

5-30-2008

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Ryan C. Atwell
Iowa State University

Lisa A. Schulte
Iowa State University, lschulte@iastate.edu

Brian J. Palik
United States Forest Service

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Abstract

Traditional harvesting practices frequently result in simplification of the structure and composition within managed forest stands in comparison to their natural counterparts. In particular, loss of heterogeneity within stands may pose a problem for maintaining biodiversity in perpetuity. In this study, we survey breeding bird diversity and abundance in response to different spatial harvesting patterns in mature red pine forests located on the Chippewa National Forest of northern Minnesota, USA. Treatments are designed to increase structural complexity over time and include three overstory manipulations (dispersed retention, aggregate retention with small gaps, and aggregate retention with large gaps), one understory manipulation (brush removal), and controls (no harvesting, and/or no brush removal). In 2003, the first breeding season following the harvest, we found little difference in bird community composition between control and treatment stands. In 2005, the third breeding season following harvest, avian abundance, richness, and diversity were all greater within treatments. Species associated with edge, shrub, and early successional habitats generally show positive response to treatments (e.g. Chestnut-sided Warbler [*Dendroica pensylvanica*], Mourning Warbler [*Oporornis philadelphia*], Chipping Sparrow [*Spizella passerine*]), as do some species associated with mature forest (e.g., Pine Warbler [*Dendroica pinus*], Rose-breasted Grosbeak [*Pheucticus ludovicianus*]). Ovenbirds (*Seiurus aurocapilla*) and Black-throated Green Warblers (*Dendroica virens*) were more abundant in control stands. There are, as of yet, no discernable differences in avian community composition among the three overstory treatments or between the single understory treatment and the understory control, but differences are expected as the treatments diversify due to understory development. While overstory retention harvests provide habitat for a diverse and abundant bird community, the temporal divergence in avian community composition that we observed between treatment and control stands reveals the importance of uncut, mature red pine forest as a component of a biodiverse landscape.

Keywords

avian ecology, biodiversity, Minnesota, partial overstory retention, restoration, structural complexity, timber harvesting

Disciplines

Ecology and Evolutionary Biology | Natural Resources Management and Policy

Comments

This article is from *Forest Ecology and Management* 255, no. 10 (2008): 3621–3631, doi:[10.1016/j.foreco.2008.02.049](https://doi.org/10.1016/j.foreco.2008.02.049).

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Ryan C. Atwell^{a,*}, Lisa A. Schulte^a, Brian J. Palik^b

^a Natural Resource Ecology and Management, Iowa State University, 339 Science II, Ames, IA 50011, USA

^b US Forest Service Northern Research Station, 1831 Highway 169 E, Grand Rapids, MN 55744, USA

ARTICLE INFO

Article history:

Received 25 July 2007

Received in revised form 26 February 2008

Accepted 29 February 2008

Keywords:

Avian ecology

Biodiversity

Minnesota

Partial overstory retention

Restoration

Structural complexity

Timber harvesting

ABSTRACT

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1. Introduction

Ecologically-based forestry has been proposed as a means of meeting silvicultural objectives beyond tree regeneration, including forest restoration, biodiversity enhancement, fuel reduction, disease control, and improved aesthetics (Franklin et al., 1997; Moore et al., 1999; Palik et al., 2003a; Halpern et al., 2005; Seymour and Hunter, 1999). The use of overstory retention at harvest is one of the key implementation approaches for ecological forestry, and is grounded in the concept of biological legacies (i.e., organism, organic materials, and organic patterns that survive a disturbance and provide complexity to the new stand; Franklin et al., 1997).

Retention at harvest, particularly of large residual trees, is increasingly employed to enhance the complexity of forests traditionally managed for a single-cohort structure (Franklin et al., 1997; Palik et al., 2003a). Retained trees can be left in various spatial distributions, either uniformly dispersed or aggregated in clumps of varying sizes.

Though supported by principle, few tests of the effects of overstory retention on biodiversity response and community dynamics have been published (Schulte et al., 2006), although work in various regions is being conducted (Monserud, 2002; Palik et al., 2003a; Halpern et al., 2005). The level and spatial pattern of retention may have substantial, direct impacts on future forest composition, productivity, and diversity by altering stand-level resource availability and competitive environments (Palik et al., 2003a; Halpern et al., 2005). While studies have long shown that many wildlife species, and birds in particular, respond to the

* Corresponding author. Tel.: +1 515 294 2957; fax: +1 515 294 2995.

E-mail address: ryancardiffatwell@gmail.com (R.C. Atwell).

structural heterogeneity of habitat within forest environments (MacAurthur and MacAurthur, 1961; Hilden, 1965; Willson, 1974; Schulte and Niemi, 1998; Saab, 1999), the specific habitat elements to which wildlife respond are less well-known. It is expected that wildlife will respond positively to ecologically-based forestry practices that mimic the structural complexity of natural stands (Schmiegelow and Monkkonen, 2002), but on-the-ground tests from geographically and ecologically varied locations are needed before such practices can be broadly recommended (Erhlich, 1996; Schulte et al., 2006). In particular, it is important to differentiate wildlife response to key structures which can be incorporated into forest management regimes (e.g., green tree, snag, shrub, and coarse woody debris retention) versus responses that might be more local in character (e.g., edaphic conditions, ephemeral ponds, abundance of fruit or nut bearing trees).

Ecological forestry approaches have specifically been proposed as a means of restoring and enhancing red pine (*Pinus resinosa*) forests in the northern Great Lakes region of the U.S. (Palik and Zasada, 2003). Today, the extent and dominance of red pine in the northern Great Lakes region is greatly reduced compared to pre-Euro-American settlement levels (Schulte et al., 2007). Following the initial cutover of the region between the mid-1800s and the early 1900s, red pine regenerated naturally on some of the sites that it had historically occupied; other stands were artificially regenerated in even-aged plantations. In either case, the historically important process of fire disturbance was eliminated from red pine ecosystems, resulting in structural and compositional differences in present day red pine forests relative to their historical counterparts (Heinselman, 1996; Radeloff et al., 1999). Historically, for instance, red pine forests could exhibit a multi-cohort age structure, were highly variable in tree density, and frequently contained a mixture of tree species (Frelich and Reich, 1995; Heinselman, 1973; Whitney, 1986). In locations where fire was very frequent (10–50 years), red pine even existed in a savanna condition (Heinselman, 1996; Radeloff et al., 1999). Red pine forests today are largely single-cohort and monospecific (Palik and Zasada, 2003). Where the intention is to manage these stands for ecological goods and services beyond timber production, ecological forestry approaches may assist in meeting non-timber goals, including sustainability of native wildlife communities and diversity.

To improve understanding of wildlife response to overstory retention, we tested for differences in initial bird response to experimental retention harvest of red pine forests in northern Minnesota. This research is part of the Red Pine Ecosystem Complexity Study, which seeks to develop and evaluate approaches which increase the compositional and structural complexity of red pine forests while maintaining wood production (Palik and Zasada, 2003; Seymour et al., 2006). Overstory retention was incorporated into harvests to provide residual tree legacies and, ultimately, to enhance the size, age, and compositional complexity of what were largely single-cohort, monotypic stands. Overstory treatments consist of differing spatial patterns of retention, including dispersed retention and several types of aggregate retention (Fig. 1). Stands are now being managed for a

two-cohort structure and may potentially be managed as multi-cohort in the future. Compositional diversity is being enhanced by underplanting eastern white pine (*P. strobus*), red pine, and jack pine (*P. banksiana*). Manual shrub control is also being implemented, in lieu of prescribed surface fire, to enhance understory competitive environments for tree seedlings, to improve tree recruitment, and to encourage the development of a more floristically diverse understory.

In the context of this experiment, we hypothesized that bird abundance and richness would increase concomitantly with the level of aggregation of the retained overstory trees. We based this hypothesis on the following: (1) studies showing that forest songbirds respond to the amount and configuration of vegetation heterogeneity (MacAurthur and MacAurthur, 1961; Hilden, 1965; Willson, 1974; Schulte and Niemi, 1998; Saab, 1999), including heterogeneity created by retention of residual canopy trees over decadal timeframes (Schieck and Song, 2006), (2) research showing that single-cohort red pine plantations generally have low vegetation heterogeneity (Palik and Zasada, 2003), and (3) the supposition that understory response is expected to be greatest and most diverse in the large gap retention, due to a more heterogeneous light environment (Palik and Zasada, 2003).

