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The relationship between shelterwood cuts and crown thinnings and the abundance and distribution of birds in a southern New England forest

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ABSTRACT

Forest regeneration methods such as shelterwood treatments have been shown to substantially increase the diversity of bird species, specifically of species that prefer early seral forests, now rare in the eastern United States. Stand improvement techniques such as thinnings have also been found to increase avian diversity under some conditions. A sustainably managed forest, however, must simultaneously apply regenerative harvesting with stand improvements, and the effect of such treatment combinations on bird community composition is not clear. We compared bird distribution and abundance on shelterwood cuts, crown thinnings, and unmanaged stands at the Yale Myers Forest, a large privately owned and actively managed forest in southern New England. Bird abundance and species diversity was highest in shelterwood cuts and lowest in unmanaged forest, with thinnings being intermediary. Different suites of species inhabited the three treatments, with 18 of 49 common species differing significantly in their abundances between treatments. Characteristics of the vegetation that were directly influenced by silvicultural intervention, including canopy openness, seedling regeneration and vertical structural diversity, appeared to be the dominant drivers of bird abundance. The abundances of some species or groups of species were correlated with the number of trees retained in the implementation of the forestry practices. In conjunction with the conservation of a variety of mature forest habitats, regenerative cuts and stand improvement techniques can be used together to sustain a diverse assemblage of bird species.

1. Introduction

Forest harvesting strongly influences the abundance and diversity of bird species. A rich literature has been collected on how regeneration cuts, including clear-cutting and different types of shelterwood practices, influence bird communities (Conner and Adkisson, 1975; Webb et al., 1977; Annand and Thompson, 1997; King and DeGraaf, 2000). These practices affect the structure and heterogeneity of the vegetation, which in turn is linked to birds' habitat preferences and diversity (MacArthur and MacArthur, 1961; Willson, 1974), and a high diversity of early successional bird species move in and out of logged areas (DeGraaf, 1991; Robinson and Robinson, 1999; Hobson and Bayne, 2000). A separate literature has concentrated on the effects of stand-improvement techniques, such as thinning, and has found that these measures can also affect species diversity (DeGraaf et al., 1990; Haveri and Carey, 2000; Hayes et al., 2003), usually positively. Since active forest management will include both regenerative cuts and stand improvements, however, there is a need to understand how the combination of these forestry practices affects birds.

Southern New England hardwood forests provide an excellent opportunity to study the interaction of regeneration cuts and stand improvement practices. The forests in New England were virtually eliminated by the mid-1800s (Meyer and Plusnin, 1945; Pimm and Askins, 1995; DeGraaf and Miller, 1996), but have regenerated in this century, to the point at which it is now economically feasible to harvest them (Brooks and Birch, 1988). At the same time, early successional forest has become increasingly rare in the area (Trani et al., 2001; Brooks, 2003), as have the shrubland bird species which depend on these habitats (Witham and Hunter, 1992; Askins, 1993). Forest management thus has the potential to increase the abundance of these declining, early seral species (King and DeGraaf, 2004; Askins et al., 2007). For the most part, however, studies of forestry in New England have concentrated on the northern hardwoods of Maine and New Hampshire (e.g., DeGraaf, 1991; King and DeGraaf, 2004), with less work in the "central hardwoods" of Massachusetts and Connecticut (Westveld, 1956; but see Askins et al., 2007; King et al., 2009).

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We report here on the effect of the last 20 years of forest management at the Yale-Myers Forest (hereafter, YMF) in northern CT, where an active program of combining shelterwood treatments with crown thinnings has been undertaken.

Our objectives for this study were as follows: (1) to measure the distribution and abundance of birds in shelterwoods and thinnings, in comparison to unmanaged stands, (2) to identify the vegetation parameters that may be driving these patterns, and (3) to analyze the relationship of specific aspects of the silvicultural techniques (e.g., stand size, retention of canopy trees) to bird distribution and abundance, in an attempt to provide ecological data of utility to forest managers (Sallabanks et al., 2000).

2. Methods

2.1. Study site

YMF is a 3170-ha property located in northeastern Connecticut (41°57′N, 72°07′W) that is actively managed for timber. The region was historically completely cleared of forest for agriculture (Meyer and Plusnin, 1945), with peak agricultural land abandonment (mostly poor pasture) in the 1850s. The first kind of forest that came back was usually pure "old-field" white pine (*Pinus strobus*). Many of the pine stands were heavily cut in the early 1900s, releasing the hardwoods (especially oak) that had established beneath. The secondary forest that exists today, characteristic of the 'central hardwoods' of Massachusetts and Connecticutt, is therefore comprised predominantly of even-aged 100-year-old mixed-hardwood, with a sizable eastern hemlock (*Tsuga canadensis*) component and scattered white pine stands (Westveld, 1956; Ashton and Larson, 1996). The deciduous stands typically have a dense understorey of mountain laurel (*Kalmia latifolia*). Disturbances like hurricanes, ice storms, fire, insect damage, and pathogen epidemics influence stand dynamics and succession in the forests of this region (Siccama et al., 1976; Bormann and Likens, 1979; Ashton and Larson, 1996). The area surrounding the property consists mostly of state park, state forest and private forested holdings. The region, 170–300 m above sea-level, has a gently undulating topography with the slope rarely exceeding 40% (Ashton and Larson, 1996). It experiences a temperate climate (mean temperature summer 20 °C, winter −4 °C) and receives 110 cm of rainfall annually (Ashton and Larson, 1996).

Shelterwoods are a silvicultural technique in which the tree canopy is harvested in stages to allow the more shade tolerant tree species to establish in the understorey (Smith et al., 1997). Prior to 1990, shelterwoods were not conducted because the forest was largely all even-aged and no stands were considered mature (80–120 years of age). After 1990, however, they were conducted sporadically, and then annually since 1999, with their extent in the beginning of 2006 covering approximately 380 ha. Crown thinnings (henceforth referred to as thinnings) comprise treatments to the canopy, whereby growing space is cleared around selected and appropriately spaced crop trees, usually oak (Smith et al., 1997). Stands were uniformly treated from the 1950s through release cleanings and improvement cuts that then moved to commercial crown thinnings. Since 1990 thinnings have been conducted in at least one stand per year, and the total extent stands thinned from 1990 to 2005 is approximately 690 ha.

