Boreal songbird response to understory protection harvesting in Alberta, Canada

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Ecology

Department of Biological Sciences
University of Alberta

Preface

This thesis is an original work by Connor Charchuk. No component of this thesis has been previously published, though Chapter 2 is currently under review in the journal Forest Ecology and Management.

Acknowledgments

I would like to acknowledge the mentorship of my supervisor, Erin Bayne. I am thankful for the skills and knowledge I have gained from his mentorship over the last two years. Erin's dedication to the conservation of songbirds is inspiring and motivating. Thank you, Erin, for the opportunities, challenges, inspirations, and the excellent atmosphere that you instil in your lab.

I would like to thank Jillian Cameron and Hannah Schoenberg, my field techs in 2015 and 2016, respectively. I could have never done this without your hard work. Your dedication to my project does not go unnoticed. I am ever grateful for your help.

To my committee member and industry sponsor, Elston Dzus, I thank you for always challenging me intellectually and providing oversight and support whenever I needed it. You have taught me the importance of knowledge, and the power it can have in achieving real change and real progress. I thank Alberta-Pacific Forest Industries Inc. for their tremendous economic support of this research, and recognize the importance of their dedication to research.

Thank you to my lab mates who have always been there to exchange ideas with me and let me ramble on about statistics. Elly, Emily, Nick, Scott, Dan and everyone else. Thank you.

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Chapter 1

Introduction

I. Biodiversity in Canada's boreal forest

Global biodiversity losses are being documented across habitats in all parts of the world. Recent syntheses have shown that despite integrated and coordinated efforts from world leaders, biodiversity loss has not slowed from 1970-2010 (Butchart et al. 2010). Less diverse ecosystems are less productive (Hooper et al. 2012) and contribute overall fewer ecosystem services (Cardinale et al. 2012). The boreal forest contributes significant global ecosystem services (Costanza et al. 1997) and roughly a third of it occurs in Canada (Thompson et al. 2013). Ecosystem services provided by the boreal forest include carbon sequestration (Black et al. 2000), improvement of water quality (Putz et al. 2003), and buffering against effects of climate change (Nasi et al. 2016). Because ecosystem services are greater in areas of higher biodiversity (Gamfeldt et al. 2013), conservation goals in Canada's boreal forest should prioritize the maintenance of biodiversity.

Human land use in the boreal forest contributes to the reduction of biodiversity via forest removal and fragmentation. Chiabai et al. (2011) show that by the year 2050, boreal forests are expected to face the second most forest area loss out of all major global forest biomes. Presently, boreal forest is being lost to a growing network of roads, railways, pipelines, seismic lines and other human land-use related to oil and natural gas extraction, agriculture, mining, and forestry (Venier et al. 2014) . The resulting fragmented forest hosts fewer species than its former contiguous state (Fahrig 2003, Haddad et al. 2015). It is likely that climate change impacts are also acting additively or synergistically with land use modifications, though these effects are less well quantified (Price et al. 2013). Timber harvesting represents one of the sources of human-caused alterations of forests in Canada.

Roughly one quarter of Canada's boreal forest has been harvested at least once (Venier et al. 2014). Harvesting has or will result in managed forests that are overrepresented by forest stands younger than the average harvest age, and thus less mature forests on average than might be expected naturally (Thorpe and Thomas 2007). Cyr et al. (2009) point out that while few species of birds and mammals rely solely on the oldest age classes of boreal forests, some do reach their peak abundance in those habitats. Schieck and Song (2006) suggest that in western North America, old forest stands have higher biodiversity than younger stands. However, the effects on biodiversity caused by reduction in the oldest age classes are lacking a conclusive synthesis in North America. Many Fennoscandian forests have been harvested multiple times over the past few centuries. These forests provide an idea of what North American boreal forests could become in the future unless different management regimes are applied (Imbeau et al. 2001). Berg et al. (1994) show that roughly 50% of IUCN red-listed species in Swedish boreal forests decreased due to a forestry-driven reduction in old growth forests. These findings should at least caution forest managers in North America to look for ways that ensure sufficient old growth forest in the long term in managed forests.

II. Logging Practices in Canada

To manage losses in biodiversity caused by forestry, it is important to understand the history of forestry practices, management strategies, and objectives. Mechanized timber harvesting was established in Canada in the 1960s (Venier et al. 2014). Early practices emphasized maximizing timber yield over long time periods (e.g. Sullivan and Clutter 1972, Pienaar and Turnbull 1973,) using short duration rotation periods. Harvesting practices began to face social criticism throughout the 1980s due to concerns about climate change and biodiversity loss (Hunter 1993). In response to growing concern over a lack of an ecological basis to harvesting, the natural disturbance management strategy emerged (Hunter 1990).

Harvesting under the natural disturbance regime (NDH) involves harvesting to approximate natural disturbances such as wildfire. The objectives of NDH are to ensure post-harvest conditions fall within the natural range of variation of natural disturbances in terms of pattern, structure, composition, and ultimately biodiversity (Andison et al. 2009). NDH management is hypothesized to improve post-harvest biodiversity and result in a more resilient ecosystem (Hunter 1993). The rationale behind this strategy is that organisms and ecosystems are adapted to natural disturbances, and are likely to be more resilient to changes imposed by these disturbances than novel ones created by intensive silvicultural practices (Hunter 1993). In the boreal forest, particularly in North America, wildfires represent the overwhelming majority of natural stand-replacing disturbance (Weber and Flannigan 1997). Fires typically kill most of the trees on the landscape and occur on relatively frequent intervals (Hunter 1993). Therefore, to approximate this process, forest managers often implement harvesting strategies that clear large contiguous areas and leave behind few standing trees. This harvesting strategy, herein broadly referred to as traditional harvesting, is facing increasing opposition from public opinion and conservation groups (Angelstam et al. 2003), despite being founded in ecological theory about how boreal systems work. Public opinion has historically been critical of forest management, in part driven by concerns over harvesting large areas (Booth et al. 1993). In addition to concerns over public opinion, the ecosystem resiliency and biodiversity responses to traditional harvesting practices are of general concern.

The development of natural disturbance regime harvesting was predicated on a theoretical approach rather than empirical research. Thus, studies assessing the efficacy of NDH came after its widespread implementation, and management has adapted to research as it is being conducted. Concerns have been raised over the decision to conduct NDH over other approaches. Palik et al. (2002) posed three key ecological concerns with natural disturbance harvest: unpredictable variation in natural disturbances, differential outcomes between harvesting and wildfires, and the interactive effects of the multiple components of natural disturbances. However, Long (2009) proposes that socioeconomic pressures are likely more limiting than ecological or economic ones. Drever et al. (2006) stress the importance of maintaining ecosystem resiliency post-harvest, and calls into question the ability of NDH to accomplish this goal. Therefore, forest management is faced with multiple components of uncertainty surrounding traditional harvesting practices.

The literature directly assessing the ecological success of NDH management is sparse and mostly inconclusive. One historical study from northern Quebec showed that the current age-class distribution on the landscape of managed forests fell outside the historical range driven by natural variability in fire regimes over the past 6800 years (Cyr et al. 2009). However, arthropod communities have also been shown to converge between post-fire and NDH harvesting within just 30-years post-disturbance (Buddle et al. 2006). A meta-analysis conducted by Zwolak (2009) showed small mammal abundances and communities responded differently to traditional harvesting than to wildfire within 20 years post-harvest. Huggard et al. (2014) found plant communities in post-harvest stands in Alberta were dissimilar to same-aged post-fire stands, suggesting a disconnect in the regeneration trajectory of the two disturbances. While the ecological viability of traditional management remains to be seen, the economic perspective is more clear.

III. Mixedwood Management

In the western boreal forest of North America, post-fire stands are dominated by early seral species such as trembling aspen (*Populus tremuloides*) (Johnstone and Chapin 2006). In post-fire areas, the root systems of surviving trembling aspen form clonal suckers which typically emerge the following season to dominate the disturbed area (Frey et al. 2003). Traditional forestry results in similar conditions post-harvest, and harvested areas are often dominated by aspen suckers the year after harvesting. Fire and harvesting disturbances occurring concurrently may ultimately result in the over-representation of aspen-dominated stands on the landscape, as reestablishment by conifers in these stands can be impeded by limited seed dispersal and competition with aspen (Johnstone and Chapin 2006). With an impetus to increase softwood yield, timber managers are faced with the need to devise strategies to conserve mixedwoods and conifer-dominated stands on the landscape (Lieffers and Beck 1994). In Alberta, harvest quotas are separated between softwoods and hardwoods, thus incentivizing forestry companies to maintain conifer stock in managed areas. This incentive led to the development of harvesting regimes whereby unmerchantable conifers in mixedwood forests are protected during hardwood harvest.

The majority of the boreal forest occurs in some form of mixedwood (Lennie et al. 2009), thus a large proportion of harvesting occurs in mixedwoods. Mixedwood forests typically consist of an overstory of early-seral species such as trembling aspen with an understory of later-seral species such as white spruce, *Picea glauca*. Under a maximum yield harvest system, these areas are harvested for hardwoods (i.e. trembling aspen) when the understory is still undeveloped and unmerchantable. Roughly one third of hardwood forests in Alberta have been identified as having a significant stock of understory white spruce (Navratil et al. 1994). However, up to 80% of hardwood stands are targeted for traditional harvesting without directed protection of the understory (Navratil et al. 1994). Thus, softwood stock in the form of white spruce is often lost during traditional harvesting. Brace and Bella (1988) were the first to outline the potential benefits of conserving the understory white spruce in mixedwood management. In response, several methods of understory protection harvesting (hereafter UP) were developed and tested in a series of trials known as the Hotchkiss experiments (Navratil et al. 1994).

IV. Understory Protection

The method of understory protection harvesting that showed the most economic promise is a single pass high effort strip cutting method (Grover et al. 2014). A machine corridor 6m-wide is cleared for the feller buncher machine, which reaches approximately 6m on either side to extract mature aspen without damaging the understory. A 3m-wide strip of unharvested forest remains intact between the extraction areas to act as a wind buffer. Alberta-Pacific Forest Industries Inc. (hereafter Al-Pac) first implemented this harvesting strategy in its forest management policy in 2001, and has been implementing it across their forest management area (FMA) in Alberta annually since 2004. Al-Pac's FMA spans 6.4 million hectares of northeastern Alberta wilderness, and contains 2 million hectares of harvestable forest. At least 8700 ha (conservative estimate) have been harvested using understory protection to increase the overall stock of softwood in the FMA.

Following understory protection harvesting, understory white spruce is freed from competition with the overstory aspen. The white spruce has been shown to experience accelerated growth rates of diameter, volume, and height; with up to a 40% increase in height growth rate (Man and Greenway 2004). Expedited growth of white spruce in understory protection stands therefore has economic benefits to contribute to the softwood supply faster than other methods such as planting. The rapid regeneration of superficially mature spruce (mature in size, but not in age) results in a stand of merchantable spruce that is otherwise difficult to achieve over a typical boreal forest successional pathway. Due to the unique patterning of understory protection harvesting, the types of organisms expected to colonize these areas is expected to be different than those found in traditional harvest blocks. There is only one peer-reviewed example that we are aware of that has studied an organism's response to understory protection harvesting. Fisher and Bradbury (2006) showed that red squirrels (*Sciurus vulgaris*), a conifer-dependent mammal of the boreal forest, did not decline in abundance in stands following understory protection harvest. This result suggests that understory protection has some promise to provide habitat to mature forest organisms following harvest. However, the extent to which understory protection harvesting provides habitat for forest species has yet to be comprehensively assessed.

The amount of time it takes for a harvested stand to return to pre-harvest conditions is an extensively studied, yet poorly understood dynamic. Because NDR harvesting typically seeks to approximate fire disturbance, most research compares post-harvest against post-fire reference stands. Many studies in sustainable forest management rely on bird surveys to quantify rates of change in the biodiversity and ecological community following harvesting (e.g. Harrison et al. 2005, Atwell et al. 2008, Hache et al. 2013, Carrillo-Rubio et al. 2014, Corace et al. 2014). Songbirds are frequently used as surrogates to assess human land use influences on biodiversity because they occupy a wide range of habitats, they are a highly speciose group, and they are easy to identify using vocal cues (Mac Nally et al. 2004). Some research suggests the bird communities in harvested versus fire disturbed stands reach convergence within 15-years post harvest (Huggard et al. 2014), but other research suggests it could take up to 60-years for convergence to occur (Schieck and Hobson 2000). I argue that using post-fire as the only reference condition for setting conservation objectives limits effective forest management designed to maintain biodiversity. Many of the species most directly affected by timber management are those strongly associated with old-growth forests (Mannan and Meslow 1984, Molina et al. 2006, Spies et al. 2006, Bauhus et al. 2009). As a result, many researchers have advocated for forest management that provides habitat for mature forest species and uses the old-growth forest as the reference condition that we should try and emulate after harvest (McRae et al 2001, Molina et al. 2006, Mori and Kitagawa 2014). Schieck and Song (2006) conducted a meta-analysis that suggests traditional harvesting approaches may require 100 years before recolonization by mature forest bird species occurs. Therefore, prioritizing harvesting strategies that may not model natural processes but can provide habitat to mature forest species sooner after harvest represent an approach to forest management that must be considered. From this objective, a relatively new form of forest management termed retention forestry has arisen.

Retention forestry represents any harvesting approach that seeks to maintain pre-harvest forest structure and function by focusing more on what is retained than on what is harvested (Franklin et al. 1997). The processes and patterns of retention harvesting are variable, and individual assessment of the efficacy of each approach is required. Furthermore, no consensus exists on the amount of retention that is required to facilitate patch use by mature forest species. Otto and Roloff (2012) showed that mandated retention requirements in Michigan of 3-10% were insufficient at increasing site occupancy rates of songbirds associated with mature forests. Lance and Phinney (2001) found that retention levels of 15-22% facilitated higher abundance for many forest-songbirds relative to clearcuts, but many species were dependent on mature forests and did not occur at all or at low rates in the retention sites.

The findings of Le Blanc et al. (2010) suggest that retention levels greater than 55% are required to mitigate the negative effects of harvesting on birds and mammals in old growth forests. Because species responses to retention harvesting are variable (Tittler et al. 2001), it is essential to manage communities for each harvesting system in each jurisdiction individually.

There has been no established definition in the literature that indicates the level of green tree retention required to designate a harvesting practice as retention forestry. A meta-analysis conducted by Fedrowitz et al. (2014) included 78 studies with retention levels ranging from 2-88% and an average of 36.4% ± 24.8 SD retention. A functional approach to setting target retention levels may be more appropriate whereby attaining convergence with unharvested control sites defines retention harvesting. This approach to sustainable harvesting whereby harvest stands are intended to maintain continuity with unlogged forests is increasingly influencing how foresters view the efficacy of the NDH paradigm (McRae et al. 2001, Spence 2001, Drever et al. 2006, Lindenmayer et al. 2012). Silvicultural systems that maintain higher levels of biodiversity associated with old-growth forests are an approach to NDH practices that should be considered when reductions in old-growth species below a desired threshold occur (Bauhus et al. 2009). Therefore, the “old-growthness” (Franklin and Spies 1991) that novel harvesting practices provide both immediately post-harvest and over time should be an integral component of the assessment process.

