Forest Ecology and Management 328 (2014) 26–34

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Avian communities of managed and wilderness hemiboreal forests

Edmund J. Zlonis *, Gerald J. Niemi

Center for Water and the Environment, Natural Resources Research Institute, University of Minnesota Duluth, 5013 Miller Trunk Highway, Duluth, MN 55811, USA

ARTICLE INFO

Article history:
Received 17 March 2014
Received in revised form 12 May 2014
Accepted 13 May 2014
Available online 7 June 2014

Keywords:
Hemiboreal forest
Avian community
Natural disturbance
Logging
Avian conservation
Wilderness

ABSTRACT

We compared breeding bird communities of hemiboreal forests in multiple-use managed forests and relatively unmanaged wilderness forests in northern Minnesota. A total of 240 point-count locations, 120 in each of the managed and wilderness areas, were sampled three times across ten paired transects in 2010 and 2011. Transects were paired near lotic systems that cross each management type, with half of the points adjacent to (100 m) or distant (400 m) from the riparian corridor. Total number of individuals and species richness detected per count were higher within the unmanaged forest ($F_{1,9} = 9.76$, $p = 0.01$; $F_{1,9} = 11.17$, $p < 0.01$) and forest adjacent to the riparian corridor ($F_{1,9} = 28.30$, $p < 0.001$; $F_{1,9} = 42.12$, $p < 0.001$). These results were negatively correlated with increased area of regenerating forests (mainly from logging) within the managed forest and positively correlated with tree species richness and overstory height of forest stands within the wilderness forest. Of 35 species analyzed individually, 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 more common in the wilderness forest. Only the Mourning Warbler (*Geothlypis philadelphia*) and Chipping Sparrow (*Spizella passerina*) were more common in the managed forest. Species associated with mature or mixed forests tended to be found in the wilderness area at higher densities, but most species associated with early-successional habitats did not differ between the managed and wilderness landscapes. Results suggest that forests with natural disturbance and succession regimes provide habitat for a higher density and richness of bird species. Responses by breeding birds were similar in both management types regarding distance from riparian areas. To adequately provide for effective conservation of the avian community, forested regions should include wilderness forests.

1. Introduction

Few studies have compared breeding bird composition and abundance across a broad range of forest types and ages between naturally disturbed and managed boreal or hemiboreal landscapes (Edenius and Elmberg, 1996; Drapeau et al., 2000). In boreal regions, birds are estimated to compose approximately 70–80% of all terrestrial vertebrate species (Niemi et al., 1998) and the presence of natural heterogeneity in the ecosystem has caused bird species to adapt to diverse and changing landscapes (Heinselman, 1973; Pastor et al., 1996). Forest management might change these dynamics by altering the composition, age, and complexity of forest stands in the landscape.

Fire disturbance has historically controlled the heterogeneity of boreal and hemiboreal forest ecosystems, but other natural disturbances such as wind-storms, periodic insect outbreaks, and beaver (*Castor canadensis*) activity have also been shown to affect the structure and diversity of landscapes (Heinselman, 1973; Pastor et al., 1996; Angelstam and Kuuluvainen, 2004; Kuuluvainen, 2009). The type, size, and intensity of disturbance have functioned in concert to maintain diverse species composition and ecological processes, but fire suppression efforts have resulted in human-induced changes replacing naturally occurring disturbances (Helle and Niemi, 1996; White and Host, 2008). To maintain ecological function and biodiversity, the effects of forest management must be understood and taken into account (Pastor et al., 1996; Reich et al., 2001). Logging has changed the scale and structure of landscape disturbance (Mladenoff et al., 1993; Schulte et al., 2007), but has also changed its rate (Heinselman, 1973). Historically, the rate of disturbance was highly variable while harvesting practices are at shorter, more regular intervals (Niemi et al., 1998).

* Corresponding author. Tel.: +1 6512160404.
E-mail addresses: zloni011@d.umn.edu (E.J. Zlonis), gniemi@d.umn.edu (G.J. Niemi).

http://dx.doi.org/10.1016/j.foreco.2014.05.017
0378-1127/

Although fragmentation is often implicated in controlling species diversity and extinction patterns, research indicates that fragmentation plays a lesser role in altering the distribution and populations of boreal bird communities when compared with habitat loss (Schmiegelow et al., 1997; Trzcinski et al., 1999; Schmiegelow and Mönkkönen, 2002). Forest management does not permanently alter forests (Edenius and Elmberg, 1996), and forest cut-over areas often provide habitat for many breeding bird species preferring early-successional habitats (Schulte and Niemi, 1998). However, the degree to which logging mimics natural disturbance and its effects on forest dynamics has come under question (Hobson and Schieck, 1999). Hanski et al. (1996) found that increased amounts of edge due to logging had no negative effect on bird nesting success, but Manolis et al. (2002) and Flaspohler et al. (2001) found logging edges negatively affected ovenbirds (*Seiurus aurocapilla*).

Logging reduces structural diversity, vegetation diversity, and the presence of snags that are important to breeding bird communities (Niemi and Probst, 1990). Forest stands that are more diverse structurally and in tree species composition (Niemi and Hanowski, 1984; Hobson and Bayne, 2000b) provide habitat for a greater number of bird species and individuals to forage, breed, and nest. Species richness and density of individuals depend on many factors including forest type and disturbance type, but generally increase with forest stand age (Niemi et al., 1998; *but see* Hagan et al., 1997). Hobson and Bayne (2000a) and Venier and Pearce (2005) have also supported this pattern for quaking aspen (*Populus tremuloides*) and jack pine (*Pinus banksiana*) stands, respectively.