In selecting stands for this survey, we avoided pine-dominated areas, in order to reduced the heterogeneity of the sampled habitats, and because they were relatively rare. We selected 21 shelterwood cuts, 22 crown thinnings, and 30 unmanaged stands. All shelterwood cuts created in mixed-hardwood stands after 1990 were selected; likewise, all thinnings conducted in this habitat during this same period were selected, as long as they were in sections of the forest where there had been shelterwoods cuts. For unmanaged stands, we selected the stand closest to the shelterwood cut that had not been disturbed since 1990. Many of these stands had not been disturbed since the mid-1980s; other stands had not been disturbed since 1959 or earlier. Of these control stands, approximately half were eastern hemlock-dominated stands and half were mixed hardwood stands.

Table 1
Sampling design for the 2-year study. Bird surveys were completed during six visits: three times by each observer, three times in 2006 and then again three times in 2007. In each year, two rounds were relatively early (1, starting in May), and one round late (2, starting in June).

Year	Observer[a]	Round	Dates
2006	1	1	5/4/06–6/1/06
2006	2	1	5/4/06–6/4/06
2006	1	2	6/5/06–6/30/06
2007	1	1	5/15/07–6/11/07
2007	2	1	5/14/07–6/6/07
2007	2	2	6/11/07–7/9/07

[a] 1 = PL, 2 = EG.

2.2. Bird surveys

A single point count station was placed in the center of each stand. All point count stations were at least 75 m from the stand boundary, and the recommended 250 m from another point count station (Ralph et al., 1995).

Each of the 73 point count stations was visited six times in the months of May–July in 2006 and 2007 (Table 1). The design was balanced in that the two observers both made three full rounds of the point count stations: one observer did two rounds in 2006, and one in 2007; the other observer did one round in 2006 and two in 2007. Each observer did two early rounds (beginning in May) and one later round (beginning in June). We started the second year (2007) slightly later than the first, after we saw that the avifauna was still considerably migratory in early May. All points were surveyed between 5:30 and 9:30 AM. Point counts lasted 12 min, after a 1-min period of immobility. This relatively long counting period may produce bias if birds have high mobility, but can be useful in counting birds with low detectability (Ralph et al., 1995). We estimated the distance at which each bird was first detected (see analysis Section 2.4). Point counts were stopped during precipitation or if there were heavy gusts of wind.

2.3. Vegetation measurements

Vegetation parameters were measured at each point count station using a design modified from James and Shugart (1970) and Hobson and Bayne (2000), between May and September, 2006 (plant community characteristics remained relatively consistent over the sampling period). First, four 0.04 ha circular plots were established 25 m away from the count station center in each of the four cardinal directions. All tree species within these plots were identified and each individual tree greater than 4 m height was counted, and its diameter at breast height (dbh) measured. We did not distinguish between three oak species (*Quercus rubra*, *Quercus velutina*, and *Quercus coccinea*) and between four hickory species (*Carya ovata*, *Carya glabra*, *Carya tomentosa*, and *Carya cordiformis*). Trees were placed in three height categories: canopy trees, subcanopy trees (at least 4 m below canopy trees) and understorey trees (4 m below subcanopy trees). Tree height was estimated by eye, and the number of snags and stumps (from previous logging) was noted. We measured canopy cover at the center of each circular plot using a convex spherical densitometer (an average of four readings; for some older shelterwood stands we ignored the contribution of the regenerating trees in reading the densitometer, so that the number of canopy trees could be compared among stands of different ages).

Second, two 16 m^2 square plots were established, one at each end of the diameter of the 0.04 ha circular plot, along the line of the cardinal direction in which that circular plot was established. Within these plots, we counted the number of seedlings (height class 0–1 m) and saplings (height class 1–4 m). Percent shrub (mountain laurel) cover and brush (coarse woody debris on the ground) cover, as well as shrub and brush height, were estimated by eye within these two plots.

For each of the circular plots, we calculated species diversity of trees using the Shannon–Wiener index of diversity (Krebs, 1999). We also calculated Shannon–Wiener diversity of tree height classes for each circular plot, also known as Foliage Height Diversity (MacArthur and MacArthur, 1961). This measurement served as an index of vertical stratification. We then averaged measurements made at the four circular plots and eight square plots to obtain the following vegetation parameters for each survey location: (1) percent canopy openness, (2) canopy height, (3) total trees/plot, (4) basal area of plot, (5) percent of basal area that was coniferous, (6) tree species diversity, (7) index of vertical stratification, (8) seedling number, (9) sapling number, (10) shrub cover, (11) brush cover, and (12) number of snags.

2.4. Analysis

Although we had originally planned on using distance sampling to estimate bird densities (Buckland et al., 2001), in preliminary analyses we found distance estimates to vary among observers and over time (e.g., the observers appear to changing their average estimates for a species over time). Due to the (a) balanced, two-observer design, (b) the fact that most observations were made aurally, not visually (> 85% in all treatments), and (c) the adequacy of relative abundance data in comparison to density data, we decided to use the fixed-radius point count approach. In preliminary analyses, we used fixed radii of 50 and 75 m; the patterns for these two figures were similar and we selected 75 m because it gave more data for some rarer species. Preliminary analysis of a fully factorial ANOVA model that included observer, year, and round (early or late), demonstrated that these variables did not significantly interact with the variable of interest (treatment). We therefore averaged all counts at one location to get a measure of the total and species-by-species bird abundance. Some limitations to this approach should be noted: comparing abundances between species is potentially biased by differences in species' detectability, and summing the totals of all species together may give more detectable species a disproportional impact. However, a distance model that fully adjusts for differences in detectability between species, observers, and treatments would have a sample size large enough for the analysis of only the most common species (Johnson, 2008).

