Forest Ecology and Management 483 (2021) 118730

Contents lists available at ScienceDirect

Forest Ecology and Management

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

A meta-analysis of the effects of tree retention on shrubland birds

Michael E. Akresh[a,b,*], David I. King[c], Casey A. Lott[d,e], Jeffery L. Larkin[d,f], Anthony W. D'Amato[g]

[a] Department of Environmental Conservation, University of Massachusetts Amherst, 204 Holdsworth Hall, Amherst, MA 01003, USA
[b] Department of Environmental Studies, Antioch University New England, 40 Avon St., Keene, NH 03431, USA
[c] U.S. Forest Service Northern Research Station, University of Massachusetts Amherst, 201 Holdsworth Hall, Amherst, MA 01003, USA
[d] Indiana University of Pennsylvania, Indiana, PA 15701, USA
[e] Conservation Science & Data Visualization, Boise, ID 83712, USA
[f] American Bird Conservancy, The Plains, VA 20198, USA
[g] University of Vermont, 204E Aiken Center, Burlington, VT 05405, USA

ARTICLE INFO

Keywords:
Avian
Logging
Review
Silviculture
Tree harvest
Young forest

ABSTRACT

The effects of forest management on native fauna are of key interest to managers and conservationists. Individual studies have expanded our knowledge of management impacts, but meta-analyses of multiple studies are needed to summarize and integrate findings into a more generalizable form. Most meta-analyses on the effects of tree harvesting have focused on mature forest taxa because of concerns for these species; however, early-successional specialists, such as shrubland birds in the eastern United States, are also of key conservation concern. Using data from 34 studies that examined the effects of silvicultural treatments on bird communities, we conducted a meta-analysis to determine the effects of tree retention on a suite of bird species reported to be associated with shrubland habitats within the northeastern United States. Of 21 putative shrubland bird species for which we had sufficient sample sizes for analyses, most (62%) exhibited monotonic declines of density with increasing tree retention, defined as percent basal area or canopy cover retained. Five other species (24%) exhibited quadratic relationships with tree retention. Finally, three additional species (14%) considered to be shrubland birds did not exhibit significant relationships with tree retention. We also calculated density estimates of shrubland birds in three categorical classifications of basal area retention corresponding to common management regimes: regeneration harvests with little retention (clearcut and seed-tree methods), regeneration harvests with moderate retention (shelterwoods), and high retention management regimes (commercial thinning, selection methods, no management). Many of the shrubland species had high densities in clearcuts as well as in stands with low levels (5–25%) of mature tree retention, and some species had equally high densities in stands with moderate tree retention (30–70%), supporting the use of retention forestry approaches, which can provide other benefits associated with mature trees. Overall, our findings provide managers and conservationists with robust, quantitative relationships of shrubland birds with tree retention. Managers can use these quantitative relationships for more detailed planning and evaluation of silvicultural projects, more so than what was feasible using previous findings of shrubland bird responses to discrete silvicultural treatments from disparate studies.

1. Introduction

Terrestrial wildlife communities are influenced by changes in vegetation structure and composition resulting from forest management (e.g., Webb et al., 1977; King and DeGraaf, 2000). Wildlife associated with mature, closed-canopy forests tend to decline in abundance when silvicultural harvests create more open-canopy conditions (Vanderwel et al., 2007; Semlitsch et al., 2009; Kalies et al., 2010; Tilghman et al., 2012). In contrast, other species increase in abundance in forest stands with intermediate levels of overstory tree canopy and understory vegetation density resulting from light- to mid-intensity tree harvests (Sheehan et al., 2014; Perry et al., 2018). Finally, open-canopy, shrubland specialists favor a shrubby, dense understory with few overstory trees, and are typically most abundant after high-intensity tree harvests (Freedman et al., 1981; Baker and Lacki, 1997; Kendrick et al., 2015).

Our understanding of bird and wildlife responses to tree retention is

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* Corresponding author at: Antioch University New England, 40 Avon St., Keene, NH 03431, USA.
E-mail address: makresh@antioch.edu (M.E. Akresh).

https://doi.org/10.1016/j.foreco.2020.118730
Received 17 July 2020; Received in revised form 18 October 2020; Accepted 20 October 2020

derived from individual studies conducted at discrete sites that typically compare abundance between mature closed-canopy forest and a few silvicultural treatments (e.g., Annand and Thompson, 1997; Goodale et al., 2009; Boves et al., 2013), as well as meta-analyses that synthesize effects across sites and treatment intensities (e.g., Schieck and Song, 2006; Vanderwel et al., 2007; Zwolak, 2009; Kalies et al., 2010; Verschuyl et al., 2011; Fontaine and Kennedy, 2012; Tilghman et al., 2012; Fedrowitz et al., 2014; Twedt, 2020). Meta-analyses are highly useful in quantitatively integrating findings across many studies (Arnqvist and Wooster, 1995); however, previous meta-analyses on tree harvesting have mainly focused on mature forest species or species richness and biodiversity (Verschuyl et al., 2011; Fedrowitz et al., 2014; LaManna and Martin, 2017). The focus of meta-analyses on overall biodiversity and closed-canopy forest species under-appreciates early-successional and open-canopy forests and their associated species.

Worldwide, naturally regenerating, early-successional habitats are under-valued from a conservation perspective (Swanson et al., 2011), and few meta-analyses on the effects of silviculture have focused on these early-successional wildlife communities. Most management regimes still emphasize rapid development towards closed canopy forest conditions, even though prolonged periods of open forest conditions following disturbance are increasingly being recognized as ecologically important (Donato et al., 2012; Hanberry and Thompson, 2019; Palik et al., 2020). Several regions, such as eastern North America, contain a higher proportion of early-successional, shrubland bird specialists that are threatened and in need of conservation action and targeted management compared to mature forest species (Dettmers, 2003; King and Schlossberg, 2014).

Eastern North America is an exception to the worldwide focus on mature forests, as the vulnerability of open-canopy habitats and shrubland birds in this region has received more emphasis in the past few decades (Hunter et al., 2001; Thompson and DeGraaf, 2001). Historically, these open habitats were created and maintained by natural disturbances, including beaver activity and associated flooding, as well as Native American burning regimes before European colonization (Askins, 2000). In the 19th and 20th centuries, abandoned agricultural fields also became a source of shrubland habitat (Lorimer and White, 2003). However, fire and flooding are currently suppressed, and abandoned fields have grown into middle-aged forests that are less susceptible to wind throw compared to the original old-growth forest stands (Litvaitis, 2003; Nowacki and Abrams, 2008; Shifley et al., 2014). Correspondingly, an increasingly large body of research has been generated on the effects of forest management to create habitat for birds that use young seral stages in eastern North America (King et al., 2011a; King and Schlossberg, 2014), but variability among sites, treatments, survey methods, and species compositions limit the general applicability of individual studies. Studies have found that shrubland birds decline in abundance in stands with increased tree basal area or canopy cover, although the strength of this relationship may differ among species and locales (Annand and Thompson, 1997; King and DeGraaf, 2000; Vanderwel et al., 2007; Smetzer et al., 2014). Furthermore, most studies analyze bird community response as a function of discrete management categories, whereas changes in bird community composition are more accurately characterized along a gradient of tree retention (Annand and Thompson, 1997; Vanderwel et al., 2007; Twedt, 2020). Thus, there is a great need for synthesized information to provide management guidance on the effects of silvicultural harvests on shrubland birds.

We conducted a meta-analysis on shrubland birds of the northeastern United States, to provide a quantitative assessment of species-specific responses to tree retention levels along a gradient of stand conditions, from clearcut harvests to unmanaged forest. Since information on the effects of discrete silvicultural prescriptions are also useful for planning, communication, and comparison with other studies, we also examined shrubland bird densities as a function of three common management regimes: regeneration harvests with low retention (clearcut and seed-tree methods), regeneration harvests with moderate retention (shelterwoods), and lastly, high retention management regimes (commercial thinning, selection methods, no management). Our meta-analysis provides synthesized information to forest managers on how shrubland bird densities respond to tree harvesting practices, both along a continuous gradient of tree removal and at discrete intervals. Managers can use this information in the course of their planning and evaluation activities to understand the potential impact of proposed or planned practices on shrubland species at any given retention level in a forest stand.

2. Methods

2.1. Literature search

We searched the literature for articles pertaining to the effects of tree harvesting on breeding shrubland birds in eastern North America. In May-August 2018, we searched Google Scholar and Web of Science databases, 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”, with some additional searches also including “shrubland”, “young forest”, “early-successional”, or “eastern United States” (Lott et al., 2019). We also used backward and forward ‘snowballing’ techniques to search for suitable studies (Wohlin, 2014). For instance, we examined article ‘Cited by’ lists in Google Scholar, as well as reference lists within studies, including reference lists from similar meta-analyses (Vanderwel et al., 2007; Verschuyl et al., 2011; Fontaine and Kennedy, 2012). We searched for any relevant peer-reviewed publications, unpublished theses and dissertations, and government technical reports. After reviewing manuscript titles and/or abstracts on search engines, we downloaded a total of 105 manuscripts to examine further.

2.2. Inclusion criteria

We further screened the potential studies using a number of inclusion criteria. Given that we were primarily interested in examining relationships of shrubland birds of northeastern North America, we only included studies that were conducted in southeastern Canada or the eastern United States, including USFS region 8, which extends from Texas and Oklahoma east to Florida and Virginia, and region 9, which extends from Missouri to Minnesota east to Delaware and Maine. While some eastern shrubland bird ranges extend to western North America or north into the boreal forest, examining basal area relationships for shrubland birds in forest types outside of eastern North America was beyond the scope of our study. To be included, studies needed to present either bird density estimates, or abundance data that could be standardized by unit area, for at least two northeastern shrubland bird species of interest, defined as bird species listed in Schlossberg and King (2007). Consistent with similar meta-analyses (Vanderwel et al., 2007; Kalies et al., 2010), we did not include single-species studies, which may have had different survey methods (e.g., mapping color-banded birds) and could have introduced publication bias into our study (Gurevitch and Hedges, 1999).

We included studies with a variety of different tree harvests, including single-tree selection, tree thinning, shelterwood, retention

Table 1
Studies included in the meta-analysis examining tree retention levels and shrubland bird abundance in Eastern North America.

