



Changes in breeding bird abundance and species composition over a 20 year chronosequence following shelterwood harvests in oak-hardwood forests



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ABSTRACT

Birds play an integral ecological, functional, and cultural role in New England forests and timber harvesting is known to affect their diversity and abundance. While much is known about bird communities immediately following a harvest (one to about three years), less is known about how communities shift through stand development. This study examines breeding-bird species diversity and composition in the 22 years following shelterwood harvest of second-growth oak-hardwood forests in southern New England. We documented bird species richness, Shannon diversity, abundance, and evenness in 28 regenerating shelterwood harvests and compared them with eight mature forest stands. Early-successional regenerating stands (<12 years since harvest) had higher bird abundance than regenerating stands 13–22 years old and mature stands (80–100 years old). Species richness and Shannon diversity were greater in regenerating shelterwoods compared to mature stands. Within the regenerating shelterwoods, species richness, Shannon diversity, and total bird abundance generally decreased with time since harvest. Species community composition differed between stands <12 years old and older regenerating and mature stands. Abundances of forest dwelling, ground-nesting species increased steadily with time since harvest, while early-successional, shrub-nesting species decreased with time since harvest. Specifically, we observed higher abundances of shrub-nesting species such as chestnut-sided warbler (*Setophaga pennsylvanica*) and indigo bunting (*Passerina cyanea*) in early stand-initiation (0–7 years). Ground-nesting birds, such as ovenbirds (*Seiurus aurocapilla*), are present and abundant as early as 13 years following a harvest and are not obligate to closed-canopied forest conditions. Indeed, abundances of species considered 'late-successional' were as high in early stem exclusion (13–22 years) as in mature stands and were present in moderate numbers in stands considered late initiation (8–12 years). Contrastingly, we found many early-successional species confined to stand initiation (<13 years). In summary, bird communities in shelterwood harvests are highly dynamic in the 22 years following harvesting and our understanding cannot be distilled to a single diversity number such as species richness. Our findings convey that bird abundance, richness, diversity and species composition change following a harvest, suggesting that natural resource managers in New England hoping to promote diverse and abundant bird populations should create forests composed of mosaics of differently aged managed stands, and mature forest reserves.

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1. Introduction

Birds play important ecological roles: they regulate forest insect populations, are essential seed dispersal agents, and are indicators of forest health and ecosystem integrity (Sekercioglu et al., 2004).

Many bird species in New England are declining, especially early-successional species, primarily due to habitat degradation and loss due to abandoned agricultural lands growing into second-growth forests (Askins, 1993, 2001; Litvaitis, 1993; DeGraaf and Yamasaki, 2003; Schlossberg and King, 2007). Timber harvesting and forest management techniques can combat this decline by increasing and diversifying habitats available to birds (Augenfeld et al., 2008; Cahall et al., 2013; Goodale et al., 2009; Keller et al., 2003; King and DeGraaf, 2000; Perry and Thill, 2013). In particular, shelterwood regeneration harvests in temperate-oak forests can

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increase bird populations by offering more diverse horizontal and vertical habitat compared to mature second-growth forests (Goodale et al., 2009; King and DeGraaf, 2000; Smith et al., 1997).

Shelterwood is a silvicultural term for a regeneration treatment that harvests 50–80% of the basal area leaving large, evenly-spaced trees to act as a source of seed for new recruitment and shade and protection to the regenerating stand (Smith et al., 1997). These residual trees may be harvested ten to 20 years after the initial treatment, once the regeneration has established. Shelterwood treatments can be considered “irregular” by leaving additional structures behind (reserves) that remain uncut after the final removal of parent trees. Reserves can include snags or living trees of differing species and size classes that provide supplementary habitat and food (e.g., older cavity trees, trees that provide soft and hard mast, evergreens that provide thermal cover; Smith et al., 1997). Reserves can be strategically arranged in groups or singly across the harvest treatment (Smith et al., 1997).

Bird surveys done within one to two years of a shelterwood timber harvest suggest timber harvesting can increase bird diversity and abundance by increasing the structural diversity of vegetation (Baker and Lacki, 1997; Faccio, 2003; Goodale et al., 2009; King and DeGraaf, 2000). Though short-term studies are extremely valuable, they generally only offer a fleeting glimpse of bird populations within a single successional stage following a harvest. Due to the quickly regenerating vegetation following a harvest, a single sampling point within a year or two of harvesting is not sufficient to provide adequate, long-term information about bird communities in managed forests. Few studies have looked at the long-term impacts of timber harvests, though some have: Hobson and Schieck (1999), Perry and Thill (2013) and Schlossberg and King (2009). These studies found that there was an initial increase in birds post-harvest (within one to five years), followed by a decrease in bird presence or abundance, demonstrating the need for long-term studies to capture fluctuations in bird populations over time. Stand development following a timber harvest creates substantial structural changes over short periods of time, resulting in a relatively quick turnover of bird species with varying nesting and foraging strategies (Schlossberg and King, 2009). By surveying multiple successional stages we here provide essential long-term information about bird community development following forest harvesting.

We examined bird communities in 28 regenerating shelterwood stands, across a chronosequence ranging from one to 22 years since harvest, and eight mature stands. The objective of this study is to provide foresters and natural resource managers detailed information on how forest management influences bird communities through successional development. We address the following questions: (1) How does bird abundance, richness, Shannon diversity, and evenness differ between mature stands and over a chronosequence of regenerating stands in different phases of stand development? and (2) How does bird species composition differ across the same chronosequence of stand development?

The habitat heterogeneity–animal diversity hypothesis assumes that greater diversity and abundance of vertical and horizontal habitats offered within a stand will support more species and individual birds (MacArthur and MacArthur, 1961; MacArthur, 1964). Past studies have shown that recent timber harvests can create habitat with more diverse vertical and horizontal vegetation structures than second-growth forests (Goodale et al., 2009; King and DeGraaf, 2000; Smith et al., 1997). Assuming agreement with the habitat heterogeneity–animal diversity hypothesis, we expected that bird abundance, richness and diversity would dramatically change over a short period of time, as the stand progresses from early-successional to mature habitats. We predicted bird richness, abundance and diversity would be higher in regenerating, as opposed to mature stands. In addition, we predicted bird species

richness, abundance and diversity would initially increase in early initiation and late initiation stands (due to the vigorously growing vegetation and structurally diverse regeneration) and then decrease with canopy closure upon early stem exclusion. We also expected to see bird species composition significantly differ between the age classes because of rapidly changing vegetation structures as the stands regenerated.