We used one-way analysis of variance (ANOVA) to test for differences in average species richness and total abundance of birds between the three treatments, followed by Tukey HSD post hoc comparisons. To test for overall differences in species distributions between treatments, we conducted a multivariate analysis of variance (MANOVA) using all the species that were detected in at least five sites or more as the multiple independent variables. Subsequently, we tested all species with independent ANOVA tests and Tukey HSD post hoc comparisons. Bird abundance data was square-root transformed before analysis to increase normality and reduce heteroscedasticity. All linear models were conducted in R (R Foundation for Statistical Computing, 2008).

We used a series of one-way ANOVA tests to determine differences in vegetation parameters between the three treatments. A MANOVA was also used to determine if there were overall differences in the vegetation structure between the treatments. Vegetation measures (counts) were log-transformed before analysis, except if they were percentages, in which case they were arcsine transformed.

To determine how the vegetation parameters were associated with species distribution we used canonical correspondence analysis (CCA). CCA is an ordination technique that groups species and sampling locations, creating a scatterplot in which species that have similar habitat requirements are represented closer to one another, and sites that have a similar avifaunal component are represented closer together (Ter Braak, 1987). We calculated Pearson's correlation of each vegetation parameter with the site scores of both CCA axes. Selected vegetation parameters were then plotted on the CCA scatterplot as arrows, with arrow length describing the strength of the correlation and arrow direction describing how the vegetation parameter was related to bird-abundance in the two-dimensional CCA space, using MVSP (Kovach Computing Services, 2008).

We then investigated whether stand variables, such as the age of cut, the stand size, or the intensity of the cut, were associated with changes in bird abundances. These within-treatment analyses were run separately for shelterwoods and thinnings. To give an estimate of the intensity of a cut, we counted the number of trees in the four circular plots surrounding the point station that were retained after harvest, counting oaks with dbh > 40 cm for shelterwoods and trees of all species with dbh > 30 cm for thinnings. These dbh cut-off points were adjusted for the age of the cut, using data on dbh growth in oaks in YMF over 20 years (Samuel Price and PMSA, unpublished data).

For the within-treatment analyses, we ran multiple regression models that explained each species' abundance as a function of stand age, size and intensity of cut. Because species abundances are known to rise and fall quickly in regeneration cuts (DeGraaf, 1991), we added a quadratic factor into the multiple regression model for age (age^2). Variables were stepwise dropped from the full model if F-statistics demonstrated they did not add significantly ($P < 0.05$) to the model. We subjected to this analysis all species found at more than 25 point stations (>33% of the 73 stations) as well as those species that were seen at fewer points, but demonstrated significant differences in abundance between treatments (see Table 2). We also repeated the same analysis on groups of species: those species that were most abundant in shelterwoods, those that were most abundant in thinnings, and those that were most abundant in unmanaged stands (see Table 2). All figures are shown ± SE.

3. Results

We detected a total of 72 bird species across all treatments—56 species in shelterwoods, 52 species in thinnings, and 60 species in unmanaged stands. There were significant differences in average number of species per point station ($F_{2,70} = 7.97$, $P < 0.001$) and average number of individual birds per station ($F_{2,70} = 12.55$, $P < 0.001$) between the three treatments (Fig. 1). The multiple comparisons revealed that shelterwoods had higher average species richness and total birds per stand than unmanaged forest (Tukey HSD $P < 0.001$, and $P < 0.001$, respectively). Thinnings were intermediate between the other two categories; their average species richness was significantly higher than unmanaged forest (Tukey HSD $P < 0.05$), and their total birds per stand was significantly lower than shelterwoods (Tukey HSD $P < 0.03$), with the other comparisons not being significant.

Overall, abundance of individual species differed between the treatments (Wilk's lambda, $F_{46,96} = 5.79$, $P < 0.001$). Subsequent one-way ANOVAs and Tukey's HSD tests revealed that the abundances of 18 out of 49 species that were seen at more than 5 points significantly varied between the treatments (see Table 2,

Table 2
Relative abundance of species at the Yale Forest, northeastern Connecticut, in the three silvicultural treatments: shelterwoods, thinnings, and unmanaged stands. All species seen in at least 25 of the 73 points (>33%) are included, as well as those species that were seen at fewer points, but demonstrated significant differences in abundance between treatments. Values are the mean number of birds within a 75-m radius area surrounding the point station (±SE). Values with the same letter or no letters were not significantly different at $\alpha < 0.05$, by Tukey HSD multiple comparison tests.