Study	Location	Survey type	Survey area	Years since treatment	Retention levels	Forest Type
Annand and Thompson, 1997	MO	10-min Pt Count	unlimited	3 to 6	15, 55, 78, 78, 100	O-H
Atwell et al., 2008	MN	Transects	5 ha	3	50, 100	RP
Baker and Lacki, 1997	KY	12-min Pt Count	50 m	1 to 2	0, 11, 26, 100	O-H
Boardman and Yahner, 1999	PA	5-min Pt Count	30 m	1 to 5	27, 100	NH-M
Doyon et al., 2005	QC	10-min Pt Count	60 m	9 to 12	85, 100	NH-M
Duguid et al., 2016	CT	12-min Pt Count	50 m	1 to 7	44, 100	NH-M
Fink et al., 2006	MO	Spot mapping		3 to 5	10	O-H
Flaspohler et al., 2002	MI	10-min Pt Count	50 m	2 to 10	81, 100	NH
Freedman et al., 1981	NS	Spot mapping		3 to 5	0, 51, 100	NH
Goodale et al., 2009	CT	12-min Pt Count	75 m	1 to 16	40, 89, 100	NH-M
Greenberg et al., 2014	NC	Transects	0.875 ha	0 to 2	39, 100	O-H
Hache et al., 2013	NB	Spot mapping		4	69, 100	NH
Hagan et al., 1997	ME	10-min Pt Count	50 m	1 to 5	10, 100	NH
Harrison and Kilgo, 2004	SC	Transects	50 m	2	0, 100	BH
Heltzel and Leberg, 2006	LA	10-min Pt Count	unlimited	1 to 5	67, 100	BH
Holmes et al., 2012	ON	5-min Pt Count	50 m	5 to 7	54, 56, 70, 100	NH
Holmes et al., 2004	ON	Transects	2 ha	2 to 6	54, 68, 100	NH
Jobes et al., 2004	ON	10-min Pt Count	unlimited	1 to 5	54, 100	NH
Kendrick et al., 2015	MO	Spot mapping		3 to 5	10, 100	O-H
King and DeGraaf, 2000	NH	10-min Pt Count	50 m	3 to 5	4, 68, 100	NH
King et al., 2009	MA	10-min Pt Count	50 m	4 to 7	10	NH
King et al., 2011b	MA	10-min Pt Count	50 m	1 to 4	45, 100	PPSO
Margenau et al., 2018	AL	Spot mapping		2	6, 46, 50, 100	O-H
McDermott and Wood, 2009	WV	10-min Pt Count	50 m	6 to 11	0, 100	NH
Newell and Rodewald, 2012	OH	Transects	200 m long	1 to 3	44, 100	O-H
Perry and Thill, 2013	OK/AR	10-min Pt Count	40 m	5	40, 59, 100	O-H S
Rankin and Perlut, 2015	VT	10-min Pt Count	50 m	1 to 3	82, 100	NH-M
Robinson and Robinson, 1999	IL	6-min Pt Count	50 m	2 to 3	68, 100	NH
Rodewald and Yahner, 2000	PA	10-min Pt Count	50 m	2 to 6	21, 100	O-H
Thatcher, 2007	TN	Spot mapping		1 to 4	71, 100	O-H
Thompson et al., 1992	MO	Transects	500 m × 75 m	1 to 10	10, 100	O-H
Tozer et al., 2010	ON	5-min Pt Count	unlimited	2	75, 100	NH
Wilson et al., 1995	AR	8-min Pt Count	40 m	1 to 14	68, 100	O-H S
Ziehmer, 1993	MO	Transects	50 m	1	76, 100	O-H

Forest type abbreviations: BH = Bottomland Hardwoods, NH = Northern Hardwoods, NH-M = Northern Hardwoods-Mixedwoods, O-H = Oak-Hickory, O-H S = Mixed Oak-Hickory Shortleaf Pine, PPSO = Pitch Pine-Scrub Oak, RP = Red Pine.

harvest, even-aged reproduction (EAR), seed-tree, and clearcuts. We also included studies with group selection cuts (e.g., Robinson and Robinson, 1999; Holmes et al., 2004), as long as they were < 0.5 ha (range $= 0.05–0.4$ ha), because openings of this size would be interspersed throughout a stand. We did not include studies with group selection cuts between 0.5 and 1 ha, as we were often uncertain of the proportion of bird surveys that were conducted within these larger openings or in the adjacent, unharvested forest. We included studies that surveyed birds in clearcuts if the treated stands were > 1 ha, as clearcuts < 1 ha may have lower abundance due to patch size (Chandler et al., 2009; Shake et al., 2012; Roberts and King, 2017).

We only included studies that examined bird abundance in harvested stands < 16 years since treatment, as most shrubland birds typically decline in abundance in stands older than 15–20 years (Schlossberg and King, 2009). All included studies had at least some managed stands between 0 and 10 years since treatment (Table 1). We did not analyze time since treatment because studies often present averaged bird abundances across a range of stands with varying years since treatment. Furthermore, we could not assign a year since treatment value for abundance of birds in mature forest stands. Relationships with years since treatment have been reported elsewhere in other studies (Keller et al., 2003; Perry and Thill, 2013), including at least one meta-analysis (Schlossberg and King, 2009). We excluded studies that had canopy cover loss due to fire or other natural disturbances, and studies in tree plantations, which have inherently different management regimes than naturally regenerating forests (Iglay et al., 2018).

Almost all the studies that we included in our analysis contained information on the forest characteristics in control and treated stands, such that we could determine the tree retention levels in the treated stands (Vanderwel et al., 2007). Within each study, we primarily used the ratio of the mean basal area of treated stands versus the control mature forest stands to compute the percent tree retention level in the treated stands. All mature forest stands were classified as having 100% tree retention. The percent tree retention values were highly correlated with basal area values ($n = 51$, $r = 0.93$; Appendix A: Fig. A.1a). If the study omitted basal areas, we used percent canopy cover to determine the tree retention level, or in rare cases, we used other quantifiable metrics (Vanderwel et al., 2007). Canopy cover values were also highly correlated with percent tree retention ($n = 36$, $r = 0.86$; Appendix A: Fig. A.1b). As an exception, we also included studies in clearcuts ($n = 7$) which did not have vegetation and/or bird abundance data in both treated areas and in unmanaged forest stands (e.g., Thompson et al., 1992; King et al., 2009), because sample sizes for this treatment type were limited. If the study did not mention any residual trees in the clearcut stands, we assigned a 0% retention level. Alternatively, if the study mentioned that the clearcuts contained small numbers of residual trees, we assigned a 10% tree retention level (which was approximately the mean tree retention level for studies with clearcuts that had basal area data).

Meta-analysis studies can have bias because of the 'file drawer effect,' in which proportionally more published papers that contain significant results are included in the analysis, compared to unpublished

Table 2

Classifications of shelterwood treatments, given the residual basal area and forest type. We used these shelterwood classifications when analyzing bird densities among discrete treatment categories.

Forest type	Shelterwood Basal Area (m^2/ha)	Sources
Northern hardwoods	6.9–18.4	Leak et al., 2014
Oak-hickory (central hardwoods)	13.8–20.7	Gingrich, 1971; Johnson et al., 2009
Northern hardwoods-mixedwoods	6.9–18.4	Leak et al., 2014
Pitch pine-scrub oak	4.6–11.5	New Jersey Pinelands Commission, 2006
Bottomland hardwoods	11.5–18.4	Gilmore and Palik, 2006
Mixed oak-hickory shortleaf pine	9.2–18.4	Larsen et al., 2010; Mahaffey and Evans, 2016
Red pine	9.2–18.4	Kabrick et al., 2007

studies that may lack significant results (Arnqvist and Wooster, 1995; Gurevitch and Hedges, 1999). We do not foresee a 'file drawer effect' in our meta-analysis, as we included both published manuscripts and unpublished theses. Additionally, forest retention studies are readily published irrespective of significant differences in bird abundance between control and treatment stands because lack of significant results are equally useful to managers and conservationists (e.g., Weakland et al., 2002; Otto and Roloff, 2012). Furthermore, all of the included studies examined the effects of forest retention on multiple bird species in a community-based approach and studies included species-level data regardless of significant differences between control and treated stands. We did not examine if effect sizes in our study were biased (Gurevitch and Hedges, 1999) because we were not directly examining effect sizes in our analyses (see statistical analysis below). Regardless, we have no reason to believe publication bias would occur in our type of study (Kalies et al., 2010; Fontaine and Kennedy, 2012).

2.3. *Data extraction*

For each study, we recorded the study's location, survey method, area of the forest stands, forest type, shrubland bird species, raw mean abundance or density and their standard errors (SEs) for each species in mature forest and treated sites, time since treatment for treated sites, and values of tree retention (mean basal area, canopy cover, and/or other metrics). Most studies had data presented in tables, but for a handful of studies we used Web Plot Digitizer Version 4.1 (Rohatgi, 2018) to obtain bird and/or tree retention data from figures. The majority of studies (68%) had bird abundance data in unmanaged control stands and in treated stands with just one level of tree retention. A smaller number of studies had unmanaged stands and treatment stands with multiple tree retention levels ($n = 9$, 26%), and a few studies ($n = 2$, 6%) only had data from clearcuts (Table 1). In a given study, we included the abundance or density of a given shrubland bird species if the species had an abundance > 0 in either treated or mature stands.

After recording the raw mean abundance or density and their standard errors in mature forest and harvested stands for each species within a study, we standardized all avian data to the number of birds/ha. Some studies did not have density data, but instead presented mean abundance per point count. For these data, we recorded the point count circle radius (e.g., 40 m, 50 m, 75 m), and divided the mean abundance by the circle area to convert the data to a standardized density estimate. Four studies used unlimited-distance point counts and for these studies we assumed a 75 m radius to obtain standardized density values (i.e., abundance values per point divided by 1.77). We used a 75 m radius for these unlimited-distance counts because detection probability of most species likely declines past 50 m (Schieck, 1997; Reidy et al., 2011; Newell et al., 2013), and density values standardized by a 75 m radius appeared to be more reasonable and similar to estimates from other studies, in comparison with standardizing with a 100 m radius (dividing abundance values by 3.14).

2.4. *Statistical analysis*

We conducted a regression-type meta-analysis (Schlossberg and King, 2009), using primary data of mean densities of shrubland birds recorded in forest stands with different tree retention levels, rather than using effect sizes, response ratios, or relative abundance indices in our analyses (Hedges et al., 1999; Kalies et al., 2010; Tilghman et al., 2012). Common meta-analytical approaches using effect sizes and metrics such as Hedges' d or Cohen's d are calculated with sample sizes and standard deviations (Hedges et al., 1999), yet many relevant studies did not present these data. Moreover, determining the true sample size in forest biodiversity studies is difficult (Hurlbert, 1984; Spake and Doncaster, 2017), because bird surveys at point or transect locations were often conducted multiple times within a year and among years, and were often replicated within the same stand or forestry block. To circumvent the lack of sample sizes and standard deviations, previous studies on the effects of retention forestry on wildlife have computed meta-analyses with relative abundance indices or response ratios, rather than using effect sizes (Vanderwel et al., 2007; Kalies et al., 2010; Tilghman et al., 2012). However, response ratios were not viable for our study because shrubland birds often have negligible abundance in mature forest stands; therefore, treated stands have unmeasurable relative increases in abundance compared to control stands. Moreover, clearcut stands could not be defined as the baseline/control retention level, because most relevant studies in the literature did not examine bird abundance in clearcut and partially harvested stands, but rather compared abundance in harvested stands with mature forest controls.

