Effects of burn severity and time since fire on songbird communities in the northern boreal forest

by

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Abstract

Wildfire shapes the boreal ecosystem in western Canada and thereby enhances and diminishes important breeding habitat for many songbird species. Two aspects of wildfire, burn severity and time since fire, fundamentally alter the forest structure that songbirds use. The objectives of this study were to test the effects of burn severity (control, unburned/ low, medium, and high) one and two years post-fire and time since fire (1 to >50 years post-fire) on songbirds in the Northwest Territories, Canada. Specifically, I quantified changes in species richness, community composition, functional diversity, and species-specific responses in uplands and peatlands using data from 777 sampling stations using autonomous recording units (ARUs). Species richness and function diversity were inversely related to burn severity. Community composition converged between uplands and peatlands when burn severity was high. Both species richness and functional diversity were significantly lower one year post-fire compared to controls (>50 years post-fire). Species richness was higher than unburned controls between 3 and 50 years post-fire, while functional diversity showed no other significant changes with time since fire. There was no shift in community composition with increasing time since fire. Results suggest that burn severity, time since fire, and their interactions with vegetation type have a noticeable, but not extreme influence, on the songbird community suggesting moderate resistant and high resilience to fire disturbances. Such information may prove useful in understanding responses to songbirds under different climate change and fire scenarios and thereby inform local conservation and management actions.

Preface

This thesis is an original work by Michelle Knaggs. Samuel Haché and Erin Bayne conceived the study design. Erin Bayne, Samuel Haché, and Scott Nielsen provided input and feedback on analysis and writing.

Acknowledgements

I'd like to express my appreciation to Erin Bayne and Scott Nielsen for the opportunity to be involved with this project. Thank you Erin for entertaining my wishes to do fieldwork in boreal forest that is slightly different than in northern Alberta. Thank you Sam Hache for envisioning the project, participating in the whole first season of fieldwork, and the mentoring throughout. Thank you to the significant funding provided by the Canadian Wildlife Service Northern Region landbird program. Thank you to the CREATE-EI program for providing funding as well as professional development opportunities. I was lucky to have great field partners: Rhiannon, Emily and Emony. Thank you Bayne and Nielsen lab folks, especially Natasha and Caitlin. I appreciate the advice and support of my family and non-school related friends. Thank you to the guy who hands out the free newspapers in front of the LRT station with the funny costumes and one-liners. Most of all, thank you Alex and Kittycoo.

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Chapter 1 - General Introduction

Songbirds in the northwestern Canadian boreal forest

The boreal biome in North America provides breeding grounds for several billion migratory songbirds each year (Blancher 2003, Rosenberg et al. 2016). While some generalist boreal species have recently increased in abundance (Rosenberg et al. 2016), other species are experiencing long-term population declines (Ballard et al. 2003). Overall, songbird abundance in the western boreal forest is in decline (Rosenberg et al. 2016). The Taiga boreal ecozone of the Northwest Territories (604,628 km^2, 6.2% of Canada's area) is relatively unaltered by human disturbances, including energy development, forestry, agriculture, and urbanization (Grondin and Gauthier 2014). This area therefore provides nesting habitat for migratory species that face conservation threats, such as habitat loss, in the more developed southern boreal, at migratory stop-over sites, or on wintering grounds (Kirk et al. 2011). As songbird monitoring of the boreal largely takes place in readily accessible and more populated southern areas, there are substantial gaps in our knowledge on distribution, abundance, and habitat associations for birds breeding in more northern regions of the boreal (Blancher 2003; Environment Canada 2013).

Northwestern boreal wildfire regime and ecology

The Canadian boreal forest is characterized by low productivity and low tree diversity, but still has substantial variability in forest structure because of regional differences in fire regimes, climate, human disturbance, and the proportion of wetlands. Overall, the northern boreal forest is cooler, slower growing, and less biologically diverse than southern boreal ecozones. Regional fire regimes can be characterized by typical fire intensity (the amount of energy released during fire, Keeley 2009), frequency, timing, size, and effects on soils (Weber and Flannigan 1997). Fires are often ignited by lightning and occur during periods of drought which are more typical in the Canadian western boreal region than in the east (Parisien et al. 2011). In the Taiga Pains ecozone within the Northwest Territories, the fire regime is characterized by large, frequent, and intense fires and has the second highest annual average area burned of all boreal ecozones of Canada (ESTR Secretariat 2013). Although the wildfire season shortens with increasing latitude, the length of daylight in summer increases, enabling the fast drying of fuels as well as increasing the duration of the burning period during the day. The proportion of deciduous trees decreases with increasing latitude, making northern forests more conifer-dominated and therefore flammable during summer months when lightning occurs. High burn intensity results in high burn severity. Burn severity measures the ecological responses to a fire including a reduction in structure due to loss of canopy, understory vegetation, and groundcover. Wildfire reduces the vegetation structure that birds use for foraging, nesting, and refuge. However, new structure also arises, including standing snags for cavity nesting species and perches for birds that forage and hunt in open spaces.

Climate change

Climate change is a major threat to songbirds in North America (Rosenberg et al. 2016). Weather and climate are the primary drivers of wildfire in the boreal (Brandt et al. 2013) and predicted climatic changes will result in increases in fire frequency, severity, and area burned (Kochtubajda et al. 2006; Grissom et al. 2000). Unlike southern boreal regions where human presence and intervention may limit the amount of wildfire, the northern and more undeveloped regions will be more likely to experience increases in wildfire with less human interference (Campos-Ruiz et al. 2018). This study took place in a region that is expected to experience more wildfire in the future due to climate change because of increased evapotranspiration (more fuel), more lightning (ignition sources), and a longer fire season (Parisien et al. 2011). This will have significant effects to the forest available to birds. Over the past 50 years there has been an increase of ~2º C in the western boreal with general circulation models (GCMs) predicting additional warming into the future (Schneider 2013; Price et al. 2013). Shifts in climate and the fire regime will also alter how forests regenerate (Schneider 2013). Some changes in the past 50 years have already been documented: Bonan et al. (1990) found that tree species in interior Alaska, USA could only grow with a maximum of 1º C of warming and were further inhibited by reduced soil moisture, while Hogg and Wein (2005) found that decreased precipitation post-fire resulted in slowed regeneration of white spruce and aspen in the Yukon, Canada.

Resistance and resilience

Ecological stability is the ability of an ecosystem or community to withstand change by resistance (the ability to withstand change), and/or resilience (the ability to return to return to the previous state after disturbance; McCann 2000). Resistance to wildfire is generally measured soon after fire occurs across a gradient of burn severities while resilience is measured over time after the disturbance has ceased (Lake 2013). Birds are good indicators of ecosystem resilience and resistance because they are easy to survey and have a diverse range of habitat requirements (Carignan and Villard 2002). To my knowledge there have been no studies on how wildfire affects songbirds in the northwestern boreal forest of Canada.

Research objectives

The objectives of this thesis were to assess the resistance and resilience of songbirds to wildfire across two forest types in an understudied region of the northwestern Canadian boreal forest. On the one hand, the songbird community in the northwestern boreal forest may be resistant and resilient to wildfire because species have co-evolved with frequent wildfire (Schmiegelow and Villard 2009). Alternatively, low species diversity may result in low resilience. Therefore, in Chapter 2 I tested for resistance by assessing changes in species richness, community composition, and functional diversity across a burn severity gradient in recent fires across two major forest types (upland forests versus peatlands). In chapter 3, I tested for resilience in the songbird community by quantifying differences in the same metrics of species richness, community composition, and functional diversity by time since fire and forest type. The implications of the resistance and resilience of songbirds to wildfire in the context of climate change are discussed in the thesis discussion (chapter 4).

Chapter 2 – Resistance of songbird communities to wildfire in the northern boreal forest

Abstract

Wildfire is the dominant natural disturbance in the boreal ecosystem of western Canada. The degree that fire alters forest structure is described as burn severity and the resistance of songbird communities to fire severity remains largely unknown. We tested for effects of burn severity (control, unburned/ low, moderate, and high) in uplands and peatlands on species richness, community composition, and functional diversity using avian point count data ($n = 1156$) from two large burns in the Northwest Territories, Canada. Species richness decreased between control and high burn severity categories in both forest types, and although there was no significant interaction of burn severity and forest type, the decrease in peatlands was more pronounced than in uplands. Functional diversity was lower in high severity burns than in controls in both uplands (-27%) and peatlands (-28%). Lastly, community composition became more similar between uplands and peatlands with increasing burn severity (5.4% variation explained by the interaction; $P \leq 0.001$). Relatively small effect sizes of burn severity indicated moderate resistance of the bird community to wildfire, particularly in upland forest types. Results from this study provides a better understanding of how songbirds respond to this important natural disturbance in northern boreal regions and this information can be used to predict how they may respond to an expected increase in burn severity due to climate change.

Introduction

Ecological resistance is the ability of ecosystems to withstand environmental change (Lake 2013). Species richness and diversity are often used to measure resistance of communities to disturbance (Leupin et al. 2004; Hoover et al. 2014), but ignore the composition of the community which may prevent an accurate assessment of impacts. For example, species richness and diversity have been shown to be stable, while beta diversity and/or functional diversity change with increasing amounts of human disturbance (Schmiegelow et al. 1997; Imbeau et al. 1999) or climate change (Virkkala and Lehikoinen 2017). Thus, metrics that incorporate species identity or ecological functions are required to fully understand how resistant a community is to change. Functional diversity measures the redundancy of traits in a community and links species with habitats by measuring species' traits that are associated with particular forest types (Schleuter et al 2010). Functional diversity has therefore been proposed to be a more appropriate indicator of resilience than species richness or abundance (Woodward and Diament 1991; Gagic et al. 2015). Functional diversity is increasingly being used to characterize responses in bird communities to disturbance with decreases in functional diversity often observed (Devictor et al. 2008; Edwards et al. 2013; Cosset and Edwards 2017; Vollstädt et al. 2017).

The boreal forest of North America contains a significant portion of the world's remaining intact forests (Potapov et al. 2008) and includes the breeding ranges of half of all bird species in North America (Wells and Blancher 2011). Wildfire is the most important natural disturbance in this biome (Weber and Flannigan 1997) and variation in severity, frequency, and area burned creates spatio-temporal heterogeneity in forest structure and composition (Weber and Stocks 1998; Bourgeau-Chavez et al. 2000). In extreme fire years, large and intense crown fires result in high severity burns where most trees are killed (de Groot et al. 2013). However, approximately 15% of disturbed areas remain unburnt in high severity burns (Eberhart and Woodard 1987) due to the presence of water, topographic variation, or changes in weather conditions during the fire (Rowe and Scotter 1973). Additionally, less severely burned areas where only some trees, understory vegetation, and groundcover are killed are also common in parts of high severity burns (Madoui et al. 2010).

Birds breeding in boreal regions may be resistant to the effects of wildfire given their adaptation to high frequency wildfire since the last ice age (Telfer 1993). Studies in North America have shown that aerial insectivores and cavity nesters tend to respond positively to burn severity, as more food and nesting locations become available (Hutto 1995, Latif et al. 2016). Species associated with early seral forest, including some ground nesters also respond positively to high severity fires (Nappi et al. 2004), while mature forest specialists generally respond negatively (Hutto and Patterson 2016). However, these studies were done in southern boreal regions with a different fire regime (Boulanger et al. 2014) and tree growth rates higher than those in northern regions (Hogg and Wein 2005). How the mosaic of post-fire stand conditions affects songbird communities at the northern edge of the boreal forest remains largely unknown. A more comprehensive understanding of the resistance of songbird communities to wildfire is needed to inform conservation and management strategies, particularly given the observed increases in warmer and drier conditions associated with rapid climate change (Kochtubajda et al 2006, Grissom et al. 2000, Héon et al 2014).

In the northwest boreal region of Canada, peatlands, defined as wetlands with a thick (> 40 cm) layer of organic matter (National Wetlands Working Group 1997), make up almost half of the landbase (Ecosystem Classification Group 2009) and provide important songbird habitat (Calme et al. 2002). Peatlands have characteristics that may make them resistant to wildfire, such as a high water table (Kettridge et al. 2015) and groundwater connectivity (Hokanson et al. 2015). Wetter peatlands, such as fens (Flannigan et al. 2008) and peatland interiors, are thought to be particularly resistant to wildfire (Hokanson et al. 2015). However, peatlands contain a large fuel supply with a thick layer of organic matter that can be highly flammable under extremely dry conditions (Flannigan et al. 2008). Treed fens and bogs also contain volatile ericaceous shrubs (Rowe and Scotter 1973) and black spruce that retains its dead branches, adding to the availability of fuels and ability of fires to spread to tree crowns. Because bird assemblages in areas with higher disturbance frequency were found to be more resistant to disturbance than areas with less frequent disturbance (Latif et al. 2016; Drapeau et al. 2016), the songbird community in peatlands may be less resistant than in uplands where fire disturbance is traditionally more frequent. To my knowledge, there have been no similar boreal studies to test the effects of wildfire in peatlands.

The objectives of this study were to quantify the resistance of songbird communities to wildfire in the northwest boreal region of Canada by testing for effects of burn severity (unburned, low, moderate, and high) in uplands and peatlands on different community metrics (species richness, community composition, and functional diversity). Avian point count data were collected during the first two years following large wildfires in the Northwest Territories, Canada. Complete resistance would be indicated by no changes in species richness, functional diversity, or community composition with increasing burn severity. Because of the adaptation of songbirds to frequent wildfire, we predicted that the songbird community in this region should be highly resistant to wildfire. Based on this hypothesis, we also predicted that the upland songbird community would be more resistant to wildfire than the peatland songbird community.