Species	# point	Shelterwood	Thinnings	Undisturbed	$F_{2,70}$	*P*
Abundance highest in shelterwoods						
Chestnut-sided Warbler, CSWA *Dendroica pensylvanica*	37	1.32 (0.14)[a]	0.43 (0.12)[b]	0.03 (0.01)[c]	56.23	2.7×10^{-15}
Eastern Towhee, EATO *Pipilo erythrophthalmus*	48	1.17 (0.12)[a]	0.50 (0.08)[b]	0.12 (0.04)[c]	40.16	1.3×10^{-10}
Gray Catbird, GRCA *Dumetella carolinensis*	23	0.50 (0.10)[a]	0.02 (0.02)[b]	0.03 (0.01)[b]	32.38	1.1×10^{-10}
Common Yellowthroat, COYE *Geothlypis trichas*	43	1.10 (0.15)[a]	0.21 (0.06)[b]	0.12 (0.03)[b]	32.11	2.4×10^{-12}
Chipping Sparrow, CHSP *Spizella passerina*	22	0.27 (0.06)[a]	0.08 (0.03)[b]	0.02 (0.02)[b]	18.26	4.2×10^{-7}
Blue-winged Warbler, BWWA *Vermivora pinus*	14	0.19 (0.06)[a]	0.01 (0.01)[b]	0.01 (0.01)[b]	15.76	2.2×10^{-6}
Baltimore Oriole, BAOR *Icterus galbula*	47	0.62 (0.12)[a]	0.37 (0.06)[a]	0.11 (0.03)[b]	11.87	3.6×10^{-5}
Rose-breasted Grosbeak, RBGR *Pheucticus ludovicianus*	36	0.28 (0.05)[a]	0.14 (0.04)[a,b]	0.08 (0.02)[b]	7.43	0.0012
Mourning Dove, MODO *Zenaida macroura*	8	0.08 (0.03)[a]	0.01 (0.01)[b]	0.01 (0.01)[b]	5.78	0.0047
Black-and-White Warbler, BAWW *Mniotilta varia*	67	0.57 (0.06)	0.42 (0.04)	0.42 (0.06)	2.77	0.07
Brown-headed Cowbird, BHCO *Molothrus ater*	52	0.37 (0.07)	0.30 (0.07)	0.26 (0.04)	0.78	0.46
Wood Thrush, WOTH *Hylocichla mustelina*	32	0.18 (0.07)	0.16 (0.04)	0.10 (0.03)	0.6	0.55
Abundance highest in thinnings						
Black-throated Blue Warbler, BTBW *Dendroica caerulescens*	43	0.08 (0.04)[a]	0.40 (0.08)[b]	0.33 (0.07)[b]	8.77	0.0004
Downy Woodpecker, DOWO *Picoides pubescens*	30	0.07 (0.02)[a,b]	0.18 (0.04)[a]	0.07 (0.02)[b]	3.69	0.03
American Robin, AMRO *Turdus migratorius*	26	0.14 (0.06)[a,b]	0.22 (0.06)[a]	0.07 (0.02)[b]	3.23	0.05
Eastern Wood Pewee, EAWP *Contopus virens*	45	0.19 (0.04)	0.25 (0.05)	0.14 (0.03)	2.85	0.06
Eastern Tufted Titmouse, ETTI *Baeolophus bicolor*	43	0.17 (0.04)	0.32 (0.06)	0.19 (0.05)	2.76	0.07
Red-eyed Vireo, REVI *Vireo olivaceus*	67	0.46 (0.07)	0.70 (0.10)	0.54 (0.09)	1.47	0.24
Black-capped Chickadee, BCCH *Poecile atricapilla*	66	0.43 (0.08)	0.56 (0.06)	0.49 (0.07)	1.33	0.27
White-breasted Nuthatch, WBNU *Sitta carolinensis*	39	0.13 (0.03)	0.17 (0.05)	0.12 (0.03)	0.26	0.78
Abundance highest in undisturbed stands						
Ovenbird, OVEN *Seiurus aurocapillus*	66	0.46 (0.11)[a]	1.08 (0.10)[b]	1.09 (0.07)[b]	17.27	8.0×10^{-7}
Canada Warbler, CAWA *Wilsonia Canadensis*	18	0.00 (0.00)[a]	0.02 (0.02)[a]	0.28 (0.07)[b]	14.38	5.9×10^{-6}
Northern Waterthrush, NOWA *Seiurus noveboracensis*	9	0.00 (0.00)[a]	0.00 (0.00)[a]	0.10 (0.03)[b]	8.24	0.00061
Black-throated Green Warbler, BTNW *Dendroica virens*	41	0.10 (0.04)[a]	0.24 (0.07)[a,b]	0.45 (0.08)[b]	7.53	0.0011
Scarlet Tanager, SCTA *Piranga olivacea*	56	0.16 (0.05)[a]	0.33 (0.04)[b]	0.33 (0.04)[b]	6.79	0.002
Magnolia Warbler, MAWA *Dendroica magnolia*	8	0.01(0.01)[a,b]	0.00 (0.00)[a]	0.04 (0.02)[b]	4.47	0.015
Veery, VEER *Catharus fuscescens*	58	0.35 (0.05)	0.29 (0.06)	0.54 (0.09)	2.15	0.12
Great Crested Flycatcher, GCFL *Myiarchus crinitus*	26	0.08 (0.02)	0.05 (0.02)	0.11 (0.03)	1	0.37
Blue Jay, BLJY *Cyanocitta cristata*	45	0.16 (0.05)	0.21 (0.05)	0.22 (0.05)	0.82	0.45

which lists the 22 most common species seen at more than 25 points, and an additional 7 species which showed significant differences between treatments). Chestnut-sided Warbler and Eastern Towhee had abundances in shelterwoods that were significantly higher than thinnings, and abundances in thinnings that were significantly higher than unmanaged forest. Gray Catbird, Common Yellow-throat, Chipping Sparrow, Blue-winged Warbler and Mourning Dove had abundances in shelterwoods that were higher than in thinnings or unmanaged forest. Rose-breasted Grosbeak's abundance was significantly higher in shelterwoods than in the other two treatments; Baltimore Orioles had higher abundances in shelterwoods and thinnings than in unmanaged forests. In contrast, Black-throated Blue Warbler, Ovenbird and Scarlet Tanager had abundances lower in shelterwoods than in the other two treatments. Canada Warbler and Northern Waterthrush had abundances higher in unmanaged forest than in either