2. Methods

2.1. Study area

The four replicated blocks that formed our study area are located within largely single-cohort, monotypic red pine forests on the Chippewa National Forest in northern Minnesota, USA. All four experimental blocks are low in elevation, have low topographic relief, are located on an outwash ice contact landform with deep sandy soil, and are similar in climate (average annual temperature = 3.9 °C; average annual precipitation = 70.0 cm; MRCC, 2006). According to National Forest records, study stands regenerated naturally after a seed tree cut (10% residual pine) between 1910 and 1912 and have since been entered two to three times for thinning (Palik et al., 2003b). A few stands were burned in the 1990s to increase blueberry production. Pre-harvest basal areas of the study stands averaged 36 m²/ha for trees above 10 cm diameter at 1.4 m height. Red pine comprised about 90% of total basal area. Species found in lesser amounts included trembling aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidentata*), paper birch (*Betula papyrifera*), eastern white pine, balsam fir (*Abies balsamea*), northern red oak (*Quercus rubra*), red maple (*Acer rubra*), white spruce (*Picea glauca*), burr oak (*Q. macrocarpa*), and black spruce (*P. mariana*).

Our experimental design was a randomized complete block replicated four times. Blocks consisted of three overstory retention treatments and an unharvested control, each of which was further divided into an understory competition treatment and an understory control (Fig. 2). Blocks were approximately 64 ha in extent and consisted of four ~16 ha stands. Overstory treatments retained a residual basal area of ~18 m²/ha, but residual trees were left in different spatial configurations (Fig. 1), including (1) a

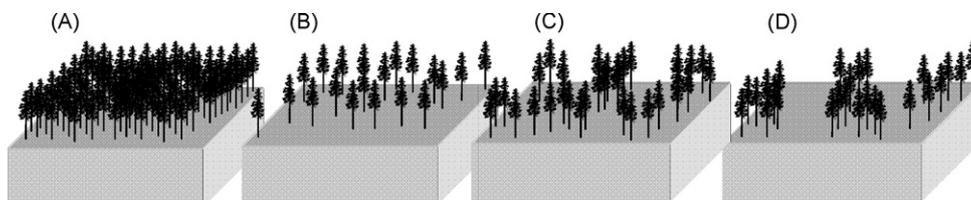


Fig. 1. Conceptual representation of overstory treatments: (A) unharvested forest (control), (B) dispersed retention of overstory trees, (C) retention of overstory trees between small gaps, and (D) retention of overstory trees between large gaps.

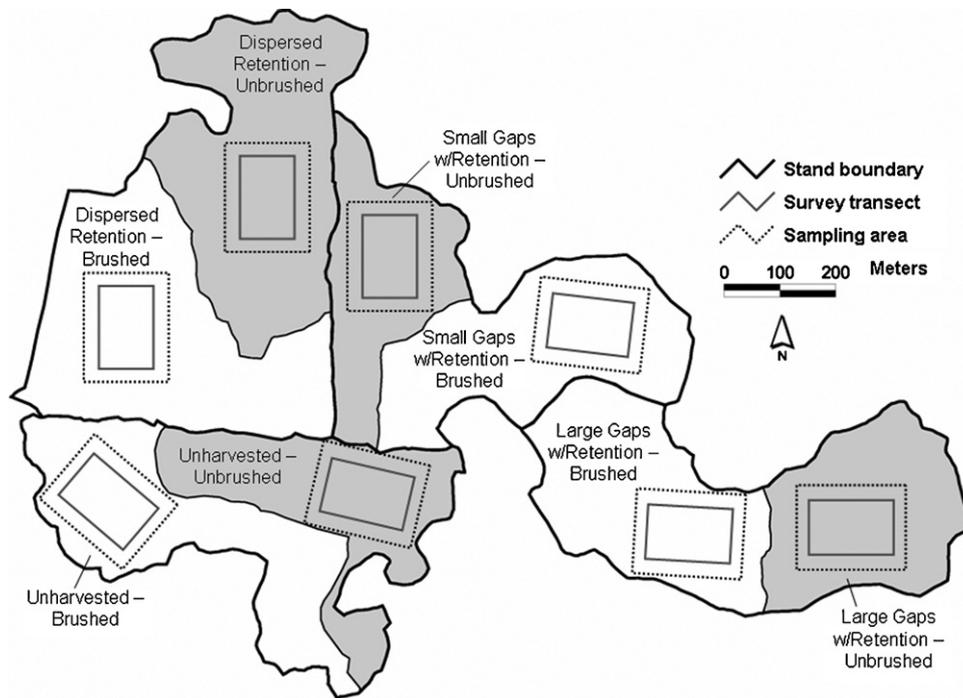


Fig. 2. Schematic of experimental block 3 within the Red Pine Complexity Study, showing layout of experimental units, bird survey transects, and bird sampling areas.

“dispersed” retention treatment, which resembled a traditional shelterwood harvest, with residual trees dispersed evenly throughout the stand, (2) a “small gap” aggregate retention treatment consisting of small (0.1 ha) gaps cut between residual overstory trees, (3) a “large gap” aggregate retention treatment consisting of large (0.3 ha) gaps cut between residual overstory trees, and (4) an “unharvested” control with no overstory manipulation. The two gap treatments created different patterns of aggregate retention among the residual trees. Stands were harvested between 15 August 2002 and 15 April 2003. Designated timber was felled and delimited at the stump then decked along existing access routes. Slash was delimited and scattered to lie within 30 in. of the ground. Disturbance to the soil and existing tree regeneration were kept to a minimum by designating skid paths and incorporating processed slash under the logging equipment. Postharvest tree species’ relative basal areas were largely the same as before treatment.

Overstory retention was combined with an understory competition treatment consisting of brushing—the mechanical removal of shrubs (primarily *Corylus cornuta* and *C. americana*). The “brushed” understory treatments were implemented in approximately one-half of each overstory treatment, with the remaining half functioning as an “unbrushed” control. As of 2005, understory vegetation was not yet well-developed within these stands due to mechanical damage during logging and because, upon initiating the experiment in 2002–2003, the entire understories of all experimental stands were manually brushed to facilitate planting.

2.2. Bird sampling

We censused each experimental stand for birds three times during the breeding season (May through mid-July) in 2003 and in 2005. Censuses were conducted between one-half hour before sunrise to no later than four hours after sunrise on days with suitable weather conditions (i.e., adequate temperature, no rain, little wind; Blake et al., 1991). We used a modified version of standard transect methodology (Ralph et al., 1993), walking 100-m by 150-m rectangular transects (Fig. 2), and spatially locating and

recording all individuals seen or heard within 50 m on either side of each transect (creating an effective sampling area of 200 m × 250 m, or 5 ha) in relation to the edge of each sampling area and the location of overstory gaps. Preliminary sampling suggested that our ability to accurately detect the spatial position of birds in relation to overstory gaps would be compromised using a standard point-count or linear transect methodology; hence, the rectangular transect design was developed and employed. Transect lengths were based on the average size and spatial orientation of the experimental units. We attempted to maintain at least 100 m distance between the sampling area and the edges of all experimental units. Transects were walked at the rate of 1.5 km/h (~20 min/transect; Hanowski et al., 1990). Two individuals (R. Atwell and L. Schulte) conducted all bird censuses and worked together to ensure accuracy.

