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Decade-long bird community response to the spatial pattern of variable retention harvesting in red pine (*Pinus resinosa*) forests

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ABSTRACT

Structural complexity is widely recognized as an inherent characteristic of unmanaged forests critical to their function and resilience, but often reduced in their managed counterparts. Variable retention harvesting (VRH) has been proposed as a way to restore or enhance structural complexity in managed forests, and thereby sustain attendant biodiversity and ecosystem function. Here we examined the decade-long response of diurnal breeding birds to a VRH experiment that, for the first time, incorporated both overstory and shrub layer treatments in red pine (*Pinus resinosa*) dominated forests in Minnesota, USA. Overstory treatments included dispersed retention, aggregated retention achieved by cutting small (0.1 ha) gaps, aggregated retention achieved by cutting large (0.3 ha) gaps, and an uncut control. A shrub layer treatment of ambient or reduced shrub density was also implemented as a split-plot design in each harvest treatment. We found a consistent increase in bird species richness and abundance with all retention harvest treatments over time compared to the control; species richness was also significantly greater in the large gap-aggregated treatment compared to dispersed and small gap-aggregated retention harvests. Among guilds, foliage-gleaning and shrub- and tree-nesting birds exhibited the strongest positive response to retention harvesting. Species associated with early-successional habitat, forest edges, and shrubs responded most positively to VRH including Chestnut-sided Warbler (*Setophaga pensylvanica*) and American Restart (*S. ruticilla*), although late-successional species such as Blackburnian Warbler (*S. fusca*) and Black-throated Green Warbler (*S. virens*) also showed positive response. We found few differences due to shrub reduction, and only at the species level: Ovenbird (*Seiurus aurocapilla*) and American Redstart were more abundant in the ambient shrub treatment, whereas Brown Creeper (*Certhia americana*), Veery (*Catharus fuscenscens*), and Chipping Sparrow (*Spizella passerina*) were more abundant with a reduced density of shrubs. Results through the first 10 years following harvest revealed differences in bird response to both VRH and shrub treatment, suggesting that management can result in forested landscapes with bird communities that are species rich, diverse, and abundant.

1. Introduction

Structural complexity—the amount, condition, size distribution, and arrangement of different structural attributes—is critical for sustaining forest ecosystem function and resilience, but is often greatly simplified in managed forests when compared to their unmanaged counterparts (Franklin et al., 1997; Puettmann et al., 2009). For example, forests of the northern Great Lakes region of North America today are widely recognized as much simpler in structure than their pre-Euro-American counterparts due to the loss of conifers, large trees, and spatial heterogeneity (Crow et al., 2002; Friedman and Reich, 2005; Schulte et al., 2007; Fraver and Palik, 2012), components that contribute to structural complexity. Declines in structural complexity have been linked to increased risk and severity of pest outbreaks (Raffa et al., 2008); altered carbon, water, and nutrient cycles (Fisk et al., 2002; Guo and Gifford, 2002); and loss of biodiversity (Schulte et al., 2005).

Variable retention harvesting (VRH) can be used to enhance the structural complexity of managed forests, thereby creating conditions that may resemble those found after natural disturbances (Gustafsson et al., 2012; Lindenmayer et al., 2012). Grounded in an understanding of natural disturbance and associated biological legacies (Franklin et al., 2007; Lindenmayer and Franklin, 2002; Lindenmayer et al., 2012), VRH approaches silviculture from the perspective of what is retained, rather than what is removed, and can be variously implemented to meet different management goals: for instance, the

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proportion of overstory retained or the specific species, size, or spatial arrangement of retained forest elements can be varied. Previous studies of VRH have documented impacts of amount of retention and its spatial pattern on microclimate conditions (Peck et al., 2012), forest growth (Palik et al., 2014), and post-harvest biodiversity (Baker et al., 2013), as well as resource availability (Boyden et al., 2012), understory plant community composition (Roberts et al., 2016), and spatial patterns of plants within the forest understory (Halpern et al., 2012). Understanding the response of forest taxa beyond trees has been less well researched, but is important where the maintenance of biodiversity is a fundamental management goal.

Structural complexity has long been recognized as important to birds and other wildlife, and forest bird communities tend to respond positively to increased heterogeneity in both horizontal and vertical planes (MacArthur and MacArthur, 1961; Willson, 1974; Robinson and Holmes, 1982; Whelan, 2001). While studies on bird community response to VRH have generally revealed a positive association between the amount of overstory retained and bird abundance and species richness (Norton and Hannon, 1997; Lance and Phinney, 2001), few studies have investigated bird response to the spatial configuration of retained trees; specifically, dispersed versus aggregated retention. Leaupin et al. (2004) found negligible bird response to different patterns of harvest up to two summers following timber removal. Atwell et al. (2008) found that retention harvesting had a positive effect on bird species richness and abundance three summers after harvest; however, no differences were associated with the spatial pattern of retention nor did birds respond to shrub layer reduction.

To better understand longer-term responses of forest birds to VRH, our study extended to 10 years post-harvest the experiment examined by Atwell et al. (2008) in a red pine (*Pinus resinosa*) forest in north central Minnesota, USA (Palik and Zasada, 2003). These VRH treatments were implemented to assess responses to variation in the spatial pattern of retained overstory trees and reduced abundance of woody shrubs in the understory. There is a growing body of research from this experiment, including work on seedling disease and mortality (Ostry et al., 2012), tree physiological processes (Powers et al., 2008, 2009a, 2009b, 2010, 2011), early survival and growth of seedlings in gaps (Peck et al., 2012), individual seedling mortality and diameter and height growth (Montgomery et al., 2013), resource availability (Montgomery et al., 2010; Boyden et al., 2012), and biomass growth (Palik et al., 2014). Here we present decade-long responses of diurnal breeding birds to VRH in red pine forests.

Based on existing knowledge of bird response to horizontal and vertical heterogeneity of forest structure (MacArthur and MacArthur, 1961; Willson, 1974; Robinson and Holmes, 1982; Whelan, 2001), we hypothesized the bird community would respond to changes in overstory, shrub density, and time since treatment. We expected greater levels of horizontal heterogeneity, as caused by aggregation of retained trees, because of increased spatial variability of light (Boyden et al., 2012). Removal of shrubs in the context of this experiment greatly reduced the vegetation cover and thus substantially reduced vertical heterogeneity. We expected time to impact stand heterogeneity in this experiment because both horizontal and vertical heterogeneity increase with post-harvest vegetation response. In terms of guild responses, we expected no differences due to our treatments among ground nesters, and we otherwise hypothesized that within the 10-year timeframe of this study:

- Overstory removal to have a negative impact on the abundance of cavity nesters and bark gleaners due to loss of nesting and foraging substrates with harvesting, but no substantial differences due to spatial pattern of retention;
- Overstory removal to have a positive impact on the abundance of aerial foragers due to an increase in air space surrounding remaining overstory trees, but no substantial differences due to spatial pattern of retention; and,
- Overstory and understory shrub removal to have an initial negative impact on the abundance of tree and shrub nesters, and foliage gleaners by removing potential nesting or foraging substrates, but also that these guilds would increase with time thereafter due to increased heterogeneity associated with forest regrowth. We expected a greater level of response among these guilds with greater levels of spatial aggregation for the reasons outlined above.

We expected treatment responses to be variable among bird species, with individual species responses consistent with guild status according to Ehrlich et al. (1988), as outlined above. For example, we hypothesized we would record lower numbers of bark-gleaning woodpeckers in the treatments versus controls because of the loss of snags and foraging substrates with logging. Similarly, we expected to record a higher abundance of aerially foraging flycatchers in treatments versus the control because of increases in air space surrounding retained overstory trees.

2. Methods

2.1. Study area and experimental design

Our study area is located on the Chippewa National Forest in north central Minnesota, USA. Mean annual temperature for this region of Minnesota is 3.9 °C and mean annual precipitation is 70.0 cm (MRCC, 2006). Study sites are located in a matrix of upland forest, bogs, and lakes and on glacial contact and outwash landforms with deep sandy soils and low topographic relief (< 10 m variation; Albert, 1995). Prior to treatment, study stands were predominantly even-aged and red pine comprised approximately 91% of basal area (Palik et al., 2003). Northern red oak (*Quercus rubra*), eastern white pine (*P. strobus*), trembling aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidentata*), paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), red maple (*Acer rubra*), white spruce (*Picea glauca*), bur oak (*Q. macrocarpa*), and black spruce (*P. mariana*) were also present, individually comprising < 0.01–2.8% of total basal area. Total basal area of study stands averaged 36 m^2/ha for trees with a diameter at breast height (DBH) greater than 10 cm.