The objective of this study was to compare the breeding bird communities in forests managed by logging and relatively unmanaged wilderness forests. We also incorporate the influence of riparian corridors within this design because of the limited data that exist comparing riparian to upland systems (Bub et al., 2004), despite the importance of forested riparian corridors for bird communities (Hannon et al., 2002; Chizinski et al., 2011). We addressed three main questions. Do breeding bird communities of the Boundary Waters Canoe Area Wilderness (BWCAW, wilderness landscape) and the surrounding Superior National Forest (SNF, managed landscape) differ in abundance, composition, and diversity? How do effects of management type compare to those of a salient landscape feature, proximity to riparian corridors? What vegetation characteristics at the stand and landscape scale are associated with these differences?

2. Methods

2.1. Study area

The SNF comprises 1.6 million hectares in northeastern Minnesota. The BWCAW makes up approximately 400,000 hectares of the SNF and lies along the border with Ontario, Canada (Fig. 1). The BWCAW is a protected wilderness area, nearly half of which is virgin forest, with the remainder having been logged in the 1800s and early 1900s (Heinselman, 1996). Since the current BWCAW boundaries were designated in 1978, natural disturbances such as fire, windstorms, and insect outbreaks have affected the landscape. There is no logging management within the BWCAW, but prescribed burns and fire control are occasionally practiced. The remainder of the SNF lies south of the BWCAW. The U.S. Forest Service has adopted a multiple use protocol in this area, and development and management practices are prevalent, logging is common, motorized recreation is allowed, and homes and towns are present. Hereafter, BWCAW refers to the unmanaged wilderness area, and SNF refers to the managed area south of the BWCAW.

Hemiboreal 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 spp.*) – birch forests. The breeding bird communities of these hemiboreal forests, near the ecotone of boreal and northern temperate forests, are amongst the most diverse in North America (Niemi et al., 1998). This region supports approximately 155 breeding species of forest-dwelling birds (Green, 1995).

2.2. Study sites

Paired transects adjacent to river systems that cross the border of the BWCAW were established. We used aerial photography (Farm Services Administration Color Orthophotos 2003–2004) and landcover maps (Landsat-based land-use land-cover) (MNDNR, 1999-2012) to identify study sites that fit criteria of being a lotic-system crossing the southern border of the BWCAW consisting of a minimum of 1.5 km of riparian habitat in both the BWCAW and SNF within 5 km of the BWCAW border (riparian habitat within 1 km of the border at an angle >45°). The habitat within 400 m of the riparian corridor had to be composed of mostly upland forest and commercial timber harvest had to have occurred on the SNF side after 1980. Ten areas spanning 138 km of the BWCAW border satisfied these criteria and were included (Fig. 1).

Each river system consisted of paired study areas, one within and one outside of the BWCAW, each a minimum of 500 m from the BWCAW border. Point counts within each study area were positioned along two parallel transects, 100 m and 400 m from the riparian corridor. Each transect consisted of six points spaced 250 m apart (Fig. 1).

2.3. Disturbance history

We summarized proportions of major habitat classes in a 1 km buffer surrounding each transect based on Landsat land-cover (Table 1). Forest cut-over areas were commercially harvested for timber between 1980 and 1995 and define the amount of younger forest. A regional analysis (Wolter and White, 2002) and recent field observations indicate the rate of forest management in this region is nearly 1% per year.

All transects within the BWCAW were likely disturbed by humans and cannot be considered virgin forest (Heinselman, 1973). Logging activities before the wilderness designation was mainly selective logging of old growth red (*Pinus resinosa*) and white pine (*Pinus strobus*). In nine of ten BWCAW transects, the most recent major disturbance was fire in the late 19th or early 20th century. The final transect was most recently disturbed by a logging operation in the early 1920s. Between 1975 and 2000, smaller-scale disturbance affected approximately 12% of the forests surrounding BWCAW count locations (Wolter et al., 2012), while forest management affected approximately 42% of locations in the SNF.

2.4. Avian surveys

At each point location, we conducted three ten-minute counts, with two between 14 May and 6 July 2010 and one between 25 May and 19 June 2011. All birds seen or heard (excepting those flying overhead) within the ten-minute interval were recorded and categorized by species, behavior (i.e., singing or calling), and distance from observer. Surveys were completed from approximately 0.5 h before sunrise to 4 h after sunrise in good weather conditions (no rain and low wind speed). In 2010, each pair of twelve points was surveyed twice by the same observer, at least 27 days apart.