We therefore chose to examine standardized mean density data for separate tree retention levels in each study, account for variation among studies using mixed-effects models (Gurevitch and Hedges, 1999), and use the standard errors of bird density to weight the data in our regression analyses (Vanderwel et al., 2007). Our approach was a viable alternative because we effectively standardized the density data among studies, and most studies included standard errors for each mean density estimate per species. To compute a weight for each bird density data point, we divided the SE by the mean density, and then standardized this weight to a value ranging between 1 and 2 (multiplying by -1 and adding 2 to all SE/mean values; Vanderwel et al., 2007). As a result, in our regression analyses, data with higher weights had relatively smaller standard errors compared to data with lower weights. In some tree retention levels within studies, mean bird densities were 0, and we could therefore not compute a real-number SE/mean weight for these data. For these 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). We also chose to include data from studies that did not present standard errors, although this was a small subset ($n = 4$, 12%) of the total included studies. For these studies that lacked standard errors, we set each bird density value to a weight of 1, the lowest weight for a sample in our analyses, given that we were uncertain of the precision of the data from these studies.

2.4.1. Continuous effect of tree retention analysis. We fit Generalized Linear Mixed Models (GLMM) separately for each species with at least

Table 3
Model comparisons of a null, linear, or quadratic relationship between tree retention and bird density for each shrubland species, fit with Gamma distributions in Generalized Linear Mixed Models. Models were compared using values of Akaike's Information Criterion corrected for small sample sizes (AIC_c). For each species, we defined the top model as the model with the lowest AIC_c value, if the difference in AIC_c from the top model to the next highest supported model (ΔAIC_c) was > 2. If multiple models were < 2 ΔAIC_c, indicating similar support, we defined the simplest model (i.e., Null or Linear) as the top model.

Species	ΔAIC_c Null	ΔAIC_c Linear	ΔAIC_c Quad	Top Simplest Model
Black-and-white warbler (*Mniotilta varia*)	0.72	0.77	0	Null
Dark-eyed junco (*Junco hyemalis*)	0.00	2.96	3.84	Null
Yellow-billed cuckoo (*Coccyzus americanus*)	0.00	0.80	5.45	Null
American goldfinch (*Spinus tristis*)	11.2	0.00	4.11	Linear
American robin (*Turdus migratorius*)	6.74	0.018	0.00	Linear
Brown-headed cowbird (*Molothrus ater*)	52.1	0.26	0.00	Linear
Carolina wren (*Thryothorus ludovicianus*)	4.40	1.74	0.00	Linear
Cedar waxwing (*Bombycilla cedrorum*)	29.9	0.00	1.09	Linear
Common yellowthroat (*Geothlypis trichas*)	77.9	0.00	1.26	Linear
Eastern towhee (*Pipilo erythrophthalmus*)	87.4	0.00	2.24	Linear
Magnolia warbler (*Setophaga magnolia*)	7.86	0.00	1.20	Linear
Northern cardinal (*Cardinalis cardinalis*)	8.23	0.00	2.81	Linear
Prairie warbler (*Setophaga discolor*)	50.8	0.00	2.97	Linear
Ruby-throated hummingbird (*Archilochus colubris*)	20.8	0.00	2.54	Linear
White-eyed vireo (*Vireo griseus*)	21.5	0.00	0.91	Linear
White-throated sparrow (*Zonotrichia albicollis*)	35.2	0.82	0.00	Linear
Chestnut-sided warbler (*Setophaga pensylvanica*)	80.4	7.14	0.00	Quadratic
Gray catbird (*Dumetella carolinensis*)	27.3	5.56	0.00	Quadratic
Indigo bunting (*Passerina cyanea*)	121.5	19.5	0.00	Quadratic
Mourning warbler (*Geothlypis philadelphia*)	46.0	23.9	0.00	Quadratic
Yellow-breasted chat (*Icteria virens*)	92.0	15.1	0.00	Quadratic

15 data points. We used bird density as the response variable, the percentage of trees retained as the main, continuous predictor variable, and included a random effect of study. The random effect accounted for different sampling methods and survey designs among studies, while also accounting for interdependence of data points in studies with multiple levels of tree retention (Fontaine and Kennedy, 2012). We used weighted regression models, in which each data point was weighted by the computed weight values described above. We fit the models using Gamma distributions with a log link, because the density data were non-negative, non-integers, and were often right-skewed (Bolker, 2008). We added a small number of 0.1 to all bird densities in order to be able to fit data values of 0 to Gamma distributions. Exploratory tests examining residual mean square errors, mean absolute errors, and figures with predicted curves and observed values showed that adding 0.1 to the data provided good model fits for the various species compared to adding a small value of 0.01, 0.001, or 0.0001 (Kalies et al., 2010).

We ran three models for each species: a null model depicting constant density (without the predictor variable), a model with a linear predictor of tree retention, and a model with a quadratic and linear predictor of tree retention. We examined models with quadratic relationships because we assumed there might be more complex relationships for some species based on the findings of prior studies (Annand and Thompson, 1997). We used an information-theoretic approach to compare the three models for each species, comparing values of Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). For two species, dark-eyed junco and magnolia warbler, one of the three mixed-effect models run per species did not converge, likely because of small sample sizes. For these two species, we compared AIC_c values using simpler, fixed-effect models without the random effect of study. We defined the top model for each species as the model with the lowest AIC_c value, if the difference in AIC_c from the top model to the next highest supported model (ΔAIC_c) was > 2 (Arnold 2010). If there were multiple models within 2 ΔAIC_c values, we chose the most parsimonious model (i.e., the one with the fewest parameters) as our top model in order to avoid extra, uninformative parameters (Arnold, 2010). After model selection, the top mixed model with the random effect converged for all the species, so model parameters and significance values were presented from mixed-effects models.

2.4.2. Discrete treatments analysis. In addition to examining a continuous effect of tree retention, we also were interested in comparing bird densities among discrete, categorical levels of silvicultural treatments. We first assigned each basal area value within a study to a treatment type classification based on forest-type-specific basal area recommendations in the literature for different regeneration methods and management regimes (Table 2). Thus, given the forest type and

Table 4
Sample size (n), the number of studies included, percent of the model variance accounted for by the random effect of study, model parameter estimates (β_0 = intercept, β_1 = linear parameter estimate) and their SEs in parentheses, t values, and p-values for shrubland bird species in which the top model included the linear predictor of tree retention. The percent of the 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). Species are listed in order of the strength of the model, based on the t value.

Species	n	No. studies	% variance	β_0 (SE)	β_1 (SE)	t	p
Common yellowthroat	26	11	0.562	0.336 (0.234)	−2.298 (0.139)	−16.6	<0.001
Eastern towhee	40	17	0.595	0.389 (0.218)	−2.010 (0.139)	−14.5	<0.001
Prairie warbler	28	12	0.472	0.056 (0.257)	−2.377 (0.229)	−10.9	<0.001
Brown-headed cowbird	34	13	0.564	0.216 (0.269)	−1.762 (0.190)	−9.3	<0.001
White-throated sparrow	21	9	0.515	0.559 (0.315)	−2.499 (0.281)	−8.9	<0.001
Cedar waxwing	23	10	0.550	−0.451 (0.224)	−1.180 (0.151)	−7.8	<0.001
White-eyed vireo	19	7	0.384	−0.135 (0.296)	−2.046 (0.317)	−6.5	<0.001
Ruby-throated hummingbird	19	9	0.395	−1.154 (0.169)	−0.991 (0.157)	−6.3	<0.001
American goldfinch	17	8	0.266	−0.525 (0.275)	−1.429 (0.322)	−4.4	<0.001
Magnolia warbler	18	7	0.497	−0.721 (0.248)	−0.733 (0.187)	−3.9	<0.001
Northern cardinal	25	11	0.766	−0.790 (0.378)	−0.708 (0.194)	−3.7	<0.001
American robin	26	11	0.695	−0.683 (0.317)	−0.531 (0.158)	−3.4	0.001
Carolina wren	21	8	0.592	−0.513 (0.376)	−0.628 (0.253)	−2.5	0.013

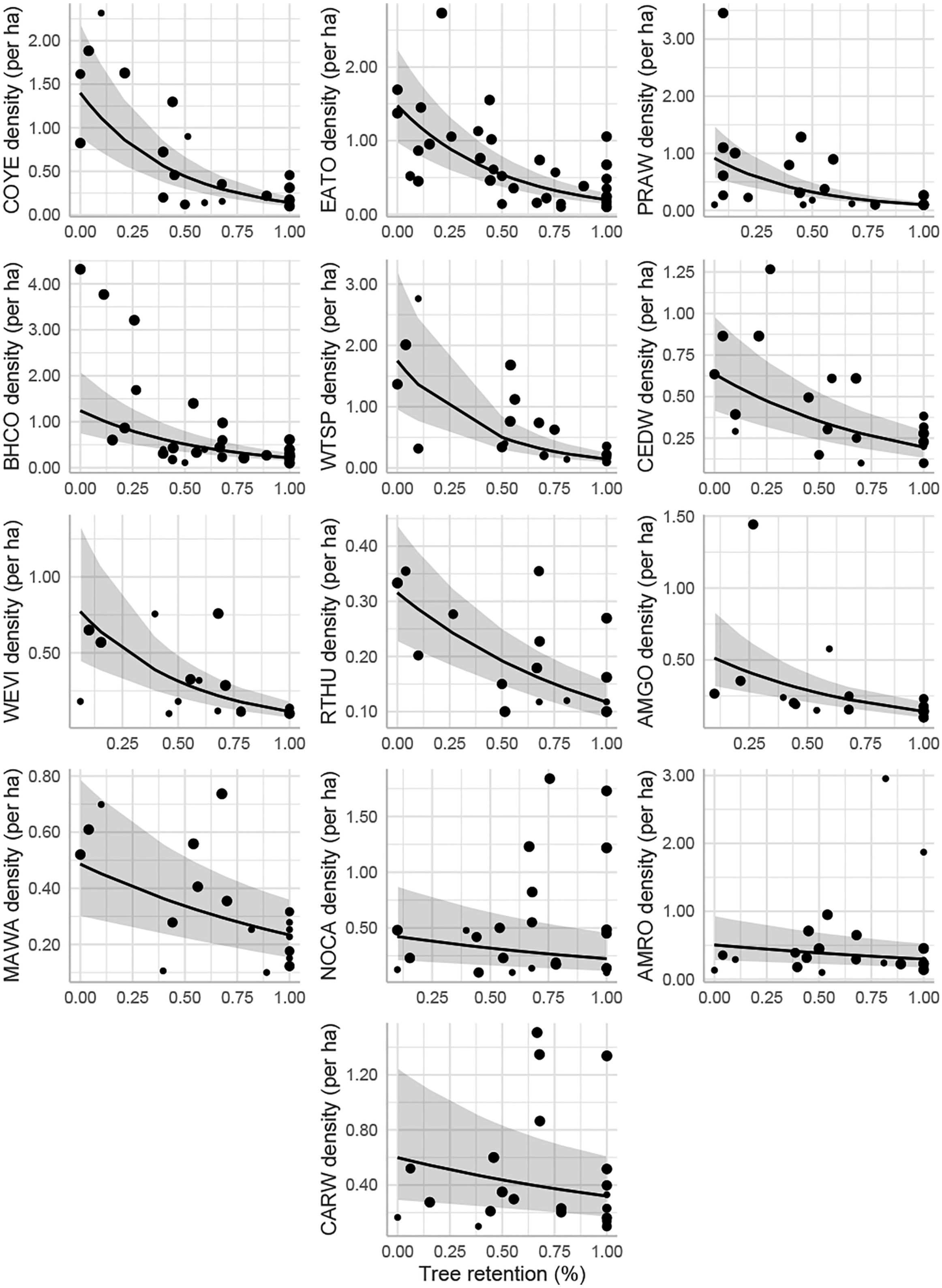

Fig. 1. Effect of tree retention on avian density in forestry stands across the eastern United States, for shrubland species in which the model with a linear predictor was the best fit. Grey lines and shading represent the weighted regression curves from the mixed models (fit to Gamma distributions) and 95% confidence intervals. Points indicate bird density values from individual studies, and larger points indicate that the data point had a higher weight in the model. To fit the models to Gamma distributions, all bird abundances had a small number of 0.1 added to them (so the lowest possible density was 0.1). COYE = common yellowthroat, EATO = eastern towhee, PRAW = prairie warbler, BHCO = brown-headed cowbird, WTSP = white-throated sparrow, CEDW = cedar waxwing, WEVI = white-eyed vireo, RTHU = ruby-throated hummingbird, AMGO = American goldfinch, MAWA = magnolia warbler, NOCA = northern cardinal, AMRO = American robin, CARW = Carolina wren.