2.3. Analyses

Analyses considered bird community and individual bird species response among the experimental treatments and between years. We assessed overall bird community response using diversity measures (i.e., species richness, Shannon-Weiner diversity) and non-metric multidimensional scaling (NMS). For each bird species, we calculated the maximum number of individuals observed across the three sampling periods within each year. We used PROC MIXED within SAS software (SAS Institute Inc., 2003) to test for differences in bird abundance, richness, and diversity among overstory and understory treatments and controls in both 2003 and 2005. We used orthogonal contrasts within PROC MIXED to assess whether combined overstory harvest treatments differed from the unharvested control, whether dispersed retention differed from aggregate retention (small gap and large gap), and whether small gap differed from large gap retention. Blocks and treatments were included as fixed effects within the mixed linear model to account for within site variation; their interaction was treated as a random effect. Control plots were used as the statistical baseline to which all treatments were compared. Bird species abundance data were also used in the NMS analysis. We performed

the NMS analysis in PC-ORD (McCune and Mefford, 1999) using the Bray-Curtis distance measure. Bray-Curtis distance is generally considered a robust measure for ecology community data (McCune and Grace, 2002). Preliminary NMS analyses were run with as many as six ordination axes, but substantial contributions to stress reduction were consistently made by only the first two axes. The specifications for the final NMS run included two axes, a random starting configuration, and 30 iterations with real data; this solution had a final stress of 22.66 and a final instability of 0.0044 based on 67 iterations of randomized data. The amount of variation explained by the two axes was relatively high ($r^2 = 0.78$) and the amount of stress in our final solution was reasonable for ecological community data (McCune and Grace, 2002). Mantel tests were used to assess dissimilarity, according to the Bray-Curtis distance measure, between the two sample periods; a Monte Carlo randomization was used to evaluate the test statistic (McCune and Grace, 2002).

Based on the results of the NMS, we tested for statistical differences between years for all observed species, but focused on a subset of bird species that were strongly correlated with the

NMS axes ($r > 0.50$; Table 3). These include the Least Flycatcher (*Empidonax minimus*), Brown Creeper (*Certhia americana*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Black-throated Green Warbler (*Dendroica virens*), Pine Warbler (*Dendroica pinus*), American Redstart (*Setophaga ruticilla*), Ovenbird (*Seiurus aurocapillus*), Mourning Warbler (*Oporornis philadelphia*), and Chipping Sparrow (*Spizella passerina*). We used species level analysis to further probe overall differences in diversity, richness, abundance, and NMS community composition. To understand what species were driving these differences, we used PROC MIXED within SAS software (SAS Institute Inc., 2003). We tested for differences in populations of all bird species between control and treatment stands in both 2003 and 2005. A difference between treatment and control is an a priori hypothesis embedded in this experimental design; thus, we report differences ($p < 0.05$) in orthogonal contrasts between control and treatment stands even when the overall *F*-test is not statistically significant ($p > 0.05$; see Table 1). Again, blocks and treatments were included as fixed effects and their interaction was treated as a random effect.

Table 1
Orthogonal contrasts between unharvested controls and combined treatments (dispersed, small gap, and large gap treatments) in the density of bird species detected by species in 2003

| Bird species | Density in controls (birds/ha) | | Density in treatments (birds/ha) | | Overall <i>F</i> -test | | Orthogonal contrast between control and treatment | |
|--|--------------------------------|------|----------------------------------|------|------------------------|-----------------|---|-----------------|
| | Mean | S.E. | Mean | S.E. | <i>F</i> | <i>p</i> -Value | <i>t</i> | <i>p</i> -Value |
| Bald Eagle (<i>Haliaeetus leucocephalus</i>) | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Sharp-shinned Hawk (<i>Accipiter striatus</i>) | 0.05 | 0.05 | 0.00 | 0.00 | N/A | N/A | N/A | N/A |
| Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>) ^a | 0.00 | 0.00 | 0.02 | 0.01 | 0.60 | 0.63 | -0.77 | 0.46 |
| Downy Woodpecker (<i>Picoides pubescens</i>) | 0.00 | 0.00 | 0.03 | 0.02 | 0.43 | 0.74 | -0.93 | 0.38 |
| Hairy Woodpecker (<i>Vermivora chrysoptera</i>) | 0.03 | 0.03 | 0.02 | 0.01 | 1.94 | 0.19 | 0.42 | 0.68 |
| Black-black Woodpecker (<i>Picoides arcticus</i>) ^{b,a} | 0.03 | 0.03 | 0.01 | 0.01 | 0.60 | 0.63 | 0.77 | 0.46 |
| Eastern Wood Peewee (<i>Contopus virens</i>) | 0.15 | 0.05 | 0.23 | 0.03 | 1.34 | 0.32 | -1.61 | 0.14 |
| Least Flycatcher (<i>Empidonax minimus</i>) ^a | 0.60 | 0.28 | 0.48 | 0.08 | 0.22 | 0.88 | 0.61 | 0.56 |
| Blue-headed Vireo (<i>Vireo solitarius</i>) | 0.03 | 0.03 | 0.00 | 0.00 | N/A | N/A | N/A | N/A |
| Red-eyed Vireo (<i>Vireo olivaceus</i>) | 0.48 | 0.08 | 0.48 | 0.06 | 0.98 | 0.44 | 0.00 | 0.99 |
| Blue Jay (<i>Cyanocitta cristata</i>) | 0.00 | 0.00 | 0.02 | 0.01 | 0.60 | 0.63 | -0.77 | 0.46 |
| Common Raven (<i>Corvus corax</i>) | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Black-capped Chickadee (<i>Poecile atricapilla</i>) | 0.05 | 0.03 | 0.10 | 0.03 | 7.36 | 0.01 | -1.57 | 0.15 |
| Red-breasted Nuthatch (<i>Sitta canadensis</i>) | 0.20 | 0.04 | 0.15 | 0.02 | 1.89 | 0.20 | 1.00 | 0.34 |
| Brown Creeper (<i>Certhia americana</i>) | 0.15 | 0.03 | 0.06 | 0.02 | 2.72 | 0.11 | 2.36 | 0.04 |
| Veery (<i>Catharus fuscescens</i>) ^a | 0.03 | 0.03 | 0.00 | 0.00 | N/A | N/A | N/A | N/A |
| Hermit Thrush (<i>Catharus guttatus</i>) | 0.03 | 0.03 | 0.05 | 0.03 | 0.57 | 0.65 | -0.38 | 0.71 |
| American Robin (<i>Turdus migratorius</i>) | 0.00 | 0.00 | 0.13 | 0.03 | 2.63 | 0.11 | -2.44 | 0.04 |
| Cedar Waxwing (<i>Bombycilla cedrorum</i>) | 0.03 | 0.03 | 0.13 | 0.04 | 1.70 | 0.24 | -1.53 | 0.16 |
| Golden-winged Warbler (<i>Vermivora chrysoptera</i>) ^{b,a} | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Tennessee Warbler (<i>Vermivora peregrina</i>) | 0.00 | 0.00 | 0.02 | 0.01 | 0.60 | 0.63 | -0.77 | 0.46 |
| Nashville Warbler (<i>Vermivora ruficapilla</i>) ^a | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>) ^a | 0.20 | 0.08 | 0.12 | 0.04 | 0.50 | 0.69 | 0.86 | 0.41 |
| Cape May Warbler (<i>Dendroica tigrina</i>) | 0.00 | 0.00 | 0.04 | 0.03 | 1.00 | 0.44 | -0.58 | 0.58 |
| Yellow-rumped Warbler (<i>Dendroica coronata</i>) | 0.18 | 0.05 | 0.18 | 0.03 | 0.82 | 0.52 | 0.00 | 1.00 |
| Black-throated Green Warbler (<i>Dendroica virens</i>) ^a | 0.13 | 0.05 | 0.05 | 0.02 | 3.11 | 0.08 | 2.06 | 0.07 |
| Blackburnian Warbler (<i>Dendroica fusca</i>) ^a | 0.05 | 0.03 | 0.13 | 0.03 | 1.72 | 0.23 | -1.65 | 0.13 |
| Pine Warbler (<i>Dendroica pinus</i>) | 0.45 | 0.09 | 0.48 | 0.04 | 0.28 | 0.84 | -0.30 | 0.77 |
| Blackpoll Warbler (<i>Dendroica striata</i>) | 0.03 | 0.03 | 0.02 | 0.02 | 0.67 | 0.59 | 0.25 | 0.81 |
| Black-and-white Warbler (<i>Mniotilta varia</i>) | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| American Redstart (<i>Setophaga ruticilla</i>) | 0.28 | 0.15 | 0.15 | 0.05 | 1.46 | 0.29 | 1.27 | 0.23 |
| Ovenbird (<i>Seiurus aurocapilla</i>) | 0.78 | 0.06 | 0.39 | 0.05 | 6.84 | 0.01 | 4.04 | <0.01 |
| Mourning Warbler (<i>Oporornis philadelphia</i>) ^a | 0.08 | 0.04 | 0.06 | 0.02 | 0.33 | 0.80 | 0.58 | 0.58 |
| Common Yellowthroat (<i>Geothlypis trichas</i>) ^a | 0.03 | 0.03 | 0.00 | 0.00 | N/A | N/A | N/A | N/A |
| Scarlet Tanager (<i>Piranga olivacea</i>) | 0.05 | 0.03 | 0.00 | 0.00 | 1.00 | 0.44 | 1.73 | 0.12 |
| Chipping Sparrow (<i>Spizella passerina</i>) | 0.08 | 0.04 | 0.42 | 0.05 | 6.82 | 0.01 | -3.78 | <0.01 |
| White-throated Sparrow (<i>Zonotrichia albicollis</i>) ^a | 0.03 | 0.03 | 0.00 | 0.00 | N/A | N/A | N/A | N/A |
| Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>) ^a | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Brown-headed Cowbird (<i>Molothrus ater</i>) | 0.03 | 0.03 | 0.00 | 0.00 | N/A | N/A | N/A | N/A |
| Purple Finch (<i>Carpodacus purpureus</i>) ^a | 0.00 | 0.00 | 0.04 | 0.02 | 1.32 | 0.33 | -1.73 | 0.12 |
| American Goldfinch (<i>Carduelis tristis</i>) | 0.00 | 0.00 | 0.02 | 0.01 | 0.60 | 0.63 | -0.77 | 0.46 |
| Evening Grosbeak (<i>Coccothraustes vespertinus</i>) | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |