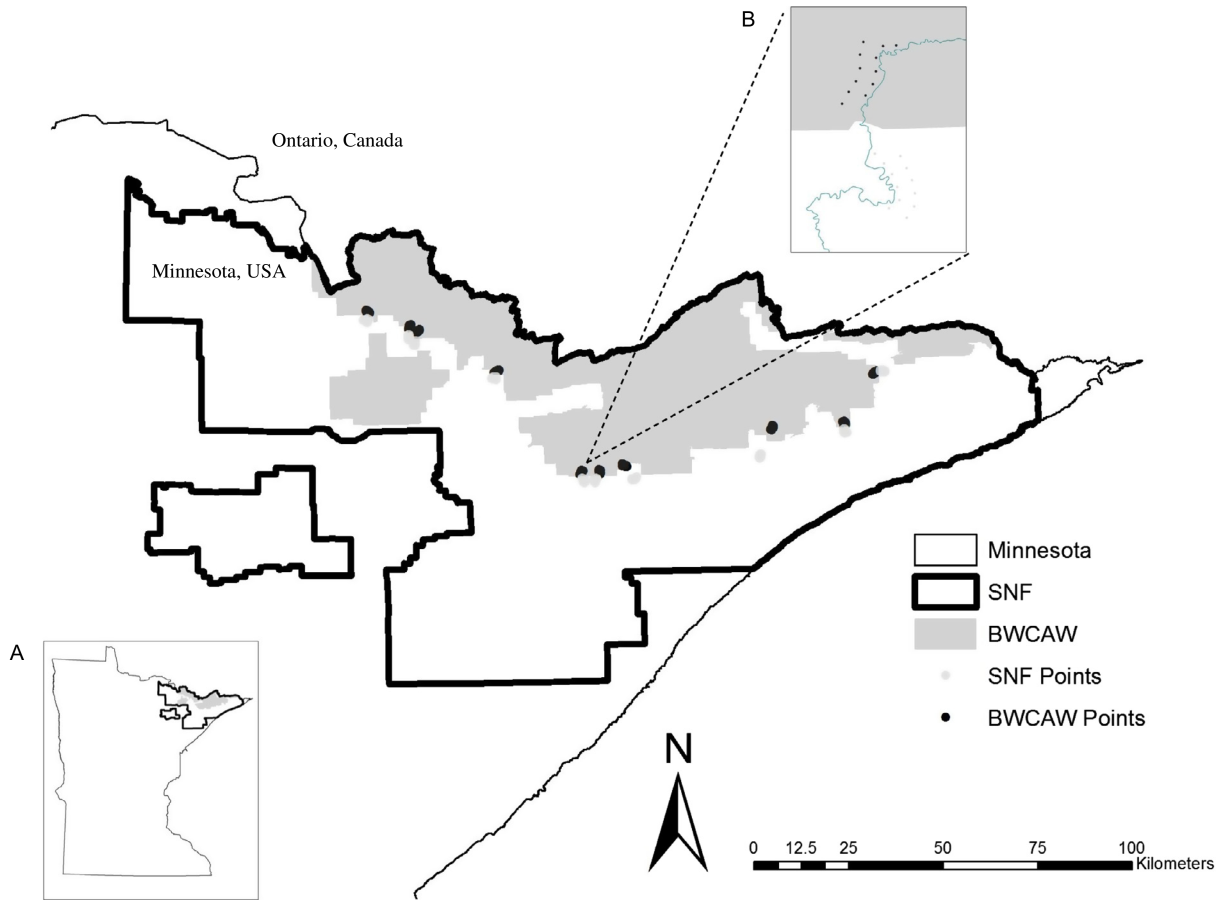

Fig. 1. Superior National Forest of Northeastern Minnesota. The region includes wilderness (BWCAW) and managed forests (SNF). BWCAW and SNF points represent paired transects near lotic systems that cross the BWCAW border. Insets show (A) Minnesota, USA (A) and an example transect, Little Isabella River, and its associated point count locations (B).

Table 1
Proportion of broad habitat classes surrounding point count transects in the Boundary Waters Canoe Area Wilderness (BWCAW; wilderness forest) and the Superior National Forest (SNF; managed forest). Values are proportions of habitat classes in a 1 km circle surrounding the center of each transect. 'Cut-over' represents forests that were harvested between 1980 and 1995.

Cover type	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

During the second survey, the order in which the point counts were conducted was reversed. In 2011, SNF and BWCAW paired transects were surveyed simultaneously by two observers. Each observer spent equal time in both management types. The order of points was randomly assigned, with half of the transects starting 100 m and half starting 400 m from the river.

2.5. Vegetation measurements

Vegetation measurements were taken at each of the point count locations in June and July 2010. Trees (dbh > 10 cm) surrounding each point were sampled using a 10 BAF prism. Tree species, status (1 = alive, 2 = dying, 3 = dead), and size class (Table 2) were recorded. Overstory height was visually estimated in 1 m measurement classes. Canopy coverage, canopy deciduous, sub-canopy coverage, sub-canopy deciduous, under-story coverage, under-story deciduous, and ground coverage were estimated in 20% increments.

2.6. Statistical analyses

To test for the differences between SNF and BWCAW paired areas on bird counts and vegetative variables, we performed Poisson or negative binomial mixed-model regressions with SAS software PROC GLIMMIX (SAS Institute, 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 from river (100 m or 400 m) were used as fixed effects; 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 transformed to the original scale through ILINK.

All individuals and species observed were included in comparisons of total individuals and species richness (Etterson et al.,

Table 2
Summary of vegetation characteristics measured in forest stands of wilderness (Boundary Waters Canoe Area Wilderness; BWCAW) and managed (Superior National Forest; SNF) forests. All variables listed were included in a Canonical Correspondence Analysis (Fig. 3). Correlations between individual variables and the first two canonical axes (R: CC1, R: CC2) are listed. Also reported are least square mean values for measurements at each point-count location and significance of statistical tests.

Variable	R: CC1	R:CC2	BWCAW	se	SNF	se	*p*-Value
Overstory height (m)	0.25	0.82	15.97	0.72	13.34	0.62	0.02
Tree richness (species/prism plot)	0.3	0.71	2.36	0.17	1.68	0.14	<0.01
BA (m^2/ha)			14.79	1.34	11.84	1.09	0.09
Tree density (TD; trees/ha)	−0.12	0.26	564.68	54.64	561.11	54.3	0.96
TD (10–14.9 cm dbh)			275.53	53.58	323.11	62.83	0.58
TD (15–19.9 cm dbh)	−0.22	0.37	148.99	29.5	139.8	27.68	0.83
TD (20–24.9 cm dbh)	0.04	0.55	70.06	17.21	56.91	13.99	0.56
TD (25–29.9 cm dbh)	0.15	0.56	38.01	10.66	24	6.74	0.28
TD (30–34.9 cm dnh)	0.08	0.5	17.51	6.26	7.92	2.84	0.15
TD (35–39.9 cm dbh)	0.28	0.35	7.97	3.26	2.17	0.9	0.05
TD (>40 cm dbh)	0.29	0.29	5.32	2.23	2.59	1.61	0.35
Snag density (trees/ha)	0.17	0.47	68.15	18.81	37.81	10.44	0.17
Canopy coverage	0.25	0.1	2.4	0.18	2.42	0.19	0.9
Canopy deciduous	0.73	−0.01	2.28	0.26	2.2	0.26	0.78
Sub-canopy coverage	0.2	0.32	2	0.14	1.72	0.13	0.14
Sub-canopy deciduous	0.68	0.09	2.21	0.25	1.9	0.22	0.13
Understory coverage	0.49	0.01	2.35	0.18	2.08	0.16	0.19
Understory deciduous	0.68	−0.32	2.88	0.31	2.83	0.3	0.84
Ground coverage	−0.31	−0.44	4.03	0.18	3.98	0.18	0.85
Shrub density	0.14	−0.03	3.08	0.17	3.18	0.18	0.67

2009). To account for potentially differing sampling areas, we analyzed metrics for both limited radius 100 m and unlimited distance counts. Similarly, rarefaction curves were created with EcoSim software (Gotelli and Entsminger, 2011) to compare tree species richness estimates from the unequal areas sampled by the prism method.