Methods

Study Area

The study took place within a ~8,000 km^2 area between Fort Providence and Behchokǫ̀, in the Taiga Plains ecozone of the Northwest Territories, Canada (Figure 1). This area was in and around two large burns (750,000 ha and 110,000 ha) that occurred in June and July 2014 and comprised nearly one third of all the area burned in the Northwest Territories during a record fire year whereby 3,400,000 ha burned compared with an average of 570,000 ha burned annually (Northwest Territories Department of Environment and Natural Resources (ENR) 2015). The ecozone is comprised of approximately 50% upland, 40% wetland (mainly peatland), and 10% open water (Ecosystem Classification Group 2007). The climate was generally dry, receiving between 288 – 387 mm of yearly precipitation and the daily temperatures averaged yearly throughout the region were between –2.5 and –4.3°C from 1981 to 2010 (Government of Canada 2018). Despite limited precipitation, there are extensive wetlands as a result of large areas of poorly-drained soils. With the exception of some shallow, inorganic mineral ponds, wetlands are primarily peatlands consisting of treed fens and bogs dominated by black spruce (*Picea mariana*; Ecosystem Classification Group 2007). For our analyses, all wetlands will hereafter be referred to as peatlands. Upland forests are dominated by jack pine (*Pinus banksiana*) with some trembling aspen (*Populus trembloides*). The study area has limited human disturbance with one highway, a few secondary roads, and limited non-commercial logging in some upland stands.

Sampling design and avian surveys

A total of 1,156 avian point count surveys was conducted between May 25 – July 1 in 2015 and 2016 using passive automated recording units (ARUs; Wildlife Acoustic SM3 model in 2015 and SM4 model in 2016). Sampling stations ($n = 405$) were grouped into study sites of either 5 × 5 (2015; $n = 16$) or 4 × 4 (2016; $n = 20$) grids with stations spaced 500 m apart. We used a stratified sampling design, where sites were randomly selected from a set of candidate sites based on overall burn severity stratified to 3 levels (low, moderate or high; Figure 2) and unburned areas (controls). The resulting sampling design consisted of 77 low severity, 87 moderate severity, 116 high severity burns, and 124 control sampling stations (Appendix 3); 173 of these stations were sampled in both years. Controls had not experienced fire in the past 43 years. For logistical reasons, stations were located within 2.5 km of truck-accessible roads, but at least 300 m from the highway to minimize interference of vehicle noise on recordings and edge effects from the road.

Burn severity was derived from a continuous differenced Normalized Burn Ratio (dNBR) layer (cell size = 30 m; Whitman 2015). DNBR was calculated as changes in reflectivity of Landsat imagery taken before and after the fire (Key and Benson 2006). Ground validation was conducted using a modified composite burn index (CBI) protocol which uses measurements of the degree of burned organic matter (Whitman 2015). For each sampling station, severity was categorized as low, moderate, or high (Rose et al. 2016, Wilkerson et al. 2016) using the average dNBR in a 100-m buffer. Unburned (control) study sites were located between 1 and 15 km from burn perimeters to limit the possibility of counting birds outside the burn perimeter. In low severity burns, less than 25% of basal area of trees was burned (Miquelajauregui et al. 2016), most trees and some shrubs survived, and soil was mostly unburned (dNBR <279). Unburned areas within the fire perimeter were categorized as low severity. In moderate severity burns, some shrubs, downed woody material and soil was consumed, as well as between 25-50% of the basal area of trees (dNBR between 279 and 525). High severity burns resulted in most trees being killed with >75% of basal area consumed, most shrubs consumed, and exposure of mineral soil (dNBR >525). The Northwest Territories Forest Inventory layer (Department of Environment and Natural Resources, 2012) was used to determine the major forest type in 100-m buffers around each sampling station (upland, n = 273 and peatland, n = 131 for peatlands).

ARUs were deployed at each study site for three or four consecutive days. Two 3-minute recordings at dawn from two randomly selected days at each sampling station were interpreted by human observers to determine the number of individuals per species using the Bioacoustic Unit Acoustic Data Analysis Protocol (Lankau et al. 2015). To minimize variation in detectability among sampling stations, recordings were randomly assigned to four trained observers and only recordings where bird vocalizations were not obscured by wind or rain were used. A species was considered present if a male primary vocalization was heard at least once at one visit to a station. Multiple individuals of the same species were identified by differences in vocalization-related directionality, amplitude, and song type. All identifiable bird vocalizations were recorded, but only passerine, grouse, and woodpecker species that breed during the survey period, defend relatively small territories, and are not gregarious were included in the analysis (see Appendix 1 for species list). For each sampling station, maximum count of individuals per species over the two recordings was used for analyses as it was preferred over mean average abundance by Toms et al. (2006).

Statistical Analysis

Species Richness

Species richness was used to measure changes in number of species per sampling station as opposed to other diversity metrics such as Shannon and Simpson indices because results were similar (see Appendix 7). A generalized linear mixed model with Poisson distribution (GLMMs) using the R (R Core Team 2016) package "lme4" (Bates et al. 2015) was used to test for a burn severity × forest type interaction. Year and study site were combined ($n = 35$) and included as a random effect to account for non-independence of sampling units. Goodness of fit between an additive model with severity and forest type as fixed effects, and a model with a severity × forest type interaction as fixed effects were tested using likelihood ratio tests using "lmtest" (Zeileis and Hothorn 2002).

Community composition

Changes to community composition were tested using partial Canonical Correspondence Analysis (pCCA; R package "vegan", Oksanen et al. 2016). CCA determines the amount of variation in the species abundance data that is explained by environmental variables (Borcard et al. 1992). The pCCA distributes sampling stations in the most parsimonious multivariate space to visually depict shifts in community composition. A permutation test with 999 permutations was used to determine the significance of the variation explained by the severity × forest type interaction after controlling for nuisance conditional variables (year sampled and study site). To partition the amount of variation that was explained by severity alone, forest type alone, and their interaction, we built models with: 1) severity as the main effect and forest type as an additional conditional variable; and 2) forest type as the main effect with severity as an additional conditional variable (*as per* Borcard 1992). A test for homogeneity of multivariate dispersion, or the amount of variability of species composition among treatment types, was used to measure beta diversity (Anderson 2006) using the R package “vegan”. Although the effects of the nuisance variables could not be partitioned, dispersion provides information about species turnover that could otherwise not be calculated. Bray-Curtis dissimilarity was used for all community composition analyses because it is suitable for analyzing count data with a high number of zeros (Clarke 1993). Results from the pCCA were presented as an ordination with 67% confidence ellipses to show where the majority of the stations of each treatment type were located in two-dimensional space. For both community composition and functional diversity, species detected at fewer than 3 sampling stations were not included (after Kardynal 2015; Murray et al. 2017).

Functional Diversity

Two measures of functional diversity, functional richness and divergence, were quantified using Rao’s quadratic entropy (hereafter “Rao’s Q”; Clark et al. 2012) in the R package “FD” (Laliberté et al. 2014). We used life history traits that describe species’ foraging and migration strategies, as well as substrates used for foraging, breeding and nesting from the Avian Life History Information Database (http://www.on.ec.gc.ca/wildlife/wildspace/project.cfm; Table 1; Appendix 7). Some of these traits can be directly linked to ecosystem functioning, such as feeding behavior, as these describe how species contribute to insect control or seed dispersal and have been identified as functionally important by Azeria et al. (2011), Murray et al. (2017), and Newbold et al. (2012). All traits were categorical and transformed to continuous values by calculating the Gower distance (Schleuter et al. 2010). Differences among burn severities, forest types, and their interactions for functional diversity were determined by using a GLMM with a Gaussian distribution in the R package “nlme” (Pinheiro et al. 2016) and the same response variables and random effects as those specified for the species richness analysis.

Results

Forty-five species were included in the analyses. Of these, six were only present in burns (Black-backed Woodpecker, Mountain Bluebird, Savannah Sparrow, White-crowned Sparrow, Yellow-bellied Sapsucker, and Yellow Warbler; see Appendix 7 for scientific names) and three were only in controls (Boreal Chickadee, Northern Waterthrush, and Ovenbird). Seven species were found in low and moderate, but not high severity burns (Blue-headed Vireo, Common Yellowthroat, Ruby-crowned Kinglet, Ruffed Grouse, Savannah Sparrow, Yellow-bellied Flycatcher, Yellow Warbler). No species were found exclusively in high severity burns.

High severity burns had significantly lower species richness than controls ($\beta = -0.19$, SE $= 0.09$, $p = 0.025$; Appendix 1). Richness was also lower in uplands than peatlands ($\beta = -0.23$, SE $= 0.04$, $p < 0.001$; Appendix 1). There was no significant interaction effect of burn severity and forest type (df = 3, $\chi^2 = 4.47$, $p = 0.214$; Figure 3); both peatlands and uplands showed similar changes in species richness with increasing severity.

The fire severity × forest type interaction explained 5.4% of variation in community composition, while the conditional variables explained an additional 6.8% ($F = 5.80$, $P \leq 0.001$; Figure 4). Forest type, when the only constrained variable, explained 1.9% of variation ($F = 14.12$, $P \leq 0.001$) and explained more of the variation than burn severity (1.5% of variation, F =

4.86, $P \leq 0.001$). The pCCA ordination showed that species in upland and peatland stations became more similar with increasing burn severity. The multivariate dispersion and subsequent permutation tests showed no significant differences among treatment types ($F = 0.93$, $p = 0.472$).

There was no significant forest type or burn severity × forest type interaction effect (df = 3, $\chi^2 = 0.20$, $p = 0.978$). Uplands and peatlands had very similar predicted functional diversity in each burn severity category ($\beta = 0.01$, SE = 0.02, $p = 0.523$). Functional diversity decreased with increasing burn severity (Figure 5). Low severity ($\beta = -0.09$, SE = 0.02, $p < 0.001$), moderate severity ($\beta = -0.14$, SE = 0.02, $p < 0.001$), and high severity ($\beta = -0.17$, SE = 0.01, $p < 0.001$) all had lower functional diversity than controls (Appendix 2).

Discussion

We hypothesized that because species have adapted to frequent wildfire the songbird community would show high resistance regardless of burn severity, particularly in upland forest type. Overall, our effect sizes were small. However, the songbird community did change in higher severity burns, which comprised a substantial proportion (40%) of the burned area in our study area (Whitman et al. 2018). Burn severity did not have a stronger effect on songbird communities in peatlands compared to uplands, suggesting that both communities have similar resistance. Overall, we argue that the songbird community in our study area showed an intermediate level of resistance.

Other studies have investigated how wildfire affects songbird communities in southern boreal forests in Alberta, Saskatchewan, Quebec, and Minnesota (e.g. Hobson and Schieck 1999; Imbeau et al. 1999; Morissette 2002; Haney et al. 2008; Van Wilgenburg and Hobson 2008;

Azeria et al. 2011; Appendix 8). Burn severity has been found to be important to bird communities in other ecological regions (studies listed in Hutto and Patterson 2016), such as the western United States and Australia, and for woodpecker species specifically in the Canadian boreal forest (Koivula and Schmiegelow 2007). However, inferences are limited to local fire regimes and ecological region (Latif et al 2016). This is, to our knowledge, the first study in the northwestern boreal region and as a result may be particularly important given the relatively large area of the Taiga Plains ecozone in which the study took place (604,628 km^2; ESTR Secretariat 2013).

The inverse relationship between functional diversity and burn severity is consistent with studies that have found decreases in functional diversity in amphibian and plant communities with increasing disturbance (Ernst et al. 2006; Collins 2017). In our study, functional diversity decreased to a greater extent than species richness because species found in high severity burns were often closely related phylogenetically or shared similar life history traits. The five most common species in high severity burns (American robin, Chipping sparrow, Dark-eyed junco, Hermit thrush, and White-throated sparrow) belong to two families (Turdidae and Emberizidae), are short distance migrants, foraging omnivores (with the exception of Hermit thrush), and nest primarily on the ground (with the exception of American robin, which although nests primarily in trees, will nest on the ground or in snags; Vanderhoff et al. (2016); Appendix 7). These few generalist species dominated high severity burns regardless of forest type, possibly because of constraints on foraging behavior and nesting sites. These species are largely responsible for the species richness at the high severity burn stations and likely contribute substantially to the resistance observed in this bird community.

Some generalist species with declining population trends may benefit from increasing fire, such as White-throated sparrows and White-crowned sparrows that had their highest abundances in high severity burns (Appendix 9). However, increasing wildfire may have negative effects on other species that are undergoing long-term population declines. For example, the Common yellowthroat, a peatland-associated species that was not found in high severity burns, has seen population declines in the boreal taiga plains region of the western boreal (Blancher 2003). Swainson's thrush is one of the most abundant boreal birds, but is also declining in Canada and although common in our study area decreased with increasing burn severity. Seven species (7/42) consisting of resident, short-distance, and neotropical migrant species were found in low and moderate burn severity patches but not in high severity patches. These species likely prefer lower severity burns because they contain more complex vegetation structure than high severity, and because unburned mature forest and recent higher severity burns are often available for nesting and foraging in the vicinity (Stuart-Smith et al. 2002; Azeria et al. 2011).

