000). Shifts in habitat may be associated with changing "priorities" across seasons such as food availability, competition, and predation risk during migration (Hutto 2000; Petit 2000) or winter, and nest sites additionally, during breeding season. Despite the use of different habitats among species and across the annual cycle, very few studies address how community composition and abundance of different species differs among seasons, between mature and young upland hardwood forests, and over time as young forests grow to canopy closure.

Most studies addressing temporal patterns of bird habitat use across post-disturbance stages of forest stand development focus only on the breeding season and do not continuously track post-harvest changes in forest structure and bird communities in the same locations over a long period of time. Studies of bird communities during non-breeding seasons are rare, short-term, and often focus on just one season (e.g., winter, or spring and/or fall migration). In an earlier article Greenberg et al. (2023*b*) examined long-term (17-year) changes in forest structure and breeding bird (summer) communities in unmanaged mature forest ($n = 16$) and young 2-age stands created by shelterwood-with-reserves regeneration harvests ($n = 15$). In this study, we used the same study design to evaluate differences in bird communities between mature, unmanaged forest, and recently-harvested shelterwoods (≤20% residual basal area (BA) retained) across all four seasons (summer, fall, winter, and spring) over 8 years; our data include the first 8 years of breeding bird data examined in the earlier article (Greenberg et al. 2023*b*), as well as data for the other seasons. Our objective was to examine how bird communities (abundance, species richness, diversity, and composition) and use by individual species differed among seasons overall, and between young and mature forest within seasons or over time as young forest structure changed with stand development toward canopy closure.

Methods

Study area

Our study sites were located throughout the Pisgah and Grandfather ranger districts of the Pisgah National Forest in Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina, USA. Sites were located across a wide range of topographic features such as aspect, slope position, percent slope, and elevation (500–1200 m). Annual rainfall in the region (Pisgah Forest, 1991–2020) averaged 165.2 cm and annual temperature averaged 13.1 °C, ranging from 4.1 °C in winter to 22.1 °C in summer (https://www.ncei.noaa.gov/access/us-climate-normals/#dataset=normals-monthly&timeframe=30&location=NC&station=USC00310724). Soils were predominantly Dystrochrepts and Hapludults (Pittillo et al. 1998). Mature forest ranged from 80–100 years old at study establishment. Forests were composed of yellow poplar (*Liriodendron tulipifera* L.), northern red oak (*Quercus rubra* L.), magnolia (*Magnolia* spp.), white ash (*Fraxinus americanus* L.), beech (*Fagus grandifolia* Ehrh.), hemlock (*Tsuga canadensis* (L.) Carrière), and silverbell (*Halesia Carolina* L.) on moister sites; drier sites were dominated by scarlet oak (*Quercus coccinea* Münchh.), chestnut oak (*Quercus montana* Willd.), black oak (*Quercus velutina* Lam.), blackgum (*Nyssa sylvatica* Marshall), and sourwood (*Oxydendrum arboreum* (L.) DC.). Red maple (*Acer rubrum* L.), hickories (*Carya* spp.), flowering dogwood (*Cornus florida* L.), and white oak (*Quercus alba* L.) were common throughout (Pittillo et al. 1998).

Study design

We selected 15 young shelterwood (SW) and 16 unmanaged mature (M) 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 regeneration harvests conducted during 1998–1999. About 80%–85% of overstory tree BA was removed resulting in open, naturally regenerating young forests; a few scattered trees—mostly oaks and hickories—were retained for aesthetics, and to maintain hard mast production (acorns and hickory nuts) and some structural heterogeneity for wildlife (T. Oprean, Pisgah National Forest, pers. comm.). Shelterwood stand sizes ranged from 3.2 to 10.5 ha (average 7.0 ha) and were generally the same age as M study stands when they were harvested (80–100 years old). Forest service personnel conducted site-preparation treatments in regenerated stands within a year of harvesting by cutting all stems 2.5–20 cm diameter at breast height (dbh) (Pisgah district) or 5–25 cm dbh (Grandfather district) and ≥1.4 m tall. The harvested tree stump surfaces of red maple, flowering dogwood, silverbell, sourwood, yellow poplar, sassafras (*Sassafras albidum*), black locust (*Robinia pseudoacacia* L.), Fraser magnolia (*M. fraseri* Walter), and blackgum, as well as rhododendron (*Rhododendron* spp.), and mountain laurel (*Kalmia latifolia* L.) were treated with herbicide (Garlon 3 A, 50–50 mix; Dow AgroSciences, Indianapolis, IN) to reduce sprouting.

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 ≥25 m from edges. We conducted bird surveys once each season in each unit for 8 years (summer 2000 through spring 2008) starting about a year post-harvest: summer (breeding season) (19 May to 13 July), fall (8 September to 25 October), winter (17 December to 27 February), and spring (14 March to 1 May). We selected season start-end dates to encompass peak breeding, winter, and spring and fall migration periods, but recognize that some overlap was likely (e.g., Bowen et al. 2007). For example, neotropical migratory birds that breed within our study area could arrive during spring migration and either remain or continue north to breed; similarly, they may linger into the fall, and (or) different individuals of the same species may pass through *en route* to their southern wintering grounds. Similarly, species that breed further north but winter within our study area could arrive during fall and either remain through winter or continue south. We slowly (about 15 min, or 1 km/1.25 h) walked transect centerlines between sunrise and 4 h after sunrise and recorded all individual birds seen or heard within an estimated 25 m on either side. Flyovers were not included in data analyses. A few transects were not surveyed in some years 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); five other highly experienced observers also conducted surveys during the study. Additionally, we used a short (25 m) fixed detection distance from transect centerline that minimized the likelihood of differences in bird detectability between treatments due to forest structure, especially because most detections were aural. We ensured that surveys in SW and M were distributed evenly throughout the study period and avoided surveys during moderate–high winds or precipitation. Abundance for each treatment unit was calculated by summing all individuals (by species and total) detected within the 1 ha transect and multiplying by 10 (number/10 ha; a more realistic scale for forest management units or stand sizes). We elected to use simple community metrics instead of a composted metric such as Hill Numbers (Jost 2006) to facilitate comparisons with other studies. Species richness represented the total number of species detected within transects each unit, season, and year; species diversity was calculated using the Shannon diversity index (Shannon 1948).

Forest structure

We quantified forest structure within a 20 × 50 m (0.1 ha) plot randomly placed within each M and SW study stand in 2004 (5 years post-harvest for SW), and again in 2009 (10 years post-harvest for SW; one (for winter and spring) or two (for summer and fall) years after seasonal bird surveys ended). Tree stems of individuals ≥0.5 m height and (or) <12.7 cm dbh were tallied by species; "individual" tree stems were defined as single stems or the largest-diameter stem within a cluster of stump sprouts. Stump sprouts were also tallied 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, so we pooled them across M and (separately) SW plots for each year and applied the average number of stump sprouts (by species) to the number of individuals (by species) 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 2004; BA for 2009 was interpolated based on tree growth 2004–2013 (measured in 2013 as part of the "fruit study"). We visually estimated percent cover of all clonal shrub species (summed across species for a total coverage estimate) 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 (2004 and 2009).

Data analysis

We recognize that a seasonal bias in bird detectability (e.g., singing during summer; minimal vocalization during migrations and winter) and the likelihood of presence during a sample transect (e.g., breeding territories during summer; flocking behavior during migrations and winter) may exist across the annual cycle. Therefore, we focused our analyses on within-season comparisons of bird communities between SW and M. We additionally conducted broad, community-level (total bird abundance, richness, and diversity) comparisons among seasons to gain a "snapshot" perspective,

despite the potential for bias. We used naïve estimates of 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) (Dail and Madsen 2011). However, both generalized linear mixed models 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 abundance of species, responded to shelterwood harvests and unmanaged mature forests across seasons, and over time as young forests matured in SW.

We used repeated measures ANOVAs (PROC MIXED; SAS 9.3) in a completely randomized design to examine differences in forest structure between treatments over time, and bird communities between treatments, both among and within seasons over our 8-year study period. Forest structure variables included small tree stem density, large tree density and BA, and clonal shrub cover. After determining there were no treatment × year interaction effects in within-season ANOVAs, we examined whether total bird abundance, richness, and diversity differed across seasons and harvest treatments overall, without consideration of possible treatment × season interaction effects. All subsequent analyses focused on within-season differences in bird communities between SW and M, and possible changes over our 8-year study period. For each season separately, we tested for treatment (M and SW), year, and treatment × year interaction effects on total bird abundance, richness, diversity, abundance of sufficiently common (≥15 total observations) species, and abundance within each of four residency categories. Residency categories were: neotropical migratory species that breed within the southern Appalachians (NMB), neotropical migratory species that do not breed within the southern Appalachians (pass-through migrants; PTM), species that winter in the southern Appalachians but breed further north (WTR), and; year-round resident species (YR). We considered elevational migrants (winter wren (*Troglodytes hiemalis*), yellow-bellied sapsucker (*Sphyrapicus varius*), slate-colored junco (*Junco hyemalis*), and hermit thrush (*Catharus guttatus*))—species that breed at higher elevations, but move to lower, warmer elevations within the southern Appalachians for winter, to be YR in our analyses. Within each season, 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 nonsignificant 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 α 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. Forest structure and bird data were natural log-transformed (ln + 0.1) for ANOVAs as needed to reduce heteroscedasticity.

Community composition patterns across seasons, treatments, and years were visualized using non-metric multidimensional scaling ordination (NMS) based on Jaccard dissimilarities. NMS was performed using the metaMDS function in R (Oksanen et al. 2015) using presence absence values. To select dimensionality, stress values from two-, three-, four-, and five-dimensional solutions were compared. We plotted final stress values against the number of dimensions and choose the five-dimensional solution, as the reduction in final stress was minimal with additional dimensions. MetaMDS uses an iterative approach with random starts and transforms data with large ranges using square root and Wisconsin double standardization. The final solution minimizes stress and is rotated so that the first axis explains the most variance. We initiated 400 independent runs (Peck 2016). Compositional differences across treatments were examined using distance-based permutational multivariate Analysis of variance (perMANOVA) in the R package vegan, blocked by plot to account for repeated sampling (Oksanen et al. 2015; R Delevelopment Core Team 2019). The test statistic is the pseudo *F*-ratio, where a large value indicates that plots within different categories differ in their species composition (i.e., plots within one category are closer to one another in multivariate space than they are to plots in the comparison group). Interactions that were not significant ($p < 0.05$) were removed from the final model. 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 subsets of the data to examine the significance of treatment differences within identified years. PerMANOVA is less sensitive to dispersion effects than other similar tests (Anderson and Walsh 2013), but may still confound location and dispersion effects. In other words, significant differences may be caused by differences in within-group variation (dispersion), differences in mean values of the groups, or both (Anderson 2001). We calculated average dispersion values (average distances to centroid values) within our groups using the betadisper function from the R package vegan and used diagnostic plots to evaluate dispersion versus location effects when dispersion was significantly different based on Tukey's honest significant differences (Anderson et al. 2006).