Bird species were grouped into migratory, nesting, and habitat guilds per Green (1995). To eliminate effects of abundant species, guild-level analysis was based on the number of species observed. Any species with ⩾72 observations was 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 version 5 (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 ($r \geqslant 0.70$) with other variables but showed lower correlation with primary axes were eliminated from ordination analyses. When the skewness of specific habitat 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, Cary, NC, USA)) was used in a descriptive mode to explore habitat differences between managed and wilderness landscapes.

3. Results

3.1. Avian point counts

We detected 13,332 individuals of 94 species. Species richness per river system (12 count locations) was significantly higher within the BWCAW (average of 38.3 species) than in the SNF (33.9 species) ($F_{1,9} = 7.98$, $p = 0.02$). Richness comparisons were congruent with diversity indices; the Shannon Wiener (H) was higher ($p < 0.01$) within the BWCAW ($H = 2.34$) than in the SNF ($H = 2.23$).

The effects of management type and distance were the same when analyzing 100 m limited-radius (LR) and unlimited distance (UD) point counts. Species richness per count was significantly higher within the BWCAW (LR, $F_{1,9} = 10.65$, $p < 0.01$; UD, $F_{1,9} = 11.17$, $p < 0.01$; Fig. 2) compared with the SNF and at point-counts 100 m from the riparian area (LR, $F_{1,9} = 11.64$, $p < 0.01$; UD $F_{1,9} = 28.30$, $p < 0.001$; Fig. 2). The total number of individuals detected was also significantly higher in the BWCAW (LR, $F_{1,9} = 18.10$, $p < 0.01$; UD, $F_{1,9} = 9.76$, $p = 0.01$; Fig. 2) and at 100 m (LR, $F_{1,9} = 11.64$, $p < 0.01$; UD, $F_{1,9} = 42.12$, $p < 0.001$) compared with the SNF and points 400 m from the riparian corridor.

For UD counts there was a significant interaction between the visit (1, 2, or 3) and the distance (100 m or 400 m) from the riparian corridor, where the discrepancy between distances was greatest for visit 1 and less substantial for visits 2 and 3. Still, the average species richness and total number of individuals was consistently higher at 100 m for all visits. There was also a significant interaction between visit and management type for total individuals (LR and UD counts), where the discrepancy between the numbers of individuals in each management type was greatest for visit 1 and less substantial for visits 2 and 3. Regardless of visit, the average number of individuals observed was consistently higher in the BWCAW than in the SNF.

The number of species detected per count station was significantly higher in the BWCAW for permanent residents (BWCAW, 1.4; SNF, 1.11 species, $F_{1,9} = 10.86$, $p < 0.01$). Although not significant at $\alpha = 0.05$, both long (BWCAW, 5.83; SNF, 5.28 species, $F_{1,9} = 3.72$, $p = 0.09$) and short distance (BWCAW, 4.49; SNF, 4.1 species, $F_{1,9} = 3.79$, $p = 0.08$) migrant species had higher average species richness in the BWCAW.

Cavity nesting species (BWCAW, 1.24; SNF, 0.73 species, $F_{1,9} = 48.01$, $p < 0.001$) were significantly more abundant in the BWCAW. At $\alpha = 0.05$, neither canopy (BWCAW, 2.58; SNF, 2.17 species, $F_{1,9} = 4.10$, $p = 0.07$) or ground (BWCAW, 5.25; SNF, 4.81 species, $F_{1,9} = 4.69$, $p = 0.06$) nesting species had significantly higher richness in the BWCAW. Shrub and sub-canopy 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,

Table 3

Summary of individual bird species analyzed in a comparison of the Boundary Waters Canoe Area Wilderness (BWCAW; wilderness forest) and the surrounding Superior National Forest (SNF; managed forest). All species with observations at >10% of point count locations were tested for management type (wilderness or managed) and riparian corridor (100 m and 400 m) effects. All species were included in a Canonical Correspondence Analysis (Fig. 3). Correlations between species and the first two canonical axes (R: CC1, R: CC2) are listed. Additional values are least squares means of each species observed per 10-minute, unlimited radius point count.

Species	Abbrev.	Obs.	R: CC1	R:CC2	BWCAW	se	SNF	se	p-Value	100 m	se	400 m	se	p-Value
Alder flycatcher (*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
Canada 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

Bold indicates species that varied by management type.

3.43; SNF, 2.79 species, $F_{1,9} = 11.75$, $p < 0.01$). Species groups associated with all other habitat-types did not differ by 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, $F_{1,9} = 1.41$, $p = 0.27$).

Of the thirty-five common species, eight were observed significantly more often in the BWCAW while two species had significantly higher abundance in the SNF (Table 3).

3.2. Vegetation sampling

Tree species composition consisted primarily of six species. BWCAW stands were dominated by black and white spruce (31%), jack pine (17%), quaking aspen (15%), paper birch (13%), and balsam fir (12%). SNF stands were composed of jack pine (29%), spruce (23%), quaking aspen (16%), balsam fir (11%), and paper birch (10%).

Neither the overall density of trees (Table 2) nor the density of deciduous (BWCAW, 116.3 trees/ha; SNF, 118.3 trees/ha; $p = 0.97$) and coniferous (BWCAW, 431.6 trees/ha; SNF 407.2 trees/ha; $p = 0.77$) trees sampled differed significantly between management types. However, the density of large trees $\geqslant 30$ cm dbh/ha (BWCAW, 31.19 trees/ha; SNF, 12.89 trees/ha; $F_{1,9} = 5.50$, $p = 0.04$) was significantly higher within the BWCAW stands.

