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ARTICLE

Effects of forest management on the conservation of bird communities in eastern North America: A meta-analysis

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Abstract

Forest management affects conditions for both early- and late-seral organisms, and managers and conservationists require information for balancing the ostensibly opposing habitat needs of both these guilds. We conducted meta-analyses that examined silvicultural systems with a range of postharvest retention and their impacts on mature-forest and shrubland bird species densities in eastern North America during the breeding season. Densities of mature-forest bird species generally declined as canopy tree retention and basal area decreased, although some mature-forest species had similar densities among unharvested and partially harvested (e.g., first-entry shelterwood) stands, and others had their highest densities in shelterwoods. We conducted a previous meta-analysis study, which showed most shrubland bird species in the region increase with harvest intensity, but some shrubland species had similar densities in clearcuts and shelterwoods. Given the contrasting effects of harvest intensity on the two avian guilds, we used Partners-in-Flight conservation values to generate objective community-wide conservation indices relative to postharvest tree retention. Clearcuts and shelterwoods typically had the highest conservation values, and unharvested and lightly thinned stands (70%–100% tree retention) had the lowest conservation scores. Many declining shrubland bird species of conservation concern are abundant in low-retention stands, thus elevating the conservation value of these stands. Additionally, high conservation values of harvested stands with 40%–70% tree retention represent the presence of both shrubland and mature-forest species; the latter are potentially responding to enhanced understory structure needed for avian nesting or foraging. In contrast, contemporary closed-canopy forests in eastern North America are generally characterized by low structural diversity and are mid-seral stands due to historical patterns of land use and tree harvesting. Although avian community conservation values were lowest in high-retention stands and many other threatened, non-avian taxa depend on open-canopy, managed forests, managers should note that late-seral, unharvested stands can

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provide important habitat for old-growth-dependent taxa and any intensive forestry should also take into account other factors. Considering the growing interest in using postharvest retention of canopy trees to meet ecological objectives, our novel synthesis can assist managers in assessing species-specific and community-wide avian responses to tree retention levels along the entire gradient of canopy treatments.

KEYWORDS
avian, retention, review, silviculture, tree harvesting, young forest

INTRODUCTION

Previous studies of forest management impacts on biodiversity report both positive and negative relationships with species abundance, depending on the taxa, geographic location, and the forestry practices employed (Franklin et al., 2019; LaManna & Martin, 2017; Paillet et al., 2010). For instance, varied effects of silviculture on species abundance have been observed for breeding birds (e.g., Akresh & King, 2016; Goodale et al., 2009; Jobes et al., 2004). High-intensity tree harvests reduce the canopy to allow for the growth of dense understory vegetation, which is preferred by many shrubland, early-successional bird species (Annand & Thompson, 1997; Smetzer et al., 2014). In contrast, unharvested forest or lightly thinned stands typically provide habitat for bird species that need closed-canopy conditions during the nesting period (Baker & Lacki, 1997; Webb et al., 1977).

Although informative, the patterns evident in individual studies are subject to variation associated with study-specific bird communities, forest compositions, tree harvest levels, and geographic locations (e.g., King et al., 2011; Perry et al., 2018; Wang et al., 2006), making it challenging to generalize the effects of forestry on birds from a single study. In eastern North America, a few studies have examined continuous gradients of tree retention or basal area (Sheehan et al., 2014; Smetzer et al., 2014), but most studies assessed discrete silvicultural treatments (e.g., clearcuts and shelterwoods; King & DeGraaf, 2000; Pagen et al., 2000), which restricts the inferences of a given study. Quantitative syntheses of previously collected information can provide generalizable findings about the effects of canopy reduction of any intensity on the entire bird community, which can then guide the activities of managers and conservationists (Schlossberg & King, 2015; Vanderwel et al., 2007).

Meta-analysis is a quantitative synthesis method that can effectively summarize findings across individual studies to reveal generalizable relationships between organisms and their environment (Arnqvist & Wooster, 1995). Previous meta-analyses have been used to better understand the effects of forest management on birds (e.g., Fedrowitz et al., 2014; Fontaine & Kennedy, 2012; Schieck & Song, 2006). However, most studies have not explicitly addressed the trade-offs among different silvicultural practices on mature-forest and shrubland birds.

Balancing the opposing needs of nesting shrubland and mature-forest birds is challenging because both species groups merit conservation attention but can occupy opposite ends of the gradient of silvicultural intensity. In eastern North America, mature-forest birds associated with some level of canopy closure during the nesting season, such as wood thrush (*Hylocichla mustelina*) and cerulean warbler (*Setophaga cerulea*), have exhibited steep range-wide declines over recent decades (Buehler et al., 2008; King et al., 2006; Sauer et al., 2019). However, a high proportion of open-canopy, shrubland bird species such as prairie warbler (*Setophaga discolor*), field sparrow (*Spizella pusilla*), and eastern towhee (*Pipilo erythrophthalmus*) are also declining range-wide (Dettmers, 2003; King & Schlossberg, 2014).

Any silvicultural practice will benefit some species and be detrimental to others (Crawford et al., 1981), and thus one approach to balancing bird species with contrasting nesting habitat requirements is with the use of community conservation scores (Michel et al., 2020; Nuttle et al., 2003). Conservation scores for a community of birds can be calculated by weighing the abundances of different individual species depending on their at-risk status and regional population abundance, and then summing across species to calculate a conservation score for the entire bird community (Götmark et al., 1986; Hunter et al., 1993). Community conservation scores can be more useful to conservationists and forest managers than solely examining species richness, which does not consider the conservation status of each individual species (Beissinger et al., 2000; Carter et al., 2000; Pons et al., 2003).

Partners-in-Flight (PIF) values from the Avian Conservation Assessment Database (Panjabi et al., 2020) are particularly useful and have been used in previous studies to characterize the conservation status of individual species in eastern North America and to create community-wide conservation values (Nuttle et al., 2003; Paquet et al., 2006). For example, Twedt et al. (2002) calculated conservation values for the entire bird community in three bottomland hardwood forest types in the southern United States, using PIF scores of individual species. More recently, a meta-analysis on the effects of time since treatment and harvest intensity on community conservation values was conducted using primary studies on bird abundance throughout North America (Twedt, 2020). Twedt (2020) revealed that community-wide conservation scores were highest in hardwood stands with 30%–50% retention and in conifer stands with 50%–70% retention, but recommended that regional examinations of bird responses to harvest intensities would be useful given the potential variation among regions.

In this study, we used meta-analyses to examine how variation in canopy tree retention affects the densities of individual mature-forest-nesting bird species in eastern North America, and then combined these mature-forest bird relationships with previous relationships that we found in shrubland birds (Akresh et al., 2021) to calculate community-wide conservation scores along the same gradient of tree retention. We weighted standardized densities of individual species using PIF conservation values. Data were analyzed along a continuous gradient of tree retention, and we also examined bird responses among three discrete silvicultural classifications (low-retention stands, shelterwoods, and high-retention management regimes [e.g., commercial thinning, single-tree selection, and no management]) that are familiar forestry prescriptions. The results from this categorical analysis can be compared with past studies and findings presented on shrubland birds in Akresh et al. (2021), which may allow for better planning and communication with forest managers (Lott et al., 2021). We ran community-wide analyses separately for four different North American Bird Conservation Regions (North American Bird Conservation Initiative, 2020), focusing on regions in northeastern North America. To assess the impacts of individual species on the community-wide conservation scores, we also tested the effects of removing specific species from the calculations. By having quantitative relationships of harvest impacts at both the individual species and community levels, forest managers can better account for the trade-offs of any given harvesting treatment on mature-forest and shrubland birds when planning management activities.

METHODS

Mature-forest birds' meta-analyses

We searched for studies examining mature-forest birds and silviculture in eastern North America, by searching Google Scholar and Web of Science Core Collection databases between May and August 2018 with the following search terms: "bird," and/or "avian," and "residual tree," "green tree retention," "shelterwood," "single-tree selection," "thinning," "seed-tree," "clearcut," "regenerating forest," or "timber harvest" (Lott et al., 2019). We also examined reference lists and used "snowballing" techniques (Wohlin, 2014). In December 2020, we additionally examined a list of references from a systematic map of bird–vegetation relationship studies in the region (Lott et al., 2022). Our literature search for mature-forest birds was conducted concurrently during our prior literature search on shrubland birds (Akresh et al., 2021). Some limitations of our search include the lack of searching for studies in other languages, the exclusion of very recent studies from the last few years, and our limited use of data from gray literature (Woodcock et al., 2014).

The geographic extent of our study was the eastern United States and southeastern Canada, and did not include the boreal forest (Figure 1). We chose to include community bird studies that presented either bird density estimates or abundance data that could be standardized by unit area. We did not include studies that focused on just one individual species because they may have had different survey methods (e.g., mapping color-banded birds) and could have introduced publication bias into our study (Gurevitch & Hedges, 1999).