Wildfire in the boreal forest is increasing in frequency, severity, and area due to climate change (Grissom et al. 2000; Kochtubajda et al. 2006; Balshi et al. 2009; Héon et al. 2014). Wildfire in peatlands in particular is expected to increase as previously wet organic layers dry out and become flammable with a warmer and drier climate (Turetsky et al. 2004, Flannigan et al. 2008) and increased fire size (Turetsky et al. 2004). The songbird community in peatlands may therefore be more susceptible to future climate change. In our study area, peatlands had higher species richness than uplands, burn with less intensity than uplands (Whitman et al. 2018), and therefore provide important habitat within burns. We did not find any differences between upland and peatland communities' responses to burn severity. However, of particular interest was the fact that upland and peatland bird communities became very similar in high severity burns, suggesting a specific group of species are best adapted to these conditions. Understanding changes to the songbird community in peatlands provides a more comprehensive understanding of how boreal songbird communities are affected by wildfire because previous studies focused on harvestable, upland forest types (Hobson and Schieck 1999; Schieck and Hobson 2000; Morissette et al. 2002; Schieck and Song 2006; Van Wilgenburg and Hobson 2008). We found that that unburned, low, and moderate burn severity patches supported higher species richness and functional diversity and provided important songbird forest types for species that are not found in high severity burns. Increasing burn severity will potentially result in smaller proportions of unburned, low, and moderate burn severity patches within the overall burned landscape.

Multiple metrics were used to quantify changes to the songbird community. Measuring changes in species richness and community composition are simple and feasible methods of detecting changes in communities and comparing results among studies even though breeding success cannot be inferred. As in other studies that found species composition to vary in different upland forest types (Morissette et al. 2002), we found differences in composition and species richness between upland and peatland forests. Azeria et al. (2011) used functional traits to detect species changes with increasing burn severity, similarly to how functional diversity and community composition detected changes in this study.

Including burn severity and habitat-specific data helps to better understand songbirds' responses to wildfire. For example, while both our study and Morissette et al. (2002) found

Dark-eyed junco and American robin in high abundance in burned forests, we found Dark-eyed junco abundance to be specifically highest in moderately burned areas, while American robin abundance was highest in high severity burns. Future studies could include both burn severity and time since fire, as Hutto and Patterson (2016) found the combination of fire variables influenced species' responses in Montana. Although the songbird community is currently somewhat resistant to wildfire in the northwestern Canadian boreal forest, incorporating projected changes to forests and wildfire due to climate change will be necessary to understand how resistance may change in the future.

Figures

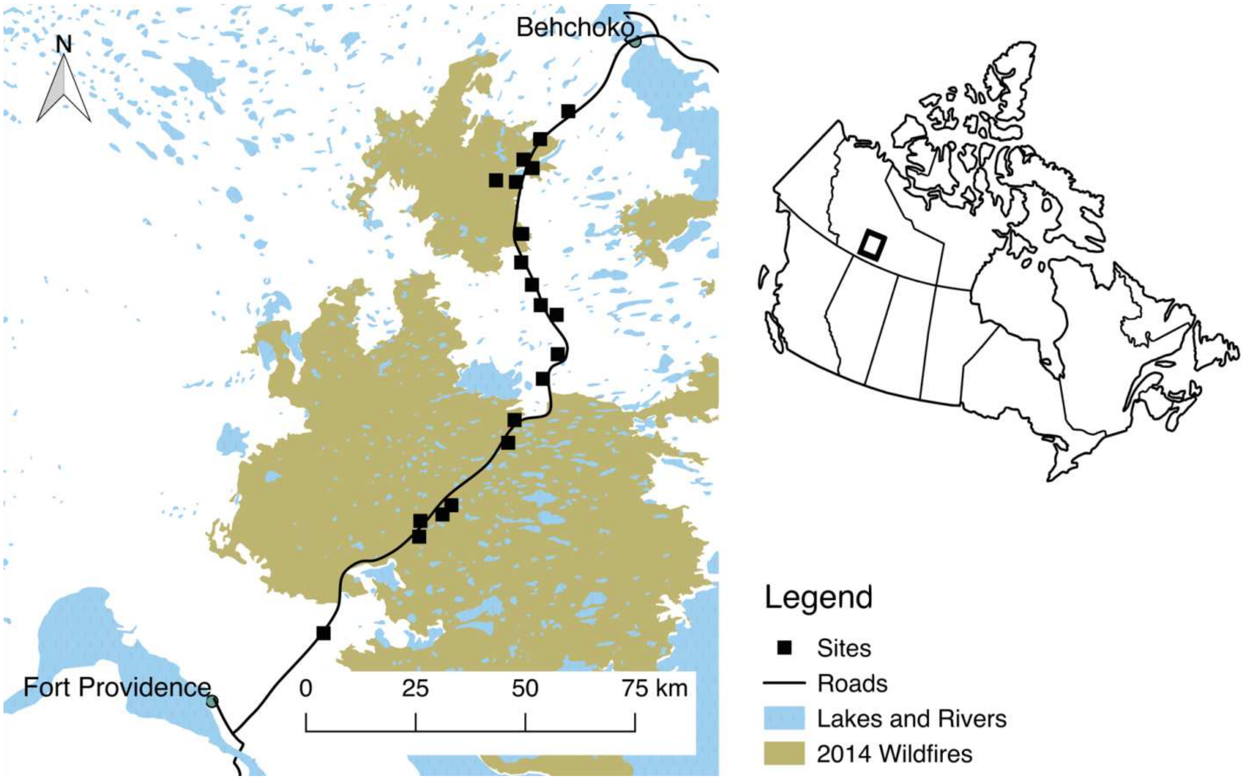

Figure 1. Location of the study sites (black squares) in the study area between Fort Providence and Behchokǫ̀, Northwest Territories.

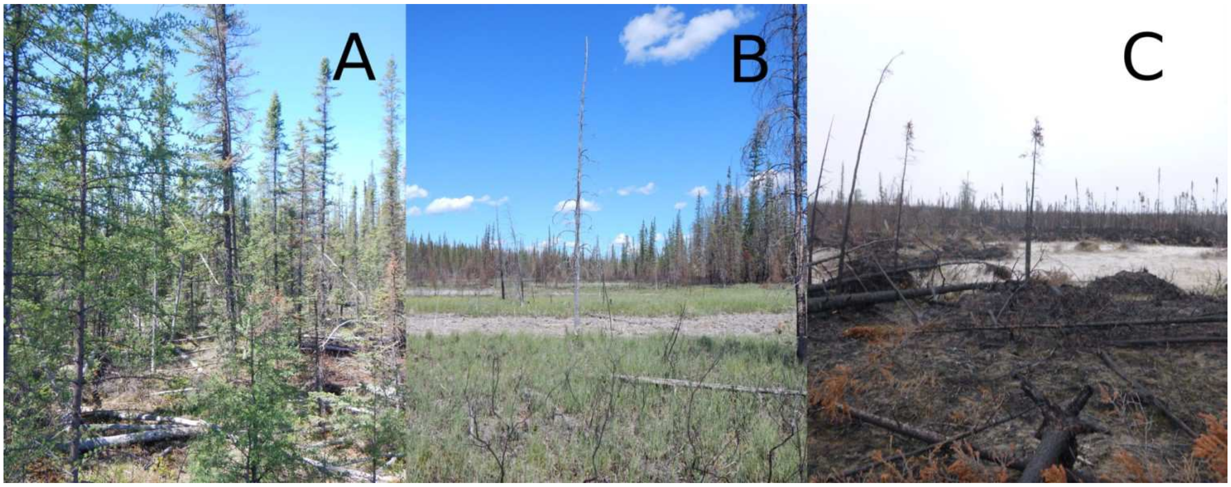

Figure 2. Examples of low (A), moderate (B) and high (C) burn severity in peatland and mineral wetlands one year post-fire in the Northwest Territories, Canada.

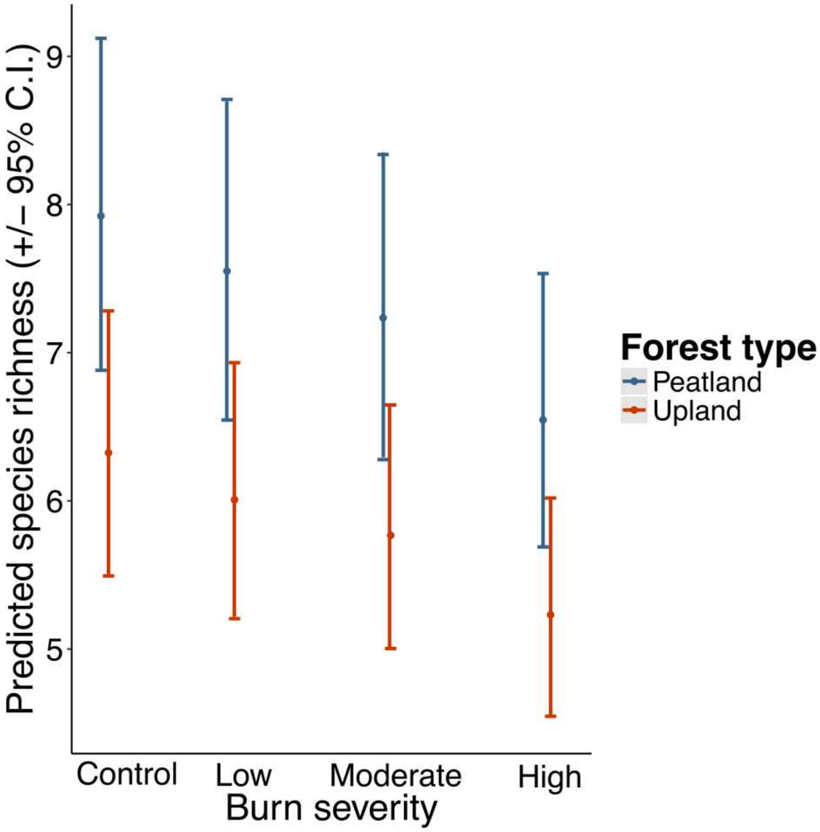

Figure 3. Predicted means for species richness (± 95 % confidence intervals) per forest type and burn severity adjusted for the random effect (site and year).

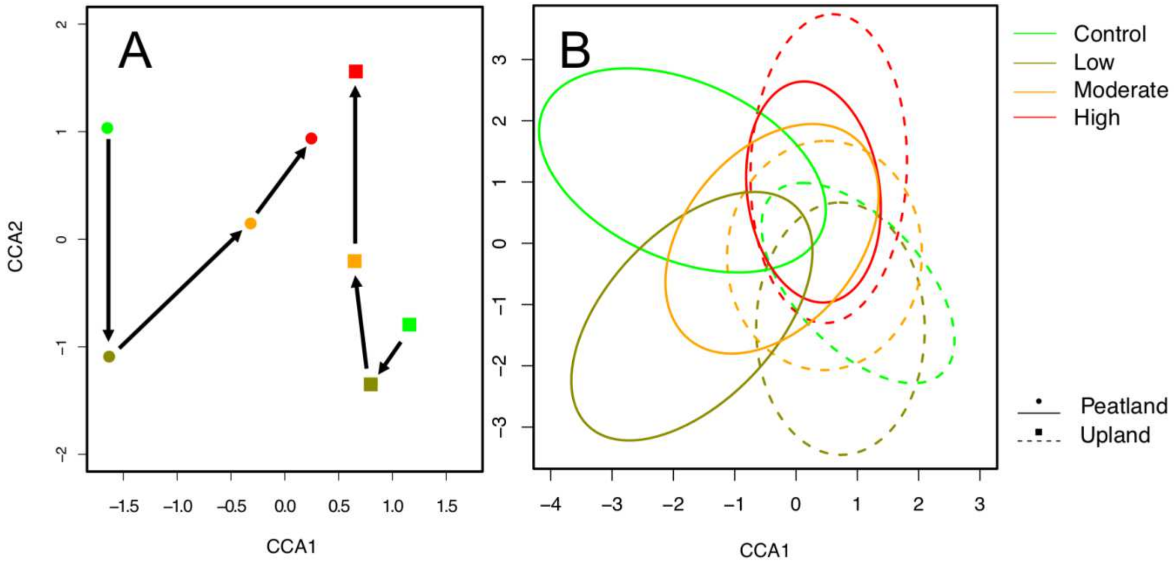

Figure 4. Partial canonical correspondence analysis ordination of bird communities in uplands and peatlands of increasing burn severity. Presented are A) centroids of each treatment type (burn severity and forest types) joined by arrows indicating the direction of increasing burn severity for uplands (squares) and peatlands (circles); B) 67% confidence ellipses around centroids (not shown) of each treatment type.

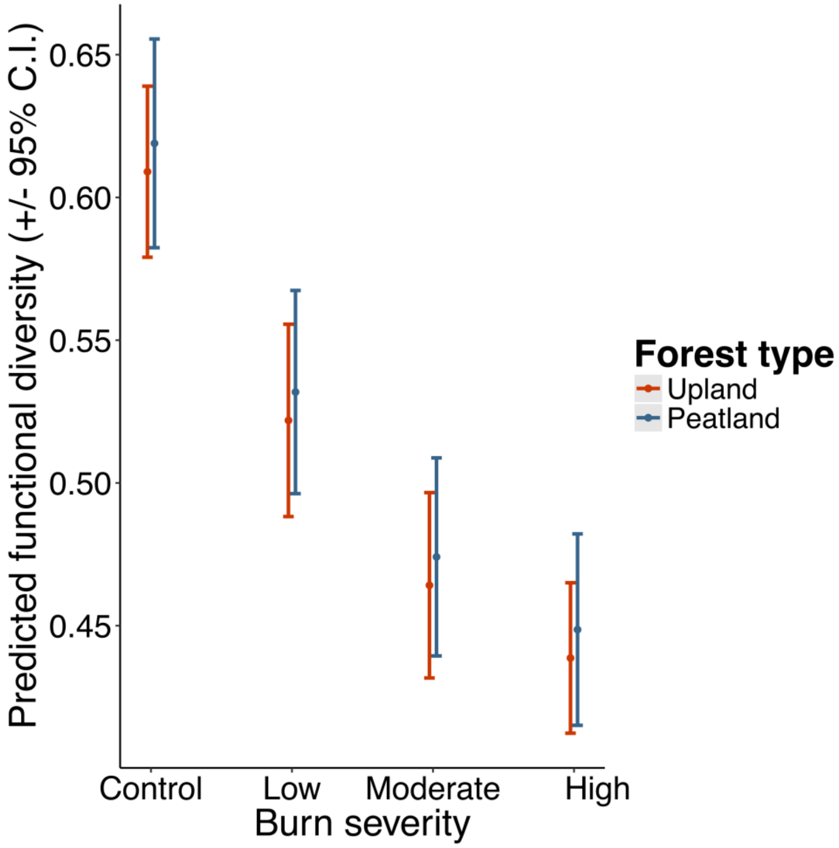

Figure 5. Predicted means of functional diversity (Q) among severity and forest type treatments adjusted for the random effect (site and year). Error bars are 95% confidence intervals.

