Avian communities of managed and unmanaged boreal forests

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Edmund Joseph Zlonis

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Dedication

This thesis is dedicated to my brother, Oliver Zlonis.

Abstract

I compared the breeding bird communities of managed and unmanaged boreal forests in northeastern Minnesota. Birds were sampled in the spring and summer of 2010 and 2011 in the Superior National Forest (SNF, managed landscape) and Boundary Waters Canoe Area Wilderness (BWCAW, unmanaged landscape). Twelve point counts were completed along each of 10 paired transects for a total of 240 points, 120 points within each of the SNF and BWCAW. The total number of individuals detected per point was significantly higher within the BWCAW ($F=9.76$, $p=0.01$). Avian species richness per point was also significantly higher within the BWCAW ($F=11.17$, $p<0.01$). These results were negatively correlated with increased amounts of regenerating forests (mainly from logging) and positively correlated with tree species richness and canopy height of forest stands. Eight species were more common in the BWCAW compared with the SNF (black-capped chickadee (*Poecile atricapillus*), brown creeper (*Certhia americana*), Canada warbler (*Cardellina canadensis*), golden-crowned kinglet (*Regulus satrapa*), least flycatcher (*Empidonax minimus*), red-breasted nuthatch (*Sitta canadensis*), winter wren (*Troglodytes hiemalis*), and yellow-bellied flycatcher (*Empidonax flaviventris*)). Only the mourning warbler (*Geothlypis philadelphia*) and chipping Sparrow (*Spizella passerina*) were more common in the SNF. Species associated with mature or mixed forests tended to be found in the BWCAW at higher densities. In general, most species associated with early successional habitats did not differ between the BWCA and SNF landscapes. Results suggest that northern Minnesota forests with natural successional and disturbance regimes provide habitat for a higher density and richness of bird species.

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Introduction

Boreal forest disturbance regimes

The heterogeneity of boreal ecosystems was historically controlled by fire disturbance (Heinselman 1973). Other natural disturbances that have been implicated in influencing the structure and diversity of the landscape include wind-storms, periodic insect outbreaks, and beaver (*Castor canadensis*) activity (Heinselman 1973; Pastor et al. 1996). The type, size, and intensity of disturbance have worked in concert to maintain diversity in species composition and ecological processes across the landscape. Through fire suppression efforts, these naturally occurring disturbances are being replaced largely by human-induced changes to the landscape, namely through forest management activity (Heinselman 1973; Helle and Niemi 1996; White and Host 2008).

The effects of forest management need to be well understood if maintenance of ecological function and overall biodiversity are to be maintained (Reich et al. 2001; Pastor et al. 1996; Niemi et al 1998; Helle and Niemi 1996). Logging is not only changing the scale and structure of disturbance on the landscape (Mladenoff et al. 1993; White and Host 2008), but is also changing the rate at which disturbance is affecting the landscape (Heinselman 1973). Historically, the rate of disturbance was highly variable, from the order of decades to more than a century (Heinselman 1973), while logging practices often affect the landscape at shorter, more regular periods (Niemi et al. 1998). Forestry can also promote monocultures that are less useful at maintaining natural ecosystem functioning (Pastor et al. 1996). A potential surrogate for understanding how management is affecting ecosystem processes is to observe differences in populations of specific taxa between managed and unmanaged landscapes.

Boreal forest bird communities

From sheer taxonomic presence to the magnitude of ecological interactions, birds make up an important component of wildlife in boreal forests. Across a range of boreal regions, birds are estimated to compose approximately 70 – 80% of all terrestrial vertebrate species (Niemi et al. 1998). Functional guilds of birds interact within the ecosystem in various ways, from dispersal of seeds (Pastor et al. 1996) to the control on insect populations and outbreaks (Niemi et al. 1998).

Due to the historic presence of natural heterogeneity in the ecosystem and presumed evolutionary relationships, it is assumed that boreal bird species are adapted to diverse and changing landscapes (Heinselman 1973; Pastor et al. 1996; Niemi et al. 1998). Forest management might alter these dynamics by increasing forest fragmentation and edge effects as well as by altering the composition, age, and complexity of forest stands in the landscape.

Fragmentation, habitat loss, and edge effects

Fragmentation is often implicated in controlling species diversity and extinction patterns, yet research indicates that fragmentation, when compared to habitat loss, might play a lesser role in affecting the distribution and populations of boreal bird communities (Schmiegelow et al. 1997; Schmiegelow and Mönkkönen 2002). Forest management does not permanently alter forests (Edenius and Elmberg 1996; Niemi et al. 1998) and forest cut-over areas often provide habitat for a variety of breeding species preferring early successional habitats (Schulte and Niemi 1998; Niemi and Hanowski 1984). Still, several studies have shown a negative effect on forest bird communities of increased human-induced fragmentation through forest management (Edenius and Elmberg 1996; Jansson and Andren 2003).

It has also been shown that edges in managed landscapes might not have any negative effect on the nesting success of birds choosing to nest near edges (Hanski et al. 1996). However, the degree to which logging can mimic the historic context of disturbance has come under question (Shulte and Niemi 1998; Hobson and Schieck 1999).

Forest stand dynamics

It is generally accepted that species richness and density of individuals increase with forest stand age (Niemi et al. 1998; Helle and Niemi 1996); however, several studies have indicated peaks in richness and density in intermediate aged stands (Hagan et al. 1997; Imbeau et al. 1999). Recent research has also supported the stand age hypothesis, specifically with jack pine, *Pinus banksiana*, (Venier and Pearce 2005) and aspen, *Populus tremuloides*, (Hobson and Bayne 2000a) dominated forests. Jansson and Andren (2003) found increased species richness in forests with both increased mature and mature mixed forests, as opposed to areas with recent management and regenerating forests.

When controlling for stand age, forest stands that are more diverse structurally (Niemi and Hanowski 1984) and diverse in tree species composition (Hobson and Bayne 2000b) provide habitat for a greater number of bird species. Increased complexity and diversity within forest stands provides more localized habitat for a greater number of species and individuals to forage, sing, and nest. Logging might reduce structural diversity, vegetation diversity, and the presence of snags that are important to breeding bird communities (Schulte and Niemi 1998; Niemi and Probst 1990).

Managed and unmanaged forests

Few studies have compared breeding bird abundances across a broad range of forest types and ages between naturally disturbed and managed landscapes. Drapeau et al. (2000) compared avian communities between three landscapes; one with pre-industrial human modification, one undergoing industrial logging, and one mainly affected by natural disturbance. They found no difference in alpha diversity between the landscapes; however, beta and gamma diversity were significantly higher in human modified landscapes, mainly due to increased amounts of early successional habitats and associated species. In a study of areas with high and low impact from forestry, Edenius and Elmberg (1996) found increased species richness and abundance of birds in areas with low forestry impact. These studies provide little consensus on how bird communities of boreal forests with little or no human impact differ from surrounding areas with more intense human disturbance.

The objective of this study is to compare the breeding bird communities of managed (primarily by logging) and unmanaged landscapes within the Superior National Forest (SNF) in northeastern Minnesota. I address the following questions: 1) Do the breeding bird communities of the Boundary Waters Canoe Area Wilderness (BWCAW, unmanaged landscape) and the surrounding SNF (managed landscape) differ in terms of abundance, composition, and diversity of breeding birds? 2) How are breeding bird communities in this region affected by proximity to riparian corridors? 3) What vegetation characteristics at the stand and landscape scale are associated with these differences? 4) How do forestry and natural disturbance differ in relation to maintaining avian diversity in this region?

Methods

Study area

The Superior National Forest (SNF) comprises 1.6 million hectares in the northeastern region of Minnesota. The Boundary Waters Canoe Area Wilderness (BWCAW) makes up approximately 400,000 hectares of the SNF and lies along the border with Ontario, Canada (Figure 1). The BWCAW is a protected wilderness area, nearly half of which is virgin forest, with the remainder having been logged in the 1800's and early 1900's (Heinselman 1973; Heinselman, 1996). Since the BWCAW was designated as a wilderness area in 1964, primarily natural disturbance such as fire, windstorms, and insect outbreaks has affected the landscape. Small areas of the

BCWAW allow motorized travel, but the vast majority is open only to limited foot and canoe travel. There is no logging management within the BWCAW; however, fire management in the form of prescribed burns and fire control are occasionally practiced. The remainder of the SNF lies adjacent to the BWCAW on its southern border. Here, the Forest Service has adopted a multiple use protocol, development and management practices are more prevalent; homes, towns, recreation, and logging are common. Hereafter, BWCAW refers to the unmanaged wilderness area while SNF refers to the managed area surrounding the southern border of the BWCAW.

