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ASSOCIATIONS BETWEEN AVIAN SPRUCE-FIR SPECIES,

HARVEST TREATMENTS, VEGETATION,

AND EDGES

By

Brian William Rolek

B.S. University of Massachusetts, 2003

M.S. Auburn University, 2009

A DISSERTATION

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Wildlife Ecology)

The Graduate School

The University of Maine

December 2018

Advisory Committee:

- Daniel J. Harrison, Professor of Wildlife Ecology and Conservation Biology, Co-Advisor
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On behalf of the Graduate Committee for Brian Rolek, I affirm that this manuscript is the final and accepted dissertation. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

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December 5, 2018

December 5, 2018

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Date: December 5, 2018

ASSOCIATIONS BETWEEN AVIAN SPRUCE-FIR SPECIES,

HARVEST TREATMENTS, VEGETATION,

AND EDGES

By Brian William Rolek

Dissertation Co-advisors: Drs. Daniel Harrison and Cynthia Loftin

An Abstract of the Dissertation Presented in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy (in Wildlife Ecology) December 2018

Habitat loss is the primary cause of species loss and declines of global biodiversity. Several birds associated with the spruce-fir forest type (hereafter spruce-fir birds) have declining populations across the continent in the Atlantic Northern Forest, and the extent of coniferous forest has declined in some areas. This region is extensively and intensively managed for timber products.

To investigate the influence from harvest treatments on the spruce-fir bird assemblage during the breeding and post-breeding period in lowland conifer and mixedwood forests, we used avian point count detection data to test for associations between avian assemblages and seven common harvest treatments. Spruce-fir avian assemblages had greatest abundance in regenerating clearcuts combined with postharvest treatments (i.e., herbicide and precommercial thinning), and within stands having $\geq 60\%$ spruce-fir tree composition. Richness of spruce-fir avian assemblages were greatest in stands with immature trees and greater spruce-fir tree composition, and clearcuts combined with postharvest treatments had greater spruce-fir tree composition compared to other treatments. Next, we tested for effects from management, years-since-harvest, and vegetation on abundance of 19 conifer associated avian focal species while accounting for the effects from detection probability. Abundance of six species differed significantly among harvest treatments, and one species was associated with years-since-harvest, indicating that management treatments provided important information. In addition, fourteen species had significant associations between abundance and vegetation variables, suggesting that managers could target specific vegetative outcomes when managing for focal species.

We tested for differences in avian abundance and richness at stand interior \geq 80 m from edges, low-contrast edges at the junction of two regenerating stands, and highcontrast road edges with managed buffers using a novel multi-species abundance model. Spruce-fir birds had greater richness at stand interior compared to high-contrast edge, and stand interior had greater spruce-fir tree composition compared to high-contrast edge, while low-contrast edge was intermediate. Road edges reduced habitat for spruce-fir birds. Combined our results suggest that management could promote habitat for sprucefir birds through: 1) application of postharvest treatments such as herbicide and precommercial thinning; 2) using management that targets focal species by using outcome-based silviculture; 3) minimizing access road edges and roadside buffers.

DEDICATION

For my grandparents Dorothy Rolek, Michael Rolek, Agnes Wroblewski, and Henry Wroblewski. You inspire me.

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CHAPTER 1

REGENERATING CLEARCUTS COMBINED WITH POSTHARVEST FORESTRYTREATMENTS PROMOTE HABITAT FOR BREEDING AND POST-BREEDING SPRUCE-FIR AVIAN ASSEMBLAGES IN THE ATLANTIC NORTHERN FOREST

1.1. Abstract

The quantity of spruce-fir forest and some conifer-associated breeding bird abundances in the Atlantic Northern Forest have declined in recent decades emphasizing the need to better understand avian responses to forest management and to identify options that proactively conserve habitat for birds during the breeding and post-breeding period. We conducted avian point counts and vegetation surveys on publicly and privately-owned lands with known management histories to assess relationships between avian assemblages in harvest and postharvest treatments that could provide habitat for passerine birds associated with the spruce-fir forest type. We sampled regenerating conifer-dominated stands 5–41 years-since-harvest (YSH) in three harvest treatments (selection, irregular first-stage shelterwood, and clearcuts) and three postharvest treatments including regenerating clearcuts treated with aerially applied herbicide (e.g., glyphosate), precommercial thinning (PCT), both herbicide and PCT, and mature stands $(\geq 48 \text{ YSH})$. Spruce-fir obligate and associate birds were more abundant in stands with greater spruce-fir tree composition (\geq 70% and \geq 60%, respectively). Avian richness of spruce-fir obligates, associates, and species of concern was greater in clearcuts and clearcuts with postharvest treatments. Vegetative features associated with greater richness and abundance of spruce-fir birds, such as greater spruce-fir composition and smaller tree

diameter at breast height, were prominent in regenerating clearcuts and postharvest treatments and suggested that these management practices promote local abundances and richness of spruce-fir birds. Richness and abundances of spruce-fir birds were least in selection, shelterwood, and mature stands, and vegetative features associated with greater richness and abundance of spruce-fir birds were diminished in these stands. Forestry trends in Maine indicate that the extent of the clearcut suite of treatments has decreased on the landscape while selection and shelterwood harvests have increased. Thus, changes in incentives for managers to apply even-aged management coupled with post-harvest applications of herbicides or precommercial thinning might mitigate further declines in habitat for spruce-fir passerines assemblages. A greater ratio of clearcuts with postharvest treatments 11–40 YSH compared to other treatments (mature forest \geq 48 YSH, selection and shelterwood 5–41 YSH) would maintain diverse spruce-fir bird communities on the landscape. Use of clearcuts with postharvest treatments in the hemiboreal forests of northern New England, southern Quebec, and Maritime Provinces of eastern Canada may enhance habitat for breeding and post-breeding spruce-fir birds especially where the quantity of conifer forests are declining and residual patches of conifers are increasingly fragmented.

1.2. Introduction

Forest management has global consequences for conservation of biodiversity. Vegetative physiognomy and composition are important for the maintenance and creation of diverse ecological communities (MacArthur 1958, MacArthur and MacArthur 1961), and management has long-term effects on vegetative structure and composition, which are important for wildlife habitat (Seymour and Hunter 1999, Keller et al. 2003,

Thompson et al. 2013). Ecologically sustainable forestry seeks to promote biodiversity and combine forest resource extraction with ecologically sound stewardship of land using disturbance-based harvest techniques (Seymour and Hunter, 1999).

Over 75% of the land area in Maine, New Hampshire, and Vermont is forested, and >70% of these forests are timberlands harvested primarily for saw logs, pulpwood, strandboard, wood pellets, and biomass energy (McCaskill et al. 2011, Morin et al. 2012). Forest managers use a diverse suite of treatments for timber extraction, but influences on forest bird communities during later stages of regeneration are poorly understood in northern New England's mixed and conifer-dominated systems. Three broad harvest treatment categories include clearcuts, partial harvests including irregular shelterwood and selection harvests, and clearcuts that subsequently receive postharvest treatments. Clearcuts have fallen out of favor because of public disapproval of their immediate postharvest appearance (Costello et al. 2000, Miller et al. 2006, McDermott and Wood 2009); forest health and hydrological effects (Costello et al. 2000, McDermott and Wood 2009); avian population declines resulting from edge and fragmentation effects (Wilcove 1989); and removal of vertical vegetation diversity that enhances wildlife diversity (MacArthur and MacArthur 1961). Partial harvests are often promoted because they retain diverse vertical forest structure compared to clearcuts and create uneven-aged stands during stages of the management cycle (Seymour and Hunter 1992, Raymond et al. 2009). While partial harvests reduce the intensity of harvest from forestry within an individual stand, managers must harvest a greater area to extract a similar value of product which may spread the effects from forestry over a larger area (Lindenmayer et al. 2012).

The shift toward partial harvests in Maine from 1982–2015 (Maine Forest Service, 2018) coincides with decreases in the area clearcut annually and a decrease in coniferous forest cover (Maine Forest Service, 2018). Legaard et al. (2015) examined remotely sensed data in northern Maine from 1975–2004 and documented a shift in tree composition from conifer to deciduous-dominated forest composition in response to widespread partial harvesting. Furthermore, studies documented preferential removal of large conifer trees by managers when conducting selection harvests (Fuller et al. 2004), and fewer regenerating conifer saplings in stands after partial harvests compared to clearcuts (Robinson 2006).

Postharvest treatments, such as precommercial thinning (hereafter PCT; elsewhere referred to as timber or forest stand improvement) and herbicide, can be applied after an initial treatment, usually clearcuts, to accelerate regrowth (Pitt and Lanteigne 2008). Clearcuts with herbicide application promote conifer sapling growth (reviewed by Lautenschlager, 1993; Newton et al., 1989) relative to partial harvests (Robinson 2006). Few studies have empirically evaluated the influence of postharvest treatments on spruce-fir bird communities (but see Kroll et al., 2017; Rankin and Perlut, 2015; Thompson et al., 2013), especially in the Atlantic Northern Forest.

The Atlantic Northern Forest (Fig. 1.1.) provides breeding and post-breeding habitat for many passerine birds (MacArthur 1958, Titterington et al. 1979, Hagan et al. 1997, DeGraaf et al. 1998, King and DeGraaf 2000), and breeding avian communities of this region are diverse (Hagan et al. 1997). Managing avian populations within this region has implications for the conservation of biodiversity, policy, and forestry certification programs. Ralston et al. (2015) showed that eastern populations of several

bird species associated with the spruce-fir forest type have declining population trends in the United States. USGS Breeding Bird Survey data and results (Sauer et al. 2017) corroborate these declines within the Atlantic Northern Forest with significant declines in abundance for 11 of 17 bird species (Sauer et al. 2017) that are associated with the spruce-fir forest type (Bicknell's Thrush is omitted because of lack of data, Ralston et al., 2015). A shift from coniferous to deciduous-dominated forest composition (McCaskill et al. 2011, Legaard et al. 2015, Simons-Legaard et al. 2016) coincides with declines in populations of coniferous forest birds in the eastern United States (Ralston et al. 2015), suggesting that the quantity and spatial pattern of spruce-fir habitat on the landscape may be affecting populations of spruce-fir birds. Figure 1.1 Study sites and sampling distribution of point count locations (n=425) and forested stands (n=114) in northern Maine, New Hampshire, and Vermont, USA, and within Bird Conservation Region (BCR) 14, Atlantic Northern Forest. The right panel illustrates study stand and point count distributions at an example field site, Telos/Baxter SP. Sample sizes of surveyed stands and number of point counts for each harvest and postharvest treatment are summarized across sites for each treatment in Table A.1.



Although effects of forestry on bird abundance and richness in the Atlantic Northern Forest have received some study (e.g. Costello et al., 2000; DeGraaf et al., 1998; Derleth et al., 1989; Hagan et al., 1997; King and DeGraaf, 2000; Rudnicky and Hunter, 1993; Titterington et al., 1979; Welsh and Healy, 1993), few have considered the breadth nor cumulative effects of forest harvest techniques over longer periods, especially for postharvest treatments that are applied extensively across this region. Additionally, few studies have considered response by entire avian assemblages to forest harvest practices and postharvest treatments that affect regeneration patterns. Here, we assess effects of forest management on vegetative attributes and spruce-fir avian communities.

Our overall objective is to identify forest management that may enhance habitat for birds associated with the spruce-fir forest type and for species of concern. To accomplish this objective, we ask three questions. (1) Does vegetation vary among harvest treatments and how does vegetation vary among treatments? (2) Do avian assemblages vary among harvest treatments? (3) How do avian assemblages respond to harvest treatments and vegetation?

1.3. Methods

1.3.1. Study Sites and Design

Our study was conducted within the hemiboreal Atlantic Northern Forest in the northeastern United States (Fig. 1.1.). This region transitions from temperate deciduous forest to eastern boreal forest (Seymour and Hunter 1992). Our study sites were located on lands actively or formerly managed by forestry, including publicly-owned lands within Baxter State Park and U.S. Fish and Wildlife Service National Wildlife Refuges (NWR; Umbagog, Aroostook, Moosehorn, and Nulhegan Division of Silvio O. Conte) in

New Hampshire, Vermont, and Maine, and privately-owned areas (Telos, Clayton Lake) in the North Maine Woods.

Within study sites, we surveyed forested stands that were ≥ 12.1 ha (≥ 30 acres) in area to minimize edge effects (King et al. 1997, Ortega and Capen 2002) and stands approximately >50% spruce or fir trees to focus on conifer-associated birds. We considered stands to be areas that were managed in a spatially contiguous manner during temporally similar periods with a prescribed forestry treatment and from polygons provided by land owners or from digital ortho quarter quad tiles from the National Agriculture Imagery Program (United States Department of Agriculture) where abrupt changes in forest structure were visible. We surveyed lowland conifer forests <500 m elevation, with dominant tree species ≥ 10 cm diameter at breast height (dbh) primarily comprised of the following tree species in descending order of abundance: balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), Atlantic white cedar (*Chamaecyparis thyoides*), black spruce (*Picea glauca*), paper birch (*Betula papyrifera*), tamarack (*Larix laricina*), and yellow birch (*Betula alleghaniensis*).

1.3.2. Harvest Treatments

We surveyed stands (Table A.1) within seven treatment types (described below) to capture a range of spruce-fir dominated and mixed-wood forest conditions on the landscape including: mature, selection, shelterwood, clearcut, clearcut with herbicide, clearcut with PCT, and clearcut with herbicide and PCT. We characterized harvest treatments using basal area and years-since-harvest (YSH, Table 1.1). We measured basal area with a two-factor metric glass prism, and summarized these data as stand-level

averages, standard deviations, and ranges across vegetation plots (Table 1.1). We could not obtain dates of PCT treatments at four stands (two clearcut-PCT and two clearcutherbicide-PCT), and could not obtain YSH for three clearcut-PCT stands, so they were omitted from data summaries involving these variables (Table 1.1, Table A.2); however, they are included in other analyses.

Selection harvest stands were partial harvests where managers removed 25–65% of overstory trees. In irregular first stage shelterwood stands (hereafter referred to as shelterwood), partial removal of overstory trees (often undesired trees) allows increased light penetration that releases new seedlings and is used to promote advanced establishment and regeneration of desired tree species prior to overstory removal. This harvest treatment creates two-aged multi-cohort vegetative structure so that mature coniferous species in the overstory propagate and promote regeneration prior to overstory removal during a second stage of harvest, not considered herein. Stands treated solely with clearcuts (i.e., without postharvest treatment) are hereafter referred to as clearcutonly stands. Clearcut-only harvest removes nearly all basal area leaving few residual trees. Some clearcut stands received postharvest treatments such as aerial application of herbicides (e.g., glyphosate) 3–21 years after harvest and PCT 15–23 years after harvest. Herbicide is applied to promote growth of coniferous trees by suppressing deciduous stem growth and results in larger yields of merchantable softwood (hereafter clearcutherbicide, Dagget, 2003; MacKinnon and Freedman, 1993; Seymour, 1992; Seymour, 1995; Wagner et al., 2004). PCT stands (hereafter referred to as clearcut-PCT) are clearcuts where less desired timber is removed prior to stem exclusion and results in faster growth (Pitt and Lanteigne 2008) of preferred timber and greater composition of

conifer trees (Brissette et al. 1999). PCT enhances tree growth by promoting spacing among desirable regenerating saplings prior to stem exclusion (Pitt and Lanteigne 2008), which reduces competition and promotes spruce-fir composition in the regenerating stand (Brissette et al. 1999). The combination of herbicide treatment followed by PCT after conifer regeneration (hereafter clearcut-herbicide-PCT) was considered as a separate postharvest treatment. Applying PCT following herbicide in clearcuts generally results in larger yields of merchantable softwood (Daggett 2003, Wagner et al. 2004). We compared harvested treatments to reference stands in mature spruce-fir and mixed-wood forest defined here as lack of forestry treatment for \geq 48 years (mean=84) and where previous forestry treatments were unknown. We note the distinction between mature stands as defined here and old growth stands that resemble stands with natural disturbance patterns. Old growth stands are >150 years since anthropogenic disturbance and are composed of long-lived shade-tolerant trees (Mosseler et al. 2003). These stands were not surveyed here because few remain on the landscape (Mosseler et al. 2003). Table 1.1 Vegetation variables and descriptions. Names with abbreviations in parentheses, stand-level means (standard deviation), units of measurement, description, and treatment means (standard deviations) for vegetation variables measured at each point count location (n=425) surveyed at 870 plots within 114 stands in seven treatments and post-treatments in northern Maine, New Hampshire, and Vermont, USA. Years-since-harvest reports mean (standard deviation, range). Ranges for vegetation variables are presented in Table A.2.

Name	Description	Mature	Selection	Shelterwoo d	Clearcut only	Clearcut- herbicide	Clearcut- PCT	Clearcut- herbicide -PCT
Basal area (BA; m ² ha ⁻¹)	Measured from trees counted "in" using wedge prism and ≥10 cm dbh	29.8 (8.4, 13.8– 49.3)	23.4 (7.1, 13.3– 41.0)	23.1 (8.4, 12.5–36.7)	8.3 (7.2, 0.0–20.0)	21.1 (10.0, 0.0–38.0)	26.4 (4.93,17. 6–32.0)	29.5 (8.5, 16.8– 38.0)
Quadratic mean diameter (QMD; cm)	Measured from trees counted "in" using wedge prism and ≥10 cm dbh along with dbh measurements	28.3 (5.0)	28.3 (5.8)	31.0 (6.2)	15.4 (11.6)	15.0 (4.3)	19.4 (1.8)	16.7 (2.0)
Tree height (HEIGHT; m)	Height of two tallest trees	21.5 (2.8)	21.1 (3.1)	20.3 (3.3)	13.0 (3.0)	13.0 (2.1)	15.5 (1.3)	14.5 (2.2)

Table 1.1 Continued

Diameter at breast height (DBH; cm)	Diameter of trees counted "in" using wedge prism and ≥10 cm dbh. Measured with Biltmore stick. Breast height=1.37 m	26.6 (4.4)	26.0 (4.3)	27.6 (5.5)	19.7 (9.4)	15.8 (1.7)	18.2 (0.8)	16.3 (1.8)
Midstory cover (MID- STORY)	Proportion of leaf cover 2 to <7.6 m height measured using plexiglass grid. Height estimated with hypsometer.	0.35 (0.21)	0.52 (0.28)	0.5 (0.22)	0.26 (0.23)	0.53 (0.2)	0.53 (0.18)	0.50 (0.21)
Canopy cover (CAN- OPY)	Proportion of leaf cover ≥7.6 m measured using plexiglass grid. Height estimated with hypsometer.	0.62 (0.18)	0.59 (0.19)	0.43 (0.25)	0.09 (0.16)	0.48 (0.29)	0.54 (0.26)	0.60 (0.27)
Ground cover (GROUN D)	Proportion of leaf cover <0.5 m, Visual estimate.	0.42 (0.2)	0.38 (0.13)	0.47 (0.12)	0.57 (0.27)	0.33 (0.12)	0.30 (0.09)	0.40 (0.19)

Table 1.1 Continued

Shrub cover (SHRUBS)	Proportion of leaf cover 0.5 to <2 m, visual estimate.	0.27 (0.15)	0.29 (0.11)	0.42 (0.17)	0.44 (0.17)	0.26 (0.18)	0.19 (0.09)	0.20 (0.13)
Canopy gaps (GAPS)	Visual estimate of proportion gaps defined as >7.6 m height and >5 m across within 30 m of vegetation plot center	0.33 (0.17)	0.28 (0.12)	0.63 (0.09)	0.76 (0.25)	0.36 (0.25)	0.29 (0.15)	0.33 (0.3)
Live crown ratio (LCR)	Measured from four tallest trees, two trees in two plots, and from the height from the top of the live crown to the lowest live branch, to the base of the tree.	0.50 (0.13)	0.48 (0.21)	0.48 (0.19)	0.51 (0.3)	0.27 (0.31)	0.70 (0.1)	0.20 (0.35)
Spruce-fir (SPFIR)	Proportion of trees that were spruce or fir and ≥ 10 cm dbh.	0.61 (0.23)	0.50 (0.25)	0.58 (0.17)	0.51 (0.42)	0.77 (0.27)	0.86 (0.09)	0.80 (0.13)

Table 1.1 Continued

Coniferou	Proportion of trees	0.81	0.62	0.86 (0.15)	0.65	0.91 (0.24)	0.90	0.95	ſ
s (CONIF)	that were coniferous	(0.23)	(0.3)		(0.38)		(0.11)	(0.05)	
	and ≥ 10 cm dbh.								
	Includes pines and								
	tamarack in contrast								l
	to SPFIR.								
Vears	Vears since a stand	83.0	22/1 (8/2	167(83	20.5 (8.9	319(56	25.8	311(31	l
since-	was harvested with	(21.6	11_{41}	5_31)	11-36	21_{-40}	(11.8	31_{30}	ł
harvest	2014 as the reference	48-	11 11)	5 51)	11 50)	21 10)	$(11.0, 11-38)^1$	51 57)	
(YSH)	vear.	113+)					11 50)		
(121)	<i>j</i> • • • • •	1101)							
Years-	Years since a stand					8–31	$18-35^2$	13–31	l
since-post-	was treated with							(herbicid	l
harvest	herbicide or PCT							e), 14–19	l
	with 2014 as a							$(PCT)^2$	l
	reference year.								l
			1						ł

¹We excluded three clearcut-PCT stands from YSH data because we could not obtain date of harvest.

²We excluded four stands from years-since-postharvest data summaries because we could not obtain dates of postharvest

treatments for two clearcut-PCT and two clearcut-herbicide-PCT stands.
1.3.3. Avian Point Count and Vegetation Surveys

We conducted avian point counts at locations >100m apart (DeGraaf et al. 1998) and >130 m from edges of our treatment stands (Costello et al. 2000) to maximize number of points within each stand, while excluding effects from adjacent edges. Our protocol followed standardized 10-min multi-species avian point count surveys (Ralph et al. 1995, Bibby et al. 2000). We surveyed birds during 1 June to 4 August, 2013–2015. This timing of annual cycle coincided with territory establishment, breeding, and postfledgling period for most species in northern New England (Rodewald 2017). Technicians were trained to identify birds by sight and sound for approximately three weeks prior to conducting surveys. Surveys were not conducted during heavy wind or rain. Technicians practiced distance estimation prior to the onset of data collection and recalibrated distance estimation with a flag placed 25 m from center of the point on at least one count location each day. Most (71%) points were surveyed three times each year for all three years with visits distributed across the breeding season. For each bird detected, we recorded species, distance interval (0-25, >25-50, >50 m), sex and age (male, female, juvenile, or unknown) and type of detection (visual, audible call, audible song, flyover). We rotated observers among repeated visits of point counts and the order that point counts were surveyed within each stand to vary time of surveys at each survey location. Some point count locations were surveyed twice during the same day owing to logistical constraints.

Vegetation surveys were conducted once during 2014 at each point, because annual vegetation structure and composition are relatively stable in this region (Scott, 2009). We established between one and four vegetation plots per point count location,

with one plot centered at each point count location and subsequent plots centered 30 m in a randomly selected direction (0°, 90°, 180°, or 270°). We used a preliminary analysis and determined that two vegetation plots per point count location were logistically feasible and adequately represented vegetation; therefore, most point count locations had two vegetation plots (94%, 398 of 425), seven had three plots, 11 had four plots, and nine had a single plot because the stand was harvested prior to completion of vegetation surveys. We retained additional vegetation plots (i.e., third or fourth plots) for analyses.

We used a two-factor metric prism to count the number of trees ≥ 10 cm dbh measured at 1.37 m height for each tree (Avery, 1975; McClure et al., 2012) within a plot to estimate basal area. We determined whether trees were included within each plot using a glass prism, and plot sizes varied as a function of the distance from the center of the plot and diameter of trees. We counted every other borderline tree as within a plot. We identified each tree species and measured dbh with a Biltmore stick. Within 5 m of each vegetation plot (Sheehan et al. 2014), we visually estimated percent cover of live vegetation (i.e., green ground cover) < 0.5 m above ground and percent shrub/regenerating cover 0.5 to <2 m in height with a visual reference (i.e., printed figure approximating the appearance of 5–95% cover at 10% intervals). We measured midstory (2 to <7.6 m) and canopy cover (\geq 7.6 m; MacArthur and MacArthur, 1961) with a transparent plexiglass grid ($25 \times 25 \text{ cm}$) divided into 25 grid cells (5×5) by holding the grid overhead and counting the number of grid cells obscured by vegetation (Hache et al. 2013). If midstory cover obscured canopy cover, we allowed up to two paces from center of the plot to avoid visual interference with the canopy layer. We approximated height for vegetation cover measurements using an analog hypsometer. We measured height of the

two tallest trees in each plot with a clinometer. We defined canopy gaps as breaks in the canopy at least 5 m in diameter across the broadest width and a distance of at least 7.6 m down from the surrounding canopy to the next vegetative strata within 30 m of the plot center (Pickett and White 1985, Perkins and Wood 2014), and we estimated the proportion canopy gaps with a printed visual reference for comparison. From these measurements, we calculated stand-level vegetation characteristics including: basal area (BA, Table 1.1), diameter at breast height (DBH), quadratic mean diameter (QMD), tree height (HEIGHT), canopy cover (CANOPY), midstory cover (MIDSTORY), shrub cover (SHRUBS), ground cover (GROUND), proportion canopy gaps (GAPS), proportion of spruce-fir trees (SPFIR), proportion of coniferous trees (CONIF), and live crown ratio (LCR). We calculated stand-level and point-level averages for vegetation variables by taking the mean of vegetation plots within each stand and point, respectively. We estimated the mean (SD) for vegetation variables in each treatment (Table 1.1), and we include ranges of values for BA, years-since-harvest, and years-since postharvest.

1.3.4. Statistical Analysis

1.3.4.1. Data Manipulation and Species Groups

We excluded species that were detected at ≤ 10 of 425 point count locations (Becker et al. 2011, McClure et al. 2012), flyovers, species with large territories, and species not sampled well with point counts (e.g., non-passerine birds, Table A.3, Scott and Ramsey, 1981). We determined that species singing at low volumes (e.g., Cape May Warbler) eluded detection beyond 50 m from density plots of distance to detection; therefore, we retained detections only for species within 50 m radius of the point count center to reduce bias of observations consistent with previous studies (Hagan et al. 1997, DeGraaf et al. 1998, Hutto 2016). We calculated stand-level annual abundance of each species by taking the maximum abundance of each species detected at all point count locations within each stand over three repeated visits.

We calculated avian richness as the total number of species detected within 50 m during three years at each point count location for seven avian groups. We surveyed most point count locations three times in each year (i.e., nine surveys total, 90% in 2013, 98% in 2014, 87% in 2015, and 91% among all years) to minimize confounding effects from detection probability.

Avian groups included: spruce-fir obligates (6 species), spruce-fir associates (7), spruce-fir obligates and associates combined (13), species of concern that are spruce-fir obligates or associates (6), species of concern (16), species of concern after omitting spruce-fir species (10), and total species richness (49; Table 1.2). The assignment of spruce-fir obligates and associates was largely based on authoritative sources listing these species as preferring or using spruce-fir forest types (Robbins 1991, DeGraaf and Yamasaki 2001, King et al. 2008, Glennon 2014, Ralston et al. 2015). Spruce-fir obligates were species that prefer and use only spruce-fir forest types, while spruce-fir associates prefer spruce-fir forest types, but will also use other forest types (Ralston et al. 2015). We created the group "species of concern" by compiling species listings from several sources including: International Union for Conservation (IUCN 2016), U.S. Federal listings (U.S. Fish and Wildlife Service, 2016), State listings from Maine, Vermont, New Hampshire, State Wildlife Action Plans from Maine (Maine Department of Inland Fisheries and Wildlife 2015), Vermont (Vermont Fish and Wildlife Department 2015), New Hampshire (New Hampshire Fish and Game 2015), Atlantic Coast Joint

Venture, Partners in Flight Watch List (Partners in Flight 2016), and species that were declining significantly across the continent or within Bird Conservation Region 14 from Breeding Bird Survey Results and Analysis (Sauer et al. 2017). We designated species of concern as those occurring on ≥ 2 species status lists (Table 1.2).

Table 1.2 Forty-nine species that met sample size requirements (points where species were detected ≥ 10) to be included in analysis and categories used to group species and estimate richness. "Listing" is the number of times a species was listed as a species of concern. "Obligates" and "associates" are spruce-fir obligates and associates (1=yes, 0=no). For excluded species see Table A.3.

Common name	Abbrev.	Genus species	Detections	Points detected	Listings ¹	Obligates ²	Associates ²
Olive-sided Flycatcher	OSFL	Contopus cooperi	49	35	6	0	1
Eastern Wood-Pewee	EAWP	Contopus virens	20	17	1	0	0
Yellow-bellied Flycatcher	YBFL	Empidonax flaviventris	512	244	0	0	1
Alder Flycatcher	ALFL	Empidonax alnorum	53	34	1	0	0
Least Flycatcher	LEFL	Empidonax minimus	134	104	2	0	0
Blue-headed Vireo	BHVI	Vireo solitaries	346	228	0	0	0
Red-eyed Vireo	REVI	Vireo olivaceus	473	240	0	0	0
Gray Jay	GRAJ	Perisoreus canadensis	115	73	1	1	0
Blue Jay	BLJA	Cyanocitta cristata	266	180	1	0	0
Black-capped Chickadee	BCCH	Parus atricapillus	665	318	0	0	0
Boreal Chickadee	BOCH	Poecile hudsonicus	390	198	2	1	0
Red-breasted Nuthatch	RBNU	Sitta canadensis	564	287	0	0	1
Brown Creeper	BRCR	Certhia americana	150	116	0	0	0

Table 1.2 Continued.

Winter Wren	WIWR	Troglodytes hiemalis	586	284	0	0	0
Golden-crowned Kinglet	GCKI	Regulus satrapa	1048	381	0	0	1
Ruby-crowned Kinglet	RCKI	Regulus calendula	242	157	1	0	1
Veery	VEER	Catharus fuscescens	43	34	4	0	0
Swainson's Thrush	SWTH	Catharus ustulatus	917	352	2	0	1
Hermit Thrush	HETH	Catharus guttatus	810	343	0	0	0
American Robin	AMRO	Turdus migratorius	245	155	1	0	0
Gray Catbird	GRCA	Dumetella carolinensis	11	11	1	0	0
Cedar Waxwing	CEDW	Bombycilla cedrorum	247	148	0	0	0
Ovenbird	OVEN	Seiurus aurocapilla	459	196	0	0	0
Northern Waterthrush	NOWA	Parkesia noveboracensis	174	113	1	0	0
Black-and-white Warbler	BAWW	Mniotilta varia	280	159	2	0	0
Nashville Warbler	NAWA	Oreothlypis ruficapilla	854	306	1	0	0
Common Yellowthroat	COYE	Geothlypis trichas	274	143	2	0	0
American Redstart	AMRE	Setophaga ruticilla	191	137	1	0	0
Cape May Warbler	CMWA	Setophaga tigrina	25	22	2	1	0
Northern Parula	NOPA	Setophaga americana	442	220	0	0	0
Magnolia Warbler	MAWA	Setophaga magnolia	1456	383	0	1	0
Bay-breasted Warbler	BBWA	Setophaga castanea	191	103	5	1	0
Blackburnian Warbler	BLBW	Setophaga fusca	317	185	0	0	0
Chestnut-sided Warbler	CSWA	Setophaga pensylvanica	73	51	3	0	0

Table 1.2 Continued.

Blackpoll Warbler	BLPW	Setophaga striata	88	43	2	1	0
Black-throated Blue Warbler	BTBW	Setophaga caerulescens	296	156	1	0	0
Palm Warbler	YPWA	Setophaga palmarum	189	77	0	0	1
Pine Warbler	PIWA	Setophaga pinus	153	113	0	0	0
Yellow-rumped Warbler	MYWA	Setophaga coronata	737	324	0	0	0
Black-throated Green Warbler	BTNW	Setophaga virens	578	246	0	0	0
Canada Warbler	CAWA	Cardellina canadensis	369	172	6	0	0
Wilson's Warbler	WIWA	Cardellina pusilla	23	21	0	0	0
Chipping Sparrow	CHSP	Spizella passerine	30	27	2	0	0
Fox Sparrow	FOSP	Passerella iliaca	56	36	1	0	0
Dark-eyed Junco	SCJU	Junco hyemalis	278	166	2	0	0

Table 1.2 Continued.

White-throated Sparrow	WTSP	Zonotrichia albicollis	708	257	1	0	0
Swamp Sparrow	SWSP	Melospiza georgiana	16	12	0	0	0
Rose-breasted Grosbeak	RBGR	Pheucticus ludovicianus	22	20	2	0	0
Purple Finch	PUFI	Haemorhous purpureus	135	106	3	0	0

¹Listings were determined from: IUCN, 2016; U.S. Fish and Wildlife Service, 2016; Maine Department of Inland Fisheries and Wildlife, 2015; Vermont Fish and Wildlife Department, 2015; New Hampshire Fish and Game, 2015, Atlantic Coast Joint Venture, State Wildlife Action Plans from Vermont, New Hampshire, or Maine, and species that were significantly declining across the North American continent or within Bird Conservation Region 14 from Breeding Bird Survey Analysis (Sauer et al. 2017). Species of concern were designated as those with ≥ 2 listings.