2. Materials and methods

2.1. Site description

We conducted our study at the Yale-Myers Forest, a 3213 ha research and demonstration forest in northeast Connecticut (41°85'N, 72°80'W). The forest is classified as central hardwood-hemlock-pine (Westveld, 1956). The forest is second-growth that originated beneath cut-over, old-field pine after agricultural abandonment in the mid-19th century. Dominant tree species include red oak (*Quercus rubra* L.), white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* L.), maple (*Acer* spp.), birch (*Betula* spp.) and hickory (*Carya* spp.; Meyer and Plusnin, 1945). The understory is composed of over 200 species of plants, though it is often characterized by dense patches of mountain laurel (*Kalmia latifolia* L.) and black birch (*Betula lenta* L.) regeneration (Ashton and Larson, 1996; Duguid et al., 2013). The topography is ridge-valley with an elevation range between 170 m and 300 m above sea level. The soils are glacial tills composed of moderate to well-drained stony loams overlying bedrock. Average temperatures in July and January are 21.2 °C and 4.1 °C, respectively (Ashton and Larson, 1996).

The Yale-Myers Forest is an actively managed working forest and is an Audubon designated Important Bird Area. The forest contains both reserve and production stands, of the total forest area, one third has been assigned as reserve and two thirds is managed for timber production. Stands that are managed for timber production are regenerated by various kinds of irregular shelterwoods, whereby after the final harvest a proportion of residual trees are left behind. One-to-two stands are regenerated through shelterwoods per year. The average stand size is about 15 acres. Shelterwood regeneration harvests usually take two harvest entries in order to secure established regeneration that can be considered free to grow. The first entry is made in stands that are reproductively mature and vary in age (depending upon site quality) between 80 and 120 years. This first cut removes almost all the sub-canopy trees and spaces the trees that are the canopy parent tree seed source between 15 and 21 m apart. At this time reserve trees are left singly or in small groups to increase wildlife habitat or economic value of the future stand (e.g., hemlock as thermal cover, cherry as a source of soft mast). Before harvest, BA within stands typically ranges between 26 and 33 m² per hectare with about 11–15 m² per hectare remaining after the first harvest. The second and final harvest occurs 10–15 years later and removes another 6–8 m² per hectare, taking every other parent tree. The remaining stems remain as seed trees and residual structures for the regenerating stand. The combination of both reserve and production stands provides a rich assemblage of stand and site conditions.

We identified 36 stands in four age classes for sampling: nine in early initiation (EI; ≤7 years since harvest), nine in late initiation (LI; 8–12 years), ten in early stem exclusion (ESE; 13–22 years) and eight mature (MAT; 80–100 years). These divisions are based on the Oliver and Larson (1990) model of stand development. In this study, we use age as a proxy for forest structure. EI stands are defined by an open canopy, sparse herbaceous vegetation, and woody debris. There is a variable presence of young

regeneration that is either germinating or being released as advanced growth. By three years there is vigorous coppice regrowth, seedling establishment and herbaceous growth. LI stands are defined by vegetative regrowth from coppice, advance growth and seedlings between 1 and 3 m in height and are dominated by woody plants that have not attained canopy closure. In ESE stands, canopy closure has occurred to form a dense uniform canopy of woody regrowth (3–4 m in height), and there is evidence of self-thinning (sapling and seedling mortality). The ground-story is densely occupied by stems but otherwise open, with leaf litter and sparse herbaceous layer. MAT stands are defined by relatively homogenous canopy tree height (10–13 m in height) and spacing. There is a sparse to clumpy herbaceous layer with a patchy understory of mountain laurel and other shade-tolerant shrubs.

2.2. Bird surveys

We used the point count method to survey bird populations (Goodale et al., 2009; Webb et al., 1977). Following King and DeGraaf (2000), we established point counts for measuring bird abundance, richness and diversity within a fixed radius of 50 m. To avoid edge effects, all points were at least 100 m away from the stand edge. In addition, point counts were at least 250 m apart to decrease the chances of recounting the same birds at different points (Ralph et al., 1995; Taulman, 2013).

We placed a point count near the center of each stand using a combination of Geographic Information Systems (GIS) and field visits (Fig. 1). In total, we examined 28 stands, regenerated from shelterwood harvests between 1992 and 2014, and eight mature stands that are 80–100 years old. Both types of stands are of similar vintage, species composition and topography (see Supplemental Table 1 in Appendix for stand descriptions). Twenty-seven of the 36 points were used in a prior study completed in 2007 (Goodale et al., 2009).

We conducted point count observations between 5:30 AM and 10:00 AM on precipitation free days with wind speeds less than 24 km per hour (Manuwel and Carey, 1991). We visited each location four times in 2015 with at least one visit in early (5:30–7:00 AM), mid (7:00–9:00 AM) and late (9:00–10:30 AM) morning. We visited all point count locations in early spring (May 9–20); mid spring (May 21–June 6); late spring (June 7–June 20); and early summer (June 21–July 1). Point counts lasted for 12 min following a one minute quiet period immediately after arriving at the site (Goodale et al., 2009; Ralph et al., 1995). At each count we recorded the count and species of each bird detected.

2.3. Data analysis

2.3.1. Bird categorization

We classified birds using species descriptions provided by the Cornell Laboratory of Ornithology (<https://www.allaboutbirds.org/guide/search/>, last accessed April 1, 2016). We were particularly interested in two categories of species: (1) birds described as preferring close-canopied mature forest habitats and that nest on the ground, which are known to be particularly sensitive to disturbance (hereafter referred to as ‘forest ground-nesting species’; Keller et al., 2003); and (2) bird species that do not prefer closed-canopied mature forest (described as preferring various types of early-successional habitats) and that nest in bushes, shrubs and small trees (hereafter referred to as ‘early-successional shrub-nesting species’). These species are closely connected to forests regenerating after disturbance (Askins, 1993, 2001).

2.3.2. Bird abundance, richness, and diversity

For each stand we calculated species richness as the total count of species per plot. We also calculated Shannon diversity and

Shannon evenness ($J' = H'/\ln S$). We used the number of detections to represent relative abundance in this study, and used the mean number of detections for each stand, across the four visits for all diversity and abundance calculations. Species accumulation curves, visualized after bootstrapping with 100 permutations (Magurran, 2004; Fig. 2), were still rising towards asymptotes when information was included from all sites, therefore we also calculated estimated species richness using the Chao richness estimator (Chao, 1987; Chiu et al., 2014). We then ran generalized linear models (GLM) on the diversity and abundance variables (measured richness, Chao estimate, Shannon diversity, Shannon evenness, and total abundance of all species) as response variables and age class as the dependent variable. We assumed normality when $P \geq 0.05$ in Shapiro–Wilk normality tests. Measured richness, Chao, Shannon diversity and total abundance were normally distributed and we used Gaussian distributions; we utilized a Poisson distribution for evenness. We carried out Tukey HSD post hoc comparisons following GLMs to determine which age classes were different from others. For shelterwood stands, we performed simple linear regressions on all five diversity and abundance variables as response variables and year since harvest as the predictor variable. We calculated Moran's I tests for all five diversity and abundance variables to confirm there was no spatial autocorrelation in our samples.