^a Listed as a regionally important species (PIF, 2007).

^b Indicates regionally sensitive species (US Forest Service, 2006).

3. Results

A total of 57 bird species were found in the experimental stands we surveyed; 42 and 51 species were observed in 2003 (Table 1) and 2005 (Table 2), respectively. Many species were common to both overstory treatments and unharvested controls, but across years, 22 species were found only in the treatment stands and four were found only within unharvested stands. Additionally, some observed species considered regionally sensitive to northern Minnesota (US Forest Service, 2006) were found only in the treatment stands (Olive-sided Flycatcher [*Contopus cooperi*], Golden-winged Warbler [*Vermivora chrysoptera*]), or only in control stands (Black-backed Woodpecker [*Picoides arcticus*]).

We found no difference in avian abundance ($F = 0.22, p = 0.88$), richness ($F = 0.72, p = 0.56$), or diversity ($F = 0.52, p = 0.68$) between the different overstory treatments and the unharvested controls in 2003, the first year following treatment (Fig. 3). By 2005, the third year following treatment, we found differences between the overstory treatments and unharvested controls according to all three measures: avian abundance ($F = 3.95, p = 0.05$), richness ($F = 26.68, p < 0.01$), and diversity ($F = 18.13, p < 0.01$). Orthogonal contrasts reveal greater avian abundance (+1.88 birds/ha; $t = 3.95, p = 0.01$), richness (+0.88 species/ha; $t = 8.64, p < 0.01$), and diversity (+0.34; $t = 7.16, p < 0.01$) in overstory treatments than in unharvested stands in 2005 (Fig. 3). Three years post-treatment, we detected no differences

Table 2

Orthogonal contrasts between unharvested controls and combined treatments (dispersed, small gap, and large gap treatments) in the density of bird species detected by species in 2005

| Bird species | Density in controls (birds/ha) | | Density in treatments (birds/ha) | | Overall F-test | | Orthogonal contrast between control and treatment | |
|--|--------------------------------|------|----------------------------------|------|----------------|---------|---|---------|
| | Mean | S.E. | Mean | S.E. | F | p-Value | t | p-Value |
| Ruffed Grouse (<i>Bonasa umbellus</i>) ^{a,b} | 0.13 | 0.13 | 0.00 | 0.00 | N/A | N/A | N/A | N/A |
| Turkey Vulture (<i>Cathartes Aura</i>) | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Bald Eagle (<i>Haliaeetus leucocephalus</i>) | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Sharped-shinned Hawk (<i>Accipiter striatus</i>) | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Broad-winged Hawk (<i>Buteo platypterus</i>) ^b | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Ruby-throated hummingbird (<i>Archilochus colubris</i>) | 0.00 | 0.00 | 0.05 | 0.02 | 0.88 | 0.49 | -1.26 | 0.24 |
| Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>) ^b | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Hairy Woodpecker (<i>Vermivora chrysoptera</i>) | 0.05 | 0.05 | 0.02 | 0.01 | 1.00 | 0.44 | 1.00 | 0.34 |
| Black-black Woodpecker (<i>Picoides arcticus</i>) ^{a,b} | 0.10 | 0.10 | 0.00 | 0.00 | N/A | N/A | N/A | N/A |
| Northern Flicker (<i>Colaptes auratus</i>) ^b | 0.00 | 0.00 | 0.13 | 0.03 | 4.65 | 0.03 | -2.19 | 0.06 |
| Olive-sided Flycatcher (<i>Contopus cooperi</i>) ^{a,b} | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Eastern Wood Peewee (<i>Contopus virens</i>) | 0.30 | 0.05 | 0.27 | 0.03 | 0.53 | 0.67 | 0.59 | 0.57 |
| Least Flycatcher (<i>Empidonax minimus</i>) ^b | 0.90 | 0.24 | 1.38 | 0.12 | 1.33 | 0.34 | -1.98 | 0.08 |
| Great-crested Flycatcher (<i>Myiarchus crinitus</i>) | 0.00 | 0.00 | 0.02 | 0.01 | 0.60 | 0.63 | -0.77 | 0.46 |
| Yellow-throated Vireo (<i>Vireo flavifrons</i>) | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Blue-headed Vireo (<i>Vireo solitarius</i>) | 0.05 | 0.03 | 0.07 | 0.03 | 0.07 | 0.98 | -0.26 | 0.80 |
| Red-eyed Vireo (<i>Vireo olivaceus</i>) | 0.58 | 0.14 | 0.53 | 0.05 | 0.87 | 0.49 | 0.38 | 0.71 |
| Blue Jay (<i>Cyanocitta cristata</i>) | 0.03 | 0.03 | 0.09 | 0.03 | 0.63 | 0.62 | -1.00 | 0.35 |
| Common Raven (<i>Corvus corax</i>) | 0.05 | 0.03 | 0.03 | 0.02 | 1.00 | 0.44 | 0.58 | 0.58 |
| Black-capped Chickadee (<i>Poecile atricapilla</i>) | 0.03 | 0.03 | 0.04 | 0.02 | 1.00 | 0.44 | -0.45 | 0.67 |
| Red-breasted Nuthatch (<i>Sitta Canadensis</i>) | 0.20 | 0.05 | 0.16 | 0.04 | 0.37 | 0.77 | 0.59 | 0.57 |
| White-breasted Nuthatch (<i>Sitta carolinensis</i>) | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| House Wren (<i>Troglodytes aedon</i>) | 0.00 | 0.00 | 0.02 | 0.01 | 1.00 | 0.43 | -0.58 | 0.58 |
| Golden-crowned Kinglet (<i>Regulus satrapa</i>) | 0.08 | 0.05 | 0.00 | 0.00 | 1.00 | 0.44 | 1.73 | 0.12 |
| Veery (<i>Catharus fuscescens</i>) ^b | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Hermit Thrush (<i>Catharus guttatus</i>) | 0.18 | 0.08 | 0.14 | 0.04 | 2.87 | 0.10 | 0.51 | 0.62 |
| American Robin (<i>Turdus migratorius</i>) | 0.13 | 0.05 | 0.35 | 0.06 | 1.71 | 0.23 | -1.99 | 0.08 |
| Cedar Waxwing (<i>Bombycilla cedrorum</i>) | 0.00 | 0.00 | 0.05 | 0.03 | 1.94 | 0.19 | -1.26 | 0.24 |
| Nashville Warbler (<i>Vermivora ruficapilla</i>) ^b | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>) ^b | 0.28 | 0.14 | 0.76 | 0.08 | 7.13 | 0.01 | -4.60 | <0.01 |
| Cape May Warbler (<i>Dendroica tigrina</i>) | 0.00 | 0.00 | 0.02 | 0.01 | 1.00 | 0.44 | -0.58 | 0.58 |
| Yellow-rumped Warbler (<i>Dendroica coronata</i>) | 0.10 | 0.04 | 0.28 | 0.08 | 1.03 | 0.43 | -1.20 | 0.26 |
| Black-throated Green Warbler (<i>Dendroica virens</i>) ^b | 0.10 | 0.04 | 0.03 | 0.01 | 1.65 | 0.24 | 2.23 | 0.05 |
| Blackburnian Warbler (<i>Dendroica fusca</i>) ^b | 0.03 | 0.03 | 0.03 | 0.02 | 0.22 | 0.88 | -0.27 | 0.79 |
| Pine Warbler (<i>Dendroica pinus</i>) | 0.45 | 0.09 | 0.67 | 0.05 | 7.22 | 0.01 | -4.33 | <0.01 |
| Black-and-white Warbler (<i>Mniotilta varia</i>) | 0.20 | 0.08 | 0.13 | 0.02 | 1.00 | 0.44 | 1.17 | 0.27 |
| American Redstart (<i>Setophaga ruticilla</i>) | 0.33 | 0.13 | 0.63 | 0.09 | 1.26 | 0.35 | -1.87 | 0.09 |
| Ovenbird (<i>Seiurus aurocapilla</i>) | 1.40 | 0.08 | 0.50 | 0.04 | 30.44 | <0.01 | 9.55 | <0.01 |
| Mourning Warbler (<i>Oporornis philadelphia</i>) ^b | 0.00 | 0.00 | 0.25 | 0.03 | 5.30 | 0.02 | -3.79 | <0.01 |
| Common Yellowthroat (<i>Geothlypis trichas</i>) ^b | 0.00 | 0.00 | 0.02 | 0.01 | 1.00 | 0.44 | -1.00 | 0.34 |
| Scarlet Tanager (<i>Piranga olivacea</i>) | 0.05 | 0.03 | 0.00 | 0.00 | 1.00 | 0.44 | 1.73 | 0.12 |
| Eastern Towhee (<i>Pipilo erythrophthalmus</i>) | 0.05 | 0.05 | 0.04 | 0.02 | 1.00 | 0.44 | 0.30 | 0.77 |
| Chipping Sparrow (<i>Spizella passerine</i>) | 0.33 | 0.10 | 0.68 | 0.09 | 2.72 | 0.11 | -2.63 | 0.03 |
| Song Sparrow (<i>Melospiza melodia</i>) | 0.00 | 0.00 | 0.03 | 0.01 | 0.67 | 0.59 | -0.74 | 0.48 |
| White-throated Sparrow (<i>Zonotrichia albicollis</i>) ^b | 0.03 | 0.03 | 0.24 | 0.07 | 1.35 | 0.32 | -1.50 | 0.17 |
| Dark-eyed Junco (<i>Junco hyemalis</i>) | 0.00 | 0.00 | 0.02 | 0.02 | N/A | N/A | N/A | N/A |
| Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>) ^b | 0.00 | 0.00 | 0.08 | 0.02 | 2.56 | 0.12 | -2.43 | 0.03 |
| Brown-headed Cowbird (<i>Molothrus ater</i>) | 0.00 | 0.00 | 0.01 | 0.01 | N/A | N/A | N/A | N/A |
| Purple Finch (<i>Carpodacus purpureus</i>) ^b | 0.03 | 0.03 | 0.13 | 0.03 | 1.29 | 0.34 | -1.60 | 0.14 |
| Pine Siskin (<i>Carduelis pinus</i>) | 0.00 | 0.00 | 0.02 | 0.02 | N/A | N/A | N/A | N/A |
| Evening Grosbeak (<i>Coccothraustes vespertinus</i>) | 0.00 | 0.00 | 0.08 | 0.05 | 1.00 | 0.44 | -0.79 | 0.45 |