Species were designated as "mature-forest" birds if they were associated with closed-canopy forest in studies of bird communities across conditions or gradients of silvicultural intensity (e.g., Annand & Thompson, 1997; King & DeGraaf, 2000). Our classification of mature-forest birds is primarily during the nesting season, as many mature-forest-nesting species disperse to shrubland habitats during the post-fledging period (Akresh et al., 2009; Stoleson, 2013). We did not include generalist bird species that occupy forests but are also present in nonforest habitats such as suburban neighborhoods and urban parks (e.g., downy woodpecker [*Picoides pubescens*] and white-breasted nuthatch [*Sitta carolinensis*]; Kluza et al., 2000). We collected data on 26 mature-forest species, although not all of these species had enough data for analysis (Appendix S1: Table S1).

Studies included a wide range of silvicultural systems, such as single-tree selection, thinning, first-entry shelterwood, retention harvest, seed-tree, and clearcuts.

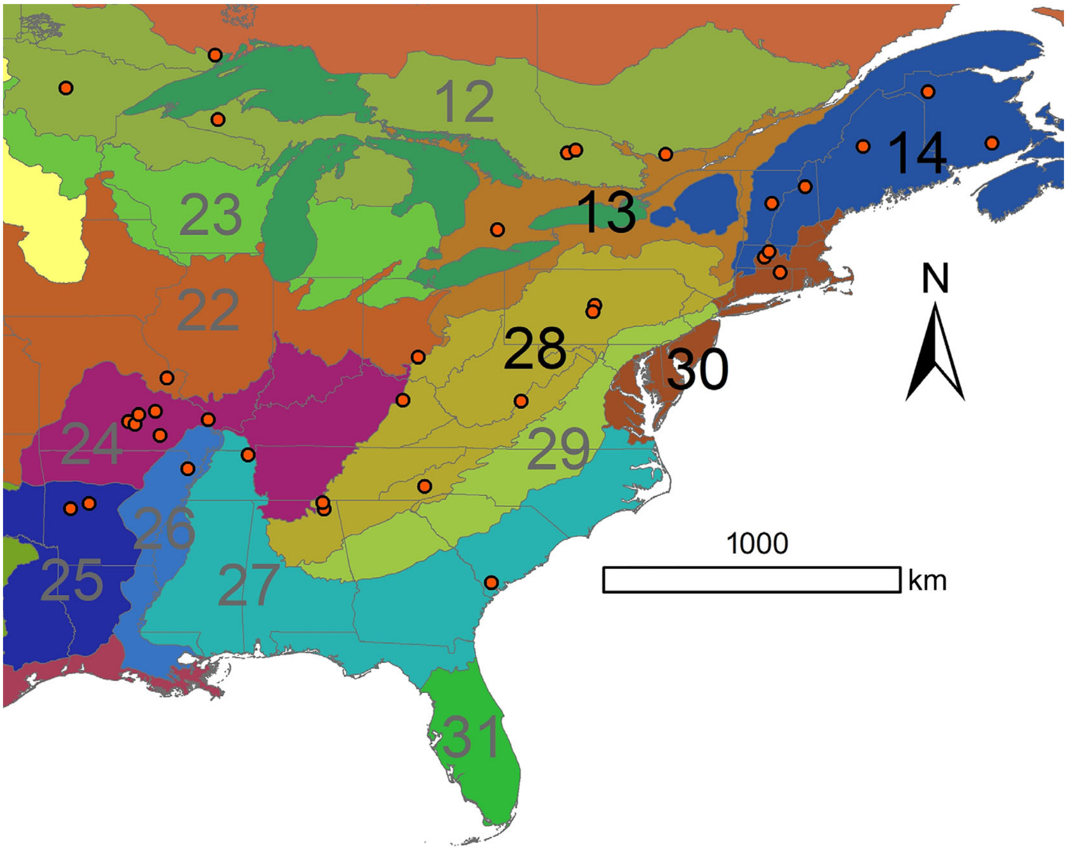

FIGURE 1 Map of Bird Conservation Regions (BCRs) in eastern North America with points denoting the approximate location of primary studies used in our mature-forest or shrubland bird (Akresh et al., 2021) meta-analyses (GIS locations obtained from the Lott et al., 2019 systematic map). Different colors denote different BCRs; BCR numbers in black indicate the four focal BCRs examined in this study.

Group selection cuts were included if the harvests were less than 0.5 ha (range = 0.05–0.4 ha), to be certain that openings were interspersed throughout a much larger, intact-canopy stand. For the few excluded studies with group selection cuts between 0.5 and 1 ha, we were uncertain what proportion of bird surveys were conducted within these larger openings or in the adjacent, unharvested forest. Our study only focused on canopy reduction in naturally regenerating forests, and thus we excluded studies examining the effects of fire or other natural disturbances, and studies in tree plantations.

We focused on studies with harvested stands <16 years since treatment (Schlossberg & King, 2009). Studies often averaged bird abundance across multiple stands with different years since treatment (Akresh et al., 2021), so we did not attempt to examine time since treatment in our analyses. Moreover, some studies did not present year since treatment values for unharvested stands, or this was complicated by historic selective tree harvesting and high-grading within stands (Akresh et al., 2022). Throughout the article, we use the terms "unmanaged" and "unharvested" forest to classify reference or control forest stands that were not recently managed, but we note that almost all eastern North American forests have likely had some tree harvesting in the last 150–200 years (Foster et al., 1998; Litvaitis, 1993) and the forest stands within the primary studies we examined were not structurally complex, old-growth (late-seral), or virgin stands found in precolonial North America (Keeton, 2006). For studies that provided information on the age of unmanaged, reference forest stands, most unmanaged stands had not been previously logged for 50–120 years (Akresh et al., 2022).

We determined the percent tree retention levels of treated stands in each study by taking the ratio of the mean basal area of treated stands versus the unmanaged forest stands (Vanderwel et al., 2007). We classified unmanaged forest stands as having 100% tree retention. The percent tree retention values were highly correlated with basal area values (Appendix S1: Figure S1, $r = 0.93$). In studies that did not present basal area, we used percent canopy cover instead to determine the tree retention percentage. Several studies in clearcuts did not present vegetation data (e.g., McDermott & Wood, 2009), but we included these studies because sample sizes for this treatment type were limited. We assigned a 0% retention level for studies that did not mention any residual trees in the clearcut stands and assigned a 10% tree retention level for studies that mentioned clearcuts that contained some residual overstory trees.

We recorded general data from each study (e.g., study location, avian survey method), as well as the raw mean abundance or density and their standard errors (SEs) for each bird species in the treated and unharvested stands, and data on basal areas and canopy cover of the stands (Akresh et al., 2022). We used Web Plot Digitizer Version 4.1 (Rohatgi, 2018) to obtain data from figures. Two of the authors (MEA and SLM) screened the articles and extracted the data from the studies, and MEA reviewed all of the extracted data. We then standardized all avian data to the number of birds per hectare (Akresh et al., 2021). For point count studies, we divided the raw mean abundance by the point count circle area (e.g., based on a 40-, 50-, or 75-m radius), to convert the data to a standardized density estimate. For a few studies with unlimited-distance point counts, we used a 75-m radius because detection probability declines past 50 m (Newell et al., 2013; Reidy et al., 2011; Schieck, 1997). For a given study, we included the species-specific abundance or density only if the species had an abundance >0 in either treated or unmanaged stands (i.e., the species was present in the study location), because studies were conducted outside of the range limits of at least some of our focal species.

As in Schlossberg and King (2009) and Akresh et al. (2021), we conducted a regression-type meta-analysis using data of mean densities of birds recorded in forest stands with different tree retention levels. We did not use more formal meta-analysis methods (e.g., Hedges et al., 1999; Kalies et al., 2010; Tilghman et al., 2012), because we were often unsure of the true sample size of surveys (Hurlbert, 1984; Spake & Doncaster, 2017) and we wanted to conduct the same standardized analysis as Akresh et al. (2021) to combine both mature-forest and shrubland bird guilds for the community conservation scores. We weighted each bird density data point by dividing the SE by the mean density and then standardizing this weight to a value ranging between 1 and 2 (Vanderwel et al., 2007). Density data with smaller SEs had higher weights. For density values of 0, we conservatively inputted the lowest real-number weight computed for the other retention level(s) in the same study for that given species (Vanderwel et al., 2007). Several studies did not present SEs ($n = 6$); for these data we used a weight of 1 (the lowest weight possible).

We conducted analyses on species with at least 15 data points (i.e., species-specific mean bird densities at different treatment levels within studies), and we ran weighted generalized linear mixed models (GLMMs) separately for each species. We used gamma distributions with a log link and added 0.1 to all bird densities in order to use gamma functions with density data that included 0s (Akresh et al., 2021; Kalies et al., 2010). The overstory tree retention percentage was a continuous predictor variable and bird density was the response variable. We included a random effect of study, which accounted for variation among studies and multiple data values for a given species within studies (Fontaine & Kennedy, 2012). We attempted to examine relationships within forest types (e.g., Oak-Hickory versus Northern Hardwoods), but the data were not sufficient within each species to run these models.

