Conserving Boreal Songbirds Using Variable Retention Forest Management

by

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Abstract

The Canadian boreal forest is vital breeding habitat for North American songbirds. Extensive anthropogenic disturbances within this biome are therefore of conservation concern. Using unharvested stands as controls, I examined the effects of variable retention management (VRM) relative to clear-cuts on songbird assemblages and individual species in a boreal mixedwood forest. Breeding season point count surveys were performed in 10-ha cutblocks applied across four dominant forest types (deciduous dominated, deciduous with spruce understory, mixedwood, and coniferous dominated), and harvested in winter 1998/99 to five retention levels (clear-cut (2%), 10%, 20%, 50%, and 75%), plus unharvested controls. Surveys were conducted prior to harvest in 1998, and subsequent to harvest in 1999, 2000, 2005, 2006, 2012, and 2013 at the Ecosystem Management by Emulating Natural Disturbance (EMEND) experiment in northwestern Alberta. In the first two post-harvest years, songbird assemblages in stands with less than 75% retention differed significantly from those in unharvested stands. After 14-15 years, assemblages in stands with 20% retention or higher no longer differed significantly from the controls, suggesting accelerated recovery within high retention stands. In the controls, however, species richness increased after 7-8 years, and species composition changed after 14-15 years, suggesting that c. 10-ha unharvested stands were too small to maintain unchanged songbird assemblages of undisturbed forest. Closer examination of six old forest-associated species – brown creeper (*Certhia americana*), winter wren (*Troglodytes hiemalis*), ovenbird (*Seiurus aurocapilla*), black-throated green warbler (*Setophaga virens*), Canada warbler (*Cardellina canadensis*), and western tanager (*Piranga ludoviciana*) - revealed that 20-75% retention prevented significant declines of all six species, and five of the six species increased significantly after 14-15 years. This suggests that variable retention management can be useful for conservation of songbird assemblages and species typical of unharvested forest. However, spatial trade-offs, lagged recovery in harvested stands, and assemblage changes in unharvested stands reinforce the importance of larger (> 10 ha) forest reserves in harvest planning.

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Chapter 1. Introduction

1.1 Background and rationale

Avian population declines in North America, detected since large-scale monitoring began in the 1970s, have led to increased scrutiny of trends, threats, and conservation strategies for species that have experienced losses. The broad, global issue of avian declines is complex and entangled. For example, the large majority of birds that breed in the boreal forest of Canada are migratory (Niemi et al. 1998) and face threats in their breeding grounds (Bohning-Gaese et al. 1993), wintering grounds (Robbins et al. 1989), and during migration (Faaborg et al. 2010). They encounter local, regional, and landscape-level threats, and these threats are cumulative, interactive, and difficult to identify and disentangle (Bohning-Gaese et al. 1993; Ballard et al. 2003).

Conserving this group requires knowledge of potential threats and the effectiveness of management approaches at different spatial and temporal scales. Sensitivities of species to local, regional, and landscape factors vary (Desrochers et al. 2010), and understanding such local effects can inform habitat-specific, as well as large-scale, opportunities for conservation. This thesis contributes to our understanding of how commercial forestry practices affect songbirds breeding in the western Canadian boreal forest, and provides one assessment of how effectively alternative silvicultural methods conserve these assemblages and some species over time.

1.1.1 Why the boreal forest?

The boreal forest is a circumpolar biome that accounts for approximately one third of Canada’s land area. In North America, it is vital breeding habitat to billions of individuals from over 300 bird species (NABCIC 2012). The estimated total anthropogenic disturbance footprint in the Canadian boreal forest was 24 million hectares as of 2010, including but not limited to agriculture, forestry cutblocks, roads, and seismic lines (Pasher et al. 2013). Industrial cutblocks have been shown to account for roughly 80% of productive forest areas studied in south-central Quebec (Boucher et al. 2013) and in north-central Alberta (Pickell et al. 2013). The large spatial extent of these disturbances, and their concentration in the more productive southern boreal forest regions, have been associated with changes to plant and animal communities, including birds (Venier et al. 2014).

Relationships between anthropogenic disturbances and breeding bird populations are complicated by the role of natural disturbances in the boreal forest. Prior to large-scale fire prevention and resource extraction, natural disturbances were the primary force shaping the boreal landscape (Rowe & Scotter 1973; Attiwill 1994). Given that boreal ecosystems and the wildlife residing therein have evolved and adapted to disturbance processes (Bunnell 1995), the conservation challenge presented by resource extraction may be defined as the reconciliation of differences, similarities, and conflicts between natural and human disturbances.

Forestry, perhaps the most spatially extensive human disturbance in the boreal forest, has evolved and expanded over the past century. Clear-cutting was firmly established as the primary harvest method in the 1950s in Finland and Sweden (“Fennoscandia”) (Lundmark et al. 2013), and in the late 1970s in Canada (e.g., Boucher et al. 2009). The small land area in Fennoscandia relative to timber demand, paired with the objective of a forest “clean” of deadwood and damaged or dying trees (Lundmark et al. 2013), has been associated with the IUCN red-listing of over 500 forest- and deadwood-associated species across numerous taxa (Fedrowitz et al. 2014). The extensive alteration of the boreal forest has negatively impacted avian populations in this region (Väisänen et al. 1986; Edenius & Elmberg 1996; Brotons et al. 2003), and demonstrates the potential risks to old forest-associated species in Canada as long as clear-cutting remains the dominant harvest method (Imbeau et al. 2001; Hobson et al. 2013).

1.1.2 Comparing clear-cuts and wildfire

Early arguments in favour of clear-cutting were based on the resemblance between a severe fire event with near-total tree mortality and a clear-cut (Smith 1986), and suggested that planned clear-cutting could produce a landscape mosaic of even-aged patches similar to a fire-dominated landscape (Attiwill 1994). This argument has been used to justify forestry policies that favour clear-cutting (e.g., Government of Alberta 2013a), even though it assumes that such severe fires are the most common (or most ecologically important) type of disturbance in the boreal forest (Hunter 1993), and that lack of post-fire carbon and woody material is unimportant.

Complete-mortality wildfire events represent only a fraction of the area disturbed by fire, as unburned residual patches are left behind by all but the most extreme boreal wildfires (Perera & Buse 2014). Clear-cuts also have different soil composition and nutrient cycling (Bergeron et al. 1999), lower volumes of snags and coarse woody debris (Brassard & Chen 2008), and different patterns of recovery (Haeussler & Bergeron 2004) than even severely burned stands.

The variability of boreal wildfires presents even more differences from clear-cutting. A number of environmental factors determine a stand's probability of burning (McRae et al. 2001), resulting in an age distribution dominated by young, frequently-burned stands, and few rarely-burned stands of ages that may far exceed the fire return interval (Bergeron et al. 2002). In contrast, clear-cutting at optimal efficiency produces a uniform distribution of stands at each age class up to the rotation age, and no stands on a fully regulated landscape that exceed the rotation age; i.e., clear-cutting results in the loss of old forests on the merchantable land base (Cyr et al. 2009).

Boreal bird populations and communities are sensitive to the differences between forests originating from wildfire and clear-cutting. Species assemblages in recently burned forests are characterised by greater numbers of woodpeckers and other deadwood associates, while young clear-cuts are dominated by open habitat associates (Imbeau et al. 1999; Drapeau et al. 2002; Schieck & Song 2006). Boreal bird assemblages differ between recently burned and clear-cut stands, driven in part by the availability of large snags (Schulte & Niemi 1998). Effects on bird assemblages also persist over time: a large variety of bird species nest in abandoned woodpecker cavities, and these species are significantly more abundant in older (> 20 years) burns than clear-cuts of the same age (Drapeau et al. 2002). Natural residual tree patterns in burned forests are also linked to increased occupancy by old forest-associated species compared with clear-cuts in the medium term (11-30 years) (Schieck & Song 2006). Overall, studies in the Canadian boreal forest have consistently shown that, in terms of the effects on boreal birds, clear-cuts and wildfire differ markedly (Imbeau et al. 1999; Schieck & Song 2006; Van Wilgenburg & Hobson 2008).

1.1.3 Variable retention management (VRM)

A number of forest management techniques have been developed under the premise that the negative effects on biodiversity and ecosystem health from forest harvests can be reduced by emulating the spatial, temporal, and structural features of natural disturbances (Morgan et al. 1994). Many predict that this approach will not only reduce the impacts of the harvest, but even restore some of the ecological conditions that have been compromised by the widespread suppression of natural disturbances (Landres et al. 1999). This thesis focuses specifically on stand-level variable retention management (VRM), also known as partial retention harvesting, as an alternative to clear-cutting in the boreal forest (Franklin et al. 1997).

Variable retention management aims to emulate the variable density and arrangement of residual structure of a burned stand through retention of merchantable trees and snags (Kafka et al. 2001). The potential conservation value of VRM for breeding bird populations is closely linked to the importance of vertical structure, which is a better predictor of forest bird-habitat responses than are floristic data about the identity of plant species (Venier & Pearce 2007; Hewson et al. 2011). In this context, VRM not only provides a continuous source of deadwood and snags for species dependent on these features (Drapeau et al. 2009), but also provides a greater diversity of nesting and foraging sites within cut-blocks. Heterogeneous structure and availability of older, large-diameter trees in turn support the persistence of old forest-associated species, whereas species associated with open-area and early-successional areas predominate in clear-cuts (Schieck & Song 2006).

1.2 Emulation of natural disturbance with VRM

The Ecosystem Management by Emulating Natural Disturbance (EMEND) experiment was developed to test and compare the effects of commercial forestry, VRM, and natural disturbance on biodiversity and ecosystem function in a northern mixedwood forest (Spence et al. 1999). This large-scale forestry experiment was established in 1998 with a planned experiment duration of 80-100 years, the average rotation age of natural forests in mesic upland boreal systems.

The EMEND experiment spans 24 km^2 of upland boreal mixedwood habitat in northwestern Alberta (experiment center: 56°46’13” N, -118°22’28” W), approximately 90 km northwest of Peace River (Fig. 1.1). The forest at EMEND is dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and white spruce (*Picea glauca* (Moench) Voss) in the overstory, with black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), lodgepole pine (*Pinus contorta* Douglas ex

Loudon) and eastern larch (*Larix laricina* (Du Roi) K.Koch) as more minor components. The shrub layer is largely comprised of prickly rose (*Rosa acicularis* Lindl.), green and river alder (*Alnus crispa* (Aiton) Pursh and *A. tenuifolia* Nutt.), low-bush cranberry (*Viburnum edule* Raf.), and Canada buffaloberry (*Shepherdia canadensis* (L.) Nutt.) (for full details see Work et al. 2010). The project area was previously unharvested, and the 120-180 year-old mixedwood landscape originated from large fire events in 1895, 1877, and 1837, which cumulatively burned over 80% of the area (Bergeron 2012).

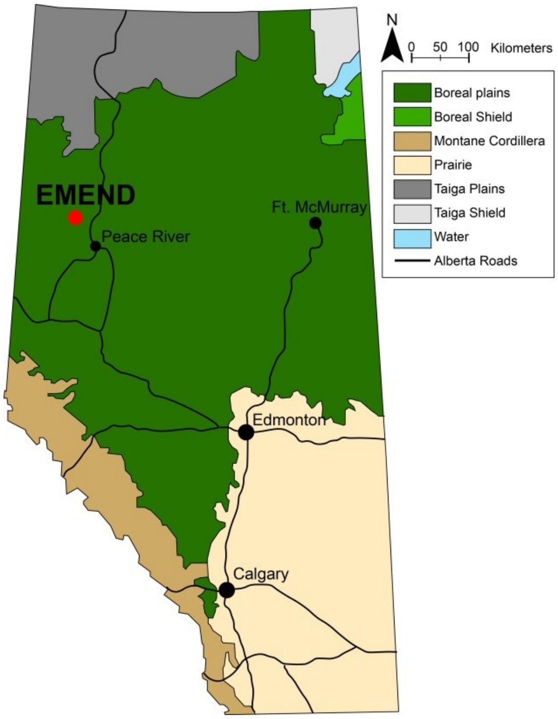

Figure 1.1. The EMEND Experiment is located c. 90 km northwest of Peace River, Alberta in the boreal plains ecoregion.

Prior to harvest in winter 1998/99, three replicates of four major forest mixedwood cover types were identified using Alberta Vegetation Index (AVI) data based on dominant tree species: deciduous-dominated (DD, ≥ 70% *Populus tremuloides* and/or *P. balsamifera*), deciduous-dominated with spruce understory (DU, ≥ 70% *Populus* spp. over *Picea* spp. in the understory), mixedwood (MX, 40-60% each of *Populus* spp. and *Picea* spp.), and conifer-dominated (CD, ≥ 70% *Picea* spp.). These four forest cover-types broadly represent the predominant successional pathway of post-fire boreal forest stands, by which shade-intolerant hardwood species (e.g. *Populus* spp.) are eventually replaced by shade-tolerant softwood species (e.g. *Picea glauca*) (Bergeron et al. 2002). Treatments consisted of five harvest retention levels – 2% (operational clear-cut), 10%, 20%, 50%, and 75% – and unharvested controls that were applied in the three replicate stands of each cover-type in approximately 10-ha “compartments” (n = 72). Residual trees, equal to a target percentage of the compartment’s original stem density, were dispersed evenly at harvest in 15 m wide strips between 5 m machine corridors. In addition, one large (0.46 ha) and one small (0.2 ha) aggregated retention patch were left in each compartment. Five-hundred meter buffers were maintained around the project area; roughly 1 400 ha have since been harvested within 5 km of EMEND, the large majority of which was harvested in 1999 as the experiment was established.