Chapter 3 – High resilience of songbird communities to wildfire in the northern boreal forest

Abstract

The resilience of animal communities and ecosystems describes their ability and the amount of time required to return to a pre-disturbance state. Songbird communities in southern boreal regions have shown high resilience to wildfire, but these ecosystems experience more rapid forest regeneration and higher songbird diversity than northern boreal regions where their resilience remains largely unknown. We tested for resilience of songbird community to wildfire in the northern boreal forest of the Northwest Territories, Canada. Specifically, we estimated songbird abundance in stands 1, 2, 3-10, 11-30, 31-50, and > 50 years post-fire and tested for effects of time since fire and forest type (uplands vs. peatlands) on species richness, community composition, and functional diversity to infer the resilience of this community. Species richness was highest between 3 and 50 years post-fire with a non-significant peak between 11-30 years (8.3), and lowest one year post-fire (5.2). There was higher species richness in peatlands compared to uplands, but there was no significant time since fire × forest type interaction. Community composition did not change with time since fire, forest, or their interaction, and functional diversity only significantly decreased one year post-fire. Because of the lack of change in composition and brief decrease in functional diversity as a function of number of years post-disturbance and forest type, we concluded that songbird communities are highly resilient to fire in northwest boreal regions. A better understanding of the resilience of northern breeding

songbirds can be integrated into simulations to generate predictions about potential changes in abundance and distribution of songbirds in response to different climatic change scenarios.

Introduction

The resilience of animal populations, communities, and ecosystems describes their ability to return to the pre-disturbance state following disturbance (Holling 1973, Walker and Salt 2006). The resilience of songbird communities to natural disturbance has been inferred by testing for statistically significant changes with increasing time since disturbance (Schmiegelow et al. 1997; Fischer et al. 2007; Jacquet and Prodon 2009). There has long been a need to understand resilience of songbirds in the southern boreal forest to harvesting practices (Schmiegelow and Villard 2009) and many studies have addressed the concept of resilience by comparing recovery over time after harvesting and wildfire, as summarized by Schieck and Song (2006). For boreal regions that do not experience harvesting, understanding the level of resilience of songbird communities is necessary to provide ecological baselines to anticipate effects of climate change (Millar et al. 2007), such as increases in area burned by wildfire in the northern Canadian boreal forest (Kochtubajda et al. 2006).

Wildfire is the primary natural disturbance in the boreal forest of Canada (Tymstra et al. 2007). The large fires that start in the northern boreal forest are typically ignited by lightning and occur during periods of drought. Such fires are more typical in the western Canadian boreal region than in the east (Parisien et al. 2011). The boreal forest also becomes more prone to fire with increasing latitude as a result of longer daylight hours in summer and greater proportion of conifer trees (Miquelajauregui et al. 2016). The northwestern fire regime is characterized by large, intense, crown fires (de Groot et al 2013), which creates spatio-temporal variation in stand age and composition resulting in diverse habitats for wildlife (Rowe et al 1973, Weber and Stocks 1998). The spread and shape of fire is highly variable and influenced by many factors such as the presence of fire breaks (e.g. water bodies or lack of vegetation), variation in moisture content of vegetation and surface substrate, changes in weather (Rowe and Scotter 1973), vegetation type, and topography (Whitman et al. 2018).

According to the "diversity-stability" hypothesis, diversity is frequently correlated with stability of an ecosystem, which in dynamic ecosystems is determined by resilience and/or resistance (McCann 2000). Two drivers of diversity in boreal forests are forest succession and latitude. Higher species diversity in southern boreal regions compared to northern regions can be partially attributed to the wide range of habitats created by succession following disturbance (Schieck and Hobson 2000; Swanson et al. 2011). Following wildfire in southern boreal regions, multiple stages of succession create a variety of habitats that a large diversity of songbird species have adapted to (Tefler 1993, Schieck and Song 2006). In northern boreal regions, stand succession is simplified because of low tree diversity (Hogg and Wein 2005), where dominant tree and shrub species present before wildfire often regenerate post-fire without intermediate successional stages. In peatlands, most understory plants can regenerate from surviving underground roots and rhizomes even when surface vegetation is consumed (Johnstone and Kasischke 2005), while black spruce stands quickly regrow from aerial seedbanks that survive fire and dominate where the organic layer has burned (Price et al. 2013). In upland stands, trembling aspen (*Populus tremuloides*) can sprout from surviving suckers and quickly recolonize, while jack pine (*Pinus banksiana*) uses the same regeneration strategy as black spruce (Price et al. 2013).

In addition to simpler forest regeneration patterns in this region of the northern boreal forest, productivity (Gauthier et al. 2015), percent of deciduous trees, tree height, and canopy cover decrease with increasing latitude (Rowe and Scotter 1973). The northern boreal region experiences short and cool growing seasons resulting in slow regeneration rates compared to southern boreal region (Hogg and Wein 2005). Schieck and Song (2006) found that boreal songbird communities in Alberta, Canada take longer (15 years) to reach intermediate successional stages than in a more southern hemiboreal region in Minnesota, U.S.A (3 years; Schulte and Niemi 1998), possibly due to a latitudinal effect on regeneration rate. The combination of slow and simplified regeneration may lead to low species diversity and therefore low resilience in wildlife communities further north.

The boreal forest provides important breeding habitats for many migratory and resident landbird species; 186 species and between one and three billion individuals nest here each year (Blancher 2003). Bird communities in regions with frequent disturbances have been found to be less sensitive to disturbance than those in regions with less frequent disturbance (Latif et al. 2016; Drapeau et al. 2016). Species that use the boreal forest, including songbirds, are thought to be resilient to large-scale and frequent disturbances (hereafter "disturbance-resilience hypothesis"; Schmiegelow et al. 1997; Weber and Stocks 1998; Schmiegelow and Villard 2009; Drapeau et al. 2016). Songbird species that prefer recently burned stands include cavity and some ground nesters (Imbeau et al. 1999, Nappi and Drapeau 2011) as well as some generalist species. In the southwestern boreal forest in the Boreal Plains ecozone, species associated with shrubby habitats in early seral stages become prevalent 11-30 years post fire (review by Schieck and Song 2006). Species associated with mature stands occurred in small patches of residual trees in recent burns but were generally more common >50 years post-disturbance. Older burns (>75 years post-fire) were structurally more diverse than younger burns and supported the greatest species richness and abundance (Schieck and Song 2006). It could be expected that songbirds would show high resilience to fire in the northern boreal forest where large-scale disturbances are common.

In the northwest boreal region of Canada, peatlands make up almost half of the landbase and are typically defined as wetlands with a thick (> 40 cm) layer of organic matter (National Wetlands Working Group 1997). Peatlands experience reduced burn severity (Whitman et al. 2018) and frequency compared to uplands due to a higher water table (Kettridge 2015), wet surface substrate (Flannigan et al. 2008), greater groundwater connectivity, and distance from uplands (Hokanson 2015). Peatlands are often composed of a large fuel load consisting of a thick layer of organic matter, black spruce that retains dead branches, and volatile ericaceous shrubs that become highly flammable when dry, such as when experiencing drought (Rowe and Scotter 1973; Flannigan et al. 2008; Kasischke et al. 2008). Previous studies have focused on testing effects of time since fire on songbird communities in upland forests (Hobson and Schieck 1999, Van Wilgenburg and Hobson 2008, Morissette et al. 2002, and Schieck and Hobson 2000, and Schieck and Song 2006), but, to our knowledge, no studies have tested for effects of time since fire in peatlands. Because peatlands burn less than uplands, songbird communities in peatlands may be less resilient to wildfire than communities in upland habitats.

The fire return interval is between 50 – 75 years in the northwestern boreal region and frequent enough that forest stands often to not reach maturity (Bergeron et al. 2002). However, wildfire frequency and area burned are anticipated to increase with climate change (Grissom et al. 2000; Kochtubajda et al. 2006; Héon et al. 2014) and northern regions are expected to experience the greatest increases (Bonan et al. 1990). Peatlands are particularly vulnerable as changes in hydrology due to climatic variations that will ultimately increase rates of wildfire (Zoltai et al. 1998). Understanding the resilience of songbird communities to wildfire in both uplands and peatlands is necessary to inform conservation strategies (Thompson et al. 2009).

In this study, we quantified the resilience of songbirds to wildfire in uplands and peatlands in the northwestern Canadian boreal forest. We conducted avian point count surveys to quantify resilience by estimating the time required (1, 2, 3-10, 11-30, and 31-50 years) for species richness, community composition, and functional diversity to return to pre-fire conditions (> 50 years). Based on the diversity-stability hypothesis, we predicted resilience to be lower in northern boreal regions than in southern regions. Alternatively, based on the disturbance-frequency hypothesis, we predicted that peatlands will show lower resilience than uplands because of less frequent fire in that habitat.

Methods

Study Area

The study took place within a ~25,000 km^2 area between Fort Simpson, Fort Providence, and Behchokǫ̀ in the Northwest Territories, Canada (Figure 6). The study area was in the Taiga Plains High Boreal and Mid Boreal ecoregions, which are comprised of approximately 50% uplands, 40% peatlands, and 10% open water (Ecosystem Classification Group 2007). Uplands are dominated by jack pine while peatlands are primarily treed fens and bogs dominated by black spruce, as well as inorganic mineral ponds (Ecosystem Classification Group 2007). The region received between 288 – 387 mm of yearly precipitation and the average daily temperature was between –2.5 and –4.3°C between 1981 – 2010 (Government of Canada 2018). The average temperature has increased by 2°C between 1950 and 2007 in this area (ESTR Secretariat 2013). There are limited roads and industrial activity in the area and no commercial forestry. Most of the study area has experienced wildfire at least once in the past 50 years. Particularly large fires in the study area occurred in 1994, 1995, and 2014 (Fig. 6).

Sampling design and avian surveys

We conducted avian point counts at 777 sampling stations between June 1 and 30, 2015 and 2016. Time since fire was classified into 1 year (*n* = 291 sampling stations), 2 (*n* = 208), 3–10 (*n* = 70), 11–30 (*n* = 86), 31–50 years (*n* = 214), and >50 years since fire (hereafter “controls”; *n* = 127; see also Smith et al. 1993). The sampling design was comprised of near-road and off-road sampling locations. Off-road surveys were conducted on and around the Horn Plateau in 2016. These sampling stations were grouped into sites with four sampling stations spaced 600 m apart in a 2 × 2 grid with the fifth station located at the centroid. Sites were systematically spaced 20 km apart. This sampling design resulted in the following sample size: 1 year (*n* = 4), 11–30 (*n* = 86), 31–50 years (n = 50), and controls (n = 56; total of 196 sampling stations). The roadside surveys, which were used in chapter 2, consisted of sites of either 16 stations (4 × 4 grid and sampling stations spaced 500 m apart; 2016) or 25 stations (5 × 5 grid and sampling stations spaced 500 m apart; 2015) using a stratified random sampling design (1 year [*n* = 287], 2 years [*n* = 208], 3–10 years [*n* = 70], 11–30 years [*n* = 0], 31–50 years [*n* = 164], and controls [*n* = 71]; Appendix 6). Some sampling stations were sampled as both year one and year two over the two years of sampling.

At each sampling station, two 3-minute point counts (n = 1,554) were conducted using recordings made by automated recording units (Wildlife Acoustic SM3 model in 2015 and SM4 model in 2016). Point counts were conducted at dawn on randomly selected dates from within 4 days of each other (roadside surveys) and from within the sampling period (off-road surveys). Bird species and abundances were manually interpreted using the Bioacoustic Unit Acoustic Data Analysis Protocol (Lankau et al. 2015). To minimize variation in detectability among sampling stations, recordings were randomly assigned to six trained observers and only recordings where bird vocalizations were not obscured by wind or rain were interpreted. A species was considered present if a male primary vocalization was heard at least once at a station. Multiple individuals of the same species were identified by differences in vocalization-related directionality, amplitude, song-type and/or quality. All identifiable bird vocalizations were recorded, but only non-gregarious passerines, grouse, and woodpeckers breeding during the survey period and defending relatively small territories were included in the analysis (see Appendix 7 for species list). For each sampling station, maximum count of individuals per species over the two recordings was used for analyses following recommendations from Toms et al. (2006).

Forest type and fire data

Remote sensing information of area burned in the study area from 1966 to 2016 was extracted from the Forest Management – Fire History GIS layer (Government of the Northwest Territories Center for Geomatics 2017). Information on fires before 1966 was not available. Time since fire was categorized into age classes similar to previous studies (Hobson and Schieck 1999; Schieck and Hobson 2000; Schieck and Song 2006; Haney et al. 2008). The Northwest

Territories Forest Inventory layer (Department of Environment and Natural Resources, 2012) and Edehzhie Vegetation Inventory (Environment and Climate Change Canada 2017) were used to determine the forest type (uplands or peatlands) for each sampling station. Information on dominant post-fire year category and forest type was summarized for a 100-m buffer around each sampling station to represent the effective detection radius of most boreal songbirds (e.g. Sólymos et al. 2013).