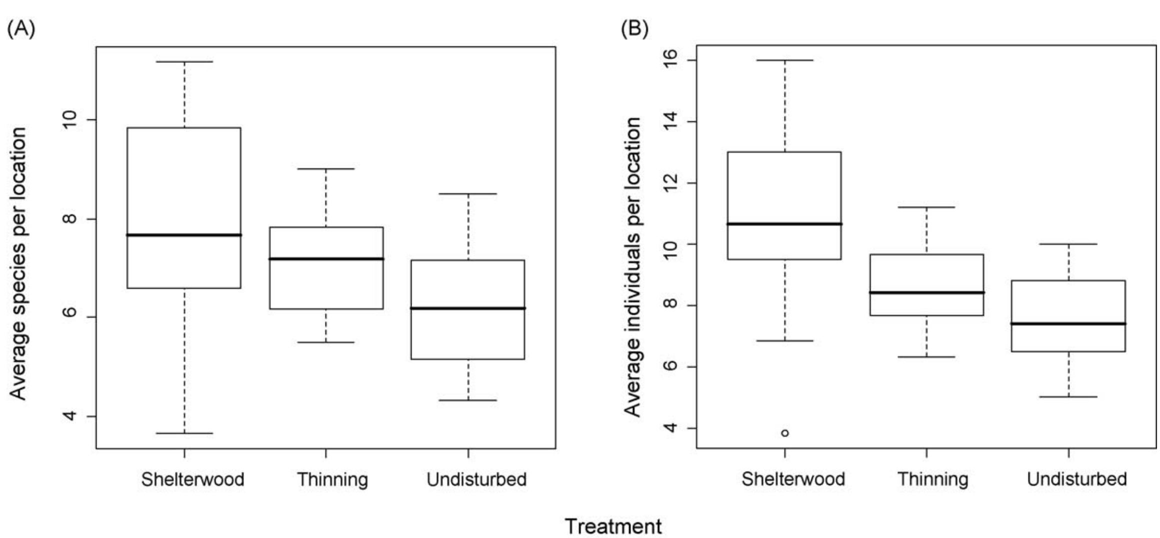

Fig. 1. The relative difference in species richness and relative abundance of all species in the three silvicultural treatments. See text for statistical analysis.

Table 3
The relative values for the vegetation variables in the three silvicultural treatments. Also shown is the Pearson's correlation coefficient between the variable and the first and second CCA axes, shown in Fig. 2. Values with the same letter or not letters were not significantly different at $\alpha < 0.05$, by Tukey HSD multiple comparison tests.

	Shelter	Thinnings	Undisturbed	$F_{2,70}$	P	CCA1		CCA2	
						Pearson	Sig	Pearson	Sig
Value highest in shelterwoods									
Canopy openness (%)	63.43 (4.78)a	17.76 (2.29)b	7.64 (0.58)c	145.73	1.0×10^{-16}	0.78	0.001	-0.01	0.98
Saplings (# per 16 m^2)	9.33 (1.89)a	2.18 (0.77)b	0.21 (0.12)c	25.07	6.2×10^{-9}	0.48	0.001	0.01	0.97
Coverage of brush (%)	16.81 (3.05)a	13.33 (2.34)a	4.35 (0.41)b	14.95	3.9×10^{-6}	0.49	0.001	−0.09	0.45
Total trees (# per 0.04 ha)	38.04 (16.45)a[a]	22.76 (1.94)a,b	27.71 (1.23)b	4.52	0.014	−0.15	0.2	0.02	0.84
Value highest in thinnings									
Vertical diversity	0.49 (0.06)a	0.99 (0.02)b	0.98(0.01)b	72.53	1.0×10^{-16}	−0.67	0.001	−0.02	0.84
Seedlings (# per 16 m^2)	16.54 (2.96)a	18.97 (3.72)a	3.53 (0.87)b	16.48	1.4×10^{-6}	0.36	0.002	−0.25	0.03
Value highest in undisturbed stands									
Basal Area (m^2/ha)	0.40 (0.06)a	0.98 (0.04)b	1.31 (0.06)c	78.13	1.0×10^{-16}	−0.82	0.001	−0.11	0.35
Species diversity	0.86 (0.09)a	1.43 (0.06)b	1.44 (0.05)b	26.91	2.2×10^{-9}	−0.66	0.001	0.08	0.5
Snags (# per 0.04 ha)	0.82 (0.33)a	1.16 (0.18)b	2.86 (0.26)c	25.14	5.9×10^{-9}	−0.63	0.001	0.05	0.68
Coniferous basal area (%)	17.15 (4.00)a	19.19 (3.66)a,b	30.00 (4.04)b	3.9	0.025	−0.3	0.01	−0.35	0.003
Coverage of mt. laurel (%)	14.52 (3.25)a	20.29 (5.24)a,b	36.46 (4.58)b	3.86	0.026	−0.25	0.03	0.69	0.001
Height (m)	21.74 (1.12)	23.41 (0.49)	23.52 (0.34)	2.56	0.08	−0.18	0.12	−0.15	0.2

[a] The large variation here was due to the two oldest shelterwoods (1990) having very high numbers of trees (325 and 176 per 0.04 ha).

shelterwoods or thinnings; Black-throated Green Warbler abundances were significantly higher in unmanaged forests than in shelterwoods, and Magnolia Warblers were significantly higher in unmanaged forests than in thinnings. Finally, Downy Woodpecker and American Robin were significantly higher in thinnings than in unmanaged forest.

We found a significant overall difference in the vegetation parameters for the three treatments (Wilk's lambda,