Prescribed burn treatments have not been fully delivered as planned, as conditions required for safe, controlled burns are uncommon. A total of seven compartments out of 14 have been burned over the period 1999-2010. In an attempt to include fire in the design, so-called “slash-burn” treatments were applied to all replicates in 2003 and 2005, in which three to four compartments originally designated for prescribed burn were instead harvested to 10% retention, with the slash residuals left within the cutblock. One half of each cutblock was subsequently burned. Due to the scarcity of bird survey data from these treatments, however, neither full-compartment burns nor “slash-burns” have been considered in the present study.

1.3 Study objectives

This thesis provides a 15-year update to the long-term breeding bird monitoring program at EMEND. Bird surveys were conducted in 1998-2000 (Harrison 2002), 2005-06 (F. K. A. Schmiegelow, unpubl. data), and most recently for this thesis in 2012-13. Due to difficulties delivering prescribed burns as planned, only survey data collected in the harvested and control compartments were considered. I therefore considered the bird assemblages of unharvested 10-ha control compartments, occasionally tempered by some data about pre-harvest assemblages collected in 1998, as targets to define recovery from forest harvest disturbance.

The objective of this study, then, is to assess the effects of clear-cutting and harvest at fixed retention levels (i.e., 10-75% retention) on boreal songbirds, relative to unharvested forest. Treatment effects were investigated at the “compartment level” in the context of dispersed green tree retention only, as the experiment was not designed to partition effects between residual retention and aggregated retention patches. Indeed, specifically in relation to avian studies, the retention patches in the EMEND compartments are too small to support such work. In Chapter 2, I examine the relationships between songbird assemblages and VRM, with particular focus on changes in species richness and composition, to provide a broad-scale assessment of the conservation value of VRM. In Chapter 3, I use data on six old forest-associated species that are predicted to be sensitive to forest harvest, and model changes in density of each species in response to VRM over time. In Chapter 4, I synthesize the main findings of this thesis, discuss challenges encountered during this study, suggest future directions for research, and weigh the management implications of VRM for avian conservation, particularly in the boreal mixedwood forest.

In setting up the work reported in Chapters 2 and 3, I predicted that clear-cutting would provoke the strongest changes to breeding songbird assemblages, and have the strongest negative effect on old forest-associated species. I expected that harvest effects would be attenuated by increased green tree retention (e.g., Norton & Hannon 1997). I also expected that harvest effects would be greatest 1-2 years after harvest (1999-2000), and that there would be substantial, albeit incomplete, recovery after 14-15 years (2012-13) post-harvest (e.g., Hobson & Schieck 1999).

This study is an important step in long-term monitoring of the effectiveness of VRM for avian conservation. The majority of studies testing impacts of forestry activities on breeding birds have assessed short-term (< 10 years) responses (Schieck & Song 2006). Longer-term studies have generally constructed chronosequences by surveying stands or cutblocks in different age classes (e.g., Schieck & Hobson 2000), and have thus had limited control over important differences in cutblock area and location, harvest intensity, spatial arrangement of residuals, pre-harvest disturbance history, and other factors that may influence responses in birds and thus inferences.

Other long-term monitoring schemes have played essential roles in identifying and quantifying the declines of many North American bird species, such as the North American Breeding Bird Survey (BBS) and provincial breeding bird atlases. Although the EMEND study lacks the sheer volume of observations made in such studies, it provides a controlled test of specific hypotheses about relative effects of different approaches to harvest and stand-level recovery of biotic elements. Such experimental results contribute an unusual perspective to the goal of improved forest management for the conservation of avian biodiversity and sensitive forest species.

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Chapter 2. Boreal songbird assemblages and variable retention management: a fifteen-year perspective on conservation in forestry

2.1 Abstract

Variable retention management (VRM) is an alternative to traditional clear-cut logging that is thought to emulate natural disturbance (e.g. wildfire), maintain the structural complexity of post-harvest landscapes, and better conserve biodiversity. Breeding songbird surveys at the Ecosystem Management by Emulating Natural Disturbance (EMEND) experiment located in the mixedwood forest of northwestern Alberta, Canada were used to assess relationships between boreal songbird assemblages and VRM over a 15-year post-harvest period. Ten-hectare experimental sites ("compartments") in stands classified as deciduous, deciduous with understory, mixed or coniferous were cut at five retention levels (clear-cut (2%), 10%, 20%, 50%, and 75%) in winter 1998/99, with matching controls left unharvested. Songbirds were surveyed in 1998 (pre-harvest) and after harvest in 1999, 2000, 2005, 2006, 2012, and 2013. Partial retention harvests leaving ≥ 20% of timber volume mitigated changes in songbird assemblages and accelerated songbird recovery. After 14-15 years, however, assemblages of unharvested controls differed significantly from those observed prior to harvest, suggesting important experiment-scale effects and/or regional trends. Large, intact forest reserves are likely crucial for an effective broad-scale conservation strategy. Although retention levels ≥ 20% show promise as an alternative to clear-cutting, trade-offs with increased harvest footprint should be investigated.

2.2 Introduction

The boreal forest is breeding habitat for many Nearctic birds, earning it the nickname of "North America's bird nursery" (Blancher & Wells 2005). Long-term monitoring of avian populations in Fennoscandia has shown a negative relationship between clear-cut forestry and old forest-associated songbirds (Helle & Järvinen 1986). While trends in North America have been less dramatic (Niemi et al. 1998), results from Northern Europe provide clear warnings about potential effects of intense forest harvesting, particularly clear-cutting (Imbeau et al. 2001). Development of boreal forests throughout Canada has rapidly increased since the 1990s, resulting in significant conservation concerns for boreal songbirds (Wells

2011), some of which stem from the direct and indirect effects of clear-cutting on breeding bird populations (Hobson et al. 2013).

Although clear-cutting can approximate stand-replacing wildfires of high intensity, boreal forest fires vary in scale, intensity, severity, and timing (Spies & Turner 1999). Most fires leave residual live and dead trees in fire skips and partially burned stands (Perera & Buse 2014), leading to landscapes characterized by a mosaic of age classes and vegetation types (Kafka et al. 2001). Extensive clear-cutting reduces or eliminates ecologically significant legacies of fire and leaves more young, even-aged stands on landscapes subjected to industrial forestry (Bergeron et al. 2002). Variable retention management (VRM), also known as partial retention harvest, has been widely promoted as a strategy to balance economic needs with conservation goals (Gustafsson et al. 2012). Like fire, VRM maintains snags, downed woody material, and live trees, which contribute to stand structural complexity and provide future sources of seed, snags, and dead wood (Franklin et al. 1997). Landscape variation of residual tree density and arrangement promotes the mosaic-like patterns of a burned forest (Hunter & Schmiegelow 2011).

The Ecosystem Management by Emulating Natural Disturbance (EMEND) experiment compares effects of prescribed burning, clear-cutting, and VRM with unharvested controls on operation-sized blocks over a full harvest rotation of 80-100 years (Spence et al. 1999). While a number of studies have assessed the immediate impacts of VRM on songbirds in the boreal forest (e.g., Harrison et al. 2005), long-term experimental studies are rare. The objective of this study is to assess the effects of clear-cutting and VRM on songbird assemblages and compare these to unharvested controls at EMEND over a 15-year post-harvest period. Unharvested controls were used as a baseline for “old” forest, or forest exceeding the rotation age, because comparable bird data from experimentally burned stands are presently unavailable.

2.3 Methods

The EMEND field site encompasses 1 000 hectares of manipulated boreal forest in northwestern Alberta (56°46’13” N, -188°22’28” W), that had not been previously harvested. EMEND is located in upland areas of a larger (c. 84 km^2) 120-180 year-old mixedwood landscape; the most recent major fires cumulatively burned > 80% of this landscape in 1837, 1877, and 1895 (Bergeron 2012). Trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and white spruce (*Picea glauca* (Moench)

Voss) are the dominant tree species at EMEND and in the surrounding forest, with minor components of black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), lodgepole pine (*Pinus contorta* Douglas ex Loudon) and eastern larch (*Larix laricina* (Du Roi) K.Koch). The shrub layer is dominated by prickly rose (*Rosa acicularis* Lindl.), alder (*Alnus crispa* (Ait.) Pursh, *Alnus tenuifolia* Nutt.), low-bush cranberry (*Viburnum edule* Raf.), and Canada buffaloberry (*Shepherdia canadensis* (L.) Nutt.). See Work et al. (2010) for more detailed description of the site.

Harvest treatments (clear-cut (2%) - CC, 10%, 20%, 50%, 75% retention, and uncut controls - CT) were applied to c. 10-ha compartments classified to four dominant tree cover-types (deciduous - DD, deciduous with spruce understory - DU, mixedwood - MX, and coniferous - CD). Treatment by cover-type combinations were replicated three times (overall *n* = 72). Compartments were harvested in the winter of 1998/99 and allowed to regenerate without intervention.

2.3.1 Data collection

One or two point count stations were established in each compartment surveyed and allocated for harvest in 1998 (*n* = 107). Stations were a minimum of 50 m from compartment boundaries, and a minimum of 150 m apart where two stations occurred in the same compartment. Breeding songbirds were surveyed at these stations in 1998, 1999 and 2000 (Harrison et al. 2005), 2005 and 2006 (F.K.A. Schmiegelow, unpubl. data), and 2012 and 2013.

This study is focused on songbirds (Order Passeriformes); however, pine siskin (*Spinus pinus*) and white-winged crossbill (*Loxia leucoptera*) were excluded due to concerns around population irruptions and grouping/colonial behaviours, and corvids (Family Corvidae) were excluded because their territory sizes exceed 10 ha. Trained observers conducted unlimited-radius 5 min. point counts (Bibby et al. 2000) at each station between 0500-1000h, over three or five survey rounds from late May to early July in all years (Harrison et al. 2005). When five survey rounds were completed in a year, I only included data from the second, third, and fourth rounds in my analysis, as the survey dates most closely matched those from years with three survey rounds. All visual and auditory observations were recorded and mapped to estimated distance intervals of 50, 100, and >100 m. Only observations within 50 m were subsequently analysed in an effort to increase spatial independence of data from each station and to reduce the likelihood of double-counting individuals at adjacent stations. Observers alternated compartments among rounds to reduce potential observer bias.

EMEND "core" forest mensuration and shrub datasets (see Spence et al. 1999) were incorporated into this analysis. Forest mensuration data were collected from six permanent 40x2 m strip plots randomly located in each EMEND compartment, and shrub data were collected from two 10x2 subplots at either end of each plot, at approximately five-year intervals. The years of vegetation measurements do not perfectly match the years that point counts were conducted, with a maximum temporal mismatch of 5 years, but the data nevertheless indicate the general characteristics of the forest compartments studied. As described below, coniferous (softwood) and deciduous (hardwood) tree and seedling/sapling densities, shrub density, and average seedling/sapling and shrub heights (Langor et al. 2006; Macdonald & Volney 2007) were analysed as explanatory variables for the bird data.

2.3.2 Data analysis

Species observations were summarized by taking the maximum count over the sampling rounds for each point count station (Toms et al. 2006), and the mean of the maximum observed abundance where two stations occurred in the same compartment. For most analyses, species abundances were averaged for each pair of years (e.g. 1999 and 2000), and pairs of years were treated as factors (time period). In all cases, 1998 (the pre-harvest year) was considered a single time period.

All analyses were performed in R (R Core Team 2014) unless otherwise noted. While numerous statistical methods exist to account for imperfect detection in single-species models (e.g., Kéry et al. 2005), well-established techniques for comparing entire assemblages are limited to estimates of diversity indices (see Iknayan et al. 2014 for a review). Thus, I used standard multivariate methods to explore assemblage responses. Although analyses are not based on estimates of absolute abundance, these data may be used in a relative sense to study trends and changes in assemblage parameters.

Multivariate analysis of species composition change was performed with package "vegan" (Oksanen et al. 2014) using distance-based redundancy analysis (dbRDA) (Legendre & Anderson 1999). Bray-Curtis distances were calculated from species counts and ordinated in response to coniferous tree density (stems/ha) (DBH > 5 cm), deciduous tree density by DBH class (5-10 cm, 10-30 cm, > 30 cm), deciduous and coniferous sapling/seedling (DBH < 5 cm) densities and heights (m), and shrub densities and heights. Only environmental variables with acceptably low collinearity ($r < 0.5$) were used in the ordination. Singletons and doubletons (species with ≤ 2 total observations) were removed prior to analysis (McCune & Grace 2002). Permutation tests ($n_{perm} = 999$ (software default)) were applied to the model and non-significant environmental variables were removed using backward selection ($\alpha = 0.05$).

I used permutational multivariate analysis of variance (PERMANOVA, Anderson 2005) to formally test treatment, time period, and interaction effects on species composition, again using Bray-Curtis distance (Anderson 2001; McArdle & Anderson 2001). Singletons and doubletons were removed prior to analysis. Permutational pairwise comparisons tested differences between harvested sites and controls within each time period (e.g., $CC_{1\text{-}2y}$ vs $CT_{1\text{-}2y}$). P-values were adjusted for multiple comparisons using the Holm method (R Core Team 2014).

I additionally tested for changes in the unharvested controls before and after harvest using PERMANOVA with package “vegan” in R (Oksanen et al. 2014). Comparisons between the single pre-harvest year and averaged species counts within paired post-harvest years violated the model assumption of homogeneity of group dispersion; thus, separate tests were conducted between the pre-harvest year and non-averaged species counts in each post-harvest time period (e.g., CT_{pre} vs (CT_{1y} & CT_{2y})). All PERMANOVA tests were conducted using 4 999 permutations ($\alpha = 0.05$).

I examined harvest effects on post-harvest occupancy of species that were present prior to harvest (“pre-harvest species”). The proportion of these species present subsequent to harvest, relative to the total number of pre-harvest species in each cover-type, was calculated for each compartment. These proportions were tested for treatment, cover-type, and time period effects using analysis of variance (ANOVA). Replication was too low to test the full range of interactions, and non-significant variables were removed from the additive model using backward selection ($\alpha = 0.05$). Pairwise comparisons of significant terms were performed using Tukey’s Honest Significant Difference test with p-values adjusted for multiple comparisons ($\alpha = 0.05$).