On average, the overstory height and tree species richness of BWCAW were significantly higher than in the SNF (Table 2). Rarefaction analysis indicated that tree species richness was higher in BWCAW stands at all sampled abundance levels.

3.3. Multivariate analyses

Results of MRPP analysis indicated significant separation in the vegetation variables between the BWCAW and SNF stands (chance-corrected within group agreement, $A = 0.02$, $p < 0.01$). DFA indicated that tree species richness, overstory height, tree density (trees 30–34.9 cm dbh), and snag density were higher in BWCAW stands, while overall tree density (trees >10 cm dbh), shrub density, and canopy coverage were higher in SNF stands.

CCA found a relationship between breeding bird species and vegetation variables for the first canonical axis (eigenvalue = 0.12%, 6.1% variation explained, species-environment correlation = 0.74, $p < 0.01$; Fig. 3). The second canonical axis also indicated a bird-vegetation relationship, with both eigenvalue (0.07%, 3.7% variation explained) and species-environment correlation (0.68) being higher than that of the maximum achieved in randomization tests.

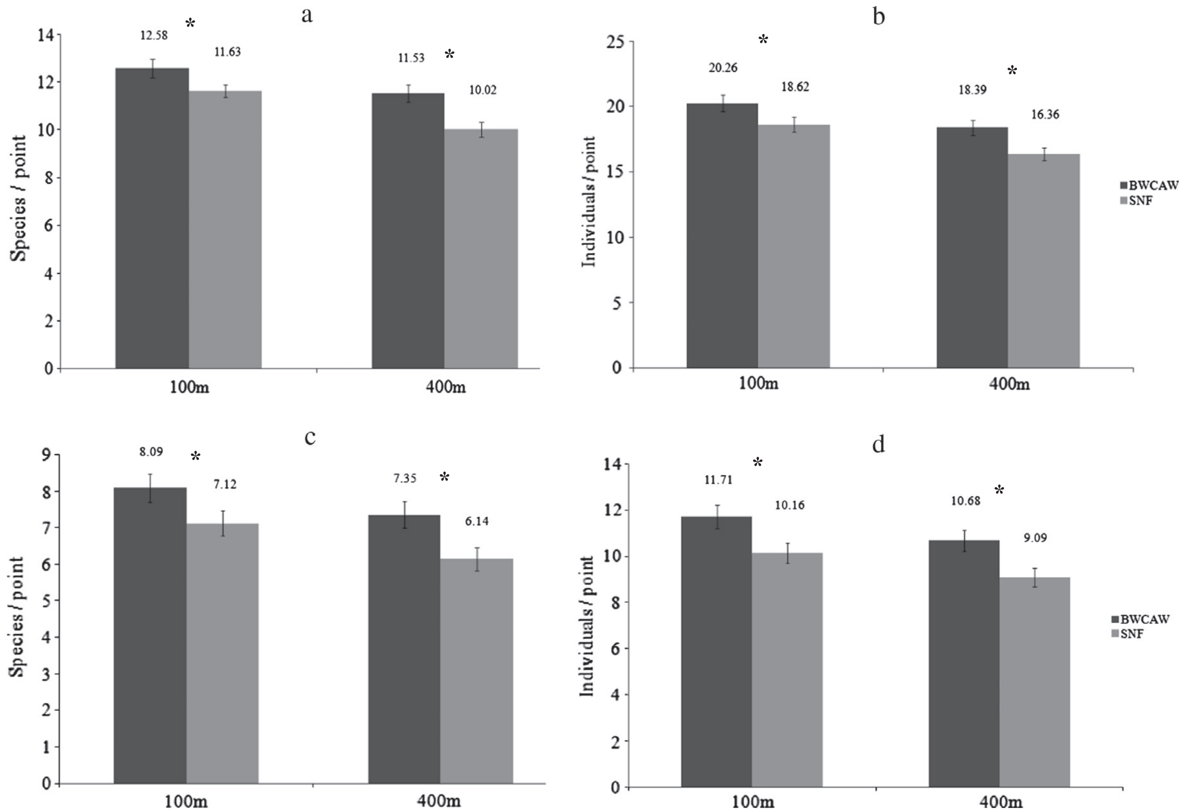

Fig. 2. Average species richness and total abundance per point count location depending on management type (wilderness or managed) and distance from riparian corridor (100 m or 400 m). Samples come from the Boundary Waters Canoe Area Wilderness (BWCAW; wilderness forests) and surrounding Superior National Forest (SNF; managed forests). Results are presented for either unlimited distance counts (a, b) or counts within 100 m of the point count location (c, d). *Results are significant at $\alpha = 0.05$ level.

4. Discussion

4.1. Bird-community patterns

Our results indicate that the relatively unmanaged forest stands within the BWCAW were providing habitat for an increased abundance and richness of breeding birds compared to the SNF. 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 (Hannon and Drapeau, 2005; Schieck and Song, 2006), more mixed (Hobson and Bayne, 2000b; Jansson and Andrén, 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 our CCA results, showing nearly all species with significantly higher abundance in the BWCAW being associated with mature, mixed, and structurally diverse forest stands (Fig. 3).

When compared to fire disturbance, the shorter rotation period of logging prevents a high proportion of stands from reaching mature, mixed status. Species richness of post-fire and post-harvest stands tends to converge in mid-successional stands (31–75 years old), but 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 hemiboreal region (Helle and Niemi 1996). Besides affecting tree species composition and structural diversity, management might prevent forest stands from supporting abundant arthropod communities (Petersson et al., 1995), an important forage-base for many bird species.

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. Although studies of managed and unmanaged landscapes are few, they have equivocal results. Drapeau et al. (2000) found no difference in alpha diversity between managed and unmanaged landscapes, but found higher beta and gamma-diversity in the managed landscape. However, studies in boreal and hemiboreal regions of Europe found that low human-impact landscapes such as those consisting of higher proportions of old and mixed forests had greater species richness than intensively managed areas (Edenius and Elmberg, 1996; Jansson and Andrén, 2003; Rosenvald et al., 2011).