Table 5
Shrubland bird species in which the top model also included a quadratic predictor of tree retention. Presented are the sample size (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.

Species	n	No. studies	% variance	β_0 (SE)	β_1 (SE)	β_2 (SE)
Chestnut-sided warbler	42	18	0.399	0.355 (0.260)	0.044 (0.833)	−2.235 (0.689)
Gray catbird	21	9	0.631	−1.361 (0.287)	1.352 (0.731)	−2.023 (0.605)
Indigo bunting	54	23	0.529	−0.102 (0.206)	0.814 (0.627)	−2.637 (0.534)
Mourning warbler	24	10	0.358	−0.956 (0.256)	2.838 (0.804)	−4.222 (0.669)
Yellow-breasted chat	29	11	0.229	0.139 (0.183)	0.371 (0.707)	−2.854 (0.612)

mean basal area of the treatment level within a study, we denoted the treatment level as a regeneration harvest with low retention, regeneration harvest with moderate retention, or a high retention stand. For low retention stands, we binned basal area values lower than shelterwoods (e.g., seed tree systems) with clearcuts, including clearcuts with reserves. Moderate retention stands were defined as shelterwoods (Table 2). High retention was defined as stands with higher basal area values than shelterwoods: unmanaged forest, basal area values consistent with uneven-aged management (e.g., single-tree selection), and commercial thinning regimes. We chose to bin treatment levels into only three categories because of the small sample sizes for some species and to assist in model convergence. Some studies only presented canopy cover and not basal area, and in these cases, we used the percent forest retained value to compute an estimated basal area value, based on a function between known basal areas and percent forest retained observed in other studies (Appendix A: Fig. A.1a). We then used this predicted basal area value to place the treatment level within the study into one of our three binned categories.

We conducted similar weighted Generalized Linear Mixed Models (GLMM), fit to Gamma distributions, separately for each species to examine categorical levels of treatment types. As before, we used bird density as the response variable, and now included a main categorical predictor variable with three retention levels: low, moderate, and high. GLMMs did not converge for five species (American goldfinch, American robin, dark-eyed junco, indigo bunting, and yellow-breasted chat), and we used simpler, fixed-effect models without the random effect of study for these species. All analyses were conducted in the R statistical program version 3.4.3 (R Core Team, 2017), and we used the lme4 and lmerTest packages to conduct mixed-effect models (Bates et al., 2015; Kuznetsova et al., 2016), and the ggeffects package for plotting predictions (Lüdecke, 2018).

3. Results

We included 34 studies in our meta-analysis (Table 1), and acquired adequate data (> 14 density estimates) to fit models for 21 species. Based on AIC$_c$ values, most species (86%) had support for either a monotonic or quadratic relationship between tree retention and bird density (Table 3). The null model was the top model for three species (black-and-white warbler, dark-eyed junco, and yellow-billed cuckoo; see Table 3 for scientific names), and thus there was little support for a relationship between bird density and tree retention for these species (Appendix A: Fig. A.2).

Models with a single linear predictor of tree retention received the most support for 13 species: American goldfinch, American robin,

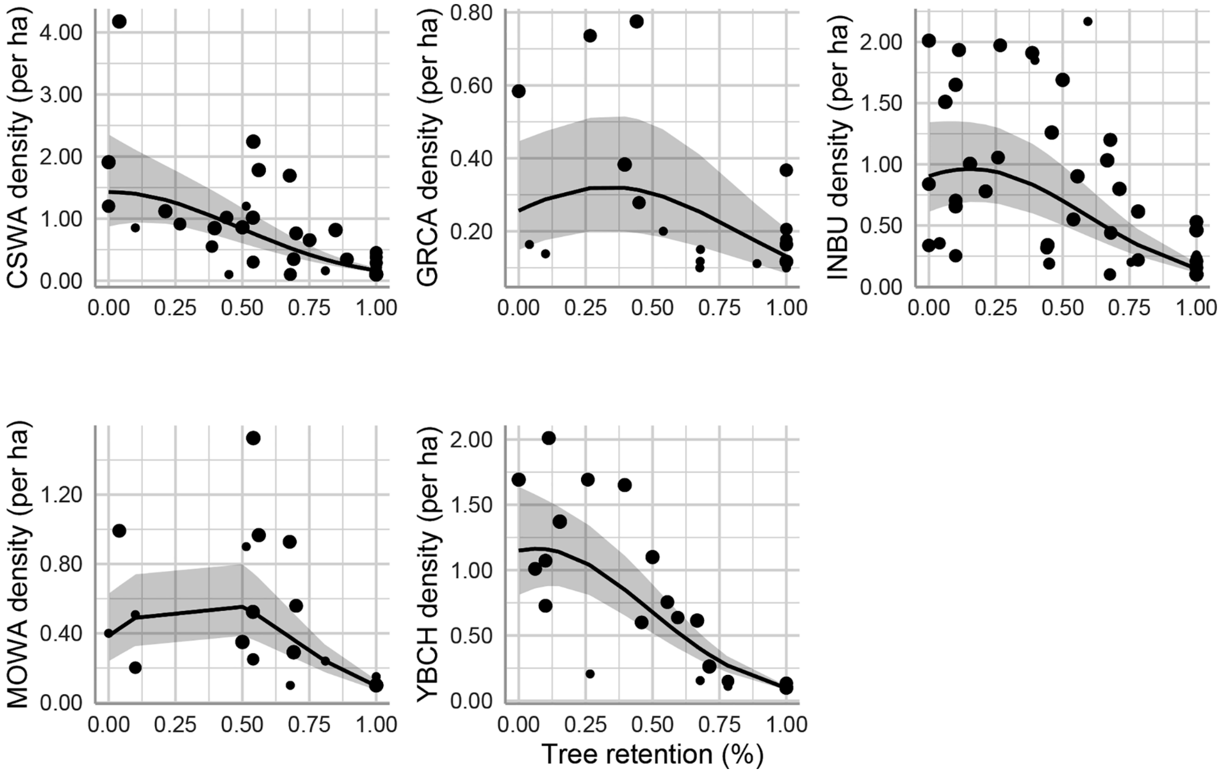

Fig. 2. Effect of tree retention on avian density in forestry stands across the eastern United States, for shrubland species in which the quadratic model was the best fit. CSWA = chestnut-sided warbler, GRCA = grey catbird, INBU = indigo bunting, MOWA = mourning warbler, YBCH = yellow-breasted chat.

Table 6

Effect of treatment type on shrubland bird density in forestry stands across the eastern United States. Values shown represent model-predicted mean density estimates per bird species and per treatment type, with 95% confidence intervals in parentheses. Low-retention harvests include any stands with basal areas less than shelterwoods, while high-retention forest includes any stands with basal areas greater than shelterwoods (see Table 2). Estimates with shared letter superscripts are not statistically different. Presented in the table header, we also used the raw basal area values from treatment levels within studies ($n = 51$), to compute a mean and SE of basal area for each of our discrete categorical treatment bins.

	Low retention harvests 5.6 m^2/ha (SE = 1.8)	Shelterwood (moderate retention) 15.7 m^2/ha (SE = 0.73)	High retention stands 24.7 m^2/ha (SE = 0.93)
Low retention > shelterwood > high retention			
Brown-headed cowbird	0.83^{a} (0.46–1.51)	0.48^{b} (0.28–0.81)	0.25^{c} (0.15–0.40)
Cedar waxwing	0.56^{a} (0.35–0.87)	0.40^{b} (0.26–0.63)	0.19^{c} (0.12–0.29)
Common yellowthroat	1.42^{a} (0.88–2.29)	0.38^{b} (0.24–0.59)	0.14^{c} (0.09–0.22)
Chestnut-sided warbler	1.71^{a} (1.05–2.80)	0.74^{b} (0.49–1.11)	0.19^{c} (0.13–0.28)
Eastern towhee	1.08^{a} (0.72–1.65)	0.41^{b} (0.26–0.64)	0.21^{c} (0.14–0.31)
Ruby-throated hummingbird	0.33^{a} (0.23–0.49)	0.18^{b} (0.13–0.25)	0.12^{c} (0.09–0.16)
White-throated sparrow	1.40^{a} (0.73–2.67)	0.60^{b} (0.31–1.14)	0.14^{c} (0.08–0.26)
Low retention = shelterwood > high retention			
Carolina wren	0.42^{a} (0.22–0.80)	0.74^{a} (0.36–1.52)	0.30^{b} (0.16–0.55)
Gray catbird	0.24^{a} (0.14–0.42)	0.32^{a} (0.20–0.52)	0.14^{b} (0.09–0.22)
Indigo bunting	1.09^{a} (0.77–1.56)	0.86^{a} (0.52–1.42)	0.25^{b} (0.18–0.35)
Magnolia warbler	0.43^{a} (0.27–0.70)	0.36^{a} (0.23–0.56)	0.22^{b} (0.15–0.34)
Mourning warbler	0.48^{a} (0.29–0.80)	0.50^{a} (0.33–0.75)	0.12^{b} (0.08–0.18)
Prairie warbler	0.55^{a} (0.33–0.90)	0.49^{a} (0.26–0.92)	0.11^{b} (0.07–0.18)
White-eyed vireo	0.35^{a} (0.21–0.56)	0.40^{a} (0.25–0.66)	0.11^{b} (0.07–0.17)
Yellow-breasted chat	1.20^{a} (0.78–1.86)	0.67^{a} (0.33–1.36)	0.16^{b} (0.10–0.25)
Shelterwood > high retention, low retention = high retention, low retention = shelterwood			
Northern cardinal	0.34^{ab} (0.16–0.69)	0.35^{a} (0.17–0.69)	0.25^{b} (0.13–0.50)
American goldfinch	0.31^{ab} (0.12–0.82)	0.46^{a} (0.26–0.83)	0.16^{b} (0.10–0.27)
Low retention = shelterwood = high retention			
American robin	0.31^{a} (0.10–0.91)	0.67^{a} (0.33–1.34)	0.38^{a} (0.22–0.66)
Black-and-white warbler	0.44^{a} (0.30–0.63)	0.32^{a} (0.21–0.47)	0.37^{a} (0.26–0.52)
Dark-eyed junco	0.34^{a} (0.15–0.78)	0.20^{a} (0.09–0.45)	0.33^{a} (0.17–0.63)
Yellow-billed cuckoo	0.14^{a} (0.08–0.26)	0.23^{a} (0.12–0.42)	0.17^{a} (0.10–0.30)

brown-headed cowbird, Carolina wren, cedar waxwing, common yellowthroat, eastern towhee, magnolia warbler, northern cardinal, prairie warbler, ruby-throated hummingbird, white-eyed vireo and white-throated sparrow (Table 3). The strength of the relationship between the tree retention gradient and bird density varied among these thirteen species (Table 4, Fig. 1). Three of the species: northern cardinal, American robin, and Carolina wren, had weak relationships with tree retention (Fig. 1). The random effect of study accounted for 59–77% of the variation in the mixed models for these three species, and post-hoc, fixed-effect models, without the random effect of study, were not significant ($P > 0.1$).