Results

Forest structure

Large (≥12.7 cm dbh) tree density was greater in M than SW; a treatment × year interaction effect with tests of effect slices indicated that within SW it was lower in 2004 than in 2009, and within both years it was greater in M than SW (Table 1). Small (≥0.5 m height and <12.7 cm dbh) tree stem density was greater in SW than M; a treatment × year interaction effect indicated that within SW it was greater in 2004 than 2009, and within both years it was greater in SW than M. Large tree BA was greater in M than SW; no treatment × year interaction effect was detected. Percent cover of total clonal shrubs did not differ between SW and M; a treatment × year interaction effect indicated that within SW it was greater in 2004 than in 2009 (Table 1).

Table 1. Mean (±SE) density (No./ha) of larger (≥12.7 cm diameter at breast height (dbh)) and small (≥0.5 m ht and < 12.7 cm dbh) tree density, large tree BA, and percent cover of total clonal shrubs measured in 2004 and 2009, and results of repeated measures mixed-model ANOVAs comparing forest structural features between shelterwood harvest and mature forest treatments, years, and treatment × year interaction effects, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

Forest structural feature	Treatment	2004 Mean ± SE	2009 Mean ± SE	p_{trt}	p_{yr}	$p_{trt \times yr}$
Larger tree density (No./ha)	Mature forest	378.1 ± 28.7	375.6 ± 31.0	<0.0001	0.0028	0.0010
	Shelterwood	73.3 ± 10.7	119.3 ± 10.4			
Small tree stem density (No./ha)	Mature forest	2349.2 ± 501.0	2352.5 ± 459.6	<0.0001	<0.0001	<0.0001
	Shelterwood	14 532.3 ± 1646.3	10 457.9 ± 1,045.5			
Larger tree BA (m^2/ha)	Mature forest	30.1 ± 1.6	31.4 ± 1.6	<0.0001	<0.0001	0.6304
	Shelterwood	6.4 ± 0.9	7.9 ± 0.9			
Total clonal shrub cover (%)	Mature forest	26.9 ± 8.1	23.3 ± 7.3	0.8338	<0.0001	0.0004
	Shelterwood	37.3 ± 7.1	17.1 ± 5.8			

Among-season bird community comparisons

We detected 3952 individuals of 82 bird species within transects across all sampled seasons and years. Total average bird abundance was greater in SW than M, and greater in summer and lower in winter than all other seasons. Average species richness and diversity were greater in SW than M, greater in summer and lower in winter than all other seasons, and greater in spring than fall (Table 2; Fig. 1).

Based on plots of final stress values against the number of dimensions, we chose a five-dimensional NMS solution, as the reduction in final stress was minimal with additional dimensions. It took 75 iterations to achieve a stable solution (when the best solution was repeated), with a final stress of 0.147. We found significant compositional differences between treatments, seasons, and years ($p < 0.0005$; Table 3). We chose to display the compositional differences by season and treatment (Fig. 2), as they explained the most variation in composition based on the perMANOVA results (Table 3). However, our significant differences are potentially confounded by significantly greater dispersion in multivariate space. To evaluate differences, we compared differences in dispersion by treatment within seasons; significant differences were detected only during spring and summer ($p < 0.0005$; Tukey's HSD). In both cases, we found evidence of both dispersion (e.g., variation) effects and location (e.g., composition) treatment effects based on the visualization of the multivariate dispersions (Fig. A1).

Summer bird communities

We detected 1328 individuals of 53 species during summer (breeding season) across all sampled seasons and years. During summer, total bird abundance (Fig. 3*a*), species richness (Fig. 3*b*), and species diversity (Fig. 3*c*) were greater in SW than M, and no treatment × year interaction effects were detected (Table 2). Only NMB and YR residents were detected during summer (Table 2; Fig. 4*a*). Total abundance of NMB and YR was greater in SW than M; a treatment × year interaction effect for YR (Fig. 4*a*) indicated that differences between SW and M varied among years. Among the 24 summer species analyzed, 8 were more abundant in SW than M, including blue-gray gnatcatchers (*Polioptila caerulea*), Carolina wrens (*Thyrothorus ludovicianus*), chestnut-sided warblers (*Setophaga pensylvanica*), hooded warblers (*Wilsonia citrina*), indigo buntings (*Passerina cyanea*), eastern towhees (*Pipilo erythrophalmus*), eastern wood-pewees (*Contopus virens*), and northern cardinals (*Cardinalis cardinalis*) (Table 2; Fig. 5). Significant treatment × year interaction effects for several species indicated that differences between SW and M varied among years (Table 2; Fig. 5). A strong directional trend was evident for indigo buntings in SW, with peak abundance in 2000 that decreased each year through 2006; by 2007 abundance did not differ between SW and M. Chestnut-sided warbler abundance in SW peaked in 2004–2005 but remained higher in SW than M thereafter. In contrast, two species, including Acadian flycatchers (*Empidonax virescens*) and ovenbirds (*Seiurus aurocapillus*), were more abundant in M than SW. Additionally, black-throated blue warblers (*Setophaga caerulescens*) showed a significant treatment × year interaction effect, indicating that differences between SW and M varied among years (Table 2; Fig. 5).

Fall bird communities

We detected 1080 individuals of 69 species during fall, across all sampled treatments and years. During fall, total bird abundance (Fig. 3*a*), species richness (Fig. 3*b*), and species diversity (Fig. 3*c*) were greater in SW than M, and no treatment × year interaction effects were detected (Table 2). NMB, PTM, WTR, and YR residents were detected during fall (Table 2; Fig. 4*b*). Total abundance of NMB did not differ between M and SW; a treatment × year interaction effect indicated that differences between SW and M varied among years. Abundance of PTM, YR, and WTR were greater in SW than M; a treatment × year interaction effects for YR indicated that differences between SW and M varied among years (Fig. 4*b*). Among the 17 fall species analyzed, 4 were more abundant in SW than M, including Carolina wrens, eastern towhees, northern cardinals, and winter wrens (Table 2; Fig. 6). A significant treatment × year interaction effect for golden-crowned kinglet (*Regulus satrapa*) indicated that abundance was greater in SW than M in 2004 (Table 2; Fig. 6).

Table 2. Total (all years and seasons) and summer, fall, winter, and spring (all years) season individual detections (obs; mature forest/shelterwood/total) of breeding birds (NMB), year-round residents (YR), pass-through migrants (PTNM), and winter residents (W) and results of repeated measures mixed-model ANOVAs comparing total abundance, species richness, diversity, and abundance of common (≥15 detections within any given season, across years and treatments) species within each season between shelterwood harvest (SW) and mature forest (M) treatments, years (2000–2008; surveyed 8 years per season, post-harvest), and treatment × year interaction effects, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

	Total	Summer				Fall				Winter				Spring			
Species[a]	Obs M/SW/Tot	p_{Trt}	p_{Yr}	p_{TxY}	Obs M/SW/Tot	p_{Trt}	p_{Yr}	p_{TxY}	Obs M/SW/Tot	p_{Trt}	p_{Yr}	$p_{T \times Yr}$	Obs M/SW/Tot	p_{Trt}	p_{Yr}	$p_{T \times Y}$	Obs M/SW/Tot
Neotropical migratory breeding birds																	
ACFL	25/3/28	*	ns	ns	25/0/25	–	–	–	0/2/2	–	–	–	0/0/0	–	–	–	0/1/1
AMRE	5/4/9	–	–	–	0/3/3	–	–	–	2/1/3	–	–	–	0/0/0	–	–	–	3/0/3
BAWW	54/55/109	ns	ns	ns	24/25/49	–	–	–	0/1/1	–	–	–	0/0/0	ns	ns	ns	30/29/59
BGGN	15/74/89	**	ns	ns	6/37/43	–	–	–	0/6/6	–	–	–	0/0/0	*	ns	ns	9/31/40
BHVI	61/27/88	ns	ns	ns	14/14/28	–	–	–	8/3/11	–	–	–	0/0/0	**	ns	ns	39/10/49
BLBW	17/18/35	ns	*	ns	7/8/15	–	–	–	2/3/5	–	–	–	0/0/0	ns	*	ns	8/7/15
BTBW	66/43/109	ns	ns	*	37/17/54	ns	**	ns	13/15/28	–	–	–	0/0/0	ns	*	ns	16/11/27
BTNW	99/56/155	ns	ns	ns	40/16/56	–	–	–	5/4/9	–	–	–	0/0/0	ns	ns	ns	54/36/90
BWHA	0/3/3	–	–	–	0/0/0	–	–	–	0/2/2	–	–	–	0/0/0	–	–	–	0/1/1
CAWA	3/11/14	–	–	–	0/5/5	–	–	–	0/3/3	–	–	–	0/0/0	–	–	–	3/3/6
CHSP	3/0/3	–	–	–	0/0/0	–	–	–	3/0/3	–	–	–	0/0/0	–	–	–	0/0/0
COYE	0/2/2	–	–	–	0/0/0	–	–	–	0/2/2	–	–	–	0/0/0	–	–	–	0/0/0
CSWA	6/150/156	****	*	**	4/106/110	–	–	–	1/6/7	–	–	–	0/0/0	**	ns	ns	1/38/39
EAWP	5/22/27	*	ns	*	2/15/17	–	–	–	3/7/10	–	–	–	0/0/0	–	–	–	0/0/0
GCFL	0/1/1	–	–	–	0/1/1	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	0/0/0
GRCA	1/11/12	–	–	–	0/0/0	–	–	–	1/10/11	–	–	–	0/0/0	–	–	–	0/1/1
HOWA	52/81/133	*	**	ns	25/44/69	ns	ns	ns	12/14/26	–	–	–	0/0/0	ns	ns	ns	15/23/38
INBU	4/144/148	****	****	****	4/120/124	–	–	–	0/5/5	–	–	–	0/0/0	**	**	**	0/19/19
LEFL	0/1/1	–	–	–	0/0/0	–	–	–	0/1/1	–	–	–	0/0/0	–	–	–	0/0/0
LOWA	4/0/4	–	–	–	2/0/2	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	2/0/2
NOPA	14/17/31	ns	ns	ns	7/14/21	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	7/3/10
OVEN	85/12/97	***	*	ns	51/4/55	–	–	–	9/2/11	–	–	–	0/0/0	*	ns	ns	25/6/31
PRAW	0/2/2	–	–	–	0/2/2	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	0/0/0
RBGR	18/23/41	–	–	–	4/7/11	–	–	–	2/9/11	–	–	–	0/0/0	ns	*	ns	12/7/19
REVI	63/56/119	ns	ns	ns	48/42/90	–	–	–	1/5/6	–	–	–	0/0/0	ns	ns	ns	14/9/23
RTHU	11/15/26	–	–	–	8/5/13	–	–	–	0/5/5	–	–	–	0/0/0	–	–	–	3/5/8
SCTA	12/24/36	ns	ns	ns	10/9/19	–	–	–	1/12/13	–	–	–	0/0/0	–	–	–	1/3/4
SWWA	5/6/11	–	–	–	2/5/7	–	–	–	2/1/3	–	–	–	0/0/0	–	–	–	1/0/1
VEER	4/2/6	–	–	–	4/1/5	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	0/1/1
WEVI	0/2/2	–	–	–	0/0/0	–	–	–	0/1/1	–	–	–	0/0/0	–	–	–	0/1/1
WEWA	24/28/52	ns	ns	ns	21/19/40	–	–	–	0/3/3	–	–	–	0/0/0	–	–	–	3/6/9
WOTH	20/13/33	–	–	–	4/5/9	ns	ns	ns	16/5/21	–	–	–	0/0/0	–	–	–	0/3/3