Boreal regions of northeastern Minnesota are made up of diverse forest and other vegetative types, with thirteen recognized upland cover types (Grigal and Ohmann 1975), and eight lowland cover types (Heinselman 1996). The most representative communities (by proportion coverage in the BWCAW) are fir (*Abies balsamea*) - birch (*Betula papyrifera*) forests, black spruce (*Picea mariana*) bog forests, black spruce feathermoss (*Hypnaceae spp*.) forests, and maple (*Acer spp*.) –aspen (*Populus tremuloides*) -birch forests (Heinselman 1996).

The breeding bird communities of the southern boreal forests, near the ecotone with northern temperate forests, are amongst the most diverse in North America (Niemi et al. 1998). The boreal region of northeastern Minnesota supports approximately 155 breeding species of forest-dwelling birds (Green and Niemi 1978; Green 1995). Regions within the boreal forests of northeastern Minnesota include both managed and relatively unmanaged forest that could provide different conditions for breeding birds.

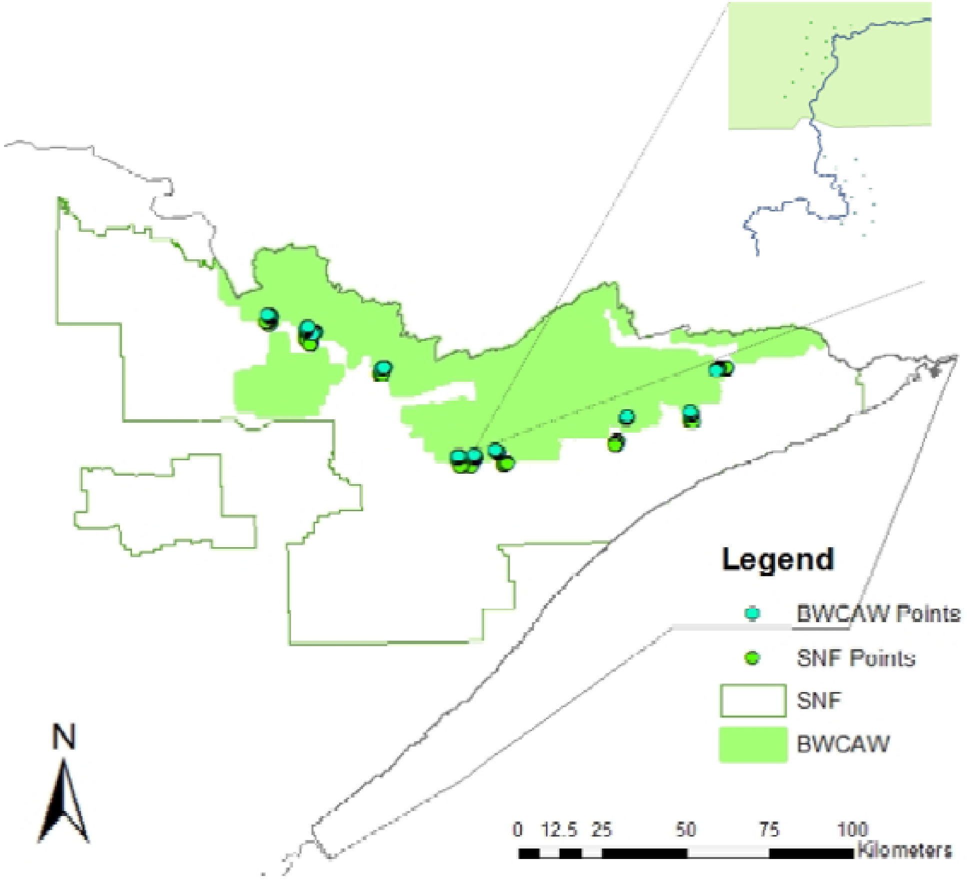


Figure 1: Superior National Forest of northeastern Minnesota. BWCAW and SNF points represent paired transects near rivers that cross the BWCAW border. Inset shows an example transect, Little Isabella River, and its associated point count locations.

Study sites

Paired transects adjacent to river systems that cross the border of the BWCAW were established. Using aerial photography (Farm Services Administration Color Orthophotos 2003-2004, FSA) and land-cover maps (LandSat-Based Land Use-Land Cover, MN DNR) lotic-systems satisfying the following criteria were selected for specific study sites: 1) medium to large lotic-system that crosses the border of the BWCAW, 2) minimum of 1.5km of riparian habitat in both the BWCAW and SNF within 5km of the BWCAW border, 3) section of the riparian habitat within 1 km of the

BWCAW border is at an angle >45° to the border, 4) upland forest constitutes the majority of the habitat within 400 m of the riparian corridor, 5) commercial timber harvest has occurred on the SNF side since 1980, and 6) timber harvest effects were not altered by the recent Cavity Lake and Ham Lake Fires. Ten systems along the southern and western borders of the BWCAW satisfied the above criteria and were included (Figure 1).

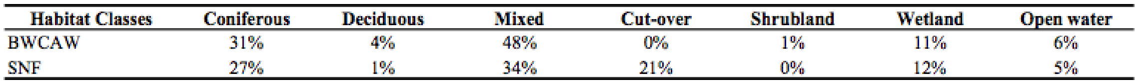
Each river system consisted of paired study areas, one within and one outside of the BWCAW. Point counts within each of these study areas were positioned along two parallel transects, 100m and 400m from the riparian corridor. Each transect consisted of six points spaced 250m apart. A 500m buffer was positioned around the border of the BWCAW, where no point counts were located (Figure 1, see inset).

Landscape features

Vegetative characteristics at the landscape scale were compared between the SNF and BWCAW transects using landcover maps developed by the Minnesota Department of Natural Resources (LandSat-Based Land Use-Land Cover, MN DNR, 1995). Proportions of habitat classes in a 1 km buffer surrounding each transect are summarized in Table 1. Forest cut-over areas are lands where commercial timber harvest occurred between 1980 and 1995 and thus define the proportion of younger forest regenerating from management in the landscape. Disturbance that occurred after the 1995 Landsat maps were created are not reflected here. Proportions of canopy height strata at point count locations describe the overall age distribution of the forested landscapes (Table 2).

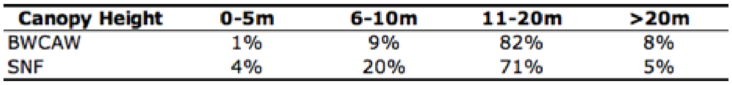
All transects within the BWCAW were likely disturbed by humans at some point and cannot be considered true virgin forest (Heinselman 1973). However, logging activities during the pre-wilderness designation mainly included selective logging of old growth red (*Pinus resinosa*) and white pine (*Pinus strobus*), interspersed with natural fire events (Heinselman 1996). In nine of ten BWCAW transects, the most recent disturbance was fire, usually in the late 19th or early 20th centuries. The final transect was most recently disturbed by a logging operation in the early 1920's. A major windstorm in 1999 affected some of the areas in both the SNF and BWCAW transects (Scheller et al. 2005), but did not cause complete stand turnover (E.J. Zlonis *personal observation*).

Table 1: Proportion of broad habitat classes surrounding BWCAW and SNF transects. Values are proportions of habitat classes in a 1km circle surrounding the center of each transect. 'Cut-over' represents forests that were harvested between 1980 and 1995.