The experiment used a randomized complete-block, split-plot design. Four blocks, each approximately 64 ha in size, were divided into four approximately 16-ha stands with three VRH treatments and an unharvested control randomly assigned to each block and crossed with a shrub layer treatment. VRH treatments included dispersed retention, which resembled a traditional shelterwood cut of evenly-spaced retained trees, aggregated retention achieved by cutting small (0.1 ha) gaps and retaining trees between the gaps, and aggregated retention achieved by cutting large (0.3 ha) gaps, again leaving trees between the gaps (Fig. 1; Palik et al., 2014). Treatments were cut between 15 August 2002 and 15 April 2003 to a basal area of approximately 17 m^2/ha. Areas of advance tree regeneration were protected and resultant basal area of each tree species remained similar to pre-harvest (Palik et al., 2003). To facilitate seedling planting, shrubs were cut with a mechanized brush cutter in mid- to late spring of 2002 across the entire stand of each VRH treatment. In spring 2003, each VRH treated stand was hand planted with red pine, eastern white pine, and jack pine (*Pinus banksiana*) seedlings at density of ~1200 trees/ha. In 2003–07, 2009, 2011, shrubs were again manually cut on one half of each treated stand but left intact (ambient) on the other half. These treatments targeted shrubs (mostly *Corylus* spp.), prolific sprouting tree species (e.g., aspens), and semi-woody herbaceous species (e.g., *Rubus* spp.) (Palik et al., 2014).

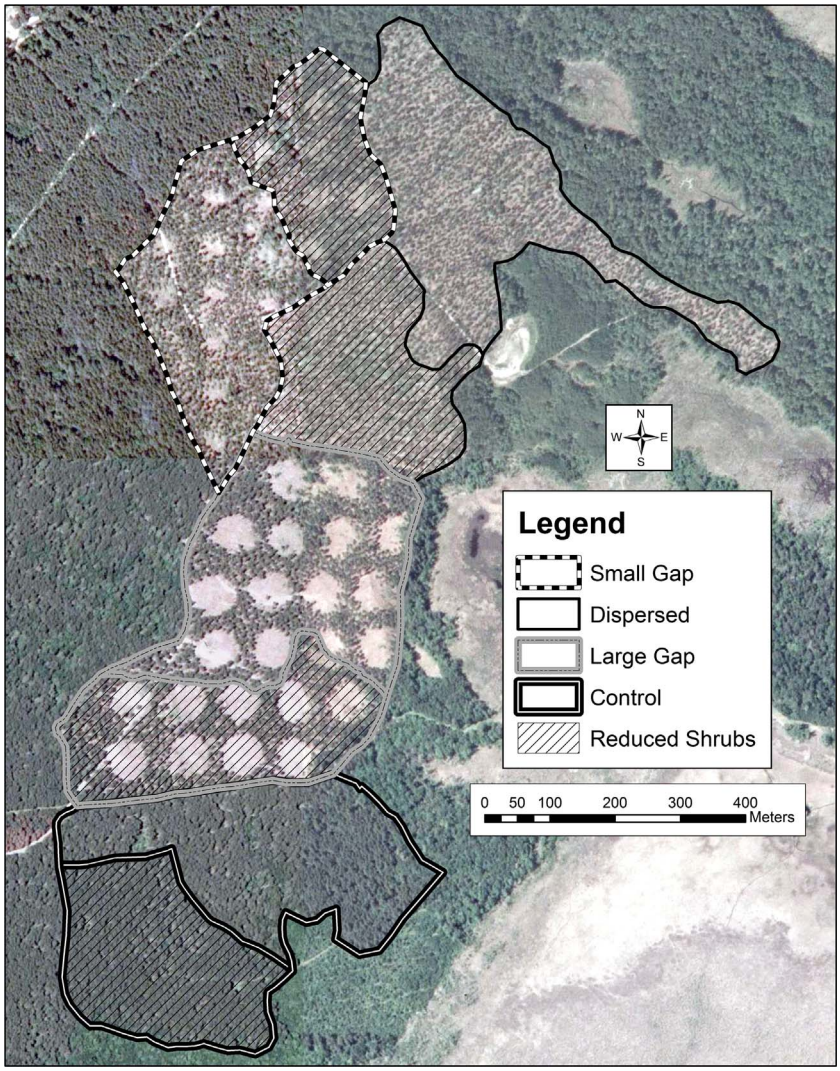

Fig. 1. Aerial image showing forest harvest treatments and shrub treatment. Combined treatments form one of four experimental blocks.

2.2. Bird sampling

Study stands were surveyed for breeding birds in 2003, 2005, 2007, 2009, 2011, and 2012. Surveys began 0.5 h before dawn and continued ≤4 h following daybreak (Blake et al., 1991) during clement weather (no rain, adequate temperature, minimal wind). Birds were surveyed three times within each retention- and shrub treatment combination between early May and mid-July using modified permanent 500-m long transects (Ralph et al., 1993; Atwell et al., 2008). Transects were randomly located, generally > 100 m from stand boundaries (Ralph et al., 1993). We recorded the spatial location of all birds seen or heard within 50 m of each transect, creating an effective sampling area of 5 ha. The order of stand visitation was alternated among survey periods. Across all sample years, a total of five individuals conducted surveys; in years when multiple surveyors conducted surveys, surveyed transects varied among surveyors.

Bird detection rates often vary among observers and species, with increased distance from observer, and over time. We did not include the observer variable in our analyses because many of the surveys in a given year were conducted by one person and, thus, observer is largely confounded with year. To minimize this source of variation, the second author trained all observers to standardized methodology. To reduce variation in detectability with distance, we employed a rectangular-transect methodology, which allowed us to use triangulation to more accurately pinpoint bird locations. Changes over time can also impact detectability, notably due to regrowth of forest understories following harvest. Therefore, we reduced the survey pace between 2003, when transects were walked at ~1.5 km/h, to ~1.0 km/h during subsequent years. We attempted to reduce the impact of differences in detectability via our survey methods, but even so, our data represent an index of bird abundance (Johnson, 2008).

2.3. Statistical analysis

We analyzed bird community, guild, and individual species responses to experimental treatments and time since harvest. Prior to analysis, we removed seven species recorded during early surveys from our analysis to avoid including birds not associated with conifer habitat (Mallard [*Anas platyrhynchos*]) or migrants (Tennessee Warbler [*Oreothlypis peregrina*], Cape May Warbler [*Setophaga tigrina*], Bay-breasted Warbler [*S. castanea*], (*Setophaga castanea*), Blackpoll Warbler [*S. striata*], Black-throated Blue Warbler [*S. caerulescens*], and Palm Warbler [*S. palmarum*]). We assessed overall community response using species richness, total bird abundance, and a nonmetric multidimensional scaling (NMS) analysis. Species richness was calculated using the total number of species across the three sample periods in a

given year; observations that we were not able to identify to species (e.g., unknown warbler; unknown sparrow) were eliminated prior to calculating species richness. Species abundance was calculated by selecting the survey with the highest number of individuals recorded from a single survey within a given breeding season at each survey location. Observations of individuals that were not identified to species were included in calculating total bird abundance. We log-transformed abundance data to meet normality assumptions.