V. Songbird response to Understory Protection

The understory protection harvesting strategy results in the retention of approximately 20% of the overstory, and 70% of the understory white spruce in any given stand. Because these rates represent moderate to high retention levels, it is expected that understory protection will provide habitat to forest species that traditional harvesting does not provide. To assess the biodiversity value of understory protection harvest blocks, we compared songbird communities between UP harvest areas, traditionally harvest areas, and unharvested controls. Conducting multi-species community analyses allows for a comprehensive comparison between harvest types to understand how birds respond to harvesting.

Comparing bird responses to different harvesting strategies allows for more informed forest management planning (Venier and Pearce 2005). By comparing understory protection harvesting against unharvested controls, we aim to assess how well understory protection function as a retention harvesting approach. By comparing the understory protection against traditionally harvested areas we quantify the degree to which this harvesting approach provides conservation benefit relative to traditional harvesting practices for old-growth species. Furthermore, we surveyed a chrono-sequence of different aged post-harvest stands to analyze the convergence of bird communities post-harvest with the unharvested forest community. We hypothesize that understory protection harvesting will result in a faster return to unharvested conditions than traditional harvesting practices.

VI. Indicator Species Assessment

An alternative approach to biodiversity management, which may simplify the multi-species management approach, is the use of indicator species for setting meaningful targets. The use of indicator species is a century-old approach to conservation (Hall and Grinnell 1919), that has become commonplace for the assessment of sustainable forest management. Choosing an appropriate indicator species depends largely on the objective (Lindenmayer et al. 2000), which in the current assessment of understory protection is its ability to provide breeding habitat to mature forest species. A conservative approach would be to select a species that is highly dependent on mature forests and sensitive to forestry practices. Ensuring the conservation of this target species would facilitate trickle-down conservation to other, less-sensitive forest species. One species that has emerged as the most suitable indicator species for North American boreal forests is the Brown Creeper, *Certhia americana*. A meta-analysis by Vanderwel et al. (2007) suggests the Brown Creeper is the species most sensitive to forest harvesting, while Lance and Phinney (2001) found it to be one of the least responsive species to partial retention, and Le Blanc et al. (2010) show that only retention levels greater than 55% facilitate use of harvest blocks by Brown Creepers. Poulin et al. (2008) call into question whether populations of Brown Creepers can be maintained at all in managed forests. Our second approach to the assessment of understory protection habitat was to determine the degree to which Brown Creepers will use UP areas relative to unharvested controls.

In addition to quantifying the degree to which Brown Creepers use understory protection, we investigated the mechanism leading to recolonization. Using measures of forest structure and composition, the objective of this research was to quantify specific habitat requirements for Brown Creepers to better inform forest management and policy. It is well established in the literature that Brown Creepers avoid harvested areas (Vanderwel et al. 2007, Mahon et al. 2008, Geleynse et al. 2016), but little is known about the mechanism underlying this avoidance. Remote sensing data can provide detailed descriptions of forest structure using light detection and ranging (LiDAR) technology. Previous research using LiDAR data has found that Brown Creepers are more likely to occupy areas with taller, denser canopies (Vogeler et al. 2013). The goal of using LiDAR in this research framework was to better understand the structural attributes of understory protection and unharveted stands that facilitate the use by Brown Creepers to better inform forest management decisions in terms of sustaining populations of Brown Creepers.

Chapter 2

Title: **Avian community response to understory protection harvesting in the boreal forest of Alberta, Canada**

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ABSTRACT

Understory protection is a harvesting approach that seeks to protect understory conifers during hardwood harvesting in mixedwood forests. While understory protection harvesting has been implemented for over a decade in Alberta, there has been no study of its ecological value to birds. We surveyed birds in understory protection (UP), natural disturbance harvest (NDH) blocks, and the nearby unharvested forest. We looked for differences in species richness and community composition between the three treatment types. We found NDH had significantly higher species richness than unharvested forests, but did not differ from UP. Higher richness in NDH may be due to birds being counted over an unlimited distance and the relatively higher sound transmission in NDH. The three treatments all had significantly different avian community compositions. UP represented an intermediary between NDH and unharvested forests. When comparing the oldest age class of UP with the unharvested forest, we found no significant difference in the bird communities just 12 years post-harvest. These results suggest that following understory protection harvest, the retained forest is quick to regenerate and provides habitat to mature forest species quite quickly. An expanded implementation of understory protection harvesting across the boreal forest may help mitigate some of the negative effects of timber management on habitat for forest dwelling birds that typically require older forests.

KEYWORDS

Understory protection, songbird, bioacoustics, ordination, ARU, retention forestry

INTRODUCTION

Approximately 30% of Canada's boreal forest is managed for timber harvest (Venier et al., 2014), of which over 60% has been harvested at least once (Burton et al., 2003). Timber harvesting in the boreal historically relied on clearcutting (Ralston et al., 2015). Proponents of clearcutting defend the practice for its economic effectiveness and efficiency (Smith and DeBald, 1978), while critics have expressed concerns about its effects on biodiversity (Lindenmayer et al., 2012). These concerns have led the forestry industry to increasingly adopt a natural disturbance model of harvesting (hereafter NDH), whereby harvesting approximates natural disturbances such as fire. NDH has been implemented based on the assumption that communities disturbed by natural processes will be more resilient than those disturbed by anthropogenic processes (Hunter 1993). NDH results in greater retention of snags and mature trees within harvested areas than clearcutting and may achieve habitat convergence relative to natural disturbances more quickly (Huggard et al., 2015). Retention of snags in NDH may serve as a "lifeboat" to promote habitat use for many species (Franklin et al., 1997), but NDH does not mimic fire disturbance exactly at any stage of succession. Communities of mammals (Zwolak, 2009), birds (Hobson and Schieck, 1999; Schieck and Song, 2006), beetles (Gandhi et al., 2004), plants (Peltzer et al., 2000), forest structure (McRae et al., 2001) and composition of soil nutrients (Kishchuk et al., 2014) have all been shown to differ between NDH areas and burns following the disturbance event. Some researchers argue NDH will never perfectly replicate fire disturbance due to the underlying differences in the disturbance process itself (Drever et al., 2006). Futhermore, Armstrong (1999) argues that knowledge of fire rotations will never be precise enough to successfully implement NDH management.

The ability for NDH to approximate natural disturbance is primarily studied in the short-term due to constraints over the time period since harvesting has taken place. At the far end of the successional gradient, concerns exist about the amount of old forest that will persist in areas managed by NDH and the species that rely on such conditions. Thus, one of the secondary objectives of NDH is to shorten the time interval for the forest to return to pre-harvest conditions to ensure habitat for such species. The assumption is that by approximating natural processes, recovery to old-growth conditions will be faster than from other forms of harvest like clearcutting. Whether or not NDH is the most effective way to return to an old-growth state quickly remains an area of active investigation. Some research suggests NDH begin to converge with post-fire disturbances just 15-years post-disturbance (Huggard et al., 2015). However, one consequence of NDH that remains poorly explored is how it influences the amount of mixedwoods that will exist on the landscape in the future.

Mixedwoods are stands containing a mixture of deciduous and coniferous trees. The successional pattern of many upland forests in western Canada following fire is the establishment of dense early-seral hardwoods such as trembling aspen (*Populus tremuloides*) immediately following disturbance, followed by the emergence of shade-tolerant species such as white spruce (*Picea glauca*) later in succession. This successional pathway means that pure stands of deciduous trees tend to dominate the landscape for decades after a fire event. Successful NDH is expected to follow a similar successional trajectory. However, NDH often operates on a rotation age of between 60-100 years. This harvest return interval may be inadequate to allow mixedwoods to develop their full ecological or economic benefit because of insufficient time for coniferous trees to regenerate. The end result is that NDH may target mixedwood forests in such a way as to reduce their availability at the landscape level over the long-term. This "unmixing of the mixedwoods" could have significant consequences for biodiversity and economic returns, as mixedwoods typically have higher species diversity than pure stands (Hobson and Bayne, 2000) and can be economically more valuable than pure stands, as softwoods and hardwoods can grow faster in mixed forests (Man and Lieffers, 1999). Thus, finding a way to maintain mixedwood structure after harvest could have significant ecological and economic benefits.

Clearcutting and NDH typically result in the accidental destruction of understory white spruce during mixedwood harvesting. By losing unmerchantable conifer stock, there is an overall reduction in long-term softwood yield for timber companies. The regeneration of white spruce stock in mixedwood forests following harvesting has been deemed one of biggest challenges facing forest managers in western Canada (Lieffers and Beck, 1994). Understory protection harvesting (hereafter UP) is a recently developed practice of harvesting that seeks to protect unmerchantable white spruce during mixedwood harvesting to facilitate future softwood timber yield. First proposed by Brace and Bella (1988), the two-pass UP harvest strategy seeks to minimize destruction of the white spruce understory during the overstory hardwood harvest to allow earlier future harvesting of softwoods (Navratil et al., 1994). Following the first-pass harvest, a mosaic of strips are left behind: a 3-meter wide unharvested strip is used to prevent windthrow of the protected understory, a 6-meter wide protection strip containing understory white spruce freed from competition with overstory aspen, and a 6-meter wide skid row cleared of vegetation (see: Grover *et al*., 2014: Figure 2). Following the first-pass harvest, the understory spruce is released from competition, and growth can be accelerated by up to 40% (Yang, 1991). This can lead to a similar conifer yield as unharvested mixedwoods within about 60 years (Grover et al., 2014).

The understory protection harvest method results in the retention of approximately 50% of the understory spruce and 20% of the residual forest on average. The retention of a higher proportion of residual forest during harvesting (i.e. retention forestry) seeks to maintain pre-harvest forest structure and conditions (Gustafsson et al., 2012). Retention forestry may provide more effective conservation of species associated with mature forest than NDH management (Lindenmayer et al., 2012). A meta-analysis by Fedrowitz et al. (2014) suggests retention forestry can maintain populations of both open-habitat species and forest species, and overall supports more diverse communities than NDH. However, the type and amount of retention required to provide habitat is highly variable and species dependent (Fedrowitz et al., 2014). Therefore, assessment of different retention cutting strategies is an ongoing and evolving process in adaptive forest management. Currently, understory protection is not recognized as a retention harvesting technique, though the benefits may be comparable to other retention forestry approaches.

Despite the growing implementation of UP, there has been a lack of research into the ecological value of understory protection harvest areas (Lieffers and Grover, 2004). The goal of this study was to compare bird diversity and communities in UP, NDH and unharvested forests. We hypothesized that bird communities in UP would differ from those in NDH due to the greater level of tree retention in UP providing habitat for mature forest birds. We further predicted that the bird community in UP would be more similar to the unharvested forest than would the NDH. Finally, we hypothesize there will be differential community trajectories in understory protection blocks relative to NDH areas because white spruce growth is expedited (Grover et al., 2014) and aspen suckering is suppressed due to soil disruption by the feller buncher (Lennie et al., 2009). We achieve this comparison by conducting bird surveys in unharvested forests paired with a chrono-sequence of UP and NDH blocks to quantify the avian community response to harvesting over time.

METHODS

Sites

This study was conducted on lands managed by Alberta-Pacific Forest Industries Inc. (hereafter Al-Pac) in the boreal forest of northeastern Alberta, Canada. NDH conducted by Al-Pac involves variable retention of an average of 5% merchantable trees and snags within each individual harvest area (for an overview of Al-Pac's harvesting at the stand and landscape level see Dzus et al. (2009)). Al-Pac has also been implementing UP since 2005 in deciduous stands with an understory of white spruce greater than 600 stems per hectare. For a detailed description of the UP harvesting procedure conducted by Al-Pac, see Greenway et al. (2006) and Grover et al. (2014). UP and NDH blocks were surveyed throughout the extent of Al-Pac's forest management area, west to 113°37'3.6"W north to 56°13'45.0"N east to 108°10'23.6"W and south to 54°50'19.1"N. For some analyses, harvest blocks were binned into two age classes: young NDH at 1-9 years and old NDH at 10+ years; young UP at 1-8 years and old UP at 9-12 years, to create age categories with relatively equal sample sizes

Bird surveys were conducted using autonomous recording units (ARU) to remotely survey vocalizing species. We used SM2+ and SM3 song meters developed by Wildlife Acoustics. ARU deployments were conducted during the breeding bird season when songbirds are most vocally active (May 25 – July 4) in 2015 and 2016. A single ARU was used to survey each harvest block or unharvested control, and is hereafter referred to as a site. Understory protection sites were selected in ArcMap 10.2 (ESRI, 2016) using a layer from Al-Pac that delineates the understory protection harvested area. Harvested areas were mapped out on-the-ground during harvesting using tracks from GPS-enabled feller bunchers; ARU locations were centered within the harvested area. NDH and unharvested sites were selected using a combination of layers developed by Al-Pac and the Alberta Vegetation Inventory (AVI). UP blocks were selected based on ease of access and age such that we surveyed a full chrono-sequence of UP blocks. NDH sites were thereafter selected based on closest proximity to UP sites, and unharvested sites were chosen based on the oldest forest patch available within 1km of the UP block. We used a randomized block design, so each block (hereafter *location*) contained one UP site, one NDH site, and one unharvested forest site. Sites were restricted to a minimum of 300-meters apart to reduce double counting birds, and a maximum of 1km away to minimize extraneous variation within the location. Within a location, NDH and UP were not typically of the same age (i.e. they were harvested in different years).

Listening

Sound files recorded by the ARUs (32-bit WAV) were manually processed in the lab to transcribe all individuals that could be identified via acoustic identification. Listening for this project was conducted by five experienced listeners (>1-year experience with western boreal songbirds). Three-minute long recordings between 04:00am-07:00am were listened to using Adobe Audition or Audacity software, and circumaural headphones. All birds vocalizing in each recording were identified and the time of first detection within each 1-minute bin was transcribed. Multiple individuals of the same species were identified using the relative strength of the vocalization on stereo microphones (i.e.

left and right channels) and/or the presence of overlapping signals. Four recordings for each site were processed (i.e. 4 visits per site). Recordings were chosen on different days whenever possible, which were usually consecutive days in the season. Recordings with moderate to strong wind or rain contamination were not processed.

Analysis

We used a randomized block design wherever possible to control for sources of variation due to geographical location, survey time within the season, forest composition in the region, and weather during the survey. We were unable to test the detection radius for each ARU and species combination; therefore, were likely dealing with varying sampling areas at each site due to differential sound attenuation as a function of vegetation structure. To reduce this effect, species richness estimates were rarefied to account for varying abundance structures resulting from differential sampling radii (Gotelli and Colwell, 2001). Rarefaction allows us to assume each site sampled the same number of individual birds, thus differences in richness should reflect true species diversity differences rather than an effect of the species-area relationship. A randomized block ANOVA was used to compare rarified species richness estimates between NDH, UP and unharvested sites. Rarefaction was conducted using the function *rarefy* in the R package *vegan* using a subsample size equal to the average species richness across all sites in our study. A Tukey's post-hoc test was conducted to investigate pairwise differences between each treatment.

To determine species-habitat associations, the Indicator Value (IndVal) method developed by Dufrene and Legendre (1997) was adapted. The IndVal method is an efficient first way to compare relative abundances and commonness of individual bird species across different habitat types. We amalgamated species data for each site by taking the maximum number of individuals of each species detected across the four visits. We used a permutative approach to obtain an exact p-value for each species-habitat association using 10, 000 iterations to randomly shuffle data across sites and species. We also calculated relative indicator values as simply:

$$RelIV_{ij} = \frac{IndVal_{ij}}{\sum_{j}^{n} IndVal_{i}} \qquad \text{Equation 1}$$

Where *RelIVij* represents the relative indicator value for species *i* at treatment class *j* across *n* treatment classes.