Statistical Analysis

Species Richness

Number of species per sampling station, i.e. species richness, was used to measure species diversity because results were similar to those from Shannon and Simpson indices and richness is a simpler metric. We created generalized linear mixed models using R (R Core Team 2016) packages “lme4” (Bates et al. 2015) to test for an effect of time since fire × forest type interaction. Year sampled ($n = 2$) and study site ($n = 69$) were included as random effects to account for the non-independence of sampling units.

Goodness of fit between an additive model with severity and forest type as fixed effects, and a model with a severity × forest type interaction as fixed effects were tested using likelihood ratio tests using “lmtest” (Zeileis and Hothorn 2002).

Community composition

We tested for changes in community composition using partial Canonical Correspondence Analysis (pCCA; R package “vegan”; Oksanen et al. 2016). CCA determines the amount of variation in species abundance that is explained by environmental variables (Borcard et al. 1992). The pCCA distributes sampling stations in the most parsimonious multivariate space to visually depict shifts in species composition. A permutation test with 999 permutations was also conducted using the pCCA results to determine the amount of variation explained by time since fire and forest type after controlling for nuisance variables (year sampled and study site). To partition the amount of variation that was explained by time since fire alone, forest type alone, and their interaction, models with time since fire as the main effect and forest type as an additional conditional variable, and a model with forest type as the main effect with time since fire as an additional conditional variable were created (*as per* Borcard 1992). The Bray-Curtis dissimilarity statistic was used for the pCCA analysis because it is considered the most suitable for analyzing count data with a high number of zeros (Clarke 1993). Results from the pCCA were presented as an ordination with 67% confidence ellipses to show where the majority of the stations of each treatment type were located in two-dimensional ordination space.

Functional Diversity

Functional diversity measures the redundancy of traits in a community and has been proposed to be a better indicator of ecosystem functioning than other metrics like species richness or abundance (Woodward and Diament 1991). Functional richness and divergence are two measures of functional diversity that were quantified based on the abundance of species' traits and using Rao's quadratic entropy (hereafter "Rao's Q"; Clark et al. 2012) from the R package "FD" (Laliberté et al. 2014). We used life history traits that describe species' feeding behaviors, reproduction and nesting locations, and migration behaviors (Table 1). These traits describe some ecosystem functions such as insect control and seed dispersal or are considered ecologically important as key avian attributes (Azeria et al. 2011; Murray et al. 2017; Newbold and Butchart 2012). These categorical traits were transformed into a continuous distance matrix using the Gower distance for analysis (Schleuter et al. 2010). We tested for effects of time since fire and forest types on functional diversity (Rao's Q) using a GLMM from the R package "nlme" (Pinheiro et al. 2016) and the same fixed and random effects as the species richness analysis. A *post-hoc* pairwise test with a Bonferroni correction using the R package "lsmeans" (Lenth 2016) was used to identify significant pairwise interactions. Species detected at fewer than 3 sampling stations were not included in all analyses (*as per* Kardynal 2015; Murray et al. 2017).

Results

Fifty species were included in the analyses (Appendix 7). The age classes between 3 – 50 years had significantly higher species richness than controls (between 11% and 35% higher; Appendix 4), with the highest mean value reported for 11 – 30 years period (Figure 7). There was no difference between controls and 2 years post-fire, but 1 year post-fire was significantly lower. Peatlands had higher mean species richness than uplands (peatland = 7.3, upland = 6.2; $\beta = 0.17$, SE = 0.03, $p = <0.001$; Figure 7), but there was no significant time since fire × forest type interaction (df = 5, $\chi^2 = 7.66$, $p = 0.176$).

The time since fire × forest type interaction explained a small amount of variation (2%, pCCA, F = 2.62, $p < 0.001$) in species composition, while study site explained considerably more variation (24%). Although statistically significant, the CCA showed no distinct shift in species composition with increasing number of years post-fire (0.69%, F = 1.91, $p < 0.001$; Figure 8) as indicated by the overlap in 67% confidence ellipses around the centroids of each treatment type and low amount of variance explained. There was also a statistically significant difference in species composition between birds breeding in uplands versus peatlands, but the amount of variation explained was low (0.72%, F = 10.03, p <0.001). Overall, there was little change in the community due to either time since fire or forest type.

There was no significant change in functional diversity between forest types. Functional diversity was significantly lower one year post-fire than in controls (Appendix 5). There were no other age classes that were significantly different from the controls, although there was a slight, insignificant increase in functional diversity in the 11–30 years age class. The time since fire × forest type interaction was significant (df = 4, χ^2= 15.60, p = 0.004). However, the pairwise comparison found that the only difference between the response to time since fire in uplands and peatlands was that functional diversity was significantly lower in year one compared to the 11 – 30 year age class in peatlands. There was no difference in uplands (Figure 9).

Discussion

This study tested the resilience of songbird communities to wildfire in uplands and peatlands of the northwestern boreal forest, a region with relatively little anthropogenic disturbance. This analysis was based on the assumption that wildfire, the major natural disturbance that shapes the boreal landscape (Weber and Flannigan 1997), would have important effects on songbird communities immediately post-fire and the time required for communities to return pre-fire conditions could be quantified. We did not detect a significant biological change in community composition, functional diversity only decreased significantly in the first year post-fire, and species richness peaked early in regenerating stands (11–30 years), suggesting high resilience to wildfire. Similarly, Imbeau et al. (1999) found no change in species richness with succession in black spruce stands in boreal forest in Quebec. Our results were consistent with the disturbance-resilience hypothesis, where high resilience of the songbird community may be explained by the historical prevalence of wildfire on the landscape and subsequent adaptation by species found there. The diversity-stability hypothesis was not a good explanation of resilience. Unlike southwestern boreal forests where bird communities are diverse and change throughout succession (Schieck and Hobson 2000), species diversity in this study was low (49 species, 6.95 ± 0.16 species per sampling station) and did not shift dramatically.

The prevalence of generalist species may help explain the lack of change in species richness, community composition, and functional diversity with increasing time since fire. Nearly half (46%, 23 species) of the species included in analyses are considered to be among the 25 most abundant species in the Canadian boreal forest (Blancher 2003). These common boreal species use a wide variety of forest types and at varying stages of regeneration; no species in our analyses was limited to just one time since fire class. Haney et al. (2008) found species richness and diversity to be highest between 19–30 years. Our findings are similar, with highest species richness and functional diversity in the 11–30 years-since-fire class (35% higher than controls). The community composition ordination showed that the 11–30 years-since-fire class was between the younger and older forest age classes, indicating that this age class is used by both early and late-successional species and/or generalists. A meta-analysis on the effects of forestry on birds at different latitudinal gradients found that changes in species richness and composition in response to logging were greater in tropical than in temperate forests (LaManna and Martin 2017). The authors hypothesized that these results could be explained by large-scale natural disturbance being more common in temperate regions, which in turn, would result in a larger proportion of habitat generalist species using both undisturbed and disturbed forests. Our results support this hypothesis for natural disturbances as well.

Species diversity may be relatively low because plant species and vegetation structure may not change enough to provide sufficiently different habitats for new species. This lack of change in structure is likely due to many factors driven by increasing latitude and relatively poor productivity, such as the lack of successional changes in stand structure, low tree height, and low tree diversity. The lack of change in functional diversity reported in our study further suggests that the habitat used by songbirds did not functionally change. We did not find resilience in this study to be lower than more southern studies, and therefore did not find support for the prediction that resilience would decrease with increasing latitude. In Alberta and Saskatchewan boreal studies summarized by Schieck and Song (2006), community changes were due to the addition of shrubby species occurred within 10 years post-fire and species that use old forests becoming abundant between 31 – 75 years post-fire. Instead of longer times to reach these stages as hypothesized, our study showed that these distinct shifts did not occur.

Salvage logging in southern boreal may increase the change in community composition after wildfire in southern forests. Schieck and Song (2006) found that communities in recent burns with and without salvage logging were different and did not converge until thirty years after fire, when dead standing trees had mostly fallen. For example, cavity nesters and species that eat beetles were abundant immediately post-fire and while were present for up to 30 years post-fire where snags were left intact, declined in stands where salvage logging occurred. While there were small amounts of incidental salvage logging in our study area, there were no large-scale commercial operations. Presence of snags in our study area likely further contributed to the lack of change in community composition.

Forest type had a greater effect on species richness and community composition than time since fire. Peatlands had the highest species richness but there was no significant time since fire × forest type interaction. Similarly, Kirk et al. (2011) found that in southwestern boreal regions, the gradient from dry to wet forests was the strongest driver of species assemblages. This result is particularly important given that peatlands are expected to be disproportionately affected by wildfire in the future; climate change models predict a warmer climate and more frequent drought (Price et al. 2013) that may lead to more drying out of peatlands and subsequently more fires.

The limited change in community composition contrasts with other studies from more southern regions (e.g. Haney et al. 2008; Lowe et al. 2012). In these studies, shifts in community composition may have been due in part to higher abundances of woodpeckers in younger forest age classes after wildfire (summarized by Nappi et al. 2004) and mature forest specialists that were only found in old forests (e.g. Lowe et al. 2012). Only four woodpecker species were detected in our study, likely because surveys took place after the primary woodpecker breeding season. Lack of woodpeckers in the younger age classes may have contributed to the lack of change in community composition and lower species richness in younger age classes; our results may have differed if additional surveys for woodpeckers had been conducted in May to determine different patterns in community composition might emerge.

The temporal extent of the time since fire data were only available for the past 50 years. Forest stands in the region do not reach an old seral stage until between 101 – 131 years where tree growth has slowed (The Forestry Corp. 2010). However, fires typically re-occur before stands reach an old seral stage (Johnson et al. 2001), so our sampling design likely captured representative forest age classes. Study site, as a random effect, explained more variation than time since fire or forest type. Ideally sampling in different burn age classes would have been stratified over the entire study area to ensure that there was limited geographical correlation and to reduce the amount of variation explained by site, but the sampling design was implemented prior to developing this study.

Differences between our results and those from more southern studies highlight the regional differences in the responses of songbirds to natural disturbances. To our knowledge, this is the most northerly study of fire impacts of songbird communities conducted in the western boreal forest. This region has the highest frequency, intensity, and size of wildfires and seems to be an area particularly susceptible to climate change (Boulanger et al. 2014). Of particular concern are predicted shorter fire-return intervals, which have been found to prevent regeneration of black spruce (Brown and Johnstone 2012). A larger proportion of more recent burns may have negative effects on songbird communities by temporarily reducing species richness and functional diversity. This study also highlights the necessity to consider variation in forest type and fire regime when investigating the effects of wildfire on songbirds in boreal forest ecosystems. In this study we differentiated uplands from peatlands, which is important because peatlands had higher species richness, have not been surveyed in similar previous studies, and are expected to persist on the landscape longer than uplands with climate change (Stralberg et al. 2018). Data from this study should be combined with predictions from fire simulation tools and climate change models as in Stralberg et al. (2018), where prediction from species distribution models based on different climate scenarios could help land managers to better understand potential effects of climate change on songbird breeding in northern boreal regions.

Tables

Table 1. Life history traits used in the functional diversity analysis and the number of species in each category (in parentheses). Traits are from the Avian Life History Information Database (http://www.on.ec.gc.ca/wildlife/wildspace/project.cfm).

Migration	**Feeding Class**	**Breeding substrate**	**Foraging**	**Nesting substrate**	**Nesting Habitat**
Short distance migrant (22)	Insectivore (28)	Ground (23)	Forager (20)	Ground (20)	Coniferous woodlands (10)
Neotropical migrant (21)	Omnivore (22)	Lower canopy / shrub (10)	Gleaner (20)	Coniferous tree (11)	Bogs (7)
Resident (6)		Upper canopy (7)	Sallier (5)	Deciduous tree	Mixed woodlands (7)
Nomadic (1)		Air (6)	Excavator (2)	Shrub (5)	Open woodlands (5)
		Bark (3)	Scaler (1)	Snag (5)	Deciduous woodlands (4)
		Freshwater (1)	Scavenger (1)	Grass (2)	Early successional (3)
			Other (1)	Other (2)	Other (14)

Figures

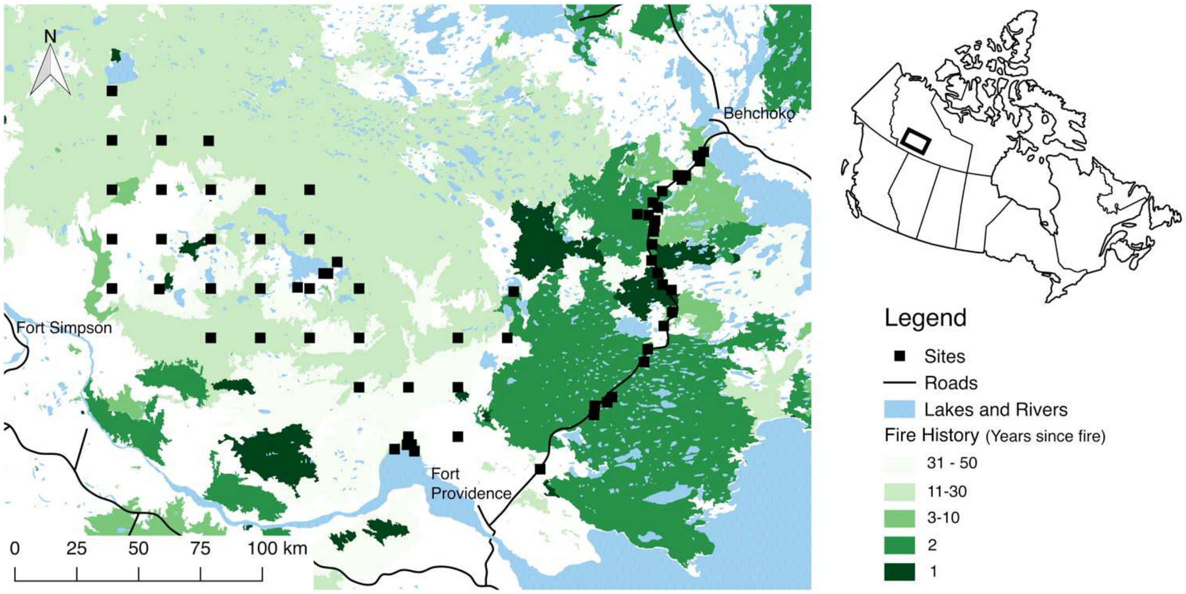

Figure 6. Map of the study area, fire history, and location of the 69 study sites (roadside and off-road sampling design) in the Northwest Territories, Canada.