Community data were analyzed using a linear mixed-effects statistical model (PROC MIXED) in SAS (version 9.4; SAS Institute Inc. 2013). We observed evidence of an establishment year effect and a linear effect over time in preliminary graphing of the data, so both were incorporated into the model as fixed effects. Additionally, overstory treatment, shrub treatment, the interaction between overstory and shrub treatments, and the interaction between time and overstory treatment were included as fixed effects. We used an AR1 covariance structure for repeated measures to account for the fact that surveys were conducted at the same locations over time (Diggle, 1988). For hypothesis testing, we included a Satterthwaite adjustment to approximate the denominator degrees of freedom. We carried out post hoc multiple comparisons among the three different VRH treatments when the main effect for treatment or interactions between treatment and time significantly differed using a 95% confidence interval. Bird community data were also used in a NMS analysis with PC-ORD (McCune and Mefford, 2011) using the Bray-Curtis distance measure (McCune and Grace, 2002). Initial NMS analyses were run with up to six ordination axes, but substantial contributions to stress reduction only occurred in the first two axes. For the final NMS run we used two axes, a random starting configuration, and 35 iterations with real data, which produced a final stress of 16.31 and a final instability of 0.000001 based on 121 iterations of randomized data. This model explained a relatively high proportion of data ($r^2 = 0.83$) and our level of stress was considered good for community-level data (McCune and Grace, 2002). We tested dissimilarity between the two sample periods using Mantel tests; a Monte Carlo randomization was selected to evaluate the test statistic (McCune and Grace, 2002).

Analysis was conducted on nesting and foraging guilds to understand treatment influence on specific components of the bird community. Nesting guild categories included tree or shrub, cavity, and ground (Ehrlich et al., 1988). Foraging guild categories included aerial, foliage gleaning, bark gleaning, and ground (Ehrlich et al., 1988). Unknown species were excluded from guild analysis. Separate analyses were conducted for bird abundance within each guild type with PROC GLIMMIX using the Poisson distribution and logit link in SAS. We added guild, the interaction of guild with VRH treatment, and the interaction of guild with shrub treatment to the model as fixed effects but otherwise used the same statistical model structure described for the community analyses.

Finally, we assessed changes in the abundance of individual species over the entire study period. Separate analyses were carried out for each species with PROC GLIMMIX using the Poisson distribution and logit link in SAS. We present results for 24 species for which statistical models successfully converged.

3. Results

The total number of birds observed per survey ranged from 1 to 86 individuals, with an average of 22.74. Seventy-nine bird species were recorded over the entire study period, ranging from 42 species in 2003 to 62 species in 2012. Foraging guilds consisted of ground foragers (23 species; 29.11%), foliage gleaners (31 species; 39.24%), bark gleaners (9 species; 11.39%), and aerial foragers (11 species; 13.92%), while nesting guild species were categorized into shrub and tree (50 species; 63.29%), ground (16 species; 20.25%), or cavity (12 species; 15.19%) nesting groups. The majority of species recorded across the survey years were common among VRH treatments and unharvested control stands. Two species were found only within unharvested control stands – the Red-tailed Hawk and Common Grackle – although neither requires old conifer forest. Twenty-two species were found only within VRH treatment stands (Table 1), but no species was unique to any one of the three VRH treatments. Several species of greatest conservation need in Minnesota were recorded at our experimental sites (Table 1), but none clearly in response to our treatments.

3.1. Response to VRH

We expected increases in species richness and total bird abundance to correspond with higher levels of spatial aggregation of trees among VRH treatments and over time, and found a significant interaction effect between VRH treatment and time for species richness and total abundance; the differences were largely driven by the positive effect of VRH over time compared to unharvested controls (Fig. 2; Table 2; Appendices A and B). Among the VRH treatments, species richness was greater in large gap-aggregated treatments than either dispersed ($t = 3.01$, $P = 0.01$) or small gap-aggregated ($t = 3.37$, $P = 0.01$) treatments, but no differences were found for bird abundance. In 2012, the last survey year, species richness was greater in the large gap-aggregated treatment compared to the small gap-aggregated treatment (+3.11 species/5 ha, $P < 0.01$), but no difference was detected between large gap-aggregated and dispersed treatments ($t = 2.36$, $P = 0.10$).

We expected increases in foliage gleaning and tree and shrub nesting guilds over time and with higher levels of spatial aggregation for retention. Among foraging guilds, we detected a significant three-way interaction among guild class, VRH treatment, and time for abundance (Appendix C). Foliage gleaning species increased in abundance within VRH treatments, whereas in unharvested treatments foliage, bark, and ground gleaners showed no response and aerial gleaners declined over time in all treatments except large-gap aggregate treatment (Fig. 3; Appendix D). Ground foragers showed no change over time (Fig. 3; Appendix D).

Analysis of nesting guild abundance revealed significant interactions between guild class and VRH treatment, guild class and time, and VRH treatment and time, but the three-way interaction among guild class, VRH treatment, and time was not significant (Appendix C). Cavity nesting species increased over time at a rate higher than shrub and tree nesting species ($t = 2.44$, $P = 0.02$), although their overall abundances were lower (Fig. 4). Within shrub and tree nesting species, we found greater abundances within the large gap-aggregated treatment ($t = 9.41$, $P < 0.01$), small gap-aggregated treatment ($t = 8.38$, $P < 0.01$), and dispersed retention treatment ($t = 10.47$, $P < 0.01$) compared to the unharvested control (in 2012, abundance for each treatment was, respectively: 52.4 birds/5 ha, 44.5 birds/5 ha, 62.5 birds/5 ha, 25.5 birds/5 ha). Shrub and tree nesting species also increased in abundance within VRH treatments whereas in control treatments abundance of these birds remained unchanged (Appendix E). No differences in abundance were detected for cavity or ground nesting species among the VRH treatments (Fig. 4).

The NMS analysis of 2003 and 2012 data revealed clear and growing divergence between VHR treatments and unharvested controls (Fig. 5); although a significant relationship remains between the two time periods, as measured by a Mantel test ($r = 0.40$, $P < 0.01$). Axis 1 ($r^2 = 0.37$) and Axis 2 ($r^2 = 0.47$) accounted for most of the variation in the bird community data. Eight species were strongly ($r > 0.50$) correlated with Axis 1, whereas five species were strongly correlated with Axis 2 (Fig. 5; Appendix F). Cedar Waxwing, Red-eyed Vireo, Pine

Table 1
Bird species observed along with species codes and nesting and foraging guild designations. C = Cavity nester; G = Ground nester; ST = Shrub or tree nester; A = Aerial forager; B = Bark forager; F = Foliage forager; G = Ground forager; O = Other forager (not included in analysis).

