Landscape-level responses of boreal forest bird communities to anthropogenic and natural disturbance.

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Steven L. Van Wilgenburg

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ABSTRACT

In an attempt to manage values other than timber production, forestry companies have sought a new paradigm to manage forest resources. Based on the hypothesis that wildlife in the boreal forest has adapted to habitat structures created by natural disturbances, some forest harvests have been modified to approximate patterns left after natural disturbance. Attempts at approximating natural disturbance have included retention of patches of live trees within cutblock boundaries, cutting to natural stand boundaries and application of harvest plans with spatio-temporally aggregated cutblocks (single-pass harvests). Single-pass harvesting is a recent attempt to better approximate natural disturbance in the boreal and has not been evaluated for its potential to sustain wildlife. I therefore contrasted residual patch pattern and composition, as well as landscape-scale avian abundance and composition in 1) single-pass; 2) multi-pass; and 3) salvage logged post-fire harvests, and contrasted these with unsalvaged post-fire sites. Post-fire sites were used to define the Natural Range of Variation (NRV). Seventy-two plots (12 post-fire, 15 post-salvage harvest, 16 single-pass harvest, and 29 multi-pass harvest) were surveyed for avian community composition and abundance one to five years post disturbance.

I contrasted the composition of remaining live forest stands at the landscape-scale and in residual patches by pairwise comparison of pre- and post-disturbance composition. At the landscape-scale, non-metric mutlidimensional scaling suggested post-disturbance landscape composition of post-fire and salvage-logged plots was similar to pre-disturbance landscape composition, with a tendency toward greater survival of hardwoods and lower survival of jack pine (*Pinus banksiana*) or black spruce (*Picea mariana*). However, harvesting of hardwoods and

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mixedwood stand types in single and multi-pass harvests led to landscapes with more bog and swamp habitats.

Comparison of residual patch composition with pre-disturbance composition was made using blocked multi-response permutation procedures. Post-fire plots (i.e. NRV) had residual patches that were representative of pre-disturbance composition, but with slightly more hardwoods and less black spruce/jack pine than expected by chance. All harvested treatments had similar biases among residuals to those left by fire, except that multi-pass harvests tended to leave less mixedwood habitat than expected. Multi-pass harvests also had less area in residual patches, and patches were smaller, more isolated and less complex in shape. Single-pass harvests had residual patches that were more representative of the size, shape, complexity, and change in composition seen post-fire. Multi-pass harvests only had 14% of the residual patch area in patches at least 5 ha in size, whereas this proportion was higher in fire (83%), salvage-logged areas (42%), and single-pass harvests (57%). Old-growth associated species might only persist in patches 5 ha or larger, and so multi-pass harvesting may have negative consequences for these forest birds.

Redundancy analysis indicated that bird communities differed from the NRV in all harvest treatments. However, single-pass harvests provided a slightly better fit to NRV than did multi-pass harvesting. Community similarity was influenced by non-linear responses to area harvested, residual retention, residual composition and pre-disturbance forest composition. An optimization routine was used to select harvest characteristics that would maximize community similarity to NRV. Optimization suggested that community similarity to NRV can be maximized by using single-pass harvests over multi-pass harvests, harvesting 66-88% of of a planning unit, and retaining 5-19% of the harvest area as live residual patches.

My results suggest that single-pass harvesting may be ecologically more sustainable than multi-pass harvests. Future studies are required to determine whether both harvesting treatments converge with NRV through time. Greater overlap of salvage-logged avian communities with NRV suggests that experimentation with prescribed fire as a post-harvest treatment may be the best method to bring harvests ecologically closer to NRV, and highlights the need to conserve early post-fire habitats.

To my wife Enid, I am eternally indebted for your love, support, and assistance in transcription of recorded bird songs, and in the field surveys. Furthermore, the patience, love and support of Enid and my sons Declan and Dylan, has made the past few years the best of my life.

DEDICATION

For my father. I owe much of my curiosity and love of the natural world to you. Thank you.

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CHAPTER 1. GENERAL INTRODUCTION

1.1 Avian responses to traditional forestry

The southern boreal mixedwood forest of western Canada supports one of the richest

communities of breeding birds in North America (Hobson and Schieck 1999; Kirk et al. 1996,

Kirk et al. 1997). This is due, in part, to the diversity and mosaic of habitats historically created

by natural disturbances within the boreal forest (Hobson and Schieck 1999). Boreal forest bird

communities are affected by many factors, particularly stand age, composition, vertical structure

and understory composition (Cumming and Diamond 2002; Hobson and Bayne 2000a; Hobson

and Bayne 2000b; Kirk et al. 1996, Kirk et al.1997). Relative to natural disturbance scenarios,

forest management and fire suppression will likely result in changes to forest composition and

structure that affect bird communities at scales ranging from within stand to across landscapes

(Schieck and Hobson 2000). Due to the evolved adaptations of bird communities to forest

structures shaped by wildfire, there is concern that harvesting practices may put those bird

communities associated with early post-fire or late successional habitats at risk (Hannon and

Drapeau 2005; Hobson and Schieck 1999).

Traditionally, forest management has sought to maximize the yield of timber products

available for harvesting operations (maximum sustained yield, hereafter MSY). Forest age

structure favoured by MSY follows an even-age class distribution which is truncated at the forest

rotation age (Thompson et al. 2003). Concern over truncation of forest age structure due to

forestry practices has led to several recent investigations examining the response of birds to stand

age. These investigations suggest that species richness tends to be greatest in forest stands

beyond rotation age, and that significantly more species reach their greatest abundance in post-

rotation aged stands than in younger stands (Cumming and Diamond 2002; Hobson and Bayne 2000a; Kirk and Hobson 2001; Schieck et al. 1995; however, see Westworth and Telfer 1993). As many as 34 species in the western boreal reach their highest densities in post-rotation aged stands (Cumming and Diamond 2002; Hobson and Bayne 2000a; Kirk and Hobson 2001; Schieck et al. 1995). As stands mature, canopy nesters, cavity nesters, and species associated with the white spruce component of mature/old aspen or mixedwood stands contribute proportionately more to the bird community than in early succession (Cumming and Diamond 2002; Hobson and Bayne 2000a). However, the greatest divergence between post-fire and post-harvest bird communities occurs immediately following disturbance, with early post-fire sites having high densities of post-fire specialist cavity nesting species (Hobson and Schieck 1999). Thus, early seral stages also are important to boreal birds (Hobson and Schieck 1999).

Forest harvesting and silvicultural practices designed to maximize timber yield may also cause conversion of mixedwood stands into monospecific coniferous or deciduous stands (Hobson and Bayne 2000b, Thompson et al. 2003). "Unmixing" of mixedwood forests could occur either through active management for monocultures, or through difficulties of forest succession under short-rotation management (Haeussler and Kneeshaw 2003). Although recent policies generally favour regeneration of mixedwood stands, there is still substantial concern that forest stands will not regenerate along the same successional trajectories as under natural disturbance (Haeussler and Kneeshaw 2003). This concern led Hobson and Bayne (2000b) to examine whether bird communities in mixedwood forest harbour unique species assemblages, or whether bird communities in mixedwood stands were simply an amalgamation of communities associated with "pure" forest stands. Hobson and Bayne (2000b) found that mixedwood stands actually had both greater richness and abundance of individuals than their pure stand

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counterparts. In particular, Chipping Sparrow (for all scientific names, refer to Appendix A),

Pine Siskin, White-winged Crossbill, Red-breasted Nuthatch, Swainson's Thrush, and Tennessee

Warbler were more abundant in mixedwood stands than in pure stands. These trends were

consistent among nesting guilds and migratory strategies. Targeted harvesting of old aspen- and

white spruce-dominated mixedwood stands may therefore have a particularly negative influence

on bird communities if silvicultural practices that promote mixedwood regeneration are not

employed on a sufficiently wide scale (Hobson and Bayne 2000b).

In addition to changes in forest age structure and composition, forest harvesting leads to

habitat fragmentation. The effect of habitat loss and fragmentation on forest bird communities

has been a very active area of research for the past two decades. The degree to which bird

communities are affected by habitat change or loss, as opposed to configuration effects, is

difficult to separate, and is poorly studied in areas dominated by forestry. In general, research

into forest fragmentation has been conducted in habitats dominated by agriculture or with long

disturbance histories (Schmiegelow and Mönkkönen 2002). Investigations examining

fragmentation within industrial forest contexts have often found much smaller effects than seen

in more disturbed habitats (Schmiegelow and Mönkkönen 2002; Trzcinski et al.1999). This may

be due to lower levels of disturbance, forest re-growth effects, the relatively short disturbance

history, or less change in predator communities relative to agricultural landscapes (Schmiegelow

and Mönkkönen 2002). However, as industrial forestry progresses through rotations, the

possibility that threshold levels of forest fragmentation are reached increases (Villard et al.

1999). Recent work in landscape ecology suggests that such thresholds exist and more work is

required to assess their role in the forestry context (Rempel et al. 2004; Villard et al. 1999).

Recent work by Rempel (2007) in the boreal forest of Ontario, suggests that although both amount and configuration are important, there was no strong evidence of threshold effects.