²Designated from sources listing spruce-fir as preferred or utilized habitat types (DeGraaf and Yamasaki, 2001, Glennon,

2014; King et al., 2008; Ralston et al., 2015; Robbins, 1991).

1.3.4.2. Dominant Vegetation Variables

We used a preliminary analysis (Appendix B) to identify dominant vegetation variables that were orthogonal (statistically independent) and explained the most variance in avian assemblages using a combination of principal component analysis (PCA), nonmetric multidimensional scaling (NMDS), and generalized additive models (fully described in Table B.1). We determined that BA, DBH, SPFIR, and MIDSTORY were relatively statistically independent and represented unique vegetative characteristics that explained the greatest variance in avian assemblages; therefore, we refer to these four vegetative characteristics as "dominant vegetation variables" hereafter and use these variables in several subsequent analyses.

1.3.4.3. Vegetation

We tested whether vegetation variables differed among treatments (objectives, question 1) with a redundancy analysis (RDA) on stand-level vegetation variables. RDA regresses multiple response variables as a function of multiple explanatory variables, assuming a linear relationship between response and explanatory variables (Zuur et al. 2007). We modeled stand-level vegetation variables as response variables and included six harvest treatments as categorical explanatory variables. One categorical covariate must be omitted to avoid collinearity for RDA, so we omitted mature treatments (Zuur et al. 2007). We estimated p-values using permutation tests with 9999 iterations (Zuur et al. 2007), and we determined significance by setting α =0.05. To visualize treatments relative to vegetation, we plotted 67% confidence ellipses as visual aids which approximate ±1 SD (Hobson and Schieck 1999).

We identified how vegetation differed between treatments (objectives, question 1) by comparing point-level estimates of dominant vegetation variables among harvest treatments with Bayesian hierarchical models. The RDA described above tests for an overall difference in vegetation or assemblages among harvest treatments, and Bayesian hierarchical models provide estimates of the mean response with 95% credible intervals for each treatment that allowed direct comparisons of vegetation between treatments. We constructed a hierarchical model for estimating stand-level vegetation means from pointlevel vegetation data with harvest treatments as categorical explanatory variables (X). We used point-level vegetation data and included stand identity as a random effect, $y_i \sim Normal(\alpha_{i[i]}, \sigma^y)$, where y is a vegetation variable at point count location i, the point-level intercept (α) is indexed by stand *j*, and σ is the standard error (note that superscript is not exponentiation here and is used only to distinguish between two standard errors). We modeled stand-level response by dominant vegetation variables to harvest treatments as $\alpha_i \sim Normal(\gamma_{1:7} \mathbf{X}, \sigma^{\alpha})$, and γ is a vector of coefficient estimates for harvest treatments. This model is similar to an ANOVA on stand-level vegetation means with harvest treatments as covariates.

1.3.4.4 Avian Assemblages

We tested whether avian assemblages differed among harvest treatments (objectives, question 2) with annual mean abundance of each species within each stand with NMDS for ordination and linear regression. NMDS is an unconstrained ordination technique that is well suited for data with a large number of zeros such as avian abundance data, because it uses ranks to ordinate and is ideal for use with nonlinear data. We applied NMDS using R and the metaMDS function within the vegan package

(Oksanen et al. 2017) with Bray-Curtis dissimilarity. We selected the appropriate number of ordination axes with Shepard diagrams and scree plots of stress to evaluate the goodness-of-fit while varying the number of dimensions between one and six. We considered stress <0.1 to be a good fit, 0.1–0.2 moderate fit, and >0.2 problematic (Zuur et al. 2007). We assessed whether stand-level bird abundance provided a reasonable fit with R^2 values and stress plots.

We tested for an association between avian assemblages and harvest treatments (objectives, question 2) using ordinated scores from NMDS from avian abundance data and harvest treatments (Oksanen et al., 2017; Sheehan et al., 2014), and we fit linear models to categorical harvest treatments and survey year using the envir function in the vegan package (Oksanen et al. 2017) in R (R Core Team 2015). We determined significance for linear models using p-values from permutation tests with 9999 iterations α =0.05 and plotted 67% confidence ellipses for each treatment that approximate one standard deviation as a visual aid (Hobson and Schieck 1999, Kardynal et al. 2009).

1.3.4.5 Avian Richness

We identified how avian assemblages responded to harvest treatments (objectives, question 3) with hierarchical generalized linear models to estimate richness as a Poisson-log normal distribution with harvest treatments as explanatory variables. We included stand identity as a random effect to model richness at the stand-level:

 $y_i \sim Poisson(\alpha_{j[i]} + \gamma_1 surveys + \gamma_2 surveys^2 + \varepsilon_i)$, $\varepsilon_i \sim Normal(0, \sigma^y)$, and $\alpha_j \sim Normal(\gamma_{3:9}\mathbf{X}, \sigma^\alpha)$, where *y* is richness at point *i*, point-level intercept (α) is indexed at stand *j*, ε is an error term, $\gamma_{3:9}$ is a vector of coefficient estimates for harvest treatments, *surveys* is the number of surveys over three years at each point count location (centered and scaled), and $\gamma_{1:2}$ are the estimated slopes for *surveys* and its quadratic term. We modeled stand-level mean richness as a linear function of seven harvest treatments (**X**).

We identify how avian assemblages responded to vegetation (objectives, question 3) with an additional set of hierarchical generalized linear models that include avian richness as a response variable and PCA axis scores derived from vegetation variables as explanatory variables. First, we selected dominant vegetation variables in our preliminary analysis described elsewhere (section 2.4.2, Table B.1). We tested one assumption of regression analysis, a lack of collinearity between explanatory variables, by comparing dominant vegetation variables with Pearson's product moment correlation coefficients using the cor.test function in base R package (R Core Team 2015) and considered correlations significant when $r \ge 0.3$ (Cohen 1988) and $p \le 0.05$ (Fig. B.2). Our selected dominant vegetation variables (BA, DBH, SPFIR, and MIDSTORY) were collinear, which violates the assumptions of regression. We addressed collinearity using a PCA on all vegetation covariates and extracted principal component scores for axes one through four as explanatory variables for richness of species groups, because principal components are orthogonal and statistically independent. We modified the formula above for α_j to $\alpha_j \sim Normal(\gamma_3 + \gamma_{4:7} \mathbf{X}, \sigma^{\alpha})$ where **X** is a matrix of continuous covariates comprised of site scores from four principal components described post hoc as: tree density, tree maturity, tree composition, and midstory, while γ_3 is the estimated yintercept and $\gamma_{4:7}$ is a vector of slope estimates. Similar to our previously described richness analyses with treatments as explanatory variables, we included a quadratic covariate accounting for the number of avian surveys at each point count location.

We implemented Bayesian hierarchical regression models in JAGS version 4.2.0 (Plummer 2003) with the package jagsUI version 1.4.2 (Kellner 2016) in R version 3.2.3 (R Core Team 2015). For each model, we ran three chains with 10,000 iterations for burn-in, and another 100,000 iterations to obtain posterior distributions while thinning one of every five posterior draws (Gelman and Hill 2007). We assessed convergence among chains by viewing traceplots, and calculating the Gelman-Rubin convergence statistic, where $\hat{R} < 1.1$ indicated convergence (Gelman and Rubin 1992). For all regressions, we considered categorical groups to be significantly different when 95% credible intervals for slope estimates did not overlap zero.

1.4. Results

1.4.1. Dominant Vegetation Variables

Among the four dominant vegetation variables describing vegetation structure and composition, BA had the most variance explained by avian abundances along the first and second axes of NMDS ordination. Among the group of variables describing tree immaturity, DBH had the most variance explained by the first two axes from avian abundance ordinations. Among variables describing tree composition, SPFIR had the most variance explained by the first two axes from avian significantly associated with avian abundance across the first two axes of ordination, but had less variance explained relative to tree density, tree immaturity, and composition. Overall, BA, DBH, SPFIR, and MIDSTORY were the most statistically independent variables (Table 1.3) and had relatively large proportion of variance explained by NMDS axes from avian abundance.

Generalized additive models regressing vegetation with NMDS axes that were used to identify dominant vegetation variables indicated that avian assemblages had associations with DBH and SPFIR (described below), but these groups did not show clear patterns of association with BA and MIDSTORY. Peak abundance of spruce-fir obligates and associates was greatest in stands with smaller diameter trees, and 10 of 13 species were most abundant when average dbh of trees was <25 cm dbh (Fig. B.1.B). Peak abundance by spruce-fir obligates and associates was greatest in stands with greater composition of spruce and fir trees (averaging \geq 0.7 and \geq 0.6 SPFIR, respectively), and nine of 13 spruce-fir obligates and associates had greatest abundance in stands >0.65 SPFIR (Fig. B.1.C). Spruce-fir associates coincided with a large range of BA and DBH (Figs. B.1.A and B.1.B). Two spruce-fir associates, Palm Warbler (*Setophaga palmarum*) and Olive-sided Flycatcher (*Contopus cooperi*), were primarily associated with clearcutonly treatments, and reached greatest abundance in stands with sparse large diameter trees (Fig. B.1.B) and less overall basal area (Fig. B.1.A).

1.4.2. Avian point count and vegetation surveys

We sampled 30 mature stands at 118 point count locations, 23 selection stands at 83 point count locations, 11 shelterwood stands at 37 point count locations (seven stands added after 2013), 14 clearcut-only stands at 58 point count locations, 17 clearcut-herbicide stands at 66 point count locations, 12 clearcut-PCT stands at 44 point count locations, and seven clearcut-herbicide-PCT stands at 19 point count locations. Overall, we surveyed 114 stands with 425 point count locations at seven study areas (Fig. 1.1., Table A.1). The number of point count locations within each stand ranged from one to 14.

We conducted avian point count surveys at 397 point count locations in 107 stands in 2013 and at 425 point count locations in 114 stands in 2014 and 2015. Of 139 avian species, we retained 49 passerine species (Table 1.2 and Table A.3 for exclusions) detected at \geq 10 point count locations ranging from 11 (Gray Catbird) to 383 (Magnolia Warbler) point count locations. We measured 870 vegetation plots in 2014 at 425 point count locations.

1.4.3. Vegetation

Vegetation was significantly different among harvest treatments (RDA; p<0.001, R^2 =34.5%; Fig. 1.2., objectives, question 1). Clearcut-herbicide, clearcut-PCT, and clearcut-herbicide-PCT stands had greater SPFIR than all other harvest treatments. Both selection and shelterwood treatments had reduced SPFIR compared to postharvest treatments (Fig. 1.2., Table 1.1). Mature and selection stands had greatest BA, while clearcut-only stands had the least BA.

Figure 1.2 Triplot of redundancy analysis with vegetation as response variables and harvest treatment categories as explanatory variables showing the first two axes of ordination for seven harvest and postharvest treatments. Polygons are 67% confidence ellipses for each treatment for visual aid.



We compared how dominant vegetation variables differed among treatments (objectives, question 1) using hierarchical generalized linear models. Parameter estimates for dominant vegetation variables had adequate convergence with $\hat{R} < 1.1$. Basal area, dbh, proportion of spruce fir trees, and midstory cover differed among harvest treatments. Basal area was significantly less in clearcut-only stands than in all other treatments (Fig. 1.3.). Tree dbh in selection and shelterwood was similar to mature stands, and clearcut-only, clearcut-herbicide, clearcut-PCT, and clearcut-herbicide-PCT had significantly smaller diameter trees. The proportion of spruce-fir trees was significantly greater in clearcut-herbicide, clearcut-PCT, and clearcut-herbicide-PCT compared to selection and shelterwood treatments, whereas clearcut-only stands had a more mixed conifer-deciduous composition and credible intervals that overlapped with all other treatments. Midstory cover was significantly less dense in mature and clearcut-only treatments compared to selection, clearcut-herbicide, and clearcut-PCT, whereas, shelterwood and clearcut-herbicide-PCT had intermediate midstory cover (Fig. 1.3.).

Figure 1.3 Mean stand-level vegetation estimates from Bayesian hierarchical models. 95% credible intervals are depicted using pointlevel data for three harvest treatments (clearcut-only, irregular shelterwood, and selection), three harvests with postharvest treatments (clearcut-herbicide, clearcut-PCT, and clearcut-herbicide-PCT), and mature stands. Treatments with overlapping credible intervals are statistically similar and share letters.



1.4.4. Avian Assemblages

To test whether avian assemblages differed among harvest treatments (objectives, question 2), we used NMDS with four ordination axes with stand-level avian abundance data because four axes had moderate stress (stress=0.15) indicating reasonable fit. Combined, these four axes explained 82% of the variance in avian abundances. A linear model regressing the first two NMDS axes and harvest treatments explained 38.8% of the variance in avian assemblages indicating significant differences among treatments (p<0.001, Fig. 1.4.). Year of avian point count had a significant effect on the first two axes (p=0.032) but explained little variance (R²=1.7%) suggesting that temporal variation had little influence on avian abundance. Therefore, we did not consider year as an explanatory variable in analyses.

Figure 1.4. A linear regression of nonmetric multidimensional scaling axes (NMDS, axes one and two) from abundance of 49 bird species modeled with treatment as an explanatory variable. Ellipses 67% confidence intervals are shown for each harvest treatment for visual aid. Spruce-fir species (obligates and associates), and species of concern are displayed here. All other species are omitted for visual clarity. R² and p value are shown for treatment effects. Text represents avian species and species codes are referenced in Table 1.2.



Abundance of spruce-fir obligates was greatest in stands treated with clearcutonly, clearcut-herbicide, clearcut-PCT, clearcut-herbicide-PCT, but three (Cape May Warbler, Gray Jay, and Magnolia Warbler) of the six species did not have clear associations with treatments (Fig. 1.4.). Abundance of spruce-fir associates coincided with clearcut-only stands, clearcut-herbicide, clearcut-PCT and clearcut-herbicide-PCT; however, Red-breasted Nuthatch (*Sitta canadensis*) was abundant in mature, selection, and shelterwood treatments, and Golden-crowned Kinglet (*Regulus satrapa*) was abundant in mature and shelterwood stands (Fig. 1.4.).

Abundance of species of concern did not coincide with specific harvest treatments (Fig. 1.4.). Species having greater abundance in postharvest treatments and greater spruce-fir composition included Bay-breasted Warbler, Boreal Chickadee (*Poecile hudsonicus*), Ruby-crowned Kinglet (*Regulus calendula*), Swainson's Thrush (*Catharus ustulatus*), and Yellow-bellied Flycatcher (*Empidonax flaviventris*). Several species of concern had greater abundance in clearcut-only stands, such as Blackpoll Warbler (*Setophaga striata*), Palm Warbler, Olive-sided Flycatcher, and Common Yellowthroat (*Geothlypis trichas*). Several species had greater abundance in selection, shelterwood, and mature stands including Veery (*Catharus fuscescens*), Black-and-white Warbler (*Mniotilta varia*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), and Red-breasted Nuthatch.

1.4.5. Avian Richness

To identify how richness differed by treatments (objectives, question 3), we used hierarchical generalized linear models that had adequate convergence with $\hat{R} < 1.1$ for all parameters. Total avian richness was similar across treatments (Fig. 1.5.). Richness of

spruce-fir obligates was significantly greater in clearcut-only, clearcut-herbicide, clearcut-PCT, clearcut-herbicide-PCT compared to selection and mature stands, whereas richness in clearcut-only and shelterwood stands were intermediate. Richness of sprucefir associates was significantly greater in clearcut-only compared to selection and mature stands, whereas richness in clearcut-herbicide, clearcut-PCT, and clearcut-herbicide-PCT did not statistically differ from richness in all other treatments. Combined richness of spruce-fir obligates and associates was significantly greater in clearcut-only, clearcutherbicide, clearcut-PCT, and clearcut-herbicide-PCT when compared to selection and mature stands. Richness of spruce-fir species of concern was significantly greater in clearcut-only, clearcut-herbicide, clearcut-PCT, and clearcut-herbicide-PCT compared to selection, shelterwood, and mature stands. Richness of species of concern was greatest in clearcut-only, clearcut-herbicide, clearcut-PCT, and clearcut-herbicide-PCT stands, and least in selection and mature stands, while shelterwood stands had intermediate richness. Richness of non-spruce-fir species of concern was significantly greater in clearcut-only stands compared to selection, mature, clearcut-herbicide, and clearcut-PCT, whereas richness of non-spruce-fir species in shelterwood stands was intermediate (Fig. 1.5.).

Figure 1.5 Stand-level richness (number of species per point count location) response to treatments using hierarchical generalized linear models with treatments as explanatory variables. Mean model estimates and 95% lower and upper credible intervals are displayed. Treatments with overlapping credible intervals are statistically similar and share letters. The number of surveys at each point count location was assigned its mean value (8.5 surveys) for display.



To identify how avian assemblages responded to vegetation (objectives, question 3), we regressed richness from avian groups on vegetation using PCA axes scores from vegetation variables as explanatory variables. Tests for collinearity between dominant vegetation variables using Pearson's correlation coefficients indicated that dominant vegetation variables were correlated (BA and SPFIR r=0.3, p<0.05, DBH and SPFIR r=-0.45, p<0.05, Fig. B.2), so we used scores from PCA axes as covariates for richness to avoid collinearity. The first four principal components explained the majority of variance across vegetation variables (33, 24, 13, and 11%, respectively; 80% cumulatively), and these four components had eigenvalues ≥ 1.0 (Table 1.3). We assigned post hoc descriptive labels to variables associated with each PC: tree density, tree immaturity, tree composition, and midstory. Principal component one (PC1) described tree density and was significantly and positively correlated with BA and CANOPY, and inversely correlated with GAPS and SHRUBS (Table 1.3). PC2 described tree immaturity and was inversely correlated with DBH, HEIGHT, and QMD. PC3 described tree composition and was positively correlated with CONIF, SPFIR, and LCR. PC4 was positively correlated with MIDSTORY.

Table 1.3 Eigenvalues, eigenvector loadings, and variance explained from a principal components analysis of vegetation variables. Shown are the first five principal components used to ordinate stand-level means of vegetation variables among seven harvest treatments in northern forests of Maine, New Hampshire, and Vermont, USA. Bold text indicates significance for eigenvector loadings (absolute value ≥ 0.4) and principal components (eigenvalues ≥ 1.0), with labels describing groups of variables assigned post hoc. A correlation matrix of vegetation variables is provided in Fig. B.2.

PC label	Variable	PC1	PC2	PC3	PC4	PC5
Tree density	BA	0.44	-0.08	0.02	-0.23	0.02
	CANOPY	0.42	-0.12	-0.16	-0.24	-0.07
	GAPS	-0.42	-0.01	0.28	-0.01	0.18
	SHRUBS	-0.41	-0.16	0.07	-0.02	0.25
Tree immaturity	DBH	0.03	-0.54	0.15	0.13	0.14
	HEIGHT	0.16	-0.50	0.04	-0.04	-0.01
	QMD	0.17	-0.43	0.28	0.25	0.21
Tree composition	CONIF	0.21	0.22	0.58	-0.07	0.35
	LCR	0.04	0.02	0.43	0.45	-0.73
	SPFIR	0.21	0.36	0.41	-0.09	0.17
Midstory	MIDSTORY	0.09	0.14	-0.27	0.71	0.35
Other	GROUND	-0.35	-0.17	0.15	-0.29	-0.15
Summary statistics	Eigenvalues	1.95	1.67	1.23	1.12	0.84
	Proportion of variance	0.33	0.24	0.13	0.11	0.06
	Cumulative proportion					
	of variance	0.33	0.57	0.70	0.80	0.86

Hierarchical generalized linear models were used to identify how richness of species groups differed by vegetation using principal component scores as covariates and model parameters had adequate convergence with $\hat{R} < 1.1$. Richness responded to three (tree density, tree immaturity, tree composition) of four principal components describing variance in vegetation across stands, however, responses varied by species group (Fig. 1.6.). Richness of total bird species, species of concern, and non-spruce-fir species of concern decreased as tree density increased (PC1). Richness of spruce-fir obligates, spruce-fir associates, spruce-fir obligates and associates, spruce-fir species of concern, and species of concern increased with tree immaturity (PC2). Richness increased as coniferous tree composition increased (PC3) for total species richness, spruce-fir associates, and spruce-fir obligates and spruce-fir associates combined, but richness of spruce-fir obligates was not significantly associated with greater coniferous tree composition (γ_6 =0.069, 95% CIs=-0.004–0.146); however, its insignificance was marginal. Midstory (PC4) was not significantly associated with richness of any species group.

Comparing the relative magnitude and direction of effect sizes from principal components on richness of species groups provided additional insights (Fig. 1.6.). Species groups considered here had similar directions of significant responses (positive or negative) for each principal component. For example, all species groups that significantly responded to SPFIR had positive relationships. The relative magnitude of effect sizes suggested that tree immaturity played a dominant and positive role influencing richness of species groups, especially spruce-fir species of concern and spruce-fir obligates, whereas tree density and tree composition were associated with richness of species groups, but with less magnitude. Total species richness was significantly associated with tree density and tree composition; however, effect sizes were small and marginal.

Figure 1.6 Stand-level richness response to principal components from vegetation variables. Means are depicted as points with 95% credible intervals displayed as horizontal lines. Gray points and lines indicate that 95% credible intervals intersect zero, while black points and credible intervals indicate significance. Principal components were returned as standardized site scores allowing direct comparisons of effect sizes. The number of surveys at each point count location was assigned its mean value (8.5 surveys) for display.



1.5. Discussion

1.5.1. Forest Management for Spruce-fir Birds and Species of Concern

The clearcut suite of forestry treatments (10–40 years after initial clearcut harvest) followed by postharvest treatments (3–23 years after initial harvest) had greatest abundance and richness of most spruce-fir obligates, associates, and species of concern. Furthermore, clearcut treatments had vegetation characteristics that were preferred by spruce-fir obligates and associates; however, clearcuts have been restricted in Maine since 1991 by legislation (e.g., Maine Forest Practices Act).

Spruce-fir composition varied among harvest treatments, and passerines responded to these conditions, suggesting that strategic forest management could reduce recent losses in coniferous forest (McCaskill et al. 2011, Legaard et al. 2015, Simons-Legaard et al. 2016) and increase local abundance and richness of spruce-fir birds. Herbicide and PCT promote spruce-fir composition (Brissette et al. 1999, Thompson et al. 2013), and stands examined here that received postharvest treatments 3–23 years after clearcutting had a greater proportion of spruce-fir trees than other treatments. Herbicide and PCT 11-40 years post-clearcut promote spruce-fir regeneration and increase tree density, resulting in basal area approaching that of mature stands \geq 48 years postharvest, however, individual trees were smaller in diameter than those in mature stands. Rankin and Perlut (2015) documented immediate decreases in basal area one to three years after PCT, and our PCT stands 15–23 years after clearcut had average basal area similar to our mature stands (48–113+ years after treatment). Our selection and irregular shelterwood stands 5–41 years post-harvest were similar in tree maturity, tree density, and tree composition to mature stands, and they differed from the clearcut suite of harvest and

postharvest treatments by having a lesser proportion of spruce-fir trees. Average sprucefir tree composition ranked least in selection harvest stands, likely from selective removal of coniferous trees during harvest (Fuller et al., 2004; Robinson, 2006). Greater retention of spruce and fir trees in selection and shelterwood stands could potentially benefit spruce-fir birds; however, understanding effects on avian assemblages would require further study.

We speculate that benefits provided by greater spruce-fir composition to sprucefir bird species are diverse and vary by species, such as foraging and nesting attributes that potentially enhance demographic rates. Several spruce-fir birds (e.g., Bay-breasted Warbler, Cape May Warbler, and Tennessee Warbler) have breeding distributions that coincide with eastern spruce budworm prey (Choristoneura fumiferana, MacArthur, 1958) and have evolved to increase populations during periodic budworm outbreaks (MacArthur 1958, Venier et al. 2009). Spruce budworm were relatively scarce during our study compared to outbreak years, which preceded our study by >30 years (Maine Forest Service, 2015), thus our avian abundance estimates were unlikely to be influenced by short-term changes in budworm densities. Other forage provided by spruce trees includes mast that is preferred food for some resident species and partial migrants such as Boreal Chickadee (Haftorn 1974) and Red-breasted Nuthatch, and those foods can be critical for winter survival (Ficken et al. 1996, Ghalambor and Martin 1999). Species such as Olivesided Flycatcher, Ruby-crowned Kinglet, and Golden-crowned Kinglet prefer to nest in spruce trees (Swanson et al. 2008, 2012, Altman and Sallabanks 2012). Collectively, these ecological relationships highlight the mechanistic importance of tree composition to spruce-fir bird populations and the potential importance to bird conservation in the

Atlantic Northern Forest from harvest treatments that promote spruce-fir composition such as clearcuts with postharvest treatments. These treatments also promote abundances and richness of spruce-fir obligates, associates, and species of concern.

Selection and irregular shelterwood treatments remain important for conserving species that use large trees. Red-breasted Nuthatch requires mature forest structure such as snags for nest sites and conifer mast for winter food, and these resources are diminished in recently harvested even-aged stands (Adams and Morrison 1993). Non-passerine birds (e.g., woodpeckers) and other taxa that were not considered here may require mature forest structure such as snags and woody debris. If the conservation objective is to promote habitat in the managed Atlantic Northern Forest for the broadest array of spruce-fir birds and species of concern, then clearcuts 11–40 years since harvest, especially those combined with postharvest treatments, achieve a greater response in abundance and richness of avian assemblages than other harvest treatments investigated here.

1.5.2. Biodiversity

Vertebrate diversity generally decreases as forest stands reach canopy closure, and thinning of stands increases or maintains diversity (reviewed by Demarais et al. 2017). Our results roughly reflected these relationships: mean total avian richness ranked greatest in clearcut-only stands 11–36 years postharvest indicating increased richness with greater intensity of management. Harvested stands peak in bird diversity approximately 5–10 years after harvest followed by rapid declines (Conner and Adkisson 1975, Hagan et al. 1997, Keller et al. 2003) that are often attributed to decreases of early successional bird species (McDermott and Wood 2009) in response to increased canopy

closure, lack of structural diversity, and loss of ground foraging and nesting sites (Keller et al. 2003). Regenerating clearcut-only stands (11–36 years post-harvest) were species rich, and likely bolstered by the presence of early successional species. Stands that we surveyed spanned 11–40 years since clearcut harvest and 5–41 years since partial harvest, capturing the post-harvest period when we expect near peak diversity (5–10 years after harvest, Keller et al., 2003).

Forest birds partition niches among complex structures (MacArthur 1958), and vegetation with diverse vertical structure promotes richness of forest birds (MacArthur and MacArthur 1961, Goetz et al. 2007). Keller et al. (2003) showed a secondary smaller peak in richness in older stands 55 to 125 years post-harvest as more complex forest structures develop, which may explain our non-significant but consistently greater richness in mature stands compared to selection stands. Selection and shelterwood harvests created stands that were more similar to mature stands in vegetation composition, vegetation structure, passerine richness, and passerine assemblages. Partial harvests may maintain important vegetative features for retaining species that select late successional forest (e.g., Red-breasted Nuthatch); however, they lack characteristics selected by many other spruce-fir associated birds.

1.5.3. Forest Management

Our study captured a snapshot of the landscape in the Atlantic Northern Forest managed with harvest treatments applied 5–41 years prior and mature stands 48–113+ years-since-harvest. Some of our study stands were inherently later succession, such as those with postharvest treatments that were applied 3–23 years after a clearcut. Vegetative characteristics change as stands mature, and both basal area and dbh were

correlated with years-since-harvest (Fig. C.1). Despite large variation in years-sinceharvest, we found distinctive emergent features of harvest and postharvest treatments, such as greater spruce-fir composition in postharvest treatments, suggesting that effects on vegetation and bird abundance may be persistent and directed by management.

The average length of time each treatment remains on the landscape may vary because of inherent differences in stand age or maturity. For example, postharvest treatments are costly to implement, but increase gross merchantable volume of residual spruce and fir trees (Pitt and Lanteigne 2008), which makes stands economically desirable for harvest sooner after treatments compared to stands with less intensive management. Consequently, the longevity of stands after postharvest treatments may also be an important consideration for the conservation of spruce-fir birds. Even within a managed stand, forest dynamics from natural disturbance change habitat availability for birds. Thompson et al. (2013) showed that 31-52 years after stands had been harvested and subsequently received postharvest treatments that avian communities were more similar to those in mature spruce-fir stands compared to stands without postharvest treatments. Other research from the northwestern United States has documented decreases in abundance (Betts et al. 2013) and richness (Kroll et al. 2017) of leaf gleaning insectivorous birds one to four years after postharvest treatments, although no differences were apparent after five years (Kroll et al. 2017). Future research that explores dynamics of forest structure, composition, harvest and postharvest treatments, and management intervals in relation to habitat selection will enhance our understanding of effects from forest management on long-term conservation of forest biodiversity and spruce-fir passerines.

We focused on spruce-fir avian assemblages; however, if conservation goals are to emulate natural disturbance or promote habitat for wildlife that require old growth forest, selection and shelterwood harvests may be more appropriate (Seymour et al. 2002). Stand structure was the dominant predictor of avian assemblages (Table A.4), with a large amount of variance explained by basal area (50.8%) in separate regressions, followed by spruce-fir tree composition (40.4%), and dbh (37.0%). Basal area was least in clearcut stands, but stands managed with both clearcuts and postharvest treatments had basal area that was comparable to mature stands (Fig. 1.3.). Tree dbh in selection and shelterwood harvests (averaging 26.0 and 27.6 cm, respectively) was more similar to tree dbh expected in old growth forests (averaging 35–53 cm, Mosseler et al., 2003) compared to the suite of clearcut treatments (averaging between 15.8 and 19.7 cm, Fig. 1.3.). Stands with greater richness of spruce-fir birds contained more immature trees and these stands will continue to be created on the landscape while forests are harvested. More research is required to understand how forest management emulates natural disturbance and the consequences for avian assemblages.

We relied on relative abundance as a metric for habitat quality; however, density does not always reflect demographic rates, because preferred habitat may not convey a fitness advantage (Fretwell and Lucas 1969, Gates and Gysel 1978, Van Horne 1983). However, abundance and occupancy are often positively correlated with demographic rates (Ferrer and Donazar 1996, Sergio and Newton 2003, Germain et al. 2018), and data on demographics can be costly and difficult to obtain (Johnson 2007).

1.5.4. Conclusions

We clarified how avian assemblages and richness within conifer-dominant stands in the Atlantic Northern Forest respond to dominant management approaches and identified vegetative components associated with these responses. Furthermore, our results indicate that clearcuts coupled with postharvest treatment (3–23 years after clearcut) promote coniferous trees (11–40 years after initial harvests) that may be beneficial to populations of spruce-fir associated passerines in the Atlantic Northern Forest. Important structural and compositional characteristics are influenced by forest management approaches, some of which are regulated, controversial, or costly (e.g., clearcuts and herbicide are controversial and PCT is expensive).

Spruce-fir obligates and associates reached greatest abundance when spruce-fir comprised \geq 70% and \geq 60% of trees, respectively (Fig. B.1.C). Spruce-fir obligates and associates reached greatest richness in stands with small diameter trees and greater coniferous tree composition (Fig. 1.6.). More information about relationships between demographic parameters of individual species with conditions created by forest management would further clarify appropriate management approaches for priority species of concern.
Our research may be relevant to other regions with similar forest composition (conifer-dominated and mixed woods), forest structure, and avian assemblages, which includes much of the boreal region across North America, and similar results were observed outside our study region (e.g. Ontario, Thompson et al., 2013). Abundance and richness of spruce-fir birds responded to common forestry practices in our region, however, these practices also can be detrimental to other taxa, and their effects likely are dependent upon habitat availability on the landscape and prevailing trends in wildlife populations. Given the extent of forestry within our study region, more research is needed on the cumulative effects across the landscape of changing composition, configuration, succession, and fragmentation of habitats used by spruce-fir birds.

CHAPTER 2

INFLUENCE OF HARVEST TREATMENTS AND VEGETATION ON ABUNDANCE OF BREEDING AVIAN FOCAL SPECIES IN REGENERATING FORESTED STANDS

2.1. Abstract

Forests are subject to anthropogenic effects from forest management that influence demographic rates of breeding and post-breeding birds. Numerous studies have focused on the immediate effects from forest management on wildlife soon after harvest treatment (e.g., 0–5 years), but fewer studies have examined changes in focal species abundance over longer durations of time as forest regenerates after disturbance. To understand how harvests influence conifer-associated birds during the breeding and postbreeding period over the forest regeneration period, we used avian detection data from point count surveys of 19 conifer-associated birds in lowland conifer and mixed-wood forests and distance-removal models to estimate abundance and associations with seven common harvest treatments, years-since-harvest (YSH, 5–120+), and seven vegetation variables. We adapted previously described hierarchical distance-removal models to parse associations with YSH and harvest treatments corresponding to the unit of forest management at the stand-level. Abundance of six species differed significantly among treatments, demonstrating that management treatments provided information predicting the abundance of single species. Fourteen species had significant associations between abundance and vegetative variables, suggesting that managers could target vegetative outcomes when directing management toward focal species (sensu retention forestry). All vegetation variables were important for some species including basal area (9 species),

midstory cover (5 species), spruce-fir composition (4 species), live crown ratio (3 species), tree diameter at breast height (3 species), shrub cover (3 species), and shrub composition (1 species). Only one species was associated with YSH; Blackpoll Warbler (*S. striata*) abundance decreased as YSH increased. We discuss harvest treatments that may benefit focal species based on their vegetative characteristics and focal species associations with vegetation. Our results provide essential information about associations between abundance of focal species, forest management, and vegetation that can guide practitioners toward management that is associated with greater abundance of focal species, species and conservation of biodiversity.