Models with a linear and quadratic predictor variable of tree retention received the most support for five species: chestnut-sided warbler, gray catbird, indigo bunting, mourning warbler and yellow-breasted chat (Table 3). These five species had more complex relationships with tree retention, with a decline of bird density only when > 40–50% of the trees were retained (Table 5, Fig. 2).

Examining densities among the three discrete treatment levels, brown-headed cowbird, cedar waxwing, common yellowthroat, chestnut-sided warbler, eastern towhee, ruby-throated hummingbird and white-throated sparrow had the greatest densities in regeneration harvests with low retention, significantly lower densities in shelterwoods (moderate retention) compared to stands with low retention, and lowest densities in high retention stands (Table 6). Carolina wren, gray catbird, indigo bunting, magnolia warbler, mourning warbler, prairie warbler, white-eyed vireo and yellow-breasted chat were equally abundant in low-retention harvests and shelterwood cuts, and less abundant in high retention stands compared to either low retention or shelterwoods. Northern cardinal and American goldfinch were significantly more abundant in shelterwoods than high retention stands, but abundance was not significantly different in low-retention versus high retention stands, and in low-retention versus shelterwood cuts. Finally, American robin, black-and-white warbler, dark-eyed junco and yellow-billed cuckoo did not differ among any of the discrete treatment levels.

4. Discussion

Using data from studies across eastern North America, our meta-analysis illustrates that shrubland bird abundance declines with tree retention along a continuous gradient, consistent with individual studies that have compared only a few discrete tree retention levels at relatively small geographic scales (e.g., King and DeGraaf, 2000; Goodale et al., 2009). In addition to high densities in complete clearcuts, numerous shrubland species had high densities in stands with low levels of mature tree retention (5–25%), lending support to retention forestry (Gustafsson et al., 2012; Otto and Roloff, 2012; Grinde et al., 2020). Overall, our results across studies can be applied to specific, proposed management scenarios, to specify the level of basal area or tree retention that provides habitat for specific shrubland bird species.

The association of the shrubland bird guild with open canopy conditions and their absence from closed canopy forest has led some investigators to conclude that silvicultural treatments that retain a low level of canopy retention are the most efficient for conserving these species (King and DeGraaf, 2000; DeGraaf and Yamasaki, 2003). Our observation that most shrubland species decreased monotonically with tree retention supports this view — (i.e., 13 of 21 species, 62%, were best fit with a linear predictor) — which has also been borne out by field investigations in specific landscapes (e.g., Smetzer et al., 2014). Nevertheless, we also found several species were equally abundant in forest stands with 25–50% tree retention as they were in stands with 0–25% tree retention, consistent with findings on some individual species (Harrison and Kilgo, 2004; Roth et al., 2014; Margenau et al., 2018). Some shrubland bird species likely respond favorably to silvicultural treatments that mimic natural disturbance conditions, including wind events and ice storms that leave remnant standing trees singly or in groups (Faccio, 2003; Holmes et al., 2004). Moreover, some shrubland birds may be adapted to the partially-open, woodland conditions historically associated with oak and pine forests in portions of the eastern United States prior to the suppression of historic fire regimes (Hanberry and Thompson, 2019).

The association of shrubland birds with recently disturbed sites is clearly due to changes in vegetation structure and composition. Herbaceous growth and low, woody vegetation are less developed under conditions of greater tree retention, and characteristics of the herb and shrub layer influence the presence and abundance of shrubland bird species (Keller et al., 2003; Schlossberg et al., 2010). Many shrubland birds nest, forage, and hide from predators in or under shrubs, grasses, or herbaceous forbs and ferns (Schlossberg et al., 2010; Akresh, 2012; Greenlaw, 2020). As fewer trees are retained and basal area decreases in a stand, the amount of sunlight increases, and subsequently the understory vegetation is enhanced and can support insect prey, afford suitable nests sites, and can promote concealment from nest and post-fledging predators (Annand and Thompson, 1997; Smith et al., 1997; Akresh et al., 2009). Shrubland birds are likely responding to these changes in ecological conditions and vegetation structure resulting from silvicultural treatments.

Besides needing dense understory vegetation, shrubland birds may be using retention trees within harvested areas, or closed-canopy forests adjacent to clearcuts, for singing, foraging, and other behaviors (Akresh and King, 2016; McNeil et al., 2018). Roth et al. (2014) speculated that golden-winged warblers (*Vermivora chrysoptera*) were associated with some retained canopy because trees provide elevated singing posts to broadcast their songs. Other shrubland bird species, like the chestnut-sided warbler, forage extensively in closed-canopy forests adjacent to openings (Roberts and King, in press) and females make forays into the forest to collect bark from birch (*Betula* spp.) trees for nest-building (King, Pers. Obs.), suggesting that retained trees can afford additional values to shrubland birds in managed stands (Grinde et al., 2020). We note that our analyses could not incorporate treatment area, and a small amount of retention throughout the stand may be especially important for shrubland birds in very large (e.g., > 50 ha) harvested stands where there is less mature forest edge (Roth et al., 2014).

To our knowledge, Vanderwel et al. (2007) is the only other meta-analysis to examine individual bird species responses to silviculture as a continuous function of tree retention in North America; however, that study focused on mature forest birds and only included seven putative shrubland species. Their findings for five of these species were similar to ours: indigo buntings, white-throated sparrows, brown-headed cowbirds, and American robins increased with canopy removal and black-and-white warbler abundance was unrelated to canopy retention. In contrast to our results, Vanderwel et al. (2007) found dark-eyed juncos increased in response to canopy removal, whereas juncos were found to be unaffected by tree retention in our study. Lastly, Vanderwel et al. (2007) observed mourning warblers were unaffected by tree retention, whereas they increased with tree removal in our study.

Black-and-white warbler, dark-eyed junco and yellow-billed cuckoo were not influenced by tree retention in our study, despite being considered shrubland birds in at least some classifications (DeGraaf and Yamasaki, 2001; Hunter et al., 2001). Unlike other species that are virtually never present in the absence of open-canopy conditions, these three species appear more variable in their response to silviculture (King and DeGraaf, 2000; Rodewald and Yahner, 2000; Goodale et al., 2009; Otto and Roloff, 2012). Habitat features needed by these three species likely vary independently from silvicultural treatments. Both black-and white warblers and juncos are ground nesters, and for these species, suitable nesting sites might be less likely to be affected by silvicultural treatments than for birds that nest in shrubs or trees. Schlossberg and King (2007) attempted to generate a list of species that should be considered shrubland birds by calculating the percentage of studies in which a given species was more abundant in shrubland habitat, and black-and-white warbler, dark-eyed junco and yellow-billed cuckoo all had relatively low values for this index (≤ 0.64), whereas species that exhibited a significant relationship in our study with tree retention typically had higher values (mean = 0.83). The variability in response to silviculture by these three species suggests they should not be generally considered shrubland species, although they might be associated with disturbance in certain systems.

Unsurprisingly, most of the species that we found to exhibit significant relationships with a continuous gradient of tree retention also differed among discrete silvicultural categories in our analyses. Specifically, cedar waxwing, common yellowthroat, eastern towhee, ruby-throated hummingbird, and white-throated sparrow had the highest densities in low retention harvests, then shelterwoods, then high retention stands, and also were best fit with a single linear predictor variable of tree retention. All of these species except cedar waxwings are widely considered shrubland species (Schlossberg and King, 2007). Species similarly abundant in low retention harvests and shelterwoods, and also best fit with a quadratic model, consisted of gray catbird, indigo bunting, mourning warbler, and yellow-breasted chat. These species are also widely considered shrubland birds, given that the shrubland bird designation is typically made in the context of abundance in treated stands relative to unmanaged forest (e.g., Schlossberg and King, 2007). Several other species exhibited monotonic relationships with our continuous variable, yet were still equally similar between the low retention harvests and shelterwood discrete categories (Carolina wren, magnolia warbler, prairie warbler and white-eyed vireo). Our continuous variable was based on percent tree retention, while our discrete silvicultural categories were based on shelterwood basal-area classifications, which can vary depending on the forest type. These slight differences in classifications may explain our varied results for these latter four species. All four species exhibited some higher density values around 50% retention, which, despite the strong monotonic relationship with the continuous variable, were enough to obscure the differences we expected in the discrete, categorical analysis.

We were unable to robustly analyze the effects of tree retention for shrubland bird species which were detected in relatively few primary studies. Nevertheless, exploratory examinations of some other putative shrubland bird species that had small sample sizes, such as song sparrow (*Melospiza melodia*), blue-winged warbler (*Vermivora cyanoptera*), and alder flycatcher (*Empidonax alnorum*), suggested similar declining densities as tree retention increased (Akresh unpublished data), consistent with previous knowledge of these species' habitat requirements (Arcese et al., 2020; Gill et al., 2020). Highly threatened shrubland species such as golden-winged warblers were not detected in the community-based studies we examined in our meta-analysis, but other studies that have focused on golden-winged warblers have observed highest abundances in basal areas between 0–12 m^2/ha (Leuenberger et al., 2017; McNeil et al., 2018).

The goal of our analyses was to identify conditions suitable for breeding birds in managed forests, however these findings are based only on abundance, and do not necessarily reflect habitat quality as manifested by bird survival and reproductive success (Van Horne, 1983). Brown-headed cowbirds are a brood parasite that can decrease the nesting success of host bird species, and we found cowbirds increase in abundance with decreasing canopy retention. Our results on cowbird abundance are consistent with the findings of others (Annand and Thompson, 1997; Vanderwel et al., 2007), and raise the possibility that decreased basal retention could potentially compromise bird nesting success in some landscapes. Cowbird abundance and brood parasitism can be especially detrimental in landscapes with extensive agricultural development (Robinson et al., 1995). Nevertheless, cowbirds tend to be scarce and cowbird parasitism low in extensively forested landscapes (Annand and Thompson, 1997; King and DeGraaf, 2000; Chandler et al., 2009; King et al., 2009), and shrubland birds may be able to endure impacts of low levels of parasitism via re-nesting and other mechanisms (Smith, 1981; Guigueno and Sealy, 2010; Akresh, 2012). Similarly, nest predator abundance is not typically elevated by silviculture in extensively forested landscapes (King et al., 1996; King and DeGraaf, 2000; Chandler et al., 2009). Thus, landscape context may be important when considering tree harvests and potential impacts on bird productivity.