Until recently, little attention has been paid to the impacts of post-fire salvage logging on forest bird communities (Lindenmayer et al. 2004; Morrisette et al. 2002). The practice of salvage harvesting of fire-damaged trees before they decay or are further damaged by insects may be of particular concern for post-fire specialists such as Black-backed and Three-toed woodpeckers (for scientific names, see Appendix A). Concerns regarding the conservation of post-fire specialist species are exacerbated by the fact that many of these species are also associated with late-seral habitats targeted by forestry activities (Hobson and Schieck 1999; Imbeau and Desrochers 2002; Koivula and Schmiegelow 2007; Schmiegelow et al. 2006). In a study conducted in the boreal forest of Saskatchewan, Morrisette et al. (2002) found that unsalvaged post-fire forest stands contained unique assemblages of species relative to their salvage logged and unburned counterparts. In particular, salvage logging negatively influenced all cavity nesting species (except House Wren and Tree Swallows) and resident birds such as Boreal Chickadee, Red-breasted Nuthatch, and Brown Creeper (Morrisette et al. 2002). Similar results were seen in the boreal forest of Alberta, where salvage logging caused lower abundance of cavity nesters and fewer species than seen in burned and unsalvaged stands (Koivula and Schmiegelow 2007; Schmiegelow et al. 2006). Cavity nesting species may be negatively influenced by salvage logging due to reductions in abundance of standing dead material and the nesting and foraging substrates that they provide. Salvage logging is also expected to target larger trees that may be more suitable for cavity nesters.

1.2 Natural Disturbance Emulation

Industrial-scale forest harvesting is relatively recent (<30 years) in western Canada, and the primary disturbances structuring the forest landscape are large wildfires (Cumming 2001; Weber and Stocks 1998). However, with increasing forest harvesting and fire suppression, forestry could replace fire as the primary disturbance agent. Concern over the ecological sustainability of maximum-sustained yield forestry has lead researchers and foresters alike to search for a new paradigm with which to manage forestry operations. This has led to the forest industry moving toward the adoption of ecosystem-based management approaches to incorporate values other than timber supply (Boutin and Hebert 2002). The ecosystem management approach to forestry in the boreal assumes that wildlife has adapted to forest disturbances such as large, stand-replacing fires and other natural disturbances (Hunter 1993). Based on this premise, ecosystem management in boreal forests has become a paradigm of natural disturbance "emulation"; attempting to approximate, where possible, patterns created by disturbances such as fire (Bergeron et al. 2002; Hobson and Schieck 1999; McRae et al. 2001).

Operationally, it is not the process of fire that the foresters seek to approximate; it is only the physical structure and patterns resulting from fire and subsequent forest succession that foresters can most practically emulate (Bergeron et al. 1999). In keeping with this paradigm, forestry has moved away from conventional two- or three-pass clear-cut logging with cut and leave blocks toward partial cut or variable-retention harvesting (Schieck et al. 2000, Tittler et al. 2001). These approaches retain structure within the boundaries of harvests by leaving single trees or "island" remnants of standing trees from the previous stands. In addition to retaining in-block structure, other methods of emulating the patterns left after fire include cutting to natural boundaries (e.g. previous stand boundaries, wetland edges, etc.), and basing target age class distributions on those

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predicted by natural fire frequency such as the negative exponential age class distribution (Hunter 1993; Hunter 1999; Bergeron et al. 1998; Bergeron et al. 2002).

Thus far, the ability of Natural Disturbance Emulation (hereafter NDE) forestry to maintain bird communities similar to those seen post-fire have primarily been made for island remnant patches. Comparisons made at a patch scale between post-fire and post-harvest sites over a chronosequence up to 30 years post-disturbance suggest that emulation forestry results in only partial convergence of bird communities with post-fire sites (Hobson and Schieck 1999; Schieck and Hobson 2000; Schulte and Niemi 1998; Simon et al. 2002) with closer convergence at 60 years. These studies suggest that leaving more complex vegetation structure in cutblocks has resulted in maintaining some characteristics of old growth forest (Hobson and Schieck 1999; Schieck and Hobson 2000); however, there is still difficulty in maintaining components of vegetation and bird communities in clear-cuts relative to early post-fire sites (Hobson and Schieck 1999; Schieck and Hobson 2000; Simon et al. 2002). In particular, approximation of natural disturbance is limited to structural characteristics within the disturbed portion of the landscape. Forestry, by default, removes a substantial proportion of the aboveground (tree) biomass from the landscape, whereas fire burns a great deal of material yet leaves significant standing dead structure (snags) within the disturbed area. In addition, fire disturbs the understorey of many live residual stands where fire intensity was low. These differences between fire and harvest lead to very different habitats available for forest bird communities early in succession, until snags begin to fall and forest structure becomes more similar with forest re-growth (Hobson and Schieck 1999; Schieck and Hobson 2000).

The spatial and temporal aggregation of cutblocks associated with single-pass harvesting whereby harvesting is done in one time period and operations do not reoccur until the next

rotation, represents another potential advance toward natural disturbance emulation (Delong 2002; Öhman and Lämås 2003). This harvest technique can also incorporate variability of disturbance size classes seen in natural disturbances, an aspect of "emulation" forestry that has received little attention until recently. Most jurisdictions limit cutblock size to 150 ha or less, whereas fires may burn areas up to 100s or 1000s km^2 (Bergeron et al. 2002; McRae et al. 2001). While creation of larger cutblocks might allow the forest industry to decrease the "footprint" of roads and habitat fragmentation of the remaining forest (Delong 2002; Öhman and Lämås, 2003), other benefits may be less clear. In addition, increased isolation of residual patches within larger cutblocks may lead to differences in probability of occurrence or abundance for some species. However, greater ranges in variation of remaining structure are generally seen in larger disturbances (Bergeron et al. 2002; Schulte and Niemi 1998), therefore, larger cutblocks may overlap with post-fire forests in structural attributes. To my knowledge, no field study has explicitly examined the impacts of single-pass harvesting on forest birds. Several simulation studies suggest that traditional multi-pass harvest planning leads to bird communities that diverge from the Natural Range of Variation (hereafter NRV) expected under natural disturbance, whereas plans favouring larger harvest blocks and spatio-temporal deferment of harvests show a lesser degree of divergence from NRV (Loehle et al. 2002; Loehle et al. 2006; Rempel et al. 2007).

1.3 Thesis Outline and Objectives

The objective of this thesis is to test the hypothesis that natural disturbances emulation forestry can bring harvesting practices ecologically closer to fire disturbed areas. My specific objectives were to assess; 1) how are bird communities influenced by each anthropogenic disturbance relative to natural disturbance (fire); and 2) which attributes (residual composition,

configuration and pattern) of these landscapes are critical to the maintenance of forest-bird communities? I predicted that songbird community composition would be most similar relative to fire-generated landscapes in the following order, ranked from most to least similar; post-fire sites with salvage logging, single-pass post-harvest sites with residual standing structure left on site, and conventional multi-pass harvest sites with residuals. Furthermore, I predicted that avian similarity to that in unsalvaged post-fire sites will be driven by amount and variability in distribution (within the disturbance area e.g. cutblock) of residual trees (clumps and single trees). More specifically, I hypothesized that the larger disturbances (single-pass harvesting and salvage logging), will be more similar in avian composition and relative abundance to that in post-fire sites than in multi-pass harvesting, due to greater variability in amount, location and configuration of residual patches. Where differences in avian communities between post-fire and single-pass/multi-pass harvest sites occur, I hypothesized that these differences will be due to differences in early successional plant community composition.

To gain a full understanding of how forest bird communities are influenced by anthropogenic and natural disturbances at the landscape scale, a thorough understanding of the habitats created by each disturbance is necessary. To that end, Chapter 2 examines "island" remnant area and composition and how it is influenced by disturbance type and pre-disturbance forest characteristics. In Chapter 3, I test the hypothesis that emulating natural disturbances can bring bird communities closer to those seen in post-fire landscapes, and examine the role of residual retention in achieving this goal. Due to the statistical complexities of the data, I provide Appendices outlining the modeling and estimation of detectability for the point-count data used in Chapter 3. Finally, in Chapter 4, I discuss the effects of natural versus anthropogenic disturbances on forest bird communities.

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CHAPTER 2. DOES FORESTRY SUCCESSFULLY "EMULATE" POST-FIRE PATTERN AND COMPOSITION OF RESIDUAL FOREST PATCHES?

2.1 Abstract

Retaining islands of remnant habitat within forest harvest areas is a key method in approximating patterns left after natural disturbance. Creation of such patterns is one potential method to conserve biodiversity where forest harvesting occurs. However, fire and forestry are different processes, and therefore are expected to leave different patterns on the landscape. The degree to which fire versus forestry result in different patterns of residual material after disturbance has not previously been described. Such a description is necessary if island remnants within forestry operations are to approximate those patterns found post-fire. This is particularly crucial if the objective of maintaining similar biodiversity to naturally disturbed landscapes is to be met, since many wildlife groups (e.g. birds) have unique inter-specific differences in habitat requirements. I therefore contrasted pre-disturbance landscape composition with composition of residual patches following single-pass harvests, multi-pass harvests, post-fire salvage logging, and fire (without salvage logging). I also quantified fragmentation of the resulting residual patches and contrasted fragmentation and area of residuals between treatments. Post-fire plots that were not salvage logged were disturbed stochastically, leaving residual patches that were fairly representative of pre-disturbance composition, but with a slight bias toward leaving more hardwoods and disturbing more black spruce and jack pine than expected. The harvested treatments all showed similar biases to those of fire, except that multi-pass harvests tended to leave less mixedwood habitat than expected. Multi-pass harvests also had much less area in residual patches than the other three treatments, and the patches were smaller, more isolated and less complex in shape. Single-pass harvests were more representative of the size, shape, complexity, and relative change in composition seen after fire. Structurally, single-pass harvests

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and salvage harvests provide a better fit to natural range of variation (NRV) than multi-pass harvests.

2.2 Introduction

The shift towards ecosystem-based management approaches within the forest industry (Boutin and Herbert 2002), can be seen as a coarse-filter approach to addressing sustainability. Forestry operations in the boreal forest of western Canada have largely adopted natural disturbance emulation as the coarse-filter approach for biodiversity conservation, on the assumption that maintaining the breadth of habitat types and configurations created by natural disturbances can preserve biota adapted to habitats created by forest disturbances such as large, stand-replacing fires and other natural disturbances (Hunter 1993). Operationally, natural disturbance emulation has been implemented by studying and emulating disturbance patterns, sizes and disturbance rates described from studies of natural disturbances. Within the boreal forest, the focus has been on attempting to approximate, where possible, patterns created by wildfire since fire is the primary disturbance agent in this ecosystem (Bergeron et al. 2002; Hobson and Schieck 1999; McRae et al. 2001).