We used an information-theoretic approach to compare three models for each species: a null model, a model with a linear predictor of tree retention, and a model with a quadratic and linear predictor of tree retention. We used corrected Akaike information criterion values (AIC_c) for small sample sizes (Burnham & Anderson, 2002) to compare among models. We defined the top model as the model with the lowest AIC_c, if the top model was more than two AIC_c values compared with the next highest supported model. If there were several models within two ΔAIC_c values, we chose the simplest model as our top model (Arnold, 2010). A few mixed models did not converge when conducting model selection (for four species); in these cases, we ran simpler fixed-effects models without the random effect of the study.

In addition to testing a continuous predictor of tree retention, in separate models we compared bird densities among discrete, categorical levels of silvicultural treatments. Following Akresh et al. (2021) and based on basal areas and forest type, we assigned treatment levels in each study to either regeneration harvests with low-retention, regeneration harvests with moderate-retention (e.g., shelterwoods) or high-retention (often unmanaged) stands (Appendix S1: Figure S2). Separately for each species, we conducted similar weighted GLMMs to examine categorical levels of treatment types. Bird density was still the response variable, and we now included a main categorical predictor variable with three retention levels: low, moderate, and high. The GLMM did not converge for hermit thrush, and we used a simpler, fixed-effects model for this species. All analyses were conducted using the R statistical program version 4.0.3 (R Core Team, 2020), and we used the lme4 and lmerTest packages to conduct mixed-effects models (Bates et al., 2015; Kuznetsova et al., 2016) and the ggeffects package for plotting predictions (Lüdecke, 2018).

Although publication bias in meta-analyses can occur because proportionally more published papers may contain significant results compared with unpublished studies that may lack significant results (Arnqvist & Wooster, 1995; Gurevitch & Hedges, 1999), we do not foresee this "file drawer effect" occurring in our meta-analysis. Studies examining the effects of tree harvests on bird abundance are often published regardless of significant differences within certain individual species, because studies are focused on examining community-wide patterns using point counts or transect surveys (e.g., Goodale et al., 2009; King et al., 2011). As noted in similar meta-analyses, we have no reason to believe that publication bias would occur in our type of study (Fontaine & Kennedy, 2012; Kalies et al., 2010). We did not examine effect sizes in our analyses, and thus could not examine publication bias as done in some other meta-analyses (Nakagawa et al., 2022). Nevertheless, using the performance package (Lüdecke et al., 2021), we examined the influence of individual data points on the predicted functions. We found no points had a large influence within any of the individual mature-forest species' models using a continuous predictor of tree retention (Cook's distances <0.8), and there were few influential data points in models using the categorical predictor of silvicultural treatments (Cook's distances <0.8, except for one influential point in the model for least flycatcher). Including the random effect of study in the analyses also accounted for heterogeneity among studies.

Community-wide analyses

In order to determine the impact of silvicultural intensity on the entire bird community, we also examined the relationship between percent canopy retained and a community-wide conservation index incorporating both shrubland and mature-forest birds. We first selected the top model (a null, linear, or quadratic relationship with tree retention), for each shrubland and mature-forest species, using the shrubland bird relationships from a previous study (Akresh et al., 2021). Shrubland bird species (synonymous with "young forest," "open forest," or "early-successional" bird species; Hanberry & Thompson, 2019; King & Schlossberg, 2014) consisted of 16 species (Appendix S1: Table S1). With the top mixed model fit for each species, we then predicted the mean density of each species as overstory tree retention increased at 1% increments between 0% and 100%. We then standardized the predicted density values per species to values between 0 and 1, because we wanted to compare the impact of tree retention on individual species, regardless of variation in density due to geography, study, or site-level factors that were unrelated to tree retention. Several shrubland birds also had relatively high recorded densities (>1 bird/ha; Akresh et al., 2021) compared with mature-forest birds, but we were unsure if this was due to increased detectability of females of shrubland birds in clearcuts or other survey-related biases (Pagen et al., 2002). Therefore, our meta-analysis approach differed from previous studies (e.g., Twedt, 2020; Twedt et al., 2002) in that we created community-wide indexes that were not location specific, but rather were based on standardized densities across the tree retention gradient and were only using selected bird species that had sufficient data to determine quantitative relationships with tree retention.

We obtained region-specific values of per-species conservation scores based on PIF criteria (Carter et al., 2000). Specifically, from the PIF database, we obtained Regional Concern Scores (breeding season; RCS-b) for each species, for each of the following Bird Conservation Regions (BCRs): 13, 14, 28, and 30 (North American Bird Conservation Initiative, 2020). The RCS-b conservation score is a combination of scores from individual elements of conservation status, such as global population size, breeding distribution, population trend, threats to breeding populations, and regional density, all of which are ranked on a scale of 1–5 (Panjabi et al., 2020). We focused on BCRs in the northeastern United States and southeastern Canada; we did not include BCR 29, a more southern region that did not have PIF scores for seven of our focal species, or other BCRs (e.g., 24 and 12) that lacked some of our focal species (Figure 1).

Across the gradient of tree retention (0%–100%), we multiplied the standardized predicted density values from our models with the regionally specific PIF conservation scores, for each given species (Nuttle et al., 2003). This effectively integrated and weighted the species relative density values with their conservation values. Lastly, we computed a community-wide conservation score for each percentage of tree retention by summing up the per-species values across both mature-forest and shrubland species (Nuttle et al., 2003). We computed the community-wide conservation scores separately for each BCR. We were primarily interested in the mean relationships between community conservation scores and tree retention, and did not incorporate study-specific or species-specific variation around the mean predicted values.

We chose to include an equal number of shrubland and mature-forest bird species when computing our community-wide conservation scores, in order to effectively examine a balance of sustaining and conserving both mature-forest and shrubland bird populations. We did not include species in which the null model was the top model, or species in which the effect of tree retention on bird density was not significant (using an alpha level of 0.05). These species were not greatly influenced by tree retention and would only add a constant value to our community-wide conservation index, but would not change the relationship of the index with tree retention. Given that there were a few more shrubland species compared with mature-forest species for which we observed a significant effect of tree retention, we discarded two shrubland bird species (Carolina wren [*Thryothorus ludovicianus*] and American robin [*Turdus migratorius*]) in our community-wide conservation scores; these two species had weak relationships with tree retention (Akresh et al., 2021) and are weakly associated with shrublands (Schlossberg & King, 2007). Our community-wide conservation scores in BCRs 13, 28, and 30 combined the values from 16 mature-forest species and 16 shrubland species, all 32 of which had a stronger relationship with tree retention, and had >14 data points to effectively analyze and predict relative densities in our meta-analysis. BCR 14 is a more northern region and is mostly outside the range of the yellow-breasted chat (shrubland species) and blue-gray gnatcatcher (mature-forest species; Sullivan et al., 2009). Thus, we excluded these two species in our community-wide conservation scores for BCR 14.

Overall, we note that although our community-wide conservation scores were tallied from a representative group of species found in the forests of northeastern North America, the community-wide conservation scores are specific to the species that we were able to include in our analyses. Given this, we tested how much the community-wide conservation scores changed if certain species were taken out of the calculations. Separately for each region, we conducted a "delete-one" jackknife analysis (Crowley, 1992; Princé & Zuckerberg, 2015), in which we iteratively deleted one species from the calculations of the community-wide conservation scores for every predicted value of tree retention between 0% and 100%. We then used the 0.025, 0.50, and 0.975 quantiles of the jackknifed conservation scores to examine the variation in the relationship between tree retention and the community-wide conservation scores when deleting individual species from our original candidate set of species.

Finally, we calculated community conservation scores among discrete categories of silvicultural intensities: low, moderate, and high tree retention. Within categories, we used the mean basal area from treatments within studies: 5.6 m^2/ha for low retention, 15.7 m^2/ha for moderate retention, and 24.7 m^2/ha for high retention (Akresh et al., 2021). We then converted these basal area values to percent tree retention levels (27%, 61%, and 91% retention, respectively) using a predicted linear relationship between basal area and tree retention (Appendix S1: Figure S1). Lastly, we presented the 0.025, 0.50, and 0.975 quantiles of the jackknifed conservation scores at these three tree retention levels to examine community-wide conservation scores in representative silvicultural categories.

RESULTS

Mature-forest bird relationships

We used data from 33 studies across eastern North America (Figure 1) and acquired adequate data (>14 density estimates) to fit models for 22 putative mature-forest bird species (Akresh et al., 2022). Based on AIC_c values, most species had support for models with either a linear, or linear and quadratic, continuous predictor of overstory tree retention on bird densities (Table 1).