Species richness was estimated using coverage-based rarefaction (Chao & Jost 2012) with program iNEXT (Hsieh et al. 2013). Rarefaction provides richness estimates given an incomplete sample, and more generally, given imperfect detection within the sample (Chao & Jost 2012). “Coverage” refers to percent sampling completeness, estimated using the number of uncommon species (singletons and doubletons) that are observed in each sample. This rarefaction method discards fewer data than traditional individual-based rarefaction, and provides less biased comparisons between assemblages (Chao & Jost 2012). Species richness was standardized to the minimum coverage across all samples and 95% bootstrap confidence intervals calculated for each estimate using the maximum number of permutations allowed by the software ($n_{perm} = 500$). Where confidence intervals do not overlap, statistical significance at $\alpha = 0.05$ is assured (Chao & Jost 2012).

2.4 Results

The final dbRDA model of species composition includes a constrained variance of 0.211. Only the first two canonical axes are shown in Fig. 2.1; despite being statistically significant, axes 3-5 each account for less than 5% of the total variance. Axes dbRDA1 and dbRDA2 explain 10.3% (F = 34.9, p = 0.001) and 5.6% (F = 19.0, p = 0.001) of the total variance, and 47.0% and 25.6% of the constrained variance, respectively. The model contains nine environmental variables: density of deciduous trees with DBH > 30 cm (variance (‘var’) = 1.69, F = 5.7, p = 0.001), DBH 10-30 cm (var = 4.47, F = 15.1, p = 0.001), and DBH 5-10 cm (var = 3.14, F = 10.6, p = 0.001); coniferous tree density (var = 5.1, F = 17.2, p = 0.001); deciduous sapling (var = 2.33, F = 7.9, p = 0.001) and coniferous seedling (var = 0.62, F = 2.1, p = 0.01) densities; shrub density (var = 2.07, F = 7.0, p = 0.001); and shrub (var = 1.01, F = 3.4, p = 0.001) and deciduous sapling (var = 1.55, F = 5.3, p = 0.001) heights (Fig. 2.1a).

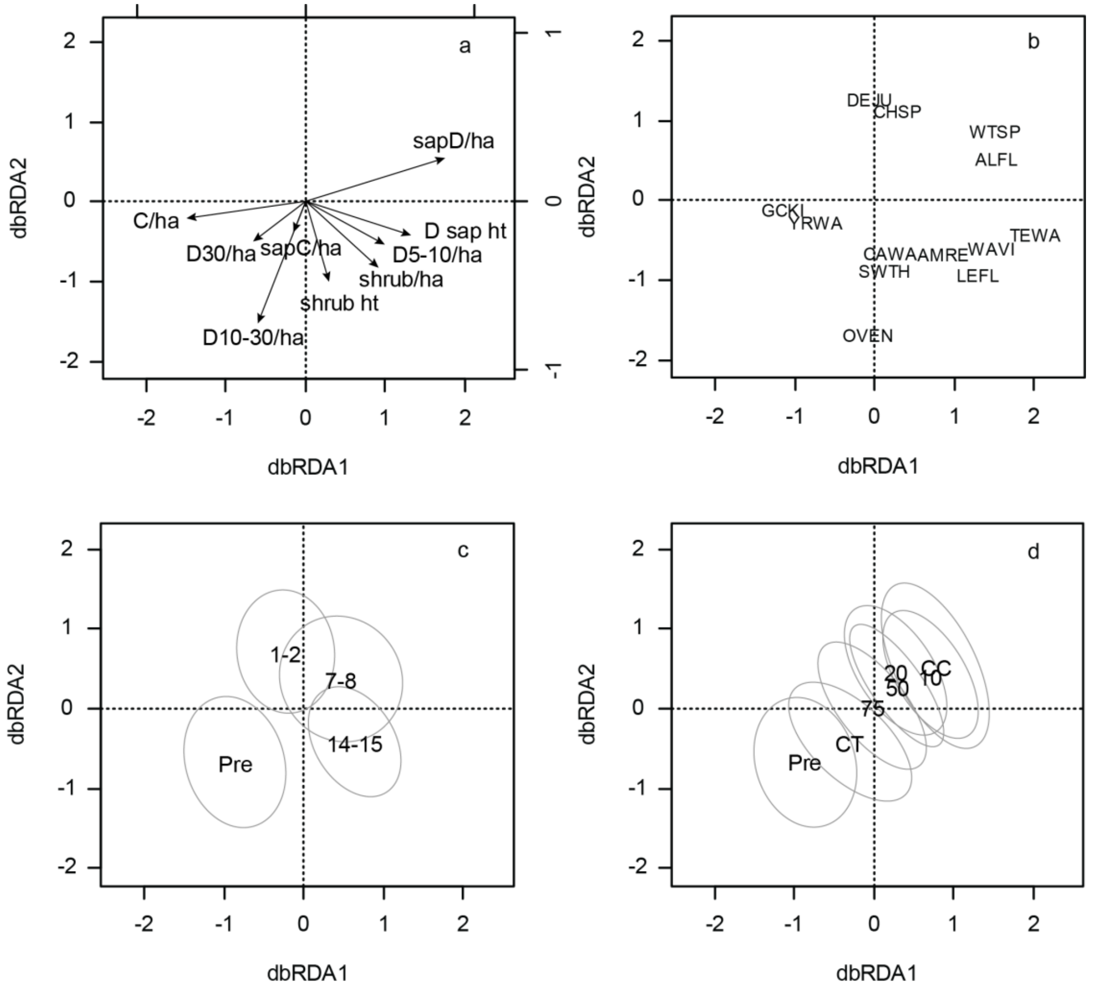

Figure 2.1. Relationships between species assemblages and tree, sapling, and shrub variables using distance-based redundancy analysis (dbRDA) with Bray-Curtis distance (constrained variance = 0.211). a) Vectors representing correlation scores of environmental variables, including deciduous ('D') and coniferous ('C') stem densities per hectare ('/ha'), deciduous sapling and coniferous seedling densities per hectare ('sap'), heights (m, 'ht'), and diameter at breast height classes (cm). b) Selected species scores (for species codes see Table 2.1). c) Ellipses representing time period (one standard deviation around the group centroid). d) Ellipses representing treatment/retention level (one standard deviation around the group centroid), including pre-harvest ('Pre'), unharvested controls ('CT'), and clear-cuts ('CC').

For illustrative purposes, only species with the strongest positive or negative scores were plotted to reduce congestion (Fig. 2.1b). Golden-crowned kinglet (GCKI, *Regulus satrapa*) and yellow-rumped warbler (YRWA, *Setophaga coronata*) are correlated with high densities of coniferous trees, and ovenbird (OVEN, *Seiurus aurocapilla*) with medium-large deciduous trees (DBH 10-30 cm). Dark-eyed junco (DEJU, *Junco hyemalis*) and chipping sparrow (CHSP, *Spizella passerina*) characterise assemblages at high dbRDA2 values; this plot region, roughly corresponding with the magnitude opposite of the vector representing medium-diameter (10-30 cm) deciduous trees, indicates low densities of these stems. White-throated sparrow (WTSP, *Zonotrichia albicollis*) and alder flycatcher (ALFL, *Empidonax alnorum*) are associated with dense deciduous saplings. Several species are correlated with shrubby stands with medium-diameter deciduous trees, including Tennessee warbler (TEWA, *Oreothlypis peregrina*), warbling vireo (WAVI, *Vireo gilvus*), and least flycatcher (LEFL, *Empidonax minimus*). For a list of species codes see Table 2.1.

Ellipses illustrate a trajectory of species composition change over time (Fig. 2.1c) and as retention level decreased (Fig. 2.1d). Forest harvest triggered a shift in species composition that remained evident after 14-15 years (Fig. 2.1c). Even at 75% retention, this shift was only partially mitigated (Fig. 2.1d). The ellipses, viewed alongside Figs 2.1a and b, demonstrate that stands with higher retention (dbRDA1 values approaching zero) were associated with denser and taller shrubs, while low-retention and clear-cut stands (dbRDA1 values near one) were related instead with high densities of deciduous saplings.

PERMANOVA (Fig. 2.2) revealed significant post-harvest effects of time period ($F = 20.7$, $df = 2$, $p < 0.001$), harvest treatment ($F = 6.2$, $df = 5$, $p < 0.001$), and the interaction between the two ($F = 1.6$, $df = 10$, $p < 0.001$). In all years, assemblages at 75% retention did not differ significantly from the controls. Additional recovery was evident only after 14-15 years at 20% (dist = 61.5, $p_{adj} = 0.41$) and 50% (dist = 62.0, $p_{adj} = 0.11$) retention, which at that time did not differ significantly from the controls.

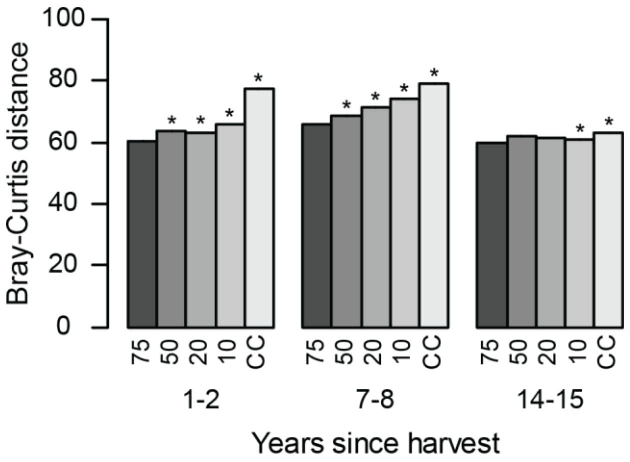

Figure 2.2. Average Bray-Curtis distance (dissimilarity) between species assemblages in each harvest treatment versus the controls in each time period. Significance determined for α = 0.05 using permutation tests (n_{perm} = 4 999) with adjustment for multiple comparisons.

Additional PERMANOVA tests for changes in the unharvested controls before and after experiment-wide harvest revealed that assemblages in the unharvested controls changed over time. Assemblages were not significantly different from pre-harvest assemblages after 1-2 years (dist = 0.71, F = 1.26, df = 1, p = 0.24); were marginally significant after 7-8 years (dist = 0.74, F = 1.78, df = 1, p = 0.063); and had changed significantly after 14-15 years (dist = 0.74, F = 2.87, df = 1, p = 0.005).

Of the species present prior to harvest ("pre-harvest species"), the proportion also observed post-harvest was significantly affected by time period (F = 21.4, df = 2, $p < 0.001$) and harvest treatment (F = 5.68, df = 5, $p < 0.001$) (Fig. 2.3). Some species were lost, or occurred less frequently after harvest, including in the unharvested control compartments (e.g. golden-crowned kinglet (*Regulus satrapa*) and ovenbird (*Seiurus aurocapilla*)). Over all treatment types, significantly fewer pre-harvest species were present 1-2 years after harvest than the two subsequent time periods (Fig. 2.3a). Over all post-harvest time periods, unharvested controls and 75% retention stands supported significantly more pre-harvest species than the clear-cuts, while stands with ≥ 10% retention displayed intermediate pre-harvest species losses (Fig. 2.3b). It is important to note, however, that only 69% of pre-harvest species (95% confidence interval (CI_{95}) = 64%, 75%) were retained on average in the unharvested controls. While none of the pre-harvest species were lost altogether from the controls during the post-harvest period, observed assemblage changes reflect an average loss of 25-36% of species in each control compartment.

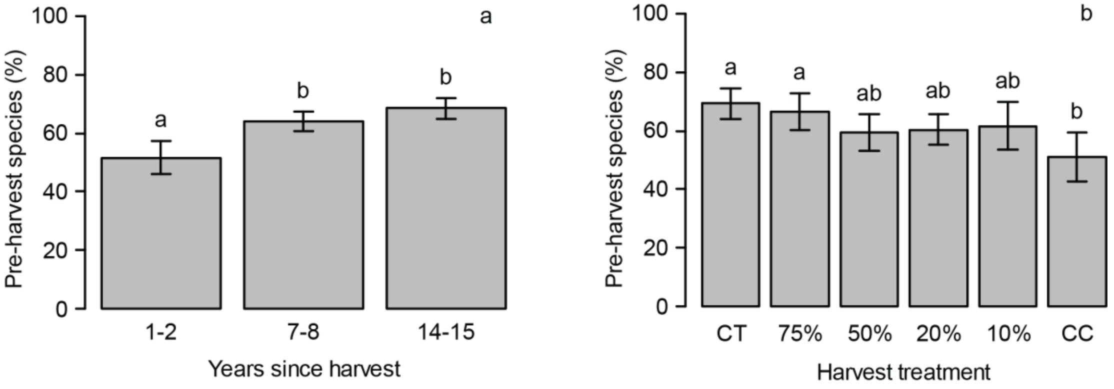

Figure 2.3. Average proportion of pre-harvest species, relative to the total number of pre-harvest species, observed in each a) post-harvest time period, and b) post-harvest treatment.

Species richness (R), rarefied to 96% sampling coverage, was 31 on average across all sites in the year prior to harvest (CI_{95} = 29.3, 32.8) (Fig. 2.4). Richness decreased significantly in the clear-cuts (R = 21, CI_{95} = 18.2, 24.3) and marginally at 20% retention (R = 26, CI_{95} = 23.5, 29.1) in the first two years post-harvest. After 7-8 years, richness increased significantly across all stands with ≥ 10% retention, with the exception of those with 20% retention (R = 34, CI_{95} = 31.8, 37.2). After 14-15 years, richness stabilized in three harvest treatments to pre-harvest values, but remained significantly higher at 50% and 75% retention. These two treatments continued to be characterized by high numbers of new species, including but not limited to mourning warbler (*Geothlypis philadelphia*), alder flycatcher (*Empidonax alnorum*), American robin (*Turdus migratorius*), and cedar waxwing (*Bombycilla cedrorum*).