Ecosystem management based on natural disturbance "emulation" necessitates detailed knowledge of regional patterns and rates of disturbance in order to provide defensible management planning. Therefore, detailed studies of natural disturbance patterns are becoming increasingly common in order to manage for biological values, without having to manage on a species-by-species basis (Baker, 1992; Cissel et al. 1999). If boreal wildlife has adapted to natural disturbance, the probability of maintaining appropriate biodiversity might be maximized by "emulating" as closely as possible the local rates and patterns of disturbance that occurred historically (Bergeron et al. 2004; Hansen et al. 1991, Landres et al. 1999). In the case of boreal

forest birds, numerous species are habitat specialists, requiring specific combinations of forest age, composition and/or structure (Cumming and Diamond 2002; Hobson and Bayne 2000a; Hobson and Bayne 2000b; Hobson and Schieck 1999; Rempel 2007; Schieck and Hobson 2000; Schieck et al. 2000; Villard et al. 1999). In addition, the response of forest birds to forest residual retention has been shown to be dependent on habitat type (Harrison et al. 2005; Schieck and Song 2006). Given the greatest divergence between post-fire and post-harvest bird communities occurs immediately following disturbance (Hobson and Schieck 1999; Schieck and Hobson 2000), it is particularly important that retained habitats within cutblocks reflect as closely as possible those seen post-fire. This may be even more crucial as several of the species at greatest risk due to forestry activities are associated not only with preferentially targeted old-growth forests, but also with early post-fire habitats (Hobson and Schieck 1999).

The boreal forest of Canada is extremely diverse, with disturbance rates varying regionally due to climatic and topographic conditions. Stand-replacing fires that initiate forest re-growth, have fire-return intervals averaging from 130-700 years across Canada (Bergeron et al. 2004; Stocks et al. 2002); however, fire return intervals are extremely variable and show geographic variation, with more northerly and westerly portions of the boreal having short return intervals as low as ~50 years since the end of the Little Ice Age (Belleau et al. 2007). Local topographic effects, climatic conditions and soil moisture conditions lead to significant variability in the degree of tree mortality occurring during a wildfire event (Eberhart and Woodard 1987). Extremely dry climatic conditions tend to lead to fires with more stochastic effects due to extremes in burning periods and influences of variable climatic conditions during the fire (Bessie and Johnson 1995; Eberhart and Woodard 1987). However, in less severe conditions, forest composition affects stand susceptibility to fire ignition and/or mortality due to fire, with

hardwood stands having lower likelihood of mortality (Bessie and Johnson 1995; Cumming 2001). Estimates from previous studies suggest that island remnants of live residuals within fire boundaries make up 3-37% of the disturbance area (Eberhart and Woodard 1987; Smyth et al. 2005). Recent estimates from 29 historic fires in Saskatchewan suggest mean area of island remnants is approximately 27% of the disturbed area, but ranged from 5-50% (Andison 2006).

The degree to which forest harvests can encapsulate the natural range of variability (NRV) of post-fire forest age, complexity and composition has not previously been described. The technical, financial and regulatory constraints on forest harvesting in general leads to targeted harvesting of the largest and most economically valuable forest stands. It is therefore unlikely that harvesting could completely encompass NRV since forest fires are typically stochastic in burn patterns and consume stands that are not necessarily commercially viable. This is particularly the case for the largest fires which make up only two to three percent of fires, but account for approximately 98% of the total area disturbed annually (Weber and Stocks, 1998). Furthermore, where bias in the fuel "preference" of fires occurs, it tends to be towards greater consumption of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*), and less hardwoods than would be expected based on pre-fire landscape composition (Cumming 2001). Forest harvesting in the boreal of western Canada on the other hand, preferentially harvests hardwood, white spruce and mixedwood dominated habitats and make less use of black spruce (Cumming 2001).

Previous research has focused on comparing pre- and post-disturbance landscape characteristics at the scale of entire fires (e.g. Cumming 2001). These studies tended to use medium resolution data, and hence did not capture small (i.e. <2 ha) island patches. Given the emphasis on residual patches in Natural Disturbance Emulation (NDE) forestry, there is a need

to examine whether patterns at the scale of entire fires hold true at smaller scales and how well NDE forestry emulates these patterns. The objective of this study was to examine how island remnant area and residual forest composition differ between early post-fire habitats and three key forest-harvesting approaches (post-fire salvage harvesting, multi-pass harvests with residual retention, and single-pass harvests with retention).

2.3 Methods and Study Design

The study area extended from Candle Lake, Saskatchewan in the east (53° 50' N; 105° 50' W) to the House River Fire in north-eastern Alberta (approximate location 56° 44' N; 111° 23' W; Figure 2.1). This area was located within the Boreal Plain Ecozone, a gently rolling plain, covered by boreal mixedwood forest including trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), white birch (*Betula papyrifera*), jack pine, white spruce (*Picea glauca*), black spruce, balsam fir (*Abies balsamea*) and tamarack (*Larix laricinia*) (Acton et al. 1998; Rowe 1972). Successional patterns within the Boreal Plain are complex, with a heterogeneous mosaic of habitats created through multiple-stand disturbance patterns (Weir et al. 2000).

Site selection was limited by the number of existing aggregated harvests in the study area. I therefore attempted to select disturbances in the other treatments that were as similar as possible in pre-disturbance vegetation composition to the single-pass harvests. In order to avoid bias associated with forest succession following disturbance, I first selected areas within the study area containing recent (<5 years prior to sampling) disturbances. A series of 400 ha overlays were used to select areas within recent disturbances having approximately 50% of the stands being rotation age and classified as hardwood and/or hardwood- or softwood-dominated mixedwood stands. Due to many of the fires having lower proportions of stands meeting my selection criteria, I selected a subsample of 1.6 by 1.6 km (256ha) plots from within the overlays

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that had composition closest to the selection criteria. The 256 ha plots were then treated as the

sample units. Based on these plots, proportions of the plots meeting the selection criteria were

reasonably similar between disturbance types (Fires $=0.43 \pm 0.22$ SD; Salvage$=0.41 \pm 0.19$ SD;

Single-pass$=0.51 \pm 0.22$ SD; Multi-pass$=0.49 \pm 0.29$ SD). In addition, plots in the salvage-

logged, single-pass and multi-pass harvesting treatments were selected for similar levels of

harvesting between treatments. For multi-pass harvest sites, I restricted sampling to areas that

had recent harvest; of theses sites, four had only the first pass completed (median cutblock age=

2 years, min= 0 y, max= 6 y), 21 had the second pass completed (median cutblock age= 2.5

years, min= 0 y, max= 17 y), and four had the third pass completed (median cutblock age= 4

years, min= 0 y, max= 25 y). Attempts were also made to cover similar spatial gradients across

all treatments (Figure 2.1).

Seventy two plots were selected amongst four treatments (Figure 2.1). These plots consisted

of 12 post-fire, 15 post-salvage harvest, 16 single-pass, and 29 multi-pass harvest plots. Twelve

post-fire control plots were located in areas burned in 1998 (Cobra Fire), 2002 (Chitek Fire,

House River Fire, Timber Fire, Milo Fire) and 2003 (Pasture/Rawhide Fire). Fifteen post- fire

salvage plots were surveyed in the eight separate fires (Chitek Fire, Dore Fire, House River Fire,

Timber Fire, Milo Fire, Pasture/Rawhide Fire). Single-pass plots were distributed among three

large-scale (1200-2700 ha harvested) and five small-scale aggregated harvests (250-400 ha).
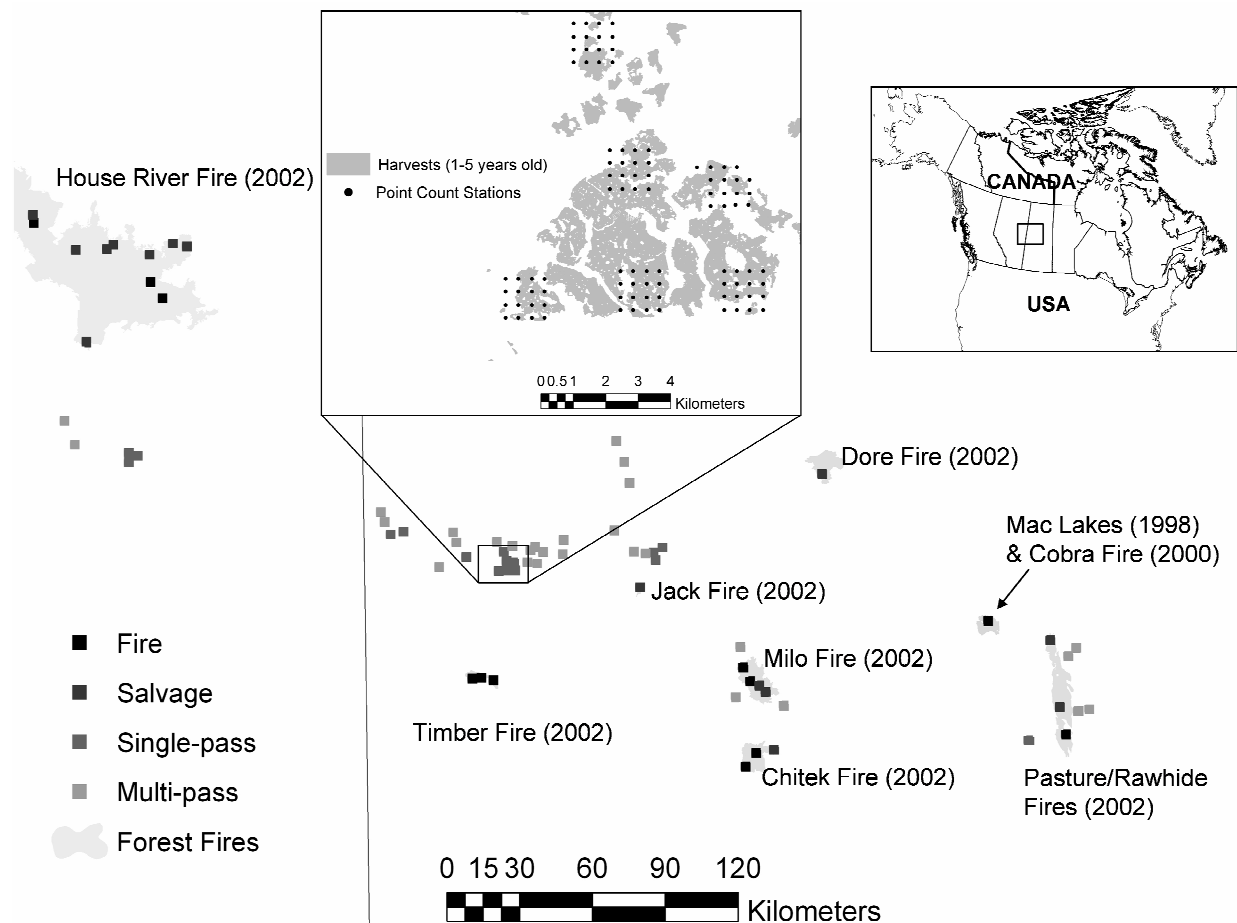
Figure 2.1. Study design in the boreal forest of western Saskatchewan and eastern Alberta, Canada. Upper right, location of the study area in Canada. Large map: spatial arrangement of 72 plots across the study area by type of treatment; names and year burned are given for sampled forest fires. Inset (centre): example layout of point count stations within plots at a single-disturbance event; white background represents undisturbed habitats.