Eight species had models that fit better with a single linear predictor of tree retention, based on the AIC_c values (Table 2). Predicted bird densities increased as a higher percentage of trees were retained for seven species: ovenbird, Acadian flycatcher, hermit thrush, black-throated green warbler, brown creeper, red-breasted nuthatch, and wood thrush (Figure 2). Although the top model for rose-breasted grosbeak had the linear predictor of tree retention, the effect was not significant (based on the β_1, SE, and p values; Table 2).

Nine species had models that fit better with quadratic relationships: blue-gray gnatcatcher, blue-headed vireo, blackburnian warbler, black-throated blue warbler, eastern wood-pewee, least flycatcher, red-eyed vireo, scarlet tanager, and yellow-bellied sapsucker. These nine species had more complex relationships with the continuous variable of tree retention (Table 3, Figure 3), but all of these species had lower densities in stands with low tree retention.

The null model was the top simplest model for five putative mature-forest species: American redstart, great-created flycatcher, hooded warbler, veery, and yellow-rumped warbler. Thus, there was little support for a relationship between bird density and a continuous variable of tree retention for these five species, as well as for rose-breasted grosbeak (Appendix S1: Figure S3).

Examining densities among three discrete silvicultural regimes (low, moderate, and high tree retention;

TABLE 1 Model comparisons of a null, linear, or quadratic relationship between percent tree retention and bird density for each putative mature-forest species.

	ΔAIC_c			
Species	**Null**	**Linear**	**Quadratic**	**Top simplest model**
American redstart	0	1.691	4.198	Null
Great-crested flycatcher	0	2.522	1.587	Null
Hooded warbler	0	2.362	5.224	Null
Veery	0	2.422	5.219	Null
Yellow-rumped warbler	0.736	4.152	0	Null
Acadian flycatcher	82.1	1.582	0	Linear
Brown creeper	8.505	0	4.363	Linear
Black-throated green warbler	51.751	0	0.988	Linear
Hermit thrush	18.982	0	2.378	Linear
Ovenbird	67.938	0	1.79	Linear
Rose-breasted grosbeak	2.123	0	2.438	Linear
Red-breasted nuthatch	2.799	0	4.231	Linear
Wood thrush	3.875	0	2.706	Linear
Blue-gray gnatcatcher	2.588	3.896	0	Quadratic
Blue-headed vireo	14.325	13.745	0	Quadratic
Blackburnian warbler	17.183	4.429	0	Quadratic
Black-throated blue warbler	22.095	5.814	0	Quadratic
Eastern wood-pewee	26.658	28.877	0	Quadratic
Least flycatcher	16.904	20.072	0	Quadratic
Red-eyed vireo	77.305	12.725	0	Quadratic
Scarlet tanager	13.963	2.72	0	Quadratic
Yellow-bellied sapsucker	29.932	23.219	0	Quadratic

Note: We compared models using values of corrected Akaike information criterion (AIC_c). For each species, we defined the top model as the model with the lowest AIC_c value, if the difference in the AIC_c value from the top model to the next highest supported model (ΔAIC_c) was >2. If multiple models had <2 ΔAIC_c values, indicating similar support, we defined the simplest model of these (i.e., null or linear) as the top model.

TABLE 2 For mature-forest bird species in which the top model included the linear predictor of tree retention, we present the number of data points (n; i.e., mean bird densities in different treatment levels within studies), the number of studies that had data for the given species, percent of the model variance accounted for by the random effect of study, model parameter estimates (β_0 = intercept and β_1 = linear parameter estimate) and their SEs in parentheses, t values, and p values.

Species	n	**No. studies**	**Percent variance**	β_0 **(SE)**	β_1 **(SE)**	t	p
Ovenbird	62	26	0.648	−2.284 (0.218)	2.313 (0.121)	19.2	<0.001
Acadian flycatcher	30	13	0.789	−2.113 (0.265)	1.124 (0.072)	15.6	<0.001
Hermit thrush	22	10	0.593	−2.315 (0.267)	1.681 (0.161)	10.5	<0.001
Black-throated green warbler	33	15	0.619	−1.860 (0.248)	1.509 (0.145)	10.4	<0.001
Brown creeper	16	7	0.169	−2.328 (0.236)	1.154 (0.275)	4.2	<0.001
Red-breasted nuthatch	15	7	0.774	−1.915 (0.282)	0.290 (0.101)	2.9	0.004
Wood thrush	36	15	0.495	−1.667 (0.195)	0.361 (0.140)	2.6	0.01
Rose-breasted grosbeak	31	14	NA	−0.514 (0.453)	−0.711 (0.589)	−1.2	0.24

Note: The percentage of variance accounted for by the random effect of study was computed by dividing the variance of the random effect with the total variance in the model (the variance of the random effect plus the residual variance; Zuur et al., 2009). The mixed-effects model did not converge for rose-breasted grosbeak, and we used a fixed-effects model for this species. Species are listed in order of strength of the model, based on the t value.

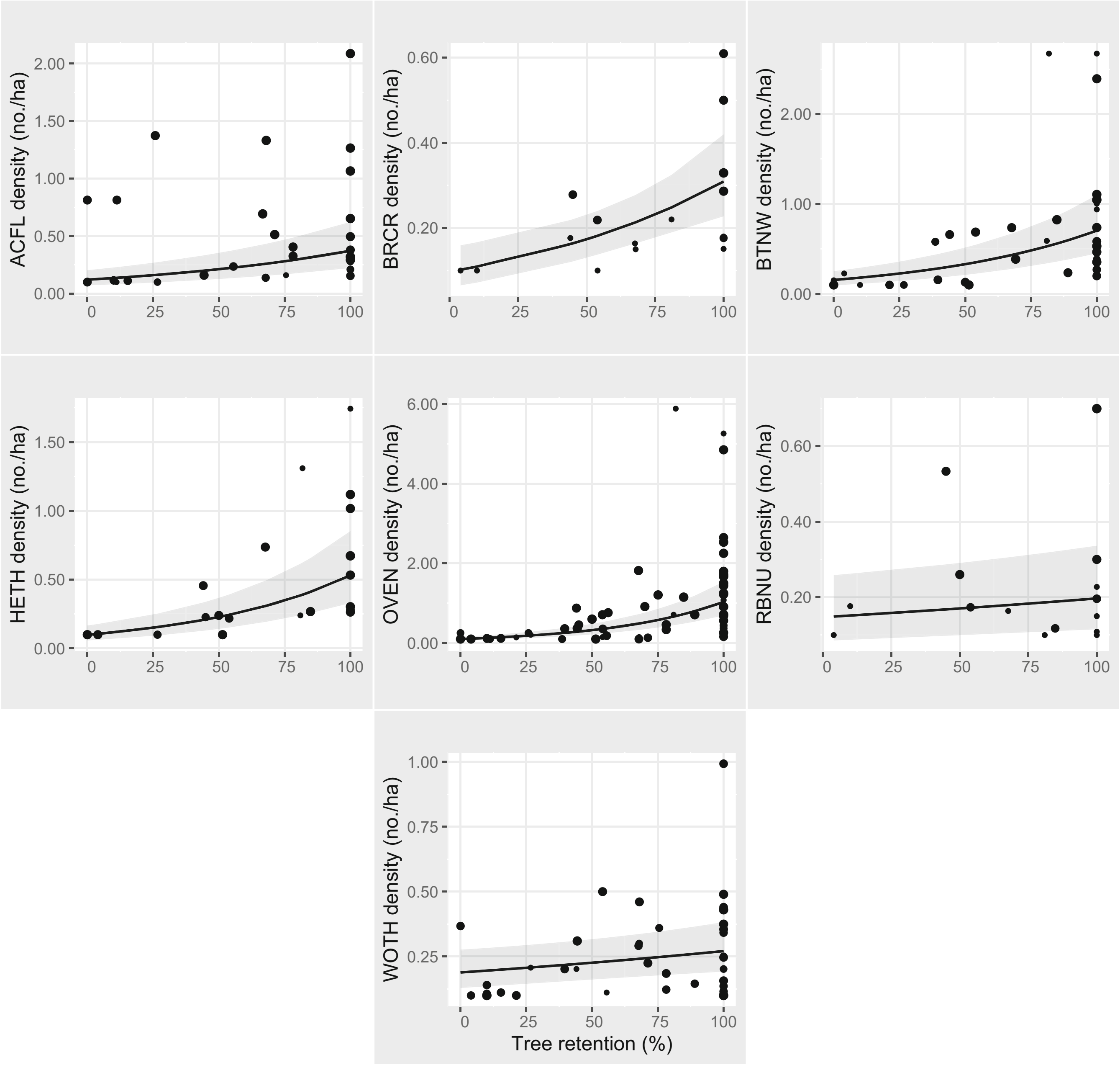

FIGURE 2 For mature-forest species where a linear predictor was the best fit, we present the effect of tree retention on avian density. Points indicate bird density values from individual studies, and larger points indicate that the data point had a higher weight in the model. Lines and gray shading represent the weighted regression curves and 95% confidence intervals. To fit the models to gamma distributions, all bird densities had a small value of 0.1 added to them (so the lowest possible density was 0.1). ACFL, Acadian flycatcher; BRCR, brown creeper; BTNW, black-throated green warbler; HETH, hermit thrush; OVEN, ovenbird; RBNU, red-breasted nuthatch; WOTH, wood thrush.