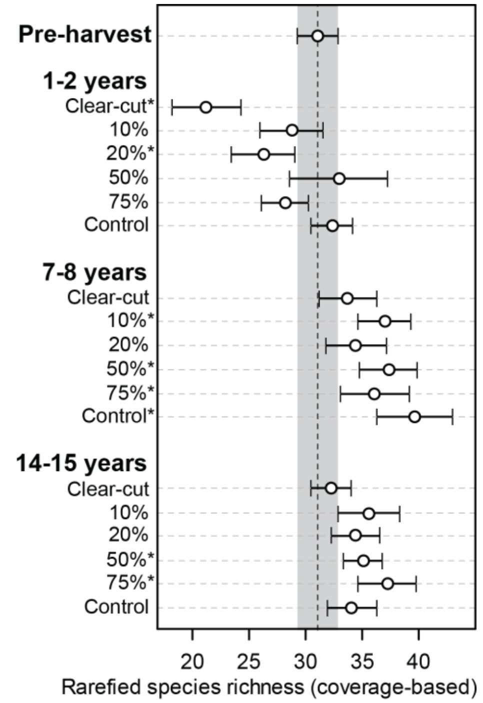

Figure 2.4. Species richness estimates rarefied to 96% sampling coverage for each time period and treatment, with 95% bootstrap confidence intervals. Significant changes from pre-harvest conditions are indicated with asterisks.

2.5 Discussion

Results of this study encourage optimism about use of VRM for biodiversity conservation, but emphasize that forest harvesting nevertheless drives songbird assemblage change at the stand and, very likely, landscape levels. However, with significant reserves large enough to support species that do best in old forest, species loss is less likely with VRM than with clear-cut prescriptions, and songbird recovery in harvested stands is likely to be faster.

Species composition changed drastically after harvest, first in response to the removal of medium- to large-diameter trees in 1998/99, then in response to the rapid regeneration of deciduous saplings after 7-8 years (Figs 2.1a, c). These environmental changes were most pronounced in the clear-cuts, where species composition differed most from assemblages in the controls, and where significant differences persisted 14-15 years after harvest (Fig. 2.2). By 14-15 years, the clear-cuts were vegetated primarily by tall, dense aspen saplings, while higher retention stands had more shrubs and medium-diameter trees

(Figs 2.1a, c, d). This more complex vertical structure may have contributed to the accelerated songbird assemblage recovery evident in stands with ≥ 20% retention, in which species composition did not differ significantly from the controls after 14-15 years (Fig. 2.2). Similarly, stands with ≥ 10% retention lost moderately fewer pre-harvest species than did clear-cuts, relative to the controls (Fig. 2.3b), and supported a higher overall number of species (Fig. 2.4).

These results suggest that 20% tree retention partly mitigated harvest effects and accelerated recovery in species composition compared to clear-cuts. However, assemblage changes in the 10-ha controls suggest that these changes may be due in part to larger landscape changes and/or regional trends. Increasing dissimilarity between control and pre-harvest assemblages may have resulted from increased post-harvest habitat heterogeneity across the EMEND experiment and the surrounding landscape (Desrochers et al. 2010) and/or regional trends in songbirds. Five-hundred meter unharvested buffers were maintained around the experiment, but roughly 1 400 ha were harvested within 5 km of EMEND during the study period, primarily in 1999. Furthermore, forest edges support higher bird diversity than forest interior (Šálek et al. 2010), and this may have contributed to increases in richness in EMEND compartments. After harvest, open-area, edge-associated, and generalist species were increasingly observed in the controls, including but not limited to American robin, cedar waxwing, chipping sparrow, and dark-eyed junco.

While species richness remained stable or increased in the controls, shifts in assemblages over time, in particular reduced overall occupancy by pre-harvest species, raise questions about their usefulness as refugia for old forest species. However, among pre-harvest species lost from the unharvested controls were species normally associated with second-growth (e.g. American redstart, *Setophaga ruticilla*) or open habitats (e.g. chipping sparrow), whose presence prior to harvest may be explained by transience or occupancy of suboptimal habitat. Following harvest, many of these species occurred more frequently in the harvested stands (e.g., Fig. 2.1b), reflecting possible shifts toward more suitable habitat rather than outright losses, and accounting in part for pre-harvest species losses from the controls. In contrast, many species more typically associated with old forests were frequently observed in the post-harvest controls (e.g. Canada warbler (*Cardellina canadensis*) and black-throated green warbler (*Setophaga virens*)), and no pre-harvest species were entirely absent subsequent to harvest. In terms of occupancy, this result suggests that 10-ha unharvested controls were moderately effective as refugia for old forest associates, in spite of the relatively high rate of species loss overall, as well as increased occupancy by new species.

Lack of bird survey data from burned stands precludes conclusions about the utility of VRM in emulating burned habitats. In light of the growing scale of harvest, however, it is perhaps more appropriate to consider undisturbed forest as the limiting factor for boreal wildlife (Bergeron & Harper 2009), particularly in productive forest regions (Venier et al. 2014). Within the context of the EMEND experiment, there are promising indications that 20% tree retention accelerated avian assemblage recovery compared to unharvested stands. Concerns remain, however, around the experiment-wide increase in species richness after seven years, and a shift away from pre-harvest species assemblages after 14-15 years. Ten-hectare unharvested compartments may have functioned less as controls than as fragments within the harvested landscape. They provided adequate refugia for continued occupancy by some old forest species, but may have been affected by large-scale changes across the harvested region and/or regional population trends. Widespread application of 20% retention, with annual harvest volumes remaining constant, would result in a larger annual harvest footprint, and reduce areas of potential forest reserves. These results suggest that VRM with on average ≥ 20% retention coupled with a matrix of larger (> 10 ha) reserves might promote recovery of songbird assemblages characteristic of older forest on harvested landscapes.

2.6 Conclusions

VRM was associated with a number of positive effects on songbird assemblages relative to clear-cut harvesting, and the potential biodiversity benefits of the inclusion of 20% green tree retention in harvest plans are clear. However, in light of species composition changes observed in 10-ha reserves, the usefulness of high retention levels could be offset by the increased harvest footprint that results if harvesting pressure remains the same. Research in larger (> 10 ha) partial retention stands is a logical next step to determine to what extent the small cutblocks at EMEND influenced patterns of avian assemblage change. Species composition change in unharvested fragments is of concern in a landscape where stands exceeding the rotation age of 80-100 years become scarcer every year.

2.7 References

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Table 2.1. Key to species codes from Figure 2.1.

Code	**Species**	
ALFL	Alder flycatcher	*Empidonax alnorum*
AMRE	American redstart	*Setophaga ruticilla*
CAWA	Canada warbler	*Cardellina canadensis*
CHSP	Chipping sparrow	*Spizella passerina*
DEJU	Dark-eyed junco	*Junco hyemalis*
GCKI	Golden-crowned kinglet	*Regulus satrapa*
LEFL	Least flycatcher	*Empidonax minimus*
OVEN	Ovenbird	*Seiurus aurocapilla*
SWTH	Swainson’s thrush	*Catharus ustulatus*
TEWA	Tennessee warbler	*Oreothlypis peregrina*
WAVI	Warbling vireo	*Vireo gilvus*
WTSP	White-throated sparrow	*Zonotrichia albicollis*
YRWA	Yellow-rumped warbler	*Setophaga coronata*

Chapter 3. Effects of high green tree retention on boreal songbird species of old forest over a 14-15 year post-harvest period

3.1 Abstract

Long-term songbird declines in managed forests are a persistent conservation issue, linked to the extensive spatial footprint of clear-cutting and reduction of old forest habitats. I assessed the effects of variable retention management (VRM) on the abundance of six old forest-associated songbird species - brown creeper, winter wren, ovenbird, black-throated green warbler, Canada warbler, and western tanager - using point count surveys at the Ecosystem Management by Emulating Natural Disturbance (EMEND) Experiment in northwestern Alberta. Ten-hectare compartments of upland boreal mixedwood forest were cut in winter 1998/99 at five retention levels (clear-cut (2%), 10%, 20%, 50%, and 75%), with control compartments left unharvested, in stands classified as deciduous, deciduous with spruce understory, mixed, or coniferous. Breeding songbirds were surveyed in 1998 (pre-harvest) and after harvest in 1999, 2000, 2005, 2006, 2012, and 2013. Significant declines in abundance (density) were prevented at 20% retention for western tanager, 50% retention for brown creeper, winter wren, black-throated green warbler, and Canada warbler, and 75% for ovenbird. All species but winter wren increased significantly 14-15 years after harvest. Although high retention levels supported higher species densities than clear-cuts, trade-offs must be considered because widespread application of high retention comes at the cost of larger harvest footprints.

3.2 Introduction

The boreal forest of Canada provides breeding grounds for more than 300 bird species, comprising roughly three million birds annually, and is thus an important region for bird conservation in North America (Blancher and Wells 2005, NABCIC 2012). Anthropogenic disturbances in the boreal forest, including industrial forestry, have been shown to cause species declines and community changes (Beese & Bryant 1999; Drapeau et al. 2000; Hobson & Bayne 2000a; Imbeau et al. 2001). Thus, we seek to modify industrial natural resource extraction and management practices, including forestry, to accommodate conservation goals.

Boreal ecosystems have historically been affected by natural disturbances; in western Canada, mainly wildfire (Rowe & Scotter 1973). The intensity, area, and severity of wildfires are highly variable, resulting in different rates of tree mortality, complex edges, and a variety of regeneration patterns (Attiwill 1994; Burton et al. 2008; Bergeron et al. 2014). Residual live and dead trees produce a patchwork of uneven-aged stands with variable and complex vertical structure (Eberhart & Woodard 1987; Kafka et al. 2001). Although regionally high fire return intervals have historically limited the proportion of old forest stands (Bergeron & Harper 2009), this landscape component provides important habitat to many species (Stelfox 1995; Imbeau et al. 2001).

In contrast to wildfire, traditional clear-cutting removes most or all merchantable trees from uniform blocks with sharp edges. Many of these stands are subsequently managed as single-species, even-aged crops of timber, and are re-harvested at rotation ages generally shorter than the fire return interval (Hobson & Bayne 2000a; Bergeron et al. 2002). Replacement of natural disturbance processes with clear-cutting has reduced the proportion of old forest (forest exceeding the rotation age) in large areas, and had negative long-term impacts on biodiversity, particularly on old-forest and deadwood-associated species in Fennoscandia, where intensive forest management has a long history (Helle & Järvinen 1986; Väisänen et al. 1986; Edenius & Elmberg 1996).

Variable retention management (VRM) is a strategy intended to balance harvest and biodiversity values by emulating structural aspects and patterns of a burned forest (Attiwill 1994; Landres et al. 1999). A pre-determined proportion of merchantable trees is retained within cutblocks to increase structural heterogeneity, provide a future source of seeds, snags, and dead wood, and provide more suitable habitat for forest specialist species (Franklin et al. 1997). From an avian perspective, VRM may maintain nesting and foraging sites that are no longer present in clear-cuts, and allow disturbance-sensitive species to persist in harvested landscapes.

The Ecosystem Management by Emulating Natural Disturbance (EMEND) Experiment was established, in part, to address the effects of VRM on forest productivity, function, and biodiversity, in comparison to effects of operational clear-cutting on unharvested forest (Spence et al. 1999). EMEND has a planned duration of a full timber rotation (80-100 years), providing a unique opportunity to assess not only the short-term effects of VRM on boreal birds, but the medium- and long-term consequences as well. The scale and design of EMEND are additional advantages, as large, fully replicated forestry experiments are rare (see Gustafsson et al. 2012).

This study uses breeding bird survey data collected over the 15-year post-harvest period to assess effects of VRM treatments on stand-level densities of six old forest-associated songbird species over the short- and medium-term at EMEND. In Chapter 2, I showed that high green tree retention mitigated harvest impacts on songbird assemblages associated with uncut forest. It seemed possible, however, that patterns of species composition change masked the effects of harvest on older forest specialists.

The objective of this study is to examine the impacts of VRM on estimated densities of six old boreal forest-associated songbird species: brown creeper (*Certhia americana*), winter wren (*Troglodytes hiemalis*), ovenbird (*Seiurus aurocapilla*), black-throated green warbler (*Setophaga virens*), Canada warbler (*Cardellina canadensis*), and western tanager (*Piranga ludoviciana*). These species were selected based on known associations with old boreal forest, sensitivity to disturbance and/or fragmentation, and/or association with burned forest (see Table 3.1). All six of these species were predicted to decline steeply in clear-cuts, but to be less affected as retention level increased toward the baseline of unharvested compartments. All species except western tanager were predicted to be most abundant in the uncut controls. As a species associated with openings in older forests, western tanager was expected to reach its highest numbers at high (50-75%) green tree retention (Hudon 1999). Possible green tree retention thresholds, above which declines were dampened relative to stands with less retention, were of primary interest.

3.3 Methods

The Ecosystem Management Emulating Natural Disturbance (EMEND) experiment covers approximately 24 km^2 of previously unharvested upland boreal mixedwood forest in northwestern Alberta (experiment center: 56°46’13” N, -118°22’28” W), the majority of which was last burned 120-180 years ago (Bergeron 2012). The tree overstory is dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and white spruce (*Picea glauca* (Moench) Voss), with black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), lodgepole pine (*Pinus contorta* Douglas ex Loudon), and eastern larch (*Larix laricina* (Du Roi) K.Koch) as minor components. The shrub layer is dominated by green and river alder (*Alnus crispa* (Aiton) Pursh and *A. tenuifolia* Nutt.), prickly rose (*Rosa acicularis* Lindl.), Canada buffaloberry (*Shepherdia canadensis* (L.) Nutt.), and low-bush cranberry (*Viburnum edule* Raf.) (see Work et al. 2010).