2.2. Introduction

Habitat loss and fragmentation are regarded as major causes of species loss for birds (Schmiegelow and Mönkkönen 2002, Johnson 2007) and other taxa globally (Ehrlich and Ehrlich 1981, Wilson 1988, Newbold et al. 2015). Forest covers approximately 31% of the Earth's terrestrial area (MacDicken et al. 2016), and anthropogenic causes of disturbance are widespread; however, only 13% of global forests were set aside for conservation prior to 2016 (MacDicken et al. 2016). Combined, the boreal and hemiboreal zones of North America comprise 34% of the terrestrial area in Canada and the United States (Brandt 2009). Birds represent a large percentage of terrestrial vertebrate taxon in the boreal forest (>75%, Smith 1993, Mönkkönen and Viro 1997), and these forests provide habitat during the breeding and post-breeding periods of the annual cycle (Hagan et al. 1997, DeGraaf et al. 1998) when the entirety of recruitment occurs for many bird species in the hemiboreal subzone (e.g., Cape May Warbler, Olivesided Flycatcher, and Yellow-rumped Warbler, and numerous others). Concurrently,

these forests are extensively and intensively managed influencing vegetative composition, vegetative structure (Sader et al. 2003, Legaard et al. 2015, Rolek et al. 2018), and habitat quality for breeding (e.g., Flaspohler et al. 2001) and post-breeding birds (reviewed by Cox et al. 2014).

Populations of several conifer-associated birds in the eastern United States declined between 1989 and 2013 (Ralston et al. 2015) and USGS Breeding Bird Survey results corroborate these declines for 11 of 17 birds (Sauer et al. 2017) that are associated with the spruce-fir forest type in the Atlantic Northern Forest between 1966 and 2015 (Rolek et al. 2018). This region is intensively managed and >70% of the land area in Maine, New Hampshire, and Vermont are timberlands (McCaskill et al. 2011, Morin et al. 2012). Given the extent of forest management on the landscape coupled with declines in conifer-associated birds, research on the influences from forestry on avian abundance can aid in identifying management techniques that optimize habitat for focal species.

Numerous studies have recognized the relevance of spatiotemporal components associated with configuration of habitat (e.g., Weakland and Wood 2005, Fraterrigo et al. 2009, McClure et al. 2012) and intervals of disturbance (e.g., Hunter 1993, Seymour et al. 2002) in managed stands for conserving habitat and biodiversity. The spatial and temporal intervals between disturbance control habitat availability (Hunter 1993, Seymour et al. 2002) for many focal species in the Atlantic Northern Forest because most of the landscape is comprised of timberlands (McCaskill et al. 2011, Morin et al. 2012); therefore, many forested stands that occur on the landscape exist between periodic disturbances from harvest. These temporal intervals occur on average roughly every 50

years in northern New England (Seymour et al. 2002), greatly exceeding natural disturbance intervals in the region (typically >150 years, Lorimer and White 2003, Mosseler et al. 2003). Regenerating forests are dynamic, and tree composition and structure changes immediately after disturbance during succession to >150 years after disturbance (Mosseler et al. 2003). Information on the availability of avian habitat five to 120 YSH is poorly understood, despite that regenerating and second- and third-growth forest compose a majority of the region's landscape (>70% in Maine, New Hampshire, and Vermont, McCaskill et al. 2011, Morin et al. 2012). Identifying the temporal interval when species reach greatest abundance would provide essential information for detailed conservation planning of focal species in extensively harvested landscapes (e.g., McDermott and Wood 2009, McDermott et al. 2011). Numerous studies have focused on the immediate effects of forest management on wildlife (e.g., Titterington et al. 1979, King and DeGraaf 2000, Betts et al. 2013, Rankin and Perlut 2015, Kroll et al. 2017); however, studies have rarely investigated long-term effects of forest management on birds spanning large portions of the stand regeneration period (but see Hobson and Schieck 1999, Thompson et al. 2013). Hierarchical models provide opportunities to parse the effects from management treatments and time since harvest on demographic rates of focal species.

Conservation of biodiversity relies on identifying high quality habitat that provides enhanced demographic rates that allow populations to persist. Quantifying habitat quality can be challenging, because demographic rates may be costly to measure in the field (Johnson 2007). Habitat selection, the proportional use of habitats, is a pivotal component of habitat quality because additional components of demography, including

abundance, survival, and fecundity, arise from occupied habitat (Germain et al., 2017). Habitat selection during the breeding and post-breeding periods can play disproportionately large roles in population changes for some species, because the duration of the breeding season is brief (2–3 months) for some birds especially Nearctic-Neotropical migrants (e.g., Bay-breasted Warbler, see Table 2.2 for latin names, Rodewald 2017). For example, the relative effect from habitat loss on breeding grounds is at least three to six times greater than habitat loss on nonbreeding grounds for the Wood Thrush (*Hylocichla mustelina*, Rushing et al., 2016), a Nearctic-Neotropical migrant.

Occurrence (e.g., species richness) can be valuable for assessing the effects on species assemblages (Rolek et al. 2018); however, these data may provide limited information when attempting to understand single-species responses to anthropogenic habitat changes. Abundance or density arise from habitat selection (e.g., occurrence, Boyce et al. 2016) and these data can be less costly to collect compared to other demographic rates (e.g., survival and fecundity, Johnson 2007). Abundance and density are often correlated with other demographic rates that are important components of habitat quality (Ferrer and Donazar 1996, Sergio and Newton 2003, Bock and Jones 2004, Germain et al. 2018), although exceptions exist (Fretwell and Lucas 1969, Van Horne 1983). Abundance can provide richer information about demographic processes compared to occurrence estimates alone because abundance includes habitat selection by multiple individuals and density dependent processes (Boyce et al. 2016) that can be important to the regulation of populations. Some statistical methods that account for imperfect detection require repeated visits and the assumption of closure over repeated

visits (i.e., no immigration, emigration, mortality, or reproduction, MacKenzie et al. 2002, Tyre et al. 2003); however, violating the closure assumption can result in biased parameter estimates (Rota et al. 2009). This closure assumption can be unreasonable in many circumstances, and 71–100% of avian species violated this assumption during repeated point count visits (Rota et al. 2009). Recent advances in statistical techniques (e.g., Amundson et al. 2014) enable estimation of abundance while accounting for imperfect detection using single-visit surveys that do not require the closure assumption over longer durations. We use these models (Kéry and Royle 2015) to improve our estimates of relationships between abundance of 19 conifer-associated birds, vegetation characteristics, and forest management.

We used a dataset designed to assess the influence from harvest treatments on avian abundance combined with space-for-time substitution of harvested stands to estimate abundance of breeding and post-breeding focal species that use the spruce-fir and mixed-wood forest types. We considered seven treatment categories spanning a variety of harvest intensities and YSH that are common across the Atlantic Northern Forest. Our overall objective was to evaluate the influences from management, YSH, and vegetation on abundance of 19 avian species (Table 2.2) in these managed forests, and by identifying associations between avian abundance and (1) forestry treatments, (2) YSH, and (3) vegetative characteristics.

2.3. Methods

2.3.1. Study Sites

Our study was restricted to sites within the Atlantic Northern Forest (Bird Conservation Region 14, Williams and Pashley 1999), which coarsely corresponds to the Acadian Forest Region that transitions from temperate deciduous to eastern boreal forest (Seymour and Hunter 1992) and the hemiboreal subzone (Brandt 2009). Our study sites (Fig. 2.1.) were located on managed public and private lands in Vermont, New Hampshire, and Maine including privately-owned Telos and Clayton Lake in the North Maine Woods region and publicly-owned lands in Baxter State Park and four U.S. Fish and Wildlife Service National Wildlife Refuges (hereafter NWR; Nulhegan Division of Silvio O. Conte, Umbagog, Aroostook, Moosehorn). Figure 2.1 Sampling design for conifer-associated avian point count surveys at seven study sites within the hemiboreal Atlantic Northern Forest, Bird Conservation Region 14. We surveyed birds and vegetation at seven study sites on private and public lands within the United States in Maine, Vermont, and New Hampshire. We surveyed 425 point count locations over three years (2013–2015) and 870 vegetation plots (surveyed in 2014) in 114 forested stands. Pie charts depict the proportion of stands within each treatment category at each site. Coordinates are displayed for zoomed-in maps using UTM Zone 19N.



We surveyed conifer-associated passerines in 114 stands in lowland conifer forests <500 m elevation that were comprised of approximately >50% coniferous trees and were ≥ 12.1 ha in size to reduce edge effects (King et al. 1997, Ortega and Capen 2002). We restricted surveys to stands with data of historical management. We sampled seven management treatments including selection $11 \leq YSH \leq 41$, first stage shelterwood $5 \le YSH \le 31$ (hereafter shelterwood), and regenerating clearcut $11 \le YSH \le 40$. We further divided regenerating clearcut into stands receiving only clearcut treatment (hereafter clearcut-only) 11 ≤ YSH ≤ 36 and stands receiving intensive forest management via postharvest treatments including: aerially applied herbicide 8–31 years prior to surveys and $21 \le YSH \le 40$ (clearcut-herbicide); precommercial thinning 18–35 years prior to surveys and 11≤YSH≤38 (clearcut-PCT), or both herbicide and precommercial thinning 13–31 years prior to surveys and $31 \le YSH \le 39$ (clearcut-herbicide-PCT). Overall, managed stands, excluding mature, ranged 5-41 YSH (Fig. 2.2.). Mature stands were previously managed \geq 48 YSH to >113 YSH, but previous harvest treatment is unknown. We note that mature stands considered here are distinct from old growth stands, because old growth within the region is considered >150 YSH (Mosseler et al. 2003).

Figure 2.2 Box-and-whisker plots of years-since-harvest (YSH) and seven common forestry treatments surveyed at 114 stands in the Atlantic Northern Forest on both private and public lands. The median (50th percentile) is depicted by a vertical line; the 25th and 75th percentiles are depicted by box edges; and data are depicted as points.



2.3.2. Avian Point Counts and Vegetation Surveys

We conducted standardized multi-species avian point count surveys (Ralph et al. 1995) at 425 points spaced >100 m apart (DeGraaf et al. 1998) and >130 m from stand edges (i.e., 80 m from the periphery of a 50 m point count circle, Costello et al. 2000) during the breeding and post-fledgling period (1 June–4 August, Rodewald, 2017) during the annual cycle for most species in northern New England. We conducted stationary counts for a duration of 10 minutes, and we recorded the time interval of initial detection (0–2, 2–4, 4–6, 6–8, 8–10 minutes), and distance to initial detection for each individual (Buckland et al. 1993) in three intervals: 0–25, 25–50, and >50 m. After we detected and recorded individuals, we omitted them from subsequent recording of data during a survey. Technicians were trained to avoid double counting individuals. We recorded flyovers, which were omitted from analyses. We collected ancillary data during surveys to account for variation in detection probability: observer identity (OBS, 28 total); background noise (NOISE, mean=0.73, SD=0.85) as the perceived noise from any nonavian sounds on a scale from one to five; overhead canopy density (DENS, mean=0.28, SD=0.33) as the proportion of overhead leaf cover measured using a convex densiometer before each survey from the point count location; Julian date (DATE, mean=44.3, SD=18.6) as number of days after 1 June that a survey was conducted; and hours after civil dawn (HR, mean=2.1, SD=1.3). We also included basal area of trees as a covariate for detection probability (described below), because vegetation density causes sound attenuation and is negatively associated with perceptibility of bird song (Yip et al. 2017). We conducted avian surveys at most point count locations (75%) three times each year for three subsequent years (2013–2015), totaling nine surveys. Some point count

locations (10% in 2013, 2% in 2014, 13% in 2015) were surveyed less than three times some years due to logistical constraints. We added seven shelterwood stands in 2014 to increase sample sizes; therefore, these stands we not surveyed in 2013.

We conducted vegetation surveys at each point count location during 2014, using one plot centered at the point count location and one to three additional plots selected using a random number generator to determine a cardinal direction $(0^{\circ}, 90^{\circ}, 180^{\circ}, or$ 270°) located 30 m from the center of the point count location. We determined that two vegetation plots per point count location adequately represented vegetation and were logistically feasible; therefore, we surveyed most point count locations (398 of 425) with two vegetation plots. However, we surveyed some point count locations using three or four plots (seven and 11 point count locations, respectively), Forest managers harvested some stands prior to collection of a second vegetation plot, resulting in one vegetation plot per point count location (nine point count locations). We measured structural and compositional vegetative characteristics including: basal area (BA), diameter at breast height (DBH), canopy cover (CAN), midstory cover (MID), shrub cover (SCOV), shrub composition ratio (SCOMP), proportion of spruce-fir trees (SPFIR), and live crown ratio (LCR, Table 2.1, Table E.1, Fig. G.1). These vegetative measurements were summarized by averaging vegetation plots at each point count location.

Table 2.1 Variable names with abbreviations in parentheses, point-level means (standard deviation), units of measurement, description, and treatment means (standard deviations) for variables measured at each point count location (n=425). Variable were surveyed at 870 subplots within 114 stands in seven treatments and post-treatments in northern Maine, New Hampshire, and Vermont, USA. Years-since-harvest reports stand-level mean (SEs, range) because it was modeled at the stand-level. All covariates were centered on the mean and scaled for analyses. For stand-level means of basal area spruce-fir composition, diameter-at-breast-height, midstory cover, and shrub cover see Rolek et al. (2018).

Name	Description	Mature	Selec-	Shelter-	Clearcut-	Clearcut-	Clearcut-	Clearcut-
			tion	wood	only	herbicide	PCT	herbicide
								-PCT
Basal area (BA;	Measured from trees	34.4	28.04	25.6	8.5 (1.1)	21.5	25.4	29.1
m ² ha ⁻¹ . BA2 is	counted "in" using	(1.0)	(1.3)	(2.3)		(1.5)	(1.9)	(1.8)
BA^2)	wedge prism and							
	≥10cm dbh							
Spruce-fir	Proportion of trees that	0.57	0.52	0.52	0.65	0.83	0.84	0.84
composition	were spruce or fir and	(0.03)	(0.03)	(0.04)	(0.04)	(0.03)	(0.03)	(0.03)
(SPFIR)	≥ 10 cm dbh.							
Diameter-at-breast-	Diameter of trees	27.4	25.8	28.9	16.3	15.8	19.2	16.4
height (DBH; cm)	counted "in" using	(0.6)	(0.6)	(1.1)	(1.8)	(0.5)	(0.8)	(0.5)
	wedge prism and							
	\geq 10cm dbh. Measured							
	with Biltmore stick.							
	Breast height=1.37m							
Midstory cover	Proportion of leaf	0.38	0.55	0.47	0.32	0.53	0.58	0.48
(MID)	cover \geq 7.6m measured	(0.03)	(0.04)	(0.06)	(0.04)	(0.03)	(0.05)	(0.06)
	using plexiglass grid.							
	Height estimated with							
	hypsometer.							

Table 2.1 Continued.								
Shrub cover	Proportion of leaf	0.27	0.29	0.44	0.41	0.27	0.22	0.18
(SCOV)	cover <0.5m, Visual	(0.02)	(0.02)	(0.03)	(0.02)	(0.03)	(0.02)	(0.03)
	estimate.							
Shrub composition	Ratio of coniferous to	0.22	0.16	0.30	0.34	0.13	0.11	0.09
ratio (SCOMP)	deciduous shrub cover	(0.02)	(0.01)	(0.03)	(0.02)	(0.03)	(0.01)	(0.01)
Live crown ratio	Measured from four	0.49	0.46	0.43	0.50	0.14	0.64	0.27
(LCR)	tallest trees, two trees	(0.02)	(0.03)	(0.04)	(0.04)	(0.03)	(0.04)	(0.07)
	in two subplots, and							
	from the height from							
	the top of the live							
	crown to the lowest							
	live branch, to the base							
	of the tree.							
Years-since-harvest	Number of years since	83.9	22.4	16.7	20.5 (2.4,	31.9 (1.4,	25.8 (3.1,	34.4 (2.9,
(YSH, YSH2 is	a stand was harvested	(3.9,	(1.7,	(2.5, 5–	11–36)	21–40)	11–38)	31–39)
YSH ²)	with 2014 as the	48–	11-41)	31)				
	reference year.	113+)						

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We sampled 114 stands with 425 point count locations and 870 vegetation plots. Of these stands, we surveyed 30 mature stands (\geq 48 YSH) containing 118 point count locations; 23 selection stands containing 83 point count locations; 11 shelterwood stands containing 37 point count locations; 14 clearcut-only stands containing 58 point count locations; 17 clearcut-herbicide stands containing 66 point count locations; 12 clearcut-PCT stands containing 44 point count locations; and seven clearcut-herbicide-PCT stands containing 19 point count locations (see Chapter 1 Table A.1 for details).

We restricted analyses to species detected at ≥10 point count locations and those detected ≤50 m from the center of the point (Hagan et al. 1997, DeGraaf et al. 1998, Hutto 2016) that are passerines (order Passeriformes) associated with mixed-wood or coniferous forests, and whose distributions roughly coincide with boreal and hemiboreal forests of North America (Rodewald 2017). We analyzed 19 species that fit these criteria. They included Olive-sided Flycatcher, Yellow-bellied Flycatcher, Gray Jay, Boreal Chickadee, Red-breasted Nuthatch, Winter Wren, Golden-crowned Kinglet, Rubycrowned Kinglet, Swainson's Thrush, Hermit Thrush, White-throated Sparrow, Cape May Warbler, Magnolia Warbler, Bay-breasted Warbler, Blackburnian Warbler, Blackpoll Warbler, Palm Warbler, Yellow-rumped Warbler, and Canada Warbler (see Table 2.2 for binomial nomenclature, abbreviations, and number detected). Table 2.2 Nineteen conifer-associated avian species that met sample size requirements (detected at \geq 10 points). We included these species in analysis from 425 point count locations across Northern New England in Maine, New Hampshire, and Vermont over three years, 2013–2015.

Common nomo	Abbrou	Comus species	Detections	Points	
Common name	Abblev.	Genus species	Detections	detected	
Olive-sided Flycatcher	OSFL	Contopus cooperi	49	35	
Yellow-bellied	VDEI	Empidonax	510	244	
Flycatcher	IDL	flaviventris	512		
Grov Joy	CDAI	Perisoreus	115	73	
Olay Jay	UKAJ	canadensis	115		
Boreal Chickadee	BOCH	Poecile hudsonicus	390	198	
Red-breasted Nuthatch	RBNU	Sitta canadensis	564	287	
Winter Wren	WIWR	Nannus troglodytes	586	284	
Golden-crowned	CCVI	Deculus saturana	1049	201	
Kinglet	UCKI	Kegulus saltapa	1040	301	
Ruby-crowned Kinglet	RCKI	Regulus calendula	242	157	
Swainson's Thrush	SWTH	Catharus ustulatus	917	352	
Hermit Thrush	HETH	Catharus guttatus	810	343	
Cape May Warbler	CMWA	Setophaga tigrina	25	22	
Magnolia Warbler	MAWA	Setophaga magnolia	1456	383	
Bay-breasted Warbler	BBWA	Setophaga castanea	191	103	
Blackburnian Warbler	BLBW	Setophaga fusca	317	185	
Blackpoll Warbler	BLPW	Setophaga striata	88	43	
Palm Warbler	YPWA	Setophaga palmarum	189	77	
Yellow-rumped	MVWA	Satonhaga ooronata	727	374	
Warbler		Selophaga coronala	131	524	
Canada Warbler	CAWA	Cardellina	360	172	
	CAWA	canadensis	509	172	
White-throated	WTSP	Zonotrichia albicollis	708	257	
Sparrow	** 101		700	231	

2.3.3. Statistical Analysis

We used distance-removal models that hybridize statistical methods to maximize statistical inference for avian point counts while incorporating detection processes (Farnsworth et al. 2005, Amundson et al. 2014, Kéry and Royle 2015). Assumptions of ;the distance-removal model include: 1) animals are distributed uniformly in space; 2) detection probability is a function of distance; 3) individuals are detected at their original location, 4) distances are measured without error; 5) counts are instantaneous samples; and 6) individuals are detected only once (Kéry and Royle 2015). Distance-removal models approximate an instantaneous sample for point counts of birds (Farnsworth et al. 2005, Amundson et al. 2014), providing a snapshot of density and abundance that lacks confounding affects from movement (e.g., temporary emigration, Chandler et al., 2011). This instantaneous sample of abundance scales to the second or third orders of habitat selection, i.e., home range selection or selection within home range (Johnson 1980) for the species investigated here.

We modeled the detection parameter associated with distance sampling, i.e., perceptibility (p^p) , as a monotonically decreasing function of distance from observer from the center of the point count location using the radial distance function, and perceptibility decreased with the half-normal distance function $g(r) = \exp(-\frac{r^2}{2\sigma^2})$ (Buckland 2001) where r is the detection radius and σ is a distance scale parameter that varies by site i at time t. Note that superscripts with letters were used to differentiate between parameters and do not indicate exponentiation unless specified otherwise. We specified the distance scale parameter as a function of covariates using the log link function and included the covariates background noise level (NOISE), overhead canopy density (DENS), and basal area (BA), while observer identity (OBS) was included as a random effect: $\log(\sigma_{it}) = \log(\gamma_0) + w_1\gamma_1 \text{NOISE}_{it} + w_2\gamma_2 \text{DENS}_i + w_3\gamma_3 \text{BA}_i + \varepsilon_{OBS}$ and $\varepsilon_{OBS} \sim Normal(0, \sigma^{OBS})$. We used indicator variable selection to identify important covariates (denoted as w, see full description below). We modeled availability (p^a) as a function of covariates including days after 1 June (DATE), days after 1 June squared (DATE2), and hours after civil dawn (HR) using the logit link: $\log it(p_{it}^a) = \delta_0 + w_4\delta_1 \text{DATE}_{it} + w_4w_5\delta_2 \text{DATE}_{it}^2 + w_6\delta_3 \text{HR}_{it}$.

We used the combined detection probabilities, $p_{it} = p_{it}^a * p_{it}^p$ with a N-mixture model to estimate abundance $n_{it}|N_{it} \sim Binomial(N_{it}, p_{it})$ (Kéry and Royle 2015). We modeled abundance (N) as $N_{it} \sim Poisson(\lambda_{it})$ and used a zero-inflated Poisson distribution for species where Poisson distributed models had poor fit and the zeroinflated distribution improved model fit. We did not use a negative binomial distribution because we observed difficulties with convergence that were documented elsewhere using similar models (Kéry 2018).

2.3.4. Avian Abundance Response to Vegetation

Abundance was a function of vegetation covariates basal area (BA), spruce-fir tree composition (SPFIR), tree diameter at breast height (DBH), midstory cover (MID), shrub cover (SCOV), shrub composition (SCOMP), and live crown ratio (LCR): $log(\lambda_{it}) = \beta_0 + w_7\beta_1BA_i + w_7w_8\beta_2BA2_i + w_9\beta_3SPFIR_i + w_9w_{10}\beta_4SPFIR2_i + w_{11}\beta_5DBH_i + w_{12}\beta_6MID_i + w_{13}\beta_7SCOV_i + w_{14}\beta_8SCOMP_i + w_{15}\beta_9LCR_i + \varepsilon_s + \varepsilon_t$, where "2" indicates the quadratic form of a covariate (e.g., SPFIR2). Vegetation covariates and abbreviations are fully described in Table 2.1. The random effect, ε_s , was indexed by stand identity (*s*) and accounted for pseudoreplication of point count locations within each stand where $\varepsilon_s \sim Normal(0, \sigma^s)$, and ε_t was a random effect for site visit *t* where $\varepsilon_t \sim Normal(0, \sigma^t)$.

2.3.5. Avian Abundance Response to Harvest Treatments, and Years-since-harvest.

We specified a second set of models to determine focal species abundance response to treatments and YSH as $\log(\lambda_{it}) = \alpha_{0s} + \varepsilon_t$ where $\alpha_{0s} \sim Normal(\mu_s, \sigma^s)$ and $\mu_s = \alpha_{1 treatment} + w_{15}\alpha_2$ YSH_s + $w_{15}w_{16}\alpha_3$ YSH2_s, where ε_t was a random effect that allows abundance to vary by site visit (t), $\varepsilon_t \sim Normal(0, \sigma^t)$. This model assumed a linear or quadratic response to YSH, and allowed the intercept to vary by harvest treatment. Thus, we considered each stand a sample unit for harvest treatments and μ_s was the average abundance among point count locations within a stand (s).

2.3.6. Implementation, Model Selection, and Goodness-of-Fit

We used indicator variable selection for abundance and detection covariates to estimate the probability that each covariate should be included in the model. Each covariate is assigned a Bernoulli indicator w and included in the model as $w_1\beta_1x_i$ or as $w_1\beta_1x_i + w_1w_2\beta_2x_i^2$ for quadratic terms (Kéry and Royle 2015) with priors assigned as *Bernoulli*(0.5). We calculated the mean probability that a variable should be included in a model from each indicator. We excluded harvest treatment intercepts from indicator variable selection because we were primarily interested in parameter estimation for treatments rather than whether a treatment differed from the overall mean.

We present parameters as mean point estimates and 95% credible intervals with indicator variable selection weights. We considered variables significant when 95% credible intervals for parameter estimates did not intersect zero and we attributed substantial support when indicator variable selection weights were ≥ 0.75 , weak support when ≥ 0.50 and < 0.75, and not supported when < 0.50. These criteria roughly corresponded to Jeffreys scale for Bayes factors given our prior (Jeffreys 1961, Kass and Raftery 1995, Mutshinda et al. 2013).

We used JAGS 4.2.0 (Plummer 2003) from R version 3.3.1 (R Core Team 2015) and the package jagsUI (Kellner 2016). We centered and scaled all continuous covariates so that each had a mean=0 and SD=1 to aid convergence (Schielzeth 2010). We used standard vague priors for all intercepts and slopes of p^a , p^p , λ , and mean stand abundance (μ_s , Table F.2). We implemented each model with an adaptation period of 10,000, burn in period of 50,000, and an additional 50,000 posterior iterations thinned by one of 10 iterations using 3 chains, resulting in a total of 15,000 posterior iterations. We evaluated convergence by visually assessing traceplots of abundance from MCMC iterations and used the Gelman-Rubin convergence statistic, where $\hat{R} < 1.1$ indicated convergence (Gelman and Rubin 1992). We evaluated goodness-of-fit for abundance using Bayesian P values generated from posterior predictive distributions, where values near 0.5 indicate a good fit and values near zero or one suggest poor fit (Kéry 2010). We considered models with Bayesian P values >0.90 and <0.10 to have poor fit (Sollmann et al. 2015) and reran these models using a zero-inflated Poisson distribution. We retained models (Poisson or zero-inflated distributed) with Bayesian P values nearest to 0.5 for further inference. We estimated the average magnitude of effect for abundance covariates across all species by calculating the average of the absolute value of each regression coefficient. JAGS model code is provided in Appendix H.

2.4. Results

2.4.1. Avian Point Count, Vegetation Surveys, and Detection Probability

Of the 19 species analyzed, we detected Cape May Warbler at the fewest number of point count locations (22) and Magnolia Warbler at the greatest number of point count locations (383, Table 2.2). The number of detections ranged from a minimum of 25 for Cape May Warbler to a maximum of 1456 for Magnolia Warbler.

Detection probability varied with covariates. Availability was associated with DATE for five species in vegetation models (Table I.1) and six species in treatment models (Table I.2). Only one species had a quadratic relationship with DATE in treatment models. Availability was not associated with TIME in treatment or vegetation models. Perceptibility was associated with BA for five species for treatment models, and two species in vegetation models. Perceptibility was not associated with DENS or NOISE for any species in both vegetation and treatment models.

2.4.2. Avian Abundance Response to Vegetation

Five of 19 species (Boreal Chickadee, Golden-crowned Kinglet, Gray Jay, Magnolia Warbler, and Yellow-bellied Flycatcher) had poor model fit indicated by Bayesian *P* values when using a Poisson distribution on abundance in vegetation models. Substituting the Poisson for a zero-inflated Poisson distribution for abundance provided adequate model fit for two species (Boreal Chickadee and Gray Jay, Table I.1). We retained models for species with the distribution (Poisson or zero-inflated) that provided the greatest fit despite a lack of fit, and we recommend caution when interpreting results from these species including: Golden-crowned Kinglet, Magnolia Warbler, and Yellowbellied Flycatcher.

Abundance of 14 species (excluding Boreal Chickadee, Cape May Warbler, Hermit Thrush, Swainson's Thrush, and Winter Wren) associated with vegetation (Fig. 2.3., Table 2.3, Table I.1). Abundance of nine species associated with basal area. Abundance of four species (Blackburnian Warbler, Golden-crowned Kinglet, Gray Jay, and Red-breasted Nuthatch) increased with greater basal area, abundance of three species (Blackpoll Warbler, Magnolia Warbler, and Ruby-crowned Kinglet) decreased with greater basal area, and two species (White-throated Sparrow and Palm Warbler) decreased quadratically with basal area. Abundance of five species associated with midstory cover: two species (Bay-breasted Warbler and Blackburnian Warbler) increased abundance with greater midstory cover, while three species (Olive-sided Flycatcher, White-throated Sparrow, and Palm Warbler) decreased. Abundance of four species associated with spruce-fir composition: two species (Bay-breasted Warbler and Yellowrumped Warbler) abundance increased linearly with greater spruce-fir composition and two species (Golden-crowned Kinglet and Red-breasted Nuthatch) increased quadratically. Abundance of three species associated with live crown ratio: two species (Blackpoll Warbler and Yellow-rumped Warbler) increased abundance with greater live crown ratio, and one species (Bay-breasted Warbler) decreased. Abundance of three species associated with diameter at breast height: two species (Blackburnian Warbler and Red-breasted Nuthatch) increased abundance with greater diameter at breast height and one species (Yellow-bellied Flycatcher) decreased. Abundance of three species associated with shrub cover: one species (White-throated Sparrow) increased with shrub cover, while two species (Bay-breasted Warbler and Yellow-rumped Warbler) decreased

with shrub cover. One species, Canada Warbler, increased abundance in stands with greater conifer shrub composition.

Figure 2.3 Vegetation associations with abundance of 14 conifer-associated birds during the breeding and post-breeding periods estimated from distance-removal abundance models that account for detection probability. Each panel displays abundance for one species with the covariate on the bottom x-axis (solid lines, blue CIs) having the greatest effect size and the top x-axis (dashed lines, red CIs) having the second greatest effect size. All other covariates were held at their mean value. Vegetation variables include basal area (BA), diameter at breast height (DBH), spruce-fir tree composition (SPFIR), midstory (MID), shrub cover (SCOV), and live crown ratio (LCR).



Table 2.3 Summary of abundance estimates from Bayesian distance-removal models. This analysis tested for associations between species abundance and vegetation variables in Atlantic Northern Forest located in New Hampshire, Vermont, and Maine (for covariate abbreviations see Table 2.1). For each species (see Table 2.2 for abbreviations) results are provided for the best fitting model (Poisson or zero-inflated distribution) with the Bayesian P value nearest to 0.5, and we provide the probability of inclusion from indicator variable selection (Weight), mean slope coefficient estimate (Mean), and 95% lower (LCI) and upper (UCI) credible intervals. For brevity, detection covariates were excluded and these details are included in Appendix I.

Species	Bayesp	Covariate	Weight	Mean	LCI	UCI
BBWA	0.85	SPFIR	1.00	0.57	0.28	0.85
		MID	0.62	0.25	0.10	0.39
		SCOV	1.00	-0.53	-0.73	-0.32
		LCR	0.98	-0.36	-0.54	-0.19
BLBW	0.76	BA	1.00	0.40	0.21	1.00
		DBH	1.00	0.50	0.38	0.62
		MID	0.51	0.19	0.07	0.31
BLPW	0.58	BA	1.00	-1.27	-1.66	-0.69
		LCR	0.82	0.35	0.16	0.54
BOCH	0.34					
CAWA	0.86	SCOMP	1.00	0.35	0.21	0.47
CMWA	0.37					
GCKI	1.00	BA	1.00	0.37	0.18	0.69
		SPFIR	1.00	0.88	0.61	1.16
		SPFIR2	1.00	-0.57	-0.82	-0.32
GRAJ	0.16	BA	0.75	0.45	0.09	0.79

Table 2.3 Continued.