Table 2. (*continued*).

Species[a]	Total Obs M/SW/Tot	Summer p_{Trt}	Summer p_{Yr}	Summer p_{TxY}	Summer Obs M/SW/Tot	Fall p_{Trt}	Fall p_{Yr}	Fall p_{TxY}	Fall Obs M/SW/Tot	Winter p_{Trt}	Winter p_{Yr}	Winter $p_{T\ x\ Yr}$	Winter Obs M/SW/Tot	Spring p_{Trt}	Spring p_{Yr}	Spring $p_{T\ x\ Y}$	Spring Obs M/SW/Tot
YBCH	0/1/1	–	–	–	0/1/1	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	0/0/0
YBCU	1/0/1	–	–	–	1/0/1	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	0/0/0
YTVI	0/1/1	–	–	–	0/0/0	–	–	–	0/1/1	–	–	–	0/0/0	–	–	–	0/0/0
Total NMB	677/908/1585	**	*	ns	350/525/875	ns	*	*	81/129/210	–	–	–	0/0/0	ns	*	ns	246/254/500
Pass-through neotropical migratory birds																	
BBWA	4/1/5	–	–	–	0/0/0	–	–	–	1/1/2	–	–	–	0/0/0	–	–	–	3/0/3
GCBT	2/0/2	–	–	–	0/0/0	–	–	–	2/0/2	–	–	–	0/0/0	–	–	–	0/0/0
MAWA	1/7/8	–	–	–	0/0/0	–	–	–	1/6/7	–	–	–	0/0/0	–	–	–	0/1/1
OCWA	0/5/5	–	–	–	0/0/0	–	–	–	0/5/5	–	–	–	0/0/0	–	–	–	0/0/0
PAWA	1/3/4	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	1/3/4
SWTH	7/10/17	–	–	–	0/0/0	ns	ns	ns	7/10/17	–	–	–	0/0/0	–	–	–	0/0/0
TEWA	0/11/11	–	–	–	0/0/0	–	–	–	0/11/11	–	–	–	0/0/0	–	–	–	0/0/0
Total PTNM	15/37/52	–	–	–	0/0/0	*	ns	ns	11/33/44	–	–	–	0/0/0	–	–	–	4/4/8
Year-round resident birds																	
AMCR	19/12/31	–	–	–	1/3/4	ns	ns	ns	13/17/20	–	–	–	0/1/1	–	–	–	5/1/6
AMGO	9/42/51	–	–	–	0/10/10	ns	ns	ns	2/25/27	–	–	–	0/1/1	–	–	–	7/6/13
AMRO	8/6/14	–	–	–	2/1/3	–	–	–	4/0/4	–	–	–	1/4/5	–	–	–	1/1/2
AMWO	0/1/1	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	0/1/1	–	–	–	0/0/0
BHCO	0/1/1	–	–	–	0/101	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	0/0/0
BLJA	27/30/57	–	–	–	6/5/11	ns	ns	ns	9/21/30	–	–	–	3/2/5	–	–	–	9/2/11
BRCR	9/0/9	–	–	–	0/0/0	–	–	–	3/0/3	–	–	–	6/0/6	–	–	–	0/0/0
BRTH	1/5/6	–	–	–	0/1/1	–	–	–	1/2/3	–	–	–	0/0/0	–	–	–	0/2/2
CACH	132/136/268	ns	ns	ns	16/34/50	ns	**	ns	41/49/90	ns	ns	ns	39/19/58	ns	**	ns	36/34/70
CARW	20/93/113	***	*	*	1/28/29	*	*	ns	11/30/41	*	ns	ns	4/4/18	***	ns	ns	4/21/25
CEDW	0/12/12	–	–	–	0/7/7	–	–	–	0/3/3	–	–	–	0/2/2	–	–	–	0/0/0
CORA	7/0/7	–	–	–	0/0/0	–	–	–	2/0/2	–	–	–	5/0/5	–	–	–	0/0/0
DOWO	35/30/85	–	–	–	6/6/12	ns	*	ns	11/8/19	–	–	–	8/6/14	ns	ns	ns	10/10/20
EABL	0/2/2	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	0/2/2	–	–	–	0/0/0
EAPH	5/16/21	–	–	–	1/3/4	–	–	–	1/11/12	–	–	–	0/2/2	–	–	–	3/0/3
EATO	59/376/435	****	ns	ns	26/132/158	****	ns	ns	8/77/85	*	ns	ns	3/41/44	****	ns	*	22/126/148
ETTI	108/65/173	ns	ns	ns	22/20/42	ns	ns	ns	36/22/58	ns	ns	*	30/12/42	ns	ns	ns	20/11/31
WITU	3/1/4	–	–	–	1/0/1	–	–	–	1/0/1	–	–	–	0/0/0	–	–	–	1/1/2
FISP	0/1/1	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	0/1/1	–	–	–	0/0/0
GCKI	40/49/89	–	–	–	0/0/0	ns	ns	*	8/13/21	ns	ns	ns	28/24/50	ns	ns	ns	6/12/18
HAWO	4/11/15	–	–	–	2/4/6	–	–	–	2/5/7	–	–	–	0/1/1	–	–	–	0/1/1
HETH[b]	4/3/7	–	–	–	0/0/0	–	–	–	4/0/4	–	–	–	0/1/1	–	–	–	0/2/2
MODO	0/10/10	–	–	–	0/6/6	–	–	–	0/1/1	–	–	–	0/0/0	–	–	–	0/3/3
NOCA	9/55/64	*	ns	ns	5/19/24	**	ns	ns	0/19/19	–	–	–	3/4/7	–	–	–	1/13/14
NOFL	7/17/24	–	–	–	0/202	–	–	–	6/8/14	–	–	–	0/1/1	–	–	–	1/6/7

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Table 2. (*concluded*).