Relative indicator values were calculated to determine which species were utilizing UP to a greater degree than NDH or unharvested forests.

Comparisons of bird communities between the three forest types were visualized using non-metric multidimensional scaling (NMDS). Using an iterative approach, we established the optimal settings to be a 3-dimensional ordination at 50 iterations, resulting in a final stress of 0.199. We visualized differences between the communities using centroid ellipses to encompass what we deem as core species for each habitat. We define core species as those that fall within an ellipse that was drawn around each habitat centroid such that the overlap between the ellipses is minimized while maximizing overall coverage. We determined an ellipse size of 70% S.D. using an iterative approach to best visualize these core communities. Centroid points were then drawn for each age class of NDH and UP to visualize changes in community composition as the harvest blocks age.

We used multivariate randomized block permutation procedures (MRBP) (Mielke and Berry, 2007) to test for differences in the communities between the three treatment types while maintaining the randomized block design. MRBP was conducted using the *mrbp* function in the *Blossom* package in R. We used a permutative method for establishing exact p-values, and chose 2000 permutations. Pairwise comparisons were made between each treatment type using a Bonferonni correction as suggested by McCune and Grace (2002). Block alignment and variable commensuration were applied following recommendation from McCune and Grace (2002). This test is akin to an ANOVA, and tests the null hypothesis that dissimilarity between groups is equal to or less than the dissimilarity between sites within a group.

Finally, we investigated community differences between NDH and UP age classes against the unharvested forest. However, this design was not blocked as the same age classes of UP and NDH did not always occur within the same location. We instead used a multivariate randomized permutation procedure (MRPP) to analyze this data using the *mrpp* function from the *Blossom* package in R; again a Bonferroni correction was applied. We lacked data to test for differences between the harvest types, and in total made four pairwise corrections tested at significance of α = 0.0125.

RESULTS

Species Richness

In total, 98 species of birds and mammals were detected in our recordings, including 69 species of passerines. The most ubiquitous species was White-throated Sparrow (*Zonotrichia albiconicus)* found at 96.7% of sites (261/270), while eight species were detected at only one site. Of these, 53 passerine species were detected at 5 or more sites and were included in the analyses.

NDH sites had the highest species richness at 46 out of 79 locations, UP at 29 out of 79 locations, and the unharvested site at 18 out of 90 locations (12 two-way ties, 1 three-way tie). Species richness at the site level ranged from 2 species to 25 species. We found a significant difference in rarefied species richness between the three treatments (p = 0.027). The post-hoc Tukey test showed that NDH had significantly higher species richness than unharvested sites (p = 0.027). The UP sites did not significantly differ in richness from unharvested sites (p = 0.12), nor from NDH sites (p = 0.81) (Figure 1).

Indicator Value Analysis

Of the 54 species tested using the indicator value method, 26 were significant indicators at α = 0.1 for a single habitat type (Table 1). 12 were indicators of NDH, 9 were indicators of unharvested forest, and 5 were indicators for UP. The five species that were significant indicators for UP were: Chipping Sparrow, Connecticut Warbler, Magnolia Warbler, Tennessee Warbler, and White-throated Sparrow.

Community Analysis

The NMDS plot showed that the UP community centroid occurred in between the NDH centroid and the unharvested forest centroid (Figure 1a). There was considerable overlap of the UP ellipse and both the NDH ellipse and unharvested ellipse, suggesting the UP community is an intermediary between the other forest types. Furthermore, almost none of the UP ellipse did not overlap the unharvested or NDH ellipses, suggesting few species use UP exclusively. The centroids for the youngest UP age classes (1-3 years) occurred in the region of UP and NDH overlap; intermediate age classes (4-11 years) were distributed in the overlap region of all three ellipses, and the oldest age class (12 years) occurred in the overlap region of the UP and unharvested ellipses.

Species of birds shown to be associated with older forests, such as Golden-crowned Kinglet, Bay-breasted Warbler, Red-breasted Nuthatch, and Western Tanager occurred outside the ellipses, but were most closely associated with the unharvested forest sites. Early successional species such as Song, Le Conte’s and Clay-coloured Sparrows occurred most closely associated with NDH, but outside the ellipse. Red-eyed and Philadelphia Vireo, Dark-eyed Junco, Common Yellowthroat, Lincoln’s Sparrow, and Orange-crowned Warbler were exclusively associated with NDH (Figure 2). American Robin, Mourning Warbler, Least Flycatcher, and Rose-breasted Grosbeak were core species in NDH and UP communities. Warbling Vireo, Magnolia Warbler, White-throated Sparrow, Tennessee Warbler, and American Redstart were the most generalist species, representing core species for all three forest types. Ruby-crowned Kinglet, Winter Wren, Wilson’s Warbler, Olive-sided Flycatcher, and Swainson’s Thrush occurred exclusively in UP and unharvested core communities. Finally, Ovenbird, Cape May Warbler, and Brown Creeper were exclusively associated with the unharvested habitat.

The MRBP analyses revealed a significant difference between all pairwise comparisons of forest types (Table 2); NDHs were significantly distinct from UP (delta = 16.97, $p < 0.001$) and unharvested forests (delta = 16.18, $p < 0.001$), and UP was significantly distinct from unharvested forest (delta = 17.67, $p < 0.001$). The MRPP analyses showed that both young (delta = 19.12, $p < 0.001$) and old NDH (delta = 20.58, $p = 0.01$) had significantly different bird communities from unharvested forests. Young UP bird communities were significantly distinct from unharvested forest communities (delta = 20.15, p = 0.01), though old UP blocks were not significantly different from unharvested forests (delta = 21.4, p = 0.03).

DISCUSSION

Areas harvested using NDH had higher species richness than unharvested forests, while UP richness was intermediate and did not differ from the other treatments. There are two possible reasons for this result. First, it may reflect ecological reality whereby younger forests provide necessary resources for a higher number of species. However, it may also be an artefact of using unlimited distance point counts with ARUs. ARUs that are surrounded by denser vegetation tend to survey a smaller area, given that sound travels further and with less attenuation in open relative to forested environments (Yip et al., 2017). Due to the low vegetation typically expected in young NDH areas, it is possible that we could hear birds farther away, and thus the ARU was sampling a larger area. We therefore attribute higher richness in the NDH as simply an example of the species-area relationship (McGuinness, 1984). Using rarefaction to generate our richness estimates was intended to account for different sampling effort as a function of the number of individuals sampled between the habitat types (Gotelli and Colwell, 2001); however, these results may suggest simple rarefaction techniques may be inadequate at accounting for differences in sampling areas when comparing between ARUs in different habitats. Because UP is intermediate between NDH and mature forests in terms of vegetation structure, it is our interpretation that the sampling area and thus species richness would be intermediary too. The application of ARUs in avian point count surveys is still in its infancy, and further advances in understanding detection distances and survey radii would benefit future studies.

Our MRPP and NMDS results suggest that the bird community in understory protection is a unique intermediary between NDH and unharvested forest communities. We argue this is due to use of UP by both early- and late- seral specialists as well as by habitat generalists. The UP community may therefore be the result of three distinct groups of birds using the same location: 1) the establishment in the cleared strips by species otherwise associated with young forest (i.e post-fire or clearcuts), 2) the expected colonization by habitat generalists, and 3) some degree of utilization by mature forest species otherwise typically absent from NDH or clearcuts. It is this later group from which the greatest conservation implications arise.

Previous research has shown that retention forestry does facilitate some degree of use by species associated with mature forests (Atwell et al., 2008); though the amount of retention required is species-dependent and highly variable (Tittler et al., 2001). The strip cutting nature of UP harvesting means retention levels are difficult to quantify and highly variable between blocks, but will result in cutblocks with on average 20% retention of mature aspen and 70% retention of young white spruce. Out of the 9 species found in our study to be significant indicators of unharvested habitat ("mature forest species"), 7 of them were found to be stronger indicators of UP than NDH, 1 was found in equal levels in both harvest types, and 1 was found more in NDH. The relative indicator values suggest these species are more abundant in UP sites than NDH; therefore, the retention levels resulting from UP harvesting are having a positive effect on many mature forest species relative to NDH within 12-years post-harvest. Future research should focus on quantifying responses of reproductive success for these species to understory protection harvesting at the landscape scale.

Understory protection harvesting has potential to provide habitat to mature forest species that are otherwise sensitive to deforestation and timber harvesting. In contrast, many species have been shown to benefit from fragmentation and habitat alteration caused by NDH (Harrison, 2005). Twelve species were found to be significant indicators of NDH, all of which were found to be stronger indicators of UP than unharvested forests. The NMDS plot shows a relatively large area of the NDH ellipse is overlapped by the UP ellipse, suggesting most species that benefit from NDH would also benefit from UP. However, these species may be more confined to younger UP blocks as older UP blocks may introduce competition with mature forest species. In contrast, NDH may provide higher quality habitat to these species for a longer time period as convergence with mature forest communities may take up to 75 years (Schieck and Song 2006). In contrast, species that depend on coniferous trees for nesting and breeding habitat maybe be found in young UP harvest blocks that would be absent from NDH for several decades before spruce regeneration occurs.

We found evidence to suggest the protected understory white spruce is providing important habitat to some species that are not typically found in NDH. For example, the Magnolia Warbler, *Setophaga magnolia,* has been shown to select for young spruce trees during the breeding season, and is suggested as an indicator species for young spruce habitats (Ralston et al. 2015). Our study shows Magnolia Warbler is one of the strongest indicator for UP habitat, suggesting this harvesting approach can provide important breeding habitat to a species otherwise shown to respond negatively to forest harvesting (Niemi et al. 1997). Similarly, Reynolds and Knapton (1984) show that the vast majority of Chipping Sparrow, *Spizella passerina,* nest sites were located in white spruce trees, supporting the results from our indicator value analysis which showed Chipping Sparrows were a strong indicator of UP. Finally, Lapin et al. (2015) show that Connecticut Warbler, *Oporornis agilis,* abundance is positively associated with conifer density, while ABMI (2016) analyses show the species reaches its highest density in 60-120 year old deciduous stands where a white spruce understory would be expected to occur. Connecticut Warblers were another strong indicator of UP, suggesting the retained spruce are providing important habitat for this species. Ultimately, our results support the conclusion that understory protection provides important breeding habitat to conifer-dependent species.

Our ordination plots suggest that the UP community is on the trajectory to return to pre-harvest conditions more quickly than NDH. Because Al-Pac only started implementing UP harvesting in 2004, our oldest available sampling blocks were only 12 years old. The NMDS showed the oldest age class of UP blocks had an avian community very similar to the average (i.e. centroid location) community of unharvested forests (Figure 2). We found that our old UP age category showed no significant community distinctness from unharvested forests. We interpret this result to suggest that within 12 years post-harvest, the understory protection habitat is on the right trajectory to recover to pre-harvest avian community conditions. Understory protection blocks are likely showing community convergence with mature forests due to the colonization by mature forest species. For instance, we observed a male Bay-breasted Warbler, *Setophaga castanea,* defending territory, singing, and carrying nesting material in one of our 12-year old UP blocks. Bay-breasted Warblers are a species typically associated with the oldest age class of mixedwood forests (Kirk and Hobson, 2001). UP is likely able to support species associated with mature conifers sooner because of the release of understory white spruce following aspen harvesting. For instance, previous research has shown that growth rate of white spruce released from competition can increase by up to 350% (Lieffers and Grover, 2004).

The density of birds that can be supported by UP was not quantified in this study due to the sampling restraints of ARU technology. The importance of quantifying numerical effects of harvesting has been established in the literature (Hache et al. 2013). Numerical responses of these species are difficult to quantify, and typically require high effort spot mapping techniques (Bibby et al., 2000), but relative abundances can be inferred from our unlimited distance ARU point counts. The use of ARU technology in bird surveys is still a relatively new monitoring procedure, and thus far we feel our conclusions should be limited to community differences, rather than density, due to uncertainty of the sampling radius over which the point counts are being conducted. However, research has shown that ARU data allows for similar detectability as human point counts (Alquezar and Machado, 2015), and poses substantial advantages in the amount of data that can be collected (Brandes, 2008). We encourage researchers to implement ARU monitoring and continue to develop the methodologies for analyzing bioacoustics data that allow for density estimation.

We conclude that UP represent a mosaic habitat that is used by mature forest specialists, habitat generalists, and post-disturbance specialists. Forestry management policies that prioritize UP harvesting over clearcutting or NDH in mixedwood forests may facilitate local ecosystems more suitable to sustaining functionally diverse avian communities that need these conditions. Currently, UP is only implemented in areas with very high densities of understory spruce. In areas with 400-600 stems per hectare of white spruce understory, an avoidance harvesting approach is implemented that may be less tenable to the conservation of forest species, but has yet to be assessed. We recommend an assessment of the avoidance understory protection harvesting procedure to follow. Many of the boreal avian species showing the steepest declines are those associated with the oldest forest age classes, and our research suggests that expanded implementation of UP harvesting has the potential to provide habitat to those species.

Table 1. Summary table of indicator values for 54 species across the study. Indicator values given for each habitat type, NDH = Natural disturbance harvest. Relative indicator values for each species for each habitat type (out of 100%) are given. P-values < 0.1 indicated in bold.