Prior to harvest, stands within the experiment area were selected and blocked according to four dominant tree cover-types: deciduous-dominated (DD, ≥ 70% *Populus tremuloides* and/or *P. balsamifera*), deciduous-dominated with spruce understory (DU, ≥ 70% *Populus* spp. over *Picea* spp. understory), mixedwood (MX, 40-60% each *Picea* spp. and *Populus* spp.), and conifer-dominated (CD, ≥ 70% *Picea* spp.). Treatment compartments, approximately 10-ha in area, were harvested in winter 1998/99 at five retention levels (2% (operational clear-cut, CC), 10%, 20%, 50%, and 75%) as a percentage of pre-harvest tree stem density. In addition, unharvested controls (CT) were included in each cover-type block. Blocks were replicated three times over each cover-type (*n* = 72). Five-hundred meter unharvested buffers were established and maintained around harvested stands.

3.3.1 Data collection

3.3.1.1 Bird surveys

Breeding songbirds were surveyed using the point count method (Bibby et al. 2000) at one or two randomly-located points per compartment as allocated to pre-harvest stands in 1998 (*n* = 107), and re-surveyed after harvest in 1999 and 2000 (Harrison et al. 2005), 2005 and 2006 (F.K.A. Schmiegelow, unpubl. data), and 2012 and 2013. Point count stations were a minimum of 50 m from compartment boundaries and 150 m from adjacent stations (Harrison et al. 2005). All surveys were conducted between 0500h and 1000h, between late May and early July, following Harrison et al. (2005). Alternating observers conducted five-minute surveys, three to five times during the breeding season. All birds heard or seen were recorded and distance to each observation estimated at intervals of 0-50 m, 50-100 m, and >100 m. Birds flying over or through compartments were excluded from analysis, as these observations did not reliably indicate the existence of a territory within the compartment being surveyed.

3.3.1.2 Vegetation data

Experiment-wide forest mensuration, shrub, and snag data were collected at approximately five-year intervals by a ‘core’ research team. Forest mensuration data were collected from six permanent 40x2 m strip plots (PSPs) placed randomly in each compartment perpendicular to machine harvest corridors (Langor et al. 2006). Shrub data were collected from two 10x2 m subplots at either end of each PSP (Macdonald & Volney 2007), and snag data were collected from 40x10 m strip plots centered on the PSPs (Langor 2007). Vegetation data were not collected in the same years as the bird survey years, with differences ranging up to a maximum of five years; the most recently available forest mensuration and snag data were collected in 2008, compared with bird surveys performed in 2012-13. These differences were deemed too large to test the relationships between environmental features and densities of the avian study species, but provided context for discussion (Section 3.5).

3.3.2 Data analysis

Where two point count stations occurred in a single compartment, a single station was chosen in order to minimize the following (in decreasing order of importance): proximity to adjacent cutblocks and/or other point count stations, proximity to buffer, and proximity to unharvested retention patches. In years when five survey rounds were conducted, only rounds two through four were analysed to ensure comparability of survey dates over the entire data set. Analysis was performed at the “compartment-level” using the maximum number of observations for each species over the three sampling rounds, as the maximum is considered a more reliable index of abundance than the mean number of counts (Toms et al. 2006).

Because compartment shapes were irregular, approximately half of the point count stations were located less than 100 m from compartment boundaries. In previous work, the full data set was limited to counts observed within a 50 m radius to improve the spatial independence of the surveys (see Chapter 2). For the present species-level analysis, however, this condition proved too restrictive given resulting sample sizes. Instead, observations assigned to >100 m from plot centre were excluded from the entire data set, and observations estimated to be beyond 50 m were excluded only for those survey stations that were < 100 m from the compartment boundary. The resulting differences in sampling area will be addressed in the following section.

3.3.2.1 Generalised linear mixed model (GLMM)

For each species, density (birds/ha) was modelled using species counts within a given sampling area, in response to three categorical fixed effects: time period, harvest treatment, and forest cover-type. Each pair of adjoining survey years (e.g. 1999 and 2000) was treated as a single time period. Unfortunately, the single year of pre-harvest data (1998) provided too few counts to produce compartment-level density estimates or formally test for differences between pre- and post-harvest densities. However, the existing data can be used to generally assess the suitability of the unharvested controls as recovery targets. All analyses were conducted using the statistical software, R (R Core Team 2014).

The statistical dependence introduced by repeated visits to the same point count stations over multiple years (temporal auto-correlation) was addressed using generalised linear mixed models (GLMMs) with a random compartment-level intercept (package “glmmML”, Broström 2013). A temporal auto-regression of order 1 (AR1) structure was considered for the models, but it introduced more complexity than could be accommodated by a solution. Considering compartment effects to be random was considered the next-best alternative, functioning as a compound symmetric correlation structure (Zuur et al. 2009; Vittinghoff et al. 2012), or compartment-level error term.

The problem of imperfect detection was addressed using package “detect” (Sólymos et al. 2013, 2014), which uses the offset method to produce point density estimates by accounting for sampling area and variables affecting detectability. Distance and/or time-of-detection (removal) data can be used to model effective detection radius and singing rate for each species, in response to study-specific variables, to produce detectability offset coefficients .Time-of-detection data were only collected for this study during 2012-13, and distance estimation in dense forested environments is prone to high error rates (Alldredge et al. 2007), precluding our ability to confidently estimate detectability offset coefficients using data from this study alone. However, this package also includes species-specific detectability offset coefficients calculated for selected variables using the Boreal Avian Modeling (BAM) project database (Cumming et al. 2010), consisting of nearly 90 000 unique survey visits across the North American boreal forest (Sólymos et al. 2013). These BAM coefficients are available for percent forest cover, land cover class

(LCC), time since sunrise, and Julian date. Regardless of the method used, these offsets can be subsequently included in generalised linear models or extensions thereof to account for differences in detectability under variable survey situations.

I used the BAM coefficients by using the harvest treatments at EMEND to approximate percent forest cover (e.g., 10% retention ≅ 0.10 forest cover), and assigning LCC according to treatment and forest cover-type in consultation with the package developer (Table 3.2, P. Sólymos, pers. comm.). These offsets additionally accounted for point count radius in order to produce a density estimate (D, birds/ha). The structure of the base model follows for counts *Y* observed at site *i* during survey round *j* and time period *k*:

(Eq. 1) $Y_{ik} \sim \text{Poisson}(\mu_{ik})$

(Eq. 2) $\log(\mu_{ik}) = \log(D_{ik}) + \log(\text{offset}_{ijk})$

(Eq. 3) $\log(D_{ik}) = \alpha + \boldsymbol{\beta}_{ik} + \varepsilon_i \quad \text{and} \quad \varepsilon_i \sim \text{Normal}(0, \sigma^2_{\varepsilon})$

(Eq. 4) $\text{offset}_{ijk} = f(\text{species, survey area}_i\text{, Julian date}_{ijk}\text{, time since sunrise}_{ijk}\text{, \% forest cover}_i\text{, LCC}_i)$

(Eq. 5) $\boldsymbol{\beta}_{ik} = \text{subset}(\beta 1_k^{time}; \beta 2_i^{trt}; \beta 3_i^{type})$

Five *a priori* candidate models were constructed, differing only in fixed effects (i.e. $\boldsymbol{\beta}_{ik}$) (Eq. 5). The reference levels included in the intercept are the first time period (1-2 years after harvest), the unharvested controls, and the coniferous-dominated cover-type, for β1, β2, and β3, respectively. Interactions were initially considered due to their likely ecological relevance but had to be excluded because sample sizes were too limited to support the analysis. Candidate models are provided in Table 3.3, and include four different combinations of the factors time period (time since harvest), harvest treatment, and cover type, as well as an intercept-only model. Models including time period were expected to perform well for species that are sensitive to habitat edges and/or fragmentation, or species capable of exploiting moderately open, shrubby habitats. These species would be expected to respond positively to regeneration of the harvested matrix over time. Harvest treatment (percent green tree retention) was expected to be included in the final solution for all six species, as these old forest associates are all known to be sensitive to logging (Poole 2005). Cover-type was expected to be significant for species with strong associations to one or more forest cover-type to the exclusion of others. Finally, the intercept-only model would be expected to perform best when there are too few observations to detect changes using the statistical methods given above, or for species with much more general habitat affinities than any of these six species.

Models were compared using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) (Burnham 2004), and model averaging employed for models where $\Delta AIC_c < 4$ using package "MuMIn" (Barton 2014). Where model averaging was used, the natural average method (i.e. no shrinkage) was selected because the treatment variable was of particular interest (Nakagawa & Freckleton 2011). Models were checked for overdispersion and/or failure to converge, as evident in excessive standard errors of parameters (Grueber et al. 2011). Statistical significance of parameters was assessed at $\alpha = 0.05$; however, p-values obtained using mixed effects models are considered more approximate than those obtained by fixed effects models (Zuur et al. 2009).

Nearly all Canada warbler observations (80%) occurred in the *Populus*-dominated (DD) stands. Analyses of Canada warbler therefore include data collected in the DD stands alone, and density estimates are indicative of these stands rather than the experiment area as a whole. This data restriction, predicated on the assumption that Canada warbler densities were low enough in the other cover-types as to be negligible, improved model performance and provided density estimates that were not biased toward zero due to the scarcity of observations outside of the DD stands.

Parameter estimates and standard errors (i.e., effect sizes) are in the log-scale, and densities for each time period, treatment, and cover-type were estimated using Eq. 3 and back-transformed for each species.

Statistical thresholds for density changes were of primary interest for each species. A "threshold" was considered for this analysis as the point at which a model parameter (e.g. a treatment level) differed significantly from the intercept (reference level), as indicated by a significant p-value ($\alpha = 0.05$). For example, a species that significantly declined in the clear-cuts relative to the controls (controls being the parameter intercept, or reference level), but did not significantly decline in the 10% retention treatments or higher, would be described as having a treatment threshold at 10% green tree retention. Temporal and cover-type thresholds are statistically significant deviations from the first time period (1-2 years) and the coniferous-dominated cover-type, respectively, which are included in the intercept term in addition to the unharvested controls.

It is important to note that “threshold” is used in this analysis in the statistical sense, and does not reflect ecological or management thresholds per se. The ecological and management implications of the statistical results will be more explicitly discussed in Section 3.5 - Discussion.

3.4 Results

The full model, in which density was considered a function of time period, harvest treatment, and forest cover-type, was the single most supported model for ovenbird and western tanager (Table 3.3). I used weighted model averaging (model weights = w_{aic}) to find solutions for the remaining four species. Black-throated green warbler and brown creeper densities were modeled in response to a combination of the full model (w_{aic} = 0.66 and 0.56, respectively) and the time period plus harvest treatment model (w_{aic} = 0.34 and 0.44, respectively). Winter wren density was modeled in response to an average of treatment plus cover-type (w_{aic} = 0.74) and the full model (w_{aic} = 0.26). Canada warbler densities were only modeled using data from deciduous-dominated stands, thus models containing a cover-type term were not considered. The most supported model solution for Canada warbler included time plus treatment (w_{aic} = 0.60), intercept-only (w_{aic} = 0.25), and treatment-only (w_{aic} = 0.15). The full model was included in the final solution ($\text{w}_{\text{aic}} > 0$) for five of the six species, suggesting the importance of all three candidate variables for explaining density for the old forest associates considered here (excluding Canada warbler, for which the full model was not a candidate).

All species except winter wren increased significantly after 14-15 years, compared with 1-2 years post-harvest (Table 3.4), indicating a degree of recovery following the initial disturbance that would not have been detected by a shorter-term study.

Responses to retention level varied among the six species (Table 3.4). The lowest statistical threshold was evident at 20% retention for western tanager, followed by 50% retention for Canada warbler (considering only the deciduous-dominated stands) and winter wren, and 75% retention for ovenbird. Black-throated green warbler declined significantly in the clear-cuts and at 20% retention, and declines were marginally significant at 10% retention (effect = -1.12, SE = 0.58, p = 0.052). Brown creeper declined significantly at 10% and 20% retention, but declines in the clear-cuts were confounded by the high standard error (effect = -9.50, SE = 28.9, p = 0.74). This species was not observed in a regenerating clear-cut at any time subsequent to harvest. The high standard error appears to reflect a lack of observations at this treatment level rather than unexpectedly high variation in counts. In both cases, a threshold at 50% retention is reasonably concluded.

Estimates for all species were higher in one or more of the cover-types (Table 3.4), suggesting that green tree retention is a more effective tool for a given species when applied to forest stands with which it has a positive relationship (Fig. 3.1). Significantly higher densities were evident for black-throated green warblers in the mixedwood compartments, and ovenbirds in all non-coniferous stands (Table 3.4, Fig. 3.1). Brown creeper densities were significantly lower in deciduous stands with understory, and western tanager and winter wren were less dense in deciduous and deciduous stands with spruce understory, than they were in the coniferous stands (Table 3.4, Fig. 3.1). As stated above, Canada warbler had dramatically higher densities in the deciduous stands than any other cover-type.