HETH	0.16					
MAWA	1.00	BA	1.00	-0.20	-0.25	-0.14
MYWA	0.40	SPFIR	1.00	0.25	0.15	0.35
		SCOV	1.00	-0.28	-0.37	-0.19
		LCR	0.60	0.15	0.06	0.23
OSFL	0.40	MID	0.98	-0.74	-1.13	-0.38
RBNU	0.30	BA	0.99	0.23	0.13	0.43
		SPFIR	0.76	0.82	0.47	1.19
		SPFIR2	0.76	-0.90	-1.27	-0.53
		DBH	1.00	0.23	0.14	0.31
RCKI	0.62	BA	0.96	-0.40	-0.60	-0.19
SWTH	0.20					
WIWR	0.75					
WTSP	0.65	BA	1.00	-0.98	-1.30	-0.57
		BA2	0.86	0.46	0.20	0.73
		MID	1.00	-0.28	-0.37	-0.2
		SCOV	1.00	0.24	0.15	0.35
YBFL	0.91	DBH	0.99	-0.24	-0.35	-0.14
YPWA	0.34	BA	1.00	-1.53	-2.31	-0.98
		BA2	0.55	0.94	0.24	1.60
		MID	0.75	-0.35	-0.58	-0.16

Basal area had the greatest average magnitude of effect on abundance ($|\beta_1| = 0.46$ and $|\beta_2| = 0.25$, Appendix I) across species when significant. Coefficients for other vegetation covariates had smaller magnitudes SPFIR $|\beta_3| = 0.41$ and SPFIR2 $|\beta_4| = 0.43$, MID $|\beta_6| = 0.21$, SCOV $|\beta_7| = 0.16$, DBH $|\beta_5| = 0.14$, LCR $|\beta_9| = 0.11$, and SCOMP $|\beta_8|$.

2.4.3. Avian Abundance Response to Harvest Treatments, and Years-since-harvest

Six species (Boreal Chickadee, Golden-crowned Kinglet, Gray Jay, Magnolia Warbler, Yellow-bellied Flycatcher, and Palm Warbler) had poor model fit using a Poisson distribution for abundance with treatments and YSH as covariates, Table I.2). However, substituting a zero-inflated Poisson distribution improved model fit for two species (Boreal Chickadee and Gray Jay). We retained models for species with the distribution (Poisson or zero-inflated) that provided the greatest fit regardless of Bayesian P values and urge caution when interpreting model results for species with poor model fit (i.e., Golden-crowned Kinglet, Magnolia Warbler, Yellow-bellied Flycatcher, and Palm Warbler).

Abundance of one of 19 species had significant associations with YSH (Fig. 2.4., Table I.2). Blackpoll Warbler decreased abundance with greater YSH ($w_{15} = 0.76$, $\alpha_2 = -2.26$, and 95% CIs=-4.25 and -0.43). YSH and YSH2 tended to have insignificant, but large magnitude of effect among species compared to vegetation covariates ($|\alpha_2| = 0.49$ and $|\alpha_3| = 0.61$).

Figure 2.4 Associations between years-since-harvest (YSH), harvest treatments, and avian abundance from Bayesian hierarchical distance-removal models for Blackpoll Warbler. Model estimates of avian abundance (points) and 95% credible intervals (vertical lines) are depicted. Abundance estimates are plotted at the mean (middle and 3rd point), quartiles (25% and 75%, 2nd and 4th points), minimum (1st point), and maximum (5th point) YSH for each treatment type.



Abundance of six species differed significantly among treatments (Fig. 2.5.). Blackburnian Warbler had greater abundance in mature and selection stands compared to shelterwood stands. Canada Warbler had greater abundance in selection stands compared to clearcut-herbicide and clearcut-PCT stands. Gray Jay had greater abundance in mature, selection, shelterwood, and clearcut-only stands compared to clearcut-herbicide-PCT stands. Olive-sided Flycatcher had greater abundance in mature stands compared to clearcut-herbicide-PCT stands. White-throated Sparrow had greater abundance in selection stands compared to clearcut-herbicide stands. Palm Warbler had greater abundance in clearcut-only stands compared to clearcut-herbicide stands. Detections per survey (not corrected for detection probability) are summarized for each species in each harvest treatment in Appendix J. Figure 2.5 Associations between harvest treatments and avian abundance from Bayesian hierarchical distance-removal models for six focal species. Estimates include mean abundance in harvest treatments (points) within a 50 m radius and 95% credible intervals (vertical lines). Y-axis intervals are spaced on the log scale.



2.5. Discussion

Fourteen species had abundance that was significantly associated with vegetation; six species had significant differences among harvest treatments; and one species was significantly associated with YSH. Combined, our results suggest there is large variability in vegetative outcomes within harvest treatments and that practitioners managing for focal species could target vegetative outcomes rather than use strict prescriptions of management treatments when managing for focal species.

YSH was only important for abundance of Blackpoll Warbler, and confidence intervals tended to be large for focal species. However, YSH was the explanatory variable that had the greatest average magnitude of effect among all species. We speculate that abundance of more species would have correlations with YSH if we had surveyed stands over the full range of harvest intervals (0-150 YSH) for each treatment, because forest structure changes greatly over this period (Mosseler et al. 2003). For example, Bay-breasted Warbler avoids recently disturbed early successional forest (Titterington et al. 1979) and stands with short harvest intervals (Venier et al. 2011), but this relationship was not detected using our approach likely because we did not survey stands with fewer YSH (e.g., 0-5 YSH). Larger spans of time-since-disturbance combined with hierarchical models that incorporate nonlinear relationships or higherorder polynomials (greater than quadratic) with covariates might provide additional insight into species abundance relationships with YSH. Increasing sample size of the number of stands might further clarify these relationships, because YSH and harvest treatments were modeled at the stand-level.

Blackpoll Warbler was more abundant at point count locations with less basal area and greater live crown ratio. High elevation montane spruce-fir is considered habitat for Blackpoll Warbler (Wilson Jr. 2013), and the lowland spruce-fir habitat examined here may provide population sinks (Wilson Jr. 2013). Indeed, many Blackpoll Warblers detected here were surrounded by higher elevations (e.g., Nulhegan NWR), suggesting that immigration from nearby high elevation sites may have been important for maintaining populations in lowland spruce-fir habitat.

Bay-breasted Warbler is often noted as a species of concern because populations in Atlantic Northern Forest are declining (Environment and Climate Change Canada 2017, Sauer et al. 2017). This species is described as selecting mature spruce-fir forests (Hagan et al. 1997, Venier et al. 2011) and young (e.g., 8–36 YSH) mixed-wood stands during spruce budworm outbreaks (Venier et al. 2009). In lowland conifer and mixedwood forests examined here, Bay-breasted Warbler had greatest abundance at locations with greater spruce-fir composition and midstory cover, and less shrub cover and live crown ratio (Fig. 2.3), and tended toward greatest abundance in shelterwood stands (5–31 YSH).

Blackburnian Warbler has greatest abundance in mature forest where trees are large (summarized by Morse 2004), and here Blackburnian Warbler had greatest abundance in stands with less disturbance from harvest, i.e., mature and selection stands examined here. Consistent with previous studies, abundance increased with mature forest structure such as greater basal area, diameter at breast height, and midstory cover, and Blackburnian Warbler avoided shelterwood treated stands.

Canada Warbler, a species of concern, had greatest abundance in stands with light disturbance such as selection harvests, and our results are consistent with a previous study that observed greater abundance in stands treated with light partial harvests at the southern margins of its distribution (Becker et al. 2012). Canada Warbler also had greater abundance with greater conifer shrub composition, which differs from previous studies that observed Canada Warbler in more mature forest with deciduous understory and early successional forests (Titterington et al. 1979, DeGraaf et al. 1998).

Cape May Warbler, another regionally declining species of concern (Environment and Climate Change Canada 2017, Sauer et al. 2017), did not select for any vegetation variables that we measured in our study. However, sample sizes were small for this species (n=25) primarily because detection probability was low, and perceptibility decayed rapidly with distance, with $\sigma=20.7$ in treatment models and $\sigma=29.0$ in vegetation models, this species was never detected beyond 50 m. Similarly, availability during a two minute interval was low, with $p^a = 0.10$ in treatment models and $p^a=0.07$ in vegetation models. Distance sampling typically requires about 70 detections for robust estimates (Buckland 2001). Abundance estimates for Cape May Warbler would be improved with modified surveys for this species. For example, future studies could increase point count duration and survey more point count locations without repeated visits to increase sample sizes. Importantly, more targeted surveys focusing on fewer species would likely increase detection rates of Cape May Warbler by observers, because their high-pitched vocalizations (Baltz and Latta 1998) are poorly perceived. Another alternative to increase inference might be to include informative priors on detection probability that have been

estimated from other studies (e,g., Boreal Avian Modeling Project, Sólymos et al. 2013), thereby incorporating the results from previous studies to models.

We analyzed a dataset that was designed to assess associations between management and abundance of focal species, however, application of our results is limited to the post-harvest temporal intervals in each treatment that we examined here (see YSH, Table 2.1). Some harvest treatments can only exist during specific temporal intervals, restricting their occurrence. For example, postharvest treatments using herbicide were applied 3–21 YSH after initial harvest, and precommercial thinning was applied approximately and 15–23 YSH. These stands exist in the clearcut-only treatment category prior to application of postharvest treatments. Longitudinal studies on focal species and avian assemblages in stands with known or experimentally-induced harvest treatments would provide a more complete picture of the effects from management on focal species.

Despite the small number of direct relationships between focal species abundance and harvest treatments, we can identify vegetation characteristics that could be promoted to benefit focal species based on the tendencies of directed silvicultural treatments to create specific vegetative outcomes. Managers seeking to improve habitat for spruce-fir birds could enhance habitat by increasing spruce-fir composition because four of 19 species examined here responded positively to spruce–fir composition, and a previous study observed that spruce-fir avian assemblages had peak abundance where tree composition was >60% spruce or fir (Rolek et al. 2018). Our results confirm the importance of spruce-fir composition for some focal species. Clearcut stands combined with postharvest treatments (i.e., herbicide and PCT) have greater spruce-fir composition

(averaging 83–84%, Table 2.1) compared to other treatments considered here (52–65%), and other studies have confirmed that postharvest treatments have greater conifer composition (Newton et al. 1989, Lautenschlager 1993, Brissette et al. 1999, Thompson et al. 2013, Rolek et al. 2018). Postharvest treatments could be used to increase spruce-fir composition in stands with <60% if management objectives include enhancing habitat for conifer-associated birds.

A diversity of tree density (e.g., basal area) and tree maturity (e.g., diameter-atbreast height) on the landscape would increase habitat for species studied here because responses to these vegetation variables differed markedly among species, consistent with other studies (Hagan et al. 1997, Hunter et al. 2001, McDermott and Wood 2009). Harvest treatments with greater residual basal area and larger residual trees (e.g., mature, selection, and shelterwood, Table 2.1) would promote abundance of Blackburnian Warbler, Golden-crowned Kinglet, Gray Jay, and Red-breasted Nuthatch; however, other species would be expected to avoid these stands including Blackpoll Warbler, Magnolia Warbler, Ruby-crowned Kinglet, White-throated Sparrow, Palm Warbler, and Yellowbellied Flycatcher. Species with greater abundance in stands with less basal area and smaller trees could be managed using clearcut-only treatments that have substantially less basal area and diameter at breast height (Table 2.1). Several species may require a combination of vegetative traits for managers to produce beneficial habitat, for example both Golden-crowned Kinglet and Red-breasted Nuthatch had greater abundance in stands with both greater spruce-fir composition and basal area. Furthermore, Redbreasted Nuthatch had greater abundance at sites with trees having greater diameter at breast height which suggests that a lengthy harvest interval could provide benefit to this
species. Outcome-based silviculture or retention forestry could be used to encourage and retain desired vegetation characteristics and may provide more direct outcomes for conservation of habitat directed toward focal species.

Our results combined with results from other studies that focus on temporal dynamics after harvest could be used simulate conservation planning in dynamic landscapes dominated by anthropogenic forest management to reach population objectives for focal species (e.g., Partners in Flight 2016). Abundance provides richer information about demographics of focal species compared to occurrence data; however, abundance remains an incomplete measure of demographic rates. Future research could investigate other demographic consequences of forest management and vegetation on focal species, because greater abundance does not necessarily reflect greater habitat quality (Fretwell and Lucas 1969, Van Horne 1983). While demographic rates can be challenging to collect (Johnson 2007), dynamic occupancy and abundance models show promise for estimating detailed demographics from occupancy or abundance data (Olatz et al. 2017), and studies on more detailed demographics using abundance models (e.g., McClure et al. 2013) would provide additional insight into habitat quality for coniferassociated species.

CHAPTER 3

A MULTI-SPECIES MODEL REVEALS EDGE EFFECTS FROM LOGGING ROADS ON BIRD ABUNDANCES AND RICHNESS IN EXTENSIVELY FORESTED LANDSCAPES

3.1. Abstract

Several species within the spruce-fir avian assemblage are declining regionally and continentally. We examined how richness of avian assemblages, abundances of individual species, and vegetation differed among high-contrast edge, low-contrast edge, and stand interior to identify important habitat and potential stressors affecting the spruce-fir avian assemblage. We coupled passive multi-species avian point count surveys with vegetation plots to sample high-contrast edges created by logging roads, lowcontrast edges created by discontinuous stand management from harvest treatments, and stand interior >80 m from edge. We developed two non-mutually exclusive hypotheses based on previous studies. First, we predicted that high-contrast edges would contain less spruce-fir and coniferous tree composition, less species abundances and richness of conifer and spruce-fir associated birds, and greater species abundances and richness of deciduous birds (composition hypothesis) compared to stand interior, because light conditions influence the composition of vegetation at high-contrast edges and composition of vegetation influences species assemblages. Secondly, we predicted that early successional habitat that is associated with roads and managed roadside buffers adjacent to high-contrast edge would contain less basal area, midstory cover, and tree diameter at breast height and would result in increased species abundances and richness of early successional birds and decreased species abundances and richness of late

successional birds compared to stand interior (structure hypothesis). We developed a multi-species abundance model designed specifically for inference on avian point count surveys to compare the abundances of species and the richness of avian assemblages among these three habitat conditions while controlling for management history and intrinsic stand characteristics. The composition hypothesis was well supported, with high contrast edges having decreased spruce-fir and coniferous tree composition and decreased avian species abundances and richness of conifer-associated and spruce-fir assemblages compared to forest interior. The structure hypothesis was also well supported with decreased basal area and midstory cover, increased richness of early successional birds, and decreased richness of late successional deciduous bird species and late successional coniferous bird species at high-contrast edge compared to stand interior. Our results demonstrate that stand interior supports greater abundances and richness of spruce-fir and late successional avian assemblages compared to high-contrast edge. Low-contrast edges mostly mimicked stand interior or were intermediate in species abundances, richness, and vegetation compared to high-contrast edges and stand interior. Observed differences appear to be driven by shifts in both tree composition and structure at road edges. Our results suggest that unpaved logging roads and their managed buffers (approximately 5-30 m wide) create high-contrast edges that detrimentally influence richness and abundances of spruce-fir birds. These edge effects may compose between 8 and 24% of the landscape. The effects from roads could be reduced by limiting the extent and width of roads and their buffers that are cleared or treated with herbicide, because high-contrast road edges represent direct habitat loss from suppression of forested habitat.

3.2. Introduction

Loss and degradation of habitat, fragmentation, and prevalence of habitat edges are interdependent contributors (Desrochers et al. 2003, Fletcher Jr. et al. 2007) to the loss of global biodiversity (Ehrlich and Ehrlich 1981, Wilson 1988, Pereira et al. 2010, Pimm et al. 2014, Newbold et al. 2015). Edges represent an abrupt change in habitat (Murcia 1995) at the junction of two different landscape elements (e.g., plant community type, successional stage, or land use, Yahner 1988). Edges are important contributors to the loss and fragmentation of habitat and can be the primary driver of area effects on wildlife in fragmented landscapes (Banks-Leite et al. 2010), because edges represent discrete boundaries that restrict the area of habitat patches and determine patch geometry.

Edge effects are dependent on contrast (Schneider et al. 2012), where contrast refers to the degree of structural (Thomas et al. 1979) or compositional differences (Yahner 1988) along the boundary of two habitats. Effects from anthropogenicallyinduced edges on wildlife can occur at both high- and low-contrast edges and can compose a large proportion of landscapes affecting a diversity of taxa (reviewed by Rytwinski and Fahrig 2012). These edges influence microclimates and alter vegetation (Kremsater and Bunnell 1999) and abundance of wildlife (Rytwinski and Fahrig 2012) including birds (e.g., Watson et al. 2004), mammals (e.g., Fuller et al. 2007), amphibians (e.g., c), and invertebrates (e.g., Van Wilgenburg et al. 2001). Meta-analysis demonstrated that birds have decreased density (22–36%) near edges (within 2.6 km) created by roads and infrastructure (Benítez-López et al. 2010), because edges attract light demanding vegetation and may be avoided by some wildlife (Kroodsma 1984, Bolger et al. 1997, Vos and Chardon 1998, Ortega and Capen 1999).

Conservation practitioners can intervene using conservation planning and habitat management from numerous perspectives and ecosystem scales (e.g., focal species, assemblages, ecosystems, functional traits; Franklin 1993, Block et al. 1995). Therefore, researchers often seek to quantify responses by species to habitat or management at several scales of biodiversity (e.g., DeGraaf 1992). Species abundances and richness are directly related to each other, and abundance plays a pivotal role in determining the demographics and habitat quality of focal species (Germain et al. 2018). Hierarchical multi-species models foster a unified analysis to estimate abundance of species (Yamaura et al. 2011) and richness of assemblages (Iknayan et al. 2014) while accounting for uncertainty introduced by imperfect detection at multiple ecological scales.

The boreal and hemiboreal zones of North America provide important habitat for wildlife and compose over 34% of terrestrial land area of the United States and Canada (Brandt 2009). Birds compose a large percentage (>75%) of vertebrate taxa within boreal forest (Smith 1993, Mönkkönen and Viro 1997). Birds that are associated with the spruce-fir forest type in North America, hereafter referred to as spruce-fir birds (sensu Ralston et al. 2015, Rolek et al. 2018), are an assemblage that requires forested habitat. The spruce-fir avian assemblage inhabits the boreal and hemiboreal zones, and tends to reach maximum abundance in areas with a predominance of spruce and fir trees (Rolek et al. 2018). Several species within this assemblage have declining populations in the eastern United States (Ralston et al. 2015, Sauer et al. 2017) and regions of Canada (e.g., Atlantic Northern Forest, Environment and Climate Change Canada 2017, Sauer et al. 2017), warranting empirical investigations into factors that may influence abundances of these species and contribute to declining populations. Forested habitat in this region is extensively managed for resource extraction, and most of the land area (>70% in Maine, New Hampshire, and Vermont) of the Atlantic Northern Forest within the United States (Fig. 3.1.) is considered timberlands (McCaskill et al. 2011, Morin et al. 2012).

Figure 3.1 Maps of study sites and sampling design to test for associations between avian abundance, richness, and edge contrast levels in the Atlantic Northern Forest during the breeding and post-breeding periods in 2013–2015. Study sites included Nulhegan Silvio O. Conte Division National Wildlife Refuge (NWR), Umbagog NWR, Aroostook NWR, Moosehorn NWR, Baxter State Park, and privately owned Telos and Clayton Lake. Telos and Baxter State Park are combined on the map because of close spatial proximity.



Management that is prescribed for the extraction of forest resources directly alters wildlife habitat (Schmiegelow and Mönkkönen 2002, Wood et al. 2006) and creates both high- and low-contrast edges, especially when adjacent stands are harvested using different techniques or are harvested at different times and succession proceeds so that boundaries transition to low-contrast edges over time. Furthermore, these managed forests often require unpaved roads to transport resources from extraction sites for processing and market consumption, and these roads create high-contrast edges. Unpaved logging roads and their adjacently managed buffer zones (hereafter collectively referred to as road edges) compose a large proportion of the landscape in some regions (previously estimated as approximately 11% of the landscape at one of our study sites, Fuller et al. 2007). Buffers are managed by mowing and applying herbicide to prevent encroachment of vegetation on roads, thereby maintaining early successional vegetation adjacent to roads. Managers may apply herbicide, typically glyphosate, with sufficient quantities so that both deciduous and coniferous trees and saplings are eradicated. These road edges have been characterized as having less basal area and density of coniferous saplings relative to other stand types, and had the greatest density of deciduous saplings (Fuller et al. 2007). Forest edges permit increased light penetration (deMaynadier and Hunter 1998, Kremsater and Bunnell 1999, Harper and Macdonald 2001), and facilitate increased composition of shade-intolerant deciduous tree species (reviewed by Kremsater and Bunnell 1999, Fuller et al. 2007). However, the effects from road edges on wildlife are poorly understood in the Atlantic Northern Forest, especially for declining spruce-fir birds. Balsam fir, Abies balsamea, and red spruce, Picea rubens, rank among the most shade tolerant conifer tree species in the temperate northern hemisphere (Forbes and

Meyer 1955, Hart 1959, Niinemets and Valladares 2006, Kuehne et al. 2016), and these tree species provide important habitat for spruce-fir birds (Rolek et al. 2018).

We examined how anthropogenically-created edges influence abundance and richness of an avian community composed of song birds (Passeriformes) and woodpeckers (Piciformes), with an emphasis on spruce-fir avian assemblage and two ubiquitous sources of contrast in managed forests: 1) road edges (high-contrast edge) and 2) harvest-induced (5 to >113 years-since-harvest) edges at transitions between forested stands that were managed using different harvest treatments or were harvested at different times (low-contrast edge). We compare these contrast levels to stand interior >80 m from edge (no contrast).

We predict that birds associated with coniferous and spruce-fir forest will have reduced species abundances and richness at high-contrast edges compared to stand interior, while birds associated with deciduous and mixed-wood forest will have greater species abundances and richness at high-contrast edges (hereafter the composition hypothesis), and that these associations will be reflected in vegetation characteristics with reduced coniferous and spruce-fir tree composition. Secondly, high-contrast edges create breaks in the canopy that transition from early succession or disturbed habitat to later succession (Benítez-López et al. 2010); therefore, we hypothesize that early successional birds will have greater species abundances and richness at high-contrast edges (hereafter the structure hypothesis) and that these associations will be reflected in vegetation characteristics with reduced basal area, midstory cover, and tree diameter at breast height at high-contrast edges. We predict that for both hypotheses, low-contrast

edges will have avian species abundances and richness that are intermediate between high-contrast edge and stand interior, because vegetation structure and composition are intermediate by definition, and reduced light penetration compared to high-contrast edges will enable more shade tolerant species including conifer trees such as red spruce and balsam fir to outcompete shade intolerant deciduous species (Forbes and Meyer 1955, Hart 1959, Niinemets and Valladares 2006).

To address our hypotheses: (1) we used standardized avian point counts to survey road edges (representing high-contrast edge), stand transitions created by harvest treatments (representing low-contrast edge), and areas isolated from edges (stand interior >80 m from roads and harvest edges) while controlling for differences in harvest treatment and individual stands; (2) we developed a novel multi-species abundance model to estimate avian abundances and account for imperfect detection of birds with point count survey data; (3) we compare abundances of individual species and assemblages using species richness at high-contrast edges, low-contrast edges, and stand interior; and (4) we compare vegetation characteristics among contrast levels to provide a mechanism for observed differences in avian abundances and richness.

Advances in statistical modeling using multi-species occupancy and abundance data have fundamentally changed the capability of researchers to study associations between habitat and wildlife (reviewed by Iknayan et al. 2014), because researchers can simultaneously assess responses to habitat by individual species, assemblages, and entire communities. Multi-species models provide numerous additional benefits over singlespecies models (Zipkin et al. 2009, 2010, Iknayan et al. 2014), because they can simultaneously estimate abundance, occupancy , or demographic rates for single species

and groups of species, enabling a detailed assessment of tradeoffs between species and assemblages in a unified framework. Furthermore, multi-species models allow species to share information about state variables (e.g., abundance) or observation processes (e.g., detection probability) via partial-pooling of parameter estimates, thereby increasing the precision of estimates (Gelman and Hill 2007) especially for species with smaller sample sizes (Zipkin et al. 2010, Linden et al. 2012, Iknayan et al. 2014, Sollmann et al. 2015, Yamaura and Royle 2017). Improved estimates of state variables for multiple species can inform management and infrastructure planning for wildlife that may be sensitive to the alteration of habitat. The effects from habitat loss at multiple scales of biodiversity (e.g., species, assemblages, and meta-communities) may provide insights that are difficult to estimate using single-species approaches.

3.3. Methods

3.3.1. Avian Point Count and Vegetation Surveys

We conducted our study in the Atlantic Northern Forest (Bird Conservation Region 14) within the northeastern United States. Bird Conservation Regions were delineated to contain similar bird communities, habitats, and resource management issues (fully described at http://nabci-us.org/resources/bird-conservation-regions/). The Atlantic Northern Forest roughly corresponds to the hemiboreal subzone (Brandt 2009) within the northeastern United States and Acadian forest where temperate deciduous forest in the south transitions to eastern boreal forest in the Canadian north (Seymour and Hunter 1992). Our study sites were comprised of both privately (North Maine Woods) and publicly-owned lands including a state park (Baxter) and four U.S. Fish and Wildlife Service National Wildlife Refuges (Nulhegan Division of Silvio O. Conte, Umbagog, Aroostook, and Moosehorn, Fig. 3.1). All study sites were actively or formerly managed for forest resource extraction and were located within lowland conifer forests <500 m in elevation, excluding high elevation spruce-fir habitat. Because these focal species included the spruce-fir avian assemblage (Table 3.1); therefore, we surveyed mixed-wood or conifer forest stands that were comprised of approximately \geq 50% spruce or fir trees (Rolek et al. 2018). Table 3.1 Bird species detected during point count surveys (476 locations) at seven sites in the Atlantic Northern Forest to test for associations of abundance and richness between contrast levels (stand interior, high-contrast edge, and low-contrast edge). Abbreviations for each species (Abbrev.), common name, Latin name, number of detections, and species assemblages are shown. Missing values in species assemblage indicate that a species was uncategorized.

				Species assemblage		
Abbrev.	Common name	Genus species	Detections	Succession	Composition	Spruce-fir
ALFL	Alder Flycatcher	Empidonax alnorum	63	early	deciduous	
AMGO	American Goldfinch	Spinus tristis	15	early	deciduous	
AMRE	American Redstart	Setophaga ruticilla	299		deciduous	
AMRO	American Robin	Turdus migratorius	407	early	deciduous	
BAWW	Black-and-white Warbler	Mniotilta varia	363	late		
BBWA	Bay-breasted Warbler	Setophaga castanea	282	late	coniferous	obligate
BBWO	Black-backed Woodpecker	Picoides arcticus	62		coniferous	
BCCH	Black-capped Chickadee	Parus atricapillus	870		deciduous	
BHVI	Blue-headed Vireo	Vireo solitaries	409			
BLBW	Blackburnian Warbler	Setophaga fusca	433	late		
BLJA	Blue Jay	Cyanocitta cristata	312			
BLPW	Blackpoll Warbler	Setophaga striata	131		coniferous	obligate
BOCH	Boreal Chickadee	Poecile hudsonicus	508		coniferous	obligate

Table 3.1 Continued.

BRCR	Brown Creeper	Certhia americana	169	late		
BTBW	Black-throated Blue Warbler	Setophaga caerulescens	476	late	deciduous	
BTNW	Black-throated Green Warbler	Setophaga virens	857		coniferous	
CAWA	Canada Warbler	Cardellina canadensis	598			
CEDW	Cedar Waxwing	Bombycilla cedrorum	299	early		
CHSP	Chipping Sparrow	Spizella passerine	42	early	coniferous	
CMWA	Cape May Warbler	Setophaga tigrina	22		coniferous	obligate
COGR	Common Grackle	Quiscalus quiscula	10	early		
COYE	Common Yellowthroat	Geothlypis trichas	613	early		
CSWA	Chestnut-sided Warbler	Setophaga pensylvanica	106	early	deciduous	
DOWO	Downy Woodpecker	Picoides pubescens	52	early	deciduous	
EAPH	Eastern Phoebe	Sayornis phoebe	10	early		
EAWP	Eastern Wood-Pewee	Contopus virens	45		deciduous	
FOSP	Fox Sparrow	Passerella iliaca	76	early	coniferous	
GCFL	Great Crested Flycatcher	Myiarchus crinitus	6		deciduous	
GCKI	Golden-crowned Kinglet	Regulus satrapa	1664	late	coniferous	associate
GRAJ	Gray Jay	Perisoreus canadensis	120		coniferous	obligate
GRCA	Gray Catbird	Dumetella carolinensis	17	early	deciduous	

Table 3.1 Continued.

HAWO	Hairy Woodpecker	Picoides villosus	99			
HETH	Hermit Thrush	Catharus guttatus	1146			
LEFL	Least Flycatcher	Empidonax minimus	172	late	deciduous	
LISP	Lincoln's Sparrow	Melospiza lincolnii	2			
MAWA	Magnolia Warbler	Setophaga magnolia	2602	early	coniferous	obligate
MOWA	Mourning Warbler	Geothlypis philadelphia	8	early		
MYWA	Yellow-rumped Warbler	Setophaga coronata	997	late	coniferous	
NAWA	Nashville Warbler	Oreothlypis ruficapilla	1317			
NOCA	Northern Cardinal	Cardinalis cardinalis	1	early		
NOPA	Northern Parula	Setophaga americana	685	late		
NOWA	Northern Waterthrush	Parkesia noveboracensis	240			
OSFL	Olive-sided Flycatcher	Contopus cooperi	37		coniferous	associate
OVEN	Ovenbird	Seiurus aurocapilla	881	late		
PIWA	Pine Warbler	Setophaga pinus	169		coniferous	
PIWO	Pileated Woodpecker	Dryocopus pileatus	41	late		
PUFI	Purple Finch	Haemorhous purpureus	170		coniferous	
RBGR	Rose-breasted Grosbeak	Pheucticus ludovicianus	31		deciduous	
RBNU	Red-breasted Nuthatch	Sitta canadensis	772	late	coniferous	associate
RCKI	Ruby-crowned Kinglet	Regulus calendula	287		coniferous	associate
RECR	Red Crossbill	Loxia curvirostra	7	late	coniferous	

Table 3.1 Continued.

REVI	Red-eyed Vireo	Vireo olivaceus	924		deciduous	
RUBL	Rusty Blackbird	Euphagus carolinus	5		coniferous	
RWBL	Red-winged Blackbird	Agelaius phoeniceus	6	early		
SAVS	Savannah Sparrow	Passerculus sandwichensis	15	early		
SCJU	Dark-eyed Junco	Junco hyemalis	375		coniferous	
SCTA	Scarlet Tanager	Piranga olivacea	4	late	deciduous	
SOSP	Song Sparrow	Melospiza melodia	26	early		
SWSP	Swamp Sparrow	Melospiza georgiana	27	early		
SWTH	Swainson's Thrush	Catharus ustulatus	1497		coniferous	associate
TEWA	Tenessee Warbler	Oreothlypis peregrina	12			
VEER	Veery	Catharus fuscescens	70		deciduous	
WBNU	White-breasted Nuthatch	Sitta carolinensis	10	late	deciduous	
WIWA	Wilson's Warbler	Cardellina pusilla	37	early		
WIWR	Winter Wren	Troglodytes hiemalis	865	late	coniferous	
WTSP	White-throated Sparrow	Zonotrichia albicollis	1300			
WWCR	White-winged Crossbill	Loxia leucoptera	9		coniferous	obligate
YBFL	Yellow-bellied Flycatcher	Empidonax flaviventris	769		coniferous	associate
YBSA	Yellow-bellied Sapsucker	Sphyrapicus varius	182			
YEWA	Yellow Warbler	Setophaga petechia	6	early	deciduous	
YPWA	Palm Warbler	Setophaga palmarum	184		coniferous	associate
YSFL	Northern Flicker	Colaptes auratus	135			

We conducted passive multi-species avian point count surveys (Ralph et al. 1995) separated by >100 m (DeGraaf et al. 1998) during territory establishment, breeding, and post-fledgling periods for most passerines in this region (1 June through 4 August, 2013– 2015, Rodewald, 2017). We recorded time interval to detection (1-2, 2-4, 4-6, 6-8, 8-10 min) and we estimated distance to initial detection (0-25, 25-50, and >50 m) for each individual bird detected during a point count survey. We trained technicians to visually estimate distance to avian detections, and technicians recalibrated their distance estimates each day of surveys by flagging 25 m from the center of a point count location during a single point count survey. We alternated observers between each point count survey to avoid bias introduced by observers. Additionally, we changed the starting point count location within each stand between visits to account for effects from time after sunrise on detection probability and to vary the time after sunrise when each survey was conducted. We accounted for effects from date of survey on detection probability by surveying stands intermittently throughout the breeding and post-breeding season. For example, we attempted to survey all stands during the first rotation of point count surveys before moving on to a second round of surveys. This sampling scheme distributed the temporal spacing of point count surveys across the breeding and post-breeding periods. We retained detections within 50 m of the point count center for perching song birds (i.e., order Passeriformes) and woodpeckers (i.e., order Piciformes, Chesser et al. 2018). We excluded flyovers, species with large territories, and other species that are inadequately surveyed using the point count survey method (i.e., corvids and raptors, Scott and Ramsey 1981).