Habitat Classes	Coniferous	Deciduous	Mixed	Cut-over	Shrubland	Wetland	Open water
BWCAW	31%	4%	48%	0%	1%	11%	6%
SNF	27%	1%	34%	21%	0%	12%	5%

Table 2: Proportion of canopy height classes for BWCAW and SNF stands



Canopy Height	0-5m	6-10m	11-20m	>20m
BWCAW	1%	9%	82%	8%
SNF	4%	20%	71%	5%

Avian surveys

I conducted ten-minute point counts for birds between May 14, and July 6, 2010. All birds seen or heard within the ten-minute interval were recorded and categorized by species, behavior (i.e. singing or calling), and distance from observer. Surveys were conducted from approximately ½ hour before sunrise to 4 hours after sunrise in generally good weather conditions (no rain and low wind speed). Each set of twelve points was surveyed on two separate days, one earlier and one later in the field season. During the second survey, the order of point counts was reversed, allowing the replicated points to have one earlier morning and one later morning survey (or two middle-hour surveys). Observations of birds flying over the point count station were eliminated from analysis; only those utilizing the local habitat in some way were included.

All transects were surveyed a third time between May 25, and June 19, 2011 by myself and a second, trained observer. SNF and BWCAW transects were randomly assigned to an observer and were surveyed on the same day. Each observer spent equal time in both management types. The start point (either 100m or 400m) was randomly determined, with half of the river transects having early morning (i.e. starting ½ hour before sunrise) surveys of 100m points and half of 400m points.

Vegetation measurements

Vegetation measurements were taken at each of the point count locations after the second round of avian surveys was complete (June and July 2010). Trees (DBH > 10cm) surrounding each point were sampled using a 10 BAF prism and were recorded based on species, status (1=alive, 2=dying, 3=dead), presence of potential nesting cavities, and presence of woodpecker activity. Sampled trees were placed into seven size-classes (Table 4). Canopy height (m) was visually estimated in 1m increments. Canopy coverage (%), canopy deciduous (%), sub-canopy coverage (%), sub-canopy deciduous (%), under-story coverage (%), under-story deciduous (%), and ground coverage (%) were estimated in 20% increments at each point count location.

Statistical analyses

To test for the effects of management type on bird counts and vegetative variables we performed Poisson or Negative Binomial mixed-model regressions with SAS software PROC GLIMMIX (SAS Institute Inc., Cary, NC, USA). The Laplace method of maximum likelihood estimation was used for parameter estimates. Management type (BWCAW or SNF), visit (1, 2, or 3), and distance (100 m or 400 m) were used as fixed effects, while river transect (and its interactions with fixed effects) was considered a random effect. Each model responded to inclusion of random effects in different ways. When covariance parameters of random effects were estimated to be zero, they were removed from the model. When the scale parameter (for Negative Binomial distribution) was estimated to be zero, a Poisson distribution was used. All reported mean values are least squares means (LSM) transformed to the original scale through ILINK.

All individuals and species observed, except those flying over the point count, were included in comparisons of total individuals and species richness. Species were grouped into migration and nesting guilds per Green (1995) and Danz et al. (2008). Any species with ≥72 observations (10% of point counts) was considered common enough to warrant individual comparison between management types and distances from river corridor. Thirty-five species met this criterion (Table 3).

Multivariate analyses of vegetation and bird data were conducted in PC-ORD (McCune and Mefford 2006). Canonical Correspondence Analysis (CCA) was used to explore the relationships between common bird species (Table 3) and habitat variables. Habitat variables that were highly correlated ($r \geq 0.70$) with other variables (but showed lower correlation with primary axis) were eliminated from ordination analyses. When the skewness of specific variables was ≥1, square root or log transformations were used. A randomization test (Monte Carlo permutations test, 999 runs) was used to test the significance of bird-vegetation correlations (McCune and Mefford 2006).

Multi-response Permutation Procedures (MRPP) was used to test the statistical hypothesis of no difference in vegetation components between BWCAW and SNF stands. Data were relativized by vegetation variable and Euclidean distance measures were used to test within group clustering. Discriminant Function Analysis (PROC CANDISC (SAS Institute Inc., Cary, NC, USA)) was used in a descriptive mode to determine which habitat variables helped differentiate management types.

Results

Avian point counts

We detected 13,332 individuals of 94 species. Seventy-seven species were observed in both the SNF and BWCAW. Seven species were unique to the SNF (84 total species), while 10 species were unique to the BWCAW (87 total species). Species richness per river transect was significantly higher within the BWCAW (average of 38.3

species) than in the SNF (33.9 species) (F=7.98, p=0.02). Richness comparisons are congruent with diversity indices, both the Shannon Weaver (H) and Simpson's index (D) were higher (p<0.01) within the BWCAW (H=2.34, D=0.89) than in the SNF (H=2.23, D=0.87).

Species richness per point count station (unlimited distance counts) was significantly higher within the BWCAW (F=11.17, p<0.01; Figure 2a) and at point-count stations 100 m from the riparian area (F=28.30, p<0.001). The total number of individuals detected was also significantly higher in the BWCAW (F=9.76, p=0.01; Figure 2b) and at 100m (F=42.12, p<0.001). For both of these analyses there was a significant interaction between the visit (1, 2, or 3) and the distance (100m or 400m) from the riparian corridor. Yet, the species richness and total number of individuals was higher at 100m between all visits. There was also a significant interaction between visit and management type (BWCAW and SNF) for total individuals. However, regardless of visit, the average number of individuals observed was higher in the BWCAW than in the SNF.

The effects of management type and distance were similar when analyzing point count data for birds detected within 100m of the point count station, as opposed to unlimited distance. Species richness was significantly higher in the BWCAW (F=10.65, p<0.01) and at 100m from the riparian corridor (F=12.91, p<0.01; Figure 2c). The total number of individuals detected was significantly higher within the BWCAW (F=18.10, p<0.01) and at 100m (F=11.64, p<0.01; Figure 2d). There was a significant interaction between management type and visit for total individuals; however, regardless of visit, the number of individuals detected within 100m of the point count station was higher in the BWCAW stands. There were no significant interactions when analyzing species richness within a fixed distance (100m) of the point count location.

Avian guilds. To eliminate effects of abundant species, I analyzed migration, nesting, and habitat-association guilds based on the number of species observed. The number of species detected per count station was significantly higher in the BWCAW for permanent residents ($F=10.86$, $p<0.01$; Figure 3a). Although not significant at $\alpha=0.05$, both long ($F=3.72$, $p=0.09$; Figure 3a) and short distance ($F=3.79$, $p=0.08$; Figure 3a) migrant species nearly had higher species richness in the BWCAW.

Cavity nesting species ($F=48.01$, $p<0.001$; Figure 3b) were significantly more abundant in the BWCAW. At $\alpha=0.05$, both canopy ($F=4.10$, $p=0.07$; Figure 3b) and ground ($F=4.69$, $p=0.06$; Figure 3b) nesting species did not have significantly higher richness in the BWCAW. Sub-canopy or shrub-nesting species were not different between management types.

On average, significantly more species associated with mixed forests were observed in the BWCAW point counts (BWCAW, 3.43 species; SNF, 2.79 species, $F=11.75$, $p<0.01$). Species dependent upon both lowland-conifer forests (BWCAW; 0.66 species, SNF; 0.46 species, $F=4.44$, $p=0.06$) and wetlands (BWCAW; 0.33 species, SNF; 0.24 species, $F=4.43$, $p=0.06$) were potentially associated with BWCAW forest stands. Species groups associated with all other habitat-types did not vary depending upon management type. Specifically, species richness of birds associated with early-successional habitats, often characterized by recent logging disturbance, did not vary between BWCAW and SNF (BWCAW; 1.67 species, SNF; 1.89 species, F=1.41, p=0.27).

Individual species. Thirty-five species were observed at >10% of the point counts (observations at 72 or more different point counts) (Table 3). Eight of these species, black-capped chickadee (*Poecile atricapillus*), brown creeper (*Certhia americana*), Canada warbler (*Cardellina canadensis*), golden-crowned kinglet (*Regulus satrapa*), least flycatcher (*Empidonax minimus*), red-breasted nuthatch (*Sitta canadensis*), winter wren (*Troglodytes hiemalis*), and yellow-bellied flycatcher (*Empidonax flaviventris*) were observed significantly more often in the BWCAW. Only the mourning warbler (*Geothlypis philadelphia*) and chipping sparrow (*Spizella passerina*) had significantly higher abundance in the SNF.