2.3.3. Bird species composition

We tested for differences in bird species composition between age classes using nonparametric MANOVA (NPMANOVA), a multivariate analysis of variance using permutations. We ran all NPMANOVA models with Bray-Curtis distance and 1000 permutations. To visually examine the clustering of significant factors from the NPMANOVA, we used non-metric multidimensional scaling (NMDS). We used Bray-Curtis distance, conducted several random starts on the same data, and used square root and Wisconsin double standardization transformations and step-across dissimilarities. We scaled and rotated final results for maximum variance in the first dimension. We completed five randomized runs before finding a convergent solution and examined a Shepard plot to confirm that original dissimilarities were well preserved in three dimensions.

To explore differences in individual bird species' abundances across different aged regenerating stands, we used one-way analysis of variance (ANOVA) models for each observed species with abundance as the response variable and age class as the predictor. On species with significant ANOVA results ($\alpha < 0.10$) we calculated Tukey post-hoc pairwise comparisons between age classes. We also performed indicator species analysis (ISA), a statistical analysis of association between species and an *a priori* grouping of sites (Dufrene and Legendre, 1997). Indicator species signify which species can be used as predictors of certain environmental conditions, using our forest development age classification (EI, LI, ESE, MAT). ISA uses the relative abundance of species to calculate an indicator value (IV) as a percentage between 0 and 1, reported here as the square root of that value (De Cáceres and Legendre, 2009). A high IV reflects high fidelity to a single age class. A species with an IV of 1 would be found in all samples of the age class and only in that single age class. We then ran a Monte-Carlo test with 999 permutations to evaluate the statistical significance of this indicator value. We also examined changes in the abundance of the two categories of birds—forest ground-nesting species and early-successional shrub-nesting species in shelterwoods of different ages. We summed all individuals of these species at a point, and ran simple regressions with age of regeneration as the predictor variable. When residual plots indicated non-linearity, we also ran quadratic regressions to see if they improved the fit. We removed insignificant terms until we had a minimum adequate model and

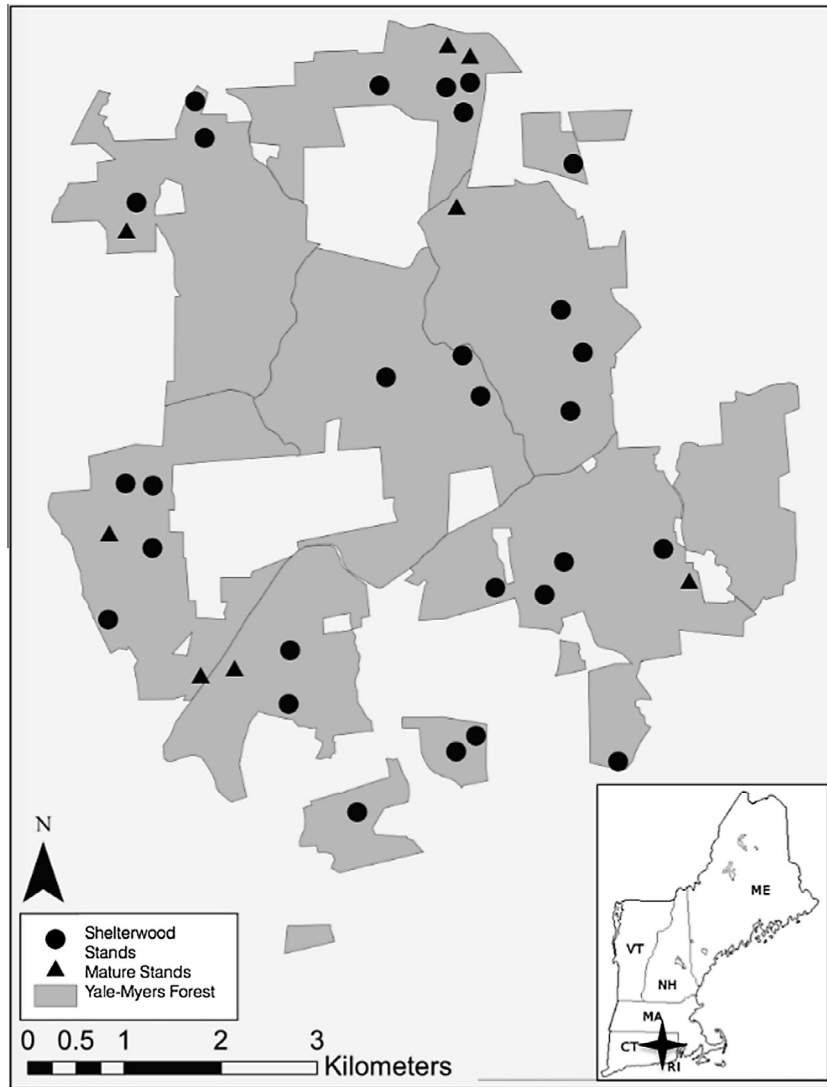


Fig. 1. The 36 point count locations throughout the Yale-Myers Forest in northeastern Connecticut. Twenty-eight point counts were placed in shelterwood stands harvested between zero and 22 years ago. The remaining eight were in mature forests that have not been harvested for at least 80 years.

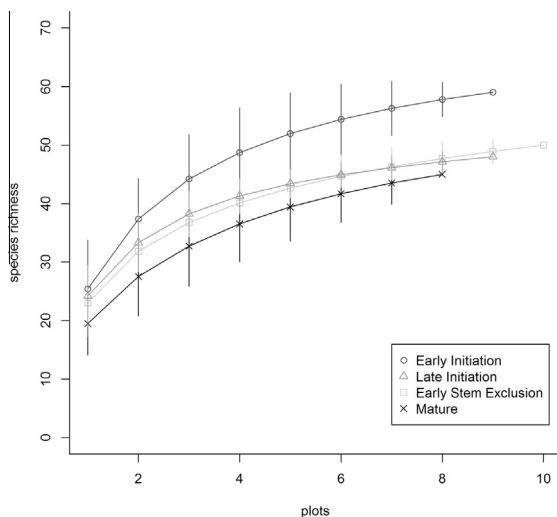


Fig. 2. Species accumulation curves for the four age classes based on bootstrapping with 100 permutations.

examined residual plots to confirm model acceptability. For all regressions we examined simple linear, quadratic, and Poisson distribution GLMs for each regression to find the best model.

All statistics were carried out using R 2.11.1 (R Development Core Team, Geneva, Switzerland, 2010) with the additional packages *Vegan*, *BiodiversityR*, *indicspecies*, *mgcv*, and *agricolae* (De Cáceres and Legendre, 2009; DeMendiburu, 2012; Kindt and Coe, 2005; Oksanen et al., 2013; Wood, 2006). With the exception of the aforementioned ANOVAs we assumed statistical significance when $\alpha < 0.05$.