We conducted detailed vegetation surveys in 2014 because annual vegetation structure and composition are relatively stable in this region across three years (Scott 2009). We measured vegetation at one to four plots at each point count location. Point count locations had one vegetation plot at the center with subsequent plots randomly placed at 0°, 90°, 180°, or 270° from magnetic North and 30 m from the point count center. We measured three or four vegetation plots at a subset of point count locations to assess representation by the number of vegetation plots at each point count location and logistical feasibility. We concluded that two vegetation plots per point count location, one plot at the point count center and one plot in a random direction, adequately represented the vegetation at each point count location and was logistically feasible. However, we retained additional vegetation plots in analyses to contribute to vegetation estimates. We measured a total of 969 vegetation plots at 476 point count locations, two vegetation plots at 443 point count locations, three vegetation plots at 10 point count locations, and four vegetation plots at 10 point count locations. We measured 13 point count locations with a single vegetation plot, because managers harvested these stands prior to the completion of vegetation measurements. We calculated vegetation characteristics for each point count location including: basal area of trees ≥ 10 cm diameter, diameter at breast height (1.37 m height) for trees ≥ 10 cm diameter, proportion of spruce-fir trees for trees ≥ 10 cm diameter, proportion of conifer trees for trees ≥ 10 cm diameter, midstory cover (2 to <7.6 m height measured using plexiglass grid), and shrub cover (proportion of leaf cover 0.5 to <2 m, visual estimate). Avian point counts and vegetation surveys are described in detail elsewhere (Rolek et al. 2018).

We placed point count locations >100 m apart within each stand, and surveyed three contrast classifications (hereafter contrast level): stand interior, high-contrast edge and low-contrast edge (Fig. 3.1.). We placed point count locations so that each contrast level was represented by ≥ 1 location within each stand; therefore, each stand had a minimum of three point count locations, (range 3–17, mean=6). We placed point count locations representing stand interior (no contrast) >130 m from edges to avoid edge effects on vegetation (deMaynadier and Hunter 1998, Kremsater and Bunnell 1999, Fuller et al. 2007), leaving an 80 m buffer to edges beyond the 50 m radius of point count surveys. We placed point count locations representing high-contrast edge at abrupt transitions from forest to non-forest at persistent edges on unpaved logging roads because this edge type is ubiquitous within forested landscapes examined here. High-contrast road edges had 5–30 m wide management buffers located perpendicularly and adjacent to both sides of the road surface and buffers were maintained using herbicide (e.g., glyphosate), brush cutting, and removal of large trees to reduce obstruction from tree blowdown and encroachment of vegetation adjacent to the road surface. We identified high-contrast edges using digital ortho quarter quads (DOQQs) from the National Agriculture Imagery Program (NAIP, accessed from https://earthexplorer.usgs.gov/) from 2012 and 2013 with 1 m resolution in a geographic information system (ArcMap 10.6.1) to visually locate breaks in canopy cover that were contiguous with managed stands. We considered lowcontrast edges as the junction between two forested and managed stands. We selected stands where the previous harvest treatment was known and these stands were adjacent to stands where the previous harvest treatment was unknown. We identified point count locations to survey low-contrast edge at the periphery of stands where differences in

vegetation density, succession, timing of harvest, composition, or canopy cover were visible using DOQQs and shapefiles of management history where available. We confirmed that locations of point counts represented the assigned contrast level of high-contrast or low-contrast edge during site visits. Occasionally point count locations did not represent the contrast levels described above, and we repositioned surveys (<50 m) to locations that better represented the assigned contrast level.

Point count locations for high- and low-contrast edges were positioned with approximately half of the survey area within known harvest treatments, and stand interior was positioned entirely within known harvest treatments (Fig. 3.1). We included a nested random effect in abundance and vegetation models for stand identity and harvest treatment at each point count location (see details in Statistical Analysis section). The random effect for stand identity implicitly corrected for differences in vegetation, yearssince-harvest, spatial location or orientation, pseudoreplication within a stand, and effectively created paired comparisons among contrast levels within a stand. We assigned one of seven categories of harvest treatment to each stand including mature ≥ 48 yearssince-harvest (YSH, unknown previous harvest treatment), selection $11 \le YSH \le 41$, shelterwood $5 \le YSH \le 31$, clearcut-only $11 \le YSH \le 36$, clearcut with herbicide 21 ≤ YSH ≤ 40, clearcut with precommercial thinning 11 ≤ YSH ≤ 38, clearcut with herbicide and precommercial thinning $16 \le YSH \le 39$. Additional details describing harvest treatments and avian community responses to those treatments are described in Rolek et al. (2018).

3.3.2. Avian Assemblages

We assigned bird species to habitat assemblages representing two successional categories (early or late, including many bird species that remained uncategorized) and five forest composition categories (deciduous, coniferous, spruce-fir obligates, spruce-fir associates, spruce-fir birds combined, also including many uncategorized bird species). We extracted classifications for habitat assemblages from the Birds of North America (Rodewald 2017) section titled "Habitat in the Breeding Range", Ralston et al. (2015), and authoritative sources within (e.g., DeGraaf and Yamasaki, 2001; Glennon, 2014; King et al., 2008; Ralston et al., 2015; Robbins, 1991). We assigned species to habitat assemblages where they had peak abundance in previous studies. For a detailed description of criteria used to categorized spruce-fir assemblages see Rolek et al. (2018) and Ralston et al. (2015).

3.3.3. Statistical Analysis

We developed a multi-species distance-removal model designed for inference using multi-species point count surveys of birds. We used a hybrid distance-removal model, because the model fostered multi-species inference; accounted for bias for imperfect detection; and accounted for detection probability using an approach that is biologically and behaviorally relevant to our study species and descriptive of the avian point count methodology (Farnsworth et al. 2005, Amundson et al. 2014). The singlespecies version of this model is described in detail elsewhere (Amundson et al. 2014, Kéry and Royle 2015), and we describe the multi-species model in detail below. The hybrid model approximates instantaneous density (Farnsworth et al. 2005) and second

(i.e., home range) or third order (i.e., within home range) habitat selection (sensu Johnson 1980).

We used distance sampling, a method where surveyors estimate initial detection distance to each individual from a surveyed point or transect, to estimate abundance while correcting for detection probability (Buckland 2001, Royle 2004, Conn et al. 2012). Here the detection parameter refers to perceptibility, the probability that an individual is perceived during a survey (Farnsworth et al. 2005, Nichols et al. 2009, Amundson et al. 2014). Hereafter, we use letter superscripts to apply labels to variables for identification purposes unless otherwise noted. The cell probabilities for perceptibility (π^p) can be expressed as a categorical distribution for observed distance class data (dclass_l for l in 1 ... L observations) in each distance class (b), site (i) and species (s) as $dclass_l \sim Categorical(\pi_{isb}^{Cp})$ and $\pi_{ish}^{Cp} = \frac{\pi_{isb}^p}{p_{ic}^p}$. We assume that perceptibility monotonically decreases by some function of distance, and use the half-normal distance function $g(r)_{isb} = \exp(-\frac{r_b^2}{2\sigma_{ic}^2})$, where r is the midpoint of the category for radius to detection (e.g., category 0–25 m has a midpoint of 12.5 m), and σ is the scale parameter that governs the distance function. We included the radial distance function to account for increasing area of survey at further distances from the center of the point count as $f(r)_b = 2r_b\delta/B^2$, where δ is the width of each distance band and B is the maximum distance to detections (50 m here). We specified σ so that it varies with site-specific covariates $\log(\sigma_{is}) = \log(\gamma_{0s}) + \gamma_{1s}x_i$. We modeled perceptibility as a function of basal area, because dense vegetation can attenuate bird vocalizations (Yip et al. 2017) and could potentially confound abundance estimates.

We used the time-removal method to estimate the probability that a species was available for detection, hereafter availability (Farnsworth et al. 2005, Nichols et al. 2009, Amundson et al. 2014). Availability has been described as equivalent to singing rates of birds (Farnsworth et al. 2005, Sólymos et al. 2013) because they are primarily detected aurally while singing (82% singing of detections here, 14% calling, 4% visual), but we note that a modest percentage were detected while vocalizing. Removal sampling (referred to elsewhere as time-to-detection, time depletion, or time-removal) is a method where only the initial detection of an individual is recorded, and time interval of each initial detection is recorded (here 0-2, 2-4, ...8–10 min, interval). This method is descriptive of the point count process, because surveyors mentally remove each individual after detection (Farnsworth et al. 2005). We constructed a removal model where *interval*₁~*Categorical*(π_s^{Ca}) (Farnsworth et al. 2002, Amundson et al. 2014).

The conditional cell probabilities for availability are described as $\pi_{sj}^{Ca} = \frac{\pi_{sj}^a}{p_s^a}$, for time interval (*j*) and the time interval specific probability of availability by an individual is calculated by $\pi_s^a = p_s^a (1 - p_s^a)^{j-1}$ where p_s^a is availability of each species during a single time interval and j - 1 indicates exponentiation. We summed the probability of availability specific to each time interval π_{js}^a , across time intervals j = 1, ..., J as $p_s^a = \sum_{j=1}^J \pi_{js}^a$ to obtain probability of availability p_s^a .

3.3.4. Abundance of Avian Species

We estimate abundance as a latent variable with the combined detection probabilities, $p_{its} = p_{its}^a * p_{its}^p$ from both perceptibility and availability in a N-mixture model to estimate abundance (N) from counts (n) as $n_{its}|N_{its} \sim Binomial(N_{its}, p_{its})$ (Kéry and Royle 2015). Abundance is modeled by some distribution function $N_{its} \sim h(x)$ and we considered Poisson, negative binomial, Poisson log-normal, or zero-inflated Poisson distribution. We avoided use of the negative binomial distribution because of previously described identifiability problems when used with N-mixture models (Kéry 2018), and we did not use the Poisson log-normal distribution because we had difficulty fitting this distribution. We used a zero-inflated Poisson distribution (Lambert 1992) here, because we observed a number of species with large frequencies of zero detections, and negative binomial distributions were found to have identifiability problems when used with N-mixture models (Kéry 2018). We fit abundance as a zero-inflated Poisson distribution as $N_{its} \sim Poisson(\lambda_{its}\omega_s)$ and $\omega_s \sim Bernoulli(\psi)$.

Abundance was a linear function of covariates and we tested for edge effects as $log(\lambda_{its}) = \beta_{es} + \varepsilon_{1ks} + \varepsilon_{2ms} + \varepsilon_{3ts}$ where the intercept β was indexed by contrast level e (indicating high-contrast, low-contrast, or stand interior) and species, and $\varepsilon_{2:3}$ are random effects for study site (*m*) and visit (*t*), respectively, with a mean of zero $\varepsilon_{2ms} \sim Normal(0, \sigma^{\varepsilon_2})$ and $\varepsilon_{3ts} \sim Normal(0, \sigma^{\varepsilon_3})$, and ε_1 is a nested random effect for management indexed by stand identity (*k*) and harvest treatments (*n*) $\varepsilon_{1ks} \sim Normal(\varepsilon_{4ns}, \sigma^{\varepsilon_1})$, and $\varepsilon_{4ns} \sim Normal(0, \sigma^{\varepsilon_4})$. Note that the nested random effect including stand identity and harvest treatment enables direct comparisons among contrast levels by accounting for variation within stands and harvest treatments, thereby controlling for implicit stand characteristics. We did not include covariates for the zeroinflation parameter (ω_s).

Sharing a common distribution among parameters is more computationally efficient and allows species to share information using partial pooling (Gelman and Hill 2007, Iknayan et al. 2014). We assume that availability, perceptibility, and abundance are normally distributed among species $logit(p_s^a) \sim Normal(\mu^{pa}, \sigma^{pa})$,

 $\gamma_{0s} \sim Normal(\mu^{\gamma_0}, \sigma^{\gamma_0}), \beta_{es} \sim Normal(\mu_e^{\beta}, \sigma_e^{\beta}), \text{ and the coefficient for perceptibility is a function of basal area and we assumed a normal distribution among species <math>\gamma_{1s} \sim Normal(\mu^{\gamma_1}, \sigma^{\gamma_1}).$

3.3.5. Richness of Avian Assemblages

We evaluated how edges influenced avian assemblages by calculating detection corrected species richness for each of seven avian assemblages across three years of surveys. We calculated species richness for avian assemblages as a derived parameter by converting detection corrected abundance (while accounting for the effects from harvest treatments, stands, visits, and study sites as a random effects) to occupancy when abundance was ≥1, then calculating the maximum species occupancy at each point count location across three years of surveys (nine surveys total for most point count locations). Next, we summed occupancy across species within each habitat assemblage and calculated mean richness across point count locations at each of the three contrast levels. Some studies have used data augmentation to account for species that were not detected during surveys when estimating richness. Similar to other studies (e.g., Linden et al. 2012, Kroll et al. 2017), we did not use data augmentation to estimate species richness, and instead conditioned our model on the set of species that were observed during our study.

3.3.6. Vegetation

We examined potential mechanisms for variation in abundance and richness of birds by modeling the effects of contrast level on vegetation characteristics using hierarchical models. We tested whether contrast levels differed by selected vegetation

covariates that were previously described as important to avian assemblages considered here (Rolek et al. 2018). We included average basal area of trees (≥ 10 cm dbh), tree diameter at breast height (≥ 10 cm dbh), spruce-fir tree composition (≥ 10 cm dbh), conifer tree composition (≥ 10 cm dbh), midstory cover (2 to <7.6 m), and shrub cover (0.5 to <2 m). We modeled each vegetation variable as $y_i \sim Normal(\mu_e^y + \varepsilon_{5k}, \sigma^{y_2})$ including a nested random effect for stand identity (ε_{5k}) where $\varepsilon_{5k} \sim Normal(\varepsilon_{6n}, \sigma^{\varepsilon_5})$ and harvest treatment $\varepsilon_{6n} \sim Normal(0, \sigma^{\varepsilon_6})$. The overall mean for each vegetation variable (μ_e^y) varied by contrast level (e). We used an arcsine transformation on vegetation variables that were calculated as proportions for analysis.

We used JAGS 4.2.0 (Plummer 2003) from R version 3.3.1 (R Core Team 2015) and the package jagsUI 1.4.9 (see Appendix K for JAGS code, Kellner 2016). We centered and scaled continuous covariates for detection so that each covariate had a mean=0 and SD=1 to aid in interpretation and convergence (Schielzeth 2010). We implemented models with 40,000 iterations for adaptation, 150,000 iterations for burn-in, and 150,000 iterations for the posterior distribution that were thinned one of every 150 iterations. We used three chains to estimate posterior distributions. We evaluated convergence with Gelman-Rubin statistic (Gelman and Rubin 1992) and considered adequate convergence for parameters with $1 \ge \hat{R} \le 1.1$ and by visually assessing traceplots. We used 85% HDIs to determine significance, because our model propagates detection error into abundance estimates to realistically account for uncertainty and we were concerned that the propagation of error would result in poor statistical power and a greater number of Type II errors, i.e., not rejecting the null hypothesis when a relationship is significant. We present parameters as median point estimates and 85%

highest posterior density intervals (hereafter HDIs, Chen and Shao 1999, Krushke 2011) and considered contrast levels significantly different when 85% HDIs did not overlap (Arnold 2010). We used Bayesian *P* values generated from posterior predictive distributions to assess model fit where values near 0.5 indicate good model fit (Kéry 2010) and values >0.90 and <0.10 indicate poor model fit (Sollmann et al. 2016).

3.4. Results

We surveyed birds at 476 point count locations in 79 stands (Table 3.2) with 4,102 point count surveys and 969 vegetation plots. We totaled 25,458 avian detections of 72 species that were retained for analysis.

Table 3.2 The number of avian multi-species point count locations in each contrast level (stand interior >80 m from edge, high-contrast road edge, low-contrast harvest edge) and harvest treatment. Most stands contained \geq 1 high-contrast, low-contrast, and stand interior point count locations.

	Numbe			
	in eac			
Harvest treatment	High- Low- Stand		Number	
	contrast	contrast	interior	of stands
Mature	21	20	75	18
Selection	19	21	65	18
Shelterwood	5	5	16	5
Clearcut-only	10	9	44	9
Clearcut-herbicide	16	16	61	16
Clearcut-precommercially thinned	9	10	29	8
Clearcut-herbicide-	5	5	15	5
precommercially thinned				

3.4.1. Model Assessment

Traceplots of posterior MCMC samples indicated adequate convergence of parameters and hyperparameters, and $1.0 \ge \hat{R} \le 1.1$ for all parameters. The mean Bayesian *P* value for our model was 1.0 indicating a lack of fit overall. Estimates of community hyperparameters are presented as backtransformed medians.

Hyperparameters are estimates among all species for availability, perceptibility, and abundance, and we report them here because these parameters govern detection and abundance estimates for all species. Availability among species was low during a two minute interval $(logit^{-1}(\mu^{pa}) = 0.11, logit^{-1}(\sigma^{pa}) = 0.91$, Fig. L.1) and perceptibility was also low $(\mu^{\gamma_0} = 24.8, \sigma^{\gamma_0} = 5.7, \text{Fig. L.1})$. Average avian abundance among all species did not differ significantly among contrast levels (stand interior $\exp(\mu_1^{\beta}) = 0.11, \exp(\sigma_1^{\beta}) = 1.4$; high-contrast edge $\exp(\mu_2^{\beta}) = 0.12, \exp(\sigma_2^{\beta}) = 2.0$; and low-contrast edge $\exp(\mu_3^{\beta}) = 0.12, \exp(\sigma_3^{\beta}) = 1.4$).

3.4.2. Abundance of Avian Species

The composition hypothesis that predicted high-contrast edge compared to stand interior would have less abundances of conifer and spruce-fir birds and greater abundances of deciduous birds was well supported. Six species (Bay-breasted Warbler, Palm Warbler, Blackpoll Warbler, Ruby-crowned Kinglet, Yellow-bellied Flycatcher, Boreal Chickadee) classified as both conifer associated species (25 total) and spruce-fir species (14 total) had significantly greater abundance at stand interior compared to highcontrast edge (Fig. 3.2). Twenty-one of 25 conifer associated species and all of 14 spruce-fir species had greater abundance, although nonsignificant, at stand interior than those at high-contrast edges (Fig. 3.2). Although abundances of many conifer and sprucefir species were not significantly different among contrast levels, richness of these habitat assemblages were significantly different when comparing richness among contrast levels (see below). Two deciduous species, American Robin and Chestnut-sided Warbler, had greater abundance at high-contrast edges compared to stand interior. Figure 3.2 Abundance estimates (y-axis) for each species (x-axis) and edge contrast level (point shape) from multi-species distance removal model with a zero-inflated distribution. Points depict median abundance within 50 m of point count locations, thick vertical lines depict 50% highest density intervals, and thin vertical lines depict 85% highest density intervals. Species abbreviations are in Table 3.1. The y-axis is plotted on the log scale for clarity. Species are sorted by compositional habitat assemblages and then by successional habitat assemblages as coniferous associated, deciduous associated, spruce-fir associates, spruce-fir obligates, early and late succession.



The structure hypothesis that predicted greater abundances of early successional species and lesser abundances of late successional species at high-contrast edges compared to stand interior had some support. Three early successional species, Common Yellowthroat, Savannah Sparrow, and Song Sparrow, had significantly greater abundances at high-contrast edges compared to stand interior. Median abundances for 16 of 21 early succession species were nonsignificantly greater at high contrast edge compared to stand interior, and although these differences were not significant, the early succession assemblage had significantly greater richness at high-contrast edge compared to stand interior and low-contrast edge (see richness results below). Only one species (Bay-breasted Warbler) of six late successional conifer associated species had significantly less abundance at high-contrast edges compared to stand interior. Late successional deciduous bird species and late successional birds having uncategorized associations with stand composition did not differ in abundances at high contrast edges compared to stand interior.

Species abundances at low-contrast edges tended to be similar to those in stand interior (Fig. 3.2.). However, five species had significant differences in abundance between low- and high- contrast edges: Canada Warbler and Palm Warbler had greater abundance at low-contrast edges compared to high-contrast edges, and Common Yellowthroat, Song Sparrow, and American Robin had less abundance at low-contrast edges compared to high-contrast edges.

3.4.3. Richness of Avian Assemblages

The composition hypothesis predicted decreased richness of coniferous and spruce-fir assemblages and greater richness of deciduous forest assemblage at high-contrast edge compared to stand interior and assemblage-level results were largely supportive of this hypothesis (Fig. 3.3). Spruce-fir obligates, spruce-fir associates, spruce-fir obligates and associates combined, and the coniferous associated assemblage had less richness at high-contrast edge compared to stand interior. Richness of the deciduous associated assemblage was not greater at high-contrast edge compared to stand interior; however, nonsignificant trends in median estimates were consistent with predictions. Both early and late successional spruce-fir assemblages had less richness at high-contrast edge compared to stand interior. Late successional deciduous assemblage also had less richness at high-contrast edge compared to stand interior.

Figure 3.3 Richness estimates (y-axis) for species assemblages (x-axis) from multispecies distance-removal abundance model with a zero-inflated distribution testing for differences among contrast levels. Points depict median abundance, thick vertical lines depict 50% highest posterior density intervals, and thin lines depict 85% highest posterior density intervals.



The structure hypothesis predicted that early successional assemblages would have greater richness and late successional species would have reduced richness at highcontrast edges compared to stand interior and received moderate support. Richness of the early successional assemblage was greater at high-contrast edges compared to stand interior. The late successional deciduous and late successional spruce-fir assemblages both had less richness at high-contrast edge compared to stand interior (Fig. 3.3). Other species assemblages that did not differ in richness among contrast levels included: all species combined, deciduous associated, late successional, early deciduous, early coniferous, and late coniferous. Richness for most species assemblages at low-contrast edge was intermediate between stand interior and high-contrast edge (Fig. 3.3).

3.4.4. Vegetation

The composition hypothesis predicted reduced conifer and spruce-fir tree composition at high contrast edges compared to stand interior, and high contrast edge had reduced spruce-fir and coniferous tree composition compared to stand interior (Fig. 3.4). The succession hypothesis predicted greater early successional vegetation characteristics at high-contrast edges compared to stand interior, and high contrast edge had reduced basal area compared to stand interior; however, diameter of trees at breast height did not differ among contrast levels. High-contrast edge had reduced midstory cover compared to stand interior and low-contrast edge. Shrub cover did not differ significantly among contrast level.
Figure 3.4 Hierarchical regression estimates of vegetation variables (y-axis) and edge contrast level as explanatory variables (x-axis), with stand and harvest treatment included as nested random effects. Vegetation variables include basal area for trees >10 cm diameter at breast height (BA), diameter-at-breast-height for trees >10 cm (DBH), spruce-fir tree composition for trees >10 cm (SPFIR), conifer tree composition for trees >10 cm (CON), midstory cover (MID), and shrub cover (SCOV). Thick vertical lines depict 50% highest posterior density intervals and thin vertical lines depict 85% highest posterior density intervals.



3.5. Discussion

Forest interior is important habitat for mobile (Rytwinski and Fahrig 2012) and insectivorous birds (Kremsater and Bunnell 1999), and most birds in the spruce-fir assemblages investigated here have these attributes (Rodewald 2017), providing an example of a species assemblage that selects for forest interior. Responses to edge effects are often attributed to decreased reproductive success from nest predation (Gates and Gysel 1978, Wilcove 1985, Small and Hunter 1988, Robinson et al. 1995, Hartley and Hunter 1998), interspecific brood parasitism (Böhning-Gaese et al. 1993), habitat selection (McCollin 1998), or a combination of these factors (e.g., ecological traps, Weldon and Haddad 2005, Boves et al. 2013). Brood parasites (i.e., Brown-headed cowbird) were not detected during point count surveys, similar to studies in the boreal zone (Schieck et al. 1995, Schmiegelow and Hannon 1999, Manolis et al. 2002) and are unlikely to play a dominant role in the demographics of boreal and hemiboreal birds (Manolis et al. 2002, Schmiegelow and Mönkkönen 2002).

Reproductive success and clutch size of several species within the spruce-fir avian assemblage increases with abundance of spruce budworm prey (MacArthur 1958), which cycles over 35–60 year intervals (Fraver et al. 2007), and these birds exhibit functional and numeric responses to periodic budworm outbreaks (Venier et al. 2009). Spruce budworm primarily prey upon balsam fir and spruce trees (Bergeron et al. 1995), linking tree composition to nest success and clutch size (MacArthur 1958) of several birds in the spruce-fir avian assemblage; however, spruce budworm were scarce during the course of our study (Maine Forest Service 2015, BWR unpublished data). We conducted additional surveys of Bay-breasted Warbler reproductive success at point count locations where

Bay-breasted Warbler were previously detected and the probability of observing fledglings increased with spruce-fir tree composition (Appendix M), providing one example of the influence from tree composition on nest success of a spruce-fir species. Our study occurred during low abundance of spruce budworm (Maine Forest Service 2015), and Bay-breasted Warbler have been documented foraging on a diversity of invertebrate prey during spruce-budworm outbreaks (Venier et al. 2011) suggesting some flexibility in diet. Additional research is needed to identify the mechanisms of observed differences in richness and abundance, especially while spruce budworm are scarce on the landscape.

Composition is an important driver of richness for the spruce-fir avian assemblage, and both early and late successional spruce-fir birds had greater richness at stand interior. Increased and persistent light penetration along high-contrast edges (e.g., silvicultural and lake edges) promotes deciduous tree composition (deMaynadier and Hunter 1998, Harper and Macdonald 2001). Red spruce and balsam fir are considered shade tolerant trees (Forbes and Meyer 1955, Hart 1959, Niinemets and Valladares 2006) and represented less tree composition at high-contrast road edges in our study. Shifts in tree composition at high-contrast edges provide an ecological mechanism for reduced spruce-fir avian richness, and reduced spruce-fir avian abundance at road edges that has been observed in other studies (Ferris 1979). Rolek et al. (2018) observed greatest abundance of species in the spruce-fir avian assemblage within stands having \geq 60% spruce-fir tree composition and greater richness of spruce-fir avian assemblages in stands with greater spruce-fir tree composition. Thus, in our study area, forested habitat was directly lost to roads and roadside buffers with altered vegetation characteristics that were

less favorable for most spruce-fir birds. Additionally, stand interior provided improved habitat for the spruce-fir avian assemblage when considering tree composition, with approximately 73% spruce-fir tree composition at stand interior, decreasing to 65% at low-contrast edges, and 51% at high-contrast edges (Fig. 3.4) demonstrating that roads may contribute to a loss of habitat for spruce-fir birds. Degraff (1992) conducted a similar study across contrast levels in deciduous forests and found five species included in our study (Brown Creeper, Blue-headed Vireo, Northern Parula, Northern Waterthrush, and Purple Finch) that avoided high contrast edges, however, none of these species exhibited similar abundance responses during our study in mixed-wood and coniferous forests. Only Northern Waterthrush avoided high-contrast edge here and had greater abundance at low-contrast edge. These species, except Purple Finch, were classified in assemblages having no compositional preference, and significant differences in vegetative composition toward mixed-wood at high-contrast edges may have offset the effects from structural edge effects documented by Degraaf (1992). We did not analyze a mixed-wood avian assemblage here because few species were documented as having peak abundance in mixed-wood.

Stand interior (>80 m from edge) appears to provide enhanced habitat for late successional species within both deciduous and spruce-fir assemblages. Basal area and midstory cover were greater at stand interior (Fig. 3.4), resulting in both late successional deciduous and late successional spruce-fir birds having greater species richness. Rolek et al. (2018) concluded that neither basal area nor midstory cover were important predictors of richness for the spruce-fir avian assemblages; however, another study (see Chapter 2) concluded that conifer associated focal species had mixed responses to basal area and

midstory cover. Both basal area and midstory cover differed by contrast level in our study, and species responding to midstory and basal area may require targeted speciesspecific management. For example, Olive-sided Flycatcher, White-throated Sparrow, and Palm Warbler had decreased abundances as midstory cover increased, while Baybreasted Warbler, Blackburnian Warbler had increased abundance as midstory cover increased (see Chapter 2). In contrast, conifer associated focal species tended to increase abundance or have no response to spruce-fir composition (see Chapter 2), suggesting that management that would increase spruce-fir tree composition at high-contrast edges would enhance habitat or have neutral effects on the spruce-fir avian assemblage.

Effects from habitat and fragmentation on density and abundance are frequently studied, because of the relative ease with which density data can be collected (Johnson 2007). Density plays a pivotal role in other demographics (Germain et al. 2018), and tends to have positive correlations with other demographic rates (Bock and Jones 2004). A meta-analysis (Benítez-López et al. 2010) concluded that birds (excluding raptors) decrease in abundance near road edges and other infrastructure, but the avian community here did not have differences between contrast levels for mean avian abundance across all species. Most responses by birds in boreal forests can be attributed to habitat loss rather than fragmentation (Schmiegelow and Mönkkönen 2002). Our study demonstrates effects from habitat loss caused by anthropogenically induced edge, although additional effects could occur from fragmentation of habitat caused by edge. Legaard et al. (2015) used remotely-sensed data in Maine between 1973 and 2010 to identify declines in the extent of coniferous tree composition and increases in the extent of deciduous tree composition, and detailed spatially-explicit tree composition data may provide additional insight into

loss and fragmentation of habitat for the spruce-fir avian assemblage. Proximity to edge could play an important role while predicting associations between land cover and spruce-fir avian species.

Management that reduces the extent of high-contrast edge may enhance habitat for declining spruce-fir avian assemblages. Some road edges examined here were treated with herbicide (e.g., glyphosate) at concentrations sufficient to eliminate both coniferous and deciduous regeneration thereby preventing woody vegetation from encroaching into roads. Additionally, mechanical brush cutting was used along roads where herbicide application was undesirable, and trees within road buffers were frequently harvested to reduce risk of treefall and road obstruction. Thus, roads and their buffers represent direct habitat loss to spruce-fir avian assemblages because they are unforested, which also increases light penetration into adjacent forest and increase deciduous tree composition (deMaynadier and Hunter 1998).

We estimated terrestrial habitat loss for spruce-fir avian assemblages that could be attributed to roads by obtaining detailed road maps at one study site (Telos on private lands). We applied 30 m, 50 m, and 100 m buffers from the road center to assess the extent of landscape that is potentially influenced by edge effects (Appendix N), because edge effects on vegetation in forested habitat occur most frequently within 100 m and most studies on birds report edge effects in forested habitat at distances <50 m (reviewed by Kremsater and Bunnell 1999). We determined that 8, 12, and 24%, respectively, of terrestrial habitat (i.e., excluding National Wetland Inventory Areas) at the Telos study site could be affected by road edge, similar to estimates produced from other research within our study region (e.g., 11%, Fuller et al. 2007). Previous studies in similar

ecosystems (deMaynadier and Hunter 1998, Harper and Macdonald 2001) demonstrated edge effects on tree composition that extend approximately 40 m for vegetation and 25– 35 m for amphibians, and our visual assessment of buffers with aerial photography suggested that edge effects on vegetation may extend \geq 30 m on larger roads. Narrower roads appear to have less visible effects on vegetation, although the effects of road width on vegetation and abundance of birds requires further study.

Multi-species models are powerful tools that can provide novel insights into communities of organisms in a unified analysis. The model described here provides an alternative to previously described multi-species abundance models and is well-suited for the analysis of avian point count data, by approximating instantaneous density (Farnsworth et al. 2005). Further, this model does not require repeated site visits and would reduce costs of surveys in many instances. Numerous extensions of the model presented here may provide additional insights into wildlife communities, and examples include dissimilarity metrics for inference about avian assemblages (Kéry and Royle 2015); latent variables to generate hypotheses about biotic interactions or unmeasured environmental covariates (reviewed by Warton et al. 2015); species or community dynamics to understand detailed demographics (Dail and Madsen 2011); or data augmentation to assess species richness including unobserved species (Dorazio and Royle 2005). Our model runtime was approximately 1.5 weeks running parallel on 2.5 GHz processors, with 72 species at 476 point count locations and nine time intervals. Speeding up the analysis process through the increased efficiency of Markov chain Monte Carlo samplers or use of Laplace approximation will allow multi-species models to be more widely available and accessible for researchers and practitioners.

3.6. Conclusions

Our study demonstrates previously undocumented edge effects from roads on the spruce-fir avian assemblage and vegetation. Low-contrast edges represented by the harvest treatments studied here in managed stands had little effect on avian abundance, avian richness, and vegetation compared with stand interior; however, Degraaf (1992) found three species (Cedar Waxwing, Mourning Warbler, and American Goldfinch) that avoided low-contrast edges in deciduous forests. We observed greater abundance of Canada Warbler and Northern Waterthrush at low-contrast edges compared to highcontrast edge and stand interior. These differences could potentially be attributed to stand edges that are often bound by hydrology, because these bird species are associated with hydrologic features (Reitsma et al. 2009, Whitaker and Eaton 2014). Our results may provide insights into other extensively managed areas in the boreal and hemiboreal zones and for the conservation and management of biodiversity. Multi-species models provide a simplified and powerful analysis for large groups of species that can highlight the tradeoffs between species and provide greater insight into anthropogenic effects, which may be subtle, on wildlife communities.