^a Indicates regionally sensitive species (US Forest Service, 2006).

^b Listed as a regionally important species (PIF, 2007).

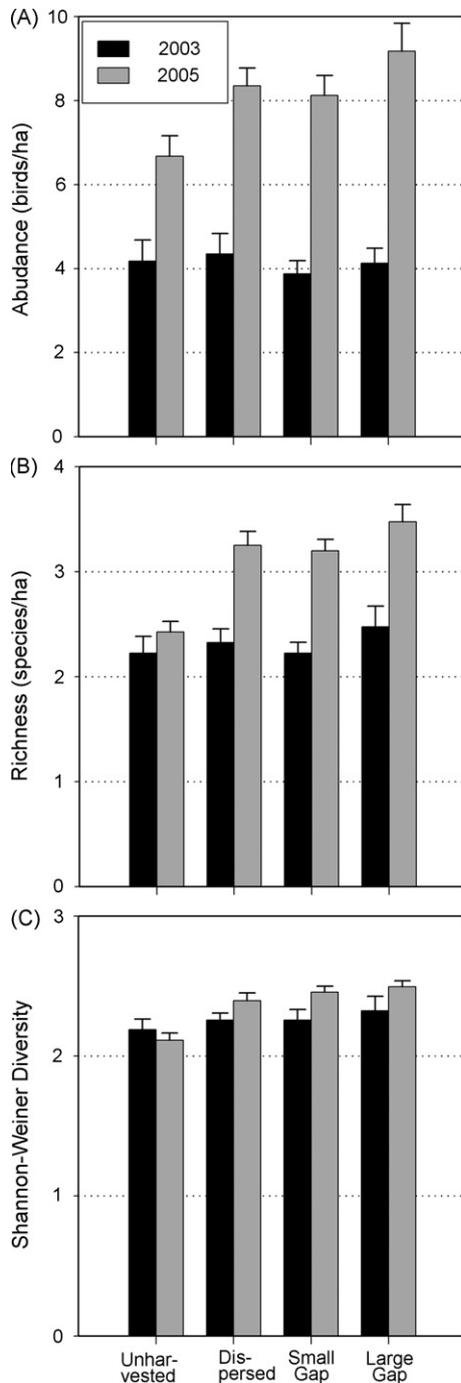


Fig. 3. Differences in bird (A) abundance, (B) richness, and (C) diversity across treatments and among years.

in abundance ($t = 0.47$, $p = 0.65$), richness ($t = 0.81$, $p = 0.44$), and diversity ($t = 1.63$, $p = 0.14$) in orthogonal contrasts between dispersed retention and aggregate retention treatments (small gap and large gap), and no differences in abundance ($t = 1.42$, $p = 0.19$), richness ($t = 2.20$, $p = 0.06$), and diversity ($t = 0.68$, $p = 0.51$) in orthogonal contrasts between small gap and large gap treatments (Fig. 3). In both 2003 and 2005, we found no difference in avian abundance (2003 $F = 0.00$, $p = 0.98$; 2005 $F = 1.27$, $p = 0.34$), richness (2003 $F = 0.01$, $p = 0.92$; 2005 $F = 0.14$, $p = 0.73$), or diversity (2003 $F = 0.04$, $p = 0.86$; 2005 $F = 0.04$, $p = 0.86$) between brushed and unbrushed understory stands.

In our NMS analysis, Axis 1 exhibited the most variation ($r^2 = 0.57$), while Axis 2 accounted for less variation ($r^2 = 0.20$). Axis

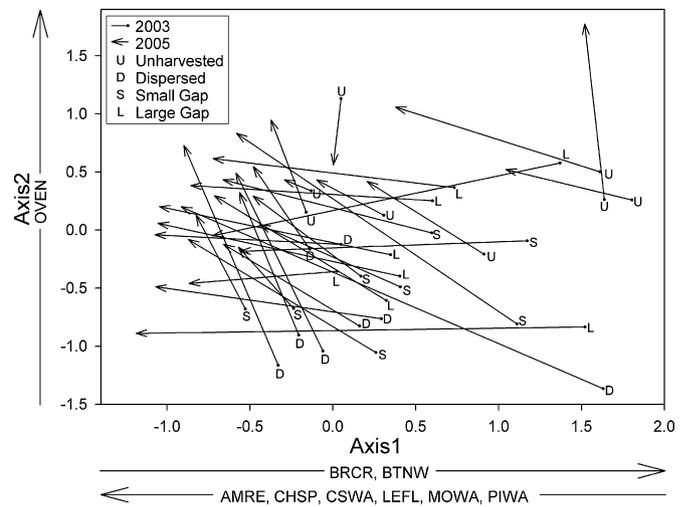


Fig. 4. Non-metric multidimensional scaling (NMS) analysis showing: (A) variation in bird community composition among overstory treatments and controls and (B) treatment-level changes in bird community composition between years. BRCR = Brown Creeper, BTNW = Black-throated Green Warbler, AMRE = American Redstart, CHSP = Chipping Sparrow, CSWA = Chestnut-sided Warbler, LEFL = Least Flycatcher, MOWA = Mourning Warbler, PIWA = Pine Warbler, and OVEN = Ovenbird.