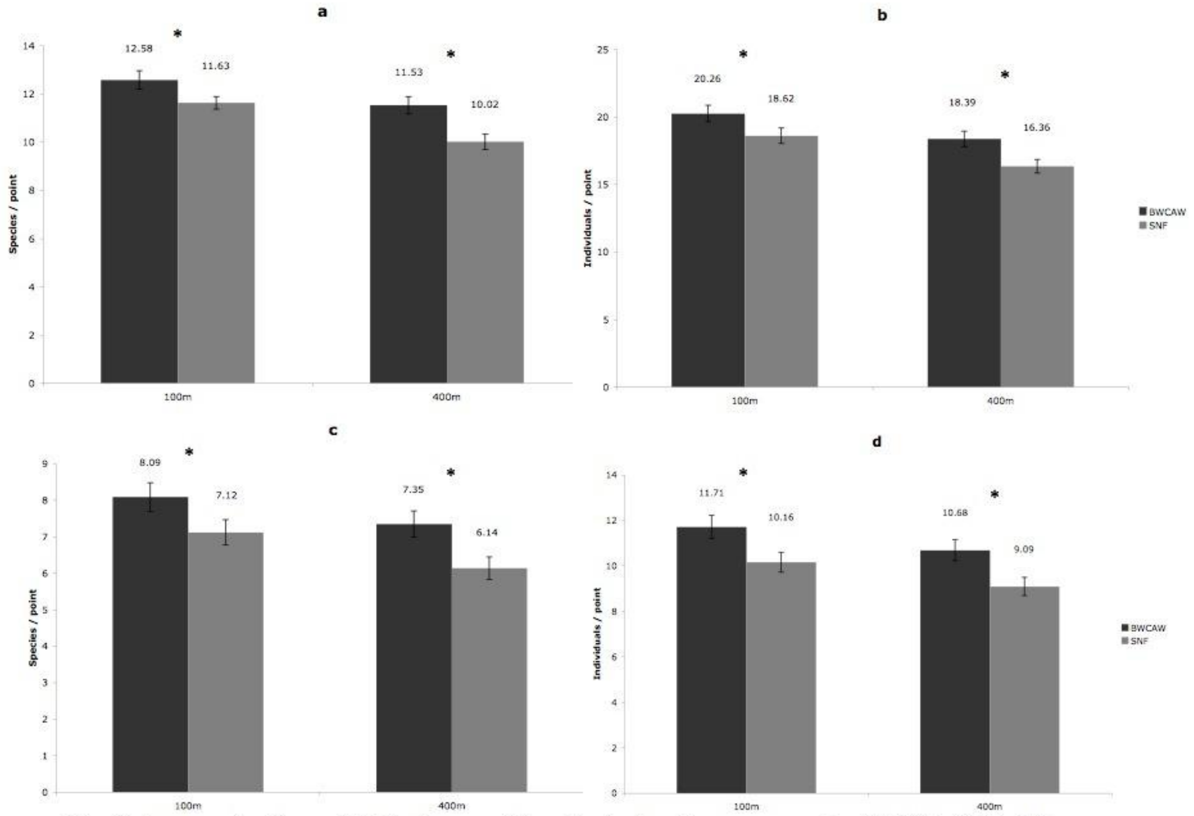


Figure 2: Average species richness and total abundance per point count location depending on management type (BWCAW or SNF) and distance from riparian corridor (100m or 400m). Results are presented for either unlimited distance counts (a, b) or counts within 100m of the point count location (c, d).
* Results are significant at α=0.05 level

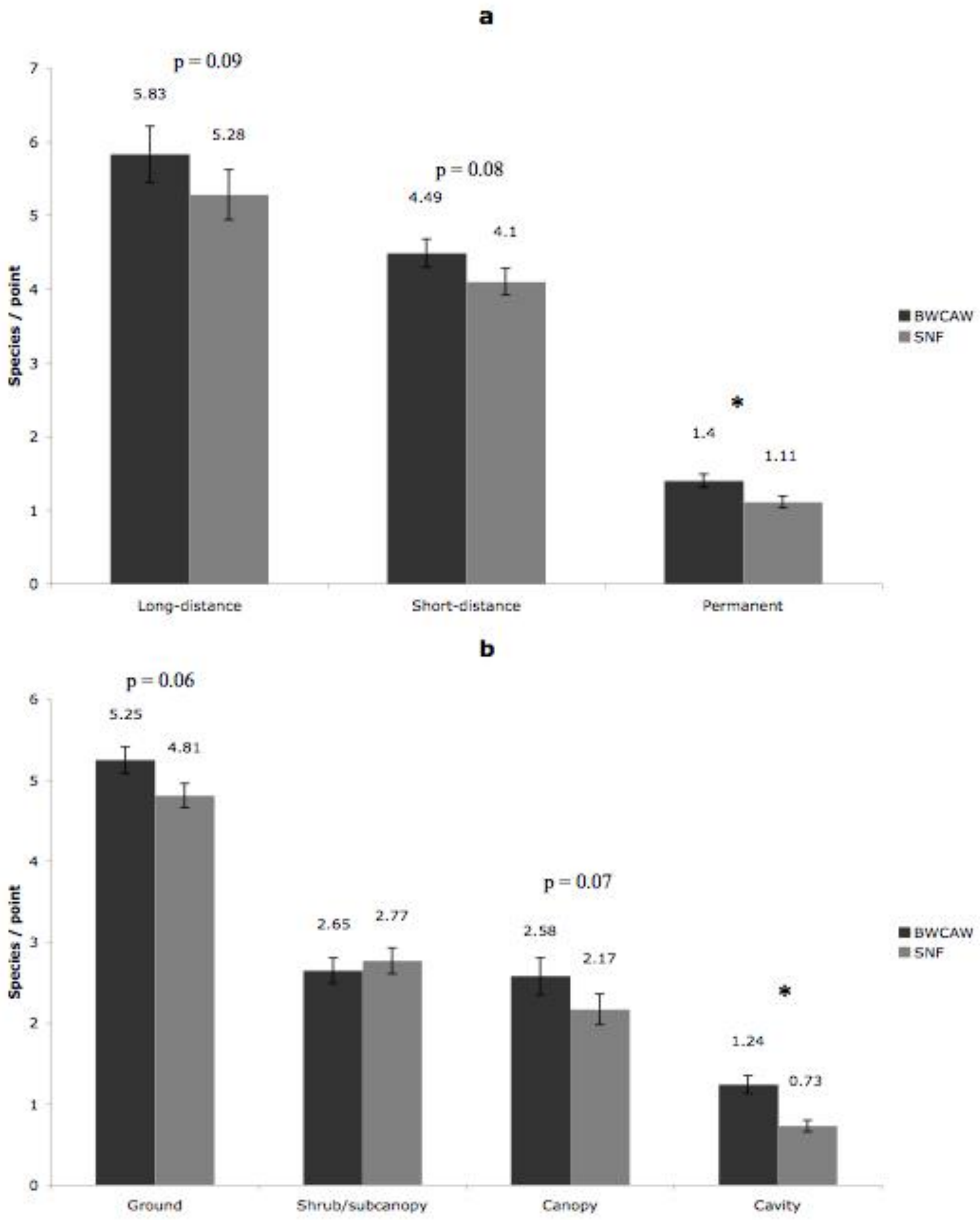
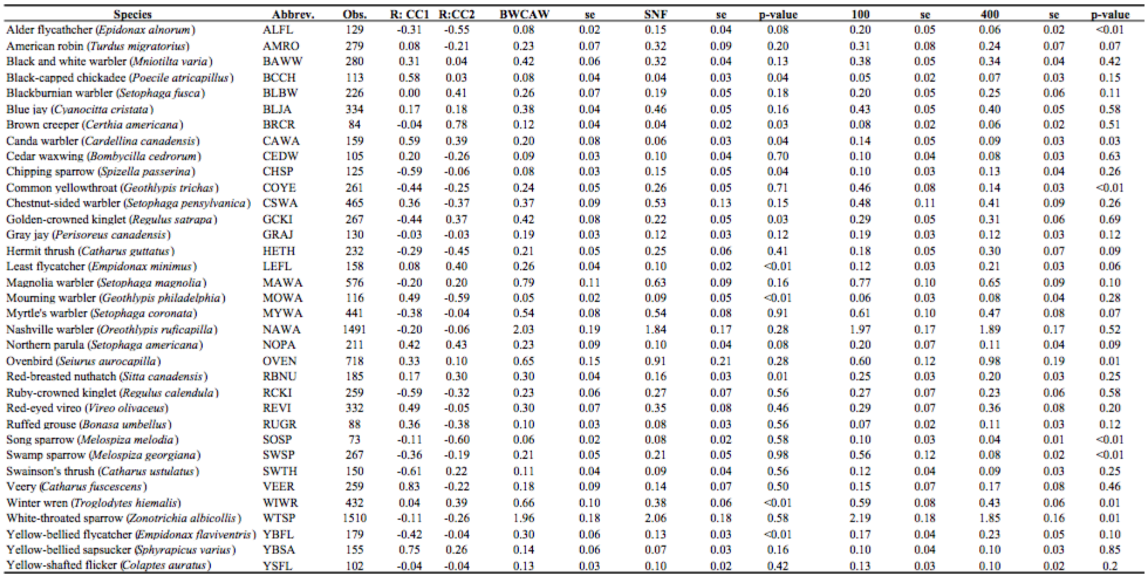