Table 4), Acadian flycatcher, blackburnian warbler, brown creeper, black-throated blue warbler, black-throated green warbler, ovenbird, and red-eyed vireo had greatest densities in high-retention stands, had lower densities in shelterwoods (moderate retention) compared with high-retention stands, and lowest densities in low-retention stands. Eleven other species had more complicated differences in densities among discrete silvicultural treatment levels (Table 4), although least flycatcher, yellow-rumped warbler, American redstart, eastern wood-pewee, rose-breasted grosbeak, and blue-headed vireo had their highest densities in shelterwoods (moderate tree retention). Wood thrush and yellow-bellied sapsucker had relatively similar densities in high-retention stands and shelterwoods, but had lower densities in low-retention stands. Blue-gray gnatcatcher, great-crested flycatcher, hooded warbler, and veery densities did not differ among the categorical treatment levels.

TABLE 3 The number of data points (n), the number of studies included, the proportion of variance accounted for by the random effect of study, and model parameter estimates (β_0 = intercept, β_1 = linear parameter estimate, β_2 = quadratic parameter estimate) and their SEs in parentheses for mature-forest bird species, in which the top model included a linear and quadratic predictor of tree retention.

Species	n	No. studies	Percent variance	β_0 (SE)	β_1 (SE)	β_2 (SE)
Blue-gray gnatcatcher	28	11	0.648	−1.476 (0.302)	1.964 (0.646)	−1.492 (0.534)
Blue-headed vireo	20	9	0.482	−3.370 (0.387)	7.507 (1.205)	−5.653 (1.034)
Blackburnian warbler	15	7	0.640	−3.123 (0.370)	4.647 (0.899)	−2.650 (0.740)
Black-throated blue warbler	28	12	0.485	−2.123 (0.283)	3.743 (0.872)	−2.215 (0.711)
Eastern wood-pewee	59	24	0.513	−1.948 (0.191)	3.217 (0.520)	−2.564 (0.414)
Least flycatcher	17	7	0.429	−2.978 (0.374)	7.835 (0.946)	−5.387 (0.724)
Red-eyed vireo	64	27	0.646	−1.464 (0.212)	2.877 (0.444)	−1.483 (0.363)
Scarlet tanager	49	21	0.566	−1.899 (0.220)	1.962 (0.636)	−1.200 (0.513)
Yellow-bellied sapsucker	19	9	0.844	−2.196 (0.428)	4.081 (0.471)	−2.689 (0.373)

Community-wide conservation scores

We found nonlinear relationships between the community-wide conservation scores and tree retention in four BCRs (Figures 1 and 4), which we examined by combining an equal number of mature-forest and shrubland bird species in the community-wide scores (Table 5; detailed results of individual species relationships for shrubland birds can be found in Akresh et al., 2021). The community-wide scores generally had two peaks: in stands with very low tree retention (0%–10%) and in stands with moderate tree retention (40%–70%). The relative importance (or amplitude) of the two peaks varied among BCRs (e.g., in BCR 30, the 40%–70% peak was relatively lower than the peak at 0%–10% tree retention, while BCR 14 showed the opposite in peak amplitude). The relationship in BCR 14 was the most different from the other regions; we did not include two species in the BCR 14 community-wide scores that were included in the other regions. In three of the four regions, forest stands with 70%–100% tree retention had the lowest community-wide conservation scores, and stands with 85%–100% tree retention had the lowest community-wide conservation scores in BCR 14.

To examine the effect of individual species on community-wide scores, we conducted a jackknife analysis and obtained confidence intervals by removing individual species from the community-wide calculations. Examining the area within the confidence intervals in BCRs 13, 28, and 30, the effect of tree retention on the community-wide scores was relatively constant between 0% and 70% tree retention (Figure 5). In BCR 14, there was a noticeable peak between 40% and 80% tree retention within the area of the confidence interval. Regardless of the individual species that were removed from the community conservation scores, 85%–100% tree retention had the lowest conservation scores across all regions. Examining the categorical classifications of silvicultural intensities, community conservation scores were highest in shelterwoods and low-retention stands, and lowest in high-retention stands (Table 4).

DISCUSSION

Understanding the trade-offs of tree retention for mature-forest and early-successional species is important for developing comprehensive conservation strategies in managed forests (Paillet et al., 2010). Our findings demonstrate the effects of overstory tree retention and basal area on individual eastern mature-forest-nesting bird species, individual shrubland bird species (Akresh et al., 2021), and on the entire shrubland–forest avian community in eastern North America. We illustrate how community conservation scores (Nuttle et al., 2003) can help better understand trade-offs of silvicultural practices for early- and late-seral guilds.

Most putative mature-forest species had their lowest densities in stands of 0%–40% tree retention, as expected from individual studies that demonstrated lower numbers in stands with high levels of canopy removal (e.g., Annand & Thompson, 1997; King & DeGraaf, 2000), and consistent with the results from a similar meta-analysis of forestry effects on birds (Vanderwel et al., 2007). Low densities of mature-forest species in stands with limited overstory retention, which included clearcuts and seed-tree harvests, likely reflect the scarcity of certain habitat elements (e.g., large-diameter trees and snags, deep leaf litter, continuous canopy) needed for these avian species' nesting and foraging requirements (Porneluzi et al., 2020; Poulin et al., 2008).

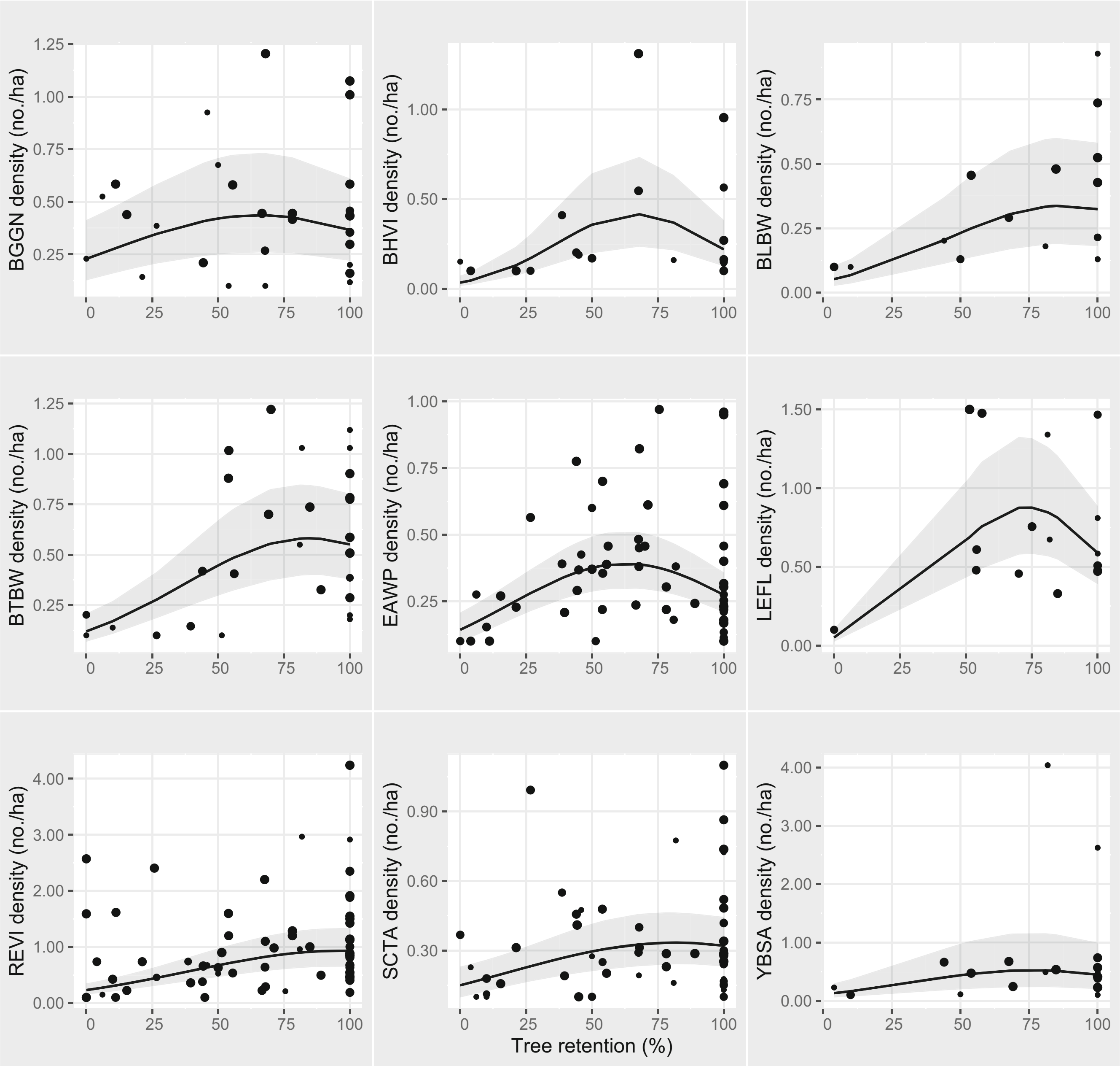

FIGURE 3 Relationships for mature-forest species in which the quadratic model was the best fit. BGGN, blue-gray gnatcatcher; BHVI, blue-headed vireo; BLBW, blackburnian warbler; BTBW, black-throated blue warbler; EAWP, eastern wood-pewee; LEFL, least flycatcher; REVI, red-eyed vireo; SCTA, scarlet tanager; YBSA, yellow-bellied sapsucker.