Species	Latin Name	Relative Indicator Value			Habitat Indicator	P-value
		NDH	Unharvested	Understory Protection		
Alder Flycatcher	*Empidonax alnorum*	61.2	4.2	34.7	NDH	**1.00E-04**
American Crow	*Corvus americanus*	44	45	11	Unharvested	0.878
American Redstart	*Setophaga ruticilla*	90.5	1.9	7.5	NDH	**0.060**
American Robin	*Turdus migratorius*	54.8	16.5	28.6	NDH	**0.029**
Black-and-white Warbler	*Mniotilta varia*	75.4	3.1	21.5	NDH	**0.017**
Bay-breasted Warbler	*Setophaga castanea*	0	89.4	10.6	Unharvested	**0.002**
Black-capped Chickadee	*Poecile atricapillus*	9.7	43.1	47.1	Understory Protection	0.549
Blue-headed Vireo	*Vireo solitarius*	10.5	62.3	27.1	Unharvested	**0.071**
Blue Jay	*Cyanocitta cristata*	44.3	11.4	44.3	NDH /Understory Protection	1
Boreal Chickadee	*Poecile hudsonicus*	1.8	90.8	7.4	Unharvested	**0.043**
Brown Creeper	*Certhia americanus*	1.2	94.1	4.7	Unharvested	**1.00E-04**
Canada Warbler	*Cardellina canadensis*	7.1	29.1	63.8	Understory Protection	0.876
Clay-colored Sparrow	*Spizella pallida*	89.2	0	10.8	NDH	**1.00E-04**
Cedar Waxwing	*Bombycilla cedrorum*	54.2	24	21.8	NDH	0.193
Chipping Sparrow	*Spizella passerina*	30.5	20.3	49.3	Understory Protection	**0.011**
Cape May Warbler	*Setophaga tigrina*	23.1	71.1	5.8	Unharvested	0.402
Connecticut Warbler	*Oporornis agilis*	18.6	20	61.4	Understory Protection	**0.021**
Common Raven	*Corvus corax*	56.8	21.8	21.3	NDH	0.240
Common Yellowthroat	*Geothlypis trichas*	70.5	4.7	24.8	NDH	**1.00E-04**
Dark-eyed Junco	*Junco hyemalis*	58.8	32.9	8.3	NDH	0.415
Evening Grosbeak	*Coccothraustes vespertinus*	18.2	41.4	40.4	Unharvested	0.910
Golden-crowned Kinglet	*Regulus satrapa*	0	98.4	1.6	Unharvested	**1.00E-04**
Gray Jay	*Perisoreus canadensis*	41.3	21.2	37.5	NDH	0.487
Hermit Thrush	*Catharus guttatus*	38.5	23.8	37.7	NDH	0.444
Le Conte's Sparrow	*Ammodramus leconteii*	96.9	0.2	2.9	NDH	**1.00E-04**
Least Flycatcher	*Empidonax minimus*	63.9	21.8	14.2	NDH	0.286

Lincoln's Sparrow	*Melospiza lincolnii*	55.6	6.9	37.5	NDH	**1.00E-04**
Magnolia Warbler	*Setophaga magnolia*	19.5	8.6	72	Understory Protection	**0.003**
Mourning Warbler	*Geothlypis philadelphia*	57.3	14.9	27.8	NDH	**0.015**
Northern Waterthrush	*Parkesia noveboracensis*	64.2	7.3	28.5	NDH	0.871
Orange-crowned Warbler	*Vermivora celata*	33.1	33.9	33.1	Unharvested	1
Olive-sided Flycatcher	*Contopus cooperi*	55.4	9.1	35.5	NDH	0.801
Ovenbird	*Seiurus aurocapilla*	23.1	55.2	21.7	Unharvested	**2.00E-04**
Philadelphia Vireo	*Vireo philadelphicus*	44.6	26.7	28.7	NDH	0.757
Pine Siskin	*Spinus pinus*	22.3	35.6	42.1	Understory Protection	0.536
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	51.5	11	37.5	NDH	**0.042**
Red-breasted Nuthatch	*Sitta canadensis*	5.4	89.1	5.4	Unharvested	**1.00E-04**
Ruby-crowned Kinglet	*Regulus calendula*	39	17.4	43.6	Understory Protection	0.614
Red-eyed Vireo	*Vireo olivaceus*	51.5	19.4	29.2	NDH	**0.002**
Red-winged Blackbird	*Agelaius phoeniceus*	74.8	12.8	12.5	NDH	0.766
Song Sparrow	*Melospiza melodia*	73.6	0.9	25.4	NDH	**0.086**
Swamp Sparrow	*Melospiza georgiana*	70.6	28.3	1.1	NDH	0.159
Swainson's Thrush	*Catharus ustulatus*	27.1	34.8	38	Understory Protection	0.226
Tennessee Warbler	*Leiothlypis peregrina*	37.5	16.1	46.4	Understory Protection	**0.003**
Tree Swallow	*Tachycineta bicolor*	33.2	11.4	55.4	Understory Protection	0.807
Warbling Vireo	*Vireo gilvus*	52.3	13.4	34.3	NDH	0.616
Western Tanager	*Piranga ludoviciana*	11.5	75.6	12.9	Unharvested	**0.004**
Western Wood-Pewee	*Contopus sordidulus*	0	50.6	49.4	Unharvested	0.627
Wilson's Warbler	*Cardellina pusilla*	16.4	67.2	16.4	Unharvested	0.623
Winter Wren	*Troglodytes hiemalis*	29.5	36.9	33.6	Unharvested	0.656
White-throated Sparrow	*Zonotrichia albicollis*	36.7	26.1	37.2	Understory Protection	**0.029**
White-winged Crossbill	*Loxia leucoptera*	25	57.6	17.4	Unharvested	0.349
Yellow Warbler	*Setophaga petechia*	60.8	10	29.2	NDH	0.614
Yellow-rumped Warbler	*Setophaga coronata*	6.1	80.1	13.7	Unharvested	**1.00E-04**

Table 2. Results of the multivariate randomized block permutation procedure test (MRBP) and multivariate permutation procedure test (MRPP). Pairwise comparisons were made using Bonferonni study-wise correction, and exact p-values calculated using 2000 Monte-Carlo permutations.

Treatment 1	Treatment 2	Test	Delta	P-value	Alpha
NDH	Unharvested	MRBP	16.18	5.00E-04**	0.017
NDH	Understory Protection	MRBP	16.97	1.50E-03**	0.017
Unharvested	Understory Protection	MRBP	17.67	5.00E-04**	0.017
Young NDH	Unharvested	MRPP	19.12	5.00E-04**	0.013
Old NDH	Unharvested	MRPP	20.58	0.012*	0.013
Young UP	Unharvested	MRPP	20.15	0.012*	0.013
Old UP	Unharvested	MRPP	21.36	0.03	0.013

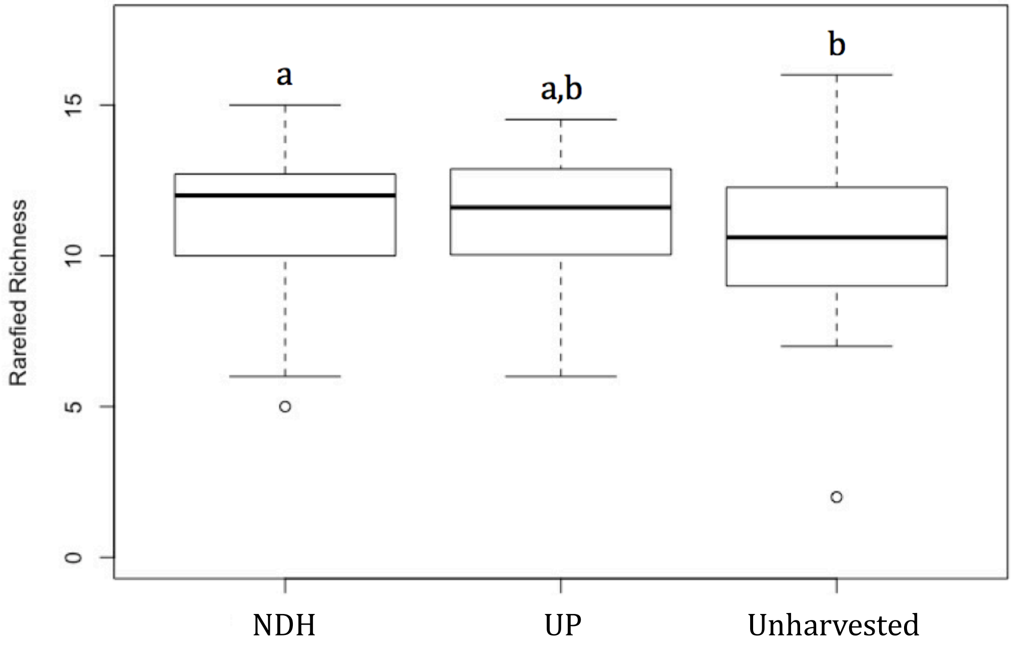

Figure 1. Box plot showing results from Tukey post hoc analysis of randomized block ANOVA with rarefied species richness values. Significant pairwise comparisons denoted with labels above boxplot.

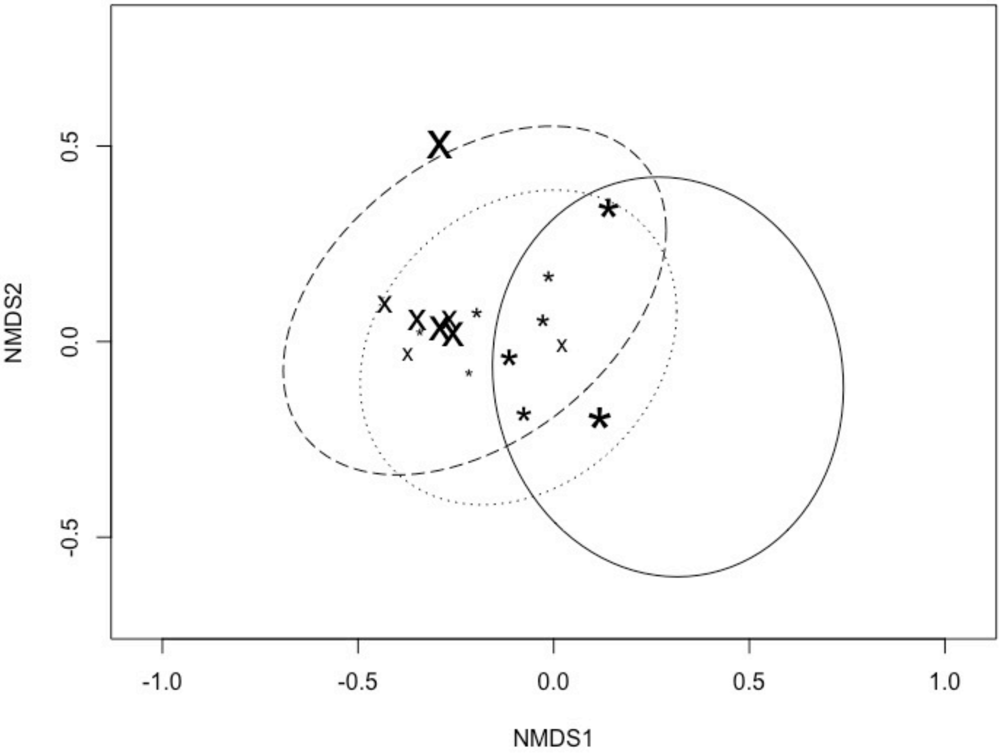

Figure 2. Non-metric multidimensional scaling (NMDS) ordination plot run on full site by species matrix data. Stress and model complexity were optimized at k=3 and n=50 iterations, distance matrix calculated using the Bray-Curtis index. Dashed line ellipse represents the centroid ellipse at 0.7 standard deviation for all NDH sites; solid line ellipse represents centroid ellipse at 0.7 standard deviation for all unharvested sites; dotted line ellipse represents centroid ellipse at 0.7 standard deviation for all understory protection sites. Stars indicate centroids for each understory protection age class (1-12 years since harvest), with larger symbols for older site classes. Crosses indicate centroids for each NDH age class (1-12 years since harvest), with larger symbols for older site classes.

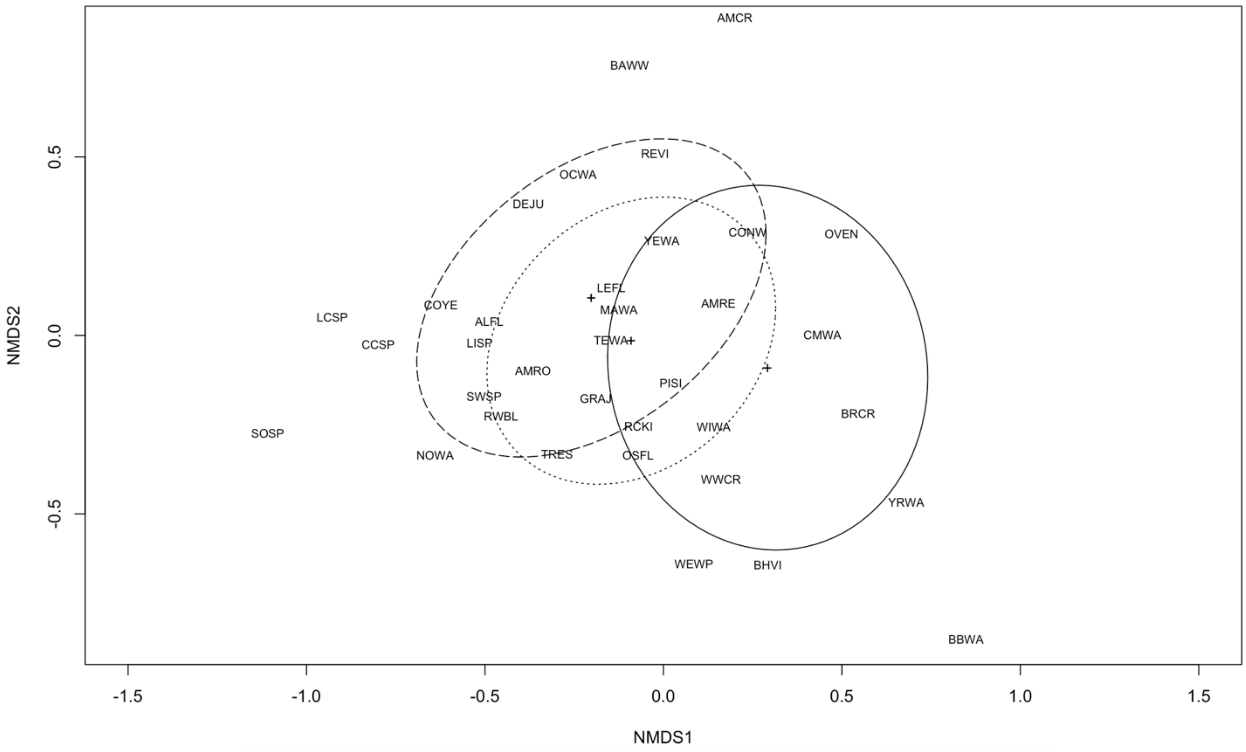

Figure 3. Non-metric multidimensional scaling (NMDS) ordination plot run on full site by species matrix data. Stress and model complexity were optimized at k=3 and n=50 iterations, distance matrix calculated using the Bray-Curtis index. Dashed ellipse represents the centroid ellipse at 0.7 standard deviation for all NDH stations; Solid ellipse represents centroid ellipse at 0.7 standard deviation for all unharvested stations; dotted ellipse represents the centroid ellipse at 0.7 standard deviation for all understory protection stations. Species four letter AOU codes indicated, with labeling priority given to most abundant species.

ACKNOWLEDGMENTS

We would like to thank E. Dzus for his ongoing intellectual contribution to the design, framework, and language of this project from start to finish. We thank J. Cameron and H. Schoenberg for their hard work in the field, along with H. Lankau and A. MacPhail for making the fieldwork possible. We would like to thank E. Knight for her assistance with analyses, N. Parayko and E. Upham-Mills for helping with conceptual framework. Funding for this project was provided by Al-Pac, the Environment Canada Habitat Stewardship Program, and the NSERC Discovery grant. Connor Charchuk was funded by the Industrial Postgraduate Scholarship from the Natural Sciences and Engineering Research Council of Canada and Al-Pac.

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Chapter 3

Title: **The use of recognizers to assess Brown Creeper response to understory protection harvesting**

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ABSTRACT

Timber harvesting has resulted in a decline in old growth representation in managed forests relative to natural forests. Designing harvesting strategies that maintain a degree of "old-growthness" on the landscape are becoming increasingly popular. In Alberta, understory protection is a form of retention harvesting that has yet to be assessed for its contribution of habitat to old growth species. To assess the old-growth quality of understory protection, we assessed an indicator species of old growth forests, the Brown Creeper (*Certhia americana)*. Brown Creepers are small songbirds that vocalize a highly detectable and unique song during the breeding season.