1 suggests that the bird community in both overstory treatment and unharvested control stands had changed between 1 and 3 years postharvest, although the results from the Mantel test show that a significant relationship between the two sample periods remains ($r = 0.40$, $p < 0.01$). The NMS analysis suggested divergence in community composition between treatment and unharvested stands in both sampling periods, and these differences became more apparent in 2005 (Fig. 4). Between 2003 and 2005, orthogonal contrasts showed substantial increases within treatment stands in both abundance (+22.17 birds/ha; $F = 409.78$, $t = 20.24$, $p < 0.01$) and richness (+4.83 species/ha; $F = 27.88$, $t = 5.28$, $p = 0.01$), with a trend towards increasing diversity (+0.17; $F = 5.96$, $t = 2.44$, $p = 0.09$). Abundance increased in unharvested control stands between the first and third year postharvest, but to a lesser degree than in treatment stands (+12.50 birds/ha; $F = 30.24$, $t = 5.50$, $p = 0.01$). There was a trend towards decreased diversity in the unharvested stands (-0.08 ; $F = 6.83$, $t = 2.61$, $p = 0.08$), while no difference was apparent in richness ($F = 3.43$, $t = 1.85$, $p = 0.16$).

In our NMS analysis, seven species were found to be correlated with Axis 1 and one with Axis 2 (Table 3). Brown Creeper ($r = 0.50$) and Black-throated Green Warbler ($r = 0.53$) abundance were positively correlated with Axis 1, while the abundance of Least Flycatcher ($r = -0.70$), Chestnut-sided Warbler ($r = -0.55$), Pine Warbler ($r = -0.57$), American Redstart ($r = -0.54$), Mourning Warbler ($r = -0.51$), and Chipping Sparrow ($r = -0.58$) were all negatively correlated with this axis. Ovenbird abundance was highly and positively correlated with Axis 2 ($r = 0.72$); other bird species were only weakly associated with this axis (Table 2).

Based on the NMS results, we compared changes in the abundance of the above species between 2003 and 2005 using orthogonal contrasts. Across overstory treatment and unharvested control sites, between 1 and 3 years post-treatment, we observed increases in average abundance of Least Flycatchers (+7.56 birds/ha; $F = 104.83$, $t = 10.24$, $p < 0.01$), Chestnut-sided Warblers (+5.00 birds/ha; $F = 25.81$, $t = 5.08$, $p = 0.01$), Pine Warblers (+1.38 birds/ha; $F = 17.29$, $t = 4.16$, $p = 0.03$), American Redstarts (+3.75 birds/ha; $F = 192.86$, $t = 13.89$, $p < 0.01$), and Ovenbirds (+2.38 birds/ha; $F = 26.41$, $t = 5.14$, $p = 0.01$), a trend towards increasing populations of Mourning Warblers (+1.25 birds/ha;

Table 3

Observed bird species and their correlations with axes from non-metric multi-dimensional scaling (NMS) ordination

| Bird species | Axis 1, r | Axis 2, r |
|--|-----------|-----------|
| Ruffed Grouse (<i>Bonasa umbellus</i>) ^{a,b} | 0.06 | 0.22 |
| Turkey Vulture (<i>Cathartes Aura</i>) | −0.17 | −0.10 |
| Bald Eagle (<i>Haliaeetus leucocephalus</i>) | −0.10 | −0.09 |
| Sharped-shinned Hawk (<i>Accipiter striatus</i>) | 0.19 | 0.14 |
| Broad-winged Hawk (<i>Buteo platypterus</i>) ^b | −0.09 | 0.07 |
| Ruby-throated hummingbird (<i>Archilochus colubris</i>) | −0.25 | 0.00 |
| Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>) ^b | −0.03 | −0.08 |
| Downy Woodpecker (<i>Picoides pubescens</i>) | 0.07 | −0.14 |
| Hairy Woodpecker (<i>Vermivora chrysoptera</i>) | −0.07 | 0.19 |
| Black-black Woodpecker (<i>Picoides arcticus</i>) ^{a,b} | 0.29 | 0.31 |
| Northern Flicker (<i>Colaptes auratus</i>) ^b | −0.45 | 0.10 |
| Olive-sided Flycatcher (<i>Contopus cooperi</i>) ^{a,b} | −0.14 | 0.04 |
| Eastern Wood Peewee (<i>Contopus virens</i>) | −0.20 | 0.02 |
| Least Flycatcher (<i>Empidonax minimus</i>) ^b | −0.70 | 0.23 |
| Great-crested Flycatcher (<i>Myiarchus crinitus</i>) | −0.17 | −0.02 |
| Yellow-throated Vireo (<i>Vireo flavifrons</i>) | −0.12 | 0.13 |
| Blue-headed Vireo (<i>Vireo solitarius</i>) | −0.27 | 0.06 |
| Red-eyed Vireo (<i>Vireo olivaceus</i>) | −0.33 | 0.09 |
| Blue Jay (<i>Cyanocitta cristata</i>) | −0.37 | −0.08 |
| Common Raven (<i>Corvus corax</i>) | −0.06 | 0.01 |
| Black-capped Chickadee (<i>Poecile atricapilla</i>) | 0.26 | −0.07 |
| Red-breasted Nuthatch (<i>Sitta canadensis</i>) | 0.14 | 0.16 |
| White-breasted Nuthatch (<i>Sitta carolinensis</i>) | −0.10 | −0.03 |
| Brown Creeper (<i>Certhia americana</i>) | 0.50 | −0.02 |
| House Wren (<i>Troglodytes aedon</i>) | −0.19 | 0.06 |
| Golden-crowned Kinglet (<i>Regulus satrapa</i>) | 0.29 | 0.38 |
| Veery (<i>Catharus fuscescens</i>) ^b | −0.05 | 0.25 |
| Hermit Thrush (<i>Catharus guttatus</i>) | −0.17 | 0.25 |
| American Robin (<i>Turdus migratorius</i>) | −0.44 | −0.05 |
| Cedar Waxwing (<i>Bombycilla cedrorum</i>) | −0.07 | −0.42 |
| Golden-winged Warbler (<i>Vermivora chrysoptera</i>) ^{a,b} | 0.01 | −0.03 |
| Tennessee Warbler (<i>Vermivora peregrina</i>) | 0.06 | −0.08 |
| Nashville Warbler (<i>Vermivora ruficapilla</i>) ^b | 0.06 | −0.14 |
| Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>) ^b | −0.55 | 0.36 |
| Cape May Warbler (<i>Dendroica tigrina</i>) | −0.09 | −0.20 |
| Yellow-rumped Warbler (<i>Dendroica coronata</i>) | −0.20 | 0.07 |
| Black-throated Green Warbler (<i>Dendroica virens</i>) ^b | 0.53 | 0.42 |
| Blackburnian Warbler (<i>Dendroica fusca</i>) ^b | 0.33 | −0.26 |
| Pine Warbler (<i>Dendroica pinus</i>) | −0.57 | −0.02 |
| Blackpoll Warbler (<i>Dendroica striata</i>) | 0.02 | −0.24 |
| Black-and-white Warbler (<i>Mniotilta varia</i>) | −0.18 | 0.49 |
| American Redstart (<i>Setophaga ruticilla</i>) | −0.54 | 0.36 |
| Ovenbird (<i>Seiurus aurocapilla</i>) | 0.18 | 0.72 |
| Mourning Warbler (<i>Oporornis philadelphia</i>) ^b | −0.51 | 0.19 |
| Common Yellowthroat (<i>Geothlypis trichas</i>) ^b | −0.13 | 0.14 |
| Scarlet Tanager (<i>Piranga olivacea</i>) | 0.04 | 0.29 |
| Eastern Towhee (<i>Pipilo erythrophthalmus</i>) | −0.20 | 0.18 |
| Chipping Sparrow (<i>Spizella passerine</i>) | −0.58 | −0.17 |
| Song Sparrow (<i>Melospiza melodia</i>) | −0.23 | −0.07 |
| White-throated Sparrow (<i>Zonotrichia albicollis</i>) ^b | −0.36 | 0.08 |
| Dark-eyed Junco (<i>Junco hyemalis</i>) | −0.09 | 0.17 |
| Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>) ^b | −0.35 | 0.16 |
| Brown-headed Cowbird (<i>Molothrus ater</i>) | −0.08 | 0.21 |
| Purple Finch (<i>Carpodacus purpureus</i>) ^b | −0.37 | 0.02 |
| Pine Siskin (<i>Carduelis pinus</i>) | −0.17 | −0.10 |
| American Goldfinch (<i>Carduelis tristis</i>) | 0.17 | −0.04 |
| Evening Grosbeak (<i>Coccothraustes vespertinus</i>) | −0.23 | −0.20 |

^a Indicates regionally sensitive species (US Forest Service, 2006).