The trend of increased bird species richness and abundance in the BWCAW was consistent for all three sampling periods, despite significant interactions. One factor that might have contributed to the interaction terms for stand-level species richness and abundance was the variation in the timing of counts. Samples from mid to late May (visit 1) 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 and the main effect of management type on abundance and richness was still significant.

4.2. 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 and long-distance migratory-guilds as well as ground and canopy nesting-guilds had similar, but insignificant

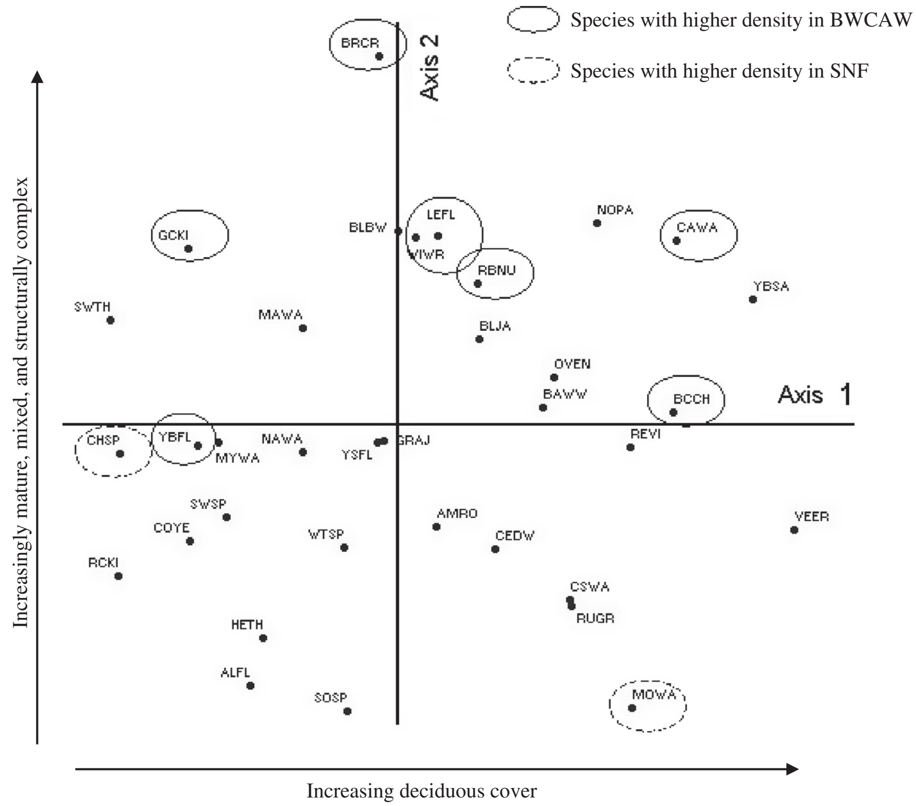

Fig. 3. Canonical Correspondence Analysis (CCA) of vegetation variables (Table 2) and bird species (Table 3) in wilderness (Boundary Waters Canoe Area Wilderness; BWCAW) and managed (Superior National Forest; SNF) forests. Abundances of each species within 100 m of point count location were used in the 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 Tables 2 and 3 for correlations between bird and vegetation variables and axes). Bird species associated with deciduous forests were positively correlated with Axis 1, while those associated with either coniferous or non-forested habitats were negatively correlated with Axis 1. Species associated with mature, mixed, and complex forests were positively correlated with Axis 2, while those associated with early-successional or non-forested habitats were negatively correlated with Axis 2.

trends ($p < 0.10$) for higher richness in BWCAW stands. Therefore, they also contributed to differences between managed and wilderness areas. These results suggest that the BWCAW is supporting 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 density of trees $\geqslant$30 cm dbh (trees potentially used by the entire cavity nesting community (Green, 1995)) in BWCAW stands provided more nest site locations for many of these species. Even though the density of snags was not different between management types, many cavities are also found in live trees, especially aspen with heartwood rot (Martin et al., 2004). Aspen trees >30 cm 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 wilderness forests were likely 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 a higher proportion of mixed-forest habitats than managed stands (Table 1). Even-aged forests regenerating from logging principally replaced mixed stands in the managed SNF transects. However, the 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). Even though the increased proportion of stands regenerating from logging activity in the managed landscape was expected to be associated with an increase in early-successional species, this was not observed likely because of the presence of natural openings in the BWCAW. These included rock outcrops, beaver ponds, tree-fall gaps, and riparian habitat that provided appropriate open, shrubby habitat. Additionally, because half of the point count locations were near or in riparian habitat, the proportion of open, shrubby, habitat was increased.

Individual species with increased abundance in the BWCAW were generally related with 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, was found abundantly in recently logged habitats (Schulte and Niemi, 1998; Hannon and Drapeau, 2005). Pitocchelli (1993) has suggested this species has expanded its population and range as logging has increased over the past 150 years. In contrast, the Chestnut-sided Warbler, another species found abundantly in early-successional habitats (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 wilderness forests of the 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.

4.3. Riparian corridor patterns

Species richness and abundance of birds was significantly higher for points in close proximity to riparian areas in comparison with 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). However, direct comparisons between riparian and forested areas for boreal or hemiboreal birds are few (Bub et al., 2004). The effect of proximity to riparian areas (points 100 m versus 400 m) was similar for both management types. The highest abundance and richness occurred at points in the unmanaged landscape that were close to riparian areas (Fig. 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 the managed (SNF) areas on transects 400 m away from the riparian area (Fig. 2). Seven species had increased abundance at 100 m point counts, while only the Ovenbird showed increased abundance at 400 m point-counts (Table 3). Within-stand vegetation measurements did not vary between 100 m and 400 m points.

4.4. Long-term effects of logging and fire suppression

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 such as 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. 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 on the conservation of bird populations are unknown, but would entail a shift in community composition (Matthews et al., 2011).