Figure 3: Average species richness of avian guilds at BWCAW and SNF point counts. Migration guilds are summarized (a), as well as nesting guilds (b).

* Results are significant at α=0.05 level

Table 3: Summary of individual species analysis. All species with observations at >10% of point count locations were tested for management type (BWCAW and SNF) and riparian corridor (100m and 400m) effects. Species are listed in order of total number of observations (Obs).



Species	Abbrev.	Obs.	R: CC1	R:CC2	BWCAW	se	SNF	se	p-value	100	se	400	se	p-value
Alder flycathcher (*Epidonax alnorum*)	ALFL	129	-0.31	-0.55	0.08	0.02	0.15	0.04	0.08	0.20	0.05	0.06	0.02	<0.01
American robin (*Turdus migratorius*)	AMRO	279	0.08	-0.21	0.23	0.07	0.32	0.09	0.20	0.31	0.08	0.24	0.07	0.07
Black and white warbler (*Mniotilta varia*)	BAWW	280	0.31	0.04	0.42	0.06	0.32	0.04	0.13	0.38	0.05	0.34	0.04	0.42
Black-capped chickadee (*Poecile atricapillus*)	BCCH	113	0.58	0.03	0.08	0.04	0.04	0.03	0.04	0.05	0.02	0.07	0.03	0.15
Blackburnian warbler (*Setophaga fusca*)	BLBW	226	0.00	0.41	0.26	0.07	0.19	0.05	0.18	0.20	0.05	0.25	0.06	0.11
Blue jay (*Cyanocitta cristata*)	BLJA	334	0.17	0.18	0.38	0.04	0.46	0.05	0.16	0.43	0.05	0.40	0.05	0.58
Brown creeper (*Certhia americana*)	BRCR	84	-0.04	0.78	0.12	0.04	0.04	0.02	0.03	0.08	0.02	0.06	0.02	0.51
Canda warbler (*Cardellina canadensis*)	CAWA	159	0.59	0.39	0.20	0.08	0.06	0.03	0.04	0.14	0.05	0.09	0.03	0.03
Cedar waxwing (*Bombycilla cedrorum*)	CEDW	105	0.20	-0.26	0.09	0.03	0.10	0.04	0.70	0.10	0.04	0.08	0.03	0.63
Chipping sparrow (*Spizella passerina*)	CHSP	125	-0.59	-0.06	0.08	0.03	0.15	0.05	0.04	0.10	0.03	0.13	0.04	0.26
Common yellowthroat (*Geothlypis trichas*)	COYE	261	-0.44	-0.25	0.24	0.05	0.26	0.05	0.71	0.46	0.08	0.14	0.03	<0.01
Chestnut-sided warbler (*Setophaga pensylvanica*)	CSWA	465	0.36	-0.37	0.37	0.09	0.53	0.13	0.15	0.48	0.11	0.41	0.09	0.26
Golden-crowned kinglet (*Regulus satrapa*)	GCKI	267	-0.44	0.37	0.42	0.08	0.22	0.05	0.03	0.29	0.05	0.31	0.06	0.69
Gray jay (*Perisoreus canadensis*)	GRAJ	130	-0.03	-0.03	0.19	0.03	0.12	0.03	0.12	0.19	0.03	0.12	0.03	0.12
Hermit thrush (*Catharus guttatus*)	HETH	232	-0.29	-0.45	0.21	0.05	0.25	0.06	0.41	0.18	0.05	0.30	0.07	0.09
Least flycatcher (*Empidonax minimus*)	LEFL	158	0.08	0.40	0.26	0.04	0.10	0.02	<0.01	0.12	0.03	0.21	0.03	0.06
Magnolia warbler (*Setophaga magnolia*)	MAWA	576	-0.20	0.20	0.79	0.11	0.63	0.09	0.16	0.77	0.10	0.65	0.09	0.10
Mourning warbler (*Geothlypis philadelphia*)	MOWA	116	0.49	-0.59	0.05	0.02	0.09	0.05	<0.01	0.06	0.03	0.08	0.04	0.28
Myrtle's warbler (*Setophaga coronata*)	MYWA	441	-0.38	-0.04	0.54	0.08	0.54	0.08	0.91	0.61	0.10	0.47	0.08	0.07
Nashville warbler (*Oreothlypis ruficapilla*)	NAWA	1491	-0.20	-0.06	2.03	0.19	1.84	0.17	0.28	1.97	0.17	1.89	0.17	0.52
Northern parula (*Setophaga americana*)	NOPA	211	0.42	0.43	0.23	0.09	0.10	0.04	0.08	0.20	0.07	0.11	0.04	0.09
Ovenbird (*Seiurus aurocapilla*)	OVEN	718	0.33	0.10	0.65	0.15	0.91	0.21	0.28	0.60	0.12	0.98	0.19	0.01
Red-breasted nuthatch (*Sitta canadensis*)	RBNU	185	0.17	0.30	0.30	0.04	0.16	0.03	0.01	0.25	0.03	0.20	0.03	0.25
Ruby-crowned kinglet (*Regulus calendula*)	RCKI	259	-0.59	-0.32	0.23	0.06	0.27	0.07	0.56	0.27	0.07	0.23	0.06	0.58
Red-eyed vireo (*Vireo olivaceus*)	REVI	332	0.49	-0.05	0.30	0.07	0.35	0.08	0.46	0.29	0.07	0.36	0.08	0.20
Ruffed grouse (*Bonasa umbellus*)	RUGR	88	0.36	-0.38	0.10	0.03	0.08	0.03	0.56	0.07	0.02	0.11	0.03	0.12
Song sparrow (*Melospiza melodia*)	SOSP	73	-0.11	-0.60	0.06	0.02	0.08	0.02	0.58	0.10	0.03	0.04	0.01	<0.01
Swamp sparrow (*Melospiza georgiana*)	SWSP	267	-0.36	-0.19	0.21	0.05	0.21	0.05	0.98	0.56	0.12	0.08	0.02	<0.01
Swainson's thrush (*Catharus ustulatus*)	SWTH	150	-0.61	0.22	0.11	0.04	0.09	0.04	0.56	0.12	0.04	0.09	0.03	0.25
Veery (*Catharus fuscescens*)	VEER	259	0.83	-0.22	0.18	0.09	0.14	0.07	0.50	0.15	0.07	0.17	0.08	0.46
Winter wren (*Troglodytes hiemalis*)	WIWR	432	0.04	0.39	0.66	0.10	0.38	0.06	<0.01	0.59	0.08	0.43	0.06	0.01
White-throated sparrow (*Zonotrichia albicollis*)	WTSP	1510	-0.11	-0.26	1.96	0.18	2.06	0.18	0.58	2.19	0.18	1.85	0.16	0.01
Yellow-bellied flycatcher (*Empidonax flaviventris*)	YBFL	179	-0.42	-0.04	0.30	0.06	0.13	0.03	<0.01	0.17	0.04	0.23	0.05	0.10
Yellow-bellied sapsucker (*Sphyrapicus varius*)	YBSA	155	0.75	0.26	0.14	0.06	0.07	0.03	0.16	0.10	0.04	0.10	0.03	0.85
Yellow-shafted flicker (*Colaptes auratus*)	YSFL	102	-0.04	-0.04	0.13	0.03	0.10	0.02	0.42	0.13	0.03	0.10	0.02	0.2

Vegetation sampling

Tree species composition consisted primarily of 6 species. BWCAW stands were dominated by spruce (*Picea mariana, glauca*; 31% of trees sampled), jack pine (*Pinus banksiana*; 17%), quaking apsen (*Populus tremuloides*; 15%), paper birch (*Betula papyrifera*; 13%), and balsam fir (*Abies balsamifera*; 12%). SNF stands were composed of jack pine (29%), spruce (23%), quaking aspen (16%), balsam fir (11%), and paper birch (10%).