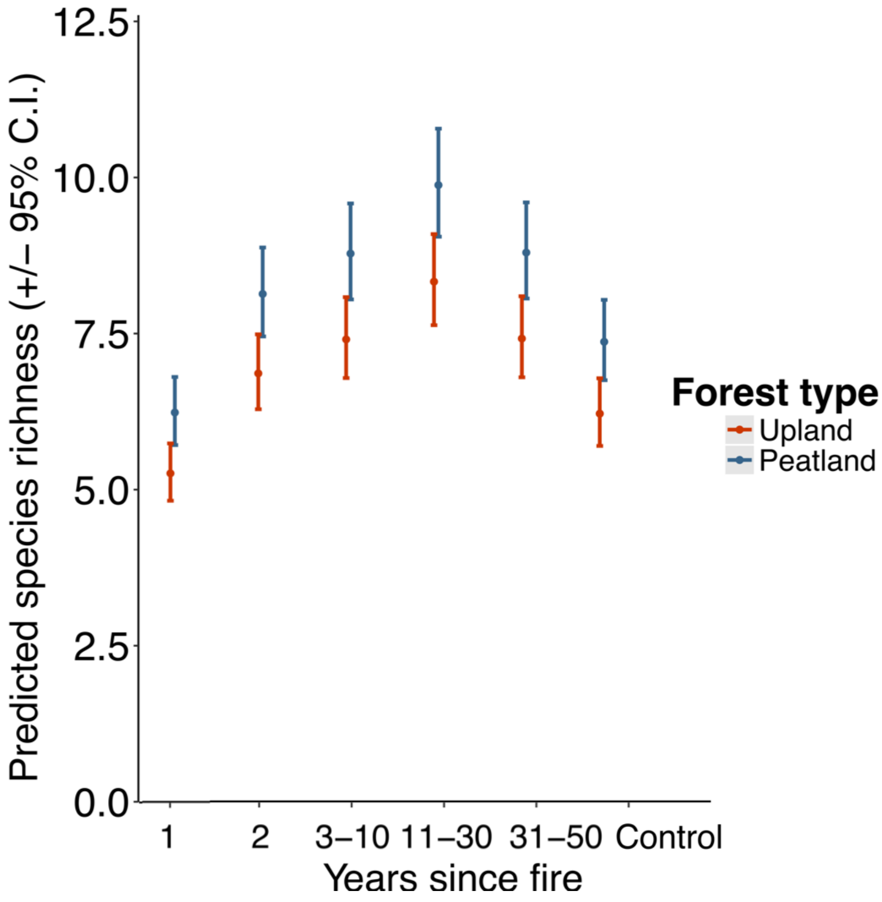

Figure 7. Mean species richness for uplands and peatlands with increasing number of years post-fire.

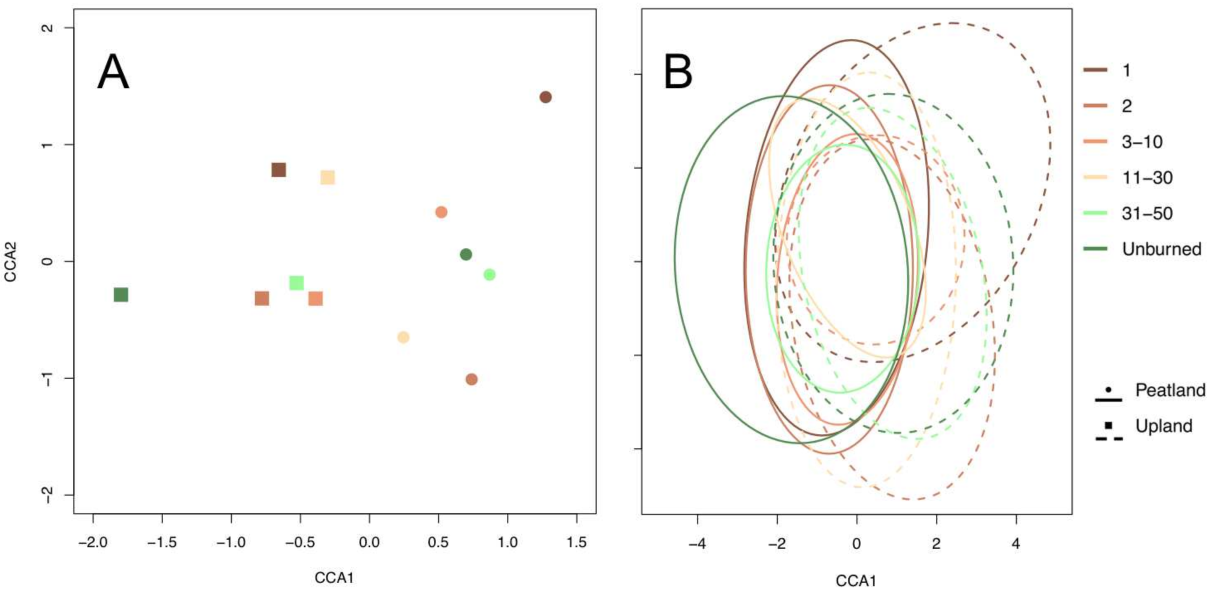

Figure 8. Partial canonical correspondence analysis ordination of bird communities in uplands and peatlands with increasing time since fire. Presented are A) centroids of each treatment type; B) 67% confidence ellipses of stations within each treatment type.

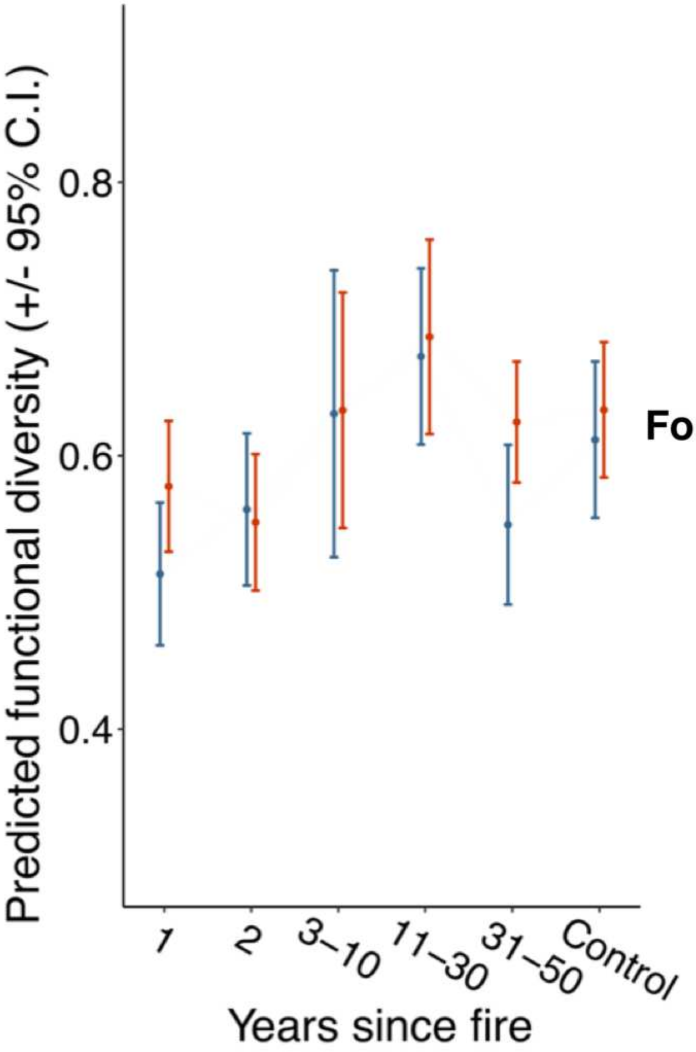

Figure 9. Functional diversity response to years since fire and forest type.

Chapter 4: General Conclusion

The heterogeneity created by wildfire is prevalent on the northwestern boreal landscape. It is therefore important to understand its effects on songbirds to gain understanding of its potential impacts to northern breeding grounds, particularly for species that have been found to be declining. The effects of wildfire were measured using burn severity and time since fire. The diversity of bird species in northern forests is relatively low; species richness at each sampling station in the study area was 6.9 ± 0.16, which was more than in black spruce dominated forests in eastern Quebec (3.4 – 5 per point count station; Imbeau et al. 1999) but less than richness in the mixedwood forests of the southwestern boreal forest (16 – 18; Macdonald 2006). Species' responses to burn severity (Appendix 9) and time since fire (Appendix 10) varied. Declines of certain common species in response to fire, such as Swainson's thrush's negative response to increasing burn severity, suggests fire does influence birds in northern regions although community shifts are not particularly dramatic.

Results from this study demonstrate the importance of using multiple metrics to understand how communities are affected by disturbance. For example, species richness is a simple metric to evaluate differences between treatment types, but alone it failed to detect changes due to burn severity that were found with community composition and functional diversity. Using functional diversity and guilds as in Imbeau et al. (1999); Morissette et al. (2002); and Azeria et al. (2011) (Appendix 7) is a useful way to compare results among studies that have different species assemblages while still describing the types of species found. Although species assemblages differed somewhat among these study areas, results were similar for guilds: ground and shrub nesters and insectivores were most common post-fire and/or in high severity burns, which were all common guilds in this study area (Table 1) and dominant post-fire. The community composition analysis in chapter 2 identified an important convergence of forest types with increasing burn severity that the other metrics were unable to detect. Community composition has also been used in similar studies (Hobson and Schieck 1999; Van Wilgenburg and Hobson 2008; Morissette et al. 2002, Hannon and Drapeau 2005) and makes it possible to compare compositional changes among studies in regions with different species. By using all of these metrics, it is possible to compare results from this study with at least certain analyses in most other boreal studies.

There are no studies to my knowledge where the songbird communities did not demonstrate at least some resistance or resilience to wildfire. However, drastic changes to the landscape with climate change may result in conditions where communities fundamentally and permanently shift, and a definitive threshold of resistance and resilience will be definable. It would be informative to test for resistance or resilience in areas where the fire regime has been fundamentally altered by human intervention and compare that to the northern boreal, where the fire regime is relatively natural.

Limitations

This study was designed to survey songbirds during their spring breeding season when most species vocalize as a way to defend territories and attract mates. However, resident species and woodpeckers that breed earlier in the year were likely not adequately surveyed. Woodpecker species were detected in the study area but at much lower rates than would be expected in recent burns, likely because sampling took place after their peak breeding season. Additionally, irruptive species such as red crossbills (*Loxia curvirostra*) have patchy abundances and were omitted because they are not adequately sampled using point count surveys (Imbeau et al. 1999). However, there is the potential to conduct more thorough bird surveys using the audio recordings collected. Each sampling station only had two three-minute recordings interpreted from an available 330 minutes of daily audio recordings for three to four consecutive days. Automated species recognizers could be used to identify species such as woodpeckers on the full set of audio recordings with technology that currently exists, increasing the likelihood of detecting individuals. Manual interpretation of audio recordings is currently the only feasible method for full community identification, but in the future automated recognizers will be capable of detecting all species on large volumes of audio recordings efficiently (Shonfield and Bayne 2017). Additionally, because species richness increases with sampling effort (Bayne et al. 2017) and only two 3-minute point counts were conducted at each sampling station, actual species richness was likely underestimated. However, two point counts at each sampling station, as in Imbeau et al. (1999); Morissette et al. (2002), were the maximum that could be completed due to time constraints in similar studies. Another limitation of the recording schedule was that all stations in each study sites were surveyed on the same days, and therefore the large effect of site in the analyses is likely due to both spatial and temporal autocorrelation.

The detection radius of surveys at each sampling station may have been influenced by differences in vegetation structure due to burn severity, time since fire, and forest type. For example, it is possible that bird vocalizations were heard over a larger distance in recent, high severity burns with little vegetation compared to unburned forests with thick vegetation. Although this was not corrected for, it is likely that any subsequent bias in the data made conclusions more conservative, as more species would have been detected in areas with higher severity or in more recent burns.