3. Results

3.1. Bird abundance, richness, and diversity

In total we detected 1987 individual birds of 69 species; 59 species in early initiation stands (EI), 48 species in late initiation (LI), 50 species in early stem exclusion (ESE), and 45 species in mature stands (MAT). Measured and Chao species richness estimates showed little difference between the three shelterwood age-classes, but all of those classes had higher estimated richness than the mature stands (Fig. 3). Shannon diversity and total abundance

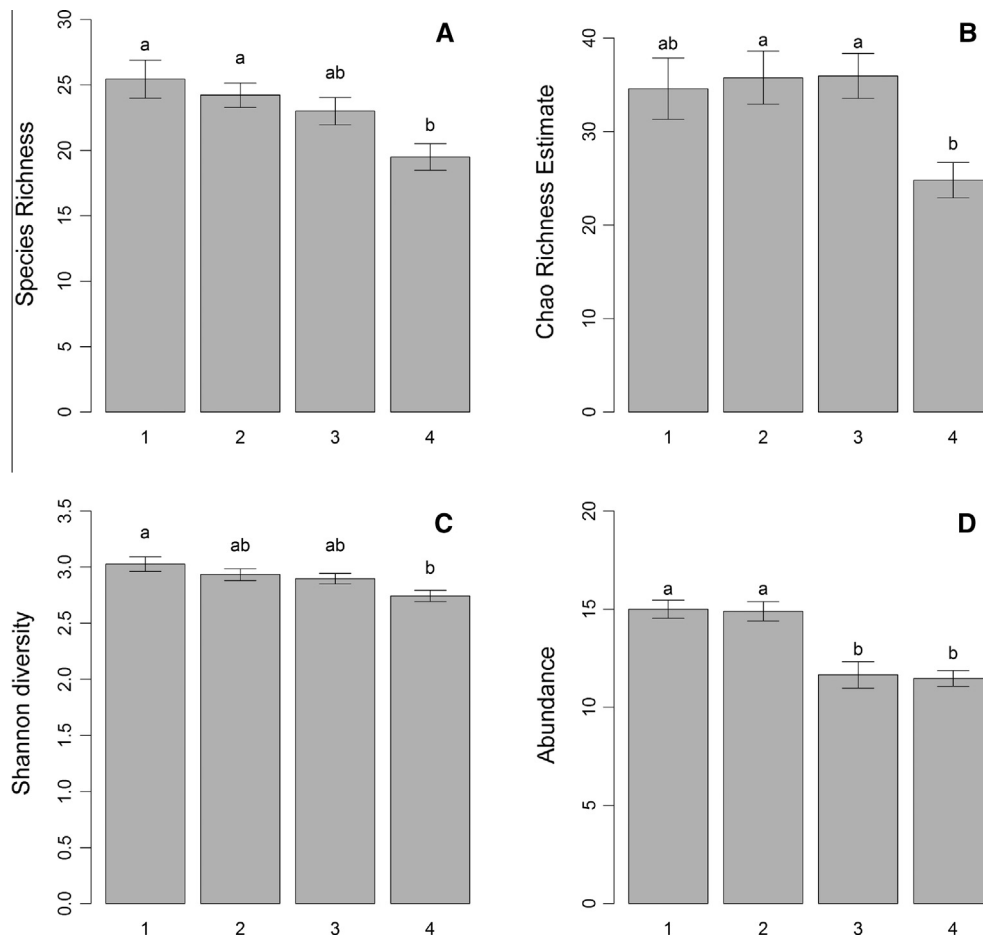


Fig. 3. Comparison of diversity between age classes. Ages classes are 1: Early Initiation (<7 years post-harvest), 2: Late Initiation (8–12 years), 3: Early Stem Exclusion (13–22 years), and 4: Mature stands (80–100 years). Barplots from top left to bottom right represent (A) measured species richness, (B) Chao richness estimator, (C) Shannon diversity, and (D) total species abundance. Bar height represents groups mean and error bars represent \pm one standard error. Letters indicate differences between treatments ($P < 0.05$) in Tukey post hoc testing after generalized linear models.

were greatest in the EI phase, decreasing through the later stand development phases, though Tukey post-hoc analyses show these differences to only be significant between the youngest (EI) and oldest (MAT) stands (Fig. 3). Within the shelterwood stands, regressions showed declines in total abundance ($\beta = -0.25$, $F_{(1, 26)} = 27.50$, $p < 0.001$, $r^2 = 0.51$); and marginally significant declines in Shannon diversity ($\beta = -0.01$, $F_{(1, 26)} = 4.12$, $p = 0.05$, $r^2 = 0.14$) and species richness ($\beta = -0.19$, $F_{(1, 26)} = 3.39$, $p = 0.08$, $r^2 = 0.12$) over time (Fig. 4). The shelterwood regressions did not show any significant trends in the Chao estimate of species richness or in Shannon evenness.

3.2. Changes in bird species composition

The NPMANOVA analysis indicated differences in bird composition between age classes ($F_{3,32} = 3.75$; $p < 0.001$, $r^2 = 0.26$), further supported by the NMDS ordination diagram (Fig. 5). Overall, there is a clear separation between the initiation stages of early stand development from the ESE and MAT stands. While there is not a clear division between the initiation stages (EI and LI), there is evidence of a continuum with EI on one end and MAT on the other (Fig. 5).

ANOVA models examining the abundance of individual species showed 19 species with significant or marginally significant differences across the classes ($p \leq 0.10$, Table 1). According to the Cornell classification, ten species are classified as early-successional shrub-nesting species. Six of these ten shrub-nesting species had

higher abundances in regenerating shelterwoods than in closed-canopied MAT stands, while the other four species showed non-significant trends in the same direction (Table 1). Of the six species classified as closed-canopied mature forest ground-nesting species, only two showed any phase association: ruffed grouse (*Bonasa umbellus*; $F_{3,32} = 3.30$, $p = 0.03$), which was most abundant in ESE stands and ovenbird (*Seiurus aurocapilla*; $F_{3,32} = 23.87$, $p < 0.001$), most abundant in MAT stands, although its abundance was not significantly different between ESE and MAT stands. The remaining four species showed substantial plasticity.