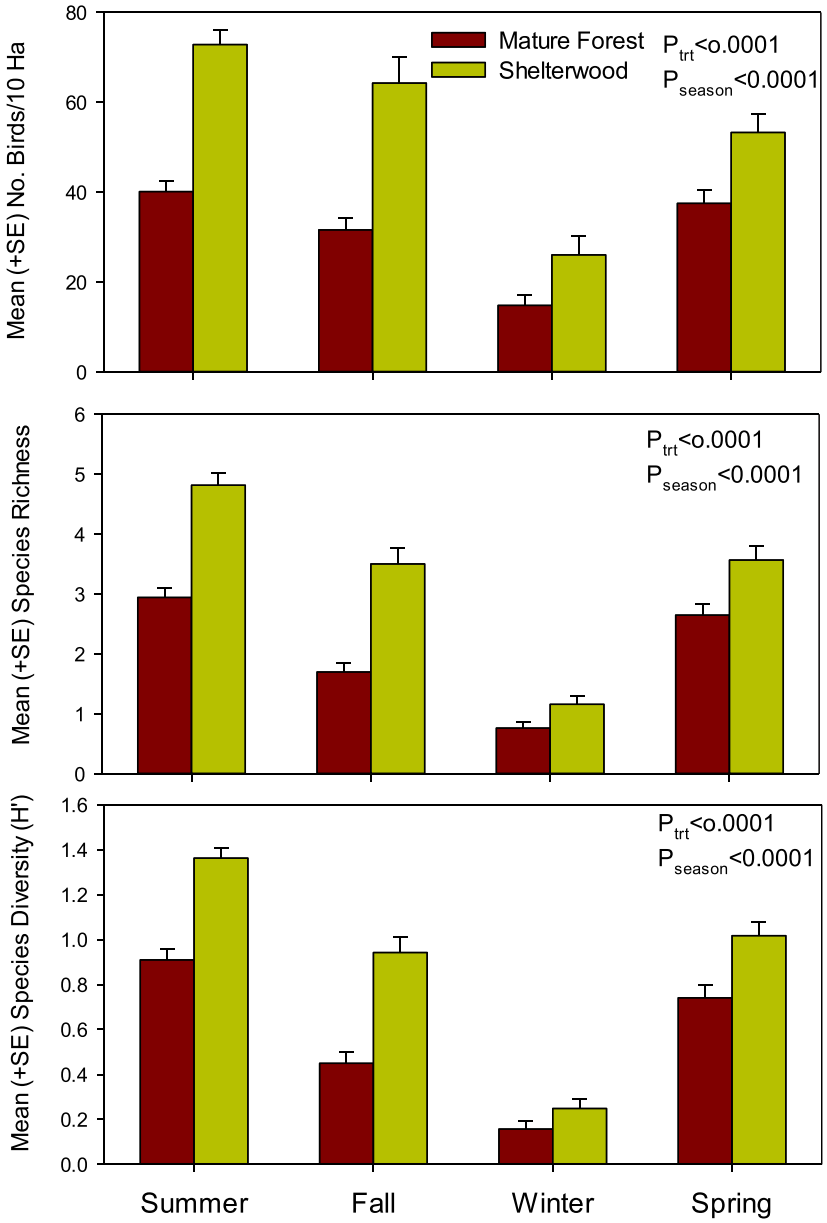
Species[a]	Total Obs M/SW/Tot	Summer p_{Trt}	Summer p_{Yr}	Summer p_{TxY}	Summer Obs M/SW/Tot	Fall p_{Trt}	Fall p_{Yr}	Fall p_{TxY}	Fall Obs M/SW/Tot	Winter p_{Trt}	Winter p_{Yr}	Winter $p_{T\ x\ Yr}$	Winter Obs M/SW/Tot	Spring p_{Trt}	Spring p_{Yr}	Spring $p_{T\ x\ Y}$	Spring Obs M/SW/Tot
PIWA	1/5/6	–	–	–	0/1/1	–	–	–	1/2/3	–	–	–	0/0/0	–	–	–	0/2/2
PIWO	21/6/27	–	–	–	8/2/10	–	–	–	3/1/4	–	–	–	5/0/5	–	–	–	5/3/8
RBWO	9/11/20	–	–	–	2/1/3	–	–	–	5/8/13	–	–	–	0/1/1	–	–	–	2/1/3
RUGR	21/5/26	–	–	–	1/0/1	–	–	–	11/2/13	–	–	–	0/0/0	–	–	–	9/3/12
SCJU[b]	84/146/230	ns	ns	ns	20/4/24	ns	ns	ns	20/45/65	*	ns	ns	22/84/106	ns	ns	ns	22/13/35
SOSP	0/3/3	–	–	–	0/0/0	–	–	–	0/3/3	–	–	–	0/0/0	–	–	–	0/0/0
SSHA	1/3/4	–	–	–	0/0/0	–	–	–	0/3/3	–	–	–	0/0/0	–	–	–	1/0/1
WBNU	49/58/107	ns	ns	ns	8/12/20	ns	*	ns	16/20/36	ns	ns	ns	20/20/40	–	–	–	5/6/11
WIWR[b]	5/42/47	–	–	–	0/0/0	**	ns	ns	2/22/24	**	ns	ns	2/16/18	–	–	–	1/4/5
YBSA[b]	20/6/26	–	–	–	1/0/1	–	–	–	9/2/11	–	–	–	5/2/7	–	–	–	5/2/7
Total YR	717/1259/1976	****	ns	*	129/302/431	****	*	*	230/409/639	ns	ns	ns	182/262/444	**	*	ns	176/286/462
Winter resident birds																	
FOSP	0/14/14	–	–	–	0/0/0	–	–	–	0/1/1	–	–	–	0/12/12	–	–	–	0/1/1
PISI	0/2/2	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	0/0/0	–	–	–	0/2/2
RCKI	11/37/48	–	–	–	0/0/0	–	–	–	1/10/11	–	–	–	0/0/0	*	****	ns	10/27/37
WTSP	0/49/49	–	–	–	0/0/0	–	–	–	0/11/11	*	ns	ns	0/21/21	*	ns	ns	0/17/17
YRWA	18/14/32	–	–	–	0/0/0	–	–	–	0/2/2	–	–	–	0/0/0	ns	ns	ns	18/12.30
Total W	29/116/145	–	–	–	0/0/0	**	ns	ns	1/24/25	ns	ns	ns	0/33/33	ns	*	ns	28/59/87
UNID	73/121/194	–	–	–	11/11/22	–	–	–	57/105/162	–	–	–	1/0/1	–	–	–	4/5/9
Total birds	1511/2441/3952	****	**	ns	490/838/1328	**	ns	ns	380/700/1080	ns	ns	ns	183/295/478	*	ns	Ns	458/608/1066
Richness	**68/82/82**	****	**	**ns**	**41/47/53**	***	*	**ns**	**47/62/69**	*	**ns**	**ns**	**16/26/30**	*	**ns**	**ns**	**45/55/61**
Diversity (H')		**	*	ns	—	***	ns	ns	—	ns	ns	ns	—	*	ns	ns	—

Note: Species data were log-transformed (ln + 0.1) for analysis. *denotes $p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ****$p < 0.0001$; ns $p < 0.05$ (non-significant).

[a]ACFL = Acadian flycatcher (*Empidonax virescens*), AMCR = American crow (*Corvus brachyrhynchos*), AMGO = American goldfinch (*Carduelis tristis*), AMRE = American redstart (*Setophaga ruticilla*), AMRO = American robin (*Turdus migratorius*), AMWO = American woodcock (*Scolopax minor*), BAWW = Black-and-white warbler (*Mniotilta varia*), BBWA = Bay-breasted warbler (*Setophaga castanea*), BGGN = Blue-gray gnatcatcher (*Polioptila caerulea*), BHCO = Brown-headed cowbird (*Molothrus ater*), BHVI = Blue-headed vireo (*Vireo solitarius*), BLBW = Blackburnian warbler (*Setophaga fusca*), BLJA = Blue jay (*Cyannocitta cristata*), BRCR = Brown creeper (*Certhia americana*), BRTH = Brown thrasher (*Toxostoma rufum*), BTBW = Black-throated blue warbler (*Setophaga caerulescens*), BTNW = Black-throated green warbler (*Dendroica virens*), BWHA = Broad-winged hawk (*Buteo platypterus*), CACH = Carolina chickadee (*Poecile carolinensis*), CARW = Carolina wren (*Thyrothorus ludovicianus*), CAWA = Canada warbler (*Cardellina canadensis*), CHSP = Chipping sparrow (*Spizella passerina*), CEDW = Cedar waxwing (*Bombycilla cedrorum*), CORA = Common raven (*Corvus corax*), COYE = Common yellowthroat (*Geothlypis trichas*), CSWA = Chestnut-sided warbler (*Setophaga pensylvanica*), DOWO = Downy woodpecker (*Picoides pubescens*), EABL = Eastern bluebird (*Sialia sialis*), EAPH = Eastern phoebe (*Sayomis phoebe*), EATO = Eastern towhee (*Pipilo erythrophalmus*), EAWP = Eastern wood-pewee (*Contopus virens*), ETTI = Eastern tufted titmouse (*Baeolophus bicolor*), FISP = Field sparrow, FOSP = Fox sparrow (*Passerella iliaca*), GCBT = Gray-cheeked Bicknell's thrush (*Catharus minimus/bicknelli*), GCFL = Great-crested flycatcher (*Myiarchus crinitus*), GCKI = Golden-crowned kinglet (*Regulus satrapa*), GRCA = Gray catbird (*Dumatella carolinensis*), HAWO = Hairy woodpecker (*Picoides villosus*), HETH = Hermit thrush (*Catharus guttatus*), HOWA = Hooded warbler (*Wilsonia citrina*), INBU = Indigo bunting (*Passerina cyanea*), LEFL = Least flycatcher (*Empidonax minimus*), LOWA = Louisiana waterthrush (*Parkesia motacilla*), MAWA = Magnolia warbler (*Setophaga magnolia*), MODO = Mourning dove (*Zenaida macroura*), NOCA = Northern cardinal (*Cardinalis cardinalis*), NOFL = Northern flicker (*Colaptes auratus*), NOPA = Northern parula (*Parula americana*), OCWA = Orange-crowned warbler (*Vermivora celata*), OVEN = Ovenbird (*Seiurus aurocapillus*), PAWA = Palm warbler (*Setophaga palmarum*), PISI = Pine Siskin (*Spinus pinus*), PIWA = Pine warbler (*Dendroica pinus*), PIWO = Pileated woodpecker (*Drycopus pileatus*), PRAW = Prairie warbler (*Dendroica discolor*), RBGB = Rose-breasted grosbeak (*Pheucticus ludovicianus*), RBWO = Red-bellied woodpecker (*Melanerpes carolinus*), RCKI = Ruby-crowned kinglet (*Regulus calendula*), REVI = Red-eyed vireo (*Vireo olivaceus*), RTHU = Ruby-throated hummingbird (*Archilochus colubris*), RUGR = Ruffed grouse (*Bonasa umbellus*), SCJU = Slate-colored junco (*Junco hyemalis*), SCTA = Scarlet tanager (*Piranga olivacea*), SOSP = Song sparrow (*Melospiza melodia*), SSHA = Sharp-shinned hawk (*Accipiter striatus*), SWTH = Swainson's thrush (*Catharus ustulatus*), SWWA = Swainson's warbler (*Limnothlypis swainsonii*), UNID = Unidentified, VEER = Veery (*Catharus fuscescens*), WBNU = White-breasted nuthatch (*Sitta carolinensis*), WEVI = White-eyed vireo (*Vireo griseus*), WEWA = Worm-eating warbler (*Helmitheros vermivorus*), WITU = Eastern wild turkey (*Meleagris gallopavo*), WIWR = Winter wren (*Troglodytes hiemalis*), WOTH = Wood thrush (*Hylocichla mustelina*), WTSP = White-throated sparrow (*Zonotrichia albicollis*), YBCH = Yellow-breasted chat (*Icteria virens*), YBCU = Yellow-billed cuckoo (*Coccyzus americanus*), YBSA = Yellow-bellied sapsucker (*Sphyrapicus varius*), YERU = Yellow-rumped warbler (*Setophaga coronata*), YTVI = Yellow-throated vireo (*Vireo flavifrons*).

[b]Short-distance migrants that breed at higher elevations and winter at lower elevations within the southern Appalachians.

Fig. 1. Mean (+SE) (summer 2000 to fall 2008; surveyed for 8 years per season post-harvest) abundance (No./10 ha), species richness, and species diversity (H') during summer (breeding season), fall, winter, and spring in shelterwood harvest and mature forest treatments, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.