2.3.1 Measuring Landscape Composition

Vegetation variables were collated from GIS analysis of digital cover maps. Since data came from three FMAs in two provinces, I standardized Forest Inventory data into a few ecologically meaningful species associations. Estimates of pre-disturbance area covered by hardwood, softwood, hardwood-dominated mixedwood, and softwood-dominated mixedwood and non-merchantable habitats were generated for each plot using ArcGIS v. 9.1 (Table 2.1).

Remnant forest islands smaller than the resolution of forest inventory data (~2-4 ha depending on FMA) were mapped by using Garmin 12XL handheld GPS receivers and position- averaging of all apex co-ordinates. To ensure acceptable precision, data collection was limited to times when 3D navigation was available and the satellite constellation provided (GPS) estimated horizontal accuracy of ≤ 7 m (Holden et al. 2002). Horizontal accuracy for consumer-grade GPS receivers is approximately 15 m (Moore et al. 2001). Residual patches in six disturbances were digitized from IRS satellite imagery (5 m panchromatic). For a subset of nine patches mapped by both IRS image and GPS survey, there was no difference in patch area, perimeter or centroid co-ordinates (unpublished data). In the case of the House River Fire, however, a classified Landsat 7 image of burn intensity was used to categorize residual islands. The Landsat 7 image was classified by Ducks Unlimited Canada (Edmonton) into three burn intensity scores (high, medium, and low) based on ground survey data; however, I reclassified this into a binary variable, categorizing the low burn intensity cells (defined as >95% canopy survival) as residual, and all other cells were classified as destroyed by fire. Overlay procedures in ArcGIS were used to generate total area of residuals per plot, and extract forest inventory variables associated with the residual patches (Table 2.1).

Table 2.1. Vegetation parameters obtained from GIS queries and field estimates used to control for differences in plot vegetation.

Variable	Description
H	%Area (ha) composed of Hardwood Dominant stands
HS	%Area (ha) composed of Hardwood Dominated Mixedwood stands
S	%Area (ha) composed of Softwood Dominant stands (bF[1] or wS[2])
SH	%Area (ha) composed of Softwood Dominated Mixedwoods (bF or wS)
OHS	%Area (ha) dominated by Hardwood stands (bS[3] or jP[4] leading)
OSH	%Area (ha) dominated by Softwood stands (bS or jP leading)
OC	%Area (ha) composed of Softwood Dominant stands (jP or bS leading)
Bog	%bS leading on wet soils
Fen	%tL[5] leading on wet soils
Swamp	%High shrub or low shrub dominant
Water	%Open water
Meadow	%Grass or sedges leading
Age0	%Area (ha) 0-2 years old
Age2	%Area (ha) 2-5 years old
Age5	%Area (ha) 5-30 years old
Age30	%Area (ha) 30-60 years old
Age60	%Area (ha) 60-80 years old
Age80	%Area (ha) 80-100 years old
Age100	%Area (ha) >100 years old

[1] Balsam Fir; [2] White Spruce; [3] Black Spruce; [4] Jack Pine; [5] Tamarack

To measure landscape structure of plots, polygons within the plots were assigned categories of either disturbed (burned and/or harvested), residual, or contiguous forest. Polygon boundaries were then dissolved (i.e. lumped together) on the basis of these categories, and landscape fragmentation metrics calculated for each of these categories using Patch Analyst extension V. 3.1 (Rempel and Carr, 2003) in ArcView V. 3.2 (ESRI, Redlands, CA). I calculated five classes of fragmentation metrics; area-based metrics, patch-density/size metrics, patch-variance metrics, edge metrics, and shape metrics (Table 2.2).

Table 2.2 Fragmentation metrics used to describe fragmentation of residual patches within plots located in early post-fire, salvage logged post-fire, single-pass harvest and multi-pass harvest landscapes within the boreal mixedwood ecozone. Landscape were reclassified into only three habitat classes (residual, disturbed, and contiguous forest) and dissolved prior to calculating fragmentation metrics.

Metric	Name
Area based	
CA	Class area (ha) for a specific habitat type
Patch size/density	
NumP	Number of patches
MPS	Mean patch size (ha)
MedPS	Median patch size (ha)
Patch variance	
PSCov	Patch size coefficient of variation
PSSD	Patch size standard deviation
Edge	
TE	Total edge (m) within the landscape
ED	Edge density (m/ha)
MPE	Mean patch edge (m)
Shape	
MSI	Mean shape index
AWMSI	Area weighted mean shape index
MPAR	Mean perimeter/area ratio
MPFD	Mean patch fractal dimension
AWMPFD	Area weighted mean patch fractal dimension

2.4 Data Analysis

2.4.1 Landscape Composition Pre and Post Disturbance

I compared overall landscape composition of pre- and post-disturbance landscapes within and between treatments using multivariate ordination. This analysis was limited to the live (unburned and/or unharvested) portion of the landscapes, including both island residuals within the disturbed portion of the landscape and adjacent leave areas and matrix residuals (e.g. corridors and peninsulas). Both pre- and post-disturbance vegetation were included in the same matrix, and samples coded separately by combination of treatment and pre- versus post-disturbance. Ordination was conducted using non-metric multidimensional scaling (NMS) in PC-ORD v. 5.0 (MjM Software, Gleneden Beach, Oregon). NMS was conducted using the Sorenson distance measure, with 40 runs of the real data and 50 runs of randomized data and dimensionality was selected using a Monte Carlo test.

2.4.2 Fragmentation and Area of Residual Islands

To reflect overall fragmentation of residuals, the metrics of which can be highly correlated, I made comparisons using multivariate methods to reduce dimensionality. Ordination was conducted using NMS with the Euclidean-distance measure, with 40 runs of the real data and 50 runs of randomized data. Differences between treatments were statistically compared using multi-response permutation procedures (MRPP) based on Euclidean distance with rank transformation of the distance matrix to make results comparable to the NMS ordination (McCune and Grace 2002), and pairwise comparisons made against the unsalvaged post-fire treatment.

I further investigated between-treatment differences in area of residuals using General Linear Models. I considered three candidate models; treatment, treatment + area harvested, treatment +

area harvested + treatment by area harvested. Model selection was made using Akaike's

Information Criterion (AICc) to select between competing models and account for both model fit

and complexity (Burnham and Anderson 1998). Prior to analysis, area of residual data were

log(x+1) transformed to achieve homogeneity of variance. In addition, I present summary

statistics on the distribution of size classes of individual patches expressed as proportion of total

residual patch area within a treatment.

2.4.3 Composition of Residual Islands

If disturbances acted stochastically, composition of residual island remnants should, on

average, reflect pre-disturbance landscape composition (i.e. each habitat type should be

represented in similar proportions pre- and post-disturbance). Therefore, I compared habitat

composition of residual patches to the pre-disturbance landscape composition using blocked

multi-response permutation procedures (MRBP), with the analyses blocked by plot. MRBP

analysis was conducted on Euclidean distances. Each treatment was analyzed separately, since I

suspected *a priori* that the treatments would differ in their "habitat preferences"; furthermore,

unequal sample sizes are not compatible with analyses designed for completely randomized

block designs. MRBP and calculation of multivariate medians was conducted using the Blossom

statistical package, all possible permutations were used in calculation of statistical significance

(Cade and Richards 2005).

To examine if specific habitats were represented more or less than expected based on chance,

I first graphed multivariate median composition of each habitat type pre and post disturbance.

Where residual composition differed from expectations within treatment (based on MRBP

analyses), those habitats showing graphical differences in pre- and post- disturbance,

multivariate median proportions and large average Euclidean distances were tested using 4999

permutations based non-parametric ANOVA (PERMANOVA) on Euclidean distances (Anderson 2001). PERMANOVA analyses were conducted using PC-Ord V. 5.0 (McCune and Medford 2006). To control for multiple comparisons, I used the False Discovery Rate (FDR) control (Benjamini and Hochberg 1995). FDR is conducted by sequentially ordering the p-values of a set of comparisons, then assessing significance at $\alpha*i/m$, where i is the comparison number and m is the total number of comparisons. Statistical significance was assessed at $\alpha=0.05$.