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.

Fire and wind disturbances are still present in both the SNF and the BWCAW. A major windstorm in 1999 affected northeastern Minnesota (Scheller et al., 2005) and during the fall of 2011 nearly 40,000 ha, approximately 10% of the entire BWCAW, was burned. Since 2006, two other fires burned another 40,000 ha in and around the BWCAW. Additionally, the U.S. Forest Service conducts occasional prescribed burns in the wilderness area. Yet, there are concerns 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 respond.

5. Conclusions

5.1. Implications for conservation of hemiboreal avifauna

Changes in forest management are a concern in hemiboreal forests, in particular the replacement of fire disturbance with logging disturbance. Our research indicated that breeding bird communities in wilderness areas mainly affected by natural disturbance are different than those in landscapes that are managed primarily for timber production. The continued modification of habitat factors that historically controlled avian species diversity in this region will have effects on populations of these species, the severity of which is unclear. If the long-term effects of logging on forest dwelling birds in Scandinavia are any indication of what might occur in North American hemiboreal and boreal forests (Imbeau et al., 2001), then the inclusion of wilderness forests and promotion of fire disturbance may be required to provide adequate conservation for several avian species.

Acknowledgements

We would like to thank Dr. Ronald Regal, and Dr. George Host for statistical and other advice throughout the design, data collection, analysis, and writing processes. We would also like to thank Kim Rewinkel for valuable comments on the manuscript. Additionally, Carly Lapin and Kyle Edgeton made extensive contributions to data collection. The University of Minnesota Integrated Biosciences program and the University of Minnesota Duluth Biology program supported E.Z. as a graduate student and Graduate Teaching Assistant 2009–2011.

References

Angelstam, P., Kuuluvainen, T., 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures: a European perspective. Ecol. Bull. 51, 117–136.
Bub, B.R., Flaspohler, D.J., Huckins, C.J., 2004. Riparian and upland breeding-bird assemblages along headwater streams in Michigan's Upper Peninsula. J. Wildl. Manage. 68, 383–392.
Carlson, D.J., Reich, P.B., Frelich, L.E., 2011. Fine-scale heterogeneity in overstory composition contributes to heterogeneity of wildfire severity in southern boreal forest. J. For. Res. 16, 203–214.
Chizinski, C.J., Peterson, A., Hanowski, J., Blinn, C.R., Vondarcek, B., Niemi, G., 2011. Breeding bird response to partially harvested riparian management zones. For. Ecol. Manage. 261, 1892–1900.
Drapeau, P., Leduc, A., Giroux, J.F., Savard, J.L., Bergeron, Y., Vickery, W.L., 2000. Landscape scale disturbance and changes in bird communities of boreal mixed-wood forests. Ecol. Monogr. 70, 423–444.
Edenius, L., Elmberg, J., 1996. Landscape level effects of modern forestry on bird communities in north Swedish boreal forests. Landscape Ecol. 11, 325–338.
Etterson, M.A., Niemi, G.J., Danz, N.P., 2009. Estimating the effects of detection heterogeneity and overdispersion on trends estimated from avian point counts. Ecol. Appl. 19, 2049–2066.
Flaspohler, D.J., Temple, S.A., Rosenfield, R.N., 2001. Species-specific edge effects on nest success and breeding bird density in a forested landscape. Ecol. Appl. 11, 32–46.
Frelich, L.E., Reich, P.B., 1995. Spatial patterns and succession in a Minnesota southern boreal forest. Ecol. Monogr. 65, 325–346.
Friedman, S.K., Reich, P.B., 2005. Regional legacies of logging: departure from presettlement forest conditions in northern Minnesota. Ecol. Appl. 15, 726–744.
Gotelli, N.J., Entsminger, G.L., 2011. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. <http://garyentsminger.com/ecosim.htm>.
Green, J.C., 1995. Birds and Forests. Minnesota Department of Natural Resources, St. Paul, MN.
Grigal, D.F., Ohmann, L.F., 1975. Classification, description, and dynamics of upland plant communities within a Minnesota wilderness area. Ecol. Monogr. 45, 389–407.