Implications

Understanding the relationship between birds and wildfire across a variety of regions will aid habitat conservation planning in the form of fire management (Latif et al. 2016). Fire management that supports biodiversity, such as the framework in Kelly et al. (2014), requires an understanding of species responses to current fire regimes. In this study, I quantified the effects of fire on the songbird community in a relatively unaltered fire regime in the northern boreal. Conversely, throughout the more populated and intensively managed southern boreal forest, fire suppression and active management has changed the structure of forests and habitat available for birds. Whitaker et al. (2008) suggested that there is a threshold at which bird assemblages will be unable to be resistant to disturbance. This threshold would likely be indicated by a dramatic decrease in species richness and / or a complete turnover of species with disturbance. Ideally, this threshold would be quantifiable, but there are, to my knowledge, no such thresholds described in the literature. It is possible that in regions with frequent disturbance where communities have adapted to frequent change, thresholds may have not been crossed under present conditions. My results suggest that the threshold in the northwestern boreal forest has not been reached under present conditions, even in areas that had burned to a high severity. Additionally, understanding which traits respond negatively to disturbance may also inform about species that share those traits but were not found in high enough abundance to statistically model effectively (Mason et al 2013).

Climate and wildfire models predict that increasing temperature, changes in precipitation and subsequent increases in wildfire will cause shifts in tree species or prevent forest regeneration after disturbance altogether in the next 100 years over much of the southwestern boreal forest (Stralberg et al. 2018). The northern boreal forest will also experience drastic changes, with the annual mean minimum temperature expected to increase up to 8° C in winter (Price et al. 2013). Northern regions with little human presence may experience more wildfire than in the south where fire suppression and conversion of forests to agriculture, logging, and industrial development may slow the spread and scale of fires. Climate change in southern boreal may cause large-scale transitions from deciduous and mixed-wood forests to grasslands and from coniferous-dominated forests to deciduous-dominated forests over much of the region, as well changes to peatlands (Schneider 2013, Stralberg et al. 2018). Northern boreal forests may not experience the extent of conversion of forests to grasslands due to increasing temperatures. However, complete loss of forests due to rapid repeat burns have been documented in the northwestern boreal forest. Fires that reoccur in an area in a short timeframe may destroy the available seed bank and mature trees with seeds, preventing regeneration of trees (Brown and Johnstone 2012).

This study shows that the songbird community in the northwestern boreal forest, although not very diverse, was able to withstand substantial changes to forest structure caused by fire. Like Imbeau et al. (1999), I found that songbird species richness did not change substantially as forests recovered, and this is likely representative of forests with simple forest structure and regeneration. However, the forest conditions in this study may not be applicable in the future as forests shift in their fundamental community composition or fail to regenerate altogether after disturbance. Additionally, the effects of high intensity fires will likely be more widespread than currently, increasing the amount of area burned to a high severity on the landscape.

Data from this thesis will also help Environment and Climate Change Canada's (ECCC) in their mandate to 'conserve and protect migratory birds and their habitat from major threats' (ECCC 2018) by providing information about species distributions, habitat associations, and how they are affected by wildfire. Data that was collected for Chapter 3 in the western portion of the study area is also being used as baseline data for a proposed National Wildlife Area (Edéhzhíe). A next step in this research will be to incorporate climate and wildfire models with information from this study to predict how northern boreal bird communities may respond to future habitat and fire regime changes. Additionally, different types of peatlands will likely be affected by wildfire based on hydrology. For example, water table fluctuations during drought tend to be greater in bogs than fens (Zoltai et al. 1998), making bogs more susceptible to wildfire during drought. Future research could differentiate among peatland types to better understand potential changes to the songbird community in response to wildfire.

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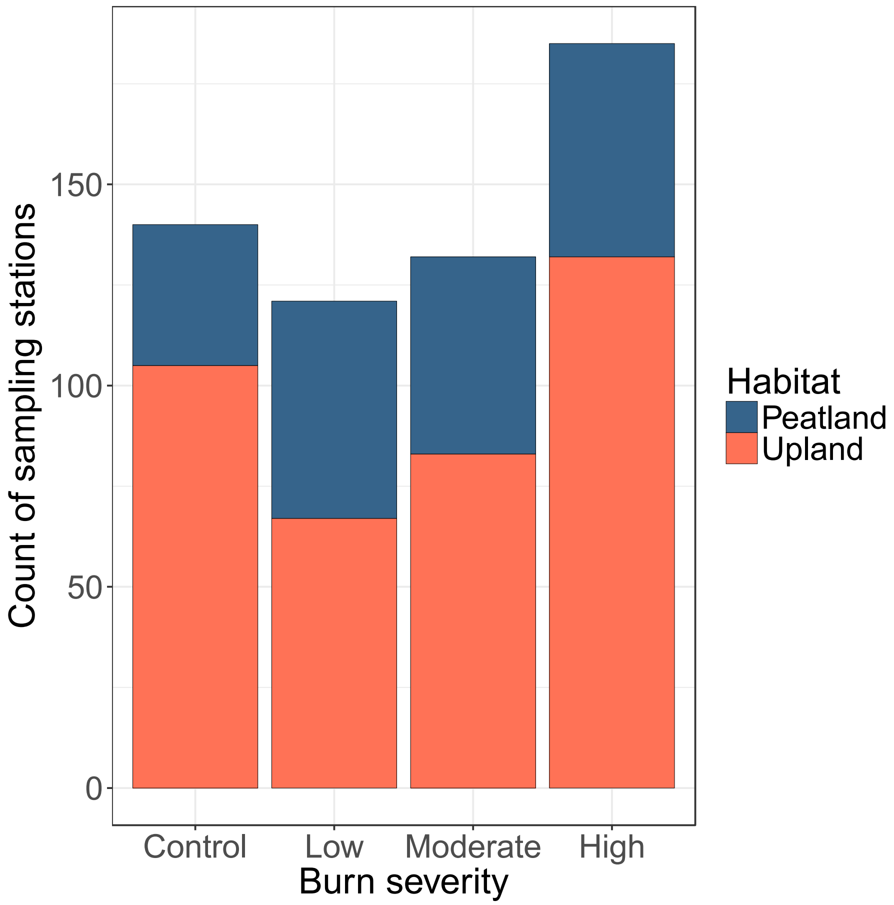
Appendices

Appendix 1. Generalized linear mixed model results testing for effect of burn severity and forest type on species richness with unstandardized beta coefficients (β), standard error (SE), and p values (*p*). The reference state in the model was peatland control.

Fixed Effect	**β**	**SE**	***p***
Intercept	2.06	0.07	<0.001
Upland	-0.23	0.04	<0.001
Low severity	-0.04	0.09	0.632
Moderate severity	-0.08	0.09	0.111
High severity	-0.19	0.09	0.025

Appendix 2. Generalized linear mixed model results testing for effect of burn severity and forest type on functional diversity with unstandardized beta coefficients (β), standard error (SE), and p values (*p*). The reference state for this model was upland control.

Fixed Effect	**β**	**S.E.**	***p***
Intercept	0.60	0.02	<0.001
Peatland	0.01	0.02	0.523
Low severity	-0.09	0.02	0.001
Moderate severity	-0.14	0.02	<0.001
High severity	-0.17	0.01	<0.001



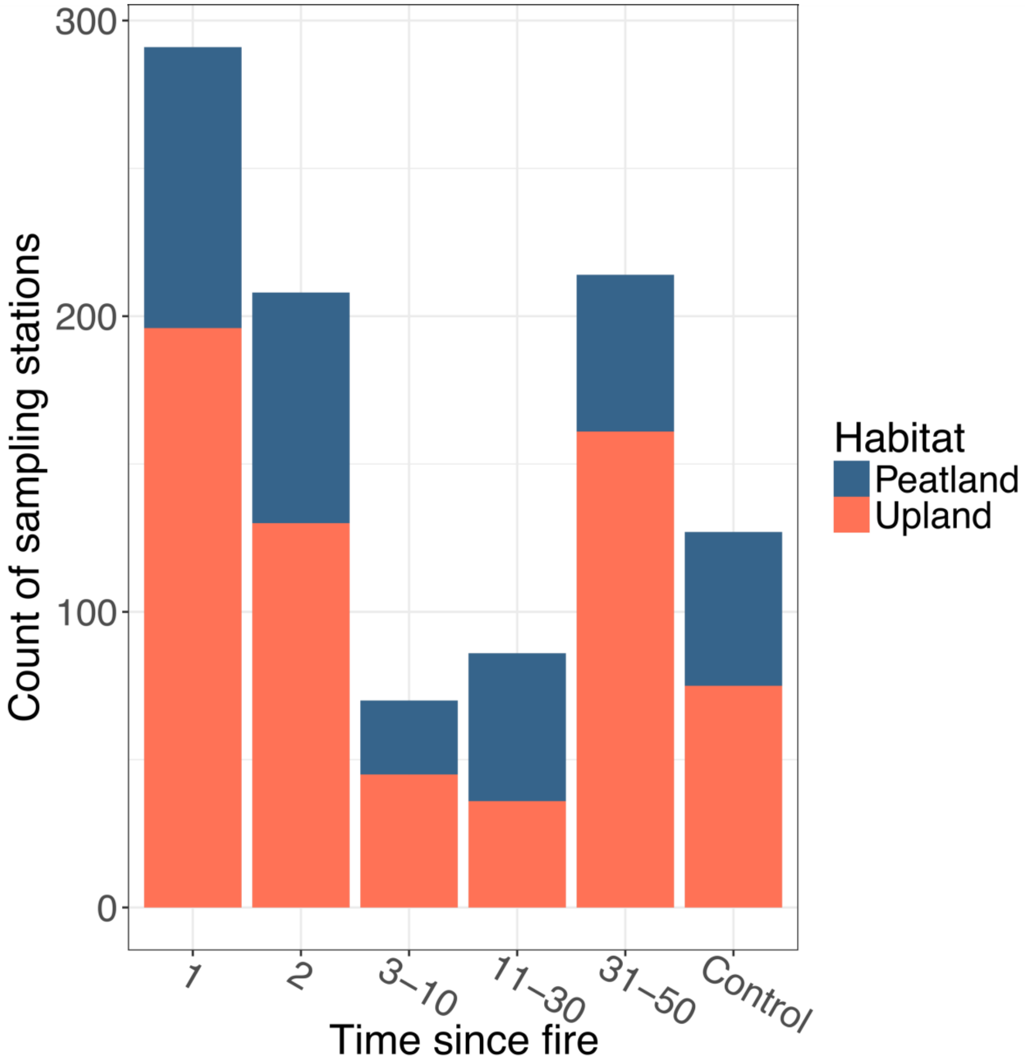
Appendix 3. Number of sampling stations for each burn severity and habitat categories.

Appendix 4. Results of generalized linear mixed model testing for effects of time since fire and forest type on species richness. Reference category is upland control.

Independent variables	**β**	**S.E.**	***p***
intercept	1.82	.04	<0.001
Peatland	0.17	0.03	<0.001
1 year	-0.17	0.05	0.002
2 years	0.10	0.05	0.057
3-10 years	0.1	0.08	0.02
11-30 years	0.29	0.061	<0.001
31-50 years	0.17	0.03	<0.001

Appendix 5. Results of linear mixed model testing for effects of time since fire, habitat type, and time since fire × habitat type on functional diversity. Reference categories are upland control and upland × control interaction.

Independent variables	**β**	**S.E.**	***p***
Intercept	0.63	0.03	<0.001
Peatland	-0.02	0.03	0.558
1 year	-0.07	0.03	0.017
2 years	-0.08	0.033	0.194
3-10 years	0.003	0.052	0.942
11-30 years	0.05	0.05	0.221
31-50 years	-0.002	0.03	0.959
1 year × Peatland	-0.02	0.04	0.607
2 years × Peatland	0.03	0.04	0.484
3-10 years × Peatland	0.02	0.060	0.780
11-30 years × Peatland	-0.002	0.054	0.966
31-50 years post-fire × Peatland	-0.06	0.05	0.222



Appendix 6. Histogram of number of sampling stations in each combination of time since fire and habitat type.

Appendix 7. Species detected at least three times in the study area, life history traits (from the Avian Life History Information Database Wildspace support system (http://www.on.ec.gc.ca/wildlife/wildspace/project.cfm)), and a rank based on the most common boreal species from Blancher (2003).