The density of deciduous (BWCA, 116.33 trees/ha; SNF, 118.26 trees/ha; p=0.97) or coniferous (BWCAW, 431.56 trees/ha; SNF 407.21 trees/ha; p=0.77) trees sampled did not differ between management type. Additionally, density of tree species with high pre-settlement abundance (tamarack, birch, spruce spp. (Friedman and Reich 2005)) (BWCAW, 311.81 trees/ha; SNF, 198.29 trees/ha; p=0.15) and post-settlement abundance (quaking aspen, balsam fir (Friedman and Reich 2005)) (BWCAW, 156.95 trees/ha; SNF, 175.27 trees/ha; p=0.78) were not different between management types.

Overall tree density (trees >10cm dbh/ha) (F=3.63, p=0.09; Table 4) did not vary significantly by management type. However, the density of large trees ≥30cm dbh/ha (trees potentially used by the entire cavity nesting community (Green 1995)) (BWCAW, 31.19 trees/ha; SNF, 12.89 trees/ha; F=5.50, p=0.04) was significantly higher within the BWCAW stands.

On average, the canopy height (F=8.47, p=0.02) and tree species richness (trees >10cm dbh)(F=13.62, p<0.01) of BWCAW point counts locations were significantly higher than in the SNF (Table 4). Due to unequal area sampled by the prism method, rarefaction curves were created for BWCAW and SNF stands. Rarefaction analysis (Gotelli and Entsminger 2011) indicated that tree species richness was higher in BWCAW stands at all sampled abundance levels.

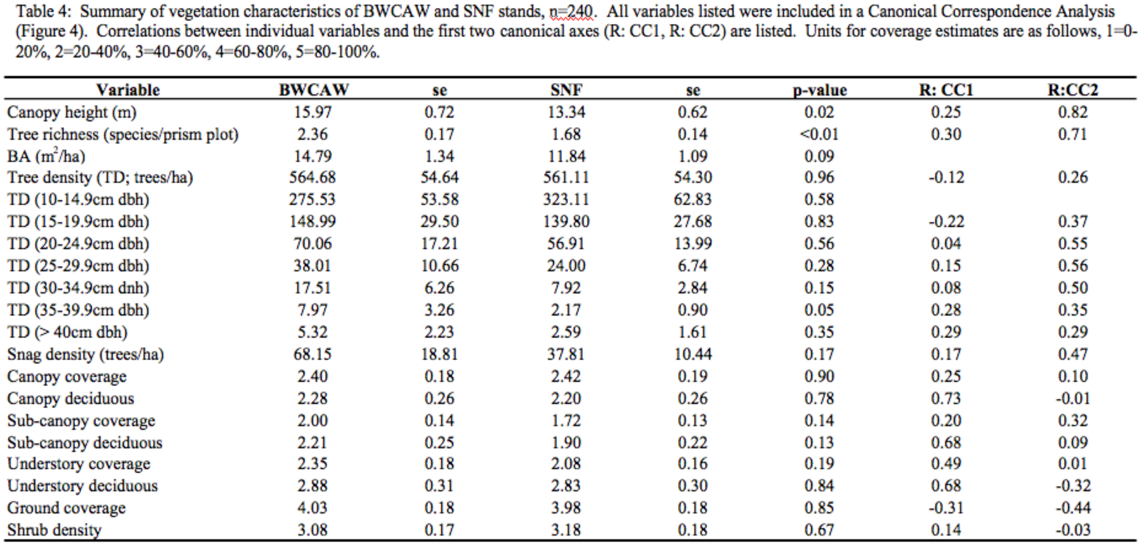


Table 4: Summary of vegetation characteristics of BWCAW and SNF stands, n=240. All variables listed were included in a Canonical Correspondence Analysis (Figure 4). Correlations between individual variables and the first two canonical axes (R: CC1, R: CC2) are listed. Units for coverage estimates are as follows, 1=0-20%, 2=20-40%, 3=40-60%, 4=60-80%, 5=80-100%.

Variable	BWCAW	se	SNF	se	p-value	R: CC1	R:CC2
Canopy height (m)	15.97	0.72	13.34	0.62	0.02	0.25	0.82
Tree richness (species/prism plot)	2.36	0.17	1.68	0.14	<0.01	0.30	0.71
BA (m^2/ha)	14.79	1.34	11.84	1.09	0.09		
Tree density (TD; trees/ha)	564.68	54.64	561.11	54.30	0.96	-0.12	0.26
TD (10-14.9cm dbh)	275.53	53.58	323.11	62.83	0.58		
TD (15-19.9cm dbh)	148.99	29.50	139.80	27.68	0.83	-0.22	0.37
TD (20-24.9cm dbh)	70.06	17.21	56.91	13.99	0.56	0.04	0.55
TD (25-29.9cm dbh)	38.01	10.66	24.00	6.74	0.28	0.15	0.56
TD (30-34.9cm dnh)	17.51	6.26	7.92	2.84	0.15	0.08	0.50
TD (35-39.9cm dbh)	7.97	3.26	2.17	0.90	0.05	0.28	0.35
TD (> 40cm dbh)	5.32	2.23	2.59	1.61	0.35	0.29	0.29
Snag density (trees/ha)	68.15	18.81	37.81	10.44	0.17	0.17	0.47
Canopy coverage	2.40	0.18	2.42	0.19	0.90	0.25	0.10
Canopy deciduous	2.28	0.26	2.20	0.26	0.78	0.73	-0.01
Sub-canopy coverage	2.00	0.14	1.72	0.13	0.14	0.20	0.32
Sub-canopy deciduous	2.21	0.25	1.90	0.22	0.13	0.68	0.09
Understory coverage	2.35	0.18	2.08	0.16	0.19	0.49	0.01
Understory deciduous	2.88	0.31	2.83	0.30	0.84	0.68	-0.32
Ground coverage	4.03	0.18	3.98	0.18	0.85	-0.31	-0.44
Shrub density	3.08	0.17	3.18	0.18	0.67	0.14	-0.03

Multivariate analyses

Multi-response Permutation Procedures (MRPP) concluded significant separation in the vegetation variables between the BWCAW and SNF stands (chance-corrected within group agreement, A = 0.02, p<0.01). Discriminant Function Analysis (DFA) indicated that tree species richness per point count, canopy height, tree density (trees 30-34.9cm dbh), and snag density were most associated with BWCAW stands, while overall tree density (trees >10cm dbh), shrub density, and canopy coverage were most associated with SNF stands.

Canonical Correspondence Analysis found a significant relationship between breeding bird and vegetation variables (Table 4) for the first Canonical Axis (eigenvalue=0.12, 6.1% variation explained, species-environment correlation=0.74, p<0.01). The second and third canonical axes indicated significant bird-vegetation relationships, with both eigenvalues (Axis 2, 0.07, 3.7% variation explained; Axis 3, 0.05, 2.3% variation explained) and species-environment correlations (Axis 2, 0.68; Axis 3, 0.60) being higher than those of the maximum achieved in randomization tests (based on Monte Carlo permutations test, 999 runs).