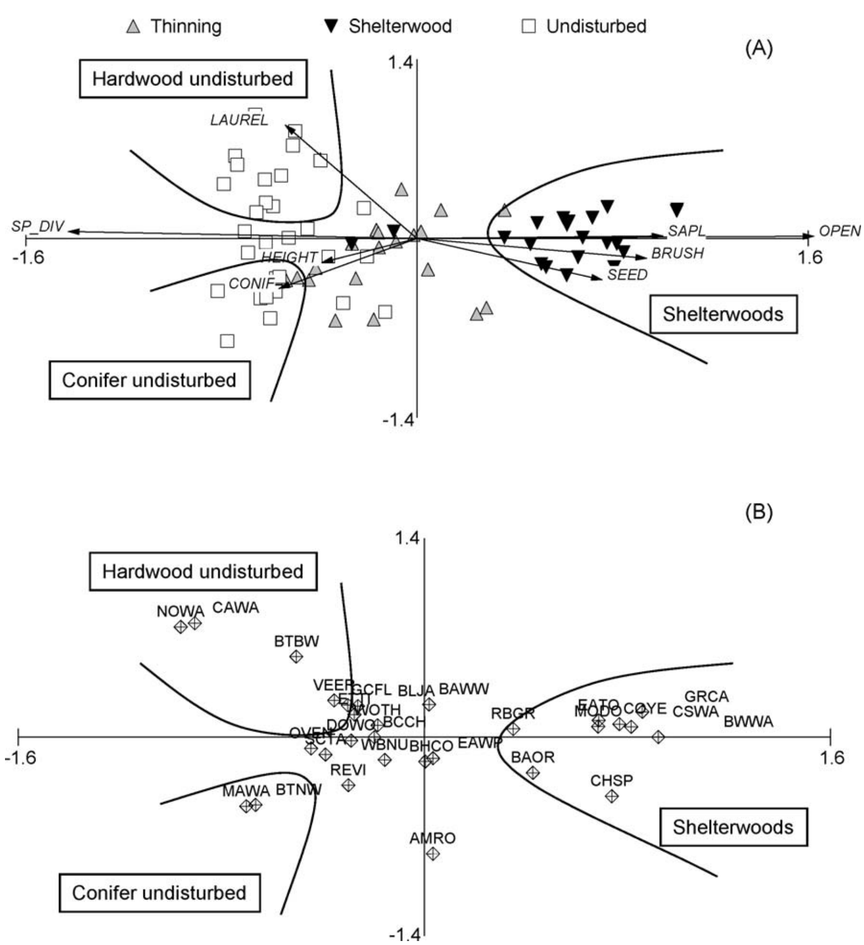

Fig. 2. CCA plots illustrate the relationship between vegetational characteristics and the distribution of bird species. (A) The point count stations are clearly differentiated between open stands with low structural diversity associated with shelterwood cuts on the right and high basal area, high diversity stands associated with unmanaged stands on the left. For clarity, several vectors that point in virtually the identical direction as species diversity (basal area, vertical diversity, the number of snags and the number of trees) have been removed from the graph. (B) The shelterwood-preferring group of species (see Table 2) are on the right, whereas on the left there are two groups of birds that prefer unmanaged stands: those that are associated with hardwood stands that have an understorey dominated by mountain laurel above the X-axis, and those the are associated with coniferous stands below the X-axis.

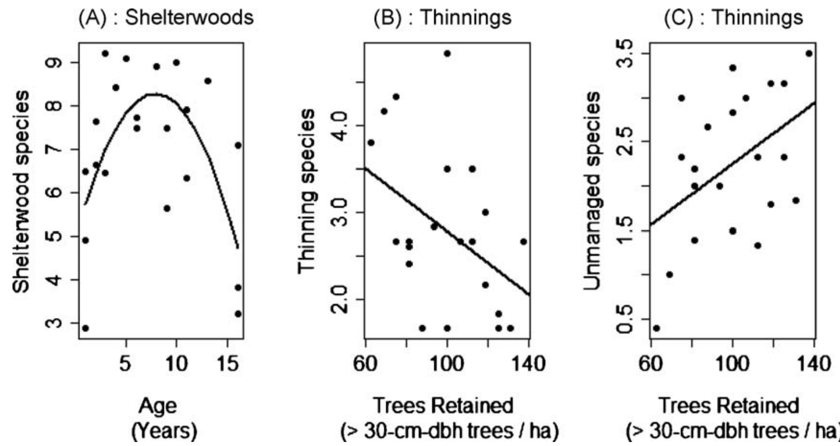

Fig. 3. Significant within-treatment effects of stand variables (age of cut, number of retained trees, size of stand). (A) Species that were most abundant in shelterwoods (see Table 1 for groupings) varied over time in shelterwood cuts, rapidly increasing in the first few years and then declining after 10 years. (B) Species that were most abundant in thinnings decreased in abundance in thinnings as the number of large (dbh > 30 cm) trees increased. (C) In contrast, species that were most abundant in unmanaged stands increased in abundance in thinnings as the number of large trees increased. For the later two graphs, the number of retained trees was measured in the circular plots surrounding the point location.

$F_{24,118} = 16.20$, $P < 0.001$). All the vegetation parameters except canopy height differed between the treatment types (Table 3). Characteristics of the vegetation that were directly influenced by intense silvicultural intervention, including canopy openness, seedling regeneration and the coverage of brush, were much higher in the shelterwood treatments. In contrast, undisturbed areas had high basal area, species diversity and number of snags. Thinnings were intermediate between the other two treatments for most variables.

The ordination illustrates the relationship between the vegetation variables and bird distributions (Fig. 2). The first CCA axis had strong positive correlations with canopy openness, the number of seedlings and saplings and the coverage of brush, and strong negative correlations with basal area, species diversity, the number of snags, the percent of basal area that was coniferous, and the coverage of mountain laurel (see Table 3). These variables appeared to have the greatest influence on bird distribution, with good separation between the shelterwood and unmanaged stands, and thinnings occurring between the other two treatments (Fig. 2A). Hence, Chestnut-sided Warbler, Eastern Towhee, Gray Catbird, Common Yellowthroat, Chipping Sparrow, Blue-winged Warbler, Baltimore Oriole, Rose-breasted Grosbeak, and Mourning Dove, occurring at the right of the ordination space (Fig. 2B), are associated with open stands, with high sapling regeneration and the high canopy openness that is characteristic of shelterwood cuts. The second CCA axis was significantly positively correlated with mountain laurel cover, and negatively correlated with the number of seedlings and the percent of basal area that was coniferous (Table 3). In Fig. 2B, the species on the left of the ordination space were associated with a closed canopy and the high structural and species diversity characteristic of the unmanaged stands (Fig. 2A). The group above the *X*-axis, includes the Canada Warbler and Northern Waterthrush, which were associated with high mountain laurel cover in hardwood stands. In contrast, below the *X*-axis, are a group of species associated with coniferous stands, including Magnolia Warbler and Black-throated Green Warbler.

In the analysis of shelterwoods, the age of the cut was the primary factor correlated with species' abundances. The age of the cut was significantly related to the abundance of the group of species most abundant in shelterwoods (see Table 2 for grouping): the abundance of this group of species was low soon after the shelterwood cut, increased to its highest point between 3 and 10 years, and then declined as the shelterwood cut got older ($F_{2,18} = 6.74$, $P = 0.007$, Fig. 3A). Several species, when analyzed independently, showed a similar rise and fall (Brown-headed

Table 4
Within-treatment relationships between relative abundance of species and variables of the cut (age, the number of retained trees, stand size).