Bird common name (Scientific name), AOU Code	Nest Guild	Forage Guild	Bird common name (Scientific name), AOU Code	Nest Guild	Forage Guild
Turkey Vulture (*Cathartes aura*)[a], TUVU	O	O	Veery (*Catharus fuscescens*)[c,e], VEER	ST	F
Bald Eagle (*Haliaeetus leucocephalus*)[d], BAEA	ST	O	Hermit Thrush (*Catharus guttatus*), HETH	G	G
Red-tailed Hawk (*Buteo jamaicensis*)[b,e], RTHA	ST	O	American Robin (*Turdus migratorius*), AMRO	ST	G
Sharp-shinned Hawk (*Accipiter striatus*), SSHA	ST	A	Gray Catbird (*Dumetella carolinensis*)[a], GRCA	ST	G
Broad-winged Hawk (*Buteo platypterus*)[a], BWHA	ST	A	Cedar Waxwing (*Bombycilla cedrorum*), CEDW	ST	F
Ruffed Grouse (*Bonasa umbellus*), RUGR	G	F	Golden-winged Warbler (*Vermivora chrysoptera*)[a,c,e], GWWA	G	F
Wilson's Snipe (*Gallinago delicata*)[a], COSN	G	G	Nashville Warbler (*Oreothlypis ruficapilla*), NAWA	G	F
Common Nighthawk (*Chordeiles minor*)[a,e], CONI	G	A	Northern Parula (*Setophaga americana*), NOPA	ST	F
Ruby-throated Hummingbird (*Archilochus colubris*), RTHU	ST	A	Chestnut-sided Warbler (*Setophaga pensylvanica*), CSWA	ST	F
Northern Flicker (*Colaptes auratus*)[c], NOFL	C	G	Magnolia Warbler (*Setophaga magnolia*)[a], MAWA	ST	F
Yellow-bellied Sapsucker (*Sphyrapicus varius*), YBSA	C	B	Yellow-rumped Warbler (*Setophaga coronata*), YRWA	ST	F
Downy Woodpecker (*Picoides pubescens*), DOWO	C	B	Black-and-white Warbler (*Mniotilta varia*), BAWW	G	B
Hairy Woodpecker (*Picoides villosus*), HAWO	C	B	Blackburnian Warbler (*Setophaga fusca*), BLBW	ST	F
Black-backed Woodpecker (*Picoides arcticus*)[d,e], BBWO	C	B	Black-throated Green Warbler (*Setophaga virens*), BTNW	ST	F
Pileated Woodpecker (*Dryocopus pileatus*), PIWO	C	B	Pine Warbler (*Setophaga pinus*), PIWA	ST	F
Olive-sided Flycatcher (*Contopus cooperi*)[a,c,e], OSFL	ST	A	Yellow Warbler (*Setophaga petechia*)[a], YWAR	ST	F
Eastern Wood-Pewee (*Contopus virens*)[c], EAWP	ST	A	Mourning Warbler (*Geothlypis philadelphia*), MOWA	G	F
Alder Flycatcher (*Empidonax alnorum*)[a], ALFL	ST	A	Canada Warbler (*Cardellina canadensis*)[c], CAWA	G	A
Least Flycatcher (*Empidonax minimus*)[e], LEFL	ST	A	Ovenbird (*Seiurus aurocapilla*), OVEN	G	G
Great Crested Flycatcher (*Myiarchus crinitus*), GCFL	C	A	Common Yellowthroat (*Geothlypis trichas*), COYE	ST	F
Yellow-throated Vireo (*Vireo flavifrons*), YTVI	ST	F	American Redstart (*Setophaga ruticilla*), AMRE	ST	F
Blue-headed Vireo (*Vireo solitarius*), BHVI	ST	F	Scarlet Tanager (*Piranga olivacea*)[c], SCTA	ST	F
Red-eyed Vireo (*Vireo olivaceus*), REVI	ST	A	Eastern Towhee (*Pipilo erythrophthalmus*), EATO[e]	G	G
Blue Jay (*Cyanocitta cristata*), BLJA	ST	G	Chipping Sparrow (*Spizella passerina*), CHSP	ST	G
Gray Jay (*Perisoreus canadensis*), GRJA	ST	G	Song Sparrow (*Melospiza melodia*)[a], SOSP	ST	G
American Crow (*Corvus brachyrhynchos*), AMCR	ST	G	White-throated Sparrow (*Zonotrichia albicollis*), WTSP	G	G
Common Raven (*Corvus corax*), CORA	ST	G	Dark-eyed Junco (*Junco hyemalis*)[a], DEJU	G	G
Black-capped Chickadee (*Poecile atricapillus*), BCCH	C	F	Rose-breasted Grosbeak (*Pheucticus ludovicianus*), RBGR	ST	F
Brown Creeper (*Certhia americana*), BRCR	ST	B	Indigo Bunting (*Passerina cyanea*)[a], INBU	ST	G
White-breasted Nuthatch (*Sitta carolinensis*), WBNU	C	B	Common Grackle (*Quiscalus quiscula*)[b], COGR	ST	G
Red-breasted Nuthatch (*Sitta canadensis*), RBNU	C	B	Brown-headed Cowbird (*Molothrus ater*), BHCO	ST	G
House Wren (*Troglodytes aedon*)[a], HOWR	C	F	Purple Finch (*Haemorhous purureus*), PUFI[e]	ST	F
Golden-crowned Kinglet (*Regulus satrapa*), GCKI	ST	F	Red Crossbill (*Loxia curvirostra*), RECR	ST	O
Ruby-crowned Kinglet (*Regulus calendula*)[a], RCKI	ST	F	Pine Siskin (*Spinus pinus*), PISI	ST	F
Eastern Bluebird (*Sialia sialis*), EABL	C	G	American Goldfinch (*Spinus tristis*)[a], AMGO	ST	G
Wood Thrush (*Hylocichla mustelina*)[c,e], WOTH	ST	G	Evening Grosbeak (*Coccothraustes vespertinus*)[c], EVGR	ST	G

[a] Only documented in VRH treatment stands.
[b] Only documented in unharvested control stands.
[c] Identified as a species of regional concern (Rosenberg et al., 2016).
[d] Listed as a regionally sensitive species (US Forest Service, 2008).
[e] Minnesota listed species in greatest conservation need (MN DNR, 2016).

Warbler, American Redstart, Chestnut-sided Warbler, Mourning Warbler, Veery, and Nashville Warbler were all positively correlated with Axis 1, whereas Chestnut-sided Warbler, Mourning Warbler, Nashville Warbler, Red-breasted Nuthatch, and Red Crossbill were positively correlated with Axis 2; no species were negatively correlated with either axis (Appendix F).

Based on criteria associated with our statistical model, 24 bird species had sufficient observations for individual analysis. We observed an interaction between VRH treatment and time for seven species including: American Redstart, Chestnut-sided Warbler, Blackburnian Warbler, Black-throated Green Warbler, Ovenbird, Veery, and Red-eyed Vireo (Table 3; Appendix G). American Redstart and Chestnut-sided Warbler strongly increased in abundance within the VRH treatments and either decreased or stayed the same within the unharvested control stands (Table 3). Blackburnian Warbler significantly increased over time in large gap- and small gap-aggregated treatments. Black-throated Green Warbler significantly increased in dispersed and small gap-aggregated treatments and displayed a near-significant negative trend in large gap-aggregated treatments. Veery significantly increased over time in large gap-aggregated treatments compared to all other treatments (Table 3). Our analysis indicated a treatment effect for American Robin (Appendix G): their abundance within dispersed retention ($t = 3.75$, df = 9, $P = 0.02$) and large gap-aggregated retention ($t = 4.82$, df = 9, $P < 0.01$) treatments was greater than in the unharvested control (mean abundance in 2012, the final survey year, was 0.75 birds/5 ha, 2.38 birds/5 ha, and 0.13 birds/5 ha, respectively). Regardless of treatment, Blue-headed Vireo, Brown Creeper, Hermit Thrush, Nashville Warbler, Rose-breasted Grosbeak, and Red-breasted Nuthatch had increased over time (Appendix G). In contrast, American Robin, Black-and-white Warbler, and Least Flycatcher decreased over time (Appendix G).

3.2. Response to shrub treatment

At the community level, we found no evidence of a significant interaction between VRH treatment and shrub treatment for species richness and total abundance (Appendix A). Similarly, we detected no differences by shrub treatment for species richness or abundance, nor for foraging or nesting guilds (Appendices A and C). For individual species, analysis by shrub treatment effect indicated American Redstart, Ovenbird, and Veery occurred in greater abundance with ambient levels of shrubs, whereas Brown Creeper and Chipping Sparrow were found in greater abundance with reduced shrub densities (Table 4).

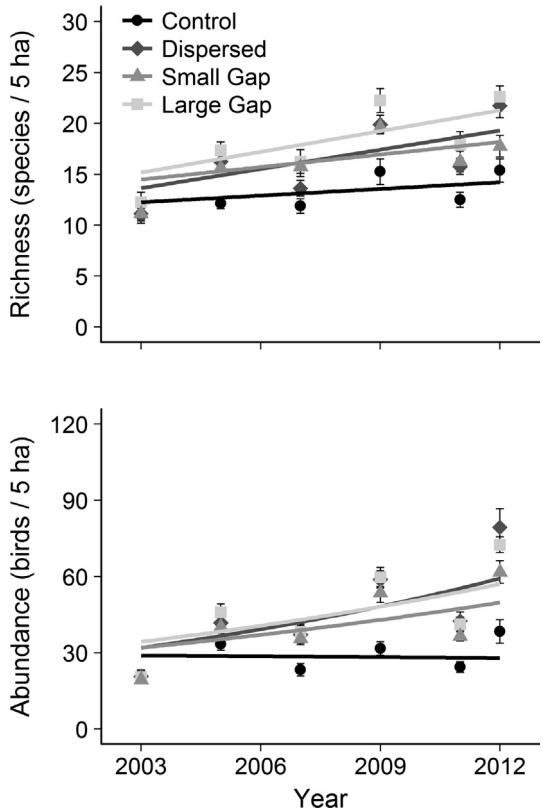

Fig. 2. Mean annual bird species richness and abundance with standard errors by VRH treatment.