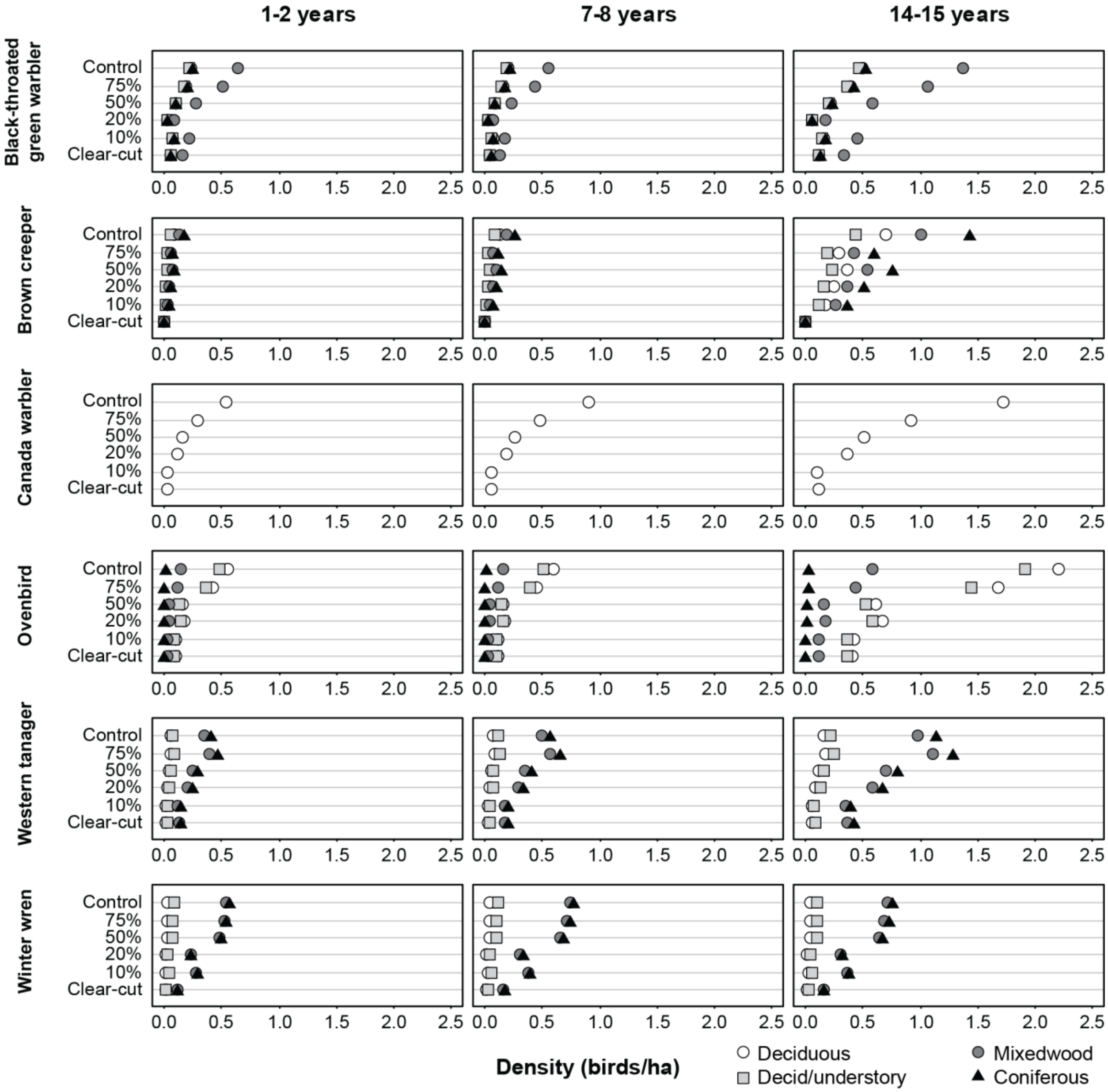

Figure 3.1. Estimated species density of six old forest associated species (birds/ha). Densities were estimated using generalised linear mixed modelling with detection offsets provided by the Boreal Avian Modelling project (BAM), accounting for differences in probability of detection according to species identity, sampling area, forest cover covariates and observation-level covariates.

3.5 Discussion

Inferences around treatment effects and changes over time must be tempered by omission of interaction terms from the candidate models due to limited degrees of freedom. Of interest, naturally, is the question of whether species densities increased at a faster rate in high-retention stands. However, visual patterns suggesting accelerated recovery in Fig. 3.1 are likely an artifact of back-transformation from the log-linked model, and do not originate from a statistical test. Thus, treatment effects and changes over time will be discussed separately, but the implications of each will be considered within the context of more complex potential recovery patterns.

3.5.1 Responses to green tree retention

Statistically evident harvest treatment thresholds were found for all six old forest-associated songbird species in this study, with important implications for the application of VRM in forest management. As little as 20% green tree retention circumvented significant declines of western tanager, but 50% retention or higher was necessary for the remaining species. Ovenbird was the most sensitive species, requiring the highest retention treatment (75%) to avoid declines (Table 3.4, Fig. 3.1). The strength of harvest effects (i.e., the magnitude of estimated declines) generally increased as retention level decreased, with the strongest declines evident in the clear-cuts and at 10% retention for all species except the black-throated green warbler, which declined the most at 20% retention. The general pattern of these results support the hypothesis that, as green tree retention decreases, so too do the numbers of species associated with old forests.

Across large landscapes, however, the benefits of VRM are less clear. Gustafsson et al. (2012) estimate that the proportion of production forests in Canada harvested with retention range from <1% in Saskatchewan (0.5-13% retention) to 75-100% in Ontario (2-10% retention, including riparian buffers), with 60% of the production forest in Alberta harvested with retention between 1-15%. Clearly, stand-level green tree retention in Canada is currently applied at levels below the minimum of 50% retention suggested by this study to be necessary to prevent declines of many old forest-associated species, including the nationally Threatened Canada warbler. It is a practice that increases costs (Ranius et al. 2005) and requires a larger harvest footprint to maintain the same harvest volume. Any plan to maximize recovery of all six species through VRM over a 15-year post-harvest period would lead to larger spatial footprints of forestry, assuming harvest volumes remain unchanged. From this perspective, unharvested reserves may be preferred by forestry companies and conservationists alike as a more cost-effective and spatially conservative strategy.

On the other hand, these results demonstrate that it is possible to extract timber without causing local population declines of some old forest-associated songbirds. In this context, the retention of 20-75% of live trees is an alternative to clear-cutting, particularly in forest areas that support high numbers of disturbance-sensitive, old forest-associated species including the six assessed in this study. In particular, these high retention treatments may yield benefits for specific target species in different forest types; Canada warbler, for example, would likely benefit from the application of 50% harvest in a high-value older *Populus* stand in lieu of clear-cutting.

3.5.2 Increases after 14-15 years

Density on the EMEND landscape increased for every species except winter wren 14-15 years after harvest, over recently harvested stands. These results suggest improved conditions, likely resulting from both stand-level and experiment-wide regeneration.

At the stand level, a number of important habitat features have changed since harvest, possibly prompting increased numbers of the study species. The midstory regenerated quickly in harvested stands, contributing to their vertical structure, and possibly improving the habitat quality of harvested stands for the old forest species over time. Shrub density steadily increased in all treatments from 2001-2010, while deciduous sapling density peaked in 2005 and remained high in 2010 (Macdonald & Volney 2007). Additionally, snag densities increased slightly from 2001-2008 (Langor 2007).

Regeneration across the entire experiment area may also explain the observed increases, particularly in the unharvested controls. Fragmentation of forested landscapes has been linked to population declines within older forest isolates (Flaspohler et al. 2002; Schmiegelow & Mönkkönen 2002; Stephens et al. 2003; Batary & Baldi 2004), but these declines have generally been measured in the short term following harvest of adjacent stands, e.g. two years (Stephens et al. 2003) or up to six years (Flaspohler et al. 2002). Fragmentation effects are generally severe at edges between old forest and agriculture (Hobson & Bayne 2000b; Schmiegelow & Mönkkönen 2002), and weaker where old forest borders clear-cuts

(Schmiegelow et al. 1997). The results of this study suggest that after 14-15 years, the harvested matrix surrounding the controls (particularly clear-cuts and low-retention compartments) regenerated sufficiently to substantially soften negative edge and fragmentation effects on these old forest-associated birds.

While comparable long-term studies are uncommon, bird community convergence between post-harvest and post-fire landscapes has been observed after 11-30 years, and it appears that VRM accelerated the recovery of old forest-associated species (Schieck & Song 2006). The results of this study are consistent with a >10 year benchmark for recovery, even given a focus on unharvested control stands rather than burns as targets for recovery. These results are also consistent with significant recovery of songbird species assemblages observed at EMEND after 14-15 years at ≥ 20% retention (see Chapter 2).

3.6 Conclusions

The high partial retention requirements found by this study echo the results of others (Norton & Hannon 1997; Tittler et al. 2001; Chizinski et al. 2011), who recommend a minimum retention of 40% or more and raise similar questions around trade-offs. Given the economic impediments to implementing high retention levels, and the proportional increase in harvest footprint, many instead emphasize the maintenance of intact forest reserves (Kirk et al. 1996; Stephens et al. 2003; Haché et al. 2013). High green tree retention nevertheless has apparent benefits for conservation of several old forest-associated species, including the nationally ‘Threatened’ Canada warbler. Given the ecological and economic advantages of diverse forest management regimes (Mönkkönen et al. 2014), the results of this study support the inclusion of VRM in balanced and diverse management plans. In particular, 20-75% green tree retention is suggested as an alternative to clear-cutting in stands that support high numbers of old forest species, in cases when forestry companies are unable to leave stands as reserves due to economic or policy constraints.

3.7 References

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Table 3.1. Selected publications indicating old forest associations of the six species chosen for analysis.

Species	Publications
Brown creeper	Hobson & Schieck 1999 Drapeau et al. 2000 Hobson & Bayne 2000a, 200b Costello et al. 2000 Poulin et al. 2013
Black-throated green warbler	Drapeau et al. 2000 Hobson & Bayne 2000b Hannon & Schmiegelow 2002 Morse & Poole 2005
Canada warbler	Drapeau et al. 2000 Hobson & Bayne 2000b COSEWIC 2008 Reitsma et al. 2010
Ovenbird	Crawford et al. 1981 Annand & Thompson 1997 Hobson & Bayne 2000b Flaspohler et al. 2002 Porneluzi et al. 2011
Western tanager	Hudon 1999 Hobson & Bayne 2000a Hannon & Schmiegelow 2002
Winter wren	Hobson & Schieck 1999 Drapeau et al. 2000 Hobson & Bayne 2000b Hejl et al. 2002

Table 3.2. Adaptation of EMEND treatment and cover-type variables to land cover class (LCC) variables for calculation of detection offsets. Retention levels were assigned using green tree retention as a proxy for percentage of tree cover; cover-types (DD = deciduous-dominated, DU = deciduous with spruce understory, MX = mixedwood, CD = coniferous-dominated) were assigned in consultation with package 'detect' developer (Sólymos et al. 2014).

Land Cover Class (LCC)	LCC definition	EMEND variable assignment
Open Habitat (OH)	< 25% cover by trees	Clear-cut, 10%, 20% [All cover-types]
Sparse Deciduous (SD)	25-60% cover by deciduous trees	50% [DD, DU, MX]
Sparse Coniferous (SC)	25-60% cover by coniferous trees	50% [CD]
Dense Deciduous (DD)	> 60% cover by deciduous trees	75%, Controls [DD, DU, MX]
Dense Coniferous (DC)	> 60% cover by coniferous trees	75%, Controls [CD]

Table 3.3. Model performance for six old forest specialists, measured by Akaike's Information Criterion adjusted for small sample sizes (AIC_c). The model with the lowest AIC_c ($\Delta AIC_c = 0$) is considered the most supported model, and candidate models with $\Delta AIC_c < 4$ were included in model averaging (Burnham 2004). Where model averaging was employed, the weight of each model within the final solution (model weight, w_{aic}) is included in parentheses. The number of observations (counts) of each species is provided (n).

Candidate Model	Black-throated green warbler (n = 89)		Brown creeper (n = 42)		Canada warbler[1] (n = 35)		Ovenbird (n = 132)		Western tanager (n = 127)		Winter wren (n = 110)	
	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c
Density ~ time + treatment + cover-type	278.8	0 (0.66)	171.8	0 (0.56)	n.a.		215.4	0	281.4	0	226.2	2.10 (0.26)
Density ~ time + treatment	280.1	1.34 (0.34)	172.3	0.5 (0.44)	87.4	0 (0.60)	276.4	60.9	327.0	45.5	271.2	47.1
Density ~ treatment + cover-type	289.5	10.8	200.6	28.8	n.a.		269.2	53.8	300.8	19.4	224.1	0 (0.74)
Density ~ treatment	290.8	12.0	201.1	29.3	90.2	2.75 (0.15)	330.0	114.5	346.5	65.1	269.1	45.0
Density ~ 1 (Intercept-only)	293.6	14.8	211.7	40.0	89.2	1.77 (0.25)	336.1	120.6	348.2	66.8	266.7	42.5

[1] Results for Canada warbler were derived from deciduous-dominated (DD) stands only. There were too few observations of Canada warbler to support hypothesis-testing of cover-type effects. n = 35 indicates the number of observations in the DD stands only for this species.

Table 3.4. Model parameter estimates for six old forest specialists using GLMM and model average when applicable (see Table 3.3). Significance is indicated where $p < 0.05$. The intercept includes the first time period (1-2 years), unharvested controls ("CT"), and (where applicable) coniferous-dominated cover-type ("CD"); all other values represent deviations from the intercept for each species. Variables include time since harvest, retention level, and dominant tree cover-type (DD = deciduous-dominated, DU = deciduous with spruce understory, MX = mixedwood).