4.1. Conclusion and management implications

Nearly all shrubland bird species were less abundant or absent from forests with high levels of canopy cover, including unmanaged forests, single-tree selection, and commercial thinning regimes, and we therefore do not recommend these practices for shrubland bird management. Based on our findings, we believe that maximizing shrubland bird abundance in any given landscape can be achieved through four potential approaches: 1) creation of open-canopy ($<$ 30%) early-successional forests via regeneration harvests, 2) short-rotation maintenance of open-canopy habitats, 3) creation of partially open-canopy (30–70%) forests via silviculture, and where appropriate 4) maintenance of partially open-canopy woodlands in fire-dependent ecosystems via prescribed burning and other practices (King and Schlossberg, 2014; Hanberry and Thompson, 2019).

As expected, regeneration harvests such as clearcuts and seed tree harvests were most efficient for creating habitat for shrubland birds. Historically, solely even-aged regeneration methods, such as clearcutting, have been suggested as strategies for creation of early-successional forest on commercial lands with high site quality (Hanberry and Thompson, 2019). Our results highlight that many shrubland bird species still attain high densities in areas where there is some low-level retention, suggesting that variable retention harvest systems maintaining live-tree legacies at densities below 25% may be an effective strategy for shrubland birds while also providing other benefits associated with large tree habitats (Fedrowitz et al., 2014; Mori and Kitagawa, 2014; Soler et al., 2016). Conditions created by retention forestry approaches more likely approximate natural post-disturbance conditions (Gustafsson et al., 2012). The habitats created through these regeneration methods will be ephemeral, but can exist throughout a landscape in a shifting mosaic or patch dynamic framework, with spatially distinct areas providing shrubland bird habitat at different times (DeGraaf et al., 2005; Akresh et al., 2015). Non-silvicultural, human-made habitats maintained with a dense understory and with few trees can also sustain large populations of shrubland birds. Maintained shrublands include wildlife openings, uncultivated land on small-scale farms, utility rights-of-way, and reclaimed surface mines (King and Schlossberg, 2014; Schlossberg and King, 2015).

Partially-open canopy conditions also provided habitat for shrubland birds, suggesting shelterwood methods and woodland restoration efforts may be used to conserve these species, especially if these stands are extensive throughout the landscape (Vander Yacht et al., 2016). Similar to low retention harvests, shelterwoods could be located on operational forests with high site quality. Shelterwoods also tend to be ephemeral in providing shrubland bird habitat, but two or three-stage shelterwoods, followed by a regenerating harvest (clearcut), could prolong habitat at a given site (Margenau et al., 2018). Alternatively, restoration and maintenance of partially-open-canopy oak-pine woodlands on low-quality, non-commercial xeric sites, maintained with low-intensity prescribed burning or other methods, could also provide habitat on a large scale (Brawn, 2006; Kabrick et al., 2014; Reidy et al., 2014). Given that some shrubland bird species have equal or higher abundance in stands with 30–70% canopy cover compared to 0–30% canopy cover, and other shrubland species occupy stands with 30–70% canopy cover to some degree, partially-open stands could be a viable management option for helping to conserve shrubland birds.

Overall, our quantitative relationships can help balance the needs of shrubland birds with other forest values, such as 1) habitat for bird and wildlife species that require the retention of canopy trees for foraging or nesting (Vanderwel et al., 2007; Tilghman et al., 2012), 2) encouraging the regeneration of tree species that require some shading or a seed source for propagation (Smith et al., 1997), or 3) softening the appearance of silvicultural openings for recreationalists (e.g., Gobster, 1999). Balancing different values is aided by having our computed continuous functions between bird abundance and tree retention, because the functions should lend themselves more readily to generating management practices that may resolve these potentially conflicting values (Toms and Villard, 2015). We also note that a number of wildlife species that breed in mature forests, including mature-forest birds, still prefer open-canopy habitat during some stage of their life cycle, such as the post-fledging period (DeGraaf and Yamasaki, 2001; Akresh et al., 2009; Chandler et al., 2012). Therefore, we suspect that many different forest and stakeholder values can be upheld by maintaining a small amount of tree retention in silvicultural harvests, and by sustaining a variety of harvest intensities, seral stages, and management approaches throughout a regional landscape.

CRediT authorship contribution statement

Michael E. Akresh: Conceptualization, Methodology, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **David I. King:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Casey A. Lott:** Writing - review & editing, Supervision. **Jeffery L. Larkin:** Writing - review & editing, Supervision. **Anthony W. D'Amato:** Data curation, Writing - review & editing, Supervision.

Declaration of Competing Interest

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

Acknowledgement

The authors wish to thank the many scientists who generated the data that was incorporated into this meta-analysis. Also, thanks to the anonymous reviewers for helpful comments on the manuscript. Support for this research was provided by the Natural Resources Conservation Service Conservation Effects Assessment Program, Award Agreement #NR183A750023C002.

Appendix A

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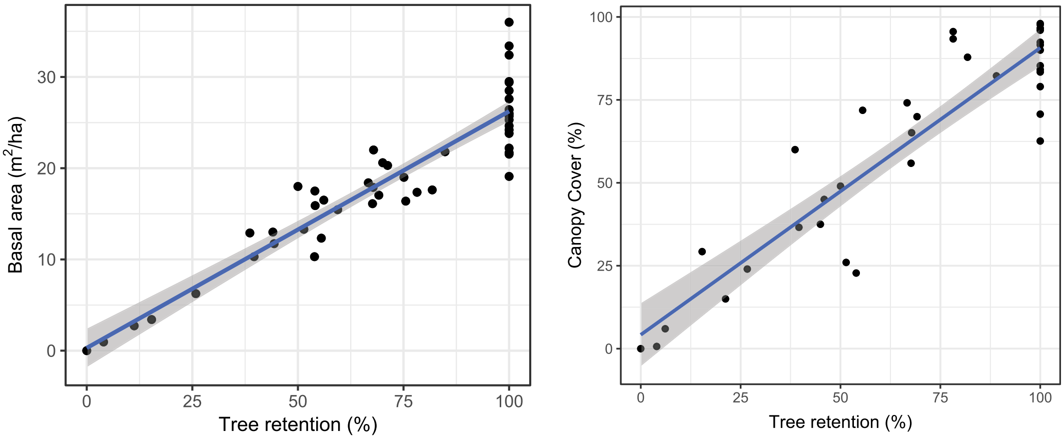

Fig. A1. Relationships between percent tree retention and the actual basal area or canopy cover recorded in different treatment levels within a study. All mature forest stands were deemed 100% tree retention, while the tree retention values for harvested stands were based on the proportion of the basal area or canopy cover of the mature forest stand for that given study (see Methods section for more details). Some studies lacked data on basal area (and just had canopy cover), and thus basal area could not be used as a baseline measure (e.g., predictor variable) for comparison among studies.

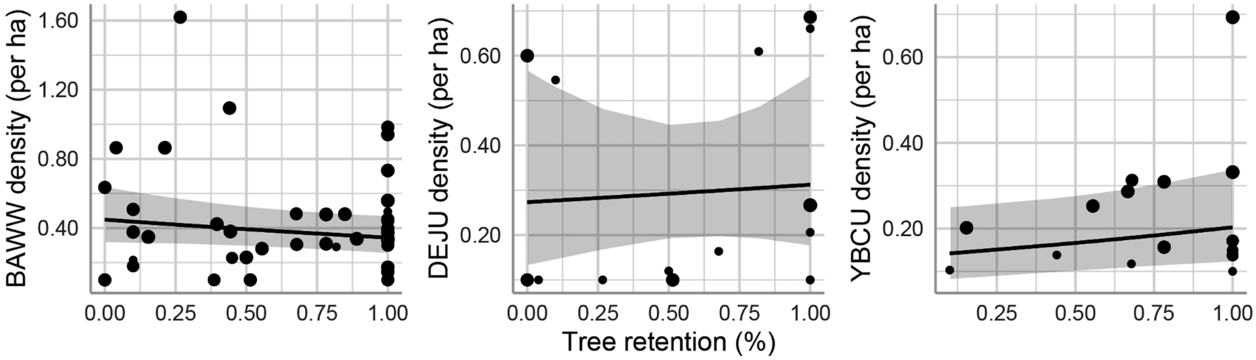

Fig. A2. Effect of tree retention on avian density in forestry stands across the eastern United States, for shrubland species in which the null model was the best fit. Black-and-white warbler (BAWW) had 43 data points from 19 studies, dark-eyed junco (DEJU) had 16 data points from 7 studies, and yellow-billed cuckoo (YBCU) had 15 data points from 6 studies.

References

Akresh, M.E., 2012. Prairie warbler nest-site selection, nest survival, and demographic response to management in a pitch pine-scrub oak barren. Master's thesis. University of Massachusetts Amherst, Amherst, MA, USA.

Akresh, M.E., King, D.I., 2016. Eastern whip-poor-will breeding ecology in relation to habitat management in a pitch pine–scrub oak barren. Wildl. Soc. Bull. 40, 97–105.

Akresh, M.E., Dinse, K., Foufopoulos, J., Schubel, S.C., Kowalczyk, T., 2009. Passerine breeding and post-fledgling habitat use in riparian and upland temperate forests of the American Midwest. Condor 111, 756–762.

Akresh, M.E., King, D.I., Brooks, R.T., 2015. Demographic response of a shrubland bird to habitat creation, succession, and disturbance in a dynamic landscape. For. Ecol. Manage. 336, 72–80.

Annand, E.M., Thompson III, F.R., 1997. Forest bird response to regeneration practices in central hardwood forests. J. Wildl. Manage. 61, 159–171.

Arcese, P., Sogge, M.K., Marr, A.B., Patten, M.A., 2020. Song Sparrow (*Melospiza melodia*), version 1.0. In: Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.

Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's Information Criterion. J. Wildl. Manage. 74, 1175–1178.

Arnqvist, G., Wooster, D., 1995. Meta-analysis: synthesizing research findings in ecology and evolution. Trends Ecol. Evol. 10, 236–240.

Askins, R.A., 2000. Restoring North America's birds: lessons from landscape ecology. Yale University Press.

Atwell, R.C., Schulte, L.A., Palik, B.J., 2008. Songbird response to experimental retention harvesting in red pine (*Pinus resinosa*) forests. For. Ecol. Manage. 255, 3621–3631.

Baker, M.D., Lacki, M.J., 1997. Short-term changes in bird communities in response to silvicultural prescriptions. For. Ecol. Manage. 96, 27–36.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Boardman, L.A., Yahner, R.H., 1999. Wildlife communities associated with even-aged reproduction stands in two state forests of Pennsylvania. North. J. Appl. For. 16, 89–95.