Table 2
Change over time in mean annual bird species richness and total bird abundance among VRH treatments. Pair-wise comparisons of change over time among overstory treatments are indicated by superscript (significance measured at the 95% confidence interval). For richness, CI = the 95% confidence interval for absolute change over time per 5 ha; for abundance, CI = the 95% confidence interval for multiplicative change over time. CL = unharvested control, DT = dispersed retention, SG = small gap-aggregate retention, and LG = large gap-aggregate retention.

Treatment	Species Richness		Abundance	
	t, *P*	CI	*t*, *P*	CI
CL	1.92, 0.06	(−0.01, 0.44)[a]	−0.43, 0.67	(0.98, 1.01)[a]
DT	5.54, < 0.01	(0.40, 0.86)[b]	7.44, < 0.01	(1.05, 1.09)[b]
SG	3.61, < 0.01	(0.18, 0.64)[ab]	5.31, < 0.01	(1.03, 1.07)[b]
LG	5.98, < 0.01	(0.45, 0.91)[b]	6.12, < 0.01	(1.04, 1.08)[b]

4. Discussion

Variable retention harvesting (VRH) has been suggested as an approach to enhance stand-scale structural complexity relative to more traditional forest management approaches (Franklin et al., 1997). Using a VRH experiment, we evaluated the response of forest birds at the community, guild, and individual species level to the spatial pattern of retained canopy trees and density of shrubs. Previous studies from this experiment found the spatial pattern of retention influenced light and nutrient availability (Boyden et al., 2012), which in turn affected the growth response of the regenerating forest (Palik et al., 2014). These findings, coupled with well-established knowledge on the influence of habitat on forest bird diversity (MacArthur and MacArthur, 1961; Willson, 1974; Robinson and Holmes, 1982; Whelan, 2001), formed the foundation for our hypotheses.

Ten years after retention harvesting, our results largely followed our predictions, but in some instances the magnitude of responses were small or opposite of what we expected. Our results document continued increases in bird species richness and total abundance with overstory VRH treatment in comparison to the relatively unchanged unharvested controls; few differences among VRH treatments; and a limited impact of shrub reduction. We also found substantial but not complete overlap in bird community composition among VRH treatment and unharvested control stands (Shea, 2013), which is consistent with other studies of forest bird response to harvesting (Flaspohler et al., 2002; Schieck and Song, 2006).

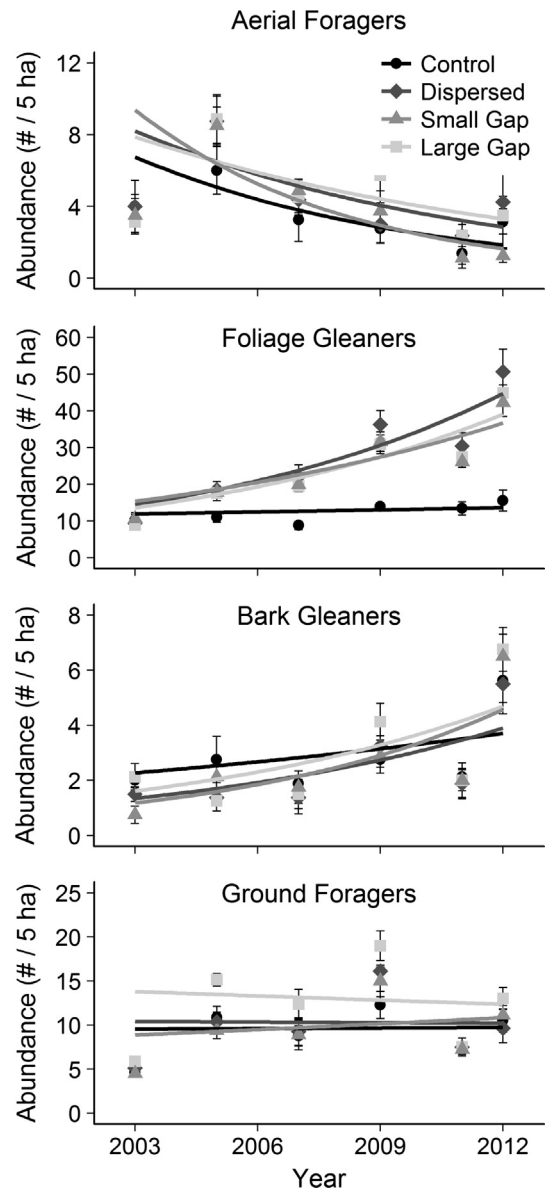

Fig. 3. Mean annual bird abundance by foraging guild with standard errors by VRH treatment.

As predicted, the bird community positively responded to VRH treatments and time, with some response to higher levels of spatial aggregation of retention. We attributed these patterns to more heterogeneous conditions following harvest, both initially and with increasing time since harvest. Forest harvest retention studies from other northern regions have also documented greater post-harvest abundance among birds that prefer open forest conditions, but suggest that the greater diversity found following harvest may last less than 20 years: early successional birds gradually become less common and birds associated with older forest become more common as the overstory closes (Schieck and Song, 2006; Perry and Thill, 2013).

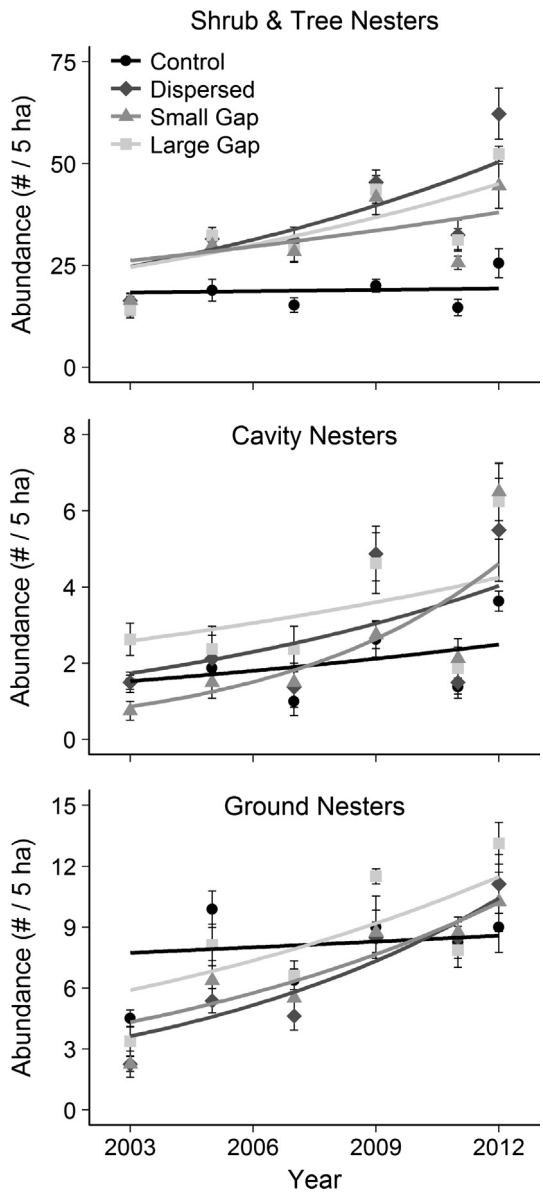

Fig. 4. Mean annual bird abundance by nesting guild with standard errors by VRH treatment.

While we documented increasing bird abundance with retention harvesting within some foraging and nesting guilds, contrary to our expectation we did not find differences with the level of aggregation. Specifically, we found positive responses in the abundance of shrub and tree nesters and foliage gleaners to retention harvesting; aerial foragers declined and all other guilds were stable in the unharvested control. Interestingly, aerial foragers declined over time in all harvest treatments except aggregate large-gap, where no changes were detected. While the reason aerial foragers declined is uncertain, our findings support other documented declines of aerial foragers on the Chippewa National Forest (Bednar et al., 2016). Combining treatments, we found a greater multiplicative rate of increase in abundance for cavity nesting birds than for shrub and tree nesting birds. However, this difference may not be ecologically significant since cavity nesting birds had low abundance in all years; small increases in abundance may appear relatively large when comparing multiplicative rates.