Winter bird communities

We detected 478 individuals of 30 species during winter, across all sampled treatments and years. During winter, total bird abundance (Fig. 3*a*) and diversity (Fig. 3*c*) did not differ between SW and M ($p < 0.10$); richness (Fig. 3*b*) was greater in SW than M, and no treatment × year interaction effects were detected (Table 2). Only WTR and YR residents were detected during winter; total abundance of both categories did not differ between treatments, and no treatment × year interaction effects were detected (Table 2; Fig. 4*c*). Among the nine winter species analyzed, five were more abundant in SW than M, including Carolina wrens, eastern towhees, slate-colored juncos, winter wrens, and white-throated sparrows (*Zonotrichia albicollis*) (Table 2; Fig. 7). A significant treatment × year interaction effect for eastern tufted titmouse (*Baeolophus bicolor*) indicated that differences between SW and M varied among years (Table 2; Fig. 7).

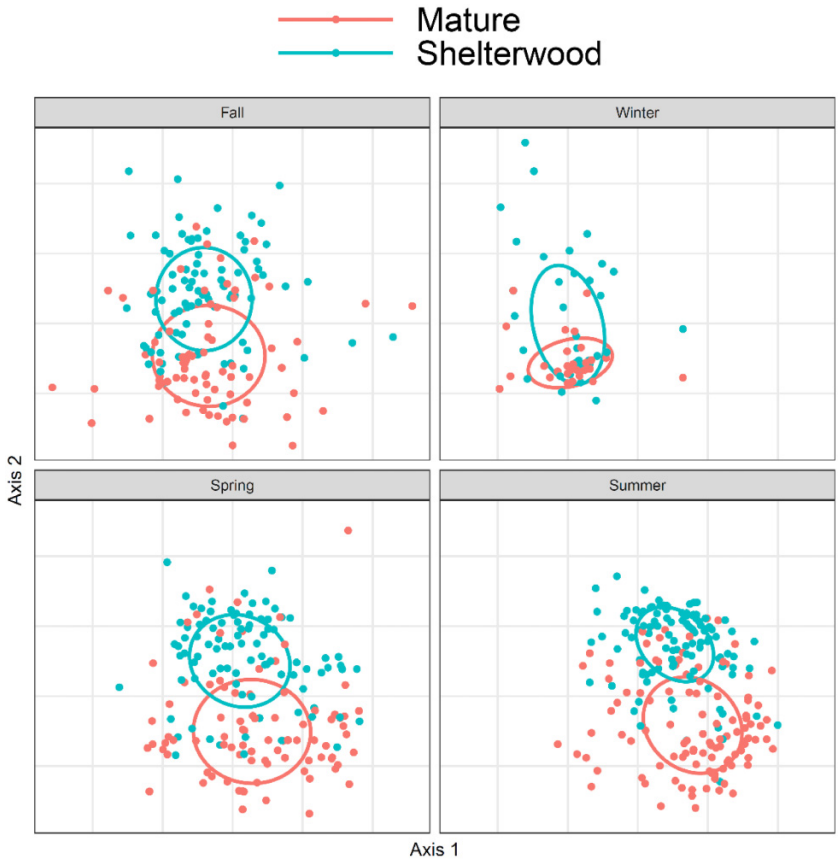
Spring bird communities

We detected 1066 individuals of 61 species during spring, across all sampled treatments and years. During spring, total bird abundance (Fig. 3*a*), richness (Fig. 3*b*), and diversity (Fig. 3*c*) were greater in SW than M, and no treatment × year interaction effects were detected (Table 2). NMB, PTM, WTR, and YR residents were detected during spring (Table 2; Fig. 4*d*). Abundance of NMB, PTM, and WTR did not differ between M and SW, whereas abundance of YR was greater in SW than M; no treatment × year interaction effects were

Table 3. Results of perMANOVA tests of bird community composition dissimilarity as a function of individual drivers (predictors) based on Jaccard distances within shelterwood harvest (harvested ca. 1999) and mature forest treatments, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

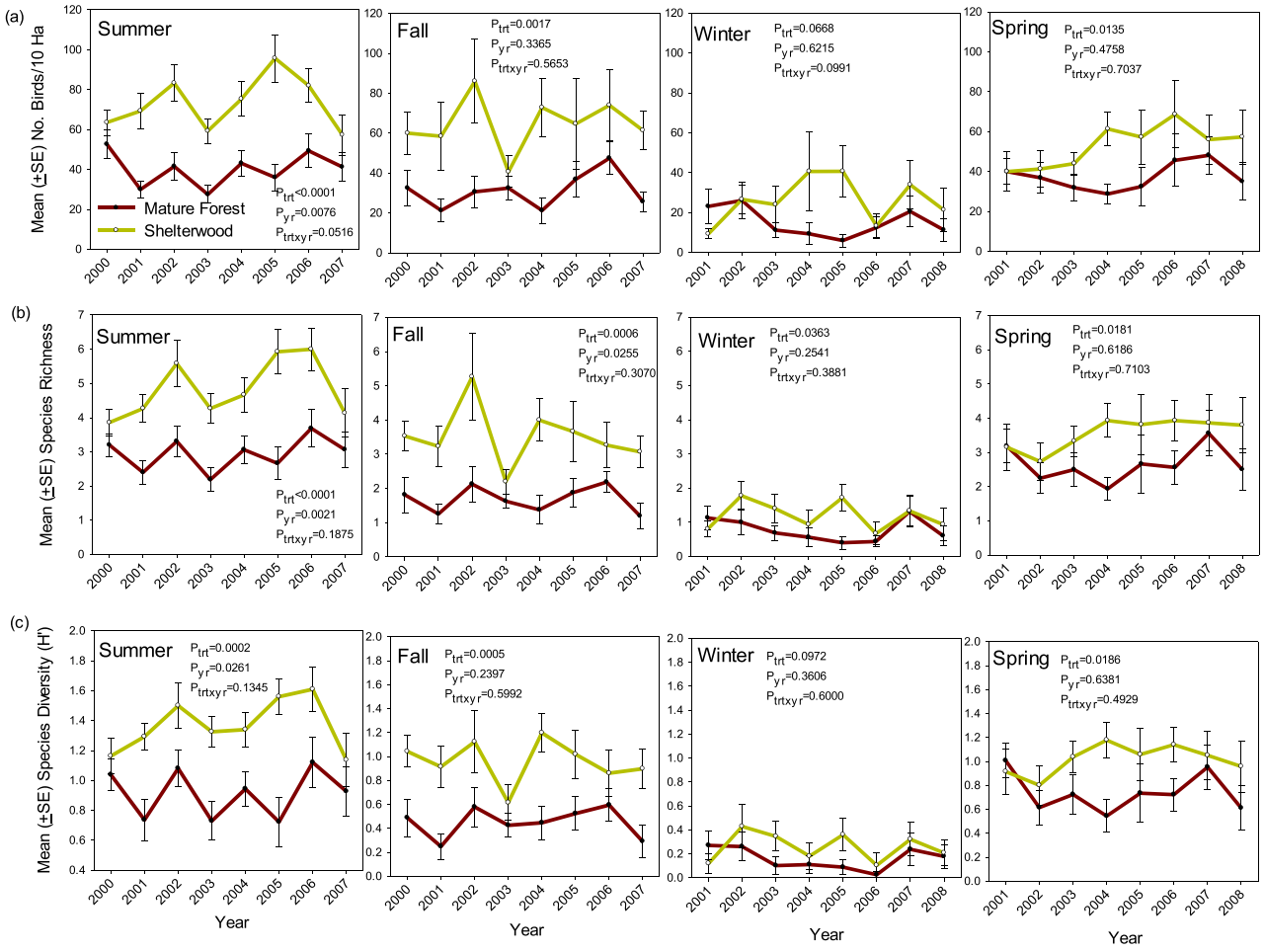
Predictor	Df	Sum of sqs	R^2	pseudo-*F*	*p*-value
Season	3	18.86	0.059	16.7878	<0.0005
Treatment	1	12.41	0.03881	33.129	<0.0005
Year	1	2.27	0.00711	6.0721	<0.0005
Season:Treatment	3	5.97	0.01869	5.3165	<0.0005
Season:Year	3	2.68	0.0084	2.3887	<0.0005
Treatment:Year	1	1.08	0.00338	2.8861	<0.0005
Residual	738	276.35	0.86461		
Total	750	319.62	1		

Fig. 2. Bird community composition within shelterwood harvest (harvested ca. 1999) and mature forest treatments, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. The figure displays nonmetric multidimensional scaling ordination based on Jaccard distances, with all years displayed by season, as season and treatment explained the most variation. The two axes explaining the most variation are displayed. Ellipses are 95% confidence ellipses for the average composition (weighted centroids).



detected for any residency category (Table 2; Fig. 4*d*). Among the 22 spring species analyzed, 7 were more abundant in SW than M, including blue-gray gnatcatcher, Carolina wren, chestnut-sided warbler, eastern towhee, indigo bunting, ruby-crowned kinglet (*Regulus calendula*), and white-throated sparrow (Table 2; Fig. 8). In contrast, two species were more abundant in M than SW, including blue-headed vireo (*Vireo solitarius*) and ovenbird (Table 2; Fig. 8). Significant treatment × year interaction effects for eastern towhees and indigo buntings were detected. Eastern towhee abundance varied among years within SW, but notably showed a delayed increase in abundance between 2001–2002 and most subsequent years. Indigo bunting abundance varied among years within SW but was greater in 2001 than all subsequent years.

Fig. 3. Mean (±SE) annual (summer 2000 to fall 2008; surveyed for 8 years per season post-harvest) summer (breeding season), fall, winter, and spring (*a*) total abundance (No./10 ha), (*b*) species richness, and (*c*) species diversity (H′) of birds in shelterwood harvest and mature forest treatments, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.