The first Canonical axis separated species based on correlations with broad forest types (deciduous, coniferous, open habitats). Canopy deciduous, sub-canopy deciduous, and understory deciduous were most highly correlated with Axis 1 (Table 4; Figure 4). Based on these correlations, Axis 1 was defined as '*increasing deciduous cover*' (Figure 4). The second Canonical Axis separated species based on correlation with mature, mixed, and structurally complex forest stands. Axis 2 was positively correlated with canopy height, tree species richness, snag density, and tree size-classes (15-19.9cm dbh, 20-24.9cm dbh, 25-29.9cm dbh, 30-34.9cm dbh, 35-39.9cm dbh, ≥40cm dbh) (Table 4; Figure 4). Based on these correlations, Axis 2 was defined as '*increasingly mature, mixed, and structurally complex*' (Figure 4).

Bird species associated with deciduous forests (veery, yellow-bellied sapsucker, canada warbler, black-capped chickadee) were positively correlated with Axis 1, while those associated with either coniferous (Swainson's thrush, ruby-crowned kinglet, chipping sparrow) or non-forested habitats (common yellowthroat, swamp sparrow, alder flycatcher) were negatively correlated with Axis 1 (Figure 4). Species associated with mature, mixed, and complex forests (brown creeper, Canada warbler, Northern parula, least flycatcher) were positively correlated with Axis 2, while those associated with early-successional (mourning warbler, chestnut-sided warbler, ruffed grouse) or non-forested (song sparrow, alder flycatcher) habitats were negatively correlated with Axis 2.

Species with significantly higher abundance in BWCAW stands, except the yellow-bellied flycatcher, were positively correlated with Axis 2. Both species (mourning warbler and chipping sparrow) with significantly higher abundance in the SNF stands were negatively correlated with Axis 2.

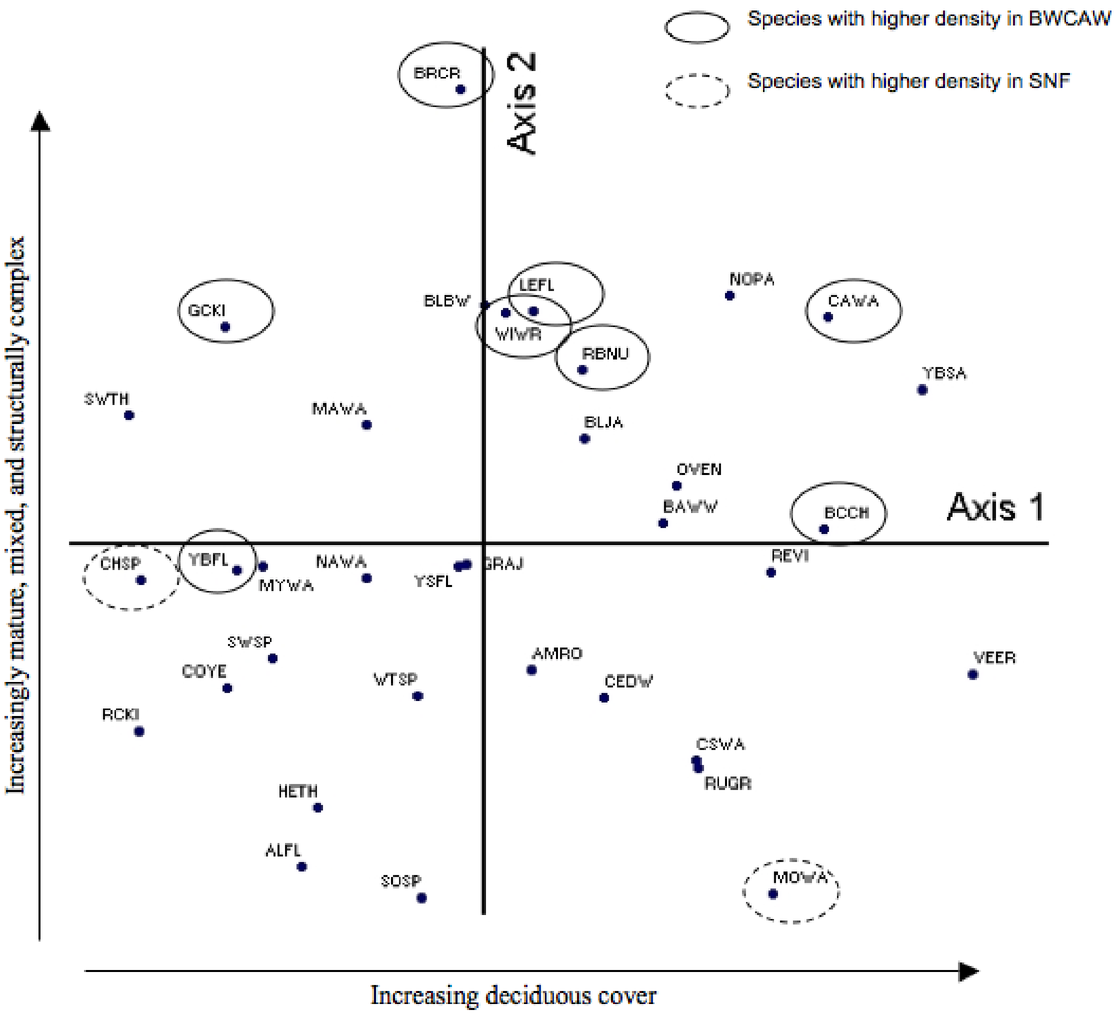


Figure 4: Canonical Correspondence Analysis (CCA) of vegetation variables (Table 4) and bird species (Table 3). Abundance of each species within 100m of point count location were used in the analysis. Canopy, sub-canopy, and understory deciduous coverage's were positively correlated with Axis 1. Variables associated with mature, mixed, and complex (mixed-aged) forest stands were positively correlated with Axis 2 (see Table 3 and 4 for correlations between bird and vegetation variables and axes).

Discussion

Bird-community patterns

My results indicate that the unmanaged forest stands within the BWCAW are providing habitat for an increased abundance and richness of breeding birds. Stands in the BWCAW were on average older, more mixed, and had a greater variety in tree size-classes than in the SNF. These results are consistent with Frelich and Reich (1995) who found that BWCAW stands were reaching mature, mixed, and uneven-aged status. Generally, stands that are older (Schieck and Song 2006; Hannon and Drapeau 2005), more mixed (Edenius and Elmberg 1996; Hobson and Bayne 2000b; Jansson and Andren 2003), and more structurally diverse (MacArthur and MacArthur 1961; Niemi and Hanowski 1984) are able to support a greater number and richness of birds. These results are further supported by CCA results, showing nearly all species with significantly higher abundance in the BWCAW being associated with mature, mixed, and structurally diverse forest stands (Figure 4).

When compared to fire disturbance, the shorter rotation period of logging (Niemi et al. 1998) prevents a high proportion of stands from reaching mature, mixed status (Schieck and Song 2006). Species richness of post-fire and post-harvest stands tends to converge in mid-successional stands (31-75 years old); however, as stands age beyond conventional harvest periods (BWCAW stands), more species of birds are able to find adequate habitat (Schieck and Song 2006). A higher proportion of mature stands appear to contribute to higher avian abundance and richness in this sub-boreal region (Niemi and

Helle 1996; Niemi et al. 1998). Besides affecting tree species composition and structural diversity, management might prevent forest stands from supporting abundant arthropod communities (Petersson, 1995), an important forage-base for many bird species.

Despite significant interactions (see results), the trend of increased richness and abundance in BWCAW counts holds for all individual visits. One factor that might have contributed to interactions is the variation in when counts were completed. For example, visit 1 (2010) began in mid-May, visit 2 (2010) in mid-June, and visit 3 (2011) in late-May. Samples from mid – late May included a high proportion of territorial permanent resident and short-distance migrant species, while long-distance migrants, although present to varying degrees, were not defending established territories. When only transects with all visits completed after 30 May (2010 and 2011) were included, the interaction between visit and management type was no longer significant, yet the main effect of management type on abundance and richness was still present.

In addition to increased abundance and richness at a stand level, average species richness was higher in unmanaged transects, and the total number of species detected was higher in the unmanaged landscape. Other studies comparing managed and unmanaged boreal landscapes have equivocal results. The most comprehensive study done by Drapeau et al. (2000) found no difference in alpha diversity between landscapes, but found higher beta and gamma-diversity in the managed landscape. However, studies in boreal regions of Scandinavia have not found similar results; low human-impact landscapes, consisting of higher proportions of old and mixed forests, generally had greater species richness than intensively managed areas (Edenius and Elmberg 1996; Jansson and Andren 2003).