As expected, the response of individual bird species was consistent with their guild classifications. American Redstart and Chestnut-sided Warbler abundance increased over time in VRH treatments, while respectively declining or remaining stable in the unharvested control. Both species prefer the more open conditions of early-successional forest with adequate shrub cover, as found within VRH treatments in general regardless of spatial pattern (Sherry and Holmes, 1997; Byers et al., 2013).

Our prediction for positive responses in bird species richness and abundance to a well-established shrub layer was not supported at the community and guild levels, but held for some individual bird species. While we find the lack of response to shrub manipulation surprising, the presence of a retained overstory may have overwhelmed bird responses to shrub density; indeed, the canopy layer has been shown to greatly influence bird guilds use of understory vegetation layers (Willson, 1974). At the individual species level, American Redstart, Ovenbird, and Veery occurred at greater abundances in the ambient shrub treatment, whereas Chipping Sparrow and Brown Creeper occurred at greater abundance where shrub cover was reduced. Greater abundance of Brown Creeper in VRH stands with a sparser shrub layer is of particular interest as this species is typically found in more closed forest conditions. While the density of large, mature trees on which Brown Creeper nests and forages influences the likelihood of their presence (Poulin et al., 2008), higher bird abundance in reduced-shrub treatments suggests that visible access to the lower portion of the bark profile may also influence this species.

Several caveats should be considered when interpreting our results. First, while abundance data are frequently used to infer habitat quality, we did not measure avian fecundity—a more direct measure of habitat quality—and thus a certain degree of caution is warranted (Van Horne, 1983). Secondly, although our 10-year study is longer than most forest wildlife studies, it is still short considering historical fire return intervals in pine forests in the region that are measured on the order of several centuries for stand-replacement events (Heinselman, 1996). Third, while we did not detect a difference in bark gleaners or cavity nesters among VRH treatments and the control, both guilds were present at low levels of abundance in all stands. In results not presented, we found the density of downed dead wood and snags to be low throughout the study area, which may account for the low abundance of these guilds. Where management priorities include maintaining structurally complex forests and associated biodiversity, more attention may need to be placed on recruiting and retaining standing and downed dead wood.

Finally, studies estimating the response of forest birds to harvest practices suggest the overall amount of intact forest may be more important to birds than the spatial configuration of remaining forest (Imbeau et al., 2001; Droblet et al., 1999), especially for species with specific habitat requirements or conditions (Schieck and Song, 2006). Our results demonstrate, however, that while the spatial arrangement of VRH and shrub control have a minor impact on community measures, they can impact individual bird species. This research suggests that silviculture approaches designed to approximate natural disturbance processes and patterns can create habitat suitable for a subset of the forest-dwelling bird community.

4.1. Conclusion

Our results indicate that retaining components of the overstory and shrub layer at harvest—approximating the structural outcomes of natural disturbance—can provide habitat for a rich, abundant, and diverse forest bird community, and create habitat suitable for many individual species. However, some individuals or guilds (e.g., late-successional species; cavity nesting birds) may require larger areas of unharvested forest or further accretion of structural attributes (e.g., snags) to utilize these treatments in greater abundance. The limited differences we found among VRH treatments suggests forest managers have flexibility in how they implement retention harvesting, i.e., dispersed versus aggregated, shrub retention versus reduction. Spatially varying the retention pattern within a harvest unit may best meet the goal of maintaining vibrant forest bird communities.

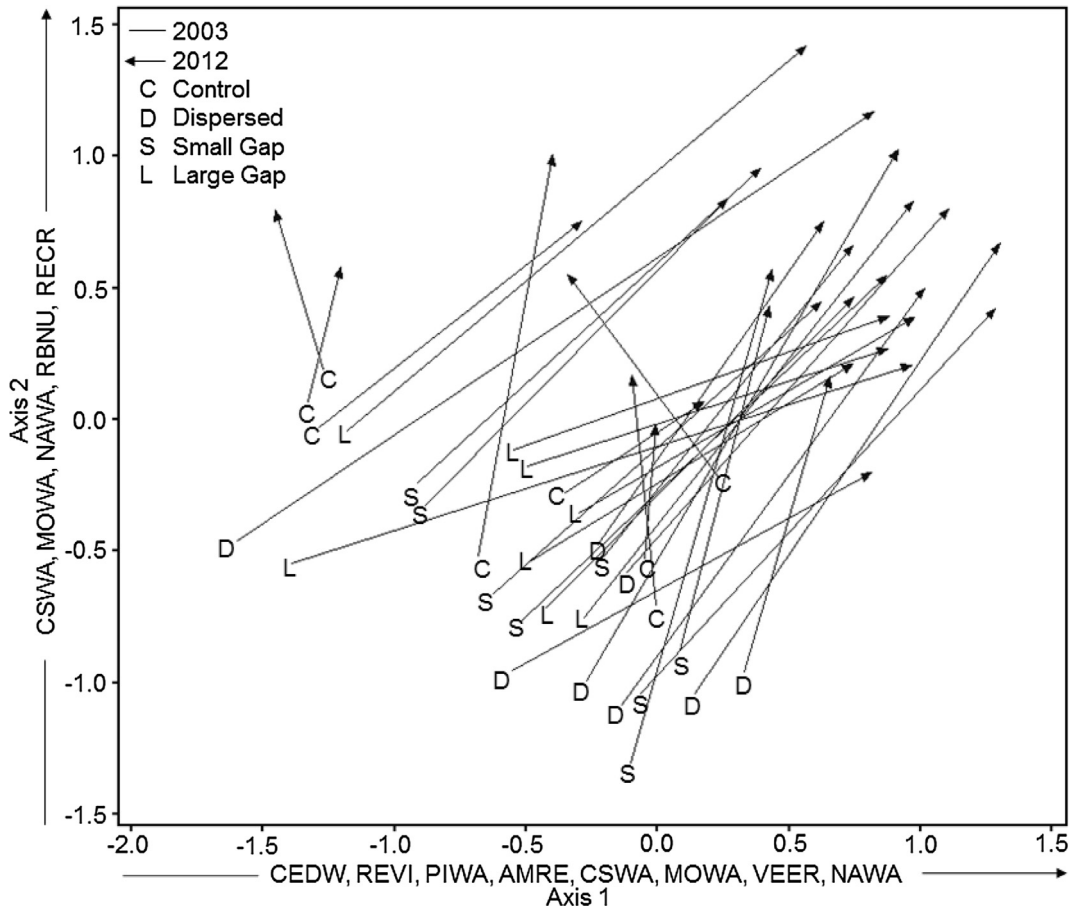

Fig. 5. Non-metric multidimensional scaling (NMS) results from 2003 and 2012 survey seasons showing variation in avian community composition among the variable retention harvest treatments and treatment-level changes in avian community composition between 2013 and 2012. Lines begin at 2003 and end at 2012 (arrow tip). Species correlations with axes are in Appendix F. Species identified along axes had correlations equal to or greater than 0.50 (CEDW = Cedar Waxwing; REVI = Red-eyed Vireo; PIWA = Pine Warbler; AMRE = American Redstart; CSWA = Chestnut-sided Warbler; MOWA = Mourning Warbler; VEER = Veery; NAWA = Nashville Warbler; RBNU = Red-breasted Nuthatch; RECR = Red Crossbill).

Table 3
Change in bird species estimated mean abundance over time. Superscript indicates significant differences ($P \leq 0.05$) among overstory treatment abundance slopes. See Table 1 for definition of species abbreviations. CI = the 95% confidence interval for multiplicative change over time.