Using autonomous recording units (ARUs) with automatic computer recognizers, we surveyed for Brown Creepers in 25 understory protection sites and 39 unharvested control sites. By using recognizers to analyze over 1000-minutes of data for each site, we compared occupancy rates and habitat use patterns assuming perfect detection. We show that Brown Creepers occupied about 16% of understory protection sites, roughly a quarter of the occupancy rate found in the unharvested controls. Brown Creepers are more likely to occupy unharvested sites when the forest canopy was taller, but were more likely to occupy understory protection sites when the canopy was shorter. By modelling habitat use patterns with more resolute data, we show that this effect is confounded by the proportion of the area that is white spruce (*Picea glauca)*. Brown Creepers were more likely to use understory protection when there was more white spruce and when this spruce reached heights of 10-20 meters. We conclude that understory protection is unique as a harvesting practice in that it is capable of supporting low densities of Brown Creepers very soon after harvest. Understory protection may represent a unique harvesting approach that is capable of contributing a significant amount of habitat to old growth species.

Due to declines in species associated with old growth forests, we encourage the implementation of understory protection harvesting over traditional approaches when possible.

INTRODUCTION

Quantifying species-habitat associations across habitat strata is often used to assess human land-use impacts on various organisms. Timber harvesting represents one of the predominant human land-use effects on habitat for many forest songbird species (Venier et al. 2014), and is increasing in many parts of North America (Masek et al. 2011). In response, forest management faces pressure to manage lands in a way that balances timber production with conservation objectives (Boutin et al. 2009). Indicator species are often recommended in forest management as a tool for understanding the effects of harvest on ecosystem diversity (Lindenmayer et al. 2000). The selection of an indicator species, or suite of species, requires an *a priori* understanding of that species' habitat needs and expected response (Noss 1990). Furthermore, the objective of a forest management plan must be considered when selecting an indicator (Failing and Gregory 2003). One objective of forest management that is increasing in priority is maintaining "old-growthness" in post-harvest stands (Bauhus et al. 2009).

One species of songbird that has consistently emerged in the North American literature as a candidate indicator species for old growth coniferous forest is the Brown Creeper *Certhia americana* (hereafter BRCR). The BRCR is a small passerine characteristic of mature mixed-conifer forests throughout North America (Adams and Morrison 1993). BRCR rely on the flaking bark of mature conifers for foraging and nesting habitat, and have been used previously as an indicator species for forest management (Wintle et al. 2005). Many studies have independently concluded that BRCR rely on the oldest age class of forests for nesting habitat (Hansen et al. 1995, Hejl et al. 2002), are highly sensitive to forest harvesting (Mahon et al. 2008, Poulin et al. 2008, Geleynse et al. 2016), and do not respond as positively to tree retention during harvesting as most other species (Lance and Phinney 2001, Le Blanc et al. 2010). Furthermore, a meta-analysis has concluded the BRCR is the species most sensitive to forest harvesting in North American boreal forests (Vanderwel et al. 2007). BRCR is listed as a sensitive species in Alberta (ASRD 2005), and the negative impacts of forestry may be causing a decline in their population (ASRD 2003).

Alberta-Pacific Forest Industries Inc. (Al-Pac) manages over 6 million hectares of land in Alberta's boreal forest, and has been implementing a method of harvesting known as understory protection annually since 2004. Understory protection harvesting (hereafter UP) seeks to protect understory white spruce, *Picea glauca,* during hardwood harvest in mixedwood forests (Grover et al. 2014). The UP harvesting strategy results in about 20% of the overstory being retained, and about 70% of the understory white spruce being retained. Following UP harvesting, white spruce is released from competition with overstory hardwoods and may experience expedited growth rates (Lieffers and Grover 2004). However, there is little known about the use of UP harvested areas by old growth species, such as the BRCR, in Alberta.

We sought to test the response of BRCR to white spruce regeneration in understory protection using a chronosequence of harvest areas. Measuring population responses directly requires considerable sampling effort, thus presence-absence data is often used as a proxy measure (Gu and Swihart 2004). Any model that relates the probability of occurrence of a species to some habitat parameters can be defined as an occupancy model (MacKenzie 2006). Traditional occupancy models may be limited in that they rely on presence/absence data to infer species-habitat associations. Ashcroft et al. (2017) argued that the use of presence/absence data in predicting species distributions is statistically limited relative to continuous metrics of abundance. Furthermore, some occupied locations represent higher quality habitat, or more heavily used habitat, than other occupied locations on the landscape (Lele et al. 2013). Occupancy models lack the resolution to tease these apart, though relative abundance metrics can be used in place of occupancy (Royle 2004), or detectability can be used to inform relative abundance (Royle & Nichols 2003). However, for relatively low-density species, whereby most observations of abundance are expected to be a 0 or a 1, it may be useful to utilize other metrics of relative use to better differentiate habitat associations. Furthermore, the link between species occurrence and habitat suffers from a potential confound when detectability rates are unequal across habitats (Gu and Swihart 2004).

Issues surrounding imperfect detection in bird surveys have been acknowledged since the 1970's (Burnham and Overton 1979), but approaches to overcoming this issue weren't popularized until decades later (Boulinier et al. 1998). The potential for an individual bird being present at a survey location, but going undetected at any given sample visit is governed by two processes: 1) the individual was available for detection but the observer failed to detect the cue; or 2) the individual did not produce a detectable cue during the survey (Nichols et al. 2009). The application of detection-corrected occupancy models (hereafter DCOMs) have since become increasingly popular in the ecological literature (Banks-Leite et al. 2014). However, Banks-Leite et al. (2014) argue that *a priori* sampling design decisions may be more appropriate than *a posteriori* modelling corrections to overcome imperfect detection. However, there is no study to date that has sought to collect sufficient data to model data under the assumption of perfect detection.

Perhaps the most feasible opportunity to increase sampling effort to the extent that is necessary to assume perfect detection comes from autonomous recording units (ARUs). ARUs are devices that can autonomously record bioacoustics data on a predetermined recording schedule and store sound file data (typically large quantities) on memory cards (Shonfield and Bayne 2017). ARUs are frequently used to remotely survey and monitor acoustically detectable species such as songbirds (Brandes 2008). However, processing of ARU data is usually done by ear by a trained human observer to identify species vocalizing in each recording (e.g. Furnas and Callas 2015). As a result, surveying sample effort has thus far only been improved marginally through the use of ARUs (Blumstein et al. 2011). However, advances in computational technology to automatically detect species may overcome this limitation.

The potential to utilize computational processing to transcribe bioacoustics data obtained from ARUs may provide an opportunity to substantially increase survey sample effort. Recent advances in automatic species identification using computer algorithms (hereafter recognizers) may provide researchers with the ability to amass orders of magnitude more data than was previously possible (Bardeli et al. 2010). Few studies have utilized recognizers to assess occupancy rates, possibly because the technology is still relatively new. Campos-Cerqueira and Aide (2016) used recognizers to detect Elfin Wood Warblers (*Setophaga angelae*) in Puerto Rico, though imperfect detection was still assumed to reduce manual validation time. The BRCR may be an ideal candidate for the application of recognizers due to its high-frequency song that is seldom masked by vocalizations of other songbirds and is unique from the song of other species.

We attempt to use the data derived from a recognizer to assess the effects of understory protection harvesting on BRCR. We attempted to overcome two shortcomings with traditional occupancy models: imperfect detection and differential site use associated with varying habitat quality. We modeled BRCR occupancy rates in the UP and adjacent old growth forest assuming perfect detection with the recognizer data. Furthermore, we utilize the number of recognizer detections of BRCR at each site to inform complex species-habitat associations. By weighting site occupancy by the number of times a species was detected at that location we assume that more heavily defended sites are associated with higher quality habitat. We used LiDAR (light detection and ranging)-derived estimates of forest structure to model specific habitat requirements for BRCR to explain differences in occupancy rates between the old growth forest and the UP.

METHODS

The study was conducted on lands managed by Alberta Pacific Forest Industries Inc. (hereafter Al-Pac) in the boreal forest of Alberta, Canada. For a detailed description of the surveying methods see Chapter 2. The project herein relies solely on data collected in 2016. We surveyed 39 understory protection harvest blocks using a single SM2 or SM3 song meter (ARU) at each site. Only 25 understory protection sites (UP) that had available LiDAR data were included in analyses. We included 39 unharvested forest control (FC) sites in this analysis. FC sites were selected using the Alberta Vegetation Inventory (AVI) layer, and were chosen based on the oldest forest class available within 1km of an understory protection harvest block. The average age of FC sites was 115 years with a range of 76-196 years since last disturbance. Bird surveys were conducted from May 25 – July 4 when BRCR are most vocally active during the breeding season. Survey locations were based on no prior knowledge of BRCR locations.

Environmental covariates were extracted for each ARU using a buffer size of 50m: the distance at which we estimate BRCR can be reliably detected given their quiet high-frequency song (~4200-7100Hz). Covariate buffer size is thus based on acoustic detectability rather than territory size, which has been estimated at 5-10 hectares (Poulin et al. 2008). LiDAR variables were averaged across the buffer for each covariate using zonal statistics in ArcMap. We extracted LiDAR data for the canopy height (P95), the average proportion of returns between

1.37-5m (S137to5), the average proportion of returns between 5-10m (S5to10), the average proportion of returns between 10-20m (S10to20), and the average proportion of returns between 20-30m (S20to30). A description of LiDAR variables, how they are derived and how they should be interpreted is provided in Table 3. We tested the effects of forest age for both the UP and FC sites and allowed this term to interact with our harvest treatment effect because age effects are expected to be different for the UP blocks than for the FC stands. Deployment date was also tested to account for seasonal variation in BRCR singing behaviour, though all recording units were deployed during the breeding season thus this effect was not expected to be significant. The percentage of spruce within a given buffer was extrapolated from the Alberta Vegetation Inventory layer and this term was allowed to interact with harvest treatment effect.

Automatic Recognition

We developed a recognizer for the BRCR primary song using the SongScope software developed by Wildlife Acoustics (Figure 4). SongScope uses hidden Markov models to match signal patterns in observed spectrograms against training data, a form of model-based classification (Blumstein et al. 2011). We built our recognizer using 92 individual BRCR song examples recorded throughout northern Alberta using SM2+ song meters. Cross-training was used to assess how well each individual annotation in the training data matched the final recognizer algorithm. Cross-training yielded an average score of 67.4 +/- 1.63%; therefore, the average true BRCR song can be expected to yield a score of 67.4%. We set our score threshold when running the recognizer at 50% to ensure poorly matching spectrograms were also returned. The trade-off therein is a greater effort in validating candidate detections returned by the recognizer (flags), as there is expected to be a high false positive rate. We felt for the purpose of this study it was more important to minimize false negative rates, by trading off an inflation of false positives and subsequently increasing the human effort required to validate all flags.

All acoustic data collected at each site was processed with the recognizer. The ARUs recorded continuously from 4:30am-10:00am to maximize data collection at dawn when BRCR are most active, and periodically throughout the day for full daily coverage. In total, each ARU day equaled 361 minutes of acoustic data, and each site had 3 or 4 ARU days of data; therefore, the recognizer processed approximately 1083 or 1444 minutes of data at each site. An experienced technician validated all flags returned by the recognizer by listening to each clip or visually confirming the spectrogram to confirm true positives (hits). The BRCR song is visually distinct, so listening to a flag was seldom necessary.

Modelling

First, we developed a BRCR occupancy model from the recognizer data assuming perfect detection. It is important to note here that we do not use the term "occupancy model" in its current usage to imply an adjustment of imperfect detection, but rather in its classical definition of any model that relates the presence/absence of a species to habitat parameters. We fit a logistic regression model using the cloglog link, where sites that the recognizer detected a BRCR at least once were assigned a '1' and sites where BRCR was never detected were assigned a '0'. The cloglog link was applied because we assume our data is derived from a censored Poisson distribution: we know only if BRCR are present or absent, but in reality the distribution is a count from $[0, \infty)$. We used forward AIC step selection to derive the final model by including further covariates that improved model fit by ≥ 2 ΔAIC. Model coefficients were interpreted in the context of the probability of that site being occupied by *at least one* BRCR.

Next we developed a model to estimate the degree of use of a site to try and establish more refined predictions of habitat associations. Using the recognizer data, we fit a logistic regression model treating each hit at a site as an individual data point. For instance, a site with 1 recognizer detection of BRCR had one replicate of associated habitat parameters in the models. A site with 100 recognizer detections had 100 replicates of associated habitat parameters. Again, we fit a logistic regression using the cloglog link to test the effects of habitat covariates on the probability of a BRCR using a given site. By replicating each hit within a site, we increase the influence of habitat parameters at sites with more detections of BRCR. However, each site is our level of replication, so while increasing the number of hits at a site results in pseudo-replication at the hit level, we maintain appropriate replication at the level of the site. We interpret λ in this model as: the predicted degree of use of site *i*, rather than probability of occupancy. Thus, values of 1 represent the highest degree of use, values close to 0 represent a low degree of use, and absolute 0 represents unoccupied sites. We used forward AIC step selection to derive the final model; additional parameters were added to the model if it improved the model fit by ≥2 ΔAIC. Through *a priori* sampling design decisions, we assume that study-level detection covariates were not confounded in this study, though habitat (UP vs. FC) may confound detectability.

We compared predictions of probability of occupancy derived from the occupancy model against predicted degree of use. The purpose of this comparison is to test the hypothesis put forth by Ashcroft et al. (2017) that occupancy models lack the resolution to derive accurate estimates of species-habitat associations because they are based on presence/absence data, whereas a continuous metric of degree of use will be better at providing accurate estimates. We re-parameterized the habitat variables in these models because with more resolute data from a degree of use model we assume subtler habitat associations will become prevalent.

RESULTS

Listening vs. Automated Recognition Detection

Human listening was conducted across 3 or 4 days at each site, for 3-minutes per visit and a total of 12-minutes total listening time. Human listeners detected BRCR at 14/39 control sites and 0/25 understory protection sites. Automatic computer recognition detected BRCR at 28/39 control sites, and 4/25 understory protection sites. Therefore, our true occupancy rates based on the recognizer data are 0.718 in forest control sites and 0.160 in understory protection sites, and based on the listening data are 0.359 in forest control sites and 0.00 in understory protection sites. On days where human listening was conducted, there were no instances where human listening detected BRCR but the computer recognizer did not; in contrast, out of 81 independent days with detections of BRCR, 58 (72%) were detected exclusively by automatic recognition. This is not due to humans failing to detect a BRCR when it was present, but a result of the BRCR vocalizing outside the 3-minute clip listened to. We did not quantify false negative rates with the recognizer, but argue that if BRCR were present the recognizer sufficiently detected them.

Recognizer Occupancy Model

Forward AIC step selection resulted in the following final model for the recognizer occupancy model (Table 4):

$$Occupancy \sim Treatment + P95 + Treatment*P95$$

The average predicted occupancy rate for BRCR was 0.717 +/- 0.332 in unharvested controls and 0.155 +/- 0.698 in understory protection blocks. The model predicted that BRCR would reach their maximum abundance in the unharvested controls at the highest canopy height, but in the understory protection at the lowest canopy height (Figure 5). The interaction between canopy height and treatment was positive and significant (β=0.499, p=0.003). BRCR occupancy was predicted to approach 1 at a canopy height of 30m in the unharvested forests. This asymptote at 100% occupancy suggests we achieved perfect detection in our study using recognizers, because otherwise even in ideal habitat, predicted occupancy should be less than 1 due to detection error.