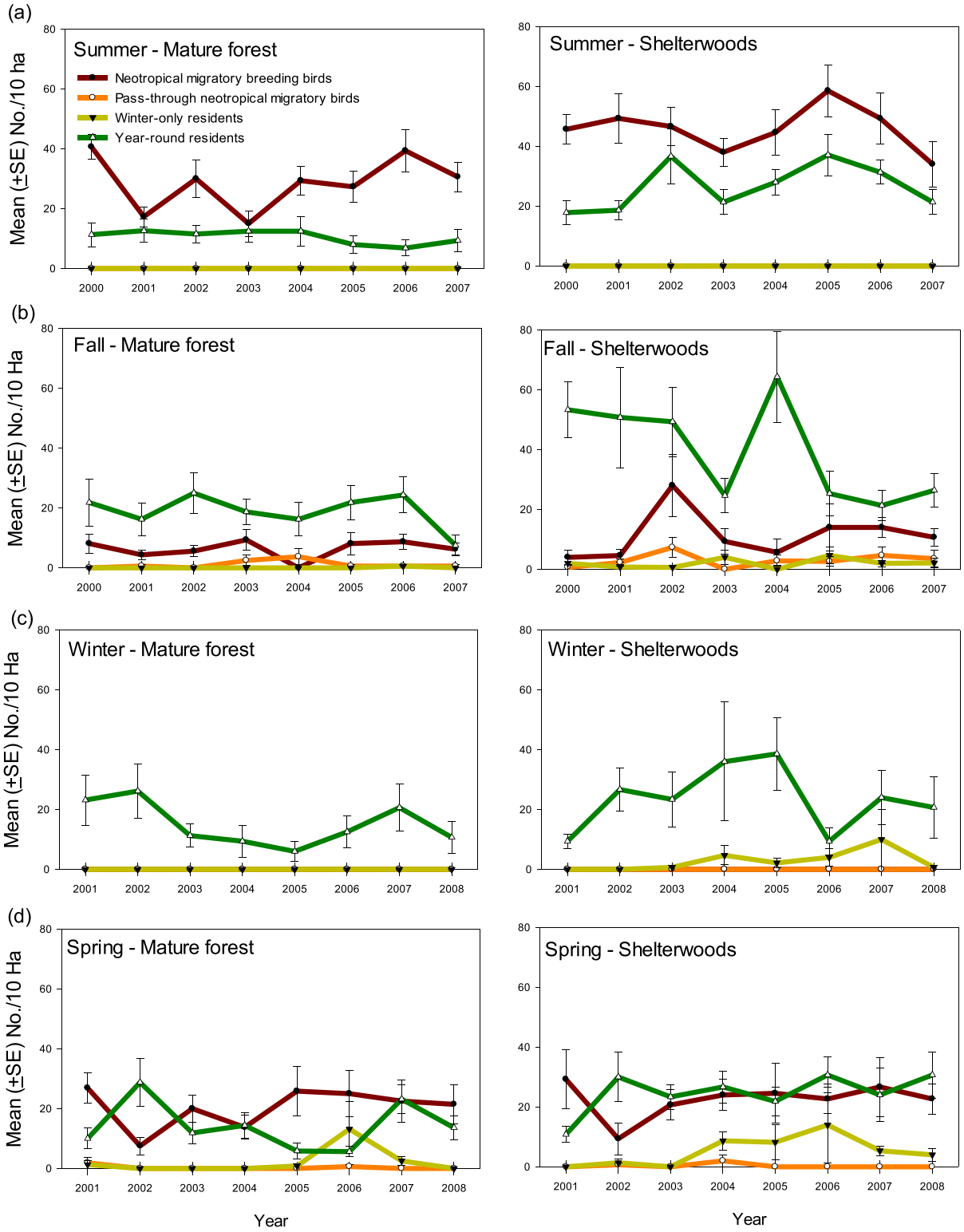
Discussion and conclusions

Our 8-year study allowed us examine differences in bird communities across and within all four seasons (summer breeding season, fall and spring migration, and winter), and how they differed between unmanaged mature- and young upland hardwood forests over time. Our results showed that bird abundance, species richness, and diversity overall were higher in summer and lower in winter than in spring or fall. Overall bird community composition differed across seasons in addition to observed differences in residency guilds. All four residency guilds (NMB, YR, WTR, and PTM) occurred during fall and spring, whereas summer bird communities included only NMBs and YR and winter included only WTR and YR residents. Our results generally correspond with those of Holmes and Sturges (1975) who additionally illustrated relationships between seasonal differences in bird abundance and communities with climate and food availability, in northern hardwood forests.

We found that bird abundance and diversity were greater in SW than M in summer, fall, and spring (with a similar, non-significant trend in winter) and species richness was greater in SW during all seasons throughout our 8-year post-harvest study period. In summer, this was largely due to an influx of shrubland species into recently disturbed SW forests, combined with a neutral or positive response by most mature forest species (also see Greenberg et al. 2023*b*); a similar pattern was seen during spring and fall migration. This was also reflected in the overall community composition, which differed between SW and M during all seasons except winter. Fewer species and individuals, flocking behavior resulting in uneven distributions of both, and similar community composition between the treatments likely confounded detection of clear differences in bird communities between SW and M in winter. In all seasons, abundances of most commonly observed species were higher in SW than M or did not differ between the treatments; a few were more abundant in M than in SW.

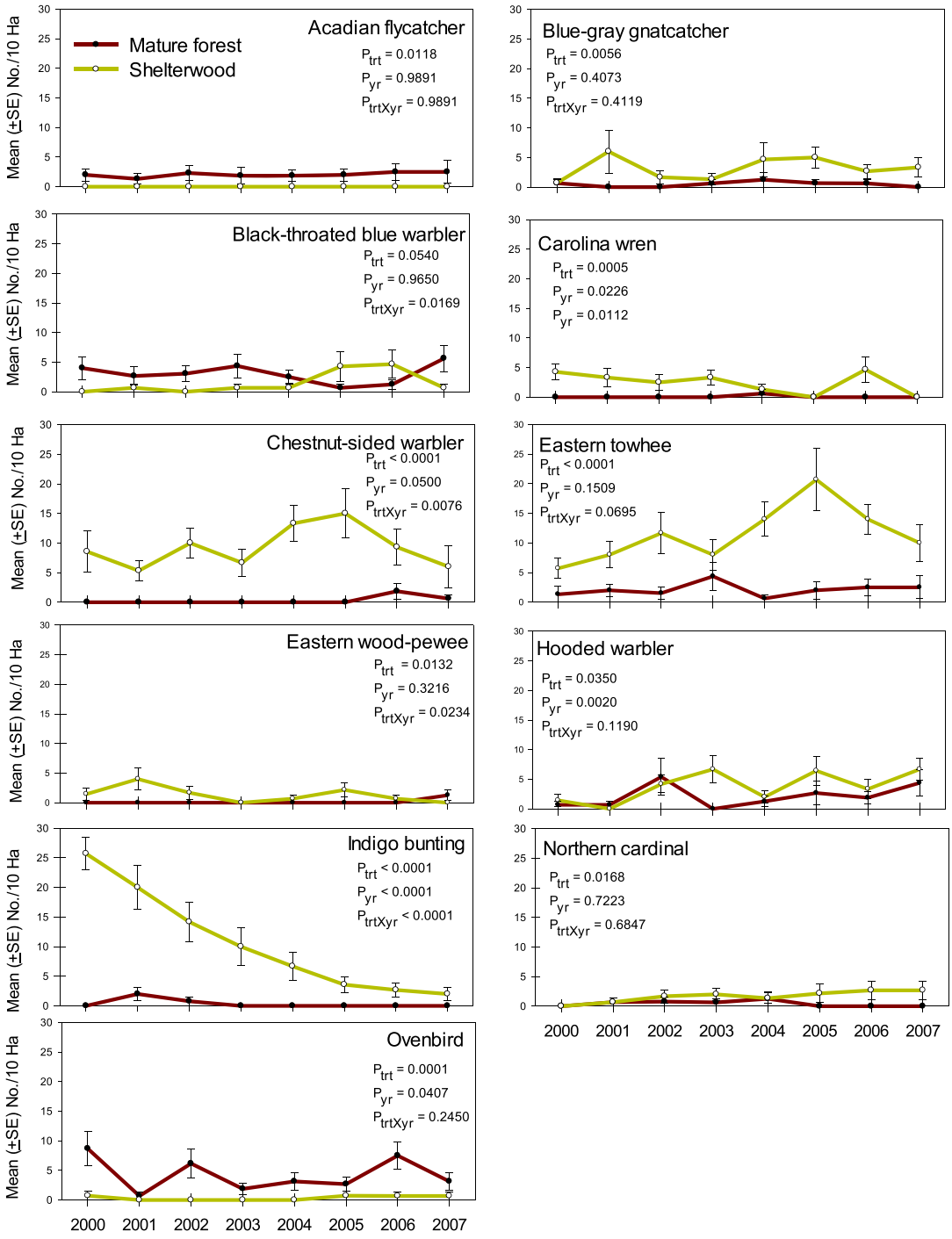
In our study, many species were detected too infrequently for statistical analysis at the species level. We did not detect any species of special conservation concern (e.g., golden winged warbler (*Vermivora chrysoptera*) or Cerulean warbler

Fig. 4. Mean (±SE) annual (2000–2008; surveyed for 8 years per season, post-harvest) abundance (No./10 ha) of breeding birds, pass-through migrants, winter residents, and; year-round residents during (*a*) summer, (*b*) fall, (*c*) winter, and (*d*) spring in shelterwood harvest and mature forest treatments, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.



(*Setophaga cerulea*)). More generally, we saw no evidence that less common species were more likely to occur in M than SW (e.g., Lešo et al. 2019). However, we suggest that a matrix of mature forests surrounding SW stands and the retention of scattered mature trees in SW may have facilitated their use by many bird species typically associated with mature for-