Hagan, J.H., McKinley, P.S., Meehan, A.L., Grove, S.L., 1997. Diversity and abundance of landbirds in a northeastern industrial forest. J. Wildl. Manage. 61, 718–735.
Hannon, S.J., Drapeau, P., 2005. Bird responses to burning and logging in the boreal forest of Canada. Stud. Avian Biol. 30, 97–115.
Hannon, S.J., Paszkowski, C.A., Boutin, S., DeGroot, J., Macdonald, S.E., Wheatley, M., Eaton, B.R., 2002. Abundance and species composition of amphibians, small mammals, and songbirds in riparian forest buffer strips of varying widths in the boreal mixedwood of Alberta. Can. J. For. Res. 32, 1784–1800.
Hanski, I.K., Fenske, T.J., Niemi, G.J., 1996. Lack of edge effects in nesting success of breeding birds in managed forest landscapes. Auk 113, 578–585.
Heinselman, M.L., 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. J. Quatern. Res. 3, 329–382.
Heinselman, M.L., 1996. The Boundary Waters Wilderness Ecosystem. University of Minnesota Press, Minneapolis, MN.
Helle, P., Niemi, G.J., 1996. Bird community dynamics in boreal forests. In: DeGraaf, R.M., Miller, R.I. (Eds.), Conservation of Faunal Diversity in Forested Landscapes. Chapman and Hall, London, UK, pp. 209–234.
Hobson, K.A., Bayne, E., 2000a. The effects of stand age on avian communities in aspen-dominated forests of central Saskatchewan, Canada. For. Ecol. Manage. 136, 121–134.
Hobson, K.A., Bayne, E., 2000b. Breeding bird communities in boreal forest of western Canada: consequences of "unmixing" the mixedwoods. Condor 102, 759–769.
Hobson, K.A., Schieck, J., 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. Ecol. Appl. 9, 849–863.
Imbeau, L., Mönkkönen, M., Desrochers, A., 2001. Long-term effects of forestry on birds of the eastern Canadian boreal forests: a comparison with Fennoscandia. Conserv. Biol. 15, 1151–1162.
Jansson, G., Andrén, H., 2003. Habitat composition and bird diversity in managed boreal forests. Scand. J. For. Res. 18, 225–236.
Kuuluvainen, T., 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: the complexity challenge. AMBIO: J. Human Environ. 38, 309–315.
MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. Ecology 42, 594–598.
Manolis, J.C., Andersen, D.E., Cuthbert, F.J., 2002. Edge effect on nesting success of ground nesting birds near regenerating clearcuts in a forest-dominated landscape. Auk 119, 955–970.
Martin, K., Aitken, K.E.H., Wiebe, K.L., 2004. Nest sites and nest webs for cavity-nesting communities in interior British Colombia, Canada: nest characteristics and niche partitioning. Condor 106, 5–19.
Matthews, S.N., Iverson, L.R., Prasad, A.M., Peters, M.P., 2011. Changes in potential habitat of 147 North American breeding bird species in response to redistribution of trees and climate following predicted climate change. Ecography 34, 933–945.
McCune, B., Mefford, M.J., 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5. MjM Software, Gleneden Beach, Oregon, USA.
Middleton, A.L., 1998. Chipping Sparrow in The Birds of North, America. No. 334.
Mladenoff, D.J., White, M.A., Pastor, J., Crow, T.R., 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecol. Appl. 3, 294–306.
Minnesota Department of Natural Resources (MNDNR) [online]. 1999–2012. The DNR data deli. <http://deli.dnr.state.mn.us/>.
Naiman, R.J., Decamps, H., Pollock, M., 1993. The role of riparian corridors in maintaining regional biodiversity. Ecol. Appl. 3, 209–212.
Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biol. Conserv. 70, 65–276.
Niemi, G.J., Hanowski, J.M., 1984. Relationships of breeding birds to habitat characteristics in logged areas. J. Wildl. Manage. 48, 438–443.
Niemi, G.J., Probst, J.R., 1990. Wildlife and fire in the upper midwest. Management of Dynamic Ecosystems. The Wildlife Society, West Lafayette, IN, pp. 31–46.
Niemi, G., Hanowski, J., Helle, P., Howe, R., Mönkkönen, M., Venier, L., Welsh, D., 1998. Ecological sustainability of birds in boreal forests. Conserv. Ecol. 2, 17.
Pastor, J., Mladenoff, D., Haila, Y., Bryant, J., Payette, S., 1996. Biodiversity and ecosystem processes in boreal regions. In: Mooney, H.A., Cushman, J.H., Medina, E., Sala, O.E., Schulze, E.D. (Eds.), Functional Roles of Biodiversity: A Global Perspective. SCOPE. John Wiley, London, UK, pp. 33–69.
Petersson, R.B., Ball, J.P., Renhorn, K.E., Esseen, P.A., Sjöberg, K., 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. Biol. Conserv. 74, 57–63.
Pitocchelli, J., 1993. Mourning Warbler in The Birds of North, America, No. 72.
Reich, P.B., Bakken, P., Carlson, D., Frelich, L.E., Friedman, S.K., Grigal, D.G., 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. Ecology 82, 2731–2748.
Richardson, M., Brauning, D.W., 1995. Chestnut-sided Warbler in The Birds of North, America. No. 190.
Rosenvald, R., Lõhmus, A., Kraut, A., Remm, L., 2011. Bird communities in hemiboreal old-growth forests: the roles of food supply, stand structure, and site type. For. Ecol. Manage. 262, 1541–1550.
SAS software, 2010. Version 9.2 of the SAS System. SAS Institute, Cary, NC, USA.
Scheller, M.S., Mladenoff, D.J., Crow, T.R., Sickley, T.A., 2005. Simulating the effects of fire reintroduction versus continued fire absence on forest composition and landscape structure in the Boundary Waters Canoe Area, northern Minnesota, USA. Ecosystems 8, 396–411.
Schieck, J., Song, S.J., 2006. Changes in bird communities throughout succession following fire and harvest in boreal forests of western North America: literature review and meta-analysis. Can. J. For. Res. 36, 1299–1318.
Schmiegelow, F.K.A., Mönkkönen, M., 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecol. Appl. 12, 375–389.
Schmiegelow, F.K.A., Machtans, C.S., Hannon, S.J., 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78, 1914–1932.
Schulte, L.A., Niemi, G.J., 1998. Bird communities of early-successional burned and logged forest. J. Wildl. Manage. 62, 1418–1429.
Schulte, L.A., Mladenoff, D.J., Crow, T.R., Merrick, L.C., Cleland, D.T., 2007. Homogenization of northern US Great Lakes forests due to land use. Landscape Ecol. 22, 1089–1103.
Trzcinski, M.K., Fahrig, L., Merriam, G., 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecol. Appl. 9, 586–593.
Venier, L.J., Pearce, J.L., 2005. Boreal bird community response to jack pine forest succession. For. Ecol. Manage. 217, 19–36.
Wallenius, T., 2011. Major decline in fires in coniferous forests – reconstructing the phenomenon and seeking for the cause. Silva Fenn. 45, 139–155.
White, M.A., Host, G.E., 2008. Forest disturbance frequency and patch structure from pre-European settlement to present in the Mixed Forest Province of Minnesota, USA. Can. J. For. Res. 38, 2212–2226.
Wolter, P.T., White, M.A., 2002. Recent forest cover type transitions and landscape structural changes in northeast Minnesota, USA. Landscape Ecol. 17, 133–155.
Wolter, P.T., Sturtevant, B.R., Miranda, B.R., Lietz, S.M., Townsend, P.A., Pastor, J., 2012. Forest Land Cover Change (1975–2000) in the Greater Border Lakes Region. Research Map NRS-3. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.