Recognizer Use Model

Forward AIC step selection resulted in the following final model for the recognizer use model (Table 4):

*Hit ~ Treatment + Canopy Height + Midstory Density + %Spruce + Understory Density + Treatment*Midstory Density + Treatment*%Spruce*

Canopy height was the strongest predictor of BRCR habitat use (Figure 6). BRCR were significantly more likely to use stands with taller canopies ($\beta=0.681$, $p=5.77\text{x}10^{-16}$). The slope of this effect can be interpreted as, for every 1-meter increase in canopy height, there was a 68% increase in the degree of use of that area. The next strongest effect was the interaction between the harvest treatment and midstory density. An increasing proportion of vegetation in the 10-20m strata results in higher BRCR use, though the effect was slightly different in the understory protection than in the unharvested controls ($\beta=1.00$, $p=0.155$). This effect was difficult to interpret when holding all other covariates constant, so we plotted the effect at P95=20m and %Spruce=10% (Figure 7), 20% (Figure 8), and 30% (Figure 9). The plots show that the effect of midstory density is highly dependent on the proportion of spruce in the understory protection, but not for the unharvested controls. These graphs can be interpreted to suggest that when the midstory is comprised of at least 30% spruce, it facilitates high degree of use by BRCR at any density, but at lower representation of spruce (i.e. 10-20%) BRCR rely on a higher midstory density to colonize the understory protection.

The proportion of spruce significantly interacted with the harvest treatment (β=0.679, $p=2x10^{-16}$), though the effect was positive in both habitat types. We plotted the effect at P95=15m to best visualize the interaction, which showed a weak linear relationship in the unharvested controls and a strong sigmoidal relationship in the understory protection (Figure 11). This result suggests there is a critical threshold of %Spruce required in the understory protection to facilitate use by BRCR. The final predictor of BRCR habitat use was understory density, which had a negative effect on BRCR use (B=0.043, p=0.0027). Increasing understory density had a similar linear negative effect on the degree of use of an area by BRCR in both the understory protection and unharvested controls (Figure 10).

DISCUSSION

Model comparison

Our recognizer habitat use model had more statistical power than the occupancy model to estimate the habitat requirements of the BRCR. The occupancy model using the recognizer data was only able to estimate the effect of an interaction between canopy height and treatment on the probability of site occupancy by BRCR. In contrast, the habitat use model was able to establish two main effects and two interactive effects on BRCR habitat preferences. The negative effect of understory density and the interactive effects of harvest treatment with %Spruce and harvest treatment with midstory density were found only using the habitat use model. Therefore, these findings support the hypothesis that presence/absence is more limited in its ability to establish habitat associations relative to other metrics (Ashcroft et al. 2017). In addition to the site occupancy model being limited in its ability to estimate BRCR habitat associations, the interactive effect in the model was in fact spurious due to a confounding effect.

Our occupancy model suggested BRCR occupancy should decline with increasing canopy height in the UP. Literature has established that taller canopies are associated with higher occupancy rates in BRCR (Vogeler et al. 2013), which was consistent with the effect found in our control sites. However, a decline in occupancy of understory protection sites with increasing canopy height could be a confounding effect of aspen dominating these canopies. The highest canopy of understory protection sites is dominated by the mature aspen (*Populus tremuloides*) that is retained in the wind-buffer strips (Navratil et al. 1994, Grover et al. 2014). BRCR respond negatively to increasing densities of mature deciduous trees (Banks et al. 1999), which may explain the declining use of understory protection areas with taller canopies. BRCR are dependent on mature conifers for foraging and breeding sites (Adams and Morrison 1993), and specifically white spruce in western Canada (ASRD 2003). The canopy in mature forests in this region are dominated by conifers, thus it is unsurprising that BRCR habitat use increased with increasing canopy height in our control sites. Therefore, the height of canopy may not be a good predictor for BRCR occupancy due to the confounding effect of the type of forest found in the canopy.

Effect of Understory Protection on BRCR

Unsurprisingly, BRCR were more likely to occupy unharvested forests than understory protection areas. The naïve occupancy rate in the understory protection (16.0%) was approximately a quarter of that experienced in the unharvested forests (71.8%). Other studies have found that BRCR avoid harvested areas entirely (e.g. Tobalske et al. 1991, Hansen et al. 1995, Steventon et al. 1998, Costello et al. 2000, Mahon et al. 2008), thus an occupancy rate of 0.16 in the UP could be considered a success. Understory protection harvesting is likely less detrimental to BRCR populations than traditional harvesting. However, BRCR occupancy rates in our unharvested controls were surprisingly high, so it is plausible that traditionally harvested areas in this region may also support some BRCR. Quantifying the BRCR occupancy rates in traditional harvest blocks within this region would better substantiate the claim that UP is better than traditional harvesting for BRCR. From human listening, no BRCR were detected in the traditional harvest blocks, but future research should use the recognizer to survey these harvest areas intensively.

BRCR also showed an overall higher use of unharvested controls ($\hat{x}$= 0. 867) than understory protection habitat ($\hat{x}$= 0.203). We interpret this result to suggest BRCR may incorporate part of the UP harvest area into their territory but are unlikely to use it exclusively. The territory of a breeding BRCR is approximately 5-10ha, and thus it is likely incorporating only part of the understory protection in the territory. Mature trees with flaking bark are required for nesting, which would not be present in the understory protection, so it is likely that BRCR are nesting in the adjacent unharvested forest. Poulin and Villard (2011) showed that BRCR experience a reduction in nest success when nests were located closer to the forest edge. BRCR in our study may be avoiding the understory protection due to edge effects resulting in reduced nesting success. Thus, future research should investigate the reproductive effects of UP harvesting on BRCR in a managed forest landscape. In contrast, the finding that BRCR are using the understory protection at all may be an indication that this harvesting strategy has less of an edge effect than other harvesting strategies, a challenge that forest management has been facing for decades (Baker et al. 2013). Quantification of the edge effect of understory protection harvest areas may help identify features and structural elements that can be improved upon in the harvesting strategy to further facilitate the colonization of these areas by forest species by reducing edge effects.

Brown creeper habitat use

Canopy height was the strongest predictor of BRCR habitat use. Tree height is an effective proxy measure for stand age, and therefore this effect is likely the result of BRCR nesting requirements for mature trees. BRCR rely on the flaking bark of old trees to build nests (Poulin et al. 2008), and therefore the positive response to canopy height is an indirect measure of nest site availability (Vogeler et al. 2013). In understory protection blocks, old trees only exist in the 3-meter wide retention strips, of which the majority are likely aspen (Grover et al. 2014). More targeted planning of retaining strips with the most mature conifers should lead to even higher rates of site occupancy and habitat use by BRCR in understory protection areas. Forest management policy should incorporate these findings into future management plans to better protect mature conifers for nesting songbirds.

The next strongest predictor of BRCR habitat use was the density of midstory vegetation. Our model predicted BRCR habitat use increases with increasing density of trees between 10-20m, though the response was inconsistent between FC and UP stands. This result is consistent with the findings of Vogeler et al. (2013) who found that the average canopy height associated with occupied BRCR sites was 12.17m +/- 1.12m. However, the density of trees in the 10-20m strata showed little effect on BRCR habitat use in unharvested forests, likely because canopy height is the stronger driver in these sites. In contrast, the density of 10-20m tall trees resulted in a strong increase in BRCR use of understory protection sites, especially when %Spruce was relatively low. We interpret this as the response of BRCR to the rapidly regenerating spruce understory. Studies have shown that the understory white spruce, when freed from competition in understory protection patches, can increase in growth rate by up to 350% (Lieffers and Grover 2004). Grover et al. (2014) measured the average height of protected white spruce trees to be

10m in understory protection sites at the time of harvest; therefore, even a conservative estimate of growth rates would suggest that these trees are reaching sizes capable of supporting BRCR within just a few years post-harvest. Furthermore, much of our LiDAR data was collected 8-10 years before surveying; thus, trees measured by the LiDAR in the 10-20m range were likely taller at the time of surveying. Ultimately, these results show that the white spruce protected in understory protection harvesting is capable of supporting low densities of BRCR almost immediately post-harvest.

The amount of spruce in a stand had a stronger positive effect on habitat use in the understory protection than in the unharvested controls. This may be due to the use of non-spruce mature trees by BRCR in the unharvested sites. Geleynse et al. (2016) showed that BRCR in eastern Canada will switch from yellow birch to balsam firs for nesting sites in logged areas, suggesting the species has some plasticity in nesting requirements. Therefore, BRCR may be less dependent on white spruce in the unharvested controls where other species of mature trees are available for nesting. However, understory protection harvesting takes place almost exclusively in trembling aspen-white spruce mixedwoods (Grover et al. 2014), and therefore the white spruce is more essential for nesting habitat. By design, understory protection occurs in locations with high density (>600 stems/ha) of white spruce; therefore, this harvesting strategy incidentally creates habitat for BRCR. Further implementation of white spruce protection harvesting strategies should benefit this species in managed landscapes.

BRCR habitat use was also negatively associated with the proportion of LiDAR returns between 1.37m and 5m. This height range represents the majority of shrubs and undergrowth vegetation, suggesting BRCR prefer habitat with a less developed understory in mature stands. Our results contradict previous research that suggested BRCR are positively associated with shrub density (Schieck and Nietfeld 1995); however, their study used a canonical correspondence analysis and thus this could be a spurious effect of other environment-species drivers. BRCR in my study appear to prefer habitat with taller canopies and less developed understories. The correlation between these covariates was weakly negative (r^2=-0.256), and thus we conclude the understory effect is not confounded.

Automatic Computer Recognition

Increasingly, autonomous recording units are being used to conduct bird surveys across North America (Shonfield and Bayne 2017); however, methods of dealing with the wealth of data that are collected by these units are lagging behind. Automatic computer recognition software showed great promise in this study at using pattern-matching algorithms to detect and identify bird songs. Here we develop for the first time a straightforward modelling procedure to handle recognizer data to estimate both occupancy and habitat use more accurately than existing methods. In an occupancy framework, we are assuming that any biases relating to the effect of habitat on detectability will be overcome by the recognizer processing power. If one habitat type is limited by lower detectability, the target species will still be detected eventually because of the amount of data being processed. Future research should test the amount of data that is required to be processed to safely assume perfect detection.

The number of singing events detected was used to weight habitat covariates associated with occupied sites to model the degree of habitat use by BRCR. Sites with more detections are inferred to be more closely overlapping with a bird's territory, whereas occupied sites with fewer detections are inferred to have little overlap with a bird's territory (Figure 9). To make this inference we must also make the assumption that the detection process is the same between sites (i.e. the species is equally detectable by the recognizer across habitat types). We argue that the relationship between use and number of hits is likely strong enough to overcome biases in the detection process. However, we recommend directly testing this assumption using field methods to quantify differential detectability to improve habitat predictions.

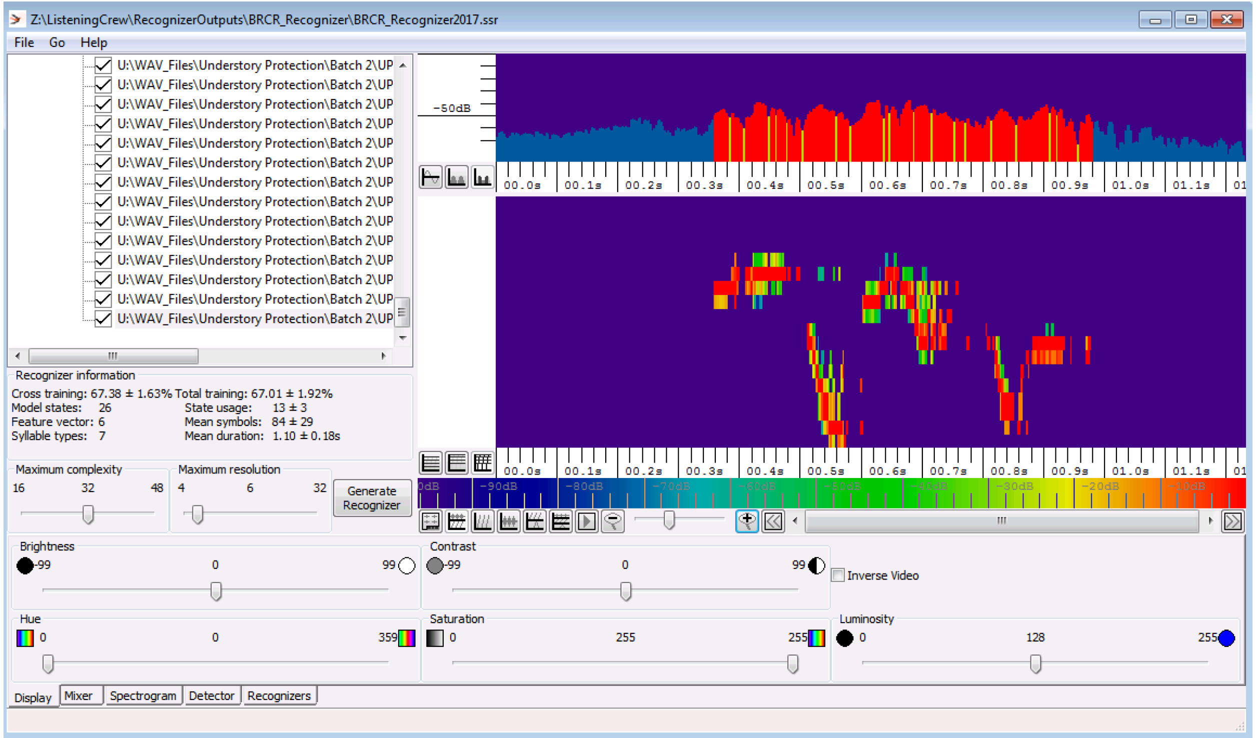
Recognizer data can be readily condensed into a format that is amenable to occupancy modelling (Campos-Cerqueira and Aide 2016), though we recommend against traditional modelling approaches that assume imperfect detection. DCOMs require a discretized detection history of detections and non-detections, but automatic recognition provides a pseudo-continuous representation of presence-only data. Therefore, periods of non-detection are likely the result of the species moving out of the detection radius of the sampling unit, or not producing detectable signals (i.e. is not singing, and therefore not actively defending territory), rather than the result of the species being present and vocalizing but the recognizer failing to detect it. Thus, we feel it is more sensible to assume perfect detection with these data than it is to *ad hoc* discretize recognizer detections into a detection history whereby 0s likely represent movement out of the survey area or non-territoriality rather than false non-detections.

The use of automatic recognizers in ecological monitoring represents a promising technological advance. While the human effort required to validate and verify recognizer results is still relatively high, we feel it is well worth the benefits reaped by increasing sample size to the point where detectability becomes a non-issue. Concerns over detectability have been prominent in the ecological literature for over a decade, with most approaches to solving the issue involving *a posteriori* modelling corrections. However, it should not be overlooked that technological advances may supersede the need to correct for detectability in some cases. We encourage a less strict view on the use of models to correct for imperfect detection when sample size can be made sufficiently large. Furthermore, the field of songbird research using ARUs may represent the most opportunistic for implementing this approach, though we feel it is not the only one. For example, advances in automatic detection of photographs from camera trap data (Villa et al. 2017) may make those data tenable to the modelling approach presented herein as well.