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APPENDICES

APPENDIX A. SUMMARY STATISTICS OF POINT COUNT SAMPLING, VEGETATION MEASUREMENTS, AND A LIST OF EXCLUDED SPECIES.

Table A.1 Distribution of 114 forest stands and 425 point counts (in parentheses) across seven harvest treatments sampled 2013–2015 across seven study sites in Northern Maine, New Hampshire, and Vermont, USA on private lands, Baxter State Park, and four National Wildlife Refuges (NWRs).

Study sites	Mature	Selection	Shelter-	Clearcut-	Clearcut-	Clearcut-	Clearcut-	Total
			wood	only	herbicide	PCT	herbicide-	
							PCT	
Aroostook NWR	8 (13)	2 (5)	0 (0)	1 (2)	0 (0)	0 (0)	0 (0)	11 (20)
Baxter State Park	2 (19)	0 (0)	7 (25)	0 (0)	0 (0)	0 (0)	0 (0)	9 (44)
Clayton Lake	0 (0)	2 (8)	0 (0)	0 (0)	8 (34)	0 (0)	0 (0)	10 (42)
Moosehorn NWR	8 (29)	0 (0)	1 (4)	0 (0)	0 (0)	0 (0)	0 (0)	9 (33)
Nulhegan NWR	2 (7)	5 (22)	1 (3)	6 (38)	0 (0)	5 (21)	0 (0)	19 (91)
Telos	4 (15)	4 (16)	0 (0)	1 (4)	9 (32)	3 (9)	7 (19)	28 (95)
Umbagog NWR	6 (35)	10 (32)	2 (5)	6 (14)	0 (0)	4 (14)	0 (0)	28 (100)
Total	30 (118)	23 (83)	11 (37)	14 (58)	17 (66)	12 (44)	7 (19)	114
								(425)

Treatment	BA	QMD	HEIG	DBH	MIDS	CAN	GRO	SHR	GAP	LCR	SPFI	CO	YS
			HT		TORY	OPY	UND	UBS	S		R	NIF	Н
Mature	13.75–	18.98–	15.55-	17.72–	0.03-	0.20-	0.10-	0.02-	0.05-	0-	0.03-	0.0	48–
	49.25	41.59	27.32	39.18	0.96	0.98	0.82	0.52	0.70	0.67	1	3–1	113
Selection	13.33-	20.15-	15.18-	20.35-	0.04-	0.14-	0.15-	0.09-	0.05-	0-	0.03-	0.0	11-
	41.00	44.19	27.50	35.36	0.98	0.90	0.69	0.55	0.52	0.76	0.91	9–1	41
Shelterwood	12.50-	21.19-	13.28–	18.98–	0.15-	0.08-	0.21-	0.05-	0.52-	0-	0.36-	0.4	5–
	36.67	36.35	24.31	33.17	0.90	0.88	0.61	0.63	0.75	0.72	0.85	5-1	31
Clearcut-only	0-	0-	7.55-	12.38-	0-0.71	0-	0.14–	0.19-	0.27-	0-	0-1	0-1	11-
	20.40	46.00	19.05	46.00		0.52	0.95	0.80	1	0.89			36
Clearcut-	0-	0-	9.45-	13.14–	0.18-	0-	0.11-	0.04-	0.12-	0-	0-1	0-1	21-
herbicide	38.00	19.52	16.67	18.35	0.90	0.97	0.57	0.77	0.95	0.81			40
Clearcut-PCT	17.60-	16.2-	13.39-	17.21-	0.23-	0.11-	0.13-	0.05-	0.08-	0.54-	0.67–	0.6	11-
	32.00	22.07	18.42	19.49	0.81	0.91	0.47	0.39	0.56	0.96	0.99	7-1	38
Clearcut-	16.75-	14.13–	11.49–	14.14-	0.21-	0.28-	0.05-	0.02-	0.02-	0-	0.55-	0.8	31-
herbicide-	38.00	19.40	16.94	19.13	0.78	1	0.59	0.37	0.76	0.85	0.94	6–1	39
PCT													

Table A.2 Ranges for stand-level averages of vegetation variables within each treatment and summarized from 870 plots in

Table A.3 Species detected during point count surveys during 2013, 2014, and 2015 in New Hampshire, Vermont, and Maine, USA, but omitted from analyses. Number of detections and number of points detected are restricted to detections within 50 m of the surveyor.

Common name	Abbrev.	Genus species	Detec tions	Points detecte d	Justification
American Black Duck	ABDU	Anas rubripes	1	1	few detections
American Bittern	AMBI	Botaurus lentiginosus	11	11	nonpasserine
American Crow	AMCR	Corvus brachyrhynchos	215	127	large territory
American Kestrel	AMKE	Falco sparverius	1	1	few detections
American Woodcock	AMWO	Scolopax minor	9	4	few detections
American Three-toed Woodpecker	ATTW	Picoides dorsalis	8	8	few detections
Bald Eagle	BAEA	Haliaeetus leucocephalus	2	2	few detections
Baltimore Oriole	BAOR	Icterus galbula	4	3	few detections
Black-billed Cuckoo	BBCU	Coccyzus erythropthalmus	1	1	few detections
Black-backed Woodpecker	BBWO	Picoides arcticus	95	68	nonpasserine
Barred Owl	BDOW	Strix varia	7	5	few detections
Belted Kingfisher	BEKI	Megaceryle alcyon	17	17	nonpasserine
Bobolink	BOBO	Dolichonyx oryzivorus	1	1	few detections
Broad-winged Hawk	BWHA	Buteo platypterus	56	47	nonpasserine
Canada Goose	CAGO	Branta canadensis	13	9	few detections
Chimney Swift	CHSW	Chaetura pelagica	4	4	few detections
Cooper's Hawk	COHA	Accipiter cooperii	4	3	few detections
Common Loon	COLO	Gavia immer	62	52	nonpasserine
Common Merganser	COME	Mergus merganser	12	3	few detections
Common Nighthawk	CONI	Chordeiles minor	15	13	nonpasserine

Table A.3 Continued.

Common Raven	CORA	Corvus corax	137	104	large territory
Downy Woodpecker	DOWO	Picoides pubescens	90	75	nonpasserine
Eastern Kingbird	EAKI	Tyrannus tyrannus	4	2	few detections
Evening Grosbeak	EVGR	Coccothraustes vespertinus	2	1	few detections
Great Blue Heron	GBHE	Ardea herodias	1	1	few detections
Great Horned Owl	GHOW	Bubo virginianus	5	5	few detections
Golden-winged Warbler	GWWA	Vermivora chrysoptera	1	1	few detections
Hairy Woodpecker	HAWO	Picoides villosus	174	145	nonpasserine
House Finch	HOFI	Haemorhous mexicanus	1	1	few detections
Indigo Bunting	INBU	Passerina cyanea	2	2	few detections
Killdeer	KILL	Charadrius vociferus	2	2	few detections
Lincoln's Sparrow	LISP	Melospiza lincolnii	18	10	few detections
Mallard	MALL	Anas platyrhynchos	1	1	few detections
Merlin	MERL	Falco columbarius	8	6	few detections
Mourning Dove	MODO	Zenaida macroura	67	48	nonpasserine
Northern Cardinal	NOCA	Cardinalis cardinalis	7	5	few detections
Northern Goshawk	NOGO	Accipiter gentilis	3	3	few detections
Northern Rough-winged Swallow	NRWS	Stelgidopteryx serripennis	1	1	few detections
Northern Saw-whet Owl	NSWO	Aegolius acadicus	1	1	few detections
Orange-crowned Warbler	OCWA	Oreothlypis celata	2	2	few detections
Osprey	OSPR	Pandion haliaetus	6	4	few detections
Pied-billed Grebe	PBGR	Podilymbus podiceps	1	1	few detections
Pileated Woodpecker	PIWO	Dryocopus pileatus	156	136	nonpasserine
Red Crossbill	RECR	Loxia curvirostra	10	10	few detections
Red-shouldered Hawk	RSHA	Buteo lineatus	1	1	few detections
Red-tailed Hawk	RTHA	Buteo jamaicensis	3	3	few detections
Ruby-throated Hummingbird	RTHU	Archilochus colubris	31	29	nonpasserine

Table A.3 Continued.

Rusty Blackbird	RUBL	Euphagus carolinus	9	7	few detections
Ruffed Grouse	RUGR	Bonasa umbellus	62	50	nonpasserine
Savannah Sparrow	SAVS	Passerculus sandwichensis	23	5	few detections
Sora	SORA	Porzana carolina	3	2	few detections
Spruce Grouse	SPGR	Falcipennis canadensis	28	18	nonpasserine
Spotted Sandpiper	SPSA	Actitis macularius	3	3	few detections
Sharp-shinned Hawk	SSHA	Accipiter striatus	14	13	nonpasserine
Tree Swallow	TRES	Tachycineta bicolor	4	4	few detections
Turkey Vulture	TUVU	Cathartes aura	3	2	few detections
Upland Sandpiper	UPSA	Bartramia longicauda	1	1	few detections
Virginia Rail	VIRA	Rallus limicola	1	1	few detections
Warbling Vireo	WAVI	Vireo gilvus	7	6	few detections
Willow Flycatcher	WIFL	Empidonax traillii	2	2	few detections
Wilson's Snipe	WISN	Gallinago delicata	24	22	nonpasserine
Wild Turkey	WITU	Meleagris gallopavo	7	6	few detections
Wood Duck	WODU	Aix sponsa	2	2	few detections
Wood Thrush	WOTH	Hylocichla mustelina	6	5	few detections
Yellow-bellied Sapsucker	YBSA	Sphyrapicus varius	490	275	nonpasserine
Northern Flicker	YSFL	Colaptes auratus	364	243	nonpasserine
Yellow-throated Vireo	YTVI	Vireo flavifrons	4	3	few detections

APPENDIX B. PRELIMINARY ANALYSES TO IDENTIFY DOMINANT VEGETATION VARIABLES.

We used preliminary analyses to identify dominant vegetation variables that were orthogonal (statistically independent) and explained the most variance in avian assemblages using a combination of PCA and NMDS. These stand-level vegetation variables explained the most variance of ordinated axes from our PCA (i.e., those with the largest eigenvalues). We retained dominant vegetation variables that contributed strongly to principal components for Bayesian hierarchical regression analyses to estimate mean effects with 95% CIs in each treatment (section 2.4.3), and eigenvalues \geq 1.0 for principal components to be important (Kaiser 1960) and eigenvector loadings \geq 0.4 (absolute value) to be significantly correlated with principal components (Stevens 1992).

To determine the variance explained by vegetation variables on avian assemblages, we used generalized additive models to regress vegetation variables against the splined axes from NMDS. We ran separate models for each vegetation variable using the ordisurf function in the vegan package (Oksanen et al. 2017) in R (R Core Team 2015), which uses generalized additive models to fit to a smooth surface with penalized splines, and allows linear and nonlinear relationships with covariates. Table B.1. NMDS preliminary analysis to identify dominant vegetation variables associated with avian abundances. Variance explained (R2) by NMDS ordination axes from avian abundance with generalized additive models that regress vegetation variables as the response variable and splined axes of ordination as explanatory variables. Bold indicates that variables were retained for additional analyses. Vegetation variables and principal component (PC) categories were retained from a previous PCA (see Table 1.3). All p-values were <0.001.

		$R^{2}(\%)$		
PC label	Variables	Axes 1,2	Axes 1,3	
Tree density	BA	50.8	47.8	
	CANOPY	49.8	48.5	
	GAPS	44.7	40.9	
	SHRUBS	23.7	19.1	
Tree immaturity	DBH	37.0	39.9	
	HEIGHT	34.3	52.9	
	QMD	25.4	35.9	
Composition	SPFIR	40.4	32.4	
	CONIF	39.5	28.2	
	LCR	16.3	8.7	
Midstory	MIDSTORY	27.8	20.7	

Figure B.1. NMDS preliminary analysis to identify dominant vegetation variables associated with avian abundances in New Hampshire, Vermont, and Maine during 2013, 2014, and 2015. Generalized additive models applied to splined ordinations of avian abundance as an explanatory variable from NMDS and vegetation response variables (A) BA, (B) DBH, (C) SPFIR, and (D) MIDSTORY. Contour lines represent average modeled response by vegetation. R2 and p value are shown for vegetation effects. Abbreviations represent avian species and species codes are referenced in Table 1.2.

Species groups

SPRUCE-FIR OBLIGATES (purple bold) SPRUCE-FIR ASSOCIATES (purple) species of concern (lowercase) OTHER SPECIES (gray)



Species groups

SPRUCE-FIR OBLIGATES (purple bold) SPRUCE-FIR ASSOCIATES (purple) species of concern (lowercase) OTHER SPECIES (gray)



Species groups

SPRUCE-FIR OBLIGATES (purple bold)

SPRUCE-FIR ASSOCIATES (purple)

species of concern (lowercase)

OTHER SPECIES (gray)


Species groups

SPRUCE-FIR OBLIGATES (purple bold)

SPRUCE-FIR ASSOCIATES (purple)

species of concern (lowercase)

OTHER SPECIES (gray)



Figure B.2. Correlation matrix showing Pearson product moment correlation coefficient (r) for relationships between vegetation variables. Darker cells have larger absolute r values. Pearson's product moment correlation coefficients were considered significant when medium correlation coefficients were estimated $r \ge 0.3$ (Cohen 1988).

	30	and		H. BI	, and	OF ND	STOR HR	JES GR	and and	- 28	° L	م م
BA	1	0.33	0.39	0.12	0.84	-0.03	-0.59	-0.4	-0.03	-0.69	0.3	0.35
QMD	0.33	1	0.7	0.84	0.3	0.04	-0.02	-0.05	0.23	-0.15	-0.15	0.16
HEIGHT	0.39	0.7	1	0.8	0.39	-0.2	-0.04	0.01	0	-0.22	-0.29	-0.17
DBH	0.12	0.84	0.8	1	0.13	-0.14	0.16	0.16	0.07	0.05	-0.45	-0.15
CANOPY	0.84	0.3	0.39	0.13	1	-0.01	-0.54	-0.39	-0.1	-0.72	0.15	0.11
MIDSTORY	-0.03	0.04	-0.2	-0.14	-0.01	1	-0.14	-0.38	0.08	-0.24	0.05	-0.07
SHRUBS	-0.59	-0.02	-0.04	0.16	-0.54	-0.14	1	0.62	-0.11	0.69	-0.38	-0.32
GROUND	-0.4	-0.05	0.01	0.16	-0.39	-0.38	0.62	1	-0.05	0.54	-0.28	-0.27
LCR	-0.03	0.23	0	0.07	-0.1	0.08	-0.11	-0.05	1	0.02	0.19	0.21
GAPS	-0.69	-0.15	-0.22	0.05	-0.72	-0.24	0.69	0.54	0.02	1	-0.19	-0.06
SPFIR	0.3	-0.15	-0.29	-0.45	0.15	0.05	-0.38	-0.28	0.19	-0.19	1	0.75
CONIF	0.35	0.16	-0.17	-0.15	0.11	-0.07	-0.32	-0.27	0.21	-0.06	0.75	1
		1	1	1				1	1			
-	1.	0.8	-0.6	-0.4	-0.2)	0.2	0.4	0.6	0.8	1

APPENDIX C. ASSOCIATIONS BETWEEN YEARS-SINCE-HARVEST AND DOMINANT VEGETATION VARIABLES FOR EACH HARVEST TREATMENT.

Figure C.1. Vegetation variables (stand means) in relation to years-since-harvest (YSH) and treatments (colors) in New Hampshire, Vermont, and Maine during 2013, 2014, and 2015. Lines indicate estimated relationships from a linear model fit to each treatment separately. Solid lines are significant (i.e., 95% CIs do not intersect zero). Three PCT stands were missing years since harvest data and were omitted.



APPENDIX D. MAINE FORESTRY TRENDS FROM 1982 TO 2015.

Figure D.1. Maine forestry trends from 1982 to 2015. (A) Annual harvested area in Maine from 1982 to 2015. Partial harvests include both selection and irregular first-stage shelterwood. (B) Annual area receiving postharvest treatments in Maine from 1982 to 2015 (Maine Forest Service, 2018).



APPENDIX E. RANGES FOR VEGETATION VARIABLES IN NEW HAMPSHIRE,

VERMONT, AND MAINE DURING 2013, 2014, AND 2015.

Table E.1. Ranges for point-level vegetation data within each treatment and summarized from 870 subplots. Units and abbreviations are described in Table 2.1.

Vegetation	Mature	Selection	Shelterwood	Clearcut-	Clearcut-	Clearcut-	Clearcut-
variable				only	herbicide	PCT	PCT-
							herbicide
BA	6–66	5–65	5–70	0–30	0-48	6–52	8–43
SPFIR	0–1	0–1	0-0.9	0–1	0–1	0.24–1	0.35–1
DBH	16.9–50.5	14.7–38.5	16.5–53.4	0–95.0	0–27.8	13.0–37.2	11.9–22.3
MID	0–1	0–1	0-1	0–1	0–1	0–1	0–1
SCOV	0–0.87	0.01–0.7	0.02–0.78	0.08–0.8	0.02–0.88	0.01–0.52	0-0.52
SCOMP	0–0.75	0–0.55	0.05-0.75	0.05–0.85	0-0.9	0–0.35	0-0.25
LCR	0–0.79	0–0.77	0-0.87	0–0.94	0-0.95	0–0.96	0–0.9

APPENDIX F. PRIORS OF PARAMETERS USED IN DISTANCE-REMOVAL ABUNDANCE MODELS TO EVALUATE ASSOCIATIONS BETWEEN ABUNDANCE, VEGETATION, HARVEST TREATMENTS,

AND YEARS-SINCE-HARVEST.

 Table F.2. Priors for estimated parameters in hybrid single-species distance-removal

 abundance models.

Model	Distribution	Parameter	Prior
Vegetation model	P, ZI	$logit^{-1}(\delta_0)$	Uniform(0,1)
	P, ZI	$\delta_{1:3}$	Normal(0,0.01)
	P, ZI	γ_0	Uniform(0,250)
	P, ZI	$\gamma_{1:3}$	Normal(0,0.01)
	P, ZI	$\beta_{1:8}$	Normal(0,0.01)
	P, ZI	W	Bernoulli(0.5)
	P, ZI	σ^s	Uniform(0,20)
	P, ZI	σ^t	Uniform(0,20)
	P, ZI	σ^{OBS}	Uniform(0,20)
	ZI	ψ	Uniform(0,1)
Treatment and YSH model	P, ZI	$logit^{-1}(\delta_0)$	Uniform(0,1)
	P, ZI	$\delta_{1:3}$	Normal(0,0.01)
	P, ZI	γ_0	Uniform(0,250)
	P, ZI	$\gamma_{1:3}$	Normal(0,0.01)
	P, ZI	<i>α</i> _{1:3}	Normal(0,0.01)
	P, ZI	W	Bernoulli(0.5)
	P, ZI	σ^s	Uniform(0,20)
	P, ZI	σ^t	Uniform(0,20)
	P, ZI	σ^{OBS}	Uniform(0,20)
	ZI	ψ	Uniform(0,1)

APPENDIX G. CORRELATION MATRIX OF VEGETATION VARIABLES.

Figure. G.1. Correlation matrix showing Pearson product moment correlation coefficient (r) for correlations between point-level vegetation variables collected in New Hampshire, Vermont, and Maine during 2013, 2014, and 2015. Darker cells have larger correlation coefficients. Pearson's product moment correlation coefficients were considered significant when $r \ge 0.3$ (Cohen, 1988).

	BR	AR.	st	Rd Str	R DEY	MID	çČ	y 202	MR . B
BA2	1	0.95	-0.09	-0.06	0.26	-0.12	-0.38	-0.19	-0.04
BA	0.95	1	-0.06	-0.02	0.29	-0.03	-0.48	-0.28	-0.03
SPFIR2	-0.09	-0.06	1	0.97	-0.41	-0.08	-0.19	-0.15	-0.01
SPFIR	-0.06	-0.02	0.97	1	-0.4	-0.07	-0.21	-0.14	-0.03
DBH	0.26	0.29	-0.41	-0.4	1	0	0.06	0.05	0.14
MID	-0.12	-0.03	-0.08	-0.07	0	1	-0.09	-0.14	0
SCOV	-0.38	-0.48	-0.19	-0.21	0.06	-0.09	1	0.68	-0.03
SCOMP	-0.19	-0.28	-0.15	-0.14	0.05	-0.14	0.68	1	0.09
LCR	-0.04	-0.03	-0.01	-0.03	0.14	0	-0.03	0.09	1
					-	-	T		
	1 -0.	8 -0.6	-0.4	-0.2	0	0.2	0.4	0.6 0	.8 1

APPENDIX H. JAGS SCRIPTS FOR SINGLE-SPECIES DISTANCE-REMOVAL

ABUNDANCE MODELS.

Models include vegetation covariates and a Poisson distribution (model 1), vegetation covariates and a zero-inflated distribution (model 2), harvest treatments and YSH with a Poisson distribution (model 3), harvest treatments and YSH with a zero-inflated distribution (model 4).

Model 1. Poisson vegetation model.

```
for (o in 2:(nCovsPA)){ pa.beta[o] ~ dnorm(0, 0.01) } #nCovsPA
pp.beta[1] ~ dunif(0, 250)
for (n in 2:(nCovsPP)){pp.beta[n] ~ dnorm(0, 0.01) } #nCovsPP
```

```
for (n in 1:nCovsLam){
lam.beta[n] ~ dnorm(0, 0.01)
w[n] ~ dbern(0.5)
} #nCovsLam
for (n in 1:3){wpa[n] ~ dbern(0.5) }
for (n in 1:4){wpp[n] ~ dbern(0.5) }
lam.beta0 ~ dnorm(0, 0.01)
stand.tau <- 1/ (stand.sig*stand.sig)
stand.sig ~ dunif(0,20)
yr.tau <- 1/ (yr.sig*yr.sig)
yr.sig ~ dunif(0,20)
obs.tau <- 1/ (obs.sig*obs.sig)
obs.sig ~ dunif(0,20)
```

} # L

```
# Distance
  for (i in 1:nsites){
  for(t in 1:YR){
  for(b in 1:nD){
  g[i,t,b] <- exp(-midpt[b]*midpt[b]/(2*dist.sigma[i,t]*dist.sigma[i,t])) # half-normal
distance function
  f[i,t,b] < (2*midpt[b]*delta)/(B*B) # radial density function for point counts,
change for line transects
  pi.pd[i,t,b] \leq g[i,t,b]*f[i,t,b]
  pi.pd.c[i,t,b] <- pi.pd[i,t,b]/pdet[i,t]
  } #nD
  pdet[i,t] <- sum(pi.pd[i,t,1:nD]) # Distance class probabilities
  # Removal
  for (r \text{ in } 1:R)
  pi.pa[i,t,r] <- p.a[i,t]*pow(1-p.a[i,t], (r-1))
  pi.pa.c[i,t,r] <- pi.pa[i,t,r] / pcap[i,t]
  } #R
  pcap[i,t] <- sum(pi.pa[i,t,1:R])
  # Detection models
  pmarg[i,t] <- pcap[i,t] * pdet[i,t]
  logit(p.a[i,t]) \le pa.beta[1] + wpa[1]*pa.beta[2]*date[i,t] +
              wpa[1]*wpa[2]*pa.beta[3]*date2[i,t] + wpa[3]*pa.beta[4]*hr[i,t]
  \log(dist.sigma[i,t]) <- \log(pp.beta[1]) + wpp[1]*pp.beta[2]*densiom[i,t] +
                 wpp[2]*pp.beta[3]*noise[i,t] + wpp[3]*pp.beta[4]*ba[i] +
obs.eps[obs[i,t]]
  nobs[i,t] \sim dbin(pmarg[i,t], N[i,t])
  \log(\text{lambda}[i,t]) <- \text{lam.beta}0 +
        w[1]*w[2]*lam.beta[1]*CovsLam[i,1] + w[2]*lam.beta[2]*CovsLam[i,2] +
        w[3]*w[4]*lam.beta[3]*CovsLam[i,3] + w[4]*lam.beta[4]*CovsLam[i,4] +
        w[5]*lam.beta[5]*CovsLam[i,5] + w[6]*lam.beta[6]*CovsLam[i,6] +
        w[7]*lam.beta[7]*CovsLam[i,7] + w[8]*lam.beta[8]*CovsLam[i,8] +
        w[9]*lam.beta[9]*CovsLam[i,9] +
        stand.eps[stand.id[i]] + yr.eps[yr_rot2[i,t]]
  N[i,t] \sim dpois(lambda[i,t])
```

} #YR #nsites

Random effects
for (s in 1:S){ stand.eps[s] ~ dnorm(0, stand.tau)}
for (y in 1:9){ yr.eps[y] ~ dnorm(0, yr.tau)}
for (o in 1:28){ obs.eps[o] ~ dnorm(0, obs.tau)}

Model 2. Zero-inflated vegetation model.

model { # see model 1 pa.beta[1] <- logit(p.pa.beta0)</pre> p.pa.beta0 ~ dunif(0,1)for (o in 2:(nCovsPA)){ $pa.beta[o] \sim dnorm(0, 0.01)$ #nCovsPA $pp.beta[1] \sim dunif(0, 250)$ for (n in 2:(nCovsPP)){ $pp.beta[n] \sim dnorm(0, 0.01)$ #nCovsPP for (n in 1:nCovsLam) lam.beta[n] ~ dnorm(0, 0.01) $w[n] \sim dbern(0.5)$ #nCovsLam for $(n \text{ in } 1:3) \{ wpa[n] \sim dbern(0.5) \}$ for $(n \text{ in } 1:3) \{ wpp[n] \sim dbern(0.5) \}$ } lam.beta0 ~ dnorm(0, 0.01) $psi \sim dunif(0,1)$

```
stand.tau <- 1/ (stand.sig*stand.sig)
stand.sig ~ dunif(0,20)
yr.tau <- 1/ (yr.sig*yr.sig)
yr.sig ~ dunif(0,20)
obs.tau <- 1/ (obs.sig*obs.sig)
obs.sig ~ dunif(0,20)
```

```
for (1 in 1:L) {
  int[1] ~ dcat(pi.pa.c[site[1], yr rot[1], ]) # removal class frequencies
  dclass[1] ~ dcat(pi.pd.c[site[1], yr_rot[1], ]) # distance class frequencies
  } # L
  # Distance
  for (i in 1:nsites){
  for(t in 1:YR){
  for(b in 1:nD){
  g[i,t,b] <- exp(-midpt[b]*midpt[b]/(2*dist.sigma[i,t]*dist.sigma[i,t])) # half-normal
distance function
  f[i,t,b] <- (2*midpt[b]*delta)/(B*B)  # radial density function for point counts,
change for line transects
  pi.pd[i,t,b] <- g[i,t,b]*f[i,t,b]
  pi.pd.c[i,t,b] <- pi.pd[i,t,b]/pdet[i,t]
  } #nD
  pdet[i,t] <- sum(pi.pd[i,t,1:nD]) # Distance class probabilities
  # Removal
  for (r \text{ in } 1:R)
  pi.pa[i,t,r] <- p.a[i,t]*pow(1-p.a[i,t], (r-1))
  pi.pa.c[i,t,r] <- pi.pa[i,t,r] / pcap[i,t]
  } #R
  pcap[i,t] <- sum(pi.pa[i,t,1:R])
  # Detection models
  pmarg[i,t] <- pcap[i,t] * pdet[i,t]</pre>
  logit(p.a[i,t]) \le pa.beta[1] + wpa[1]*pa.beta[2]*date[i,t] +
wpa[1]*wpa[2]*pa.beta[3]*date2[i,t] +
              wpa[3]*pa.beta[4]*hr[i,t]
  \log(dist.sigma[i,t]) <- \log(pp.beta[1]) + wpp[1]*pp.beta[2]*densiom[i,t] +
                wpp[2]*pp.beta[3]*noise[i,t] + wpp[3]*pp.beta[4]*ba[i] +
obs.eps[obs[i,t]]
  nobs[i,t] \sim dbin(pmarg[i,t], N[i,t])
  N[i,t] \sim dpois(lam.eff[i,t])
  lam.eff[i,t] <- lambda[i,t] * w.lam[i,t]
  w.lam[i,t] ~ dbern(psi)
  \log(\text{lambda}[i,t]) <- \text{lam.beta}0 +
       w[1]*w[2]*lam.beta[1]*CovsLam[i,1] + w[2]*lam.beta[2]*CovsLam[i,2] +
       w[3]*w[4]*lam.beta[3]*CovsLam[i,3] + w[4]*lam.beta[4]*CovsLam[i,4] +
       w[5]*lam.beta[5]*CovsLam[i,5] + w[6]*lam.beta[6]*CovsLam[i,6] +
       w[7]*lam.beta[7]*CovsLam[i,7] + w[8]*lam.beta[8]*CovsLam[i,8] +
```

w[9]*lam.beta[9]*CovsLam[i,9] + stand.eps[stand.id[i]] + yr.eps[yr_rot2[i,t]]