Bird species	Unharvested control		Dispersed retention		Small gap-aggregate retention		Large gap-aggregate retention	
	t, *P*	CI	*t*, *P*	CI	*t*, *P*	CI	*t*, *P*	CI
NOFL	0.36, 0.72	(0.71, 1.64)^{a}	−1.38, 0.17	(0.76, 1.05)^{a}	0.22, 0.83	(0.80, 1.32)^{a}	−2.91, < 0.01	(0.65, 0.92)^{a}
LEFL	−3.55, < 0.01	(0.69, 0.90)^{a}	−3.32, < 0.01	(0.75, 0.93)^{a}	−4.71, < 0.01	(0.62, 0.82)^{a}	−3.89, < 0.01	(0.71, 0.89)^{a}
EAWP	−0.17, 0.87	(0.91, 1.08)^{a}	−1.27, 0.21	(0.88, 1.03)^{a}	−0.64, 0.52	(0.89, 1.06)^{a}	0.41, 0.69	(0.94, 1.09)^{a}
BLJA	0.93, 0.35	(0.92, 1.28)^{a}	0.69, 0.49	(0.92, 1.20)^{a}	−0.03, 0.97	(0.88, 1.13)^{a}	1.27, 0.21	(0.96, 1.22)^{a}
BCCH	−0.05, 0.96	(0.76, 1.30)^{a}	1.57, 0.12	(0.97, 1.36)^{a}	2.19, 0.03	(1.02, 1.58)^{a}	0.84, 0.40	(0.92, 1.23)^{a}
RBNU	8.40, < 0.01	(1.10, 1.28)^{a}	4.35, < 0.01	(1.10, 1.28)^{a}	4.38, < 0.01	(1.10, 1.28)^{a}	5.50, < 0.01	(1.15, 1.35)^{a}
BRCR	4.98, < 0.01	(1.24, 1.64)^{a}	3.24, < 0.01	(1.14, 1.74)^{a}	4.67, < 0.01	(1.28, 1.83)^{a}	5.09, < 0.01	(1.27, 1.73)^{a}
AMRO	−1.37, 0.17	(0.69, 1.17)^{a}	−2.18, 0.03	(0.79, 0.99)^{a}	−2.94, < 0.01	(0.73, 0.94)^{a}	−0.90, 0.37	(0.88, 1.05)^{a}
HETH	1.15, 0.25	(0.95, 1.20)^{a}	1.40, 0.16	(0.96, 1.24)^{a}	2.40, 0.02	(1.03, 1.36)^{a}	0.11, 0.91	(0.91, 1.12)^{a}
VEER	2.35, 0.02	(1.03, 1.44)^{a}	5.86, < 0.01	(1.23, 1.51)^{a}	3.77, < 0.01	(1.10, 1.38)^{a}	7.16, < 0.01	(1.53, 2.12)^{b}
BHVI	0.82, 0.41	(0.91, 1.27)^{a}	2.81, 0.01	(1.07, 1.50)^{a}	1.05, 0.30	(0.92, 1.31)^{a}	1.19, 0.24	(0.95, 1.25)^{a}
REVI	0.02, 0.98	(0.96, 1.05)^{ab}	3.21, < 0.01	(1.03, 1.12)^{c}	−1.23, 0.22	(0.93, 1.02)^{b}	1.81, 0.07	(1.00, 1.09)^{ac}
BAWW	−1.90, 0.06	(0.63, 1.01)^{a}	−0.46, 0.65	(0.74, 1.20)^{a}	−2.49, 0.01	(0.42, 0.90)^{a}	0.01, 0.99	(0.76, 1.32)^{a}
NAWA	11.15, < 0.01	(1.46, 1.73)^{a}	5.63, < 0.01	(1.28, 1.67)^{a}	6.10, < 0.01	(1.40, 1.92)^{a}	5.67, < 0.01	(1.42, 2.06)^{a}
YRWA	−0.43, 0.67	(0.83, 1.12)^{a}	0.60, 0.55	(0.92, 1.16)^{a}	0.36, 0.72	(0.91, 1.15)^{a}	2.66, 0.01	(1.04, 1.31)^{a}
BTNW	1.58, 0.11	(0.98, 1.22)^{a}	2.65, 0.01	(1.08, 1.67)^{a}	2.39, 0.02	(1.03, 1.38)^{a}	−1.91, 0.06	(0.54, 1.01)^{b}
BLBW	4.39, < 0.01	(1.13, 1.39)^{a}	2.35, 0.02	(1.02, 1.24)^{ab}	0.93, 0.35	(0.95, 1.16)^{b}	1.03, 0.30	(0.94, 1.20)^{b}
CSWA	−0.27, 0.78	(0.88, 1.10)^{a}	6.28, < 0.01	(1.13, 1.25)^{b}	6.16, < 0.01	(1.13, 1.26)^{b}	6.36, < 0.01	(1.13, 1.26)^{b}
PIWA	−0.54, 0.59	(0.94, 1.04)^{a}	−1.13, 0.26	(0.93, 1.02)^{a}	−1.05, 0.29	(0.93, 1.02)^{a}	−0.01, 0.99	(0.95, 1.05)^{a}
OVEN	−1.05, 0.30	(0.95, 1.02)^{a}	1.03, 0.30	(0.98, 1.08)^{ab}	2.43, 0.02	(1.01, 1.10)^{bc}	−1.54, 0.13	(0.92, 1.01)^{a}
MOWA	−1.40, 0.16	(0.31, 1.22)^{a}	2.39, 0.02	(1.03, 1.33)^{a}	1.56, 0.12	(0.97, 1.25)^{a}	1.99, 0.05	(1.00, 1.27)^{a}
AMRE	−2.70, 0.01	(0.70, 0.95)^{a}	3.82, < 0.01	(1.06, 1.20)^{b}	2.30, 0.02	(1.01, 1.17)^{b}	1.91, 0.06	(1.00, 1.19)^{b}
RBGR	1.37, 0.17	(0.89, 1.87)^{a}	2.20, 0.03	(1.02, 1.39)^{a}	1.58, 0.12	(0.97, 1.35)^{a}	1.48, 0.14	(0.96, 1.30)^{a}
CHSP	0.45, 0.65	(0.94, 1.11)^{a}	−3.12, < 0.01	(0.85, 0.97)^{a}	−0.7, 0.49	(0.92, 1.04)^{a}	−1.49, 0.14	(0.91, 1.01)^{a}

Table 4
Bird species abundance means and pairwise comparisons of shrub treatments. Superscript represents significantly greater bird species abundance for either the ambient (AM) or reduced density (RD) shrub treatment. See Table 1 for definition of species abbreviations.

Bird species	Ambient vs. Reduced Density		
	Ambient	Reduced	*t*, *P*
NOFL	0.29	0.23	−0.85, 0.40
LEFL	2.39	3.39	1.85, 0.07
EAWP	0.97	0.99	0.42, 0.68
BLJA	0.59	0.53	−0.94, 0.35
BCCH	0.41	0.29	−1.07, 0.28
RBNU	1.34	1.42	0.10, 0.92
BRCRRD	0.35	0.57	2.51, 0.01
AMRO	0.78	1.05	0.28, 0.78
HETH	0.81	0.70	−0.60, 0.55
VEER^{AM}	0.81	0.36	−5.57, < 0.01
BHVI	0.47	0.32	−1.87, 0.06
REVI	2.64	2.59	−0.25, 0.80
BAWW	0.27	0.30	0.28, 0.78
NAWA	0.99	0.95	−0.30, 0.77
YRWA	1.15	1.10	−0.19, 0.85
BTNW	0.44	0.29	−1.87, 0.06
BLBW	0.96	0.85	0.67, 0.50
CSWA	5.71	5.20	−1.81, 0.07
PIWA	2.57	2.67	0.68, 0.50
OVEN^{AM}	3.21	2.88	−2.75, 0.01
MOWA	1.05	1.73	0.93, 0.35
AMRE^{AM}	4.38	2.65	−3.33, < 0.01
RBGR	0.43	0.32	−0.52, 0.60
CHSPRD	2.60	3.60	3.28, < 0.01

Acknowledgements

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Appendix A

Values for type three fixed effects of community-level bird responses. Significance measured at the 95% confidence interval. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom.

Model and response variable	NDF	DDF	F	*P*
Treatment + Time				
Species Richness	3	80.3	4.35	0.01
Abundance	3	78.7	15.05	< 0.01
Treatment + Shrub				
Species Richness	3	12	0.83	0.50
Abundance	3	12	0.71	0.56
Shrub				
Species Richness	1	12	1.38	0.26
Abundance	1	12	0.30	0.59

Appendix B

Pair-wise comparisons of change over time in mean annual bird species richness and total bird abundance among VRH treatments. Higher responses were recorded for starred (∗) treatments in comparisons with significant differences. CL = unharvested control, DT = dispersed retention, SG = small gap-aggregate retention, and LG = large gap-aggregate retention. For richness, CI = pairwise difference of the 95% confidence interval for absolute change over time per 5 ha; for abundance, CI = pairwise difference of the 95% confidence interval for multiplicative change over time.