Bolker, B.M., 2008. Ecological models and data in R. Princeton University Press.

Boves, T.J., Buehler, D.A., Sheehan, J., Wood, P.B., Rodewald, A.D., Larkin, J.L., Keyser, P.D., Newell, F.L., George, G.A., Bakermans, M.H. and Evans, A., 2013. Emulating natural disturbances for declining late-successional species: A case study of the consequences for Cerulean Warblers (Setophaga cerulea). PloS one 8.

Brawn, J.D., 2006. Effects of restoring oak savannas on bird communities and populations. Conserv. Biol. 20, 460–469.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference. Springer, New York, New York, USA.

Chandler, R.B., King, D.I., Chandler, C.C., 2009. Effects of management regime on the abundance and nest survival of shrubland birds in wildlife openings in northern New England, USA. For. Ecol. Manage. 258, 1669–1676.

Chandler, C.C., King, D.I., Chandler, R.B., 2012. Do mature forest birds prefer early-successional habitat during the post-fledging period? For. Ecol. Manage. 264, 1–9.

DeGraaf, R.M., Yamasaki, M., 2001. New England wildlife: habitat, natural history, and distribution. University Press of New England, Hanover, New Hampshire.

DeGraaf, R.M., Yamasaki, M., 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. For. Ecol. Manage. 185, 179–191.

DeGraaf, R.M., Yamasaki, M., Leak, W.B., Lester, A.M., 2005. Landowner's guide to wildlife habitat: forest management for the New England region. University Press of New England, Hanover, New Hampshire.

Dettmers, R., 2003. Status and conservation of shrubland birds in the northeastern US. For. Ecol. Manage. 185, 81–93.

Donato, D.C., Campbell, J.L., Franklin, J.F., 2012. Multiple successional pathways and precocity in forest development: can some forests be born complex? J. Veg. Sci. 23, 576–584.

Doyon, F., Gagnon, D., Giroux, J.F., 2005. Effects of strip and single-tree selection cutting on birds and their habitat in a southwestern Quebec northern hardwood forest. For. Ecol. Manage. 209, 101–116.

Duguid, M.C., Morrell, E.H., Goodale, E., Ashton, M.S., 2016. Changes in breeding bird abundance and species composition over a 20-year chronosequence following shelterwood harvests in oak-hardwood forests. For. Ecol. Manage. 376, 221–230.

Faccio, S.D., 2003. Effects of ice storm-created gaps on forest breeding bird communities in central Vermont. For. Ecol. Manage. 186, 133–145.

Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., 2014. Can retention forestry help conserve biodiversity? A meta-analysis. J. Appl. Ecol. 51, 1669–1679.

Fink, A.D., Thompson III, F.R., Tudor, A.A., 2006. Songbird use of regenerating forest, glade, and edge habitat types. J. Wildl. Manage. 70, 180–188.

Flaspohler, D.J., Fisher, Huckins, C.J., Bub, B.R. and Van Dusen, P.J., 2002. Temporal patterns in aquatic and avian communities following selective logging in the Upper Great Lakes region. Forest Science 48:339–34.

Freedman, B., Beauchamp, C., McLaren, J.A., Tingley, S.I., 1981. Forestry management practices and populations of breeding birds in a hardwood forest in Nova Scotia. Canadian Field Naturalist 95, 307–311.

Fontaine, J.B., Kennedy, P.L., 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in US fire-prone forests. Ecol. Appl. 22, 1547–1561.

Gill, F.B., Canterbury, R.A., Confer, J.L., 2020. Blue-winged warbler (*Vermivora cyanoptera*), version 1.0. In: Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.

Gilmore, D.W., Palik, B.J. 2006. A revised managers handbook for red pine in the North Central Region. Gen. Tech. Rep. NC-264. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station. 55 p.

Gingrich, S.F. 1971. Stocking, growth, and yield of oak stands. In: Oak Symposium Proceedings. 1971 August 16-20; U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: Upper Darby, PA. 65–73.

Gobster, P.H., 1999. An Ecological Aesthetic for Forest Landscape Management. Landscape Journal 18, 54–64.

Goodale, E., Lalbhai, P., Goodale, U.M., Ashton, P.M.S., 2009. The relationship between shelterwood cuts and crown thinnings and the abundance and distribution of birds in a southern New England forest. For. Ecol. Manage. 258, 314–322.

Greenberg, C.H., Franzreb, K.E., Keyser, T.L., Zarnoch, S.J., Simon, D.M., Warburton, G. S., 2014. Short-term response of breeding birds to oak regeneration treatments in upland hardwood forest. Natural Areas J. 34, 409–422.

Greenlaw, J.S., 2020. Eastern Towhee (*Pipilo erythrophthalmus*), version 1.0. In Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA, 10.2173/bow.eastow.01.

Grinde, A.R., Slesak, R.A., D'Amato, A.W., Palik, B.P., 2020. Effects of tree retention and woody biomass removal on bird and small mammal communities. For. Ecol. Manage. 465.

Guigueno, M.F., Sealy, S.G., 2010. Clutch abandonment by parasitized yellow warblers: Egg burial or nest desertion? Condor 112, 399–406.

Gurevitch, J., Hedges, L.V., 1999. Statistical issues in ecological meta-analyses. Ecology 80, 1142–1149.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D. B., Lõhmus, A., Pastur, G.M., Messier, C., Neyland, M., 2012. Retention forestry to maintain multifunctional forests: a world perspective. Bioscience 62, 633–645.

Hache, S., Pétry, T., Villard, M.A., 2013. Numerical response of breeding birds following experimental selection harvesting in northern hardwood forests. Avian Conservation Ecol. 8.

Hagan, J.M., McKinley, P.S., Meehan, A.L., Grove, S.L., 1997. Diversity and abundance of landbirds in a northeastern industrial forest. J. Wildl. Manage. 61, 718–735.

Hanberry, B.B., Thompson III, F.R., 2019. Open forest management for early successional birds. Wildl. Soc. Bull. 43, 41–151.

Harrison, C.A., Kilgo, J.C., 2004. Short-term breeding bird response to two harvest practices in a bottomland hardwood forest. Wilson Bulletin 116, 314–323.

Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156.

Heltzel, J.M., Leberg, P.L., 2006. Effects of selective logging on breeding bird communities in bottomland hardwood forests in Louisiana. J. Wildl. Manage. 70, 1416–1424.

Holmes, S.B., Burke, D.M., Elliott, K.A., Cadman, M.D., Friesen, L., 2004. Partial cutting of woodlots in an agriculture-dominated landscape: effects on forest bird communities. Can. J. For. Res. 34, 2467–2476.

Holmes, S.B., Pitt, D.G., McIlwrick, K.A., Hoepting, M.K., 2012. Response of bird communities to single-tree selection system harvesting in northern hardwoods: 10–12 years post-harvest. For. Ecol. Manage. 271, 132–139.

Hunter, W.C., Buehler, D.A., Canterbury, R.A., Confer, J.L., Hamel, P.B., 2001. Conservation of disturbance-dependent birds in eastern North America. Wildl. Soc. Bull. 29, 440–455.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Iglay, R.B., Greene, R.E., Leopold, B.D., Miller, D.A., 2018. Bird conservation potential of fire and herbicide treatments in thinned pine stands. For. Ecol. Manage. 409, 267–275.

Jobes, A.P., Nol, E., Voigt, D.R., 2004. Effects of selection cutting on bird communities in contiguous eastern hardwood forests. J. Wildl. Manage. 68, 51–60.

Johnson, P.S., Shifley, S.R., Rogers, R., 2009. The ecology and silviculture of oaks, second ed. CABI International, Cambridge, MA.

Kabrick, J.M., Dey, D.C.; Gwaze, D. 2007. Shortleaf pine restoration and ecology in the Ozarks: proceedings of a symposium. Gen. Tech. Rep. NRS-P-15. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 215 p.

Kabrick, J. M., Dey, D. C., Kinkead, C. O., Knapp, B. O., Leahy, M., Olson, M. G., Stambaugh, M. C., and Stevenson, A. P. 2014. Silvicultural considerations for managing fire-dependent oak woodland ecosystems. In: Groninger, John W.; Holzmueller, Eric J.; Nielsen, Clayton K.; Dey, Daniel C., eds. Proceedings, 19th Central Hardwood Forest Conference; 2014 March 10-12; Carbondale, IL. General Technical Report NRS-P-142. Newtown Square, PA: USDA Forest Service, Northern Research Station: 2-15., pp. 2-15.

Kalies, E.L., Chambers, C.L., Covington, W.W., 2010. Wildlife responses to thinning and burning treatments in southwestern conifer forests: a meta-analysis. For. Ecol. Manage. 259, 333–342.

Keller, J.K., Richmond, M.E., Smith, C.R., 2003. An explanation of patterns of breeding bird species richness and density following clearcutting in northeastern USA forests. For. Ecol. Manage. 174, 541–564.

Kendrick, S.W., Porneluzi, P.A., Iii, F.R.T., Morris, D.L., Haslerig, J.M., Faaborg, J., 2015. Stand-level bird response to experimental forest management in the Missouri Ozarks. J. Wildl. Manage. 79, 50–59.

King, D.I., DeGraaf, R.M., 2000. Bird species diversity and nesting success in mature, clearcut and shelterwood forest in northern New Hampshire, USA. For. Ecol. Manage. 129, 227–235.

King, D.I., Nislow, K.H., Brooks, R.T., DeGraaf, R.M., Yamasaki, M., 2011a. Early-successional forest ecosystems: far from "forgotten". Front. Ecol. Environ. 9, 319–320.

King, D.I., Schlossberg, S., 2014. Synthesis of the conservation value of the early-successional stage in forests of eastern North America. For. Ecol. Manage. 324, 186–195.

King, D.I., Griffin, C.R., Degraff, R.M., 1996. Effects of clearcutting on habitat use and reproductive success of the Ovenbird in forested landscapes. Conserv. Biol. 10, 1380–1386.

King, D.I., Chandler, R.B., Schlossberg, S., Chandler, C.C., 2009. Habitat use and nest success of scrub-shrub birds in wildlife and silvicultural openings in western Massachusetts, USA. For. Ecol. Manage. 257, 421–426.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2016. lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0-33. https://CRAN.R-project.org/package=lmerTest.

King, D.I., Schlossberg, S., Brooks, R.T., Akresh, M.E., 2011b. Effects of fuel reduction on birds in pitch pine–scrub oak barrens of the United States. For. Ecol. Manage. 261, 10–18.

LaManna, J.A., Martin, T.E., 2017. Logging impacts on avian species richness and composition differ across latitudes and foraging and breeding habitat preferences. Biol. Rev. 92, 1657–1674.

Larsen, D.R., Dey, Dan C., Faust, T., 2010. A stocking diagram for midwestern eastern cottonwood-silver maple-American sycamore bottomland forests. North. J. Appl. For. 27, 132–139.

Leak, W.B., Yamasaki, M. and Holleran, R., 2014. Silvicultural guide for northern hardwoods in the northeast. Gen. Tech. Rep. NRS-132. Newtown Square, PA: US Department of Agriculture, Forest Service, Northern Research Station. 46 p., 132, pp.1–46.