AOU Species Code	Common Name	Scientific Name	Migration	Feeding	Substrate Breed	Foraging type	Nesting Substrate	Nesting Habitat	Most common boreal songbird species?
ALFL	Alder Flycatcher	Empidonax alnorum	Neotropical migrant	Insectivore	Air	Sallier	Shrub	Treed/shrubby swamp	No
AMRE	American Redstart	Setophaga ruticilla	Neotropical migrant	Insectivore	Lower canopy / shrub	Gleaner	Deciduous tree	Deciduous woodlands	No
AMRO	American Robin	Turdus migratorius	Short distance migrant	Omnivore	Lower canopy / shrub	Forager	Tree - non-specific	Urban	Yes
ATSP	American Tree Sparrow	Spizella arborea	Short distance migrant	Omnivore	Ground	Forager	Ground	Bogs	Yes
BBWO	Black-backed Woodpecker	Picoides arcticus	Resident	Insectivore	Bark	Scaler	Snag	Coniferous woodlands	N/A
BHVI	Blue-headed Vireo	Vireo solitarius	Short distance migrant	Insectivore	Lower canopy / shrub	Gleaner	Coniferous tree	Mixed woodlands	No
BLPW	Blackpoll Warbler	Dendroica striata	Neotropical migrant	Insectivore	Upper canopy	Gleaner	Coniferous tree	Coniferous woodlands	Yes
BOCH	Boreal Chickadee	Poecile hudsonicus	Resident	Insectivore	Lower canopy / shrub	Gleaner	Snag	Coniferous woodlands	No
BRBL	Brewer's Blackbird	Euphagus cyanocephalus	Short distance migrant	Omnivore	Ground	Forager	Ground	Agricultural	No
CCSP	Clay-colored Sparrow	Spizella pallida	Neotropical migrant	Omnivore	Ground	Forager	Shrub	Early successional	No
CHSP	Chipping Sparrow	Spizella passerina	Short distance migrant	Omnivore	Ground	Forager	Coniferous tree	Open woodlands	Yes
CONI	Common Nighthawk	Chordeiles minor	Neotropical migrant	Insectivore	Air	Screener	Ground	Woodlands	N/A
CORA	Common Raven	Corvus corax	Resident	Omnivore	Ground	Scavenger	Cliff	Woodlands	No

CORE	Common Redpoll	Carduelis flammea	Nomadic	Omnivore	Ground	Forager	Shrub	Tundra	No
COYE	Common Yellowthroat	Geothlypis trichas	Neotropical migrant	Insectivore	Lower canopy / shrub	Gleaner	Ground	Marsh	No
DEJU	Dark-eyed Junco	Junco hyemalis	Short distance migrant	Omnivore	Ground	Forager	Ground	Coniferous woodlands	Yes
FOSP	Fox Sparrow	Passerella iliaca	Short distance migrant	Omnivore	Ground	Forager	Ground	Woodlands	Yes
GCTH	Gray-cheeked Thrush	Catharus minimus	Neotropical migrant	Omnivore	Ground	Forager	Shrub	Coniferous woodlands	Yes
GRAJ	Gray Jay	Perisoreus canadensis	Resident	Omnivore	Upper canopy	Forager	Coniferous tree	Coniferous woodlands	No
HETH	Hermit Thrush	Catharus guttatus	Short distance migrant	Insectivore	Ground	Gleaner	Ground	Coniferous woodlands	No
LCSP	Le Conte's Sparrow	Ammodramus leconteii	Short distance migrant	Omnivore	Ground	Forager	Ground	Meadows	No
LEFL	Least Flycatcher	Empidonax minimus	Neotropical migrant	Insectivore	Air	Sallier	Deciduous tree	Deciduous woodlands	Yes
LISP	Lincoln's Sparrow	Melospiza lincolnii	Short distance migrant	Omnivore	Ground	Forager	Ground	Bogs	Yes
MAWA	Magnolia Warbler	Dendroica magnolia	Neotropical migrant	Insectivore	Lower canopy / shrub	Gleaner	Coniferous tree	Mixed woodlands	Yes
MOBL	Mountain Bluebird	Sialia currucoides	Short distance migrant	Insectivore	Ground	Gleaner	Snag	Open woodlands	No
NOFL	Northern Flicker	Colaptes auratus	Short distance migrant	Insectivore	Ground	Gleaner	Snag	Mixed woodlands	No
NOWA	Northern Waterthrush	Seiurus noveboracensis	Neotropical migrant	Insectivore	Freshwater	Gleaner	Ground	Treed/shrubby swamp	Yes

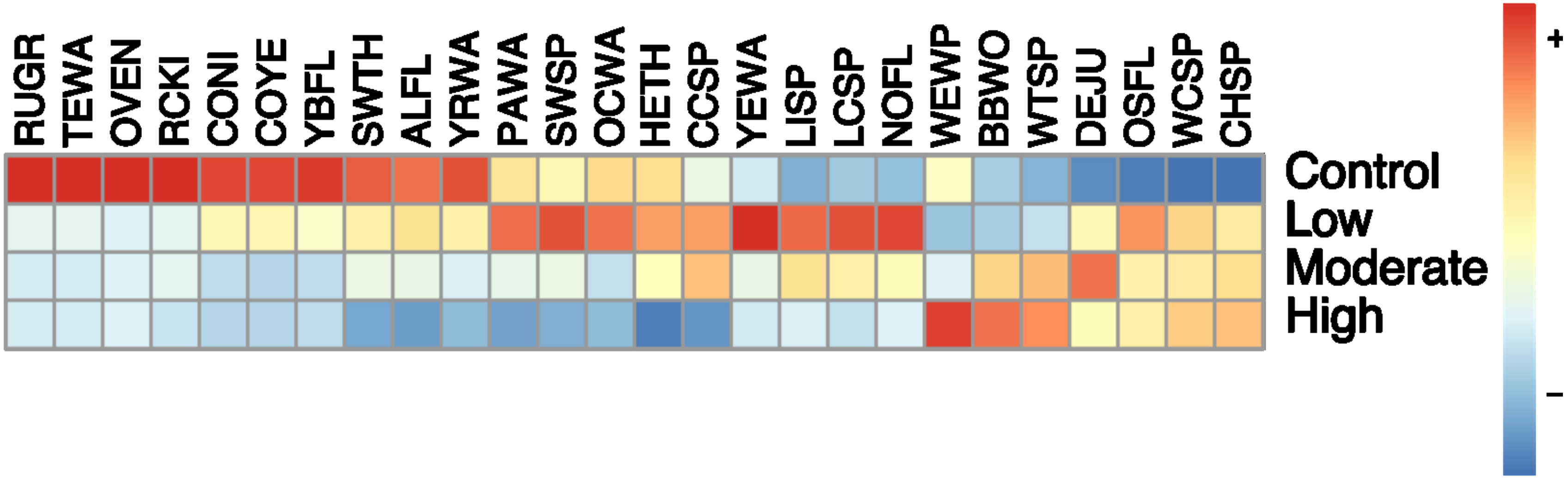
OCWA	Orange-crowned Warbler	Vermivora celata	Short distance migrant	Insectivore	Lower canopy / shrub	Gleaner	Ground	Open woodlands	No
OSFL	Olive-sided Flycatcher	Contopus cooperi	Neotropical migrant	Insectivore	Air	Sallier	Coniferous tree	Bogs	No
OVEN	Ovenbird	Seiurus aurocapillus	Neotropical migrant	Insectivore	Ground	Gleaner	Ground	Deciduous woodlands	Yes
PAWA	Palm Warbler	Dendroica palmarum	Short distance migrant	Insectivore	Ground	Gleaner	Ground	Bogs	Yes
PIWO	Pileated Woodpecker	Dryocopus pileatus	Resident	Insectivore	Bark	Excavator	Snag	Mixed woodlands	N/A
RCKI	Ruby-crowned Kinglet	Regulus calendula	Short distance migrant	Insectivore	Upper canopy	Gleaner	Coniferous tree	Coniferous woodlands	Yes
REVI	Red-eyed Vireo	Vireo olivaceus	Neotropical migrant	Insectivore	Upper canopy	Gleaner	Deciduous tree	Deciduous woodlands	Yes
RUGR	Ruffed Grouse	Bonasa umbellus	Resident	Omnivore	Ground	Forager	Ground	Mixed woodlands	N/A
RWBL	Red-winged Blackbird	Agelaius phoeniceus	Short distance migrant	Omnivore	Ground	Forager	Grass	Marsh	No
SAVS	Savannah Sparrow	Passerculus sandwichensis	Short distance migrant	Omnivore	Ground	Forager	Ground	Agricultural	Yes
SWSP	Swamp Sparrow	Melospiza georgiana	Short distance migrant	Omnivore	Ground	Forager	Grass	Marsh	Yes
SWTH	Swainson's Thrush	Catharus ustulatus	Neotropical migrant	Omnivore	Ground	Forager	Coniferous tree	Mixed woodlands	Yes
TEWA	Tennessee Warbler	Vermivora peregrina	Neotropical migrant	Insectivore	Upper canopy	Gleaner	Ground	Bogs	Yes
WAVI	Warbling Vireo	Vireo gilvus	Neotropical migrant	Insectivore	Upper canopy	Gleaner	Deciduous tree	Open woodlands	No
WCSP	White-crowned Sparrow	Zonotrichia leucophrys	Short distance migrant	Omnivore	Ground	Forager	Ground	Bogs	Yes

WETA	Western Tanager	Piranga ludoviciana	Neotropical migrant	Omnivore	Upper canopy	Forager	Coniferous tree	Coniferous woodlands	No
WEWP	Western Wood-Pewee	Contopus sordidulus	Neotropical migrant	Insectivore	Air	Sallier	Coniferous tree	Open woodlands	No
WIWA	Wilson's Warbler	Wilsonia pusilla	Neotropical migrant	Insectivore	Lower canopy / shrub	Gleaner	Ground	Treed/shrubby swamp	No
WTSP	White-throated Sparrow	Zonotrichia albicollis	Short distance migrant	Omnivore	Ground	Forager	Ground	Early successional	Yes
YBFL	Yellow-bellied Flycatcher	Empidonax flaviventris	Neotropical migrant	Insectivore	Air	Sallier	Ground	Bogs	No
YBSA	Yellow-bellied Sapsucker	Sphyrapicus varius	Short distance migrant	Omnivore	Bark	Excavator	Deciduous tree	Mixed woodlands	N/A
YEWA	Yellow Warbler	Dendroica petechia	Neotropical migrant	Insectivore	Lower canopy / shrub	Gleaner	Shrub	Early successional	Yes
YRWA	Yellow-rumped Warbler	Dendroica coronata	Short distance migrant	Insectivore	Lower canopy / shrub	Gleaner	Coniferous tree	Coniferous woodlands	Yes

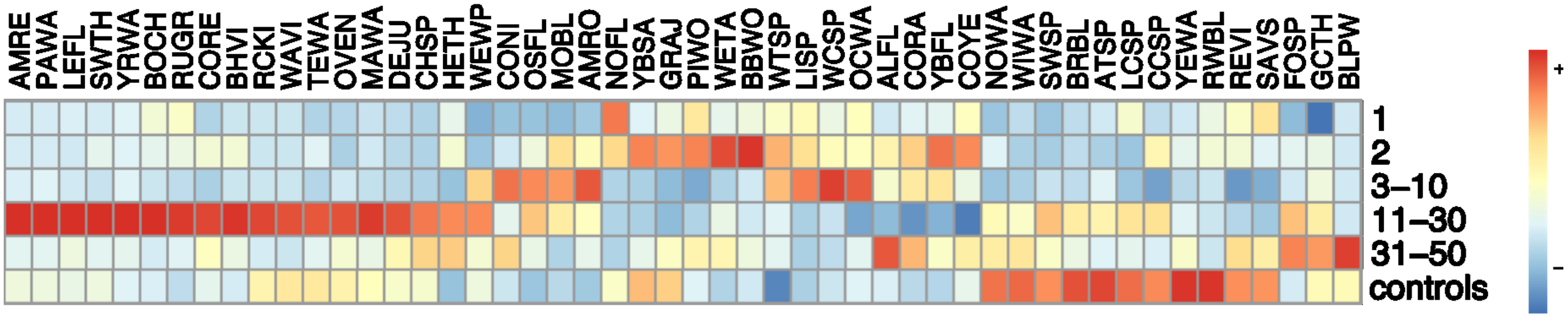
Appendix 8. Summary of similar North American boreal forest studies.

Author(s)	Study Area	Severity or time since fire (TSF)	Analyses	Findings
Hobson and Schieck (1999)	Alberta	TSF compared to logging	Indicator species analysis, community composition	1 year post-fire dominated by: open shrub, grassland, and riparian species, woodpeckers
Imbeau et al. (1999)	Quebec	TSF (gauged by tree heights)	Richness, abundance, guilds	Species richness did not change throughout time Recent burns dominated by: open-land species, cavity nesting species Mid-successional stage: ground and shrub nesting species
VanWilgenburg and Hobson (2008)	Alberta Saskatchewan	TSF (1–5 years) compared to logging	Abundance, Community composition	1–5 years dominated by: cavity nesting species
Morissette et al. (2002)	Saskatchewan	Salvage vs. salvage logging 3 yrs post-fire	Community composition, Guilds	Burned sites dominated by: OSFl, WEWP, AMRO, DEJU
Haney et al. (2008)	Minnesota	TSF	Density	Immediately post-fire: WTSP, DEJU, YRWA, BBWA 7 years post-fire dominated by: ground-brush foragers 19 years post-fire dominated by: WTSP, MAWA REVI, NAWA, SWTH Tree-foliage searchers were the most important guild throughout succession, including unburned forest Species density was greater 30 years post-fire than unburned forests
Schieck Hobson (2000)	Alberta	TSF (1 – 60 years) compared to logging	Species richness, Similarity analysis	Immediately post-fire: Species that nest in large snags Shrub nesters and foragers Old-forest species present throughout succession Generalists species most common 60 years post-disturbance
Hannon and Drapeau (2005)	Alberta, Saskatchewan, Quebec	TSF (1–25 years) compared to logging	Meta-analysis Community composition	Immediately post-fire dominated by: beetle-foragers, cavity nesting species 25 years post-fire dominated by: shrub-breeding species
Azeria et al. (2011)	Quebec	Burn Severity vs. logging	Functional diversity	Low burn severity dominated by: canopy nesters, bark and foliage insectivores High burn severity dominated by: cavity nesting and ground foraging species
Schieck and Song (2006)	Alberta, Saskatchewan, British Columbia	TSF compared to logging	Meta-analysis	0–10 years post-fire dominated by: species that live in parkland habitat and generalists. Old forest species were present where live trees persisted. 11–30 years post-fire dominated by: shrubby and young forest species

				31–75 years dominated by: generalist species dominated, old forest birds were present where live residual trees were present. 76–125 years post-fire dominated by: species richness and presence of old-forest species increased



Appendix 9. Heatmap of species that were detected at least 5 times in the study area. Each column represents a species, labelled with American Ornithologists' Union (AOU) codes. Each row represents a burn severity category. Colors from blue (never present) to red (most frequently present) represent the relative frequency that each species was detected in each severity category. Species frequency data has been standardized.



Appendix 10. Heatmap of species that were detected at least 5 times in the study area. Each column represents a species, labelled with American Ornithologists' Union (AOU) codes. Each row represents a time since fire category. Colors from blue (never present) to red (most frequently present) represent the relative frequency that each species was detected in each severity category. Species frequency data has been standardized.