Treatments	Species Richness		Abundance	
	t, *P*	CI	*t*, *P*	CI
CL vs DT*	2.85, < 0.01	(0.12, 0.70)	6.22, < 0.01	(1.05, 1.10)
CL vs SG*	1.33, 0.19	(−0.10, 0.48)	4.54, < 0.01	(1.03, 1.08)
CL vs LG*	3.20, < 0.01	(0.17, 0.75)	5.17, < 0.01	(1.04, 1.09)
DT vs SG	1.52, 0.13	(−0.07, 0.51)	1.68, 0.10	(1.00, 1.04)

DT vs LG	−0.35, 0.73	(−0.34, 0.24)	1.04, 0.30	(0.99, 1.04)
LG vs SG	1.87, 0.07	(−0.02, 0.56)	0.64, 0.53	(0.98, 1.03)

Appendix C

Model values for type three fixed effects of guild-level bird responses. Significance measured at the 95% confidence interval. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom.

Model and response variable	NDF	DDF	F	*P*
Foraging Guild Abundance				
Guild + Treatment + Time	9	319.9	1.98	0.04
Shrub	1	272.0	3.15	0.08
Nesting Guild Abundance				
Guild + Treatment + Time	6	238.5	1.81	0.10
Guild + Treatment	6	225.8	4.71	< 0.01
Guild + Time	2	238.4	4.68	0.01
Treatment + Time	3	237.9	5.53	< 0.01
Shrub	1	226.2	0.87	0.35

Appendix D

Change over time in mean annual bird abundance by foraging guild. CL = unharvested control, DT = dispersed retention, SG = small gap-aggregated retention, and LG = large gap-aggregated retention. CI = the multiplicative change in abundance at the 95% confidence interval.

Treatment	Aerial Foragers		Foliage Gleaners		Bark Gleaners		Ground Foragers	
	t, *P*	CI	*t*, *P*	CI	*t*, *P*	CI	*t*, *P*	CI
CL	−2.77, 0.01	(0.75, 0.95)	−0.08, 0.94	(0.95, 1.05)	0.78, 0.43	(0.93, 1.17)	0.51, 0.61	(0.96, 1.08)
DT	−2.75, 0.01	(0.80, 0.96)	5.34, < 0.01	(1.06, 1.15)	1.48, 0.14	(0.97, 1.26)	−0.68, 0.49	(0.92, 1.04)
SG	−3.62, < 0.01	(0.74, 0.92)	5.51, < 0.01	(1.07, 1.16)	1.94, > 0.05	(1.00, 1.31)	1.53, 0.13	(0.99, 1.12)
LG	−1.82, 0.07	(0.84, 1.00)	5.56, < 0.01	(1.08, 1.17)	1.78, 0.08	(0.99, 1.25)	−0.77, 0.44	(0.93, 1.03)

Appendix E

Change over time in mean annual bird abundance by nesting guild. CL = unharvested control, DT = dispersed retention, SG = small gap-aggregated retention, and LG = large gap-aggregated retention. CI = the multiplicative change in abundance at the 95% confidence interval.

Treatment	Shrub/Tree Nesters		Cavity Nesters		Ground Nesters	
	t, *P*	CI	*t*, *P*	CI	*t*, *P*	CI
CL	0.28, 0.78	(0.97, 1.05)	0.37, 0.71	(0.91, 1.14)	0.37, 0.71	(0.96, 1.07)
DT	4.13, < 0.01	(1.03, 1.09)	1.33, 0.18	(0.97, 1.18)	2.60, 0.01	(1.02, 1.17)
SG	3.91, < 0.01	(1.03, 1.09)	2.76, 0.01	(1.05, 1.34)	3.69, < 0.01	(1.06, 1.21)
LG	4.36, < 0.01	(1.04, 1.10)	1.09, 0.28	(0.96, 1.15)	1.69, 0.09	(0.99, 1.11)

Appendix F

Correlations of bird species observations from 2003 and 2012 with axes from non-metric multidimensional scaling (NMS) ordination.

Bird species	Axis 1, *r*	Axis 2, *r*
Turkey Vulture	0.21	0.16
Bald Eagle	0.07	0.10
Red-tailed Hawk	0.00	−0.01
Sharp-shinned Hawk	−0.22	−0.01
Ruffed Grouse	0.24	0.13
Ruby-throated Hummingbird	0.23	0.35
Northern Flicker	0.42	0.38
Yellow-bellied Sapsucker	0.38	0.20
Downy Woodpecker	0.08	−0.03
Hairy Woodpecker	0.25	0.18

Black-backed Woodpecker	−0.21	0.07
Pileated Woodpecker	0.32	0.35
Eastern Wood-Pewee	0.19	−0.02
Alder Flycatcher	0.13	0.09
Least Flycatcher	0.10	−0.33
Great Crested Flycatcher	0.25	0.20
Yellow-throated Vireo	0.27	0.13
Blue-headed Vireo	0.36	0.28
Red-eyed Vireo	0.64	0.25
Blue Jay	0.26	0.35
Gray Jay	0.10	0.27
American Crow	0.22	0.23
Common Raven	−0.03	0.22
Black-capped Chickadee	0.08	0.19
Brown Creeper	0.17	0.37
White-breasted Nuthatch	0.25	0.16
Red-breasted Nuthatch	0.43	0.75
Golden-crowned Kinglet	0.10	0.27
Eastern Bluebird	0.22	0.08
Wood Thrush	0.03	0.23
Veery	0.59	0.38
Hermit Thrush	0.29	0.46
American Robin	0.29	0.19
Cedar Waxwing	0.56	0.27
Golden-winged Warbler	0.16	0.01
Nashville Warbler	0.55	0.67
Northern Parula	−0.09	0.31
Chestnut-sided Warbler	0.82	0.65
Magnolia Warbler	0.07	0.18
Yellow-rumped Warbler	−0.08	−0.22
Black-and-white Warbler	0.32	0.22
Blackburnian Warbler	0.10	0.39
Black-throated Green Warbler	−0.28	0.33
Pine Warbler	0.60	0.10
Yellow Warbler	0.23	0.19
Mourning Warbler	0.59	0.55
Ovenbird	−0.01	0.34
Common Yellowthroat	0.20	0.15
American Redstart	0.65	0.36
Scarlet Tanager	0.34	0.28
Chipping Sparrow	0.46	0.10
White-throated Sparrow	0.39	0.37
Rose-breasted Grosbeak	0.47	0.37
Indigo Bunting	0.23	0.19
Brown-headed Cowbird	0.04	−0.04
Purple Finch	0.14	0.05
Red Crossbill	0.28	0.55
Pine Siskin	0.22	0.08
American Goldfinch	0.17	0.14
Evening Grosbeak	−0.09	−0.19

Appendix G

Values for type three fixed effects of individual bird responses. Significance measured at the 95% confidence interval. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom.

Model and response variable	NDF	DDF	F	*P*
Treatment + Time				
American Redstart	3	167	5.45	< 0.01
Chestnut-sided Warbler	3	167	3.48	0.02
Blackburnian Warbler	3	167	2.71	0.05
Black-throated Green Warbler	3	167	3.84	0.01
Ovenbird	3	167	4.02	< 0.01
Veery	3	167	5.50	< 0.01

Red-eyed Vireo	3	167	4.61	< 0.01
Treatment				
American Robin	3	9	5.98	0.02
Time (increasing trend)				
Blue-headed Vireo	1	167	7.98	0.01
Brown Creeper	1	167	37.69	< 0.01
Hermit Thrush	1	167	6.11	0.01
Nashville Warbler	1	167	124.39	< 0.01
Rose-breasted Grosbeak	1	167	8.01	< 0.01
Red-breasted Nuthatch	1	167	70.51	< 0.01
Time (decreasing trend)				
American Robin	1	167	10.06	< 0.01
Black-and-white Warbler	1	167	6.68	0.01
Least Flycatcher	1	167	50.28	< 0.01

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