Random effects
for (s in 1:S){ stand.eps[s] ~ dnorm(0, stand.tau)}
for (y in 1:9){ yr.eps[y] ~ dnorm(0, yr.tau)}
for (o in 1:28){ obs.eps[o] ~ dnorm(0, obs.tau)}

```
Model 3. Poisson treatment and years-since-harvest model.
```

```
for (o in 2:(nCovsPA)){
pa.beta[o] ~ dnorm(0, 0.01)
} #nCovsPA
```

pp.beta[1] ~ dunif(0, 250) for (n in 2:(nCovsPP)){ pp.beta[n] ~ dnorm(0, 0.01)

```
} #nCovsPP
```

```
for (n \text{ in } 1:2) \{ w[n] \sim dbern(0.5) \}
for (n \text{ in } 1:3) \{ wpa[n] \sim dbern(0.5) \}
for (n \text{ in } 1:4) \{ wpp[n] \sim dbern(0.5) \}
for (tt in 1:7) { s.beta1[tt] ~ dnorm(0,0.01) }
s.beta2 ~ dnorm(0, 0.01)
s.beta3 ~ dnorm(0, 0.01)
stand.tau <- 1/ (stand.sig*stand.sig)</pre>
stand.sig ~ dunif(0,10)
yr.tau <- 1/ (yr.sig*yr.sig)</pre>
yr.sig \sim dunif(0,20)
obs.tau <- 1/(obs.sig*obs.sig)
obs.sig ~ dunif(0,20)
for (1 in 1:L) {
 int[1] ~ dcat(pi.pa.c[site[1], yr_rot[1], ]) # removal class frequencies
 dclass[1] ~ dcat(pi.pd.c[site[1], yr_rot[1], ]) # distance class frequencies
  } # L
# Distance
  for (i in 1:nsites){
   for(t in 1:YR){
     for(b in 1:nD){
       g[i,t,b] <- \exp(-midpt[b]/(2*dist.sigma[i,t]*dist.sigma[i,t])) # half-
normal distance function
       f[i,t,b] <- (2*midpt[b]*delta)/(B*B) # radial density function for point counts,
change for line transects
       pi.pd[i,t,b] \leq g[i,t,b]*f[i,t,b]
       pi.pd.c[i,t,b] <- pi.pd[i,t,b]/pdet[i,t]
       } #nD
      pdet[i,t] <- sum(pi.pd[i,t,1:nD]) # Distance class probabilities
# Removal
  for (r \text{ in } 1:R)
   pi.pa[i,t,r] <- p.a[i,t]*pow(1-p.a[i,t], (r-1))
   pi.pa.c[i,t,r] <- pi.pa[i,t,r] / pcap[i,t]
   } #R
  pcap[i,t] <- sum(pi.pa[i,t,1:R])
# Detection models
   pmarg[i,t] <- pcap[i,t] * pdet[i,t]</pre>
  logit(p.a[i,t]) \le pa.beta[1] + wpa[1]*pa.beta[2]*date[i,t] +
```

```
wpa[1]*wpa[2]*pa.beta[3]*date2[i,t] + wpa[3]*pa.beta[4]*hr[i,t]
 log(dist.sigma[i,t]) <- log(pp.beta[1]) + wpp[1]*pp.beta[2]*densiom[i,t] +
              wpp[2]*pp.beta[3]*noise[i,t] + wpp[3]*pp.beta[4]*ba[i] +
obs.eps[obs[i,t]]
nobs[i,t] \sim dbin(pmarg[i,t], N[i,t])
   log(lambda[i,t]) <- lam.beta.s[stand.id[i]] + yr.eps[t]
   N[i,t] \sim dpois(lambda[i,t])
nobs.fit[i,t] ~ dbin(pmarg[i,t], N[i,t]) # create new realization of model
e.p[i,t] <- pmarg[i,t] * N[i,t] # original model prediction
E.p[i,t] <- pow((nobs[i,t]-e.p[i,t]),2)/(e.p[i,t]+0.5)
E.New.p[i,t] <- pow((nobs.fit[i,t]-e.p[i,t]),2)/(e.p[i,t]+0.5))
  }} #YR #nsites
for (s \text{ in } 1:S)
  lam.beta.s[s]~ dnorm(stand.mu[s], stand.tau)
  stand.mu[s] <- s.beta1[treat[s]] + w[1]*s.beta2*tsh[s] + w[1]*w[2]*s.beta3*tsh2[s]
} #S
# Random effects
for (y \text{ in } 1:9) \{ yr.eps[y] \sim dnorm(0, yr.tau) \}
for (o in 1:28) { obs.eps[o] \sim dnorm(0, obs.tau) }
for(t in 1:YR){
   Ntot[t] <- sum(N[1:nsites,t])</pre>
   D[t] <- Ntot[t] / ((3.14*B*B*nsites)/10000) # dens per ha
   } #YR
fit.p <- sum(E.p[1:nsites,1:YR])
fit.new.p <- sum(E.New.p[1:nsites,1:YR])
bayesp<-step(fit.new.p-fit.p) # Bayesian p-value for availability model. =0.5 is good fit,
near 0 or 1 is poor fit
  } # End model
Model 4. Zero-inflated treatment and years-since-harvest model.
model {
```

```
for (n in 2:(nCovsPP)){
pp.beta[n] \sim dnorm(0, 0.01)
} #nCovsPP
for (n \text{ in } 1:2) \{ w[n] \sim dbern(0.5) \}
for (n \text{ in } 1:3)\{wpa[n] \sim dbern(0.5)\}
for (n \text{ in } 1:4) \{ wpp[n] \sim dbern(0.5) \}
psi \sim dunif(0,1)
for (tt in 1:7) { s.beta1[tt] ~ dnorm(0,0.01) }
s.beta2 ~ dnorm(0, 0.01)
s.beta3 ~ dnorm(0, 0.01)
stand.tau <- 1/ (stand.sig*stand.sig)</pre>
stand.sig ~ dunif(0,20)
yr.tau <- 1/ (yr.sig*yr.sig)</pre>
yr.sig \sim dunif(0,20)
obs.tau <- 1/ (obs.sig*obs.sig)
obs.sig ~ dunif(0,20)
for (1 in 1:L) {
 int[1] ~ dcat(pi.pa.c[site[1], yr_rot[1], ]) # removal class frequencies
 dclass[1] ~ dcat(pi.pd.c[site[1], yr_rot[1], ]) # distance class frequencies
  } # L
# Distance
  for (i in 1:nsites){
   for(t in 1:YR){
     for(b in 1:nD){
       g[i,t,b] <- exp(-midpt[b]*midpt[b]/(2*dist.sigma[i,t]*dist.sigma[i,t])) # half-
normal distance function
       f[i,t,b] <- (2*midpt[b]*delta)/(B*B) # radial density function for point counts,
change for line transects
       pi.pd[i,t,b] <- g[i,t,b]*f[i,t,b]
       pi.pd.c[i,t,b] \leq pi.pd[i,t,b]/pdet[i,t]
       } #nD
      pdet[i,t] <- sum(pi.pd[i,t,1:nD]) # Distance class probabilities
# Removal
  for (r \text{ in } 1:R)
   pi.pa[i,t,r] <- p.a[i,t]*pow(1-p.a[i,t], (r-1))
   pi.pa.c[i,t,r] <- pi.pa[i,t,r] / pcap[i,t]
    } #R
  pcap[i,t] <- sum(pi.pa[i,t,1:R])
```

```
# Detection models
   pmarg[i,t] <- pcap[i,t] * pdet[i,t]</pre>
  logit(p.a[i,t]) \le pa.beta[1] + wpa[1]*pa.beta[2]*date[i,t] +
wpa[1]*wpa[2]*pa.beta[3]*date2[i,t] +
             wpa[3]*pa.beta[4]*hr[i,t]
  log(dist.sigma[i,t]) <- log(pp.beta[1]) + wpp[1]*pp.beta[2]*densiom[i,t] +
               wpp[2]*pp.beta[3]*noise[i,t] + wpp[3]*pp.beta[4]*ba[i] +
obs.eps[obs[i,t]]
nobs[i,t] \sim dbin(pmarg[i,t], N[i,t])
   N[i,t] \sim dpois(lambda.eff[i,t])
   lambda.eff[i,t] <- lambda[i,t] * w.lam[i,t]
   w.lam[i,t] ~ dbern(psi)
   log(lambda[i,t]) <- lam.beta.s[stand.id[i]] + yr.eps[t]
  nobs.sim[i,t] ~ dbin(pmarg[i,t], N[i,t]) # create new realization of model
  e.p[i,t] <- pmarg[i,t] * N[i,t] # original model prediction
  # chi-square discrepancy for the actual data
  E.p[i,t] <- pow((nobs[i,t] - e.p[i,t]),2)/(e.p[i,t]+0.5)
  # chi-square discrepancy for the simulated data
  E.New.p[i,t]<- pow((nobs.sim[i,t]-e.p[i,t]),2)/(e.p[i,t]+0.5))
  }} #YR #nsites
# Random effects
for (s \text{ in } 1:S)
lam.beta.s[s]~ dnorm(stand.mu[s], stand.tau)
stand.mu[s] <- s.beta1[treat[s]] + w[1]*s.beta2*tsh[s] + w[1]*w[2]*s.beta3*tsh2[s]
} #S
for (y \text{ in } 1:9) \{ yr.eps[y] \sim dnorm(0, yr.tau) \}
for (o in 1:28) { obs.eps[o] \sim dnorm(0, obs.tau) }
for(t in 1:YR){
   Ntot[t] <- sum(N[1:nsites,t])
   D[t] <- Ntot[t] / ((3.14*B*B*nsites)/10000) # dens per ha
   } #YR
fit.p <- sum(E.p[1:nsites,1:YR])
fit.new.p <- sum(E.New.p[1:nsites,1:YR])
bayesp<-step(fit.new.p-fit.p) # Bayesian p-value for availability model. =0.5 is good fit,
near 0 or 1 is poor fit
  } # End model
```

APPENDIX I. FOCAL SPECIES RESPONSE IN ABUNDANCE TO VEGETATION VARIABLES, YEARS-SINCE-HARVEST, AND HARVEST TREATMENTS USING SINGLE-SPECIES DISTANCE-REMOVAL MODELS.

Table I.1 Vegetation associations with avian abundance from single-species distanceremoval models. We present mean coefficient estimates, 95% credible intervals (LCI and UCI), indicator variable weights (w), and Bayesian p-values (Bayesp) to evaluate model goodness-of-fit. Note that some parameters for covariates were not estimable because they received zero weight.

Species	Bayesp	Covariate	Weight	Mean	LCI	UCI
BBWA	0.85	Lam_beta0		-2.89	-3.88	-1.94
		BA	0.02	0.30	-0.04	0.68
		BA2	0.00	-0.19	-0.38	0.26
		SPFIR	1.00	0.57	0.28	0.85
		SPFIR2	0.04	-0.03	-0.62	0.71
		DBH	0.17	-0.35	-0.70	-0.05
		MID	0.62	0.25	0.10	0.39
		SCOV	1.00	-0.53	-0.73	-0.32
		SCOMP	0.02	0.02	-0.31	0.29
		LCR	0.98	-0.36	-0.54	-0.19
		Pa_int		-0.34	-0.59	-0.10
		DATE	0.01	-0.06	-0.38	0.24
		DATE2	0.00	0.30	0.15	0.55
		TIME	0.02	0.13	-0.13	0.38
		Pp_int		17.70	15.88	19.61
		COVER	0.03	-0.06	-0.12	0.00
		NOISE	0.00	0.01	-0.05	0.06
		BAp	0.00	0.00	-0.10	0.09

BLBW 0.76 Lam_beta0 -1.08-1.40 -0.77 0.40 0.21 1.00 BA 1.00 BA2 0.16 -0.40-0.80 -0.06 SPFIR 0.12 0.00 0.01 -0.13SPFIR2 0.25 0.00 0.20 0.15 DBH 1.00 0.50 0.38 0.62 MID 0.51 0.19 0.07 0.31 SCOV 0.01 0.03 -0.14 0.15 SCOMP 0.01 0.05 -0.08 0.16 LCR 0.19 0.01 0.07 -0.10 Pa_int -1.72 -2.01 -1.39 DATE -0.90 1.00 -1.13 -1.35 DATE2 0.04 0.20 -0.14 0.54 TIME 0.01 0.02 -0.13 0.17 21.08 18.99 23.38 Pp_int **COVER** 0.00 -0.01 -0.06 0.05 NOISE 0.00 0.02 -0.03 0.06 0.00 0.02 -0.03 0.10 BAp **BLPW** 0.58 Lam beta0 -4.54 -5.48 -3.64 -1.66 BA 1.00 -1.27-0.69 BA2 0.09 -0.57 -1.700.51 **SPFIR** -0.14 0.00 0.04 0.18 SPFIR2 0.00 -0.10 -0.22 0.02 0.02 -0.27 0.29 DBH 0.04 MID 0.01 0.04 -0.170.23 SCOV -0.58 0.26 0.02 -0.09 SCOMP 0.07 0.22 0.00 0.47 0.82 0.35 0.54 LCR 0.16 -0.01 -0.37 0.31 Pa int DATE 0.01 0.15 -0.27 0.55 DATE2 -0.37 -1.49 0.65 0.00 TIME 0.10 0.34 -0.01 0.69 12.53 18.63 Pp_int 16.06 **COVER** 0.05 0.01 -0.03-0.12NOISE 0.01 0.00 -0.09 0.12 0.01 0.00 -0.20 0.16 BAp BOCH 0.34 Psi 0.54 0.45 0.66 Lam beta0 -0.47 -0.87 -0.09 -0.13 -0.25 BA 0.02 0.02 -0.07 BA2 0.00 -0.08 -0.06 **SPFIR** 0.60 0.25 -0.05 0.41 SPFIR2 0.03 0.25 -0.31 0.67

Table I.1 Continued.

0.12

-0.19

-0.35

-0.01

DBH

Table I.1 Continued.

		MID	0.01	-1.33	-22.36	19.42
		SCOV	0.01	0.05	-0.08	0.18
		SCOMP	0.01	0.03	-0.09	0.16
		LCR	0.02	0.08	-21.30	17.72
		Pa_int		-1.25	-1.56	-0.94
		DATE	1.00	0.66	0.40	0.99
		DATE2	0.21	-0.32	-0.58	-0.06
		TIME	0.06	-0.19	-0.41	0.02
		Pp_int		19.27	18.10	20.58
		COVER	0.01	-0.03	-0.07	0.00
		NOISE	0.01	-0.02	-0.07	0.02
		BAp	0.01	-0.04	-0.08	0.02
CAWA	0.86	Lam_beta0		-1.79	-2.16	-1.45
		BA	0.29	-0.20	-0.33	-0.06
		BA2	0.01	-0.16	-0.38	0.10
		SPFIR	0.01	0.09	-0.02	0.21
		SPFIR2	0.00	-0.10	-0.18	-0.02
		DBH	0.01	0.01	-0.12	0.09
		MID	0.11	-0.14	-0.24	-0.03
		SCOV	0.09	0.19	0.01	0.38
		SCOMP	1.00	0.35	0.21	0.47
		LCR	0.08	0.17	0.02	0.30
		Pa_int		-0.42	-0.60	-0.24
		DATE	0.01	-0.06	-0.21	0.15
		DATE2	0.00	0.21	0.15	0.27
		TIME	0.01	0.02	-0.18	0.18
		Pp_int		20.94	17.71	24.34
		COVER	0.07	-0.08	-0.14	-0.02
		NOISE	0.00	0.03	-0.02	0.09
		BAp	0.01	-0.02	-0.09	0.08
CMWA	0.37	Lam_beta0		-3.87	-6.46	-1.32
		BA	0.02	-0.04	-0.43	0.78
		BA2	0.00	-0.52	-1.63	0.91
		SPFIR	0.28	0.59	0.05	1.08
		SPFIR2	0.02	0.43	-0.46	1.25
		DBH	0.03	0.06	-0.38	0.44
		MID	0.02	0.10	-0.28	0.45
		SCOV	0.10	-0.51	-0.94	0.08
		SCOMP	0.03	-0.18	-0.59	0.25
		LCR	0.03	0.23	-0.17	0.60
		Pa_int		-2.54	-5.37	-0.02
		DATE	0.65	-1.70	-2.81	-0.35
		DATE2	0.08	-0.24	-2.59	3.35

Table I.1 Co	ontinued.
--------------	-----------

		TIME	0.06	0.34	-0.47	1.11
		Pp int		29.03	9.02	205.34
		COVER	0.06	-2.70	-9.23	1.92
		NOISE	0.03	-1.16	-5.94	1.66
		BAp	0.27	-1.28	-8.34	-0.08
GCKI	1	Lam beta0		0.43	0.10	0.77
		BA	1.00	0.37	0.18	0.69
		BA2	0.42	-0.27	-0.45	-0.09
		SPFIR	1.00	0.88	0.61	1.16
		SPFIR2	1.00	-0.57	-0.82	-0.32
		DBH	0.01	0.06	0.00	0.14
		MID	0.01	0.04	-0.02	0.08
		SCOV	0.11	-0.10	-0.17	-0.03
		SCOMP	0.23	-0.10	-0.16	-0.03
		LCR	0.07	0.08	0.02	0.13
		Pa_int		-0.49	-0.60	-0.39
		DATE	0.03	-0.12	-0.22	0.00
		DATE2	0.00	-0.12	-0.25	-0.01
		TIME	0.01	-0.03	-0.11	0.08
		Pp_int		17.95	17.09	18.86
		COVER	0.00	-0.01	-0.04	0.01
		NOISE	0.00	0.01	-0.01	0.03
		BAp	0.02	-0.04	-0.07	0.00
GRAJ	0.16	Psi		0.10	0.06	0.16
		Lam_beta0		-0.33	-1.91	0.90
		BA	0.75	0.45	0.09	0.79
		BA2	0.03	0.32	-0.42	1.05
		SPFIR	0.07	1.64	-0.07	2.88
		SPFIR2	0.07	-1.83	-2.90	-0.84
		DBH	0.04	0.20	-0.18	0.49
		MID	0.46	0.12	-19.22	19.51
		SCOV	0.03	-0.11	-0.60	0.36
		SCOMP	0.11	0.22	-0.05	0.48
		LCR	0.20	-0.03	-19.29	19.80
		Pa_int		-1.39	-2.11	-0.81
		DATE	0.37	1.40	0.23	2.24
		DATE2	0.32	-1.27	-2.02	-0.52
		TIME	0.03	-0.18	-0.64	0.29
		Pp_int		18.58	15.20	22.46
		COVER	0.02	-0.11	-0.27	0.04
		NOISE	0.01	-0.05	-0.19	0.09
		BAp	0.06	-0.12	-0.26	-0.01
HETH	0.16	Lam_beta0		-1.08	-1.58	-0.58

Table I.1 Continued.

		BA	0.00	0.05	-0.04	0.13
		BA2	0.00	-0.25	-0.30	-0.19
		SPFIR	0.32	-0.13	-0.21	-0.05
		SPFIR2	0.01	0.08	-0.23	0.32
		DBH	0.01	0.04	-0.04	0.11
		MID	0.00	0.00	-0.05	0.06
		SCOV	0.01	-0.02	-0.09	0.10
		SCOMP	0.00	-0.02	-0.08	0.04
		LCR	0.01	0.05	-0.03	0.14
		Pa_int		0.18	0.07	0.29
		DATE	0.01	0.08	-0.05	0.18
		DATE2	0.00	0.07	0.07	0.07
		TIME	0.01	0.06	-0.06	0.17
		Pp_int		39.54	33.65	49.20
		COVER	0.04	-0.10	-0.20	-0.02
		NOISE	0.01	-0.04	-0.12	0.04
		BAp	0.05	0.11	0.01	0.25
MAWA	1	Lam_beta0		0.51	0.28	0.73
		BA	1.00	-0.20	-0.25	-0.14
		BA2	0.01	0.02	-0.18	0.15
		SPFIR	0.01	0.04	0.00	0.10
		SPFIR2	0.00			
		DBH	0.02	-0.05	-0.09	0.00
		MID	0.00	-0.02	-0.06	0.03
		SCOV	0.00	0.02	-0.04	0.06
		SCOMP	0.02	0.05	0.00	0.10
		LCR	0.03	0.06	0.01	0.11
		Pa_int		0.07	0.00	0.14
		DATE	0.00	-0.02	-0.08	0.09
		DATE2	0.00			
		TIME	0.01	0.06	-0.01	0.12
		Pp_int		21.95	20.40	23.64
		COVER	0.00	-0.01	-0.02	0.02
		NOISE	0.00	0.00	-0.02	0.02
		BAp	0.00	0.00	-0.01	0.02
MYWA	0.4	Lam_beta0		-0.76	-1.20	-0.34
		BA	0.00	-0.04	-0.13	0.10
		BA2	0.00			
		SPFIR	1.00	0.25	0.15	0.35
		SPFIR2	0.03	-0.19	-0.55	0.16
		DBH	0.10	-0.12	-0.22	-0.03
		MID	0.00	0.00	-0.06	0.06
		SCOV	1.00	-0.28	-0.37	-0.19

Table I.1 Continued.

		SCOMP	0.02	0.09	-0.02	0.22
		LCR	0.60	0.15	0.06	0.23
		Pa_int		-0.56	-0.71	-0.43
		DATE	0.01	-0.10	-0.27	0.05
		DATE2	0.00	0.05	-0.12	0.18
		TIME	0.01	-0.04	-0.15	0.07
		Pp_int		27.32	23.79	32.20
		COVER	0.00	-0.01	-0.05	0.02
		NOISE	0.00	0.02	-0.04	0.06
		BAp	0.00	-0.02	-0.07	0.04
OSFL	0.4	Lam_beta0		-4.39	-5.83	-0.42
		BA	0.05	-0.42	-0.96	0.43
		BA2	0.00	-0.08	-0.88	0.73
		SPFIR	0.04	-1.23	-2.32	0.07
		SPFIR2	0.03	1.57	0.53	2.55
		DBH	0.02	-0.08	-0.35	0.21
		MID	0.98	-0.74	-1.13	-0.38
		SCOV	0.02	0.08	-0.28	0.46
		SCOMP	0.05	-0.24	-0.58	0.06
		LCR	0.02	-0.06	-0.35	0.30
		Pa_int		-0.90	-5.97	0.21
		DATE	0.04	0.95	-0.49	2.61
		DATE2	0.03	-2.08	-3.63	-0.30
		TIME	0.02	0.04	-0.40	0.55
		Pp_int		135.29	15.54	244.30
		COVER	0.19	-0.31	-5.46	6.13
		NOISE	0.16	0.38	-4.61	5.94
		BAp	0.97	-8.06	-18.51	-1.61
RBNU	0.3	Lam_beta0		-1.19	-1.56	-0.83
		BA	0.99	0.23	0.13	0.43
		BA2	0.04	-0.22	-0.48	0.02
		SPFIR	0.76	0.82	0.47	1.19
		SPFIR2	0.76	-0.90	-1.27	-0.53
		DBH	1.00	0.23	0.14	0.31
		MID	0.04	-0.09	-0.18	-0.01
		SCOV	0.14	0.14	0.03	0.25
		SCOMP	0.01	-0.02	-0.17	0.10
		LCR	0.01	0.00	-0.12	0.10
		Pa_int		-0.77	-1.02	-0.53
		DATE	0.95	0.39	0.20	0.59
		DATE2	0.01	0.01	-0.22	0.22
		TIME	0.01	-0.04	-0.20	0.12
		Pp_int		34.41	28.24	45.47

Table I.1 Continued.

		COVER	0.00	0.00	-0.06	0.08
		NOISE	0.01	0.08	-0.01	0.19
		BAp	0.01	-0.03	-0.13	0.12
RCKI	0.62	Lam_beta0		-2.27	-3.03	-1.58
		BA	0.96	-0.40	-0.60	-0.19
		BA2	0.03	-0.21	-0.69	0.29
		SPFIR	1.00	0.39	-0.47	0.68
		SPFIR2	0.18	0.58	0.02	1.18
		DBH	0.23	-0.27	-0.52	-0.06
		MID	0.01	-0.07	-0.20	0.07
		SCOV	0.05	-0.18	-0.35	0.03
		SCOMP	0.08	-0.18	-0.32	-0.01
		LCR	0.01	0.08	-0.03	0.23
		Pa_int		-0.98	-1.68	-0.37
		DATE	1.00	-0.66	-1.06	-0.25
		DATE2	0.41	-0.66	-1.12	-0.16
		TIME	0.02	-0.10	-0.33	0.11
		Pp_int		31.04	24.41	42.92
		COVER	0.00	-0.02	-0.16	0.09
		NOISE	0.01	0.03	-0.09	0.16
		BAp	0.02	0.11	-0.17	0.32
SWTH	0.2	Lam_beta0		-0.74	-1.00	-0.48
		BA	0.01	-0.05	-0.12	0.06
		BA2	0.00	-0.04	-0.08	0.00
		SPFIR	0.36	0.12	0.04	0.20
		SPFIR2	0.01	0.17	-0.10	0.45
		DBH	0.00	-0.02	-0.09	0.05
		MID	0.13	0.09	0.03	0.16
		SCOV	0.21	0.11	0.04	0.18
		SCOMP	0.01	0.05	-0.03	0.13
		LCR	0.02	-0.07	-0.13	0.00
		Pa_int		0.22	0.12	0.32
		DATE	0.02	-0.11	-0.22	0.02
		DATE2	0.00	-0.17	-0.27	-0.06
		TIME	0.01	-0.03	-0.14	0.06
		Pp_int		35.79	30.54	43.79
		COVER	0.00	0.01	-0.04	0.06
		NOISE	0.08	0.08	0.02	0.16
		BAp	0.01	-0.03	-0.09	0.04
WIWR	0.75	Lam_beta0		-1.26	-1.64	-0.89
		BA	0.03	0.13	0.00	0.25
		BA2	0.00	0.03	-0.10	0.15
		SPFIR	0.31	-0.13	-0.22	-0.04

Table I.1 Continued.

		SPFIR2	0.01	-0.17	-0.52	0.10
		DBH	0.01	0.05	-0.04	0.14
		MID	0.00	0.01	-0.05	0.07
		SCOV	0.07	0.12	0.01	0.26
		SCOMP	0.29	0.13	0.05	0.21
		LCR	0.10	0.13	0.02	0.22
		Pa_int		0.59	0.46	0.72
		DATE	0.00	-0.01	-0.16	0.17
		DATE2	0.00	-0.15	-0.30	0.05
		TIME	0.01	0.04	-0.08	0.15
		Pp_int		34.06	27.99	42.91
		COVER	0.01	-0.03	-0.10	0.06
		NOISE	0.01	-0.03	-0.10	0.04
		BAp	0.01	0.05	-0.02	0.14
WTSP	0.65	Lam_beta0		-1.14	-1.46	-0.83
		BA	1.00	-0.98	-1.30	-0.57
		BA2	0.86	0.46	0.20	0.73
		SPFIR	0.34	-0.44	-0.68	-0.18
		SPFIR2	0.33	0.56	0.31	0.81
		DBH	0.00	-0.02	-0.08	0.01
		MID	1.00	-0.28	-0.37	-0.20
		SCOV	1.00	0.24	0.15	0.35
		SCOMP	0.01	-0.04	-0.11	0.03
		LCR	0.01	0.02	-0.06	0.09
		Pa_int		-0.02	-0.14	0.09
		DATE	0.00	-0.02	-0.11	0.09
		DATE2	0.00	-0.10	-0.10	-0.10
		TIME	0.25	0.17	0.05	0.28
		Pp_int		30.19	26.35	35.35
		COVER	0.00	-0.01	-0.05	0.02
		NOISE	0.01	0.04	0.00	0.08
		ВАр	0.98	0.15	0.07	0.25
YBFL	0.91	Lam_beta0		-1.51	-1.93	-1.11
		BA	0.13	-0.16	-0.29	-0.05
		BA2	0.00	0.10	-0.08	0.35
		SPFIR	0.01	-0.24	-0.65	0.12
		SPFIR2	0.01	0.47	0.13	0.74
		DBH	0.99	-0.24	-0.35	-0.14
		MID	0.02	-0.07	-0.15	0.01
		SCOV	0.09	0.13	0.03	0.23
		SCOMP	0.04	0.10	0.00	0.19
		LCR	0.05	0.12	0.01	0.23
		Pa_int		-0.15	-0.36	0.00

		DATE	0.15	-0.18	-0.40	0.19
		DATE2	0.02	-0.38	-0.74	-0.04
		TIME	0.04	0.14	-0.01	0.27
		Pp_int		29.18	24.04	36.01
		COVER	0.04	-0.08	-0.17	0.00
		NOISE	0.00	-0.02	-0.10	0.06
		BAp	0.26	-0.13	-0.23	-0.05
YPWA	0.34	Lam_beta0		-3.28	-4.04	-2.60
		BA	1.00	-1.53	-2.31	-0.98
		BA2	0.55	0.94	0.24	1.60
		SPFIR	0.00	0.01	-0.10	0.14
		SPFIR2	0.00	0.02	0.02	0.02
		DBH	0.01	-0.04	-0.13	0.04
		MID	0.75	-0.35	-0.58	-0.16
		SCOV	0.04	0.16	-0.03	0.37
		SCOMP	0.01	0.03	-0.16	0.16
		LCR	0.01	0.06	-0.07	0.21
		Pa_int		-0.48	-0.76	-0.23
		DATE	0.01	0.05	-0.41	0.93
		DATE2	0.00	-0.76	-1.45	0.16
		TIME	0.16	0.31	0.03	0.57
		Pp_int		20.03	15.49	24.78
		COVER	0.00	0.01	-0.04	0.09
		NOISE	0.01	-0.04	-0.14	0.03
		BAp	0.01	0.06	-0.06	0.19

Table I.1 Continued.

Table I.2 Treatment and YSH associations with avian abundance from single-species distance-removal models. We present mean coefficient estimates, 95% credible intervals (LCI and UCI), indicator variable weights (w), and Bayesian p-values (Bayesp) to evaluate model goodness-of-fit. Note that some parameters for covariates were not estimable because they received zero weight.

Species	Bayesp	Covariate	Weight	Mean	LCI	UCI
BBWA	0.8	YSH	0.13	-0.90	-2.09	0.83
		YSH2	0.02	-0.84	-2.61	1.00
		Mature		-2.33	-3.71	-0.97
		Selection		-3.34	-5.04	-1.80
		Shelterwood		-3.58	-5.14	-1.42
		Clearcut-only		-4.33	-6.45	-2.31
		Clearcut-herbicide		-2.20	-3.82	-0.67
		Clearcut-PCT		-3.88	-5.43	-2.46
		Clearcut-herbicide-PCT		-1.43	-3.09	0.07
		Pa_int		-0.34	-0.59	-0.10
		DATE	0.01	-0.09	-0.45	0.20
		DATE2	0.00	0.21	0.13	0.35
		TIME	0.02	0.10	-0.15	0.39
		Pp_int		17.69	15.98	19.47
		COVER	0.64	-0.10	-0.16	-0.05
		NOISE	0.00	0.02	-0.03	0.08
		BAp	0.01	0.04	-0.03	0.11
BLBW	0.82	YSH	0.06	0.43	-0.04	0.93
		YSH2	0.00	-0.23	-1.35	0.42
		Mature		-0.91	-1.49	-0.37
		Selection		-1.24	-1.96	-0.61
		Shelterwood		-0.84	-1.55	-0.36
		Clearcut-only		-0.93	-1.76	-0.16
		Clearcut-herbicide		-1.27	-2.09	-0.53
		Clearcut-PCT		-0.81	-1.36	-0.28
		Clearcut-herbicide-PCT		-2.29	-3.27	-1.39
		Pa_int		-1.63	-1.96	-1.18
		DATE	1.00	-1.07	-1.30	-0.76
		DATE2	0.03	0.23	-0.09	0.60
		TIME	0.01	0.04	-0.10	0.23
		Pp_int		20.81	18.66	23.34
		COVER	0.00	0.02	-0.04	0.08
		NOISE	0.00	0.02	-0.04	0.07
		ВАр	1.00	0.14	0.08	0.21

BLPW 0.78 YSH 0.85 -2.26 -4.25 -0.43 YSH2 0.11 -0.14 -3.29 3.47 Mature -4.26 -6.04 -2.48 -4.99 -7.18 -2.79 Selection Shelterwood -1.47 -4.50 0.88 Clearcut-only -4.35 -6.67 -2.11 -9.71 -3.48 Clearcut-herbicide -6.50 -5.89 Clearcut-PCT -4.05 -2.07 -5.47 -2.70 Clearcut-herbicide-PCT -8.46 Pa int -0.02 -0.38 0.32 DATE 0.01 0.12 -0.28 0.45 DATE2 0.00 0.02 -1.44 1.10 TIME 0.10 0.35 0.00 0.73 11.29 14.27 Pp_int 8.34 COVER 0.01 -0.07 -0.15 0.03 NOISE 0.01 -0.10 0.11 0.01 -0.45 BAp 1.00 -0.30 -0.15 BOCH 0.34 Psi 0.54 0.45 0.65 YSH -0.07 -0.75 0.45 0.02 YSH2 0.16 -0.58 1.09 0.00 Mature -0.86 -1.63 -0.14 $-1.1\overline{2}$ Selection -0.33 0.40 -0.30 -0.90 0.25 Shelterwood Clearcut-only -0.64 -1.63 0.31 Clearcut-herbicide -0.34 -1.20 0.49 Clearcut-PCT -0.34 -0.99 -1.68 Clearcut-herbicide-PCT 0.17 -0.64 0.95 -1.23 -1.53 -0.91 Pa int DATE 0.95 1.00 0.64 0.38 DATE2 0.19 -0.32 -0.58 -0.06 -0.39 TIME 0.06 -0.19 0.00 19.26 18.10 20.54 Pp int COVER -0.04 -0.08 0.00 0.01 NOISE 0.00 -0.02 -0.07 0.02 BAp 0.01 -0.04 -0.09 0.01 CAWA YSH 0.02 0.06 -0.66 0.82 0.83 YSH2 0.00 0.09 -1.14 1.60 -2.75 -3.66 Mature -1.92 Selection -1.48 -2.33 -0.65 -1.48 -2.10 -0.90 Shelterwood -1.52 -2.69 -0.45 Clearcut-only Clearcut-herbicide -3.06 -4.41 -1.85 Clearcut-PCT -1.22 -1.88 -0.58

Table I.2 Continued.

		Clearcut-herbicide-PCT		-2.34	-3.45	-1.31
		Pa_int		-0.41	-0.60	-0.24
		DATE	0.01	-0.05	-0.26	0.11
		DATE2	0.00	0.23	0.12	0.35
		TIME	0.01	0.01	-0.15	0.19
		Pp_int		21.12	17.97	24.52
		COVER	0.06	-0.08	-0.14	-0.02
		NOISE	0.01	0.03	-0.05	0.11
		BAp	0.04	-0.07	-0.13	-0.01
CMWA	0.33	YSH	0.10	0.58	-2.35	1.84
		YSH2	0.02	1.23	-1.37	3.29
		Mature		-3.74	-5.85	-1.98
		Selection		-11.13	-18.36	-3.93
		Shelterwood		-4.25	-7.10	-2.19
		Clearcut-only		-4.94	-10.55	-1.90
		Clearcut-herbicide		-3.89	-6.74	-1.47
		Clearcut-PCT		-3.50	-5.85	-1.50
		Clearcut-herbicide-PCT		-4.12	-6.95	-1.72
		Pa_int		-2.24	-4.72	0.03
		DATE	0.59	-1.70	-2.79	-0.22
		DATE2	0.09	0.49	-2.70	4.58
		TIME	0.06	0.36	-0.52	1.17
		Pp_int		20.65	8.61	72.92
		COVER	0.03	-0.08	-2.25	2.79
		NOISE	0.02	-0.20	-1.75	0.39
		BAp	0.30	-0.56	-2.46	-0.09
GCKI	1	YSH	0.01	0.04	-0.51	0.29
		YSH2	0.00	0.20	-0.19	0.64
		Mature		0.37	-0.04	0.76
		Selection		0.52	0.10	0.93
		Shelterwood		0.62	0.25	0.99
		Clearcut-only		-0.09	-0.58	0.40
		Clearcut-herbicide		0.63	0.19	1.06
		Clearcut-PCT		0.41	0.02	0.79
		Clearcut-herbicide-PCT		0.59	0.16	1.03
		Pa_int		-0.49	-0.60	-0.39
		DATE	0.04	-0.12	-0.22	0.00
		DATE2	0.00	-0.16	-0.31	-0.01
		TIME	0.01	-0.03	-0.13	0.06
		Pp_int		17.97	17.13	18.89
		COVER	0.01	-0.02	-0.04	0.00
		NOISE	0.00	0.02	0.00	0.04
		BAp	0.13	0.04	0.01	0.06

Table I.2 Continued.

Table I.2 Continued.