Guild and species-level patterns

Permanent resident and cavity-nesting species contributed to the broad pattern of greater species richness in the BWCAW. However, both short-distance and long-distance migration guilds and ground and canopy nesting guilds had nearly significant trends ($p < 0.10$) for higher richness in BWCAW stands and, therefore, they also likely contributed to differences between managed and unmanaged areas. These results indicate that the BWCAW is potentially providing for the ecological needs of most breeding species, regardless of migratory or nesting affiliation.

Density of cavity nesting species can be limited by nest-site availability (Newton 1994). Higher tree density of trees ≥ 30cm dbh in BWCAW stands provides more nest site locations for many of these species. Even though the density of snags was not different between management types, many cavities may be located in live trees especially aspen, with heartwood rot (Martin et al. 2004). Aspen trees > 30cm dbh were more commonly surveyed in the BWCAW (BWCAW, 74 total trees; SNF, 20 total trees). Secondary cavity-excavators (red-breasted nuthatch, black-capped chickadee) rely heavily on trees with soft or rotten wood when excavating their own cavities. Higher abundances of these species in the unmanaged forests might be related to a combination of increased density of trees with these characteristics and previously excavated cavities.

Species richness of birds associated with mixed forests was higher in unmanaged forest stands. BWCAW transects had higher proportions of mixed-forest habitats (Table 1) than managed stands. Approximately 21% of forests in the managed SNF transects were regenerating from logging activity. However, the species richness of early-successional forest species did not vary by management type, with the exception of the mourning warbler, a species commonly found in logged areas (Schulte and Niemi 1998). The increased proportion of stands regenerating from logging activity in the managed landscape was expected to increase the abundance of species associated with this habitat type. This was the not the case for most species and the reasons may be due to the many natural openings found in the BWCAW. These included rock outcrops, beaver ponds, tree-fall gaps, and riparian habitat where these species found appropriate open, shrubby habitat. Additionally, positioning half of the point count locations near riparian habitat probably increased the proportion of open habitat that resembles early-successional vegetation over what may have been found the broader landscape of the SNF.

Individual species with increased abundance in the BWCAW are generally related to mature forests for their nesting and foraging habitat. Drapeau et al. (2000) found similar results for winter wren, golden-crowned kinglet, brown creeper, yellow-bellied flycatcher, Canada warbler, and red-breasted nuthatch, in which all were associated with naturally disturbed, old-growth, forests. With the exception of the yellow-bellied flycatcher, Schieck and Song (2006) also found these species to be indicative of old forests in the western boreal forests of Canada.

The mourning warbler, one of the few early-successional species found more commonly in the managed forests, have been found abundantly in recently logged habitats (Hannon and Drapeau 2005; Schulte and Niemi 1998) and it is suggested to have expanded its population and range as logging has increased (Pitocchelli 1993). In contrast, the chestnut-sided warbler, another species found abundantly in early-successional habitats (Niemi and Hanowski 1984, Richardson and Brauning 1995) was not found more abundantly in SNF stands. This species was observed in tree-fall gaps, shrubby rock-outcrops, and along habitat edges and hence, found adequate habitat within the unmanaged BWCAW. The chipping sparrow, the second species with higher abundance in SNF, is indicative of coniferous forests and human dominated landscapes (Middleton 1998). It was commonly found in regenerating conifer stands with relatively open understories within the SNF.

Riparian corridor patterns

Species richness and abundance of birds was significantly higher for points in close proximity to riparian areas, as opposed to those located further in the forest interior. It is generally accepted that the diversity of ecosystem processes and habitats within riparian areas support a great diversity of wildlife (Naiman et al. 1993; Naiman and Decamps 1997); however direct comparisons between riparian and forested areas for boreal birds are lacking. The effect of proximity to riparian areas (points 100m versus 400m) was similar to that of management type (BWCAW versus SNF). The highest abundance and richness occurred at points in the unmanaged landscape that were close to riparian areas (Figure 2). These measures followed a distinct trend depending upon management type and proximity to riparian corridor, with the lowest average abundance and richness occurring in managed (SNF) forest interior (400m) stands (Figure 2).

Within-stand vegetation measurements did not vary between 100m and 400m points. This is most likely due to conducting vegetation measurements at the center of the point count, 100m from the edge of the riparian corridor. However, due to the position of 100m point-counts, birds that were utilizing riparian habitat were observed in surveys. This is further indicated by the inclusion of many riparian or wetland dependent species in these surveys. Species with increased abundance at 100m point counts included; alder flycatcher, Canada warbler, common yellowthroat, song sparrow, swamp sparrow, winter wren, and white-throated sparrow (Table 3). Only the ovenbird showed increased abundance at 400m point-counts.

These results support the suggestion that few boreal species can be considered forest-interior birds (Schmiegelow et al. 1997). One possible exception is the ovenbird (Lambert and Hannon 2000). In addition, it is clear that many species in this region are either dependent upon or regularly use forest openings and riparian areas. Enhanced protection of these areas might help support greater avian diversity in boreal forests (Hannon et al. 2002).

Long-term effects of logging and fire suppression in southern boreal forests

Although much of North America’s boreal forest still maintains some form of natural fire disturbance (Hannon and Drapeau 2005), there is evidence that future forests might differ markedly from current forests (Schulte et al. 2007; Friedman and Reich 2005). In comparison to the majority of boreal Canada, areas with more extensive logging and fire-suppression histories (SNF) have much different forest composition then during pre-settlement times (Friedman and Reich 2005). Most forests were made up of dominant tree species pairs that did not exist pre-settlement (Friedman and Reich 2005). Such changes, at the periphery of the boreal forests where human settlement has persisted for longer, might be indicative of future forests throughout the boreal region of North America. The impacts of this on distributions and abundances of bird populations are unknown, but most likely would entail a shift in community composition and possibly a reduction in diversity.

Additionally, areas where logging is not present, but fire disturbance has been suppressed (BWCAW) are of equal concern (Heinselman 1996). Frelich and Reich (1995) found that unmanaged stands were generally reaching older age and becoming more mixed than during pre-settlement. Although this might have the effect of increasing within-stand compositional and structural diversity (Scheller et al. 2005) with subsequent increases in avian species richness, it is a departure from pre-settlement stands that had higher proportions of even-age forests and that historically supported the region's bird communities (Frelich and Reich 1995; *but see* Wallenius 2011). Additionally, without forest management or regular natural disturbances, populations of early-successional species might be limited, mainly being supported by riparian areas and canopy openings created by tree senescence. Further, the abundance of species associated with old-growth forests and cavity-nesting species found in the BWCAW might be related to decreasing stand turnover rates caused by infrequent fires.

This is not to say that fire-disturbance does not occur in the BWCAW. During the fall of 2011 the Pagami Creek Fire burned nearly 40,000ha, approximately 10% of the entire BWCAW. Within the last five years, two other fires burned another 40,000ha in and around the BWCAW. Additionally, the Forest Service conducts occasional prescribed burns in the wilderness area. Still, there is concern that current and future fires might have higher fire severity (burn hotter) than pre-settlement fires (Scheller et al. 2005). This might modify the characteristic mosaic pattern normally produced by fires (Carlson et al. 2011) and to which birds most certainly respond.

Conclusions: Implications for conservation of boreal avi-fauna

Change in forest management and, in particular, the replacement of fire disturbance with logging disturbance is a concern in boreal forests. My research indicates that breeding bird communities in wilderness areas mainly affected by natural disturbance are different than landscapes that are managed primarily for timber production. Dedication of additional land as wilderness could impact the populations of many species, especially mature-forest and cavity-nesting species of boreal regions. The continued modification of habitat factors that historically controlled avian species diversity in this region will have negative impacts on populations of these species, but their severity is unclear. However, if the long-term effects of logging on forest dwelling birds in Scandinavia (especially cavity nesting species) are any indication of what might occur in North American boreal forests (Imbeau et al. 2001), then changes in management activity and promotion of fire disturbance will be required to preserve avian diversity.

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