^b Listed as a regionally important species (PIF, 2007).

$F = 8.82$, $t = 2.97$, $p = 0.06$) and Chipping Sparrows (+2.56 birds/ha; $F = 5.76$, $t = 2.40$, $p = 0.10$), decreases in average abundance of the Brown Creepers (−0.81 birds/ha; $F = 46.09$, $t = 6.79$, $p < 0.01$), and no change in populations of Black-throated Green Warblers ($F = 0.86$, $t = 0.93$, $p = 0.42$).

In the initial year following treatment, only four species showed differences in mean abundance between treatment stands and unharvested controls. Species less abundant in treatment stands included Brown Creeper and Ovenbird, while American Robins *Turdus migratorius* and Chipping Sparrows were more abundant (Table 1). There was a trend towards lower abundance of Black-

throated Green Warblers in treatment stands versus unharvested control stands (Table 1). Three years post-treatment, Ovenbird abundance was much lower in treatment stands versus unharvested control stands, with only about one-third as many birds/ha (Table 2). There were also significantly fewer Black-throated Green Warblers in treatment stands (Table 2). In 2005, populations of Chipping Sparrows were again significantly greater in treatment stands than in unharvested control stands and there was a trend towards greater populations of American Robins in treatment stands (Table 2). By the third year post-treatment, other species were significantly more abundant in the treatments, including Pine Warbler, Mourning Warbler, and Rose-breasted Grosbeak (Table 2). The Northern Flicker (*Colaptes auratus*), Least Flycatcher, Chestnut-sided Warbler, and American Redstart were also more abundant in treatments, though not significantly (Table 2).

4. Discussion

This study adds to the growing body of research addressing timber harvest impacts on avian community diversity and composition (Erhlich, 1996; Hagan et al., 1997; Schulte and Niemi, 1998; Schmiegelow and Monkkonen, 2002; DeStefano, 2002; Thompson et al., 2003; Schieck and Song, 2006), and is explicitly designed to test bird community response to vertical and horizontal heterogeneity over time, as created through variable retention harvesting. It further responds to the need for “long-term, large-scale, experimental studies, which document the demographic response of forest wildlife to alterations in forest cover” (DeStefano, 2002), joining a handful of other experimental studies addressing this issue (see also Schmiegelow et al., 1997; Harrison et al., 2005; Walter and Maguire, 2005; Hanowski et al., 2006). Here we address the impacts of overstory retention on forest birds in the context of silvicultural practices designed to mimic natural disturbance. As discussed below, analyses of initial postharvest conditions show that birds respond to changes in structural complexity in ways that are complex and species specific. We also suggest some unifying landscape implications based on multi-species trends in our stand-level research.

4.1. Initial bird community response to vertical and horizontal heterogeneity

As with other studies (Thompson et al., 2003; Venier and Pearce, 2005; Schieck and Song, 2006), we found multispatial and multitemporal response of the avian community to harvesting. Only slight differences in avian community composition were recorded between unharvested control and treatment stands during the initial post-disturbance breeding season of 2003 (Fig. 4). These include (1) a qualitative difference in community composition between treatment stands and unharvested control stands suggested by the NMS analysis (Fig. 4), (2) a higher abundance of American Robins and Chipping Sparrows in treatment stands versus unharvested control stands, and (3) a lower abundance of Brown Creepers and Ovenbirds in treatment stands versus unharvested control stands. Although we have no data on pre-harvest avian community composition, we expect that the lack of an initial treatment response is due to high site fidelity (Hagan et al., 1996), with some individual birds returning to their previous breeding grounds despite intervening disturbance.

We found stronger differences in 2005, three years postharvest, including (1) significantly higher avian abundance, richness, and diversity in the treatment stands (Fig. 3), (2) significant differences in the abundance of seven bird species between treatment stands and unharvested control stands (Table 2), and (3) a divergence in the overall bird community between treatment stands and unharvested control stands (Fig. 4). We expect that these

differences are due to changes in habitat conditions, and that overstory retention harvesting has introduced heterogeneity and corresponding niche spaces beyond that found in single-cohort, monotypic red pine stands (Bourque and Villard, 2001; Flapohler et al., 2002; Lance and Phinney, 2001; Schieck and Song, 2006). For instance, nearly all species whose populations were greater in treatment stands prefer more open woodlands, shrub cover, and forest edges, and are less abundant in monotypic stands and interior forests. The Least Flycatcher, Chestnut-sided Warbler, Pine Warbler, and American Redstart are all species which prefer semi-open or second growth woodlands with ample shrubs (Briskie, 1994; Richardson and Brauning, 1995; Sherry and Holmes, 1997; Rodewald et al., 1999). The Northern Flicker, American Robin, and Chipping Sparrow are generalist, edge species that prefer areas of grass with trees for displaying, nesting, and retreating (Moore, 1995; Middleton, 1998; Sallabanks and James, 1999). The Mourning Warbler relies on thick undergrowth that often grows in response to openings in the forest canopy (Pitocchelli, 1993). In several other studies these species have been shown to be common and prolific colonizers following harvest (Flapohler et al., 2002; Hanowski et al., 2003; Holmes et al., 2004; Schieck and Song, 2006). With the exception of the Chestnut-sided Warbler and American Redstart, all of these species are common immediately following fire (Schieck and Song, 2006).

In 2005, we did not find differences in avian community composition among the three overstory retention patterns (Figs. 2 and 3) or with understory brushing to reduce shrub density. Vegetation growth in response to overstory and understory treatments was just becoming visually apparent at that time. We expect that treatment effects will be evident in the subsequent years as the forest understory becomes more fully developed, since many forest bird species in the region are known to respond positively to the presence of hazel and other understory shrub species (Schulte and Niemi, 1998). It is also possible, however, that we will always fail to record a significant response for some species due to low statistical power (four replicates) or to the small size of our experimental stands (~16 ha). While their extents are reflective of typical harvest units in the region, these stands are small in relationship to the home range size of many songbird species. In such cases, the differences reported between treatments may be too conservative.

Seventeen species that we sampled are listed as Partners in Flight species of regional importance (PIF, 2007), indicating that the maintenance of viable populations of these species in the future very likely depends upon active planning and habitat management. Several of these species, including Least Flycatcher, Chestnut-sided Warbler, Black-throated Green Warbler, Mourning Warbler, Common Yellowthroat (*Geothlypis trichas*), White-throated Sparrow (*Zonotrichia albicollis*), and Purple Finch (*Carpodacus purpureus*), were found in relatively high abundance in our sites, and the findings of our research will be helpful in contributing to their future management. Furthermore, three species found in low abundances in our study are listed as regionally sensitive species by the US Forest Service, including the Black-backed Woodpecker, Olive-sided Flycatcher, and Golden-winged Warbler (Table 3; US Forest Service, 2006).