Treatment	Species	Age	Age^2	Retained trees[a]	Size (ha)	F	P	R^2_{adj}
Shelterwoods	Eastern Wood Pewee	−0.017			−0.0087	$F_{2,18} = 14.62$	0.0002	0.58
	Brown-headed Cowbird	0.166	−0.0103			$F_{2,18} = 10.01$	0.0012	0.47
	Gray Catbird	0.17	−0.0082			$F_{2,18} = 6.45$	0.0077	0.35
	Ovenbird		0.0026			$F_{1,19} = 7.83$	0.012	0.25
	Baltimore Oriole		−0.0026			$F_{1,19} = 6.78$	0.017	0.22
	Blue-winged Warbler	0.032				$F_{1,19} = 6.69$	0.018	0.22
	Chestnut-sided Warbler	0.151	−0.0096			$F_{1,18} = 4.87$	0.02	0.28
	Wood Thrush				0.0085	$F_{1,19} = 6.26$	0.022	0.21
	Black-throated Blue Warbler			0.075		$F_{1,19} = 6.23$	0.022	0.21
	Eastern Towhee		−0.0018			$F_{1,19} = 6.14$	0.023	0.2
	American Robin		−0.0016			$F_{1,19} = 4.60$	0.045	0.15
	Eastern Titmouse		−0.0014			$F_{1,19} = 4.40$	0.049	0.15
Thinnings	Wood Thrush		0.0023			$F_{1,20} = 11.73$	0.0027	0.34
	Black-and-White Warbler	0.09	−0.0068	−0.039		$F_{3,18} = 6.11$	0.0047	0.42
	Blue Jay			0.031		$F_{1,20} = 6.80$	0.017	0.22
	Rose-breasted Grosbeak	−0.102	0.0066			$F_{1,19} = 4.98$	0.018	0.28
	Chestnut-sided Warbler			−0.071		$F_{1,20} = 4.76$	0.041	0.15

[a] For shelterwoods, the number of oaks remaining; for thinnings the number of all large trees. For specifics of methodology, see text.

Cowbird, Gray Catbird, and Chestnut-sided Warbler), or a gradual decline (Eastern Wood Pewee, Baltimore Oriole, Eastern Towhee, American Robin, and Eastern Titmouse), or a gradual increase (Blue-winged Warbler, Ovenbird, Table 4) in abundance with time since the cut was conducted. Stand size and the number of canopy oak trees that were retained were related to the abundances of fewer species than was the age of the cut. As stand size increased, Eastern Wood Pewee decreased in abundance while the abundance of Wood Thrush increased (see Table 4). Increasing the number of remaining canopy oak trees increased the abundance of Black-throated Blue Warblers.

In the analysis of thinnings, the number of large trees retained was an important variable, as well as the age of the cut. The group of species that were most abundant in thinnings (see Table 2 for grouping) declined as the number of retained trees increased ($F_{1,20} = 4.62$, $P = 0.044$, Fig. 3B); the shelterwood species also tended to decline non-significantly in the same manner ($F_{1,20} = 3.15$, $P = 0.091$). In contrast, the group of species most abundant in unmanaged stands (see Table 2 for grouping) increased in thinnings as the retained trees increased ($F_{1,20} = 5.53$, $P = 0.029$, Fig. 3C). Similar trends were seen for species individually: the shelterwood preferring Chestnut-sided Warbler and Black-and-white warbler decreased with increasing number of trees, whereas the unmanaged-preferring Blue Jay increased (see Table 4). Age of the thinning was also a factor for several species: the Wood Thrush gradually increased, the Black-and-white warbler decreased, and the Rose-breasted Grosbeak was seen in more very recent and older thinnings than in thinnings of medium age.

4. Discussion

The central hardwood forests of southern New England have now regenerated sufficiently from past human disturbance to make harvesting economically viable (Brooks and Birch, 1988). A forest of the scale of YMF is large enough to make such harvesting sustainable: at any one time, regenerative cuts are applied to some stands, while others are improved through thinning in view of a later harvest, and still other stands retained unmanaged to balance harvesting with the other wildlife management and recreational goals of the forest. Here we show that the regeneration cuts change bird distributions and abundances, favoring the early successional species that are now threatened in New England (Askins, 1993, 2001). At the same time, another suite of species prefers fairly open thinnings. At the landscape level then, the inclusion of regeneration cuts, thinning and conservation areas will result in a high diversity of birds, and to the extent that birds can be used as bioindicators, a high diversity of other species as well (Canterbury et al., 2000; Burger, 2006). Our results agree with a growing consensus that different kinds of forestry practices should be used in conjunction for the sustainable maintenance of biodiversity, and birds in particular (King and DeGraaf, 2000; Doyon et al., 2005).

The highest abundance of species was found in shelterwoods, a result that agrees with other studies that have found this harvesting method to promote diversity (see Fig. 1, Annand and Thompson, 1997; King and DeGraaf, 2000; Anderson and Crompton, 2002). Although we did not have any comparisons to clear-cuts, two lines of evidence indicate that the retention of shelter and seed trees promotes avian diversity. First, some species (e.g., Baltimore Oriole) that nest in canopy trees were more abundant in shelterwoods, in addition to the shrub-nesting species usually found in regeneration cuts. Second, a high number of retained canopy trees increased the abundance of at least one forest species, Black-throated Blue Warbler. Avian diversity was intermediate in thinnings and lower in unmanaged areas. It should be noted that there was a variety of unmanaged stands included in the analysis, including evergreen (hemlock) dominated stands as well as deciduous dominated stands. Yet bird diversity was lower in both unmanaged stands with less than 25% basal area of coniferous trees (6.63 ± 0.30 species, $n = 16$) and in unmanaged stands with greater than 25% basal area of trees (5.83 ± 0.32 species, $n = 14$), when compared to thinnings (7.15 ± 0.22 species, $n = 22$).