2.5 Results

2.5.1 Landscape Composition Pre- and Post-Disturbance

Vegetation composition was best represented by a two-dimensional solution. Final stress (goodness-of-fit) was 16.6, significantly lower than could be achieved by chance ($p<0.02$). The two axes represented a cumulative 87.0% of the variance in the landscape composition, with axis 1 representing 66.9% of the variance, and axis 2 representing 20.0 % of the variance. Axis 1 was positively correlated with area of H (see Table 2.1 for habitat acronyms; Kendall's tau=0.802) and negatively correlated with other conifer (OC) habitat (tau= -0.711) and thus represented a gradient from upland hardwoods to jack pine or black-spruce dominated sites. Plots in the single-pass and multi-pass harvests tended to be composed of more hardwoods and less black spruce or jack pine (OC) habitats than plots in the post-fire treatments both prior to and after disturbance (Figure 2.2). Axis 2 was positively correlated with hardwood dominated mixedwood (HS; tau= 0.537) and softwood dominated mixedwood (SH) habitats (tau=0.492) and negatively correlated with shrubby swamp (-0.361). Landscape composition changed very little in post-fire and salvage-logged landscapes, but considerably in multi-pass harvests (Figure 2.2). Calculation of pair-wise differences in pre- and post-disturbance compositions, and examination of the

ordination suggest that in general, H, HS and SH representation decreased in single-pass and multi-pass harvest landscapes. The harvesting of H, HS and SH habitats lead to a simultaneous increase in the proportion of the live stands composed of OC, Bog, Fen and Swamp within single-pass and multi-pass harvests (Figure 2.2). Fire and salvage-logged plots retained similar landscape composition of live stands relative to pre-disturbance conditions, however both had a tendency toward increased representation of hardwood habitats in the post –disturbance landscapes (Figure 2.2).
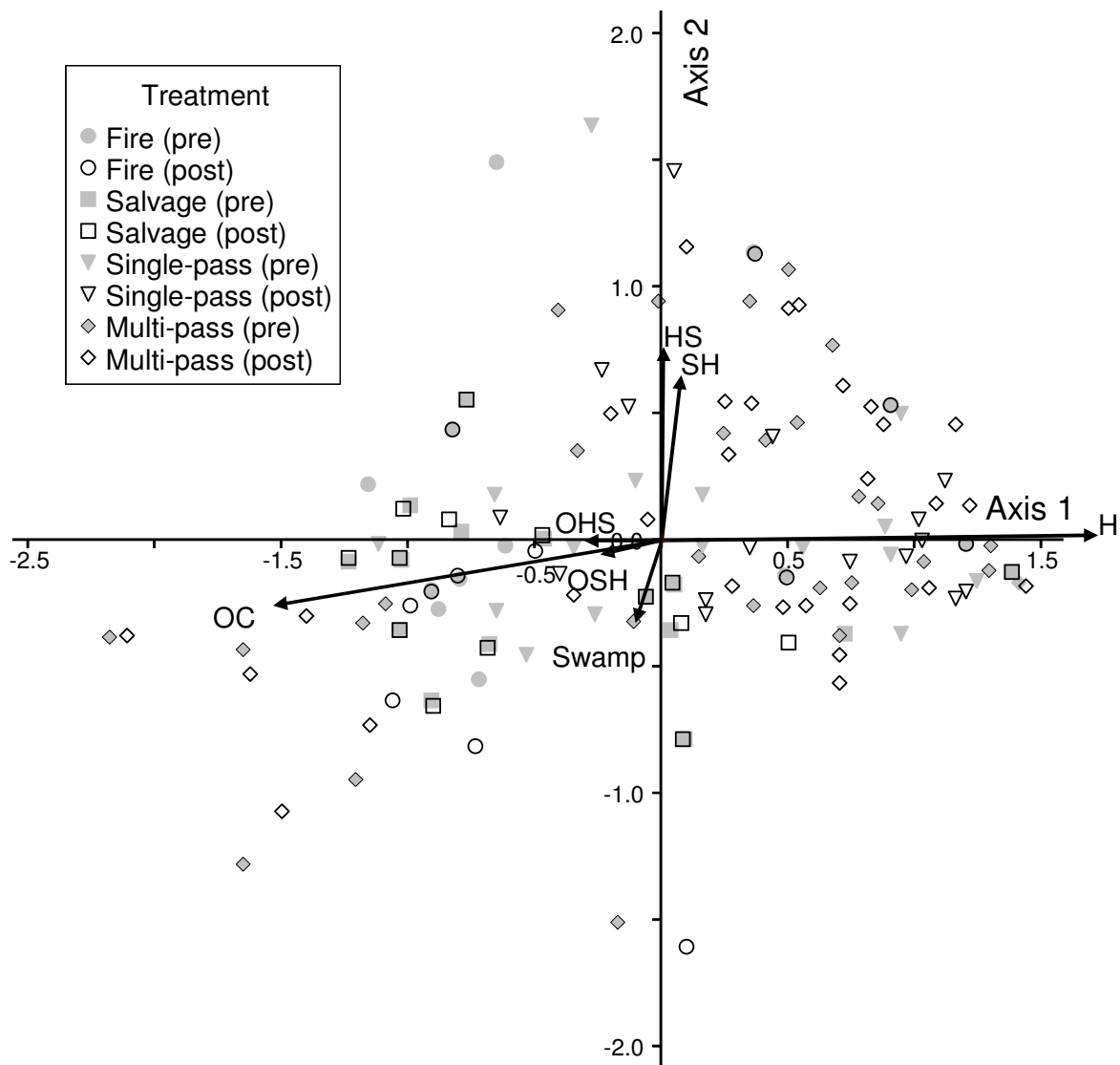
Figure 2.2. Non-metric multidimensional scaling (NMS) ordination diagram of pre- and post-disturbance live vegetation for plots in post-fire, salvage logged, single-pass harvest and multi-pass harvest landscapes. Live vegetation included (unburned and/or unharvested) portion of the landscapes, including both island residuals within the disturbed portion of the landscape and adjacent leave areas and matrix residuals (e.g. corridors and peninsulas). Vectors represent direction and degree of correlation with environment. See Table 2.1 for acronyms.

2.5.2 Fragmentation and Area of Residual Islands

Metrics describing the fragmentation of residual patches were best described by a 1-dimensional solution from the NMS ordination. Final stress was 4.9, suggesting fit was significantly better than chance (p<0.005). The single NMS axis for residual fragmentation explained 99.3% of the variance in the data. The NMS axis was most positively correlated with CA (see Table 2.2 for fragmentation metric acronyms; Kendall's tau=0.987), PSCov (tau=0.612), PSSD (tau=0.677), TE (tau=0.764), and ED (tau=0.765). I therefore interpreted this as a gradient of uniformly small, scattered patches to landscapes dominated by large- and variably sized patches (Figure 2.3). Fragmentation of residual patches differed between treatments (T=-14.81, A=0.185, p<0.001). Pairwise comparisons show that this was due to multi-pass harvests differing from fire (T=-15.10, A=0.156, p<0.001), which was the only treatment that differed from fire (Figure 2.3). Multi-pass harvests differed in having a few, small, isolated and non complex-shaped residual patches. The other treatments had higher retention, with more patches with more complex shapes, and variable sizes.
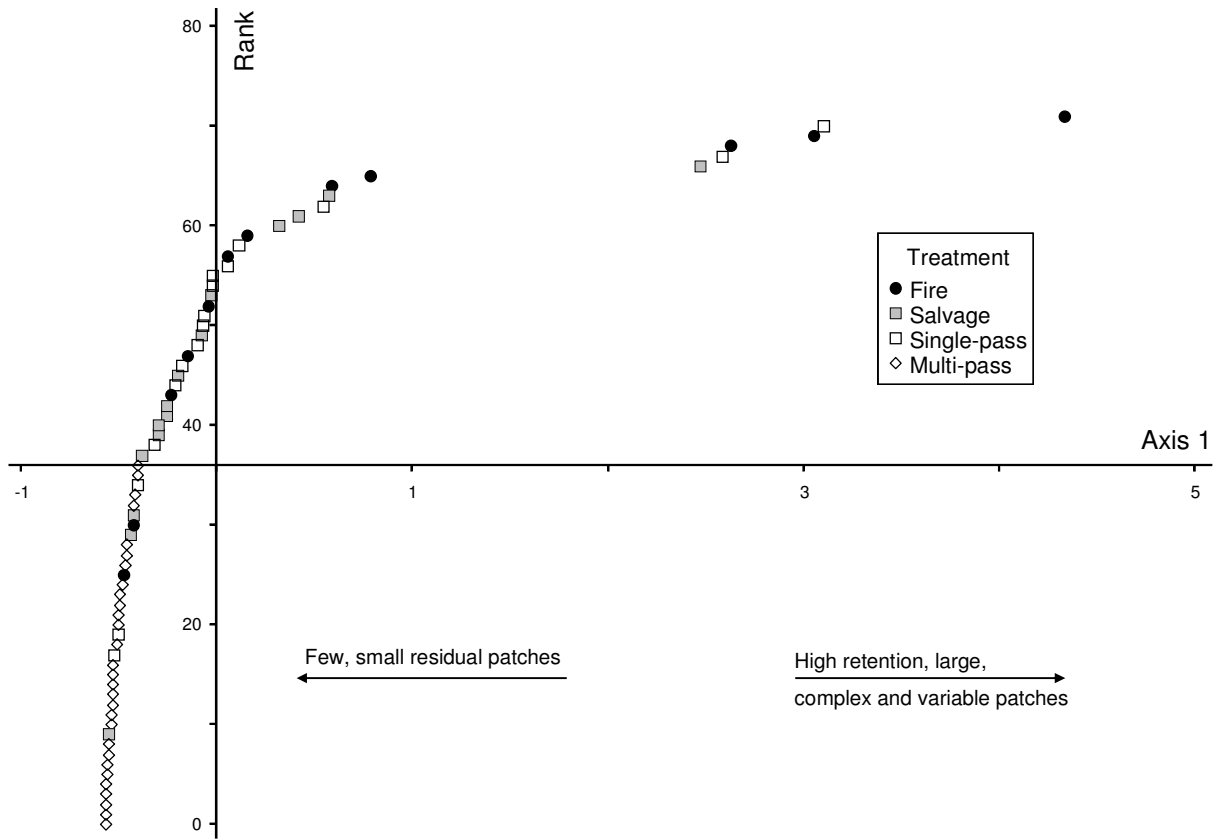
Figure 2.3. Non-metric multidimensional scaling (NMS) ordination diagram of residual patch fragmentation for plots in post-fire, salvage logged, single-pass harvest and multi-pass harvest landscapes.