4.2. Overstory retention and silviculture to mimic natural disturbance

Through various forms of variable retention harvesting, ecological silviculture seeks to enhance structural complexity and mimic structural outcomes created by natural fire or wind disturbance (Franklin et al., 1997; Palik et al., 2003a). Many studies have been conducted on responses of wildlife to the retention of mature trees in harvest operations, including a review by Thompson et al. (2003) and a meta-analysis by Schieck and Song

(2006). Several themes emerge, including that retention of 15–80% of the overstory can maintain habitat for many species found in mature, unharvested stands (Hansen et al., 1995; Schmiegelow et al., 1997; Merrill et al., 1998; Schieck et al., 2000; Leupin et al., 2004; Schieck and Song, 2006). However, in all of these studies, the bird communities observed in harvested stands always differed from those in unharvested stands. Some old growth species remained absent from retention cuts for up to 75 years following harvest (Schieck and Song, 2006). While some research shows overall reductions in diversity and abundance following harvest (Norton and Hannon, 1997), other studies have found the converse (Lance and Phinney, 2001; Bourque and Villard, 2001; Flapohler et al., 2002).

At three years postharvest, our overstory treatment stands provided habitat for a different bird community, but one that overlapped with that of unharvested stands. Our research shows that overstory retention harvests designed to mimic the structural outcomes of natural disturbances can increase overall avian community abundance, richness, and diversity over a short timeframe and can create habitat for many early successional bird species (Table 2, Fig. 3). Regardless of the spatial configuration of overstory retention, however, the removal of 50% of tree basal resulted in loss of habitat for some interior forest species, including the Black-throated Green Warbler and Ovenbird. Furthermore, the degree to which the resulting bird communities mimic those following natural canopy disturbances (e.g., fire, wind) in mature red pine forests is not clear.

Other studies comparing avian response to harvest versus fire have shown that the bird communities immediately following these two disturbances are different (Hutto, 1995, 2006; Schulte and Niemi, 1998; Hobson and Schieck, 1999; Schieck and Hobson, 2000). This body of research suggests that many cavity nesters are common only in snag rich areas following fire (Hutto, 1995, 2006; Schulte and Niemi, 1998; Kotliar et al., 2002). We found that cavity nesting species were either absent or reduced in numbers in our treatment sites, which were designed primarily to increase the diversity of vegetation and structure within regrowing stands (Palik and Zasada, 2003). Increasing the habitat of bird species most reliant on natural fire disturbance will require strategies that retain or create snags along with overstory retention (Schulte and Niemi, 1998; Nappi et al., 2004; Walter and Maguire, 2005; Hutto, 2006). Increasing the habitat of sensitive, cavity-nesting Black-backed and Three-toed (*Picoides tridactylus*) Woodpeckers through ecological silviculture will be particularly difficult. These birds primarily respond to increases in populations of pyrophilous insects that colonize recently burned stands (Hobson and Schieck, 1999; Hutto, 2006; Schieck and Song, 2006), rather than to a structural condition that is more easily retained or created through silviculture.

Several early successional species associated with more open parklands such as the Common Yellowthroat were also relatively uncommon in our study sites (Chambers et al., 1999; Schieck et al., 2000). This may be due to the relatively small scale of openings (0.1–0.3 ha) created by our treatments in comparison to the common size of clearcut harvests (10–15 ha; White and Host, 2003) or to the extent of natural fires in red and white pine systems (40–400 ha; Heinselman, 1981) in our region. Partial harvests and small patch cuts may not create adequate habitat for some early successional species, which respond to the larger extent of burns or clearcuts (Thill and Koerth, 2005; Costello et al., 2000).

4.3. Landscape lessons for ecological forestry

Although our unharvested control stands exhibited lower bird abundance, richness, and diversity in comparison to treatment stands, these unharvested stands provide habitat for an overlapping,

but distinctive, bird community (Fig. 4). This result is consistent with research across several forest types showing divergence of community composition between harvested and unharvested stands (Flapohler et al., 2002; Thompson et al., 2003; Venier and Pearce, 2005; Schieck and Song, 2006). We attribute temporal divergence between treatment and unharvested stands to individual species response (Fig. 4). Increases in the abundance of Ovenbirds, which along with other neotropical migrants have been shown to crowd retention areas in years following the initial harvest of nearby forest (Hannon et al., 2002; Schmiegelow et al., 1997), largely drive the pattern in the unharvested stands. We also found the Black-throated Green Warbler, another interior forest species (Morse and Poole, 2005), to be more abundant in unharvested stands. These two species have been shown to prefer unharvested stands in several other studies (Bourque and Villard, 2001; Hanowski et al., 2003; Venier and Pearce, 2005), likely due to the more open understory conditions, deep leaf litter, and high biomass of litter-dwelling invertebrates associated with mature forest (Bourque and Villard, 2001). Although rare within the region and on our sites, we have observed Black-backed Woodpeckers – a species that prefer post-fire habitat rich in snags (Hutto, 2006; Schieck and Song, 2006) – within the unharvested rather than treatment stands (Tables 1 and 2), which may again point to a lack of dead or hollow trees in treatment stands. Thus, while the harvest treatments created new habitat for some species, results from our unharvested stands highlight the need for reserving some undisturbed habitat patches and, perhaps, areas where natural disturbance regimes are maintained within a working forest landscape.

It is also important to note that differences we recorded in diversity in the third year postharvest were due to both increases in treatment stands and declines in unharvested stands in comparison to the first year postharvest (Fig. 3). The trend towards declining diversity in unharvested stands over time is likely due to multiple factors, but one plausible explanation may be that, within red pine forests, stands harvested with overstory retention provide more optimal habitat for many species than do mature, but monotypic stands. Another explanation may be that overstory retention harvests drastically decreased the effective patch size of intact forest stands (of which our unharvested stands were a part) in and around our study areas. Some studies on avian response to harvesting suggest that the overall amount of old-growth and natural, fire-disturbed forest in a landscape may play a more important role than the configuration of the remaining forest (Imbeau et al., 2001; McGarigal and McComb, 1995; Droblet et al., 1999). This may be especially true for old growth and fire dependent species (Thompson et al., 2003; Schieck and Song, 2006). Despite the prevalence of mature red pines in our treatments, species that rely on large stands of undisturbed forest – such as the Brown Creeper and Blackburnian Warbler (*Dendroica fusca*) – may have declined due to nearby harvesting that changed the effective habitat patch size (i.e., less forest in an interior condition; Holmes et al., 2004; Schieck and Song, 2006). Over time, patches of intact forest larger than those represented by our unharvested control stands may be necessary to maintain populations of certain old growth and/or fire-dependent species (Thompson et al., 2003; Manolis et al., 2002).

4.4. Conclusion

In summary, by the third breeding season following variable retention harvesting, avian community composition had changed in both treatment stands and unharvested control stands in comparison to the initial post-disturbance sampling period. At this time, differences were only apparent between overstory treatment stands versus unharvested controls, but not within either

overstory or understory treatments. Species that prefer interior forest and are sensitive to disturbance had declined in treatment stands and showed higher abundance in the unharvested stands; species that benefit from edge habitat and structural complexity had generally become more abundant in all overstory treatment stands. Both harvested and unharvested red pine forests provide valuable habitat for different bird species, including species listed as regionally sensitive (Table 1). Beyond these generalities, changes in community composition are not consistent within guilds or taxonomic groups, but rather appear to be complex, species and site specific, and based on the structural complexity of habitat at local to landscape scales (Schieck and Hobson, 2000; Schmiegelow and Monkkonen, 2002; Thompson et al., 2003; Schieck and Song, 2006).

Our research demonstrates that harvesting practices mimicking the spatial complexity of structure created by natural fire or wind disturbance regimes – leaving some patches of forest untouched while disturbing others – can have beneficial effects on overall avian community composition. The spatial extent of our treatment stands may be too small, however, to benefit certain bird species (Venier and Pearce, 2005; Schmiegelow and Monkkonen, 2002). Furthermore, our sites do not represent habitats and attendant bird species that would have been historically present over pine-dominated landscapes, including true old growth forest, open parkland, and recently burned snag-rich habitats (Thompson et al., 2003; Schieck and Song, 2006). Regional forest planning efforts should take a broad perspective and work to create a mosaic of habitat types over landscapes which meet the diverse needs of individual species over decadal timeframes (Norton et al., 2000; Schmiegelow and Monkkonen, 2002).

Acknowledgements

This study was funded by the US Forest Service through the Northern Research Station and Chippewa National Forest. The Deer River Ranger District of the Chippewa National Forest provided logistical support in implementing the silvicultural research design. We thank anonymous reviewers for comments improving an earlier draft of this manuscript.

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