Different suites of species inhabited the different treatments. The species composition of the shelterwoods was, as expected, dominated by species that nest in regenerating trees (e.g., Blue-winged Warbler, Chestnut-sided Warbler, Common Yellowthroat, Eastern Towhee, Gray Catbird), and these species move quickly in and then out of the regenerating cut, with slight differences among them based on the size of the regenerating trees that they prefer to nest in (e.g., larger for Blue-winged Warbler than for Chestnut-sided Warbler, DeGraaf, 1991; Hobson and Bayne, 2000). These species, and in particular Eastern Towhee, have been declining in recent years in New England due to reduced areas of early successional forest (Witham and Hunter, 1992; Hagan, 1993). Shelterwood cuts can be used as tools in the management of these species, possibly in conjunction with clear-cuts, which from recent studies nearby YMF appear to increase the abundances of some species that were very rare in our study, such as American Goldfinch *Carduelis tristis*, Cedar Waxwing *Bombycilla cedrorum*, and Prairie Warler *Dendroica discolor* (Askins et al., 2007; King et al., 2009). One caveat is the somewhat concerning tendency for the brood parasite Brown-headed Cowbird to prefer shelterwoods, sharply increasing in abundance in the ~6–10 year shelterwoods, before dropping again. This species is likely tracking the spike of nesting in the regenerating areas (Barber and Martin, 1997).

An unexpected result was the presence of some mature forest species in shelterwood areas; indeed the overall number of species that differed significantly between treatments (18/49) in this study was fairly low (compare to 29/36 species differing among treatments in Annand and Thompson, 1997). We can see two possible reasons for this. First, the forest is a mosaic of small stands of different treatments with consequently a large amount of edge area, and this could blur the distinctions between treatments. For example, the Eastern Wood Pewee was seen only in shelterwoods of small stand size; this species may prefer edge habitat. Second, some forest species like the Wood Thrush may forage facultatively in the shelterwoods, but nest elsewhere. Such species have also been reported to use open areas outside of the breeding season (Vitz and Rodewald, 2006). A clear priority in future research in YMF is to collect data on the foraging patterns and productivity of bird species in the different treatments, using spot-mapping and nest observations (Van Horne, 1983; King et al., 1996).

A separate suite of species preferred thinned stands. These are species, such as American Robin, which appear to prefer open woodlands (Hansen et al., 1995), and previous work has also shown thinning can increase their abundances (Hayes et al., 2003). Interestingly, the bark-foraging guild of birds also appears to respond favorably to thinning, despite thinnings reducing the number of potential nest-sites for these species. In this study, Downy Woodpecker showed a significant trend to be more abundant in thinnings. Interestingly, the other two bark-foraging species found in this study, the White-breasted Nuthatch and the Hairy Woodpecker (*Picoides villosus*) also were most abundant in thinnings; similar results with bark-foraging species have been seen in other studies on thinnings (Hayes et al., 2003). Perhaps nesting sites are not limiting for these species, and open woodlands facilitate their search strategy and foraging efficiency. For the group of species that preferred thinnings as a whole, it is noteworthy that their abundances decreased as the intensity of harvesting decreased (i.e., the number of trees retained increased, Fig. 3B): relatively heavy thinning is required to maintain higher abundance in these species. Thinnings, of course, require roads and landings; some of the areas with high intensity of harvest in our study tended to be points randomly located near such disturbances. Not only do these areas provide habitat for the species that prefer thinnings mentioned above, but early successional species (e.g., Chestnut-sided Warbler) also move in for a short time. Thus, at the landscape level thinnings can be used to promote diversity, in conjunction with regenerative cuts and conservation areas.

A final suite of species will require conservation of older, unmanaged stands. As mentioned above there were two types of unmanaged forests, hemlock dominated stands and deciduous dominated stands, and each kind of stand had some species that reached peak abundance in it (e.g., Black-throated Green and Magnolia Warblers in hemlock stands, Black-throated Blue and Canada Warblers in hardwood stands). It is likely that this habitat heterogeneity is responsible for the fact that the total number of species seen in the unmanaged stands (60) was higher than the number seen in thinnings or shelterwoods. Further heterogeneity in unmanaged stands is caused by topography: while there were a few upland sites, unmanaged areas tended to be wet, and hence unsuitable for harvesting, which lead to some species preferring these stands (e.g., waterthrushes). As emphasized below, long-term conservation of unmanaged stands must retain this heterogeneity to best sustain bird diversity.

4.1. Management implications

YMF is somewhat unusual for forests in southern New England in being a large privately owned entity; private owners in the area tend to own small tracts of land (Brooks and Birch, 1988; Brooks, 2003). Nonetheless, small holders can act in consortiums and in conjunction with state managers to conduct regeneration cuts, prepare other stands for eventual harvest through stand improvement, and to conserve another set of stands. Here we have shown that in addition to the early successional and threatened species that regenerative cuts can support, thinnings can also increase species diversity at the landscape level. Further, birds respond to variation in the implementation of forest practices. For example, Black-throated Blue Warblers, which are not usually found in large areas of open habitat, were present in shelterwoods that had 25 or more canopy trees per ha with dbh >40 cm. The suite of species that preferred crown thinnings declined substantially when there were more than 100 trees with dbh >30 cm retained (Fig. 3B).

Some caveats should be mentioned that might temper the generally positive findings on the effects of forest management on avian biodiversity. First, unmanaged areas are clearly important for certain species and variation in the types of these areas present (evergreen vs. hardwood, upland vs. water-logged areas) must be maintained. Second, the high species diversity of the regenerative cuts declines quickly after about 10 years (Fig. 3A, DeGraaf, 1991), and this must be considered when allocating the percentage of land to be devoted to such cuts. Third, some species that prefer unmanaged land may require a certain size of stand to be productive; spatial heterogeneity must also be maintained at a larger scale so that the whole forest is not a mosaic of patches of different treatments all of a uniform size. Further studies are needed at YMF to investigate birds species' productivity in the different treatment areas (e.g., King et al., 1996; King and DeGraaf, 2004), and to analyze species distributions at the landscape level (e.g., MacFaden and Capen, 2002).

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