Of three models describing the total area of residuals within post-disturbance landscapes, all models were within 4 AIC units. The top two models received cumulatively 87% of the support, and both included treatment and area harvested. The top model received ~63% of the support, and included treatment, area harvested and the interaction of these two variables (Table 2.3). In the harvested treatments, area of residuals tended to increase with area harvested. Area of residuals differed between treatments, however, this was primarily due to multi-pass harvests having low areas of residuals retained (Figure 2.4). On average, 20% of the area remained as residual patches in fires, 9.5% remained as residual patches in salvage logged areas, 14.9% in single-pass harvests and 1.1% in multi-pass harvests (Figure 2.4).

Across treatments, ~90% of residual patches were ≤0.5 ha in size, with all four treatments having ≥75% of the residual patches being ≤0.2 ha in size. All treatments except multi-pass harvests (max. patch size of 6.3 ha) had residual patches ≥80 ha in size. Despite the frequency of small patches, the majority of the total area of residual patches was mostly attributable to relatively rare patches ≥5 ha in size. On average, 61% of the area of residual patches was in patches >5 ha in size; however, this varied from 83% in fires, to 14% in multi-pass harvests (Figure 2.5). Overall, 76% of residual patch area was in patches larger than 1 ha, but this ranged from 93% in fires to only 43% of the area in multi-pass harvests.

Table 2.3. Model selection statistics from General Linear Models describing area of residual patches after fire, salvage logging, single-pass and multi-pass forest harvesting. Sample size is 72, k = number of parameters, AICc= Akaike's Information Criterion corrected for small sample size, and ωi = AIC weight.

Model	k	AICc	ΔAIC	ωi
Treatment+Area Harvested+Treatment*Area Harvested	5	-118.39	0.00	0.63
Treatment+Area Harvested	4	-116.43	1.96	0.24
Treatment	3	-115.36	3.03	0.14
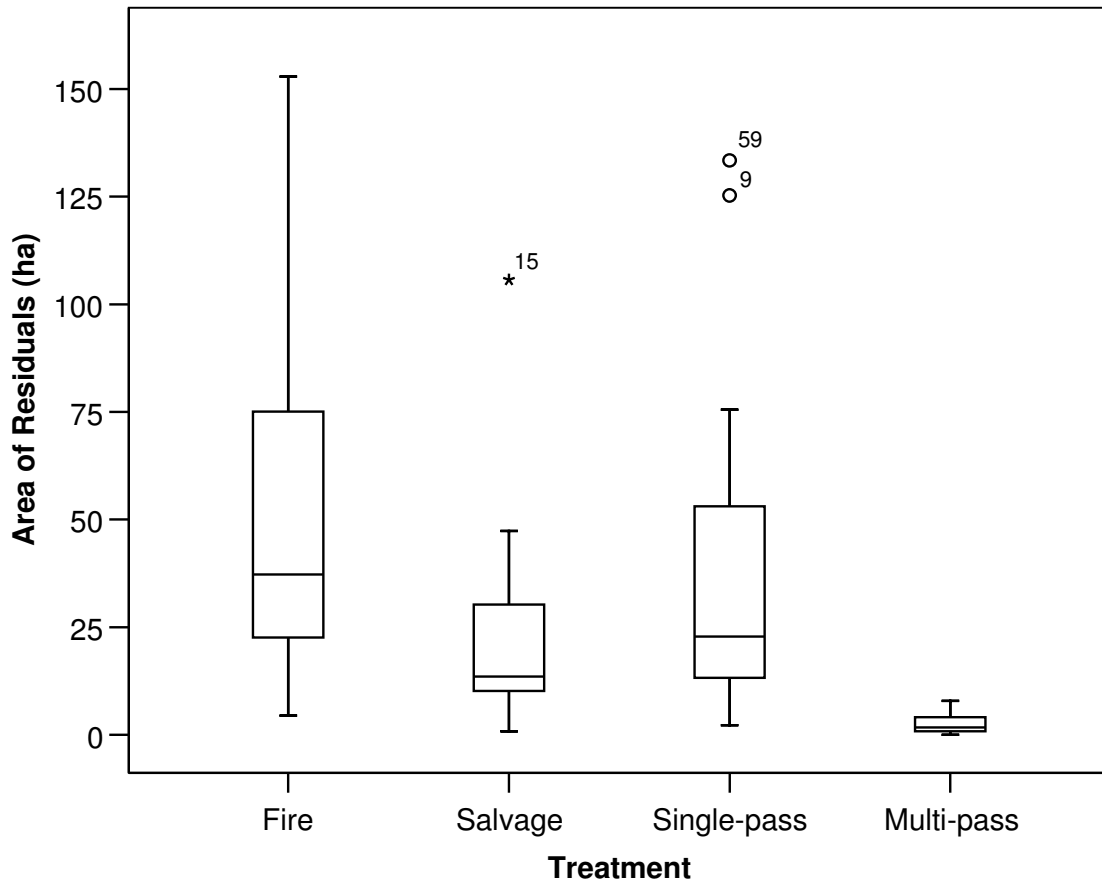
Figure 2.4. Total area of live tree residual patches within each of four key forest disturbances. Boxes indicate upper and lower quartiles, horizontal lines within the boxes are medians, whiskers indicate most extreme values that are not outliers. Outliers (1.5 to 3 inter-quartile ranges from box) are displayed as open circles, * indicates an extreme value (>3 inter-quartile ranges from boxes). Outliers and extremes are labeled by case number in the data set.
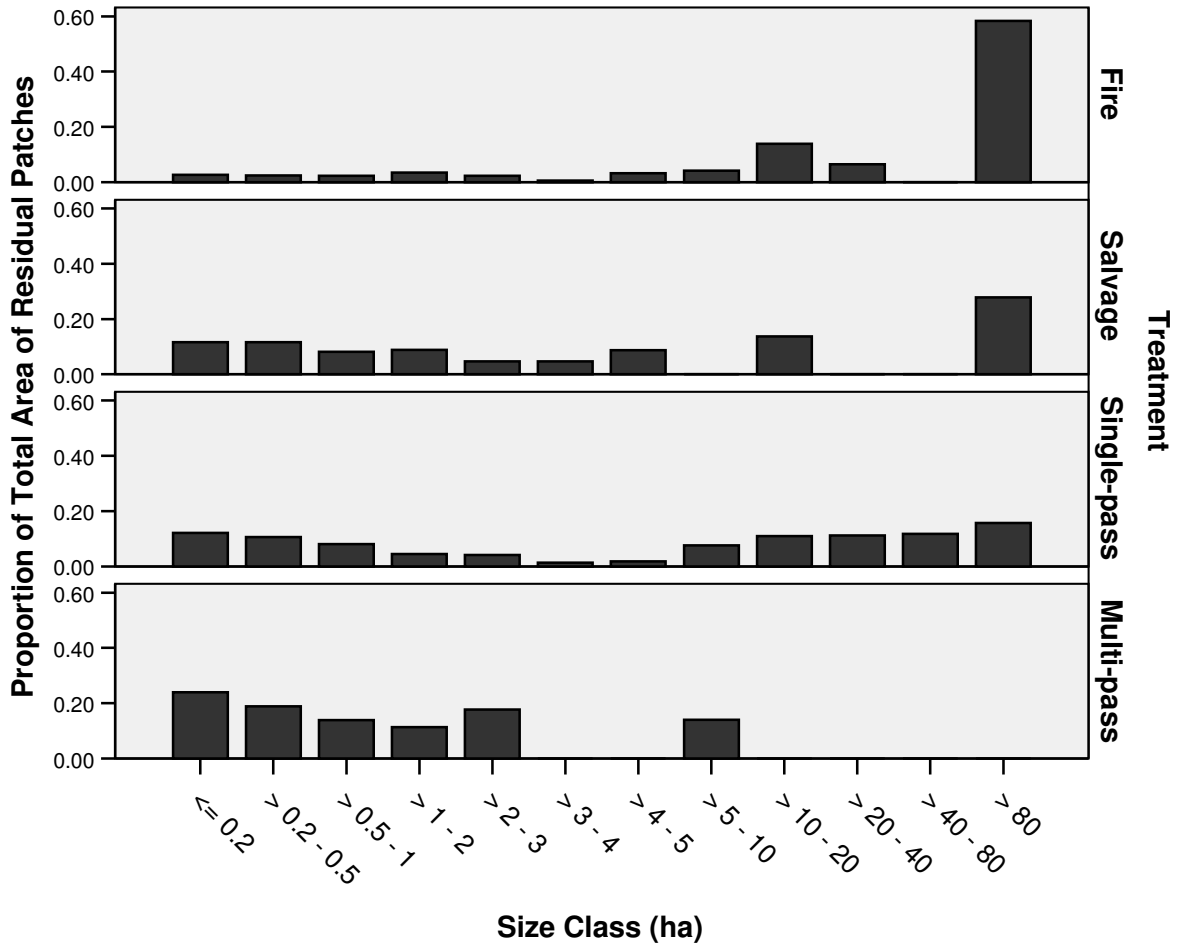
Figure 2.5. Size classes of live residual patches, expressed as a proportion of total residual patch area within treatment.