We found mature-forest species also differed in their responses to canopy reduction. Some species (such as the ovenbird and brown creeper) had lower densities in moderately harvested stands relative to unharvested forests, but the majority of the species had relatively higher or equal densities in 40%–70% tree retention compared with unharvested stands. Individual studies have also documented that several mature-forest bird species had high abundance after moderate harvests (i.e., shelterwoods), such as red-eyed vireos in Missouri (Annand & Thompson, 1997), eastern wood peewees in Arkansas (Perry et al., 2018), cerulean warblers in the central Appalachians (Sheehan et al., 2014), and black-throated blue warblers in New Hampshire (King & DeGraaf, 2000). These species may have ecological preferences that align with canopy gaps and increased understory vegetation density found in stands with 40%–70% tree retention in our study area; for instance, black-throated blue warblers prefer dense understory vegetation for nesting (Holway, 1991). In contrast, species such as ovenbirds and brown creepers promptly decline in abundance in response to any amount of tree harvesting, as found in other studies (Holmes et al., 2004, 2012; Tozer et al., 2010).

TABLE 4 Mature-forest bird density and community-wide conservation scores among categorical silvicultural treatments in eastern North America.

Species	Low-retention harvests	Moderate retention (shelterwood)	High-retention stands
High retention > shelterwood > low retention			
Acadian flycatcher	0.15^{a} (0.09–0.25)	0.27^{b} (0.16–0.46)	0.35^{c} (0.21–0.58)
Blackburnian warbler	0.05^{a} (0.03–0.10)	0.25^{b} (0.13–0.47)	0.32^{c} (0.17–0.61)
Brown creeper	0.10^{a} (0.05–0.17)	0.18^{b} (0.12–0.27)	0.30^{c} (0.22–0.40)
Black-throated blue warbler	0.15^{a} (0.09–0.28)	0.41^{b} (0.26–0.63)	0.57^{c} (0.38–0.86)
Black-throated green warbler	0.17^{a} (0.10–0.30)	0.38^{b} (0.23–0.64)	0.69^{c} (0.43–1.12)
Ovenbird	0.15^{a} (0.10–0.24)	0.41^{b} (0.27–0.63)	0.95^{c} (0.64–1.41)
Red-eyed vireo	0.36^{a} (0.24–0.53)	0.76^{b} (0.52–1.11)	0.92^{c} (0.64–1.31)
High retention > shelterwood = low retention			
Scarlet tanager	0.24^{a} (0.17–0.35)	0.25^{a} (0.17–0.36)	0.32^{b} (0.23–0.45)
High retention > low retention, high retention = shelterwood, shelterwood = low retention			
Red-breasted nuthatch	0.14^{a} (0.08–0.26)	0.18^{ab} (0.11–0.31)	0.19^{b} (0.11–0.33)
High retention = shelterwood > low retention			
Hermit thrush	0.10^{a} (0.04–0.29)	0.39^{b} (0.22–0.68)	0.58^{b} (0.36–0.91)
Wood thrush	0.18^{a} (0.13–0.27)	0.28^{b} (0.19–0.40)	0.26^{b} (0.19–0.37)
Yellow-bellied sapsucker	0.14^{a} (0.06–0.32)	0.49^{b} (0.22–1.13)	0.46^{b} (0.20–1.04)
Shelterwood > high retention > low retention			
Least flycatcher	0.05^{a} (0.03–0.10)	0.90^{c} (0.58–1.39)	0.62^{b} (0.42–0.93)
Yellow-rumped warbler	0.18^{a} (0.10–0.32)	0.36^{c} (0.22–0.58)	0.28^{b} (0.17–0.44)
Shelterwood > high retention = low retention			
American redstart	0.30^{a} (0.18–0.49)	0.53^{b} (0.35–0.82)	0.38^{a} (0.26–0.55)
Eastern wood-pewee	0.24^{a} (0.17–0.32)	0.41^{b} (0.31–0.54)	0.28^{a} (0.21–0.36)
Shelterwood > high retention, shelterwood = low retention, high retention = low retention			
Rose-breasted grosbeak	0.30^{ab} (0.17–0.54)	0.36^{b} (0.22–0.60)	0.24^{a} (0.15–0.39)
Shelterwood > low retention, shelterwood = high retention, high retention = low retention			
Blue-headed vireo	0.12^{a} (0.06–0.28)	0.39^{b} (0.20–0.76)	0.24^{ab} (0.14–0.41)
High retention = shelterwood = low retention			
Blue-gray gnatcatcher	0.38^{a} (0.22–0.63)	0.39^{a} (0.22–0.69)	0.37^{a} (0.23–0.60)
Great-crested flycatcher	0.19^{a} (0.13–0.27)	0.23^{a} (0.17–0.30)	0.18^{a} (0.15–0.23)
Hooded warbler	0.31^{a} (0.17–0.56)	0.24^{a} (0.12–0.46)	0.27^{a} (0.18–0.42)
Veery	0.42^{a} (0.24–0.75)	0.40^{a} (0.25–0.63)	0.35^{a} (0.23–0.55)
Community-wide conservation scores			
BCR 13	205 (199–210)	209 (201–213)	189 (182–194)
BCR 14	211 (204–215)	223 (215–227)	206 (199–212)
BCR 28	232 (227–238)	236 (228–240)	215 (206–219)
BCR 30	225 (219–229)	228 (220–232)	211 (201–216)

Note: Presented are model-predicted mean density estimates per bird species and per category, with 95% confidence intervals in parentheses. Low-retention harvests include any stands with basal areas less than shelterwoods, while high-retention forests include any stands with basal areas greater than shelterwoods (Appendix S1: Figure S2). For individual bird species, “>” classifies statistically significant ($p < 0.05$) differences in bird density between treatment types, while “=” denotes nonsignificance. Estimates with shared superscript letters are not statistically different. For community conservation scores, presented are the median and 95% confidence intervals of the jackknife analysis at 27%, 61%, and 91% tree retention (5.6, 15.7, and 24.7 m^2/ha, respectively).

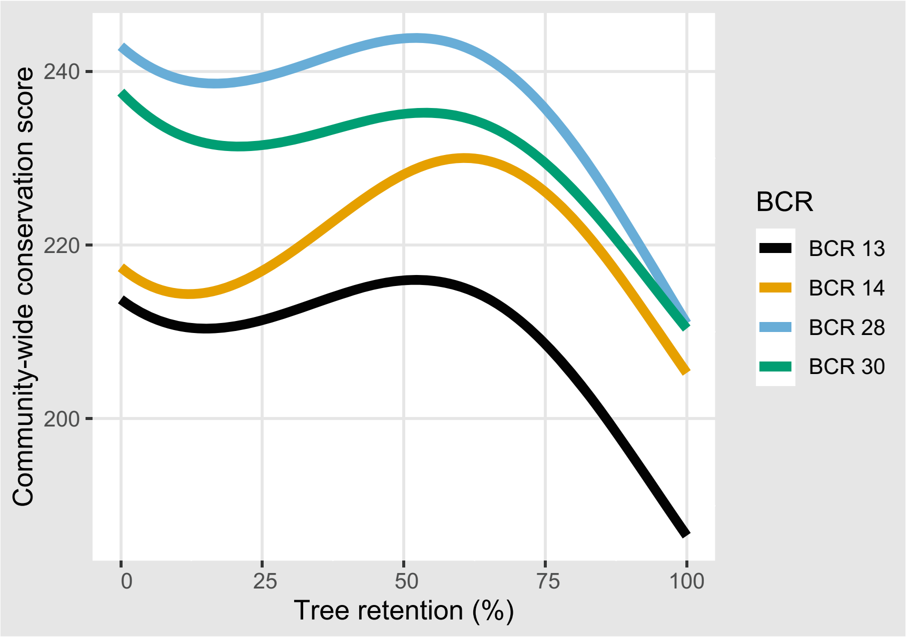

FIGURE 4 Community-wide conservation scores as a function of tree retention for Bird Conservation Regions (BCRs) 13, 14, 28, and 30.