Species	Parameter		Estimate	Standard error	Z-score	P-value
Black-throated green warbler (n = 89)	**Intercept**		**-1.38**	**0.48**	**2.87**	**0.004***
	Time period					
		7-8 years	-0.16	0.31	0.52	0.605
		14-15 years	**0.74**	**0.26**	**2.91**	**0.004***
	Treatment					
		75%	-0.24	0.51	0.48	0.634
		50%	-0.85	0.55	1.55	0.122
		20%	**-2.10**	**0.70**	**3.00**	**0.003***
		10%	-1.12	0.58	1.94	0.052
		Clear-cut	**-1.40**	**0.60**	**2.33**	**0.020***
	Cover-type					
		DD	-0.06	0.51	0.13	0.900
		DU	-0.14	0.51	0.27	0.787
		MX	**0.94**	**0.46**	**2.07**	**0.038***
Brown creeper (n = 42)	**Intercept**		**-1.73**	**0.62**	**2.78**	**0.005***
	Time period					
		7-8 years	0.41	0.65	0.63	0.530
		14-15 years	**2.09**	**0.53**	**3.94**	**<0.001***
	Treatment					
		75%	-0.88	0.46	1.90	0.058
		50%	-0.64	0.43	1.49	0.136
		20%	**-1.02**	**0.49**	**2.08**	**0.037***
		10%	**-1.36**	**0.57**	**2.40**	**0.016***
		Clear-cut	-9.50	28.9	0.33	0.743
	Cover-type					
		DD	-0.72	0.43	1.67	0.094
		DU	**-1.17**	**0.51**	**2.31**	**0.021***
		MX	-0.35	0.38	0.92	0.358
Canada warbler[1] (n = 35)	Intercept		-0.61	0.71	0.86	0.390
	Time period					
		7-8 years	0.51	0.52	0.99	0.323
		14-15 years	**1.15**	**0.47**	**2.46**	**0.014***
	Treatment					
		75%	-0.63	0.66	0.96	0.338
		50%	-1.22	0.73	1.67	0.094
		20%	**-1.54**	**0.76**	**2.02**	**0.044***
		10%	**-2.80**	**1.16**	**2.41**	**0.016***
		Clear-cut	**-2.75**	**1.16**	**2.38**	**0.017***

[1] Results are for Canada warbler observations collected in deciduous-dominated (DD) stands only. There were too few observations in the other cover-types to support hypothesis testing of this variable.

(Continued on next page)

Table 3.4, continued.

Species	Parameter		Estimate	Standard error	Z-score	P-value
Ovenbird (n = 132)	**Intercept**		**-4.80**	**1.03**	**-4.67**	**<0.001***
	Time period					
		7-8 years	0.08	0.30	0.26	0.793
		14-15 years	**1.39**	**0.24**	**5.80**	**<0.001***
	Treatment					
		75%	-0.28	0.22	-1.25	0.210
		50%	**-1.28**	**0.32**	**-3.99**	**<0.001***
		20%	**-1.19**	**0.29**	**-4.10**	**<0.001***
		10%	**-1.67**	**0.37**	**-4.50**	**<0.001***
		Clear-cut	**-1.67**	**0.37**	**-4.52**	**<0.001***
	Cover-type					
		DD	**4.20**	**1.01**	**4.17**	**<0.001***
		DU	**4.06**	**1.01**	**4.02**	**<0.001***
		MX	**2.87**	**1.03**	**2.79**	**0.005***
Western tanager (n = 127)	**Intercept**		**-0.91**	**0.28**	**-3.26**	**<0.001***
	Time period					
		7-8 years	0.35	0.26	1.34	0.181
		14-15 years	**1.03**	**0.24**	**4.38**	**<0.001***
	Treatment					
		75%	0.13	0.26	0.51	0.610
		50%	-0.34	0.28	-1.21	0.227
		20%	-0.52	0.30	-1.74	0.082
		10%	**-1.05**	**0.37**	**-2.85**	**0.004***
		Clear-cut	**-1.00**	**0.35**	**-2.90**	**0.004***
	Cover-type					
		DD	**-1.98**	**0.38**	**-5.24**	**<0.001***
		DU	**-1.65**	**0.33**	**-5.00**	**<0.001***
		MX	-0.15	0.19	-0.75	0.452
Winter wren (n = 110)	**Intercept**		**-0.57**	**0.26**	**2.18**	**0.030***
	Time period					
		7-8 years	0.32	0.24	1.33	0.184
		14-15 years	0.29	0.24	1.18	0.236
	Treatment					
		75%	-0.03	0.29	0.12	0.907
		50%	-0.12	0.28	0.42	0.677
		20%	**-0.86**	**0.35**	**2.48**	**0.013***
		10%	**-0.67**	**0.34**	**1.98**	**0.047***
		Clear-cut	**-1.53**	**0.43**	**3.54**	**<0.001***
	Cover-type					
		DD	**-2.79**	**0.59**	**4.69**	**<0.001***
		DU	**-1.93**	**0.40**	**4.77**	**<0.001***
		MX	-0.05	0.20	0.26	0.797

Chapter 4. Discussion

4.1 Main findings

This thesis revealed short- and medium-term impacts of variable retention management (VRM) on songbirds breeding in the mixedwood boreal forest of northwestern Alberta. Retention levels >20% mitigated harvest impacts on some species and assemblages associated with unharvested forest, and accelerated assemblage recovery in regenerating stands. Higher retention usefully conserved all six old forest species examined. However, assemblages also changed in the unharvested controls, raising important questions about the resilience of 10-ha forest fragments against effects from larger surrounding harvested areas. At this point it is not possible to distinguish such effects from potential impacts of other regional factors such as climate change. However, work to sort this out may provide useful information about target sizes for unharvested patches that can function as songbird reserves.

Clearly forest harvest at any level affects songbird assemblages, but recovery may be enhanced through VRM. In Chapter 2, multivariate analyses revealed accelerated recovery of the overall songbird assemblage at ≥ 20% green tree retention toward the target state defined by unharvested controls. This recovery was evident only after 14-15 years; in the earlier surveys, even assemblages at < 75% retention differed significantly from the controls. Older, higher-retention stands had more complex vertical structure (shrubs, saplings, and medium-diameter trees) than clear-cuts and low-retention stands, which were dominated by aspen (*Populus tremuloides*) saplings post-harvest. Assemblage differences between pre-harvest and unharvested control compartments, however, raise questions about the true extent of songbird assemblage recovery. After 7-8 years, species richness in the control compartments exceeded pre-harvest richness. Furthermore, after 14-15 years, significant dissimilarities in species composition were detected. Unharvested patches were likely subject to edge effects as early-successional and generalist species were attracted to adjacent harvested stands. While the potential of VRM for conserving old forest-associated assemblages by promoting recovery toward the target of unharvested controls was demonstrated, changes in the unharvested controls themselves requires further investigation.

The most worrisome conservation issue surrounding songbirds in relation to forestry has been the loss of forest older than the standard rotation age. Based on known habitat associations and previous studies, I identified six species with affinities for old forest and that were expected to be highly sensitive to forest harvest: brown creeper (*Certhia americana*), winter wren (*Troglodytes hiemalis*), ovenbird (*Seiurus aurocapilla*), black-throated green warbler (*Setophaga virens*), Canada warbler (*Cardellina canadensis*), and western tanager (*Piranga ludoviciana*). The analysis presented in Chapter 3 revealed that VRM offers similar conservation advantages for these species to those observed at the assemblage level. I showed that abundance of all of these species declined significantly below specific retention levels, relative to the unharvested controls. Significant declines were prevented at 20% retention for western tanager, 50% retention for brown creeper, winter wren, Canada warbler, and black-throated green warbler, and 75% retention for ovenbird. Significant increases were evident for all species except winter wren after 14-15 years. At high retention treatments, higher densities of large-diameter trees and snags (Langor et al. 2006; Langor 2007) may have provided more foraging and/or nesting opportunities while increased canopy closure maintained the understory characteristics favourable for these species. I am inclined to attribute increases over time to experiment-wide regeneration over the study period, with benefits spilling over all treatments, including the unharvested controls; however, regional trends or effects outside of the experiment may likewise have contributed to changes. Unfortunately, it was not computationally possible to test the hypothesis that “recovery” occurred at a faster rate in higher retention treatments using an interaction term (see Chapter 3), but evidence for accelerated change at the assemblage level (Chapter 2) suggests that this hypothesis merits targeted investigation in future work.

Change in songbird species assemblages observed in the unharvested controls raises legitimate questions about the nature of “recovery” after 14-15 years. Taken alone, the post-harvest results suggest that habitat conditions at ≥ 20% retention were moving toward the structure of those in unharvested control compartments, thus supporting recovery of similar species assemblages. Assemblage changes over time in the controls, however, beg the question: what if instead the unharvested fragments became *less* suitable for birds associated with older forest after 14-15 years? Increased species richness and average losses of pre-harvest species suggest that early-successional and generalist species might have replaced some old forest specialists in 10-ha unharvested fragments, if these fragments were able to support only a limited number of species (Wyshynski & Nudds 2009). In Chapter 3 I addressed this question by examining density responses of six old forest species. If the unharvested fragments became species-saturated after 7-8 years (Wyshynski & Nudds 2009) to the detriment of old forest associates, some or all of these species would be expected to decline at the same time.

Increases of old forest-associated species within the same time period, instead, provide further support that at some point between 7-8 years and 14-15 years after harvest, there was a shift in habitat quality that benefited old forest-associated assemblages and specialists alike. While species assemblages in the unharvested controls were apparently affected by experiment-wide harvest on the EMEND landscape, the positive responses by five of the six old forest specialists contradicts the concern raised above that habitat conditions within unharvested fragments were becoming less suitable over time.

Species assemblage changes in the harvested stands over 15 years furthermore revealed the value of unharvested reserves, not only as high-quality habitat for old forest specialists and assemblages, but also as lifeboats for their maintenance within a harvested area during the first post-harvest decade. The benefits of ≥ 20% tree retention accrued over a decade, and during this time maintenance of sufficient reserves is likely required to facilitate persistence of sensitive species in the short- and long-term. Evidence from EMEND suggests that such reserves must be > 10 ha to maintain fully intact assemblages; although the effective size limit has not yet been established, preliminary results from long-term work at the Calling Lake Experiment in Alberta (Schmiegelow et al. 1997) suggest that even 100-ha patches may be vulnerable to species declines (F. K. A. Schmieglow, pers. comm).

The findings discussed above are supported by similar studies analysing forest chronosequences (see Schieck & Song 2006), which noted substantial community changes after the first post-disturbance decade. Clearly, long-term monitoring is necessary to assess the effectiveness of forestry management practices for avian conservation, as there may be a considerable lag between management action and conservation returns.

4.2 Some caveats

Ecology is a complex field in which firm conclusions may be challenged on numerous fronts. In terms of design, experimental units cast upon nature are impossible to control in the way that they are within a laboratory, and large, accurate, and unbiased samples of living, mobile research subjects are difficult to collect. The long-term nature of this study is a mixed blessing in this respect. Monitoring at EMEND on the same plots over more than a decade underpins the most unusual and important contribution of this study to the science of forest management for avian conservation. The design and methods of the experiment, however, were therefore entrenched and could not be easily updated. Indeed, the EMEND Experiment itself was designed to accommodate a wide variety of biodiversity research without particular focus on the spatial considerations of avian surveys. This is not to say that these challenges were insurmountable; rather, that there are necessarily trade-offs when conducting research at an experiment of this scale, and as a single component of a wide-ranging project. The primary challenges arising from this study included imperfect detection, small experimental units, and the untested assumption that species density reflects habitat quality for songbirds. I consider each of these challenges, in turn, below.

4.2.1 Imperfect detection

Surveys conducted of any mobile or cryptic species in nature are invariably affected by imperfect detection, but auditory-based surveys for songbirds are subject to particular errors and bias resulting from observer, environmental, and species differences (Simons et al. 2007). Observer training reduces error (Alldredge et al. 2007), and numerous statistical methods exist to account for the error and bias that remain. One well-known method is distance sampling, by which the distances to observations are used to build a detection function and estimate the true density of a species (Buckland et al. 2008). However, accurate distance estimation is a critical assumption of distance modeling, and this is not straightforward in auditory surveys in densely forested environments (Simons et al. 2007; Alldredge et al. 2007, 2008). An analogous method is removal sampling, which builds the detection function using the time-of-detection of each observation, and assumes that detectability is primarily determined by singing rate (Farnsworth et al. 2002). Observers recorded time-of-detection in one-minute intervals in the 2012 and 2013 point counts for this study, but the detection functions developed using these data were not available for the earlier survey years, and environmental effect of a 15-year-old clear-cut on detectability surely differs from that for surveys performed in, say, a freshly harvested cutblock in 1999.

A more flexible technique using Bayesian statistics, the N-mixture (or binomial mixture) model, can build the detection function from repeated visits within a survey season (Royle 2004; Royle et al. 2007; Kéry 2008). This method seemed at first ideal for the data set at hand, but unfortunately yielded unrealistically low detection probabilities and fantastically high abundance estimates for even the most conspicuous species, most likely reflecting violation of the population closure assumption among survey rounds (P. Sólymos, pers. comm.). Although I set out on this path, it ultimately became clear that these statistical techniques, while useful where their assumptions and requirements are incorporated into survey designs, are difficult if not impossible to apply to *post hoc* data not collected by design to support them.

In Chapter 2, I made the decision to use raw counts, and restrict the data as much as was practical to limit detection bias. Indeed, while methods accounting for detection were impracticable for the reasons given above, to my knowledge they have not yet been extended to the majority of the multivariate analyses used here (Iknayan et al. 2014). For Chapter 3, work of the Boreal Avian Modelling (BAM) Project (www.borealbirds.org; Cumming et al. 2010) provided an alternative method to account for environmental effects on detection rates of different species. The R package “detect” (Sólymos et al. 2014) allows users to construct detection functions from removal and/or distance data, but additionally provides detection functions for 75 species using BAM data from nearly 90 000 survey visits to c. 35 000 points over eight years (Sólymos et al. 2013). These detection functions were constructed from variables that were measured in this study (Julian date and time since sunrise) and using variables for which I did not have perfectly matched data (proportion of forest cover and land cover class (LCC)). Applying these functions to offset the data collected at EMEND (see 3.3 Methods) was not a perfect solution, but the massive size of the BAM dataset makes it, in my opinion, the most robust option available.