2.5.3 Composition of Residual Islands

There was a tendency for Hardwood habitats to have higher than expected representation in post-fire residuals, and Other conifer habitats (OC, see Table 2.1 for acronyms) to be less represented in residual patches than expected based on pre-disturbance landscape composition (Figure 2.6A). However, the overall composition of residual patches in post-fire landscapes did not differ from that expected based on pre-fire landscape composition (T=-0.27, A=0.002, p=0.36).

The composition of residual patches in salvage-logged landscapes differed from that predicted by pre-disturbance composition (T=-2.07, A=0.007, p<0.03, FDR=0.0375). This difference appeared to be due to higher than expected proportions of hardwoods and swamp habitats, and lower than expected proportions of OC and other softwood-dominated mixed (OSH) habitats (Figure 2.6B). Based on this, I made univariate comparisons for these four habitat types. Prior to correction for multiple comparisons, OC and OSH habitats appeared to be significantly less represented than expected. However, after correcting for multiple comparisons, no single habitat differed statistically from expectation, although OC habitat had a trend toward less representation than expected ($F_{1,14}$ =7.13, p<0.02, FDR=0.0125). There was 67% less OC habitat than predicted by chance.

Residual-patch composition differed from that predicted by pre-disturbance composition in single-pass harvested landscapes (T=-2.43, A=0.011, p<0.002, FDR=0.025). This difference appeared to be due to higher than expected proportions of hardwoods, and lower than expected proportions of OC and other swamp habitats (Figure 2.6C). Both proportion H and OC appeared to differ from expectation prior to adjustment for multiple comparisons. After correction for multiple comparisons, only proportion of H in the residual patches was statistically different

from expectation, making up on average 16% more of the residual patches than expected ($F_{1,15}$ =7.39, p<0.015, FDR=0.017).

Five multi-pass harvests had no residual patches that met my mapping criteria, and were therefore excluded from further analysis. Residual patch composition in multi-pass harvests differed from that predicted by pre-disturbance composition (T=-6.31, A=0.025, p<0.001, FDR=0.0125). Residual patches appeared to have higher than expected proportions of hardwoods, and lower than expected proportions of Bog, HS, OC, OHS, and SH habitats (Figure 2.6D). Accounting for multiple comparisons, OC was represented 44% less than expected ($F_{1,23}$ =8.42, p<0.003, FDR=0.017), and SH habitat was 95% less common than expected ($F_{1,23}$ =10.00, p<0.001, FDR=0.008).
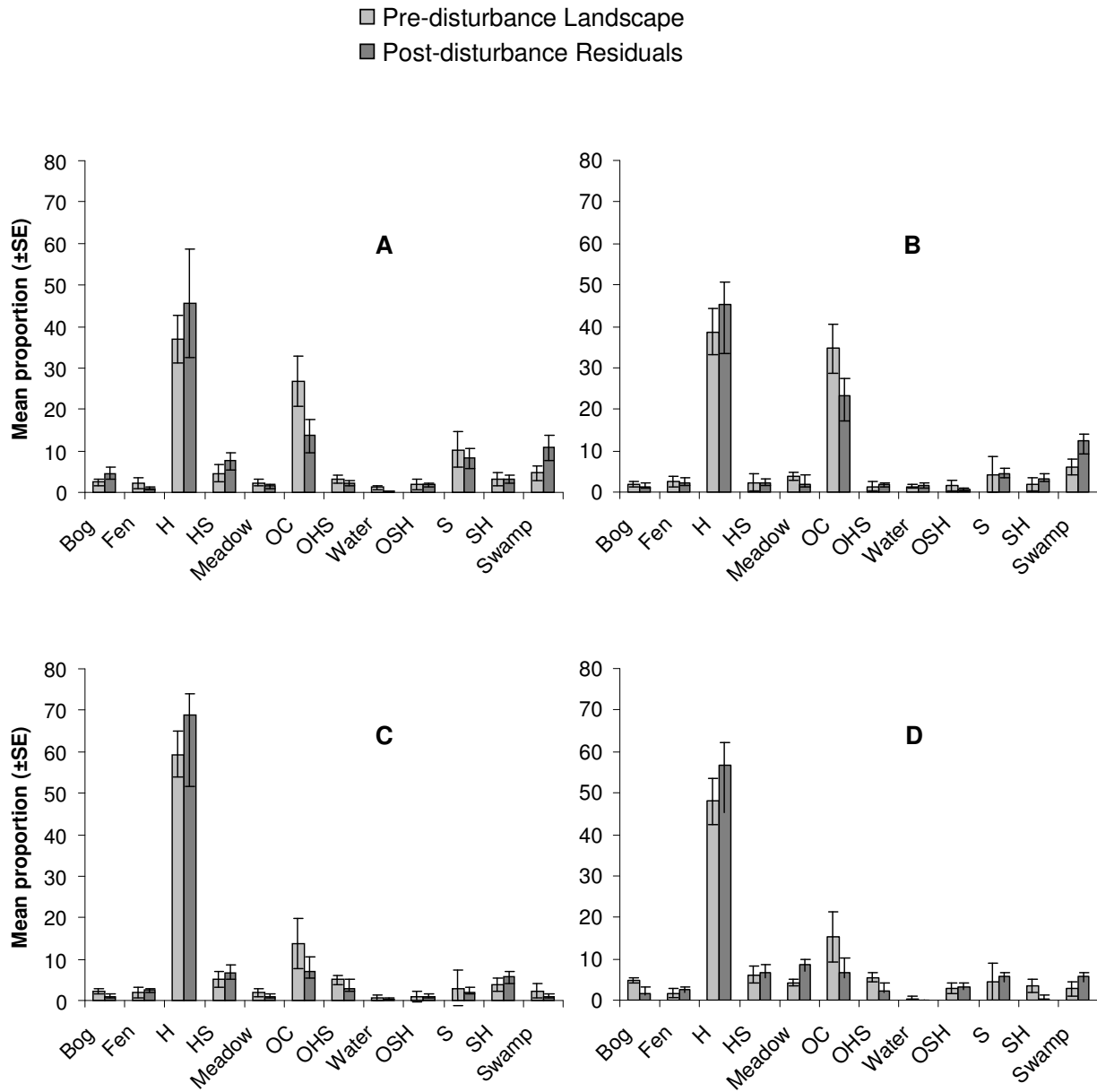
Figure 2.6 Mean proportion (%) of 12 habitat types in pre- versus post-disturbance landscapes disturbed by A) fire (n=12), B) post-fire salvage logging (n=15), C) single-pass harvesting (n=16), and D) multi-pass harvesting (n=24). Pre-disturbance composition was calculated using a GIS overlay at the scale of an entire plot, and was treated as the null expectation if disturbances acted in a stochastic fashion. Post-disturbance composition reflects the composition within island remnant residual patches (patches completely within the boundaries of the disturbance area). See Table 2.1 for acronyms.

2.6 Discussion

Landscape composition of live stands differed between post-fire (salvaged and unsalvaged) and green harvest (single- and multi-pass harvests) disturbance types. Green harvest landscapes had higher proportions of hardwoods and mixedwoods containing white spruce. Post-fire landscapes had higher proportions of swamp and OC habitats, perhaps because sampling was not strictly random. However, I attempted to select the most hardwood-dominated portions of post-fire landscapes, so it seems more likely that the actual difference in composition between fires and harvested areas was greater than described here. In addition to initial conditions being different, shifts in composition caused by the disturbances tended to be in opposite directions for fire versus green harvests. As shown by the NMS ordination of landscape composition, fires tended to remove more OC habitat from the landscape and leave more hardwoods. In contrast, green harvests tended to remove more hardwood/white-spruce mixedwood habitat types and leave more OC habitat at the landscape scale. This result was not unexpected, as the principal habitats targeted for forest harvesting are opposite to those expected to be disturbed by fire (Cumming 2001). Cumming (2001) showed that fires preferentially burned black spruce>white spruce> deciduous forest, whereas the greatest volumes of timber currently harvested by forestry companies in western Canada are ranked in the reverse order, with little black spruce harvested. While I did not directly compare pre- and post-disturbance composition of the disturbed portions of the landscape, the changes in composition discussed above reflect changes in the disturbed areas, since the entire landscape was included in the analysis, and thus any changes in composition were directly due to that portion of the landscape disturbed by either fire or forestry.

Changes in the composition of residual patches relative to the pre-disturbance conditions were similar to the shifts in composition at the landscape scale. Statistical comparison of pre- and post-disturbance composition of residual islands suggests that the disturbances investigated

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within my study did not randomly sample the habitat types within the disturbance boundaries. The only treatment that appeared to disturb the landscape in a stochastic fashion was fire, though the tendency to disturb less hardwood and more jack pine and black spruce (OC) habitats than expected was evident, and consistent with previously described trends in the boreal forest of Alberta (Cumming 2001). Similar changes were seen in the analysis of salvage-logged landscape and residual composition, where in the case of residual composition, there was 67% less OC than expected. Cumming (2001) described a tendency for wildfires to disturb less hardwood and more jack pine and black spruce than expected; however, he quantified the composition of the burned portion (excluding residuals) of entire fires for his sample units and limited his analysis to lightning-caused fires. In my sample data, plots were treated as the sample unit, and these included areas that were salvage logged. The lack of a statistically stronger bias in the amount of hardwood habitat remaining post-fire, and therefore the difference between my study and that of Cumming (2001), may be due to fire severity. Salvage-logging operations only occur in areas of relatively low fire-severity, where the wood has not been damaged beyond commercial viability, and hardwoods were the main target of salvage operations in my study area. This may have reduced my power to detect a trend in the proportion of hardwoods left post-fire, since my post-fire plots may have represented higher severity than average across an entire forest fire. Indeed, if both salvage-logged and post-fire landscapes are pooled, the proportion of hardwoods in residual patches is greater than expected ($F_{1,26} = 4.16$, $p<0.05$).