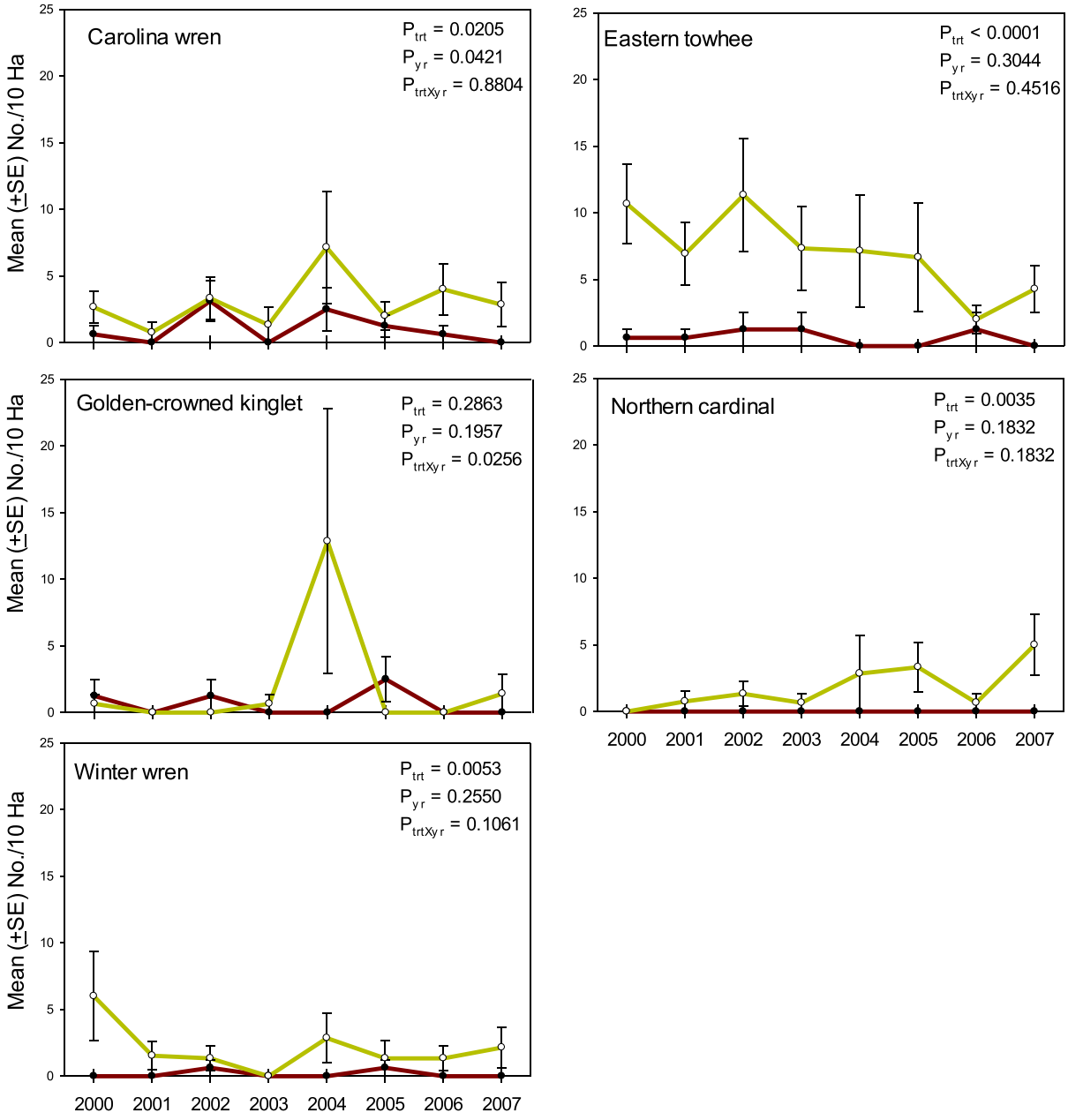
Fig. 5. Mean (±SE) annual (2000–2007; surveyed for 8 years post-harvest) summer (breeding season) abundance (No./10 ha) of common (≥15 observations within summer, across treatments and years) species having significant ($p < 0.05$) treatment and (or) treatment × year interaction effects (see Table 2), in shelterwood harvest and mature forest treatments, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.



est. Several other studies also show that bird abundance and species richness are higher in young than mature hardwood forests during breeding season (e.g., Annand and Thompson 1997; Perry and Thill 2013; Perry et al. 2018; Duguid et al. 2016; Greenberg et al. 2023*b*). Our results additionally show that young forests promote higher abundance, richness, and diversity of birds across the annual cycle, and corroborate findings of the few other studies addressing bird use of young forest (including canopy gaps) during spring and fall migration (Blake and Hoppes 1986; Martin and Karr 1986; Kilgo et al. 1999; Bowen et al. 2007; Rodewald and Brittingham 2002).

Although we cannot directly address reasons or mechanisms for greater year-round use of young SW than by birds, we suggest that differences in cover and food availability may

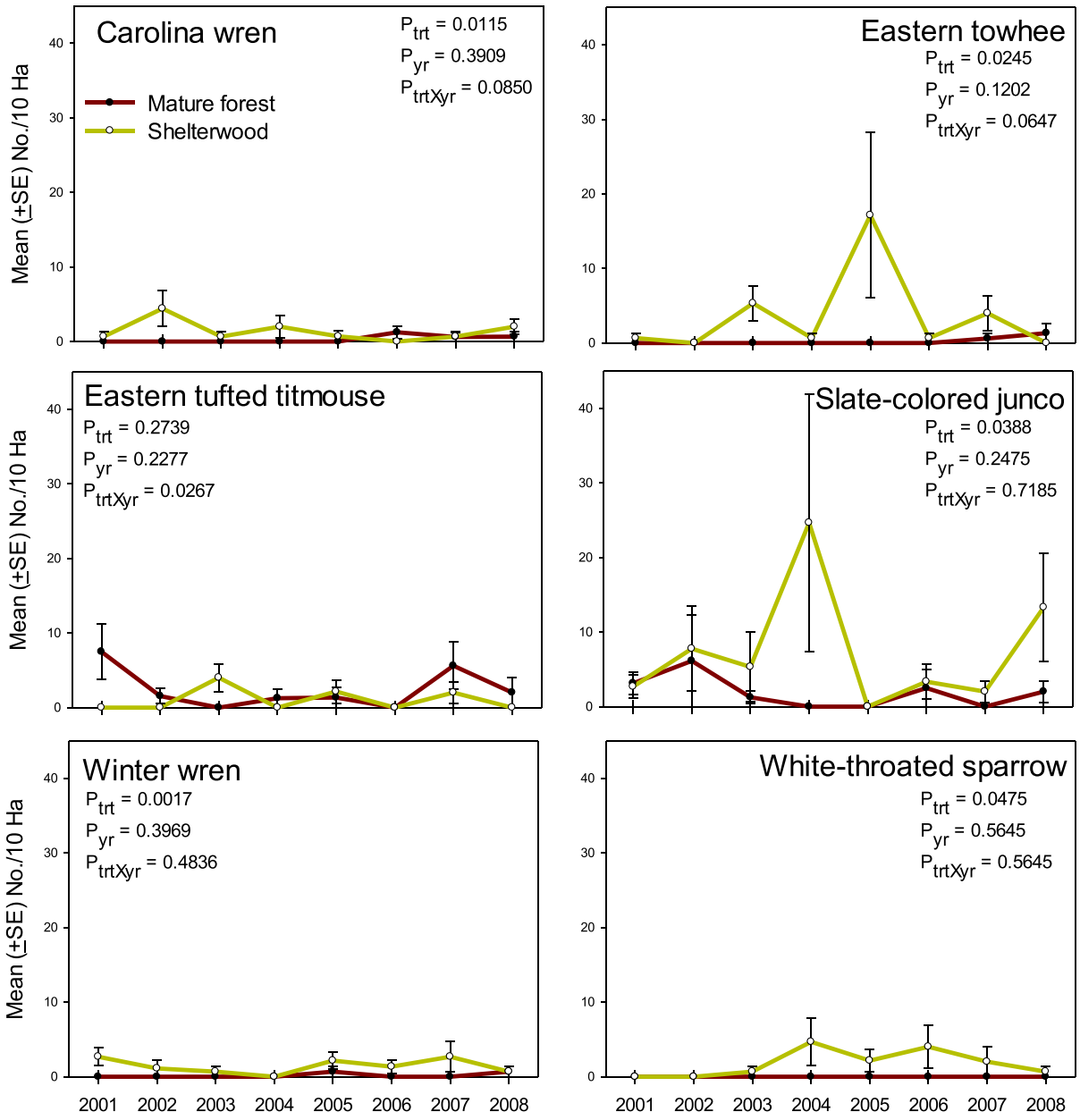
Fig. 6. Mean (+SE) annual (2000–2007; surveyed for 8 years post-harvest) fall abundance (No./10 ha) of common (≥15 observations within fall, across treatments and years) species having significant ($p < 0.05$) treatment and (or) treatment × year interaction effects (see Table 2), in shelterwood harvest and mature forest treatments, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.



be important drivers. Our results illustrated substantial differences in forest structure between SW and M throughout the 8-year study period, even as stand development in SW progressed from the stem initiation stage into early stem exclusion stage following regeneration harvests (e.g., Loftis et al. 2011). Heavy reductions in 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. Within 10 years, small tree density remained high despite substantial decreases with a concomitant increase in larger trees, as young stump sprouts and seedlings grew in girth and height, shading out less competitive young trees and blackberry. Thus, SW provided low, dense cover year-round throughout our 8-year study period. In contrast, forest structure in M was characterized by large trees that formed a closed canopy, with a relatively sparse understory of small tree stems and shrubs that changed little over time.