Indicator species analysis revealed two species as indicators of EI: indigo bunting (*Passerina cyanea*; $IV = 0.62$, $p = 0.02$) and prairie warbler (*Setophaga discolor*; $IV = 0.58$, $p = 0.04$)—both early-successional shrub-nesters. One additional species was found to be an indicator of ESE: ruffed grouse ($IV = 0.56$, $p = 0.04$), a forest ground-nesting species. Examining combinations of groups added some additional indicators. For example, the two initiation categories (EI and LI) together had significant associations with two species: chestnut-sided warbler (*Setophaga pensylvanica*; $IV = 0.87$, $p < 0.001$; an early-successional shrub-nester), and great crested flycatcher (*Myiarchus crinitus*; $IV = 0.60$, $p = 0.03$). The middle age classes of LI and ESE together are indicated by American crow (*Corvus brachyrhynchos*; $IV = 0.65$, $p = 0.04$). No species emerged as indicators of MAT only. When examining the groups of all regenerating shelterwoods (EI, LI, ESE) seven species serve as indicators: rose-breasted grosbeak (*Pheucticus ludovicianus*; $IV = 0.86$, $p = 0.03$), gray catbird (*Dumetella carolinensis*; $IV = 0.85$,

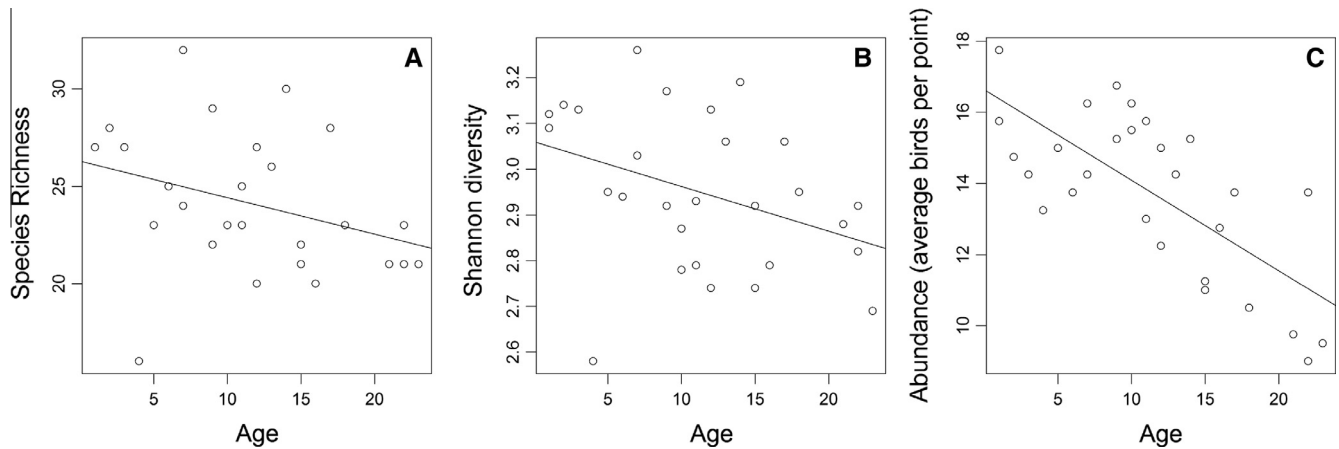


Fig. 4. Regression plots for (A) species richness, (B) Shannon diversity, and (C) abundance against time since harvest in the shelterwood stands.

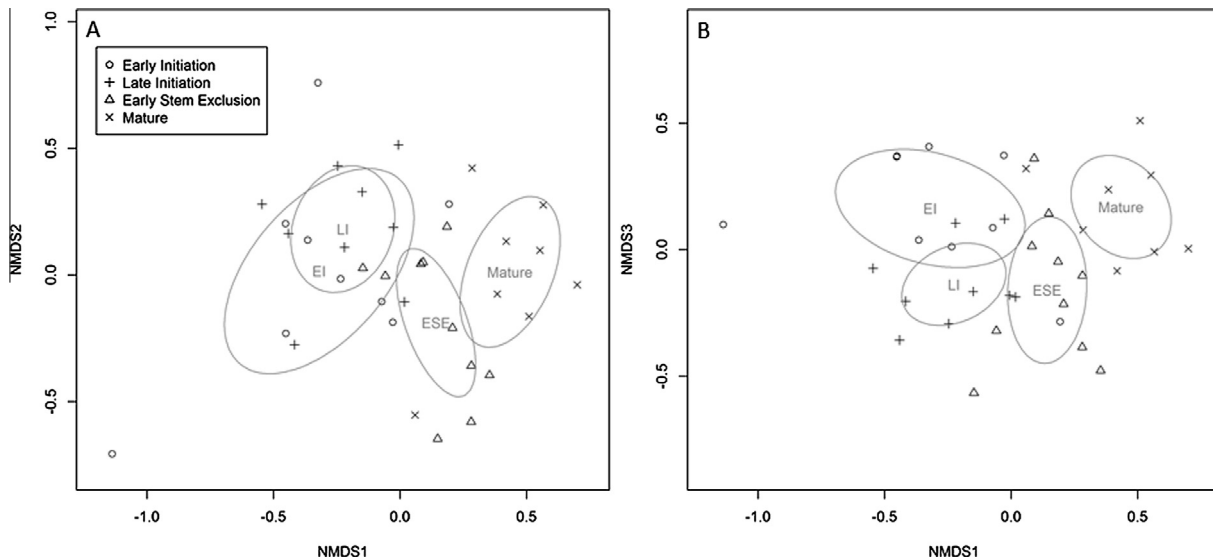


Fig. 5. Non-metric multidimensional scaling ordination diagram. Shape of points correspond with age class. All three dimensions displayed: (A) represents dimensions 1&2, (B) dimensions 1&3. Ellipses represent one standard deviation for all points within stand classification groups (EI = Early Initiation, LI = Late Initiation, ESE = Early Stem Exclusion).

$p = 0.01$; an early-successional shrub-nester), yellow-rumped warbler (*Setophaga coronata*; $IV = 0.81$, $p = 0.01$), northern flicker (*Colaptes auratus*; $IV = 0.78$, $p = 0.01$), red-bellied woodpecker (*Melanerpes carolinus*; $IV = 0.76$, $p = 0.04$), Baltimore oriole (*Icterus galbula*; $IV = 0.73$, $p = 0.03$), and mourning dove (*Zenaida macroura*; $IV = 0.73$, $p = 0.03$).

Close-canopied mature forest ground-nesting species showed a positive linear relationship with year since harvest ($\beta = 0.07$, $F_{1,26} = 6.99$, $p = 0.013$, $r^2 = 0.21$; Fig. 6A). Early-successional shrub-nesting species' abundance showed a negative linear relationship with the age of regeneration ($\beta = -0.14$, $F_{1,26} = 8.20$, $p = 0.008$, $r^2 = 0.24$; Fig. 6B).

4. Discussion

4.1. Bird abundance, richness, and diversity

Our main findings include: (1) regenerating stands (early [EI] and late stand initiation [LI], <12 years since shelterwood harvest) have higher bird abundance than regenerating early stem-exclusion

stands (ESE) between 13 and 22 years old and mature stands (MAT); (2) species richness and Shannon diversity are greatest in shelterwood stands compared to mature stands; and (3) within regenerating shelterwood stands, species richness, Shannon diversity, and total bird abundance generally decrease with time since harvest.