Leuenberger, W., McNeil, D.J., Cohen, J., Larkin, J.L., 2017. Characteristics of golden-winged warbler territories in plant communities associated with regenerating forest and abandoned agricultural fields. J. Field Ornithol. 88, 169–183.

Litvaitis, J.A., 2003. Are pre-Columbian conditions relevant baselines for managed forests in the northeastern United States? For. Ecol. Manage. 185, 113–126.

Lorimer, C.G., White, A.S., 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. For. Ecol. Manage. 185, 41–64.

Lott, C.A., Akresh, M.E., Elmore, A.J., Fiss, C.J., Fitzpatrick, M.C., Joos, C.J., King, D.I., McNeil, D.J., Stoleson, S.H., Larkin, J.L., 2019. What evidence exists for landbird species-environment relationships in eastern temperate and boreal forests of North America? A systematic map protocol. Environ. Evidence 8, 31.

Lüdecke, D., 2018. ggeffects: Tidy data frames of marginal effects from regression models. J. Open Source Software 3, 772.

Mahaffey, A., Evans, A., 2016. Ecological forestry practices for bottomland hardwood forests of the southeastern U.S. Forest Stewards Guild. 45, pp.

Margenau, E.L., Wang, Y., Schweitzer, C.J., Stringer, B.K., 2018. Responses of early-successional songbirds to a two-stage shelterwood harvest for oak forest regeneration. Avian Res. 9.

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

McNeil, D., Fiss, C., Wood, E., Duchamp, J., Bakermans, M., Larkin, J., 2018. Using a natural reference system to evaluate songbird habitat restoration. Avian Conservation Ecol. 13.

Mori, A.S., Kitagawa, R., 2014. Retention forestry as a major paradigm for safeguarding forest biodiversity in productive landscapes: A global meta-analysis. Biol. Conserv. 175, 65–73.

New Jersey Pinelands Commission. 2006. Recommended Forestry Management Practices Report. State of New Jersey, 79 pp.

Newell, F.L., Rodewald, A.D., 2012. Management for oak regeneration: Short-term effects on the bird community and suitability of shelterwood harvests for canopy songbirds. J. Wildl. Manage. 76, 683–693.

Newell, F.L., Sheehan, J., Wood, P.B., Rodewald, A.D., Buehler, D.A., Keyser, P.D., Larkin, J.L., Beachy, T.A., Bakermans, M.H., Boves, T.J., Evans, A., 2013. Comparison of point counts and territory mapping for detecting effects of forest management on songbirds. J. Field Ornithol. 84, 270–286.

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58, 123–138.

Otto, C.R., Roloff, G.J., 2012. Songbird response to green-tree retention prescriptions in clearcut forests. For. Ecol. Manage. 284, 241–250.

Palik, B.J., D'Amato, A.W., Franklin, J.F., Johnson, K.N., 2020. Ecological silviculture: foundations and applications. Waveland Press, Long Grove, Illinois.

Perry, R.W., Thill, R.E., 2013. Long-term responses of disturbance-associated birds after different timber harvests. For. Ecol. Manage. 307, 274–283.

Perry, R.W., Jenkins, J.M., Thill, R.E., Thompson, F.R., 2018. Long-term effects of different forest regeneration methods on mature forest birds. For. Ecol. Manage. 408, 183–194.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rankin, D.T., Perlut, N.G., 2015. The effects of Forest Stand Improvement Practices on occupancy and abundance of breeding songbirds. For. Ecol. Manage. 335, 99–107.

Reidy, J.L., Thompson, F.R., Bailey, J.W., 2011. Comparison of methods for estimating density of forest songbirds from point counts. J. Wildl. Manage. 75, 558–568.

Reidy, J.L., Thompson III, F.R., Kendrick, S.W., 2014. Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. For. Ecol. Manage. 313, 34–46.

Roberts, H.P., King, D.I., 2017. Area requirements and landscape-level factors influencing shrubland birds. J. Wildl. Manage. 81, 1298–1307.

Roberts, H.P., King, D.I., in press. Matrix habitat use influences avian area-sensitivity. Ecology and Evolution.

Robinson, W.D., Robinson, S.K., 1999. Effects of selective logging on forest bird populations in a fragmented landscape. Conserv. Biol. 13, 58–66.

Robinson, S.K., Thompson, F.R., Donovan, T.M., Whitehead, D.R., Faaborg, J., 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267, 1987–1990.

Rodewald, A.D., Yahner, R.H., 2000. Bird communities associated with harvested hardwood stands containing residual trees. J. Wildl. Manage. 64, 924–932.

Rohatgi, A., 2018. WebPlotDigitizer. http://arohatgi.info/WebPlotDigitizer/app/.

Roth, A.M., Flaspohler, D.J., Webster, C.R., 2014. Legacy tree retention in young aspen forest improves nesting habitat quality for Golden-winged Warbler (*Vermivora chrysoptera*). For. Ecol. Manage. 321, 61–70.

Schieck, J., 1997. Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. Condor 99, 179–190.

Schieck, J., Song, S.J., 2006. Changes in bird communities throughout succession following fire and harvest in boreal forests of western North America: literature review and meta-analyses. Can. J. For. Res. 36, 1299–1318.

Schlossberg, S., King, D.I., 2007. Ecology and management of scrubshrub birds in New England: a comprehensive review. Natural Resources Conservation Service, Beltsville, Maryland, USA.

Schlossberg, S., King, D.I., 2009. Postlogging succession and habitat usage of shrubland birds. J. Wildl. Manage. 73, 226–231.

Schlossberg, S., King, D.I., 2015. Measuring the effectiveness of conservation programs for shrubland birds. Global Ecol. Conserv. 4, 658–665.

Schlossberg, S., King, D.I., Chandler, R.B., Mazzei, B.A., 2010. Regional synthesis of habitat relationships in shrubland birds. J. Wildl. Manage. 74, 1513–1522.

Semlitsch, R.D., Todd, B.D., Blomquist, S.M., Calhoun, A.J., Gibbons, J.W., Gibbs, J.P., Graeter, G.J., Harper, E.B., Hocking, D.J., Hunter Jr, M.L., Patrick, D.A., 2009. Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. Bioscience 59, 853–862.

Shake, C.S., Moorman, C.E., Riddle, J.D., Burchell, M.R., 2012. Influence of patch size and shape on occupancy by shrubland birds. Condor 114, 268–278.

Sheehan, J., Wood, P.B., Buehler, D.A., Keyser, P.D., Larkin, J.L., Rodewald, A.D., Wigley, T.B., Boves, T.J., George, G.A., Bakermans, M.H., Beachy, T.A., 2014. Avian response to timber harvesting applied experimentally to manage Cerulean Warbler breeding populations. For. Ecol. Manage. 321, 5–18.

Shifley, S.R., Moser, W.K., Nowak, D.J., Miles, P.D., Butler, B.J., Aguilar, F.X., DeSantis, R.D., Greenfield, E.J., 2014. Five anthropogenic factors that will radically alter forest conditions and management needs in the northern United States. Forest Science 60, 914–925.

Smetzer, J.R., King, D.I., Schlossberg, S., 2014. Management regime influences shrubland birds and habitat conditions in the Northern Appalachians, USA. J. Wildl. Manage. 78, 314–324.

Smith, J.N., 1981. Cowbird parasitism, host fitness, and age of the host female in an island song sparrow population. Condor 83, 152–161.

Smith, D.M., Larson, B.C., Kelty, M.J. and Ashton, P.M.S., 1997. The practice of silviculture: applied forest ecology (No. Ed. 9). John Wiley and Sons, Inc.

Soler, R.M., Schindler, S., Lencinas, M.V., Peri, P.L., Pastur, G.M., 2016. Why biodiversity increases after variable retention harvesting: A meta-analysis for southern Patagonian forests. For. Ecol. Manage. 369, 161–169.

Spake, R., Doncaster, C.P., 2017. Use of meta-analysis in forest biodiversity research: key challenges and considerations. For. Ecol. Manage. 400, 429–437.

Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J., 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Front. Ecol. Environ. 9, 117–125.

Thatcher, B.S., 2007. Evaluation of forest management to improve breeding habitat for songbirds in oak-hickory forests at Tennessee National Wildlife Refuge Ph.D. Dissertation. University of Tennessee Knoxville, Knoxville, TN.

Thompson III, F.R., DeGraaf, R.M., 2001. Conservation approaches for woody, early successional communities in the eastern United States. Wildl. Soc. Bull. 29, 483–494.

Thompson III, F.R., Dijak, W.D., Kulowiec, T.G., Hamilton, D.A., 1992. Breeding bird populations in Missouri Ozark forests with and without clearcutting. J. Wildl. Manage. 56, 23–30.

Tilghman, J.M., Ramee, S.W., Marsh, D.M., 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. Biol. Conserv. 152, 1–9.

Toms, J.D., Villard, M.A., 2015. Threshold detection: matching statistical methodology to ecological questions and conservation planning objectives. Avian Conservat. Ecol. 10, 2.

Tozer, D.C., Burke, D.M., Nol, E., Elliott, K.A., 2010. Short-term effects of group-selection harvesting on breeding birds in a northern hardwood forest. For. Ecol. Manage. 259, 1522–1529.

Twedt, D.J., 2020. Influence of forest harvest severity and time since perturbation on conservation of North American birds. For. Ecol. Manage. 458, 117742.

Van Horne, B., 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47, 893–901.

Vander Yacht, A.L., Keyser, P.D., Buehler, D.A., Harper, C.A., Buckley, D.S., Applegate, R. D., 2016. Avian occupancy response to oak woodland and savanna restoration. J. Wildl. Manage. 80, 1091–1105.

Vanderwel, M.C., Malcolm, J.R., Mills, S.C., 2007. A meta-analysis of bird responses to uniform partial harvesting across North America. Conserv. Biol. 21, 1230–1240.

Verschuyl, J., Riffell, S., Miller, D., Wigley, T.B., 2011. Biodiversity response to intensive biomass production from forest thinning in North American forests–a meta-analysis. For. Ecol. Manage. 261, 221–232.

Webb, W.L., Behrend, D.F., Saisorn, B., 1977. Effect of logging on songbird populations in a northern hardwood Forest. Wildlife Monographs 55, 3–35.

Weakland, C.A., Wood, P.B., Ford, W.M., 2002. Responses of songbirds to diameter-limit cutting in the central Appalachians of West Virginia, USA. For. Ecol. Manage. 155, 115–129.

Wilson, C.W., Masters, R.E., Bukenhofer, G.A., 1995. Breeding bird response to pine-grassland community restoration for red-cockaded woodpeckers. J. Wildl. Manage. 59, 56–67.

Wohlin, C., 2014. Guidelines for snowballing in systematic literature studies and a replication in software engineering. In: In Proceedings of the 18th international conference on evaluation and assessment in software engineering, pp. 1–10.

Ziehmer, R.L., 1993. Effects of uneven-aged timber management on forest bird communities (Doctoral dissertation. University of Missouri-Columbia).

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY.

Zwolak, R., 2009. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. For. Ecol. Manage. 258, 539–545.