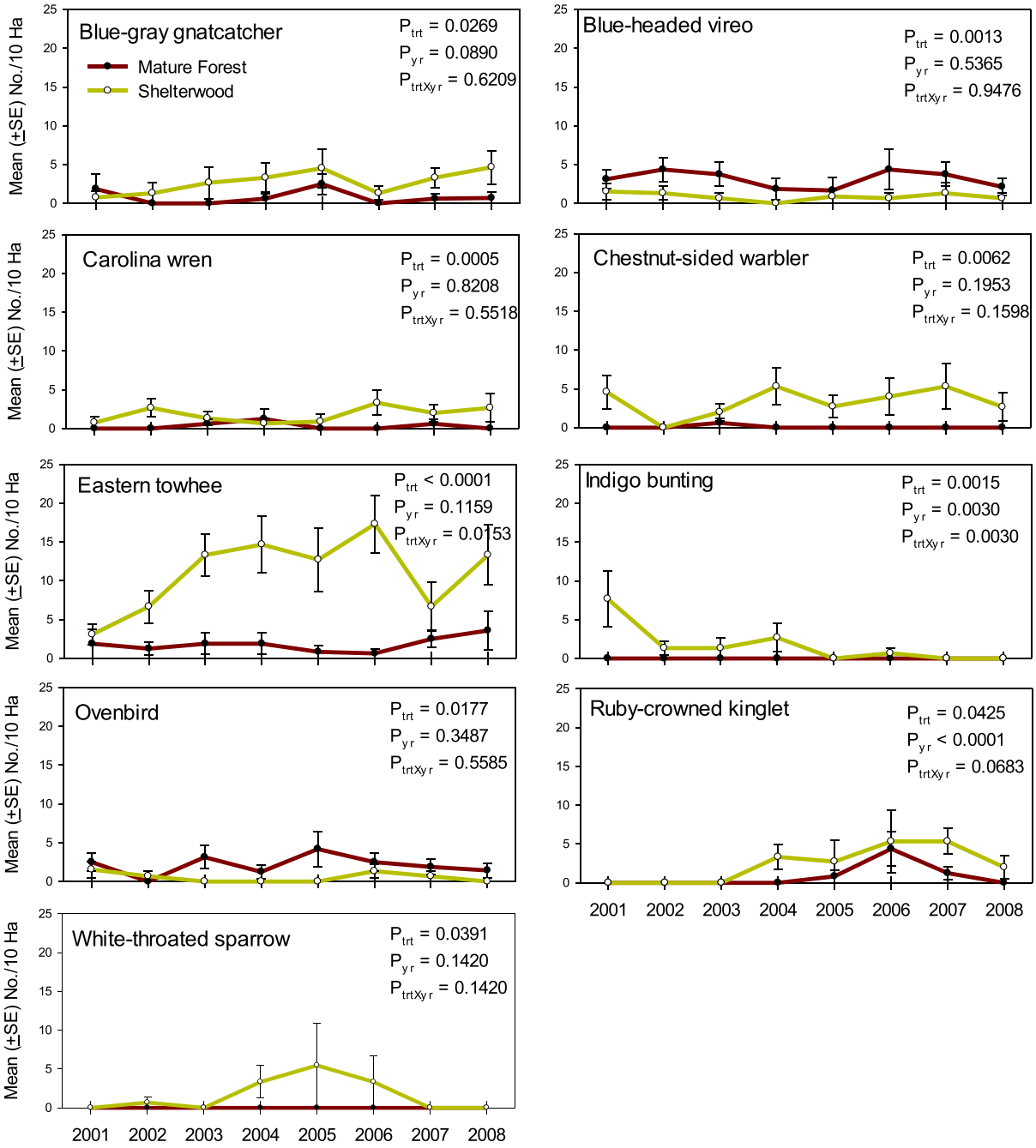
In addition to heavier protective vegetative cover, several studies indicate that food resources for birds—arthropods

Fig. 7. Mean (+SE) annual (2001–2008; surveyed for 8 years post-harvest) winter abundance (No./10 ha) of common (≥15 observations within winter, across treatments and years) species having significant ($p < 0.05$) treatment and (or) treatment × year interaction effects (see Table 2), in shelterwood harvest and mature forest treatments, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.



and fruits—are more abundant in young than mature forests, and in some seasons than in others (Holmes and Sturges 1975; Greenberg et al. 2011, 2012). Working in our study area 2–3 years after SW harvests, Whitehead (2003) reported a greater abundance of terrestrial (leaf litter) arthropods in mature forests than in shelterwood harvests, and more during fall than other seasons. In contrast, flying/foliar arthropod abundance was higher in SW than in M during breeding season and fall. and lowest during winter, with no difference between SW and M during winter and spring (Whitehead 2003). Also, within our study area, fleshy fruit biomass was 5–20 times more abundant in young SW than in M starting 2–3 years post-harvest (Greenberg et al. 2007), declining to levels similar to those in M within 10 years (Greenberg et al. 2011) as "pioneer" fruit producing species such as pokeweed (*Phytolacca americana* L.) and blackberry were shaded out with canopy closure. Fruit availability peaked during summer and fall, whereas fruit availability during winter and spring (January–May) was negligible and did not differ between SW and M (Greenberg et al. 2007). Greenberg et al. (2007) did not measure seed abundance of grasses and other non-fruit-producing plants, but in a study of herbaceous plant

Fig. 8. Mean (+SE) annual (2001–2008; surveyed for 8 years post-harvest) spring abundance (No./10 ha) of common (≥15 observations within spring, across treatments and years) species having significant ($p < 0.05$) treatment and (or) treatment × year interaction effects (see Table 2), in shelterwood harvest and mature forest treatments, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.



diversity within our study area Greenberg et al. (in review) found that grass abundance did not differ between SW and M, and abundance of many forbs was more closely associated with forest type than stand age. Thus, food resources, including flying/foliar arthropod and fleshy fruits were more abundant in SW than M primarily during summer and fall and scant in both age-classes during winter and spring.

We saw no apparent temporal trend of increase or decrease in abundance of total birds or most species, overall richness, or diversity within any season, or within SW even as forest stand development progressed from the stem initiation stage into the early stem exclusion stage over our 8-year study period. This was further supported by our results showing a lack of significant change in overall bird community composition between years within treatments in all seasons except summer. Although a few species showed abundance patterns of delayed increase (e.g., eastern towhees in spring) or peaking (e.g., chestnut-sided warblers in

2004–2005 in summer) in SW during some seasons, only one—indigo buntings—exhibited a clear trend of decreasing abundance over time (in summer and spring)—suggesting that young hardwood forest habitat suitability for most species persisted for at least 8 years across all seasons. In a longer-term (17-year) study of breeding birds (summer only) within this study design, Greenberg et al. (2023*b*) found that a higher abundance, species richness, and diversity of breeding birds and suitable habitat for scrub-shrub species (indigo bunting, chestnut-sided warbler, and eastern towhee) persisted for less than 10 years in post-shelterwood harvests, with only a few species significantly declining by year 8. The ephemerality of young forests and associated changes in bird communities over time is well established for the breeding season (e.g., Schlossberg and King 2009; Duguid et al. 2016; Greenberg et al. 2023*b*). However, virtually no studies address temporal changes in bird communities associated with development of young forests during non-breeding seasons; our 8-year study period was also likely insufficient to detect potential changes over time. Thus, longer-term research is needed to determine how long rapidly growing and changing young forests support more birds and bird species than mature forest during non-breeding seasons.

Some research indicates that the relative use of mature or young forest habitats by birds shifts within- or across seasons (Hutto 1985; Morrison et al. 1986; Petit 2000; Bowen et al. 2007). For example, during the post-fledging stage of breeding season, adults and juveniles of many mature forest species move into young forests, likely to forage under protective vegetative cover (e.g., Marshall et al. 2003; Whitehead 2003; Stoleson 2013). Similarly, several studies have shown shifts in habitat use by birds between spring and fall migration, possibly in response to availability of insect and (or) fruit food resources (e.g., Hutto 1985; Petit 2000). In our study, birds within residency guilds were more abundant in SW than M during one or more seasons but showed no preference for either treatment during others. For example, NMBs (as a group) were more abundant in SW than M during summer, but not during spring or fall migration periods. Similarly, YR residents were more abundant in SW during summer, fall and spring, but not winter, and WTR were more abundant in SW during fall migration, but not during spring migration or winter. PTMs were more abundant in SW than M during fall; spring PTM numbers were too low for statistical analysis.

Although a "broadening" of habitat use in some seasons was evident for residency guilds, we found only a few instances of this for tested individual species (only seasons having sufficient abundances of a given species could be compared); most were consistently more abundant in SW, M, or neither across seasons. For example, in both summer and spring, NMB species including blue-gray gnatcatchers, chestnut-sided warblers, and indigo buntings were more abundant in SW than M, and ovenbirds were more abundant in M than SW, whereas several species did not differ between SW and M across all tested seasons (e.g., black-and-white warbler, blackburnian warbler, black-throated green warbler, and red-eyed vireo in summer and spring; black-throated blue warbler in summer, fall, and spring). Among tested YR species, Carolina wrens and eastern towhees (across all four seasons), northern cardinals (in summer and fall), and winter wrens (in fall and winter) were more abundant in SW than M across all tested seasons, and among tested WTR species, white-throated sparrows were more abundant in SW than M in both winter and spring. In contrast, a few species were more abundant in SW in some, but not all seasons. For example, among NMB species blue-headed vireos were more abundant in M than SW in spring, but did not differ between the treatments in summer; hooded warblers were more abundant in SW than M during summer, but not during fall or spring. Among YR residents, slate-colored juncos were more abundant in SW than M in winter but not during other seasons. No PTM bird species were sufficiently abundant for statistical analysis, limiting our ability to examine whether and how they may select young or mature forests as stopover sites.

In a review, Petit (2000) found that general patterns of habitat use by birds during spring and fall migration were more variable, but generally corresponded with patterns of habitat use during the breeding season, rather than availability food, interspecific competition, or presence of predators. Our results also show that most tested species "preferred" either SW (most commonly), M, or neither, across seasons. However, cross-season changes in habitat selection by residency guilds and a few species was more aptly characterized as being more selective in some seasons, with SW used more heavily than M, and less selective in others to similarly include both SW and M, rather than "switching" habitats per se.

Although our study could not address mechanisms for observed cross-seasonal differences in the relative use of SW and M by bird residency guilds or species, shifts in habitat use both within and across seasons may be tied to changing "needs" and resource availability, such as food (Hutto 1985; Robinson and Sutherland 1999; Stoleson 2013; Carter et al. 2021) throughout the annual cycle. Food availability and cover are likely top "priorities" in all seasons; during breeding season, suitable nest sites and territories may be additional drivers of habitat selection. Carter et al. (2021) illustrated that many temperate passerine bird species switch diets from primarily insects during the summer breeding season, to also include fruits and seeds during fall and winter. In other words, the observed higher abundance of total birds and some species in SW during summer and fall may be influenced by both dense cover and ample food availability. In contrast, heavy cover in SW may be a more important attractant during winter and early spring when food resources are less concentrated in young forests, and birds may forage across a broader range of forest age-classes.

Our study corroborates many others indicating that young forest is important to birds during breeding season, but additionally highlights its important role in promoting bird diversity year-round. However, knowledge gaps remain regarding bird use of all forest age-classes during all seasons, and how long dynamically changing young forests support more birds and bird species than mature forest during non-breeding seasons. Developing timber harvest rotation schedules that provide a sustained availability of young (<10 year old) and mature forests will provide important habitats for and promote diverse bird communities year-round.

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Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

Author information

Author ORCIDs

Cathryn H. Greenberg https://orcid.org/0000-0002-2831-0989

Author contributions

Conceptualization: CHG, MW, JDL
Formal analysis: CHG, MW, CK
Investigation: CHG, MW, JT
Methodology: CHG, MW, JDL
Project administration: CHG
Supervision: CHG
Writing – original draft: CHG
Writing – review & editing: CHG, MW, MW, JDL, CK, JT

Competing interests

The authors declare there are no competing interests.

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Appendix A.

Fig. A1. Differences in dispersions between bird communities in shelterwood harvests (SW; harvested ca. 1999) and mature forest (M) treatments, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.