We believe the high bird abundance in young stands is due to the greater diversity of habitat structures that develop after shelterwood regeneration harvests. Regenerating stands comprise a large variety of available nesting and foraging habitats for different species (Goodale et al., 2009; King and DeGraaf, 2000). For instance, shelterwoods have a mix of shrubs, snags and canopy trees, all of which attract different species of birds. Further, these regenerating stands are dynamic. Initially, a dense ground-story—including herbaceous plants (e.g., ferns, graminoids, and forbs), dense deciduous shrubs (e.g., raspberry [*Rubus ideaus*] and blackberry [*Rubus allegheniensis*]), and regenerating saplings (e.g. black birch)—provide a range of nesting and foraging areas for early-successional species, such as chestnut-sided warblers and prairie warblers. Thick patches of remnant mountain laurel (an evergreen, woody shrub) are released when stands are harvested, and provide

Table 1

Summary table of all bird species detected more than three times during the study. Species are sorted by the age class in which they have the highest mean abundance. Mean (SE) of abundance in each age class: EI = Early Initiation; LI = Late Initiation; ESE = Early Stem Exclusion; MAT = Mature. For the functional group regressions ^G indicates membership in forest dwelling, ground-nesting species and * indicates early-successional, shrub-nesting species. Values in bold represent statistically significant differences. Significant ANOVAs are represented by $p < 0.1$, $p < 0.05$, $p < 0.01$, and $p < 0.001$. Letters represent differences of means in Tukey post hoc comparisons ($\alpha < 0.05$).

		EI	LI	ESE	MAT	F	Pr(>F)
<i>Most abundant in EI</i>							
Eastern Wood-Peezee	<i>Contopus virens</i>	0.53 (0.10) a	0.33 (0.09) ab	0.15 (0.08) b	0.16 (0.09) b	3.97	0.016*
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	0.22 (0.09) a	0.08 (0.04) ab	0.03 (0.03) b	0 (0) b	3.81	0.019*
Indigo Bunting*	<i>Passerina cyanea</i>	0.17 (0.08)	0.03 (0.03)	0 (0)	0 (0)	3.30	0.033*
Prairie Warbler*	<i>Setophaga discolor</i>	0.17 (0.09)	0 (0)	0 (0)	0 (0)	3.2	0.036*
Northern Cardinal*	<i>Cardinalis cardinalis</i>	0.25 (0.1)	0.14 (0.07)	0.03 (0.03)	0.03 (0.03)	2.61	0.069
Black-throated Green Warbler	<i>Setophaga virens</i>	0.44 (0.15)	0.08 (0.04)	0.4 (0.11)	0.38 (0.13)	2.01	0.13
Baltimore Oriole	<i>Icterus galbula</i>	0.33 (0.16)	0.33 (0.15)	0.13 (0.06) 0	0 (0)	1.96	0.14
Mourning Dove	<i>Zenaida macroura</i>	0.28 (0.16)	0.19 (0.06)	0.18 (0.05)	0 (0)	1.51	0.23
Chipping Sparrow*	<i>Spizella passerina</i>	0.25 (0.17)	0.03 (0.03)	0.05 (0.03)	0.03 (0.03)	1.49	0.24
White-breasted Nuthatch	<i>Sitta carolinensis</i>	0.19 (0.07)	0.14 (0.06)	0.05 (0.03)	0.09 (0.05)	1.38	0.27
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	0.44 (0.17)	0.14 (0.06)	0.13 (0.08)	0.25 (0.18)	1.34	0.28
Song Sparrow*	<i>Melospiza melodia</i>	0.22 (0.19)	0 (0)	0 (0)	0 (0)	1.33	0.28
Tufted Titmouse	<i>Baeolophus bicolor</i>	0.72 (0.17)	0.56 (0.17)	0.4 (0.07)	0.44 (0.13)	1.11	0.36
Magnolia Warbler	<i>Setophaga magnolia</i>	0.14 (0.07)	0.06 (0.04)	0.03 (0.03)	0.06 (0.04)	1.09	0.37
Northern Parula	<i>Setophaga americana</i>	0.11 (0.06)	0.06 (0.06)	0 (0)	0.06 (0.04)	1.09	0.37
Scarlet Tanager	<i>Piranga olivacea</i>	0.28 (0.08)	0.14 (0.06)	0.13 (0.06)	0.25 (0.13)	0.94	0.43
Woodpeckers	<i>Leuconotopicus villosus</i> & <i>Picoides pubescens</i>	0.5 (0.12)	0.33 (0.13)	0.33 (0.08)	0.28 (0.07)	0.82	0.49
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	0.11 (0.08)	0.06 (0.06)	0.03 (0.03)	0 (0)	0.81	0.50
Pine Warbler	<i>Setophaga pinus</i>	0.22 (0.15)	0.03 (0.03)	0.1 (0.08)	0.09 (0.07)	0.76	0.53
Brown Creeper	<i>Certhia americana</i>	0.06 (0.06)	0 (0)	0.03 (0.03)	0.06 (0.04)	0.63	0.60
Blue-headed Vireo	<i>Vireo solitarius</i>	0.08 (0.04)	0.08 (0.04)	0.08 (0.04)	0.03 (0.03)	0.38	0.77
<i>Most abundant in LI</i>							
Chestnut-sided Warbler*	<i>Setophaga pensylvanica</i>	0.72 (0.24) b	1.64 (0.14) a	0.13 (0.07) c	0.09 (0.07) c	24.15	<0.001***
Gray Catbird*	<i>Dumetella carolinensis</i>	0.53 (0.15) b	1.17 (0.27) a	0.25 (0.07) b	0.06 (0.04) b	8.73	<0.001***
Yellow-rumped Warbler	<i>Setophaga coronata</i>	0.28 (0.11) ab	0.53 (0.09) a	0.25 (0.08) ab	0.03 (0.03) b	5.52	0.004**
Common Yellowthroat*	<i>Geothlypis trichas</i>	0.94 (0.2) ab	1.06 (0.24) a	0.50 (0.19) ab	0.28 (0.12) b	3.34	0.032**
Northern Flicker	<i>Colaptes auratus</i>	0.19 (0.07) ab	0.22 (0.08) a	0.18 (0.04) ab	0 (0) b	2.94	0.048*
American Crow	<i>Corvus brachyrhynchos</i>	0 (0)	0.14 (0.06)	0.13 (0.04)	0.03 (0.03)	2.87	0.052
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	1.14 (0.23)	1.19 (0.12)	0.63 (0.17)	0.75 (0.16)	2.65	0.065
Brown-headed Cowbird	<i>Molothrus ater</i>	0.06 (0.04)	0.17 (0.08)	0.03 (0.03)	0 (0)	2.34	0.092
Black-and-white Warbler ^G	<i>Mniotilta varia</i>	0.78 (0.17)	1.08 (0.11)	0.65 (0.11)	0.66 (0.15)	2.23	0.10
Rose-breasted Grosbeak	<i>Phoebastria ludovicianus</i>	0.39 (0.11)	0.5 (0.19)	0.35 (0.11)	0.13 (0.07)	1.42	0.26
Yellow Warbler*	<i>Setophaga petechia</i>	0.14 (0.08)	0.19 (0.08)	0.03 (0.03)	0.03 (0.03)	0.98	0.42
Eastern Phoebe	<i>Sayornis phoebe</i>	0.03 (0.03)	0.08 (0.06)	0.03 (0.03)	0 (0)	0.952	0.43
Canada Warbler ^G	<i>Cardellina canadensis</i>	0.08 (0.06)	0.14 (0.06)	0.1 (0.06)	0.06 (0.04)	0.33	0.81
<i>Most abundant in ESE</i>							
Ruffed Grouse ^G	<i>Bonasa umbellus</i>	0.03 (0.03)	0 (0)	0.1 (0.04)	0 (0)	3.30	0.033*
American Goldfinch*	<i>Spinus tristis</i>	0.08 (0.04) ab	0.06 (0.04) ab	0.18 (0.05) a	0 (0) b	3.27	0.034*
Red-eyed Vireo	<i>Vireo olivaceus</i>	0.22 (0.08)	0.33 (0.09)	0.73 (0.2)	0.56 (0.11)	2.95	0.048*
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	0.19 (0.06) ab	0.11 (0.06) ab	0.25 (0.06) a	0.03 (0.03) b	2.84	0.053
White-throated Sparrow ^G	<i>Zonotrichia albicollis</i>	0 (0)	0.03 (0.03)	0.08 (0.04)	0 (0)	2.02	0.13
Wood Thrush	<i>Hylocichla mustelina</i>	0.08 (0.08)	0.14 (0.08)	0.43 (0.15)	0.19 (0.09)	1.93	0.14
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	0.06 (0.04)	0 (0)	0.13 (0.08)	0.06 (0.06)	0.94	0.43
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	0.03 (0.03)	0.06 (0.04)	0.08 (0.05)	0 (0)	0.75	0.54
Blue Jay	<i>Cyanocitta cristata</i>	0.28 (0.1)	0.42 (0.14)	0.45 (0.1)	0.38 (0.11)	0.47	0.71
<i>Most abundant in MAT</i>							
Ovenbird ^G	<i>Seiurus aurocapilla</i>	0.61 (0.14) b	0.44 (0.16) b	1.50 (0.12) a	1.91 (0.14) a	23.87	<0.001***
Hermit Thrush	<i>Catharus guttatus</i>	0.28 (0.1) b	0.39 (0.09) ab	0.40 (0.12) ab	0.72 (0.15) a	2.54	0.074
Louisiana Waterthrush	<i>Parkesia motacilla</i>	0.08 (0.08)	0 (0)	0 (0)	0.22 (0.12)	2.22	0.11
Winter Wren	<i>Troglodytes hiemalis</i>	0.11 (0.08)	0 (0)	0 (0)	0.19 (0.1)	2.11	0.12
Veery ^G	<i>Catharus fuscescens</i>	0.36 (0.14)	0.5 (0.11)	0.7 (0.14)	0.72 (0.15)	1.58	0.21
American Redstart	<i>Setophaga ruticilla</i>	0.11 (0.06)	0.19 (0.07)	0.08 (0.05)	0.28 (0.13)	1.32	0.29
Black-throated Blue Warbler	<i>Setophaga caerulescens</i>	0.25 (0.09)	0.33 (0.12)	0.33 (0.14)	0.53 (0.13)	0.89	0.46
American Robin	<i>Turdus migratorius</i>	0.17 (0.07)	0.22 (0.08)	0.23 (0.07)	0.28 (0.09)	0.36	0.79
Black-capped Chickadee	<i>Poecetes atricapillus</i>	0.5 (0.17)	0.44 (0.17)	0.38 (0.12)	0.56 (0.09)	0.31	0.82
Blackburnian Warbler	<i>Setophaga fusca</i>	0.08 (0.08)	0.06 (0.06)	0.03 (0.03)	0.09 (0.07)	0.27	0.84