We observed six putative mature-forest species (American redstart, great-crested flycatcher, hooded warbler, veery, yellow-rumped warbler, and rose-breasted grosbeak) that were not influenced by the continuous variable of tree retention. Some of these species appear to have broad ecological requirements with respect to canopy closure and are more influenced by other forest characteristics besides percent tree retention and basal area, such as the density of shrubs, saplings, or midstory trees (Hunt, 1996; Sheehan et al., 2014; Sherry et al., 2020; Wyatt & Francis, 2020). Additionally, for some species, the effect of study explained a large percentage of the variation in our meta-analysis models, which suggests that mature-forest species densities are also related to other site- and study-specific factors that we did not examine in our analyses. Potentially influential site-specific factors include the characteristics of the reference unmanaged stands, some of which may have had more complex vegetation structure due to past natural or anthropogenic disturbance or were otherwise approximating late-seral, old-growth forest conditions (Faccio, 2003; Kelty & D'Amato, 2006; Nyland, 1992). Past disturbance, as well as deer browsing, site soil class, or other factors at sites, could have muddled potential differences between reference and treated forest stands in some studies (Briggs & Lemin, 1994; Parker et al., 2020; Rushing et al., 2020).

Our findings of mature-forest bird densities among discrete silvicultural categories were similar to our results using a continuous variable of tree retention in the models, although there were some differences between the two analytical approaches. Species like black-throated green warbler and Acadian flycatcher exhibited negative relationships with the continuous variable of tree retention and also had the highest densities in unmanaged and lightly thinned (high retention) stands. Additionally, species such as yellow-bellied sapsucker and eastern wood-pewee were best fit with a quadratic relationship with tree retention and had equal or higher densities in shelterwoods (moderate retention) compared with high-retention stands. In contrast, red-eyed vireo and black-throated blue warbler had their highest densities in high-retention stands, then shelterwoods, then low-retention stands, but were still best fit with a quadratic relationship. Varied results between the categorical versus continuous tree retention models were likely due to the basal area classifications of shelterwoods we used in our categorical variable (Akresh et al., 2021). As well, small sample sizes within treatments for some species may have influenced the categorical model results (e.g., <3 samples of densities for blackburnian warbler, brown creeper, hermit thrush, least flycatcher, red-breasted nuthatch, yellow-bellied sapsucker, and yellow-rumped warbler in low-retention stands).

Our community-wide analyses incorporated both individual mature-forest species and shrubland birds, and community-wide conservation scores were highest in stands with 0%–70% tree retention in most regions. Specifically, conservation scores had a peak in low-retention stands (0%–10%) across all BCRs, likely because shrubland bird densities were high in low-retention stands (Akresh et al., 2021) and many

TABLE 5 Mature-forest and shrubland species (Akresh et al., 2021) included in the community-wide conservation scores and their relationships with tree retention during the nesting season.

Species	Guild/overall relationship with tree retention	Best model with tree retention
Acadian flycatcher	Mature-forest/positive	Linear
Brown creeper	Mature-forest/positive	Linear
Black-throated green warbler	Mature-forest/positive	Linear
Hermit thrush	Mature-forest/positive	Linear
Ovenbird	Mature-forest/positive	Linear
Red-breasted nuthatch	Mature-forest/positive	Linear
Wood thrush	Mature-forest/positive	Linear
Blue-gray gnatcatcher	Mature-forest/positive	Quadratic
Blue-headed vireo	Mature-forest/positive	Quadratic
Blackburnian warbler	Mature-forest/positive	Quadratic
Black-throated blue warbler	Mature-forest/positive	Quadratic
Eastern wood-pewee	Mature-forest/positive	Quadratic
Least flycatcher	Mature-forest/positive	Quadratic
Red-eyed vireo	Mature-forest/positive	Quadratic
Scarlet tanager	Mature-forest/positive	Quadratic
Yellow-bellied sapsucker	Mature-forest/positive	Quadratic
American goldfinch	Shrubland/negative	Linear
Brown-headed cowbird	Shrubland/negative	Linear
Cedar waxwing	Shrubland/negative	Linear
Common yellowthroat	Shrubland/negative	Linear
Eastern towhee	Shrubland/negative	Linear
Magnolia warbler	Shrubland/negative	Linear
Northern cardinal	Shrubland/negative	Linear
Prairie warbler	Shrubland/negative	Linear
Ruby-throated hummingbird	Shrubland/negative	Linear
White-eyed vireo	Shrubland/negative	Linear
White-throated sparrow	Shrubland/negative	Linear
Chestnut-sided warbler	Shrubland/negative	Quadratic
Gray catbird	Shrubland/negative	Quadratic
Indigo bunting	Shrubland/negative	Quadratic
Mourning warbler	Shrubland/negative	Quadratic
Yellow-breasted chat	Shrubland/negative	Quadratic

shrubland bird species had high per-species PIF scores (Dettmers, 2003). Habitat availability for shrubland birds is limited within our study extent (e.g., 6% of northeastern forests) and continues to decline across the eastern United States (King & Schlossberg, 2014). As a result, shrubland birds have relatively small, declining populations and are considered important targets for conservation (Askins, 2001; Litvaitis et al., 1999, 2021), as classified in their PIF conservation scores (Carter et al., 2000). In contrast, mature, unmanaged forest is far more extensive across most of eastern North America (Shifley et al., 2014), with the exception of some regions (Brooks, 2003; Hanberry & Thompson, 2019). Although a few mature-forest avian species are imperiled (King et al., 2006; Rushing et al., 2016), their overall population sizes are greater and population declines less pronounced (Dettmers, 2003; Sauer et al., 2019), resulting in lower community conservation scores on average for unharvested stands of mature forest (King & Schlossberg, 2014).

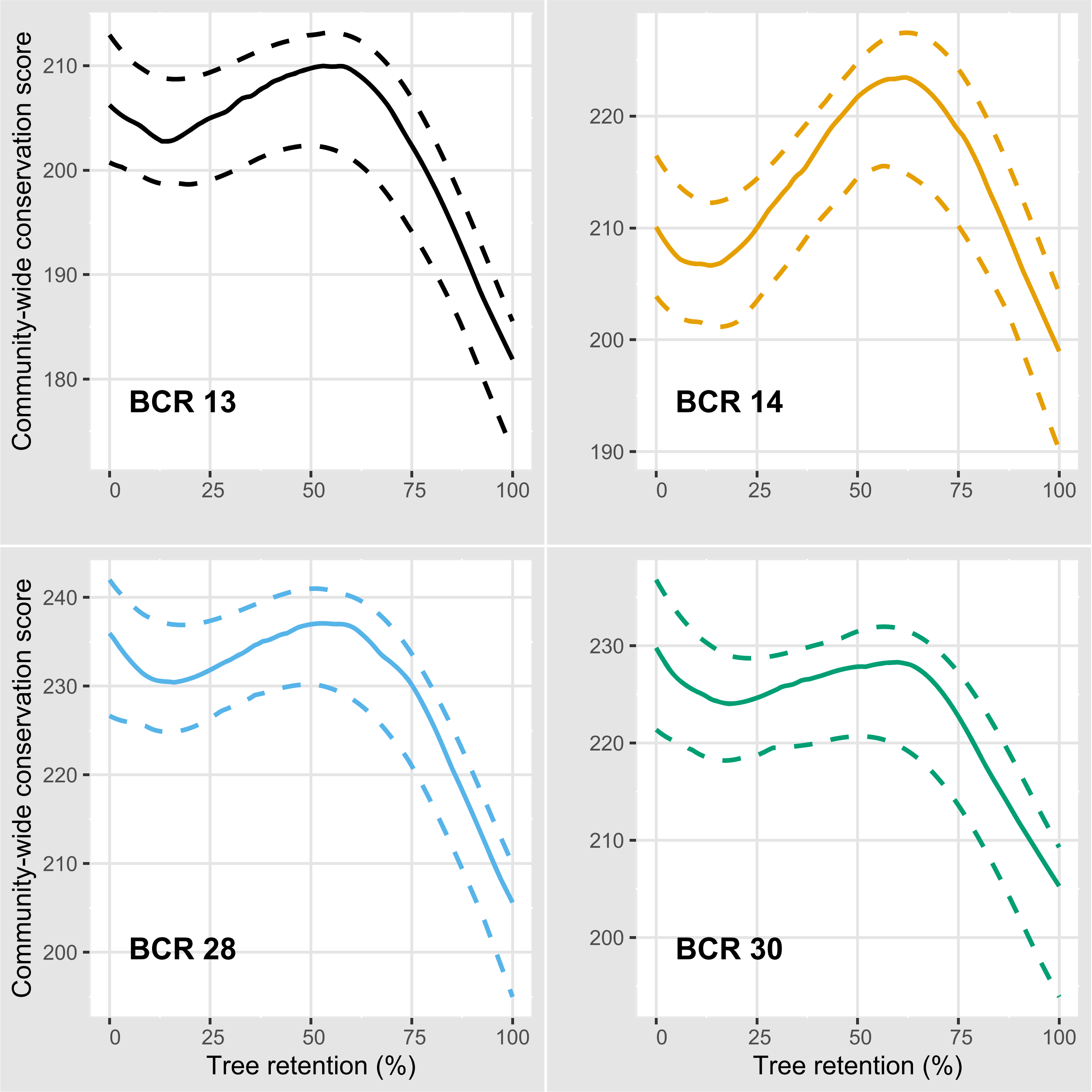

FIGURE 5 The median and 95% confidence intervals of community-wide conservation scores after conducting a jackknife analysis by iteratively removing individual species from the calculations, and then plotting as a function of tree retention. Shown are separate relationships for each Bird Conservation Region (BCR).