CONCLUSION

The BRCR is one of North America's forest species most sensitive to forest harvesting, and increasing forest management may be a risk factor for its future decline. Careful monitoring of this species using ARUs and automatic recognition will allow forest managers to make more informed decisions on policy and planning. Understory protection represents a method of harvesting that incidentally provides habitat to the BRCR. Utilizing LiDAR data represents another technological advance that we show to be effective at modelling both predicted occupancy and degree-of-use by BRCR. We show that BRCR require white spruce a minimum of 10-meters tall, but will be more likely to occupy and use a site as the canopy grows. Furthermore, we show that BRCR will use understory protection areas, likely as a result of the expedited growth of white spruce following release from competition with mature aspen post-harvest. Further monitoring of BRCR reproductive success may better quantify forestry effects on the species, though a passive acoustic monitoring approach should provide reliable knowledge on the effects of forestry. The BRCR can be used as an indicator species for a community assemblage that relies on the oldest age class of forest, which suggests understory protection may also provide habitat to other at-risk forest species.

Figures and Tables



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Recognizer information

Cross training: 67.38 ± 1.63% Total training: 67.01 ± 1.92%
Model states: 26
State usage: 13 ± 3
Feature vector: 6
Mean symbols: 84 ± 29
Syllable types: 7
Mean duration: 1.10 ± 0.18s

Maximum complexity: 16 32 48
Maximum resolution: 4 6 32

Brightness: -99 0 99
Contrast: -99 0 99
☐ Inverse Video
Hue: 0 0 359
Saturation: 0 255 255
Luminosity: 0 128 255

Figure 4. Song scope recognizer build interface. The image represents the BRCR spectrogram, where highlighted areas are signals detected by the recognizer.

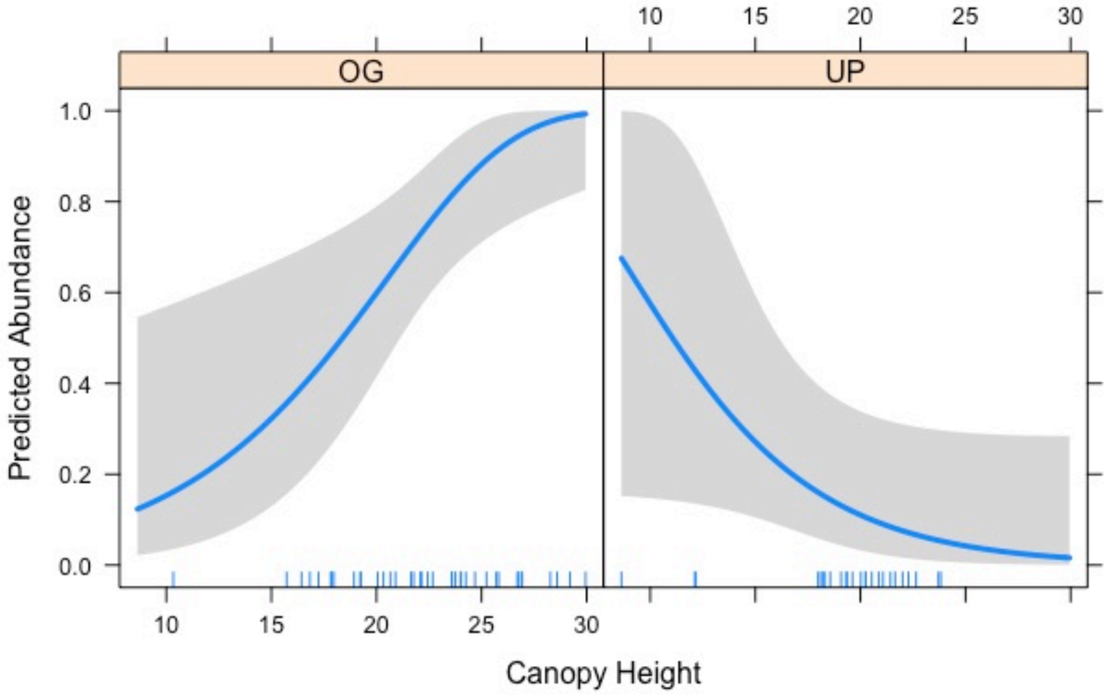

Figure 5. The predicted occupancy of BRCR in old growth habitat (left panel) and understory protection habitat (right panel) in response to the average stand canopy height (m).

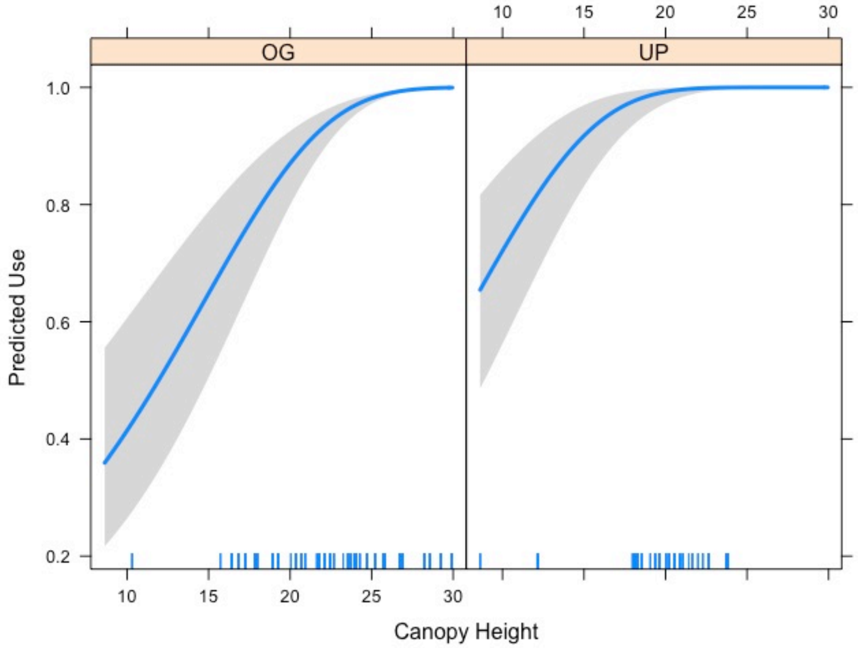

Figure 6. Predicted habitat use by BRCR in response to canopy height in old growth forest (left panel) and understory protection (right panel). All other covariates in the model held at median value.

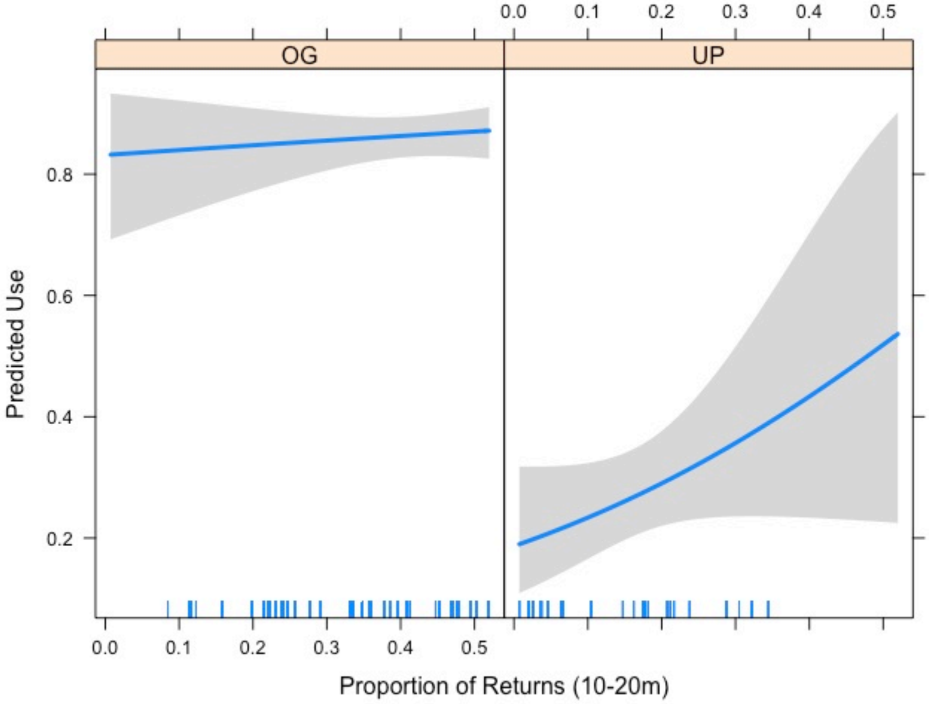

Figure 7. Predicted habitat use by BRCR in response to midstory density when the proportion of spruce in the plot is 10%. Left panel for old growth treatment and right panel for understory protection treatment.

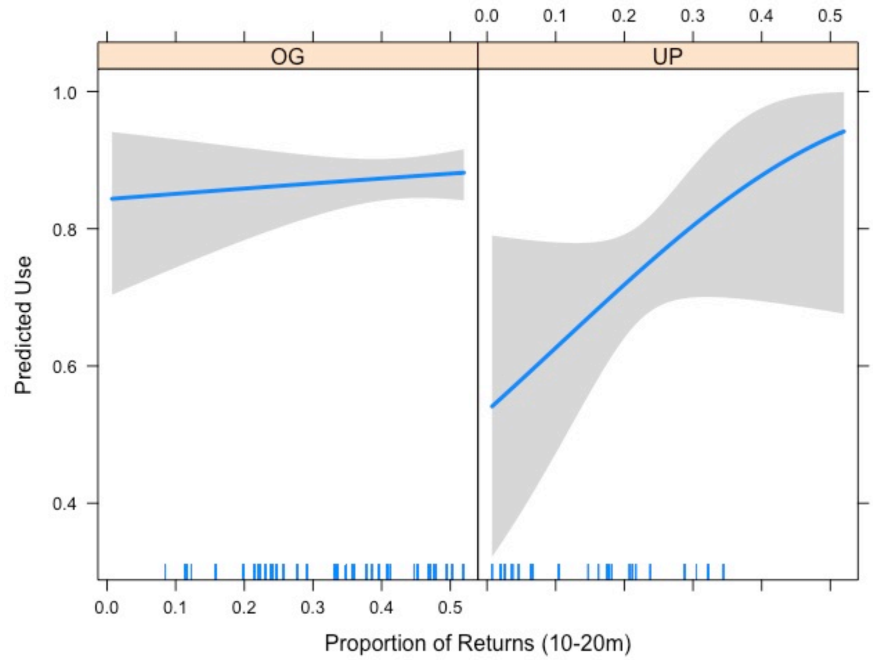

Figure 8. Predicted habitat use by BRCR in response to midstory density when the proportion of spruce in the plot is 20%. Left panel for old growth treatment and right panel for understory protection treatment.

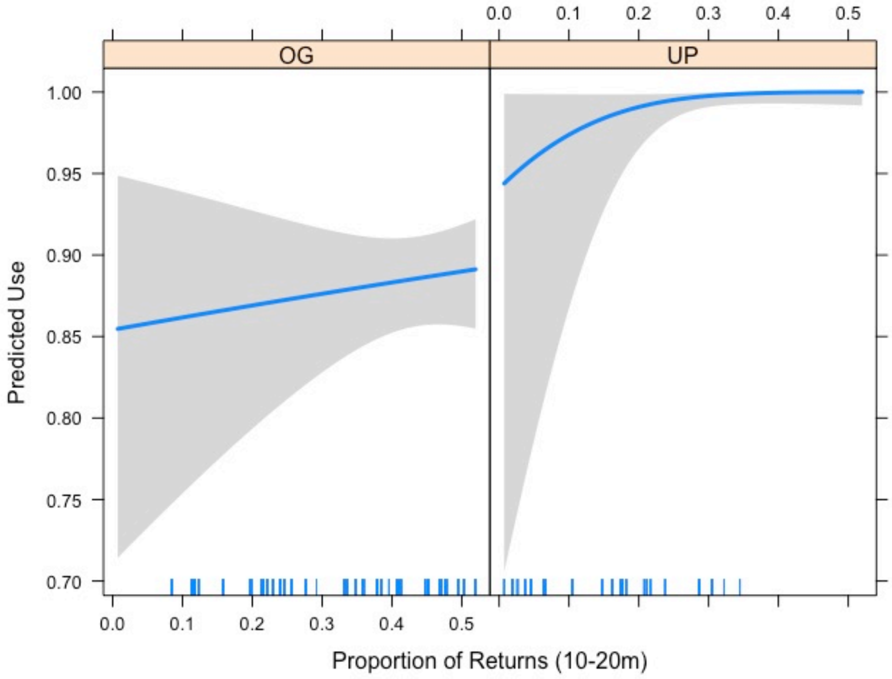

Figure 9. Predicted habitat use by BRCR in response to midstory density when the proportion of spruce in the plot is 30%. Left panel for old growth treatment and right panel for understory protection treatment.

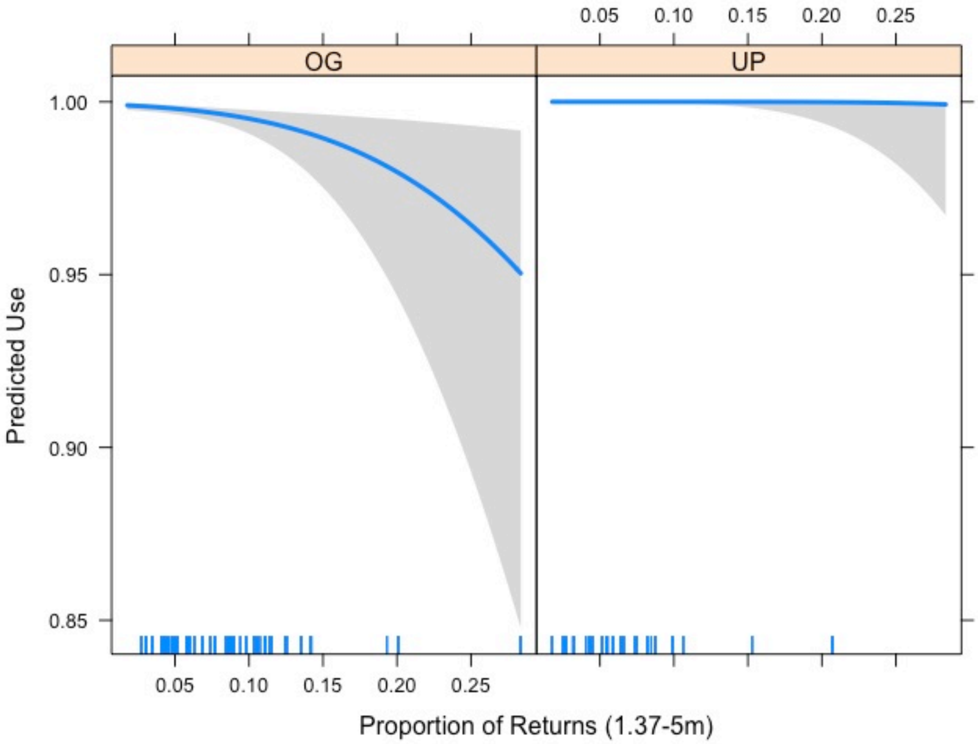

Figure 10. Predicted habitat use by BRCR in response to understory vegetation in old growth forest (left panel) and understory protection (right panel). All other covariate values held at median value.