additional cover for ground-nesting birds such as ovenbirds and eastern towhees (*Pipilo erythrophthalmus*). Residual standing trees (parent trees and reserves) provide habitat for canopy nesters such as Baltimore orioles, scarlet tanagers (*Piranga olivacea*), mourning doves and flycatchers (Tyrannidae). Snags and individually girdled trees purposely left after harvest can serve as habitat for cavity nesters such as woodpeckers (Picidae) and white-breasted nuthatches (*Sitta carolinensis*).

Additionally, our observations suggest species not normally associated with early-successional habitats are found in

regenerating forest stands (Goodale et al., 2009). Trees left as reserves in shelterwoods may provide nesting habitat for canopy and cavity nesters superior to closed-canopy forest conditions, because the large gaps between the parent trees could decrease predation from arboreal nest predators such as gray squirrels (*Sciurus carolinensis*). Another advantage of regenerating shelterwoods may be that mature forest bird species nesting in retained overstory trees would be in closer proximity to post-fledging habitat. In contrast to regenerating shelterwoods, mature second-growth oak-hardwood forests, because of their uniformly closed-canopied

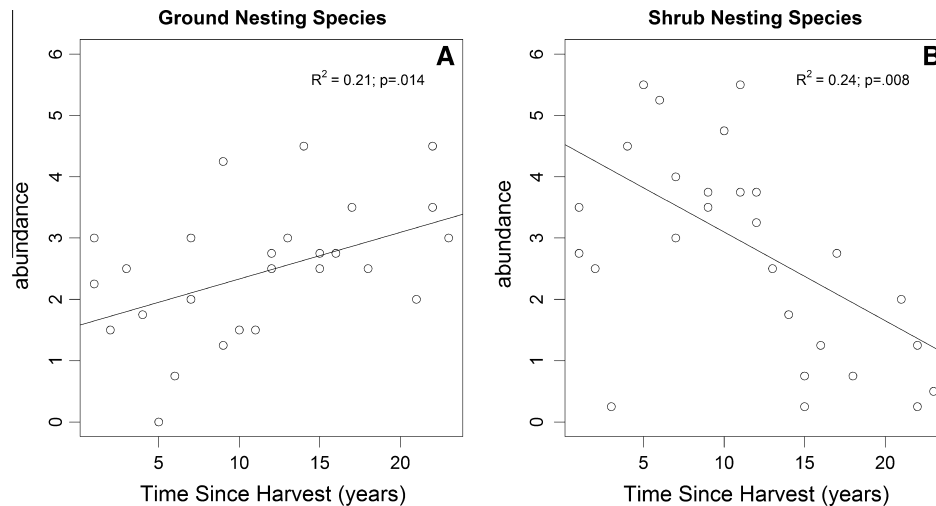


Fig. 6. Regression plots for abundance by functional group. The abundance of (A) forest dwelling ground-nesting species and (B) early-successional shrub-nesting species against time since harvest in the shelterwood stands.

conditions and relatively sparse understories, offer limited or specialized habitat opportunities. Species found in mature forests are primarily understory, ground, and canopy-tree nesters. In some cases, mature forests may host shrub nesting birds when patches of understory shrubs (e.g., mountain laurel) are present.