The second peak of high community conservation scores between 40% and 70% tree retention was perhaps due to the many mature-forest species and some shrubland species (Akresh et al., 2021), which had quadratic relationships of density with tree retention. Species richness has previously been reported to be highest in partially harvested stands due to both the presence of mature-forest species that tolerate or benefit from some reduction in basal area (and associated increases in understory development) and shrubland bird species that are generalized enough to tolerate the retained tree canopy (King & DeGraaf, 2000). Our analyses go beyond species richness to show partially harvested stands boost community-level conservation values as well. Our results are similar to the findings of Twedt (2020), whose meta-analysis examined studies across North America and observed conservation scores were highest in partially harvested stands of 30%–70% tree retention.

Interestingly, Twedt's (2020) analyses differed from our study by using absolute abundances and all species observed at individual study locations to calculate community-wide conservation scores, yet the results were mostly consistent between our two different analytical approaches and geographic extents.

We found that unharvested and lightly thinned forest stands (70%–100% tree retention) had the lowest community conservation scores across most of the BCRs. These stands do not provide habitat for shrubland birds of conservation concern (Akresh et al., 2021), and we found in our meta-analysis that even some mature-forest species do not reach their peak abundance in unharvested forests in eastern North America. Most forest stands in eastern North America are even-aged, either having regenerated on cleared agricultural land or after historical clearcut harvesting (Moola & Vasseur, 2008; Shifley et al., 2014), and thus are structurally homogeneous and quite young from a forest developmental perspective relative to the precolonial forests that would have contained a range of tree fall gap sizes and multiple age-classes (Dahir & Lorimer, 1996; Ducey et al., 2013; Keeton, 2006). As a result, unmanaged stands within the study sites we examined in our meta-analyses may have exhibited the relatively depauperate conditions typical of self-thinning stands, which generally have the least developed understory layers given high levels of canopy closure (Alaback, 1982; Moore & Vankat, 1986; Runkle, 1981). The lack of dense understory vegetation patches in unharvested stands may have led to absences of nesting and foraging sites for shrub- or midstory avian nesting species (Rankin & Perlut, 2015; Schlossberg et al., 2018). Although biologically mature, late-seral forests may have higher species richness and conservation value for birds, these old-growth stands only represent a tiny fraction of eastern forests (Keeton, 2006) and, as apparent from the studies we reviewed, are not typically subject to tree canopy management. Nevertheless, there is increasing recognition of the potential for ecological silviculture approaches to restore aspects of the structural and compositional conditions found in old-growth forests to second-growth systems (Palik et al., 2020), providing a potential pathway for rapidly increasing the conservation value of these areas for bird species (Thom & Keeton, 2020).

Our community-wide findings are generally consistent with smaller scale, primary studies that examined conservation scores in the eastern United States, which have also noted higher community conservation scores in managed and restored forests compared with closed-canopy forests (Becker et al., 2011; Iglay et al., 2018; Singleton et al., 2013; Wood et al., 2004; although see Norris et al., 2009). Our community-wide results are also consistent with a study in Europe, which found that open forest communities such as clearcuts had higher conservation scores compared with closed-canopy forests and tree plantations (Paquet et al., 2006). To our knowledge, relatively few studies outside of North America have examined community-wide conservation scores in relation to silviculture, warranting more research worldwide.

Our examination of community-wide conservation scores was limited by shrubland and mature-forest bird species for which we could obtain enough data points to test the relationship between tree retention and bird density. When we excluded individual species from calculations of the community-wide conservation scores in our jackknife analysis, there was more ambiguity in which tree retention percentages produced the highest conservation scores between 0% and 70% retention. Results between 0% and 70% tree retention were also slightly different in BCR 14, in which we removed two additional species from the analyses. We therefore caution against suggesting that specific tree retention values between 0% and 70% would be better to conserve the forest–shrubland bird community as a whole. We do note, however, that unharvested stands had the lowest community-wide conservation scores, and this finding was robust even after removing individual species from the analyses. Although we did not include rarer species in our analyses and community scores, most rare passerine species of conservation concern in eastern North American forests reside in open-canopy, early-successional communities, such as the golden-winged warbler and Kirtland's warbler (Donner et al., 2010; McNeil et al., 2020), or are abundant in partially harvested stands, such as cerulean warblers (Sheehan et al., 2014). Therefore, inclusion of rare species in our community conservation index may have increased conservation values in stands that experience moderate to heavy overstory tree removal.

Our study focused only on avian abundance during the nesting period, and both mature-forest and shrubland birds use early-successional, harvested stands extensively during the post-fledging period (Akresh et al., 2009; Chandler et al., 2012; Labbe & King, 2014). More species-specific studies are needed in order to incorporate the post-fledging period into meta-analyses of bird relationships with tree retention (Cox et al., 2014). Our community-wide conservation scores in open-canopy stands may be conservative, considering that most forest-nesting bird species use intensively harvested stands for rearing their young and preparing for migration (Chandler et al., 2012; Marshall et al., 2003), the availability of these shrublands benefits individual birds and populations (Cox et al., 2014; Stoleson, 2013; Vitz & Rodewald, 2006), and we did not incorporate the post-fledging period in our meta-analyses.

We did not examine time since treatment in our analyses, and interactions between tree retention and stand age could have influenced our results for individual mature-forest and shrubland species and the community conservation values. Some mature-forest birds, such as red-eyed vireos, can increase in abundance as low-retention stands age from 0 to 15 years since treatment (Perry et al., 2018). In contrast, shrubland bird species often monotonically decline as treated stands age over time or have a unimodal response during the first 0–20 years since management (Akresh et al., 2015; Keller et al., 2003; Schlossberg & King, 2009). Further research and long-term primary studies on the interactions between basal area and time since treatment across both shrubland and mature-forest bird communities would be useful for better understanding management effects (Lott et al., 2021).

CONCLUSION

Our results indicate that in typical, widespread second-growth forest stands in eastern North America, tree harvesting (to <70% tree retention) is beneficial for most songbird species and overall, will increase the avian conservation value of the forest stands. Given the relative homogeneity of second-growth forests in this region, moderate levels of canopy reduction via variable retention harvests, shelterwood establishment harvests, and irregular shelterwood systems can increase understory vegetation density, which can then increase foraging and nesting opportunities for many mature-forest bird species and allow stands to also be used by many shrubland birds. More intensive timber management (i.e., clearcutting, seed-tree harvests, or removal cuttings in shelterwood harvests) also supports a bird community of high conservation value, by providing open-canopy, dense understory conditions for shrubland birds, which are of high conservation priority regionally. Numerous other threatened and endangered non-avian taxa in our study region also depend on open-canopy habitats created from high-intensity tree harvests, including pollinators and other arthropods (Del Toro et al., 2013; Milam et al., 2022), mammals (Bauer et al., 2022), snakes (Akresh et al., 2017), and vascular plants (Massachusetts Natural Heritage and Endangered Species Program, 2022).

Although our results will help managers understand the trade-offs between habitat enhancement for mature-forest and shrubland bird species, they should not be construed as a blanket recommendation to engage in more intensive forestry. Other taxa should also be considered, such as terrestrial salamanders and other amphibians, which can decline after timber harvests (Semlitsch et al., 2009; Tilghman et al., 2012), as well as other site-, landscape-, and region-specific considerations (Aust & Blinn, 2004; Betts et al., 2007; Bradford & D'Amato, 2012). Some forests, especially biologically mature stands >150 years old, will already have developed important structural characteristics that can enhance habitat conditions for mature-forest birds, without a need for active forest management that targets canopy trees (Haney, 1999; Kirk et al., 2012). Rare species of fungi, invertebrates, and lichen of conservation concern can also be dependent on habitats in late-seral stands (Komonen, 2001; McMullin et al., 2008). We hope our results will help inform ecologically based treatments that allow managers to achieve a balance among forest conditions needed to maintain populations of all native bird species and other taxa that a given site or landscape can potentially support.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Akresh et al., 2022) are available from Harvard Dataverse: https://doi.org/10.7910/DVN/R2ATGU.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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