GRAJ	0.19	Psi		0.09	0.06	0.14
		YSH	0.04	0.62	-0.22	2.50
		YSH2	0.01	-0.83	-2.85	0.63
		Mature		-0.96	-2.76	0.52
		Selection		0.82	-0.81	2.14
		Shelterwood		-0.10	-1.81	1.22
		Clearcut-only		-9.15	-22.43	-1.89
		Clearcut-herbicide		-1.25	-3.35	0.58
		Clearcut-PCT		-0.01	-1.67	1.35
		Clearcut-herbicide-PCT		0.09	-1.71	1.56
		Pa_int		-1.35	-2.09	-0.80
		DATE	0.25	1.30	0.19	2.21
		DATE2	0.21	-1.23	-1.98	-0.46
		TIME	0.03	-0.16	-0.62	0.29
		Pp_int		18.59	14.96	22.75
		COVER	0.04	-0.13	-0.30	0.01
		NOISE	0.01	-0.05	-0.24	0.08
		BAp	0.00	-0.01	-0.12	0.10
HETH	0.16	YSH	0.01	-0.01	-0.33	0.31
		YSH2	0.00	-0.27	-0.57	-0.07
		Mature		-0.64	-1.19	-0.10
		Selection		-1.29	-1.89	-0.72
		Shelterwood		-1.14	-1.69	-0.62
		Clearcut-only		-1.17	-1.82	-0.53
		Clearcut-herbicide		-1.61	-2.27	-0.99
		Clearcut-PCT		-1.02	-1.57	-0.49
		Clearcut-herbicide-PCT		-0.86	-1.48	-0.26
		Pa_int		0.18	0.07	0.29
		DATE	0.01	0.07	-0.04	0.17
		DATE2	0.00	0.04	0.04	0.04
		TIME	0.01	0.05	-0.06	0.18
		Pp_int		39.54	33.45	49.09
		COVER	0.07	-0.10	-0.19	-0.01
		NOISE	0.01	-0.04	-0.12	0.06
		BAp	0.03	0.10	-0.01	0.21
MAWA	1	YSH	0.01	0.00	-0.51	0.27
		YSH2	0.00	0.37	0.03	0.81
		Mature		0.28	-0.05	0.60
		Selection		0.72	0.38	1.06
		Shelterwood		0.66	0.38	0.94
		Clearcut-only		0.39	-0.02	0.80
		Clearcut-herbicide		0.38	-0.01	0.78
		Clearcut-PCT		0.57	0.28	0.87

		Clearcut-herbicide-PCT		0.46	0.08	0.84
		Pa_int		0.08	0.00	0.15
		DATE	0.00	-0.01	-0.08	0.05
		DATE2	0.00			
		TIME	0.01	0.06	-0.01	0.12
		Pp_int		21.84	20.40	23.43
		COVER	0.00	-0.01	-0.03	0.01
		NOISE	0.00	0.01	-0.02	0.03
		ВАр	1.00	-0.05	-0.07	-0.03
MYWA	0.36	YSH	0.02	-0.29	-1.34	0.36
		YSH2	0.01	0.79	0.21	1.33
		Mature		-1.08	-1.60	-0.54
		Selection		-0.63	-1.18	-0.10
		Shelterwood		-0.61	-1.10	-0.14
		Clearcut-only		-1.01	-1.66	-0.37
		Clearcut-herbicide		-0.74	-1.33	-0.15
		Clearcut-PCT		-0.93	-1.43	-0.43
		Clearcut-herbicide-PCT		-0.30	-0.86	0.25
		Pa_int		-0.56	-0.70	-0.43
		DATE	0.01	-0.14	-0.34	0.04
		DATE2	0.00	0.32	0.15	0.55
		TIME	0.01	-0.06	-0.19	0.07
		Pp_int		27.12	23.57	31.60
		COVER	0.00	-0.03	-0.08	0.02
		NOISE	0.00	0.02	-0.03	0.08
		BAp	0.01	0.02	-0.04	0.08
OSFL	0.4	YSH	0.07	1.68	-0.52	5.98
		YSH2	0.03	-2.27	-4.96	0.50
		Mature		-6.35	-8.36	-4.56
		Selection		-4.23	-5.72	-2.79
		Shelterwood		-4.29	-6.04	-3.24
		Clearcut-only		-10.31	-17.10	-5.36
		Clearcut-herbicide		-5.43	-8.49	-3.20
		Clearcut-PCT		-4.55	-5.94	-3.35
		Clearcut-herbicide-PCT		-4.92	-7.11	-2.94
		Pa_int		-0.15	-0.91	0.35
		DATE	0.05	1.05	-0.38	2.57
		DATE2	0.03	-2.12	-3.47	-0.63
		TIME	0.02	0.04	-0.44	0.59
		Pp_int		130.01	14.34	243.61
		COVER	0.16	-0.79	-5.21	4.44
		NOISE	0.15	0.87	-3.14	5.83
		ВАр	1.00	-7.85	-18.44	-1.59

Table I.2 Continued.

Table I.2 Continued.

RBNU	0.35	YSH	0.01	0.13	-0.23	0.46
		YSH2	0.00	-0.23	-0.54	0.37
		Mature		-1.32	-1.84	-0.81
		Selection		-1.22	-1.78	-0.69
		Shelterwood		-1.04	-1.50	-0.60
		Clearcut-only		-1.41	-2.11	-0.74
		Clearcut-herbicide		-1.29	-1.91	-0.70
		Clearcut-PCT		-0.97	-1.46	-0.51
		Clearcut-herbicide-PCT		-1.27	-1.87	-0.68
		Pa_int		-0.80	-1.05	-0.56
		DATE	0.97	0.41	0.22	0.61
		DATE2	0.01	0.02	-0.21	0.23
		TIME	0.01	-0.04	-0.19	0.12
		Pp_int		33.92	28.01	43.69
		COVER	0.00	0.00	-0.09	0.10
		NOISE	0.01	0.06	-0.03	0.15
		BAp	0.38	0.12	0.05	0.20
RCKI	0.75	YSH	0.02	0.11	-0.94	0.64
		YSH2	0.00	0.67	-0.23	1.52
		Mature		-2.58	-3.48	-1.73
		Selection		-1.83	-2.73	-1.01
		Shelterwood		-2.06	-2.90	-1.33
		Clearcut-only		-1.55	-2.56	-0.61
		Clearcut-herbicide		-1.52	-2.52	-0.60
		Clearcut-PCT		-2.07	-2.94	-1.29
		Clearcut-herbicide-PCT		-1.99	-3.02	-1.04
		Pa_int		-1.23	-1.87	-0.54
		DATE	1.00	-0.73	-1.15	-0.32
		DATE2	0.61	-0.71	-1.17	-0.24
		TIME	0.02	-0.13	-0.35	0.09
		Pp_int		29.56	24.08	38.74
		COVER	0.01	-0.04	-0.14	0.07
		NOISE	0.01	0.03	-0.09	0.15
		ВАр	0.69	-0.20	-0.34	-0.09
SWTH	0.21	YSĤ	0.01	0.17	-0.14	0.48
		YSH2	0.00	0.09	-0.31	0.39
		Mature		-1.01	-1.42	-0.62
		Selection		-0.64	-1.06	-0.22
		Shelterwood		-0.64	-0.99	-0.31
		Clearcut-only		-0.33	-0.82	0.15
		Clearcut-herbicide		-0.57	-1.03	-0.11
		Clearcut-PCT		-1.07	-1.45	-0.70
		Clearcut-herbicide-PCT		-0.67	-1.13	-0.22

Table I.2 Continued.

		Pa_int		0.22	0.12	0.32
		DATE	0.02	-0.11	-0.23	0.04
		DATE2	0.00	-0.16	-0.30	0.01
		TIME	0.01	-0.05	-0.14	0.05
		Pp_int		35.91	30.64	43.73
		COVER	0.00	0.00	-0.05	0.05
		NOISE	0.08	0.09	0.02	0.16
		BAp	0.01	-0.03	-0.10	0.02
WIWR	0.74	YSH	0.03	0.39	-0.04	1.73
		YSH2	0.01	-0.66	-1.45	0.19
		Mature		-1.46	-1.99	-0.95
		Selection		-1.15	-1.71	-0.60
		Shelterwood		-1.10	-1.60	-0.65
		Clearcut-only		-1.06	-1.69	-0.45
		Clearcut-herbicide		-1.38	-2.03	-0.77
		Clearcut-PCT		-1.12	-1.60	-0.65
		Clearcut-herbicide-PCT		-2.12	-2.82	-1.45
		Pa_int		0.59	0.47	0.71
		DATE	0.00	-0.01	-0.15	0.18
		DATE2	0.00	-0.07	-0.26	0.12
		TIME	0.01	0.04	-0.09	0.19
		Pp_int		34.45	28.30	43.87
		COVER	0.01	-0.02	-0.09	0.05
		NOISE	0.01	-0.03	-0.10	0.04
		BAp	0.01	0.05	-0.03	0.13
WTSP	0.74	YSH	0.02	0.11	-0.51	0.71
		YSH2	0.00	0.12	-0.93	1.37
		Mature		-1.59	-2.23	-0.99
		Selection		-0.48	-1.13	0.15
		Shelterwood		-0.94	-1.45	-0.46
		Clearcut-only		-0.41	-1.20	0.36
		Clearcut-herbicide		-0.83	-1.59	-0.08
		Clearcut-PCT		-0.45	-0.96	0.05
		Clearcut-herbicide-PCT		-1.17	-1.92	-0.42
		Pa_int		-0.02	-0.14	0.09
		DATE	0.00	-0.03	-0.12	0.07
		DATE2	0.00	-0.11	-0.11	-0.11
		TIME	0.26	0.17	0.06	0.28
		Pp_int		25.37	23.24	28.40
		COVER	0.00	0.00	-0.04	0.04
		NOISE	0.14	0.07	0.02	0.12
		BAp	1.00	-0.17	-0.22	-0.13
YBFL	0.91	YSH	0.01	-0.10	-0.86	0.42

1 4010 112	001111140					
		YSH2	0.00	0.28	-0.55	1.16
		Mature		-2.02	-2.66	-1.40
		Selection		-1.17	-1.82	-0.54
		Shelterwood		-1.45	-2.00	-0.93
		Clearcut-only		-1.11	-1.87	-0.35
		Clearcut-herbicide		-1.77	-2.57	-0.99
		Clearcut-PCT		-1.52	-2.09	-0.96
		Clearcut-herbicide-PCT		-1.18	-1.93	-0.48
		Pa_int		-0.15	-0.36	0.00
		DATE	0.16	-0.19	-0.39	0.17
		DATE2	0.02	-0.38	-0.75	0.01
		TIME	0.05	0.14	0.00	0.27
		Pp_int		28.38	23.11	35.06
		COVER	0.03	-0.08	-0.15	0.00
		NOISE	0.01	-0.02	-0.09	0.05
		ВАр	0.71	-0.16	-0.26	-0.07
YPWA	0.94	YSH	0.05	-1.28	-4.40	0.79
		YSH2	0.03	2.20	0.53	3.95
		Mature		-4.13	-5.66	-2.82
		Selection		-1.51	-2.71	-0.43
		Shelterwood		-2.61	-3.68	-1.65
		Clearcut-only		-2.74	-4.35	-1.26
		Clearcut-herbicide		-3.45	-5.38	-1.79
		Clearcut-PCT		-2.41	-3.52	-1.41
		Clearcut-herbicide-PCT		-2.63	-4.14	-1.25
		Pa_int		-0.48	-0.76	-0.24
		DATE	0.01	0.06	-0.27	0.81
		DATE2	0.00	-0.66	-1.37	0.29
		TIME	0.18	0.31	0.04	0.57
		Pp_int		13.48	9.67	17.65
		COVER	0.01	0.03	-0.07	0.13
		NOISE	0.01	-0.06	-0.15	0.03
		BAp	1.00	-0.34	-0.45	-0.25

Table I.2 Continued.

APPENDIX J. THE MEAN NUMBER OF DETECTIONS PER SURVEY FOR 19 FOCAL BIRD SPECIES IN EACH HARVEST TREATMENT IN NEW HAMPSHIRE, VERMONT, AND,

MAINE DURING 2013, 2014, AND 2015.

Table J.1. The mean number of detections per survey for 19 focal bird species in each harvest treatment calculated from raw detection data. Zeroes with no decimal places indicate that a species was not detected in that harvest treatment.

	Treatment								
Species	Mature	Selection	Shelterwood	Clearcut-	Clearcut-	Clearcut-	Clearcut-		
_				only	herbicide	PCT	herbicide-		
							PCT		
BBWA	0.03	0.04	0.09	0.17	0.11	0.06	0.04		
BLBW	0.15	0.09	0.15	0.10	0.06	0.10	0.05		
BLPW	0.05	0.04	0.01	0.004	0.01	0.04	0.06		
BOCH	0.12	0.13	0.13	0.15	0.15	0.1	0.07		
CAWA	0.13	0.17	0.01	0.03	0.16	0.22	0.29		
CMWA	0.004	0.006	0.003	0.017	0	0.016	0.004		
GCKI	0.50	0.43	0.36	0.53	0.46	0.43	0.27		
GRAJ	0.05	0.02	0.03	0.02	0.03	0.03	0.05		
HETH	0.27	0.26	0.34	0.34	0.25	0.43	0.25		
MAWA	0.70	0.73	0.41	0.50	0.86	0.71	0.75		
MYWA	0.31	0.24	0.18	0.27	0.25	0.25	0.33		
OSFL	0.01	0.01	0.01	0.02	0.04	0.03	0.004		
RBNU	0.26	0.18	0.21	0.23	0.19	0.15	0.08		
RCKI	0.08	0.07	0.04	0.09	0.10	0.06	0.13		
SWTH	0.41	0.33	0.31	0.36	0.32	0.27	0.28		
WIWR	0.26	0.22	0.16	0.20	0.26	0.32	0.06		
WTSP	0.21	0.36	0.10	0.34	0.46	0.17	0.55		
YBFL	0.21	0.18	0.08	0.07	0.21	0.22	0.39		
YPWA	0.06	0.07	0	0.01	0.17	0.05	0.11		

APPENDIX K. JAGS MODEL CODE FOR MULTI-SPECIES DISTANCE-

REMOVAL MODEL WITH EDGE EFFECTS.

HYPERPARAMETERS AMONG SPECIES

```
pp.beta0.mu ~ dnorm(0, 0.01)
pp.beta0.tau <- 1/ (pp.beta0.sigma * pp.beta0.sigma)
pp.beta0.sigma ~ dunif(0,10)
```

```
pp.beta1.mu ~ dnorm(0, 0.01)
pp.beta1.tau <- 1/ (pp.beta1.sigma * pp.beta1.sigma)
pp.beta1.sigma ~ dunif(0,10)
```

```
for (e in 1:3){ # edge effect on abundance
lam.beta0.mu[e] ~ dnorm(0, 0.01)
lam.beta0.tau[e] <- 1/ (lam.beta0.sigma[e] * lam.beta0.sigma[e])
lam.beta0.sigma[e] ~ dunif(0,10)
}</pre>
```

```
stand.tau <- 1/(stand.sig*stand.sig)
stand.sig ~ dunif(0,10)
treat.tau <- 1/(treat.sig*treat.sig)</pre>
```

```
treat.sig ~ dunif(0,10)
ag.tau <- 1/(ag.sig*ag.sig)
ag.sig ~ dunif(0,10)
yr.tau <- 1/(yr.sig^yr.sig)
yr.sig ~ dunif(0,10)
```

```
# and links to hyperparameters
for(sp in 1:SPP){
 logit(p.a[sp]) \le pa.beta0[sp]
 pa.beta0[sp] ~ dnorm(pa.beta0.mu, pa.beta0.tau)
 pp.beta0[sp] ~ dnorm(pp.beta0.mu, pp.beta0.tau)
 pp.beta1[sp] ~ dnorm(pp.beta1.mu, pp.beta1.tau)
 w[sp]~ dbern(psi[sp])
 psi[sp] \sim dunif(0,1)
 for (e in 1:3){lam.beta0[e, sp] ~ dnorm(lam.beta0.mu[e], lam.beta0.tau[e])}
# Removal
  for (j in 1:J){ # r is time interval here need to change to j
   pi.pa[sp,j] <- p.a[sp]*pow(1-p.a[sp], (j-1))
   pi.pa.c[sp,j] <- pi.pa[sp,j]/sum(pi.pa[sp,1:J])
   } #J
for (i in 1:nsites){
# Distance
    for(b in 1:nD){
       g[i,sp,b] <- exp(-midpt[b]*midpt[b]/(2*dist.sigma[i,sp]*dist.sigma[i,sp])) # half-
normal #distance function
      f[i,sp,b] <- (2*midpt[b]*delta)/(B*B) # radial density #function for point
counts, #change for line transects
       pi.pd[i,sp,b] <- g[i,sp,b]*f[i,sp,b]
      pi.pd.c[i,sp,b] <- pi.pd[i,sp,b]/sum(pi.pd[i,sp,1:nD])
       } #nD
# Detection model for distance sampling
log(dist.sigma[i,sp]) <- log(pp.beta0[sp]) + pp.beta1[sp]*ba[i]
# combine distance and removal sampling
 for(t in 1:YR){
```

```
pcap[i,t,sp] <- sum(pi.pa[sp,1:J])</pre>
```
```
E.p[i,t,sp] <- pow((nobs[i,t,sp]- e.p[i,t,sp]),2)/(e.p[i,t,sp]+0.5)
E.New.p[i,t,sp]<- pow((nobs.fit[i,t,sp]-e.p[i,t,sp]),2)/(e.p[i,t,sp]+0.5)
```

}} #YR #nsites

Ntot[t,sp] <- sum(N[1:nsites,t,sp])
D[t,sp] <- Ntot[t,sp] / (3.14159*B*B*nsites/10000) # Abundance per #hectare
} #YR
} # SPP</pre>

```
omx[i,sp] <- max(occ[i,1:YR,sp]) # All species
} #SPP</pre>
```

```
# 2. sum occurrence within species groups (G#) at each site
r[1,i] <- sum(omx[i,G1]) # All species
r[2,i] \le sum(omx[i,G2]) # early
r[3,i] <- sum(omx[i,G3]) # late
r[4,i] <- sum(omx[i,G4]) # decid
r[5,i] <- sum(omx[i,G5]) # conif
r[6,i] <- sum(omx[i,G6]) # spfir obligate
r[7,i] <- sum(omx[i,G7]) # spfir associate
r[8,i] <- sum(omx[i,G8]) # spfir
r[9,i] <- sum(omx[i,G9]) # early decid
r[10,i] <- sum(omx[i,G10]) # early conif
r[11,i] <- sum(omx[i,G11]) # early spfir, only 1 sp
r[12,i] \le sum(omx[i,G12]) # late decid
r[13,i] \le sum(omx[i,G13]) # late conif
r[14,i] <- sum(omx[i,G14]) # late spfir
} # nsites
```

```
# 3. Calculate mean richness for edge categories
for (zz in 1:14){ #14 species groups
rmn[zz,1] <- mean(r[zz,e1])
rmn[zz,2] <- mean(r[zz,e2])
rmn[zz,3] <- mean(r[zz,e3])
} #zz</pre>
```

fit.p <- sum(E.p[1:nsites,1:YR,1:SPP])
fit.new.p <- sum(E.New.p[1:nsites,1:YR,1:SPP])
bayesp<-step(fit.new.p-fit.p) # Bayesian p-value for availability model. =0.5 #is good fit,
near 0 or # 1 is poor fit</pre>

APPENDIX L. DETECTION PROBABILITY ESTIMATES FROM MULTI-SPECIES DISTANCE-REMOVAL MODEL USING DATA COLLECTED FROM NEW HAMPSHIRE, VERMONT, AND MAINE DURING

2013, 2014, AND 2015.

Figure L.1. Detection probability estimates (y-axis) for availability, perceptibility, availability and perceptibility combined, and 72 simulated detection probabilities from model estimates.



APPENDIX M. DO RELATIONSHIPS BETWEEN ABUNDANCE AND VEGETATION CHARACTERISTICS REFLECT REPRODUCTIVE SUCCESS? A CASE STUDY OF THE BAY-BREASTED WARBLER (SETOPHAGA CASTANEA)

Introduction

Wildlife studies often investigate relationships between abundance and vegetation to assess the importance of habitat for wildlife, because these data can be less costly to accrue compared to detailed demographic rates (Johnson 2007). These studies are justified because habitat selection plays a pivotal role in subsequent demographic rates (Germain et al. 2018), and often has positive correlations with other demographic rates that contribute to habitat quality such as survival and fecundity (Bock and Jones 2004). Studies of occupancy and abundance frequently include the caveat that relationships between abundance and habitat may not reflect habitat quality because ecological traps exist (Van Horne 1983), where individuals select for habitat that provides poor demographic rates (e.g., Weakland and Wood 2005, Weldon and Haddad 2005). Several methods have been proposed to address this weakness in habitat selection studies (reviewed by Johnson 2007), but researchers rarely address this problem empirically. Conclusions within this dissertation relied on measures of species abundances or richness across species to make inferences regarding habitat quality. Here, we evaluate patterns of abundance by Bay-breasted Warbler, Setophaga castanea (hereafter BBWA), and compare these with trends of reproductive success to gain insight into differences in

habitat quality among sites with different compositional and structural characteristics of vegetation for a species with regionally declining populations (Sauer et al. 2017).

Methods

Abundance

We collected detection data for the BBWA using passive point count surveys at seven study sites in New Hampshire, Vermont, and Maine including four National Wildlife Refuges (Nulhegan Division of Silvio O. Conte, Umbagog, Aroostook, and Moosehorn), a state park (Baxter), and private lands (Telos and Clayton Lake). Information about study areas and survey locations is presented in Chapter 1.

We analyzed point count detection data using single species distance removal abundance models (Amundson et al. 2014). Our analysis is fully described in the Methods section of Chapter 2. We excluded data from flyover detections, and we truncated detections that were >50 m from the center of point count locations. This analysis detected associations between detection corrected abundance of BBWA and vegetation characteristics including spruce-fir composition, shrub cover, live-crown ratio, and midstory cover.

Reproductive success

We conducted reproductive success surveys for Bay-breasted Warbler at the Telos study site in Maine during the BBWA breeding season (Venier et al. 2011) from 2 June to 27 July 2015, because this site contained the majority of detections from regional point count surveys. We returned to point count locations (43 total) where BBWA were previously detected during point count surveys that were conducted in 2013 and 2014. We classified evidence of reproduction into 19 categories (Table M.1) that were compiled from previous studies (Vickery and Hunter 1992, Lackey et al. 2011) and citizen science programs (e.g., Breeding Bird Atlas and Ebird). We recorded the maximum reproductive success for each 10 minute interval (i.e., 0–10, 10–20, 20–30, 40–50, 50–60 minutes) during a visit.

Table M.1. Breeding codes used for Bay-breasted Warbler reproductive index surveys. Surveys were adapted from Ebird protocols, Vickery and Hunter (1992), and Lackey et al. (2011). Surveyors returned to point count locations in 2015 where Bay-breasted Warbler were previously detected in 2013 or 2014. Reproductive index surveys were conducted for a duration of 60 minutes. For each survey, we recorded the breeding code for the minimum breeding index hierarchy (i.e., the breeding code with hierarchy closest to one).

Code	Description	Level	Hierarchy
FY	FEEDING FLEDGED YOUNG	CONFIRMED SURVIVAL	1
FL	RECENTLY FLEDGED YOUNG	CONFIRMED SURVIVAL	2
NY	NEST WITH YOUNG	CONFIRMED	3
NE	NEST WITH EGGS	CONFIRMED	4
ON	OCCUPIED NEST	CONFIRMED	5
CS	CARRYING FECAL SAC	CONFIRMED	6
CF	CARRYING FOOD	CONFIRMED	7
DD	DISTRACTION DISPLAY	CONFIRMED	8
	BROOD PATCH AND		
PE	PHYSIOLOGICAL EVIDENCE	CONFIRMED	9
NB	NEST BUILDING	CONFIRMED/PROBABLE	10
	CARRYING NESTING		
CN	MATERIAL	CONFIRMED/PROBABLE	11
	TERRITORY HELD FOR 7+		
Т	DAYS	PROBABLE	12
	COURTSHIP, DISPLAY, OR		
С	COPULATION	PROBABLE	13
	VISITING PROBABLE NEST		
N	SITE	PROBABLE	14
А	AGITATED BEHAVIOR	PROBABLE	15
Р	PAIR IN SUITABLE HABITAT	PROBABLE	16
S	SINGING MALE	POSSIBLE	17
Н	IN APPROPRIATE HABITAT	POSSIBLE	18
NR	NOT RECORDED	NO INFO	19

We conducted adaptive reproductive success surveys that varied in duration up to 90 min. Reproductive success surveys began with a basic survey for a duration of 60 minutes, and these surveys were terminated immediately if breeding was confirmed. The basic survey began at the point count center where BBWA were previously detected during point count surveys. Two surveyors tracked unmarked Bay-breasted Warbler (an individual or co-occurring pair) that were closest proximity to the point count center, and conducted a joint search for evidence of reproduction. We broadcasted a mixed recording of BBWA territorial songs and calls for a duration between 1–5 minutes in two circumstances: 1) when surveyors conducted a basic search for 30 min and did not detect BBWA, and 2) when surveyors conducted a basic search for the full duration of 60 min, detected BBWA, but did not observe evidence of reproduction. In the latter circumstance, survey duration could be extended up to 90 min. The point count location was not revisited if we observed fledged young; however, if we did not observe fledglings then we returned the point count location (ranging from one to three visits total) on a different day to conduct subsequent surveys, because evidence of breeding could remain undetected as a result of secretive nesting behavior or a mistimed visit.

We reclassified reproductive success data (Table M.2) into two categories of reproductive success, whether breeding or greater evidence was observed (i.e., "CONFIRMED", hierarchy \leq 9, Table M.1) or whether successfully fledged young or greater evidence was observed (i.e., hierarchy \leq 2, Table M.1). We used generalized linear models with binomial distributions to test for associations between the probability of successfully fledging young and breeding in response to vegetation variables that were important in abundance analyses including spruce-fir composition, shrub cover, live-

crown ratio, and midstory cover. We used 85% confidence intervals to reduce the probability of Type II error as a result of small sample sizes, and we determined covariates to be significant when confidence intervals did not intersect zero.

Comparing abundance and reproductive success

We plotted responses of reproductive success to vegetation covariates, and we compared these to responses by abundance to vegetation covariates. We assessed whether BBWA had similar direction (positive or negative) of relationships with vegetation covariates for reproductive success and abundance.

Results

Fledging success and breeding success had similar associations with spruce-fir tree composition when compared to relationships with abundance (Fig. M.1), i.e., both had increased with greater spruce-fir tree composition. Other vegetation characteristics including shrub cover, live-crown ratio, and midstory cover did not have significant associations with fledging and breeding success; however, the average non-significant response to these covariates were similar in direction, and similar in magnitude for shrub cover and live-crown ratio (Fig. M.1). Fledging and breeding success had positive and negative associations, respectively, with midstory cover, but lacked significance. We conclude that associations between vegetation variables and abundance of BBWA generally reflects relationships between vegetation and reproductive success.

Summary

Directions of associations (positive or negative) between reproductive success and vegetation characteristics for BBWA largely reflect associations between abundance and vegetation characteristics., except where slope coefficients were smaller in magnitude

(e.g., midstory) and would require greater statistical power to detect an association. However, several vegetation characteristics that were significantly associated with abundance did not have significant associations with reproductive success. Here, the lack of associations between vegetation characteristics and reproductive success could be a function of statistical power, because we obtained relatively small sample sizes for reproductive success. Greater sample sizes are needed to clarify associations between vegetation characteristics and reproductive success, but our results demonstrate that maladaptive habitat selection or ecological traps, where individuals prefer habitat that provides poor demographic rates (Van Horne 1983), are unlikely to occur for the BBWA at out study sites. Furthermore, our results are consistent with a previous literature review which concluded that greater abundance and occupancy tend to correlate with improved demographic rates (Bock and Jones 2004).

Our adaptive survey was an effective method for gaining insight into reproductive success of passerine birds that can be elusive and challenging to track in dense forests. Future studies could achieve greater inference about habitat quality by using our methods combined with greater survey effort (two observers used here), or by conducting a similar study over a longer duration for multiple years.

Visit 1 Visit 2 Visit 3 Point 0-10-20-30-40-50-0-10-20-30-40-50-0-10-20-30-40-50-# 10 20 30 40 50 60 10 20 30 40 50 60 10 20 30 40 50 60 382 NR NR NR NR NR NR ---_ _ -------383 NR NR NR NR NR NR ------_ ---_ -NR S S S 403 S _ _ _ _ _ _ _ _ _ _ -_ _ S S S S FL S 404 _ _ --_ _ _ _ _ -_ _ S S Ρ Р FY 410 S _ _ _ _ _ _ _ _ -_ -S S S S S S 411 S S Η FL S S _ _ _ _ _ _ S S S S S S S S S S 412 Η S _ ---_ -S NR S S S NR NR NR Н S Η S 413 ---_ _ _ S 414 NR NR NR S NR NR NR S S NR S ------428 S S FY -_ ------_ ----_ -NR NR NR NR NR NR 433 _ -_ _ _ -_ _ _ _ _ _ S S S S 434 S S S S S NR S S _ --_ _ _ NR NR NR NR NR 436 S S S NR NR NR NR _ -_ _ _ _ S S S S S S S S Ρ S NR NR FL 437 --_ -S 438 S S S S S NR NR NR S S NR _ _ -_ -Р 439 S S S NR NR _ ---_ _ _ _ _ _ _ -440 NR NR NR NR NR FL --_ ---------441 S S S S S S _ _ _ _ -_ ---_ _ -

Table M.2. Data from Bay-breasted Warbler reproductive index surveys in 2015. Codes correspond to reproductive indices in Table M.1. Columns under each visit indicate the time interval (minutes) for each survey visit. Hyphens indicate that a survey did not occur during that time interval.

Table M.2 Continued.

442	S	NR	NR	S	NR	NR	NR	NR	NR	FL	Н	-	-	-	-	-	-	-
443	S	S	S	NR	S	S	S	NR	NR	S	S	S	NR	NR	NR	CF	-	-
446	NR	NR	NR	NR	NR	NR	-	-	-	-	-	-	-	-	-	-	-	-
467	NR	NR	NR	NR	-	NR	-	-	-	-	-	-	-	-	-	-	-	-
546	NR	NR	NR	NR	S	S	-	-	-	-	-	-	-	-	-	-	-	-
624	NR	S	S	Α	S	NR	-	-	-	-	-	-	-	-	-	-	-	-
643	NR	S	NR	NR	NR	NR	FL	S	S	S	S	S	-	-	-	-	-	-
644	NR	NR	NR	S	S	S	NR	S	S	NR	NR	S	-	I	-	-	I	-
651	NR	NR	NR	NR	NR	NR	-	-	-	-	-	-	-	-	-	-	-	-
653	NR	NR	NR	NR	NR	NR	-	-	-	-	-	-	-	-	-	-	-	-
657	NR	NR	FL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
658	NR	NR	NR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
661	NR	S	S	S	S	NR	-	I	-	-	I	-						
664	S	NR	S	S	S	S	-	I	-	I	-	-	-	I	-	-	I	-
670	NR	NR	NR	S	Р	FY	-	-	-	-	-	-	-	-	-	-	-	-
673	NR	NR	NR	NR	NR	NR	-	I	-	1	-	I	-	I	-	-	I	-
674	NR	-	-	-	-	-	-											
675	NR	NR	NR	S	S	S	-	I	-	1	-	I	-	I	-	-	I	-
676	S	S	S	S	S	S	-	I	-	1	-	I	-	I	-	-	I	-
681	Р	Р	S	S	S	S	S	S	NR	S	S	S	-	I	-	-	I	-
682	S	S	S	S	S	S	-	I	-	-	-	-	-	I	-	-	I	-
683	S	S	S	S	NR	NR	Н	S	NR	NR	NR	NR	-	-	-	-	-	-
716	NR	NR	NR	NR	NR	NR	-	-	-	-	-	-	-	-	-	-	-	-
724	NR	NR	NR	NR	NR	NR	S	FY	-	-	-	-	-	-	-	-	-	-
725	S	S	S	NR	S	NR	Н	Н	Н	Н	NR	FL	-	-	-	-	-	-

Figure M.1. A comparison of relationships for Bay-breasted Warbler between abundance collected during point count surveys conducted during 2013–2015 (see Chapter 2) and breeding indices collected during 2015 in the Telos Region of north central Maine, USA (Fig. 2.1), and their relationships with vegetation variables. Solid lines indicate that 85% CIs for slope coefficients did not intersect zero. Gray polygons depict predictions for 85% CIs. Reproductive success surveys occurred at 42 point count locations where evidence of breeding was observed at 14 point count locations and fledglings were observed at 12 point count locations. Tick marks at the top (1=success) and bottom (0=failure) of each plot represent response data for breeding and fledgling success, jittered for clarity.



APPENDIX N. A MAP OF ROAD EDGES WITH A 100 M BUFFER AT THE TELOS FIELD SITE, MAINE.

Figure N.1. A map of road edges with a 100 m buffer applied to depict the potential extent of road edge effects at the Telos study site. Road polygons were obtained from Katahdin Forest Management.



APPENDIX O. LOCATION OF ARCHIVED DATA COLLECTED DURING THIS STUDY IN NEW HAMPSHIRE, VERMONT, AND MAINE DURING 2013, 2014, AND 2015.

Scripts used in this manuscript are archived with the authors BWR and CSL at the Maine Cooperative Fish and Wildlife Research Unit, and a subset of data are available at https://doi.org/10.5066/F76Q1W53.

BIOGRAPHY OF THE AUTHOR

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