4.2.2 Small experimental units

The small size (c. 10 ha) and often irregular shapes of compartments at EMEND presented a challenge to differentiating harvest treatment impacts from experiment-wide or edge effects. In Ontario, Desrochers et al. (2010) found significant positive relationships between area-sensitivity and scale of analysis for black-throated green warbler, Canada warbler, and ovenbird, suggesting that large-scale changes may be mistaken for compartment-level treatment effects. (The other species common to this study and Desrochers et al. (2010), brown creeper, exhibited no significant scale effect.) The relatively linear nature of species and assemblage responses to retention level, however, supports the likelihood that treatment signals outweighed the statistical noise produced by experiment-wide changes.

More importantly, the limited compartment sizes may have also affected the utility of the unharvested controls as statistical baselines for undisturbed forest. One of the most promising findings in Chapter 2 was that assemblage recovery relative to unharvested stands was accelerated at 20% and higher retention levels, 14-15 years after harvest. The strength of this finding was uncertain, however, given that species assemblages in the unharvested compartments at this time were significantly different from those observed prior to harvest in 1998. As discussed in Section 4.1 – Main findings, increased densities of five old forest species alleviate concerns that the unharvested controls became less suitable for old forest associates over time. It is unfortunate that it was not possible to compare the densities of individual species within the controls before and after harvest. Such an analysis might have revealed which species drove the observed assemblage changes in the controls after 14-15 years, and whether these changes were driven by declines of old forest associates relative to pre-harvest densities. As it is, accelerated assemblage recovery at 20% retention is inferred with caution, and follow-up work to verify this result is recommended in Section 4.3 – Future directions.

4.2.3 Count data as a proxy for habitat quality

Like most studies relying on point count data, this thesis assumed that high densities of a species within a compartment indicates high-quality habitat in which individuals are successfully reproducing. Realistically, however, auditory observations alone cannot distinguish paired from unpaired males, or determine reproductive success. Thus, stands with high numbers of observations may be population sinks or ecological traps (Flaspohler et al. 2002; Hannah et al. 2008). One strategy to compensate for this assumption is to assign higher weight to observations indicating breeding success (e.g. carrying nesting material or visible brood patch) (Harrison et al. 2005). However, by 2012-13, observers rarely saw birds through dense regenerating vegetation, and were even less frequently able to discern reproductive cues, and the weighting method was consequently not used.

A number of additional research methods to address this assumption are discussed in the following section (4.3 Future directions), but could not be integrated into the tight survey schedule of this 15-year monitoring update. Although potentially misleading properties of species density estimates are certainly important to bear in mind when considering the results any study using point count data, the utility of point count surveys should not be unjustly discounted. If we reject on principle research not directly supported by, for example, reproductive data, a large body of evidence for avian declines – Breeding Bird Surveys, provincial atlases, and countless studies – would be thrown out the window. Rather, point counts reveal trends and can raise the alarm where declines are noted, prompting more in-depth research of species and habitats of concern.

4.3 Future directions

This thesis raises many questions and suggests opportunities for future research about the effects of VRM on breeding boreal songbirds and other avian groups. The most interesting gaps include the causes and extent of change in the 10-ha controls, reproductive success of species-at-risk and species of concern in response to VRM treatments, and comparisons of the experimental results with patterns from both naturally burned forests and modern industrial cutblocks. Research suggested here to address these gaps includes continued work at EMEND and research in the boreal mixedwood outside of EMEND.

4.3.1 Following up on the larger EMEND landscape

A number of useful studies for EMEND have become apparent over the course of preparing this thesis. In 2013, I identified and scouted several large (20-76 ha) unharvested forest stands meeting the criteria delineating deciduous-dominated, mixedwood, and coniferous-dominated cover-types, near EMEND experiment boundaries. My objective was to conduct point counts at three stands of each cover type in addition to the full set of counts at EMEND, for comparison between the larger stands and the 10-ha controls at EMEND. Unfortunately, these stands were not accessible by all-terrain vehicle (ATV), and the additional travel time was prohibitive. Future research could be conducted at a subset of EMEND treatments (e.g. controls, 20%, and clear-cuts) to allow time to survey these larger forested stands, or access could be improved. I believe that it is critical to determine to what extent the 10-ha controls have changed compared with intact forest, and to verify whether the retention levels associated with recovery of assemblages and sensitive species in this study are reliable when compared to targets reflecting the avifauna of larger undisturbed forest tracts.

Candidate species for more focused research at EMEND include Canada warbler, listed nationally as “Threatened” (COSEWIC 2008), and ovenbird, the species in Chapter 3 that declined with as much as 50% green tree retention. I recommend studies focused on data better connected to breeding success, using field methods that include territory mapping during the breeding season, nest identification and monitoring over the nesting and fledging periods, and collection of habitat variables adjacent to nest sites. Although labour and time intensive, these methods would yield high-resolution data which would permit, among other applications, identification of habitat features, harvest techniques, and spatial variables predicting changes in reproductive output. Additional predictive models might well be developed in conjunction with spatial environmental data (e.g., Wet Areas Mapping; Murphy et al. 2007) to identify areas of high conservation priority within the larger boreal mixedwood region of western Canada (e.g., Schuster & Arcese 2013). Such a project would also benefit from data collected within larger forested stands outside the boundaries of EMEND, as discussed above.

4.3.2 Expanding size and scope

There are a number of potential studies that would complement the existing bird monitoring program at EMEND. For example, examining the effects of VRM treatments similar to those at EMEND, but at a larger scale (i.e. > 10 ha) like those comprising DMI’s new Notekiwin cut-blocks, would shed light on the interactions between cutblock size and harvest impacts on breeding bird assemblages and disturbance-sensitive species. Larger cutblocks would additionally accommodate multiple point count stations per experimental unit, as data pooled from multiple stations are more reliable than those from a single point (Toms et al. 2006). These point count stations could furthermore be strategically placed to test spatial considerations, for example distance to cutblock or intact forest edges. Finally, larger compartments and stands could support research about species with larger territories, for example woodpeckers (Order Piciformes) or crows and relatives (Family Corvidae), which were necessarily excluded from this thesis.

Perhaps one of the greatest limitations to the present analysis was the lack of available data collected in burned stands. One of the most interesting questions around VRM is whether residual trees, in fact, benefit typical communities of burned stands, or whether the physical and chemical outcomes of a fire are of equal or greater importance to these communities. Due to the difficulties delivering whole-compartment prescribed burns as planned at EMEND, comparisons between the VRM treatments and burned stands were not possible. Future work could identify, as much as possible, naturally burned forest patches of roughly equal size for comparison against equivalent-area VRM cutblocks; two fires that burned during the summer of 2015 are close to EMEND and good candidates for such work. The logistics of this type of project would be challenging, to be sure, but this type of study is essential to fill this research gap. Alternatively, Schieck and Song (2006) identified bird community studies conducted in burned, old (not recently disturbed), and harvested stands in western Canada along a chronosequence, some of which may be candidates for re-surveying if the original datasets were made available. This work would be particularly valuable for assessing the short- and long-term effects of VRM on woodpeckers compared with fire, as populations of many woodpecker species respond strongly to burned stands but then diminish over time (Brawn et al. 2001).

Finally, the study scope at EMEND did not include numerous industry practices which are common in Alberta and across Canada. The Reforestation Standard of Alberta mandates stocking objectives for harvested stands and the maintenance of mixedwoods on the landscape (Government of Alberta 2013b). Procedures to meet these guidelines often include site preparation, planting, and stand tending (chemical or physical competition removal). Small-scale site preparation and planting trials were instituted for white spruce (*Picea glauca*) within EMEND compartments (see Gradowski et al. 2008), but these procedures were not implemented at the cutblock scale at EMEND. Companion studies outside of EMEND looking at the interaction between VRM and silvicultural interventions would particularly inform conservation decisions in softwood stands, which often require planting and chemical release of conifers from competition with deciduous regeneration (Government of Alberta 2004).

4.4 Management recommendations

While preparing this thesis, a number of forest management considerations for conserving breeding boreal songbirds, particularly old forest-associated assemblages and species, have become apparent. While there remain many avenues of investigation to strengthen the results of this study or address related conservation questions, a body of existing work supports and contextualizes the recommendations provided in this thesis. In the following section I recommend VRM for medium-term (> 10 years) conservation of sensitive breeding songbirds, discuss the importance of older stands as short-term lifeboats, and identify harvest-conservation trade-offs and challenges to implementation.

4.4.1 Diversifying harvest with VRM

There were significant conservation gains for most forest songbirds at 20% green tree retention after 14-15 years, and retention levels of 50% promoted recovery of even old forest-associated species, clearly indicating the potential utility of VRM for conserving songbird breeding in harvested landscapes. However, it remains important to consider the natural disturbance history of the western boreal forest in application of green-tree retention as a conservation strategy. In Chapter 2 I described old forest as the “limiting factor” for breeding songbirds in an industrially-harvested landscape, and recommended high (≥ 20%) green tree retention as a measure to mitigate harvest effects as forest landscapes become increasingly dominated by clear-cuts. The concept of balancing harvest techniques should govern development of this strategy: a landscape harvested entirely to 20% green tree retention would, like a completely clear-cut landscape, exclude high-quality habitat for certain groups and species. High green tree retention has a clear role in conserving species and assemblages that are excluded from clear-cuts, but this role is only part of a forest management strategy that effectively balances conservation values with economic returns.

A recent analysis of economic and biodiversity trade-offs found that a combination of methods was less expensive and provided greater ecological benefits than the best single management option (Mönkkönen et al. 2014). Increased species richness across EMEND after 7-8 years, as documented in Chapter 2, supports the notion that deployment of heterogeneous harvest methods increased biodiversity, in effect maintaining early-, mid-, and late-seral species and assemblages simultaneously on this landscape. The relationships between retention value and recovery of old forest species documented in Chapter 3 reveals the value of using between 20-75% retention for conserving the six focal old forest-associated species. Thus, this study supports adding a range of high-retention treatments to the existing forest management toolbox, and shifting away from the binary logged or unlogged state that continues to dominate boreal forest management.

4.4.2 Old forest reserves

Unharvested set-asides have been identified as important habitat for source breeding populations (Kirk et al. 1996), and as a spatially conservative strategy for concentrating high-value habitat and minimizing the breadth of fragmentation (Stephens et al. 2003). In addition to existing work advocating the maintenance of intact forest areas (e.g., Kirk & Hobson 2001; Tittler et al. 2001), this thesis provides a timeline for the relative importance of these areas: unharvested reserves were evidently important for short-term life-boating of old forest-associated assemblages while partially harvested stands regenerated (Chapter 2), and for medium-term conservation of highly sensitive old forest species such as ovenbird (Chapter 3).

Recovery of songbird assemblages was not evident until 14-15 years after harvest at EMEND, when five of the six old forest-associated species concurrently experienced significant increases. Thus, harvest effects on sensitive species and assemblages were strongest in the first post-harvest decade, when only logistically unrealistic retention (75%) significantly mitigated change. Unharvested reserves provided essential local refugia for sensitive assemblages during the first post-harvest decade until moderate- to high-retention (20-50%) cutblocks had sufficiently regenerated to support them. This thesis supports the view that unharvested set-asides could mitigate the otherwise severe short-term effects of harvest (Schieck & Hobson 2000), as well as support highly disturbance- and fragmentation-sensitive boreal species in the longer term (Haché et al. 2013).

4.4.3 Trade-offs and implementation of VRM

For conservation plans to be effectively implemented, trade-offs (including economic costs) must be considered and accounted for (Naidoo et al. 2006). An economic cost/benefit analysis was beyond the scope of this thesis, but the spatial trade-off of applying VRM regionally is clear. As discussed in Chapters 2 and 3, implementation of green tree retention requires a proportionally larger harvest footprint to maintain equal harvest volumes – i.e., replacing clear-cuts with VRM will reduce the amount of undisturbed forest. In light of this trade-off, inclusion of VRM must be carefully weighed against increased footprint, particularly given the importance of undisturbed forest in the first 10-15 years after harvest.

Additionally, large-scale application of VRM will require “buy-in” and formal approval from jurisdictions that set harvest guidelines. VRM has been included in legislation and forest management policies in Sweden, Finland, and Norway since the 1980s and 1990s (Gustafsson et al. 2012), yet a minority of provincial forest management guidelines in Canada include provisions for VRM (Thorpe & Thomas 2007), and retention levels < 20% are generally applied (Gustafsson et al. 2012). The Alberta Government’s *Partial Harvest (Non-clearcut) Planning and Monitoring Guidelines* (Greenway et al. 2006) offer no clear guidance for VRM as implemented at EMEND, and forestry companies are currently penalized if they fail to harvest “the authorised volume of timber” (Government of Alberta 2013c). In some jurisdictions, industrial activities other than forestry take precedence over timber and biodiversity values. For example, oil and gas exploration and development in Alberta unpredictably affects forest management plans (e.g. Aumann et al. 2007). These obstacles to implementation in Alberta and elsewhere in Canada highlight the need for policies and guidelines that inform, facilitate, and give incentive for industrial application of VRM in the boreal forest.

4.5 Conclusions

This thesis joins a growing body of evidence supporting harvest strategies that embrace the natural variability of boreal forests as a preferred alternative to traditional clear-cutting, while recognizing the importance of maintaining older stands (stands exceeding the rotation age) on the landscape. VRM with ≥ 20% green tree retention accelerated assemblage recovery after 14-15 years, and prevented significant declines of brown creeper, winter wren, ovenbird, black-throated green warbler, Canada warbler, and western tanager. Unharvested set-asides of at least 10 ha maintained the highest densities of all six species, and assemblage changes in these reserves over time suggest that forest fragments > 10 ha are of higher conservation value. On the strength of the results presented in the thesis, I recommend incorporation of VRM (≥ 20% retention) and unharvested set-asides as part of developing a heterogeneous forest management strategy that balances conservation objectives with economic needs.

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