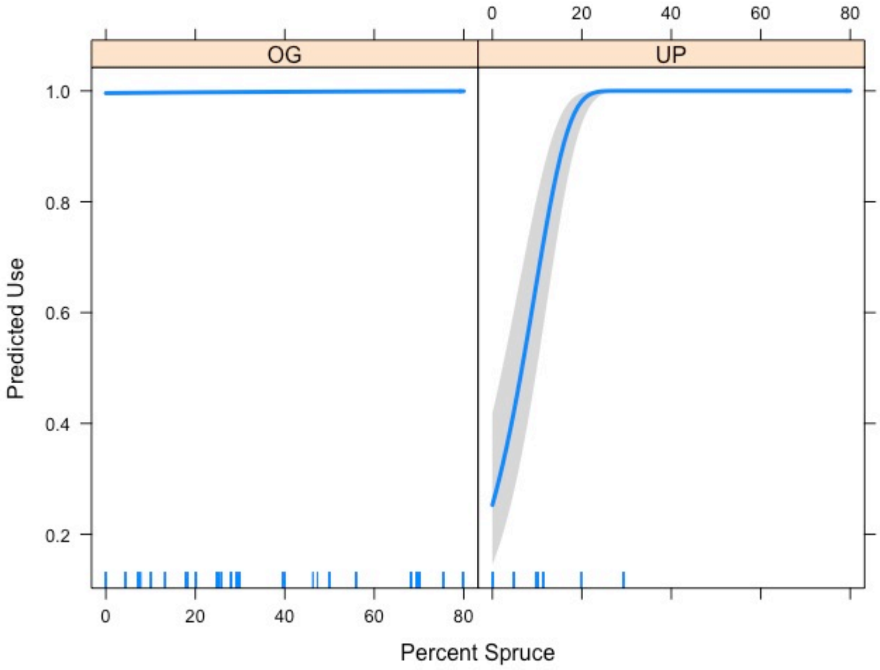

Figure 11. Predicted habitat use by BRCR in response to percent spruce in old growth forest (left panel) and understory protection (right panel). This plot shows that BRCR habitat use in the old growth is not limited by the amount of white spruce as it is in the understory protection, suggesting the species is capable of utilizing other species of old growth trees.

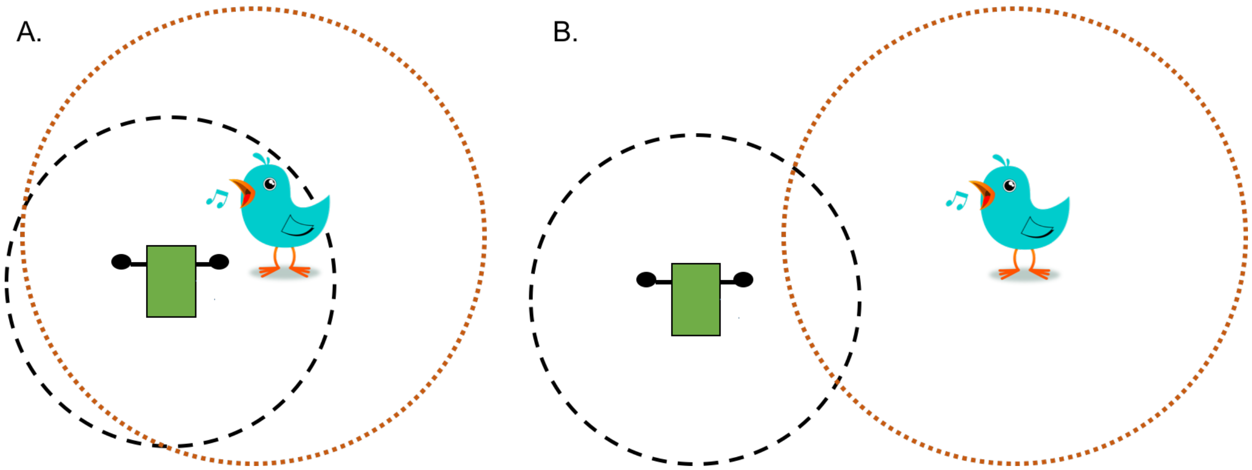

Figure 12. Two situations of occupied sites with various degrees of use. A: The bird's territory (dotted line) is highly overlapping with the ARU detection radius (dashed line); therefore, we would expect a high number of detections. B: The bird's territory is barely overlapping with the ARU detection radius; therefore, we expect the bird to be detected infrequently and thus associated with a small number of detections. In (A) we have higher certainty that the habitat covariates associated with the ARU detection radius are directly relevant to the bird's territory, whereas in (B) we are less certain about the habitat associations despite the territory being 'occupied'.

Table 3. List of covariates and their descriptions

Covariate Name	**Description**
P95	The average height at which the 95th percentile of LiDAR returns occurs within the 50m buffer. Represents a proxy measure for canopy height in meters.
S137to5	The proportion of LiDAR returns in the strata of 1.37-5meters averaged across the 50m buffer. Represents a proxy measure for understory vegetation density.
S5to10	The proportion of LiDAR returns in the strata of 5-10meters averaged across the 50m buffer. Represents a proxy measure for shrub density.
S10to20	The proportion of LiDAR returns in the strata of 10-20meters averaged across the 50m buffer. Represents a proxy measure for midstory vegetation density.
S20to30	The proportion of LiDAR returns in the strata of 20-30meters averaged across the 50m buffer. Represents a proxy measure for canopy vegetation density.

Table 4. Forward AIC step selection process for the recognizer use model

Model	**Treatment**	**+Canopy Height**	**+10-20m**	**+ Treatment*10-20m**	**+ %Spruce**	**+ Treatment*%Spruce**	**+1.37-5m**	**+ Age**
AIC	2336.42	1846.9	1707.2	1543.3	1473.5	1196.9	1188.4	1188.8
ΔAIC	NA	489.52	139.7	163.9	69.8	276.6	8.5	-0.4

Table 5. Summary table of model results. NA refers to effects that are non-interpretable due to interactions.

Data Source	Response	Covariate	β (p)	Covariate	β (p)	Covariate	β (p)	Covariate	β (p)
Recognizer	Occupancy	Station	NA	Canopy Height	NA	Station*Canopy Height	-0.501 (0.0032)		
Recognizer	Use	Treatment	NA	Canopy Height	0.6812 (5.77e-16)	10-20m	NA	Treatment * 10-20m	1.00 (0.155)
Recognizer	Use	% Spruce	NA	Treatment * %Spruce	0.6787 (2e-16)	1.37-5m	0.0433 (0.0027)		

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Chapter 4

CONCLUSION

Understory protection represents a new harvesting practice that provides a benefit to the conservation of songbirds in managed forests that generally require older forests. I show that the songbird community in understory protection harvested areas represents an intermediary between traditionally harvested areas and unharvested forests. The three main drivers of this are; 1) the use of cleared strips in understory protection by early-seral specialists, 2) the use of understory protection by habitat generalists, and 3) the rapid recolonization of understory protection by mature forest specialists. Therefore, understory protection provides habitat to a diverse group of songbirds with a wide breadth of niche requirements.

The structure and composition of vegetation left behind following UP harvest is likely driving the use of these areas by a diverse community of songbirds. Strips of forest removed for the feller buncher corridor create open habitat with relatively little vegetation regrowth. These areas likely provide habitat to the early-seral species such as sparrows that otherwise were found to prefer traditionally harvested areas. Strips of mature forest that are completely retained to act as a wind buffer for the understory protection strips may provide habitat to forest species that depend on large mature trees. These species tend to be those that are otherwise sensitive to forest harvesting. Several methods of protecting the white spruce understory from blowdown have been developed (Lieffers and Grover 2004), but the biodiversity potential of each approach has largely been overlooked. My results suggest the strip cutting understory protection method we assessed incidentally provides useable habitat to mature forest species. Lastly, the understory protection strip itself likely provides habitat to species that specialize on young spruce for nesting. However, the protected white spruce grows rapidly following harvest-mediated release from competition, resulting in available habitat to mature forest species shortly after harvesting. The rapid growth of white spruce may result in a rapid replacement of species associated with young spruce by those associated with mature spruce.

After 15 years post-harvest, we found no evidence for convergence between the songbird communities in traditional harvest areas and those in unharvested controls. My study is consistent with research suggesting traditional harvesting approaches may take over 100 years before songbirds associated with mature forests recolonize (Schieck and Song 2006). I expect the songbird community in the traditional harvest areas to be consistent with those found in post-fire areas (Huggard et al. 2014), though I argue this comparison should not always be the ultimate goal in forest management for biodiversity. Traditional harvest blocks seek to approximate natural disturbances such as wildfires, so similarly aged post-fire stands represent a valuable reference state for this objective. For understory protection harvesting however, the structure and composition of retained features is not based on the natural disturbance model. I argue that similarly aged post-fire stands do not make a valuable reference state for evaluating understory protection because fires would never create such a pattern. Instead, understory protection is more closely related to the retention forestry model, thus unlogged forests represent a more suitable reference state.

In contrast, understory protection may greatly reduce the amount of time it takes for forest species to recolonize the harvested area. My community analysis shows that just 12-years post harvest, the understory protection community has begun to converge with the unharvested forest community. I emphasize the importance of this finding given that understory protection areas are only about 60 years old at the time of harvest, yet are converging with 100+ year-old forests just 12-years following harvest. It is possible that UP harvesting is expediting habitat availability for some species due to the release of white spruce from competition with overstory aspen. By conducting a long-term study of songbird communities after UP harvest, we could better quantify the ability for UP harvesting to expedite the availability of habitat relative to unharvested control plots of the same age. In my study, control plots were substantially older than the UP harvested areas were before harvesting. Therefore, I lacked the ability to compare bird communities in the understory protection against the communities that would be expected in the same stands had they not been harvested.

The effects of forest harvesting on songbird communities is an extensive field of research, with a wealth of literature already published. However, much of this research is necessary because forest harvesting strategies are highly varied in their approaches, and assessments for each are often required. Venier and Pearce (2005) argue that local knowledge is required for effective forest management. To improve our ability to inform forest management and policy, I felt that an in-depth analysis of a single indicator species would be beneficial to this study. Species associated with old growth forests tend to be those facing the steepest declines in managed forests (Mannan and Meslow 1984) due to a decline in their available habitat (Cyr et al. 2009). Therefore, species expected to be most sensitive to forest management are those that specialize on mature trees in the boreal forest (Schieck and Song 2006). The BRCR represents one such species, and has been identified as the songbird species most sensitive to forest management in North America (Vanderwel et al. 2007). I chose to survey for BRCRs in the understory protection to quantify the "old-growthness" (Bauhus et al. 2009) value in understory protection areas. By studying a chrono-sequence of understory protection areas, I assessed old-growthness immediately post-harvest and as understory protection regenerates.

I conducted an intensive survey for BRCR in understory protection harvest areas and unharvested forests to assess their occupancy status in the harvested areas. Using computer recognizers with manual validation to detect BRCR singing events, I was able to process over 1000 minutes of data at each location. The vast majority of studies relying on presence/absence data require an adjustment of imperfect detection to estimate occupancy rates because survey effort is relatively low (Banks-Leite et al. 2014). The use of recognizers with bioacoustics data should eliminate this necessity by automatically transcribing massive amounts of data with relatively little human effort. In response to this growing availability of the technology combined with the impetus for collecting this resolution of data, it is essential that models intended to handle this data also remain up-to-date. I deemed logistic regression models assuming imperfect detection to be an obsolete and inappropriate approach to handling these data. Instead, I developed a very simple yet novel modeling approach that assumes perfect detection. I show that the data derived from recognizers can be incorporated into a classical occupancy framework, or utilized in a habitat use model. By incorporating recognizer data into a habitat use model, more precise species-habitat associations can be estimated. Further research, which I intend to pursue, should focus on comparing the findings of these models against traditional DCOMs that rely on listening-derived presence/absence data. Furthermore, quantifying false negative rates (i.e. recognizer failing to detect a species when it was present at that location) is an essential next step in utilizing these data in models assuming perfect detection.

I found BRCR occupancy rates to be substantially lower in the understory protection than the unharvested controls. However, most studies show that BRCR are entirely absent from harvested areas, so low levels of occupancy may represent a relatively successful harvesting strategy. At occupied sites, BRCR used understory protection sites to a lower degree than the unharvested forest, which may indicate they are incorporating part of the UP area in their territory but not all of it. Furthermore, I used LiDAR derived forest structure variables to predict habitat requirements by BRCRs. I showed that BRCR use of understory protection areas increases as the protected white spruce understory develops into the canopy. This result is surprising given our oldest understory protection blocks were just 12-years post harvest, and thus BRCR seem to be responding to the equivalent 70-80 year-old white spruce. BRCRs are typically associated with forests over 120 years old (Zarnowitz and Manuwal 1985), thus it is possible that understory protection harvesting is actually expediting BRCR habitat availability, through the release of white spruce from competition. Again, one limitation of this study was not having similarly aged unharvested stands to compare against. By surveying for BRCRs in stands that represent what the harvested areas would have looked like had they not been harvested, I could better quantify the direction and strength of the effect of understory protection harvesting on BRCRs.

The conservation of biodiversity in harvested areas has been one of the premier challenges for forest management. Sustainable harvesting was originally predicated on the natural disturbance hypothesis, which proposed harvesting in a way to approximate wildfire to improve ecosystem resiliency post-harvest (Hunter 1993). However, the continuing decline of organisms associated with mature forests has created impetus for a new harvesting paradigm (McRae 2001). From this concern, the strategy of retention forestry has emerged (Gustafsson et al. 2013). Retention forestry represents any harvesting strategy that seeks to maintain pre-existing levels of biodiversity and forest structure following the harvesting process. Understory protection harvesting should be considered as part of this umbrella of practices.

Understory protection harvesting facilitates the long-term harvest supply of both hardwood and softwood in managed forests using multiple harvests in the same area. Forest managers have faced the challenge of balancing offsets of socioenvironmental concerns with timber quotas, yet understory protection may promulgate an entirely new concept in forest management. Harvesting in ways that elicit both economic and ecological benefits presents advantages over other strategies, and understory protection represents the first harvesting strategy we are aware of that provides both these benefits. However, understory protection may be limited in its ability to meet hardwood annual allowable cuts due to the higher level of tree retention required. Ultimately, the best sustainable harvest practice likely requires a balance between NDH and UP harvesting in managed forests. One limitation of understory protection harvesting is its narrow application in forests that meet the criterion upon which the strategy was developed: mature aspen with >600stems/ha of understory white spruce. Al-Pac also implements high effort understory protection in areas of 400-600stems/ha understory white spruce, where clumps with high densities of white spruce are protected during harvest. These harvest areas will be inevitably more heterogeneous than strip-cutting understory protection, and further research should investigate potential benefits to songbird communities and other forest dwelling organisms. Together, these practices that protect the understory white spruce during hardwood harvesting have the potential to be integral components of a forest management plan.

The prominence of songbird species associated with mature forests found in understory protection areas suggests this harvesting approach can be used as an important tool in the toolbox of forest managers. NDH harvesting represents important habitat for many species, and had higher overall avian diversity than understory protection. To sustain healthy communities for both early-seral species and mature forest species, a combination of both NDH and UP harvesting may promote higher gamma diversity in managed forests. To meet objectives of both the ecosystem and the economy, the implementation of understory protection should be encouraged over traditional approaches in hardwood forests with dense spruce understories.

However, the long-term monitoring of understory protection areas is required to understand how species respond to these areas as they regenerate. Because understory protection is not based on mimicing a natural disturbance process, organismal responses to the regenerating forest structure may be unpredictable. I encourage continued monitoring and adaptive management as the understory protection harvesting regime is expanded in forest management planning.

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