Our finding that younger regenerating shelterwood stands less than 12 years of age have higher species richness, Shannon diversity and total bird abundance than older stands, supports prior research (King and DeGraaf, 2000; Augenfeld et al., 2008; Goodale et al., 2009; Hobson and Schieck, 1999; Keller et al., 2003; Schlossberg and King, 2009). Augenfeld et al. (2008) recorded highest diversity and bird densities within one to two years following shelterwood harvests with a dramatic decline by 12 years after harvest. Keller et al. (2003) found an initial increase in bird diversity and density in the two to six years following clear-cuts in New York followed by a decline between seven and 25 years. They assumed this decline was due to canopy closure shading out habitat for ground-foragers and nesters. We found declines to begin around 13 years after a harvest. Despite small discrepancies between these studies, taken together all demonstrate that abundance and diversity will initially dramatically increase in early and late initiation stages of stand development and then decline with canopy closure at the onset of stem exclusion. Additionally, our results suggest that the early stem exclusion stage (ESE) of development (13–22 years in age), often assumed to comprise poor habitat for birds, actually hosts the same levels of diversity as closed-canopied mature forest.

One limitation to this study is that it examines only one breeding season to assess bird diversity and abundance. However, the results were similar to a previous study, also from the Yale-Myers Forest, in which two years of data were collected (Goodale et al., 2009). Although this previous study visited many of the same stands, there were fewer shelterwood stands, harvested over a shorter time range. While detections in a single season do not necessarily represent long-term residency, they can indicate short-term habitat acceptability. We will continue to monitor stands to examine temporal trends in species compositional change. Continuing projects also examine the connection between vegetation and bird abundance. Goodale et al. (2009) found a coarse-level connection between birds abundant in shelterwoods and high canopy openness, high densities of seedlings and saplings, and large amounts of coarse woody debris on the ground. In the future, we hope to explore more detailed connections between bird distribution and abundance and the characteristics of the vegetation of

these shelterwood habitats, including variables related to remnant canopy trees and regenerating growth.

4.2. Bird species composition

4.2.1. Early-successional shrub-nesting species

This study, like several others, shows that shelterwoods offer habitat to a variety of birds, but most importantly they provide critical habitat to a group at risk in New England: early-successional shrub-nesting species such as chestnut-sided warbler, prairie warbler, and eastern towhee (Askins, 1993; DeGraaf and Yamasaki, 2003; Hagan, 1993; Litvaitis, 1993; Schlossberg and King, 2007, 2009; Witham and Hunter, 1992). Our analysis of indicator species demonstrates that there are many “generalist” early-successional species found in EI, LI and ESE stand conditions (e.g., rose-breasted grosbeak, gray catbird, yellow-rumped warbler, northern flicker, red-bellied woodpecker, Baltimore oriole, and mourning dove). Some early-successional shrub-nesting species, however, have more specific successional habitat preferences. For example, eastern towhee, chestnut-sided warbler, gray catbird, indigo bunting, and prairie warbler were all more abundant in EI and LI stands (<12 years old), than in ESE stands (13–22 years old) or MAT stands. Perry and Thill (2013) found that indigo buntings, while abundant in shelterwood stands, were more numerous in clear-cuts and concluded they peaked three to five years after harvest, which supports our findings. DeGraaf and Yamasaki (2003) suggest that chestnut-sided warblers arrive two years after clear-cut harvests, are common after four years, and decline at ten years, similar to our results where their presence peaked between seven and 12 years.

Our results suggest that early-successional bird species assemblages are continuously changing and that these changes are most rapid during the first 12 years in a regenerating forest. After this time period, bird assemblages in ESE stands have stronger similarity with mature closed-canopied forest (MAT) than with early-successional stands. One interesting caveat is that some birds generally associated with mature forests (i.e., black-throated green warbler) were most abundant in EI and ESE stands than in other stand developmental phases. This implies that ESE stand conditions may be hospitable to closed-canopied mature forest birds, while providing habitat for some early-successional species. Schlossberg and King (2009) suggest that many past studies may be overestimating the amount of early-successional habitat available to shrub-nesting early-seral species. Their meta-analysis and

model suggests that early-successional birds prefer to use stands less than ten years old, generally disappearing by 20 years. However, many studies consider stands up to 20 years old to be early-successional habitat, potentially greatly inflating the actual amount of habitat available to these obligate species. Our findings support this assertion.

4.2.2. Forest ground-nesting species

We found that forest ground-nesting species such as ovenbirds and northern waterthrush (*Parkesia noveboracensis*) were more abundant in older regenerating and mature stands. However, these species use regenerating forest stands earlier than expected. Some species such as ruffed grouse and white-throated sparrow were more abundant in ESE stands (13–22 years old) than mature stands. Even ovenbirds, a species commonly considered a mature forest species (MAT), did not have differing abundance between ESE and MAT stands and were in moderate numbers in EI and LI stands. Hermit thrushes (*Catharus guttatus*), a signature bird of mature forest in this region, were observed in ESE stands at about half the abundance, and in EI and LI at about one third abundance, as compared to mature stands. These observations suggest that forest birds return to harvested stands relatively quickly after harvesting. We explain this by the fact that by year 13 canopy closure has started to occur. DeGraaf and Yamasaki (2003) found that ruffed grouse first appear ten years after a harvest, are common 15 years after and begin to decline at 20 years; we found they were most common in stands between 13 and 20 years old. Lastly, and perhaps most important, is that none of the forest ground-nesting species were indicator species, suggesting that though some were more abundant in closed-canopied forests they were not exclusively found there. Most were recorded at some level in early-successional stand conditions (EI, LI), a contrast with early-successional species, many of which were not recorded in mature closed-canopied forest (MAT). Our results highlight the plasticity of these species in respect to habitat breadth.

5. Management implications

Shelterwood harvests have a positive impact on bird abundance, richness and diversity as compared to mature stands, and can serve as a powerful tool for landowners and natural resource managers to promote early-successional breeding birds on their property. Shelterwoods of different successional stages offer unique habitat for particular species and species assemblages, and there are distinct temporal patterns of bird populations following timber harvests associated with canopy closure conditions (Keller et al., 2003). Forest ground-nesting birds—usually indicators of interior mature forest conditions—are present and abundant as early as 13 years following a harvest and are not obligate to closed-canopied forest conditions. At the same time, many early-successional species are not found beneath closed canopied forest. Continuous management across space and time—which creates a mosaic of mature, regenerating and early-successional habitats—will help ensure bird abundance and diversity throughout New England (Burger, 2006; Cahall et al., 2013; Canterbury et al., 2000; Doyon et al., 2005; Goodale et al., 2009; Hagan et al., 1997; King and DeGraaf, 2000; McGarigal and McComb, 1995; Schlossberg and King, 2009).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.06.010>.

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