While shifts in landscape-scale composition of harvests were not representative of those seen in fires, composition of residual patches tended to be more reflective of those in post-fire landscapes. Similar to fire, all harvest types tended to leave more hardwoods than expected based on the pre-harvest conditions and OC tended to be less represented than expected. Upon first

inspection, this would seem counter-intuitive since harvesting tends to remove more hardwood- and mixedwood-dominated habitats at the landscape scale. However, harvest blocks tended to be concentrated in hardwood- and mixedwood- dominated habitats, and thus within-block residuals tended to include more hardwoods than expected based on the entire pre-disturbance landscape since they represent subsets of the harvested stands. The greatest divergence from post-fire patterns was seen in multi-pass harvests, where there was 95% less SH mixedwood habitat post-harvest than expected. This was likely due to the targeted harvesting of those habitat types, particularly in older cutblocks in the multi-pass harvest treatment, that would have been conducted prior to current residual retention guidelines.

There was significantly less area retained as within cut-block residual patches in multi-pass harvests than in all of the other disturbances. Fragmentation metrics also suggested that individual residual patches in multi-pass harvests were uniformly smaller, more isolated, less complex and less variably sized and shaped than the other disturbances. Estimates of residual patch area within non-salvage logged post-fire areas were comparable to other estimates for the boreal plain. Andison (2006) examined 29 forest fires burned prior to 1980 or areas without fire protection and without salvage harvesting, estimated that on average, 24% of the area within Saskatchewan forest fires remain as residual islands. Similarly, Smyth et al. (2005) found that in eight fires in Alberta burned between 1982 and 1991, an average of 26% of trees in burned upland mixedwoods survived fire.

The total area of residuals was less than in post-fire plots for all of the harvested treatments, including salvage-logged plots. Operating guidelines for salvage logging in the sampled fires required the forestry companies to leave live residual patches. Lower residual retention in these plots is therefore likely due to fire severity as mentioned above. The low level of residual

retention within multi-pass harvests is likely due in part to old harvests conducted prior to current residual retention guidelines, and perhaps also due to the smaller harvests allowing less flexibility in harvest operations. Single-pass harvests overlapped more with fires in amount of residuals. This may be due to harvesting and transportation efficiencies in aggregated harvest systems (Delong 2002; D'Eon 2007) allowing the forestry companies to leave more residual patches. The single-pass harvests used in my study were the first of their kind in western Canada, and thus it is unclear if future harvests will also be able to retain such high levels of residuals.

I did not address logging-road density in relation to fragmentation of the regenerating landscape. Previous simulation studies have shown that the spatio-temporal aggregation of cutblocks can reduce the footprint of roads (Delong 2002). However, this might not be the case in mountainous terrain or where older harvests may not have constrained road networks (D'Eon 2007). Anecdotally, there appeared to be fewer roads in the single-pass harvests. Future research quantifying the area and length of roads in single-pass versus multi-pass harvests would be useful. In addition, quantification of landscape fragmentation caused by roads would also be useful.

In order to assess how well natural disturbance is approximated across the scale of a forest-management area, experimentation with single-pass harvests in landscapes of different community composition is necessary. Thus far, single-pass harvests were applied to areas dominated by hardwoods. Based on patterns seen post-fire, application to landscapes dominated by black-spruce and/or jack pine would be appropriate, since these habitats tend to burn more frequently (Cumming 2001). However, current operations in western Canada make less use of these types of wood, particularly black-spruce (Cumming 2001). Therefore, to fully apply the natural disturbance model, a shift in composition of what forestry operations harvest may be

necessary. The extent to which this strategy should be employed is dependent on the degree to which harvest replaces fire as the predominant disturbance in the boreal forest, and the relative efficacy of fire suppression efforts.

A primary goal of NDE forestry is to maintain biodiversity by maintaining a natural range of habitats in patterns similar to those found following fire. Most studies examining the role of residual retention as habitat for wildlife have focused only on amount and dispersion of residual retention (Harrison et al. 2005; Schieck et al. 2000; Tittler et al. 2001). Less is known about the role of residual composition, as most studies have concentrated on residual patches of aspen or mixedwood habitats, and few have examined the interaction between residual amount and composition. Many species of birds inhabiting the boreal forest have very specific habitat requirements relating to forest age (Cumming and Diamond 2002; Hobson and Bayne 2000a), composition (Hobson and Bayne 2000b; Kirk et al. 1996; Kirk et al. 1997), and structure (Hobson and Schieck 1999; Rempel 2007; Schieck and Hobson 2000; Schieck et al. 2000; Villard et al. 1999). Furthermore, those studies that have examined the response of forest bird communities to gradients of residual retention in relation to habitat type suggest that response to retention is dependent on forest composition (Harrison et al. 2005; Schieck and Song 2006). Thus, if bird composition is to fall within NRV, where forest harvesting occurs, micro-habitats of retained patches will need to reflect the amount and composition seen post-fire. Results from this study suggest that the compositional and structural overlap in NRV was best achieved in single-pass and salvage-harvested areas. Multi-pass harvests had residual patches with greater bias in their composition and were structurally less similar to NRV. These structural differences may have important consequences, as old-growth (post-rotation age) forest bird communities may only occur in patches >5 ha (Schieck and Hobson 2000). Furthermore, 5 ha patches might not be

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sufficiently large for long-term persistence of forest birds preferring old-growth (Schmiegelow et al. 1997; Schmiegelow and Mönkkönen 2002). Multi-pass harvests only had 14% of the residual patch area in patches at least 5ha in size, whereas this proportion was much higher in fire (83%), salvage-logged areas (42%), and single-pass harvests (57%). Therefore, single-pass harvesting may be a useful alternative to multi-pass harvesting, as it appears to overlap more with NRV than multi-pass harvests. Additionally, it may be useful to use higher retention levels of residual patches than dictated by current guidelines in second- and third-pass cutblocks within multi-pass harvest landscapes, to allow residual retention at the landscape scale to fall within the range of NRV, and make up for older harvests having lower (or no) retention. However, future studies are necessary to determine how approximating the habitat "preferences" of fire affects wildlife habitat. In chapter 3, I address this knowledge gap in part, by examining avian community composition in relation to factors including residual amount and composition.

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CHAPTER 3. LANDSCAPE-SCALE DISTURBANCE AND BOREAL FOREST BIRDS: CAN LARGE SINGLE-PASS HARVESTS APPROXIMATE FIRES?

3.1 Abstract

Boreal forest birds have adapted to changes caused by natural disturbances such as fire and this adaptation forms the basis for the Natural Disturbance Paradigm (NDP) underlying recent proposed changes in forest harvesting practices in western Canada. To date, this paradigm has been evaluated primarily at the stand level and within conventional harvesting systems. The potential for improvements in avian conservation at the landscape scale by adopting the NDP approach is largely unknown. I examined the effects of landscape-scale disturbances on forest bird communities by contrasting richness and abundance of birds in 1) 16 single-pass harvest sites with residual forest patches, 2) 29 multi-pass harvest sites with residuals; and 3) 15 salvage logged post-fire sites with variable harvest intensity. I contrasted bird communities in these treatments with those in unsalvaged post-fire sites of similar age. Post-fire sites were used to provide a metric of the Natural Range of Variation (NRV) to be expected in bird communities. Sites were surveyed for avian community composition and abundance one to five years post disturbance. Redundancy analysis indicated that bird communities differed from the NRV in all of the harvest treatments. However, single-pass harvests provided a somewhat better fit to NRV than did multi-pass harvesting. Avian community similarity was influenced by non-linear responses to area harvested, amount of residual retention, residual composition and pre-disturbance forest composition. An optimization routine created from a General linear model, suggests that community similarity to NRV can be maximized by using single-pass harvests over multi-pass harvests, harvesting 66-88% of the timber in the planning unit, and retaining 5-19% of the disturbance area as live residual patches, with 50% of harvests having at least 9% of the within cutblock area retained as residuals.

3.2 Introduction

The forest industry of western Canada is moving toward ecosystem-based management approaches in an attempt to better conserve biodiversity (Boutin and Hebert 2002). This approach is based on the concept that wildlife in the boreal forest has adapted habitats and structure created by large, stand-replacing, fires and other natural disturbances (Hunter 1993). Such approximation of natural disturbance patterns provides intuitive appeal for the management of boreal forest wildlife (Bergeron et al. 2002; Hobson and Schieck 1999; McRae et al. 2001). This approach has involved reducing the two or three-pass, clear-cut logging with cut- and leave-blocks toward partial-cut or variable-retention harvesting involving leaving residual trees and patches within cutblocks (Schieck et al. 2000, Tittler et al. 2001). Comparisons made at the stand or patch scale have suggested that leaving more complex vegetation structure in cutblocks can maintain characteristics of old-growth forest in later generating stands used by boreal forest birds (Hobson and Schieck 1999; Schieck and Hobson 2000). However, maintaining components of vegetation and bird communities in harvests that are associated with those occurring in natural disturbances remains a challenge (Hobson and Schieck 1999; Schieck and Hobson 2000; Simon et al. 2002).

Another approach to approximating natural disturbance during harvest involves single-pass harvesting, whereby forest harvesting is done in one (shorter) time period and operations do not reoccur until the next rotation. This generally involves larger disturbances similar to those due to fire. This approach incorporates the variability of natural disturbance sizes currently not achieved in conventional harvesting practices. Most jurisdictions limit cutblock size to 150 ha or less, whereas fires may burn areas up to 100's or 1000's km^2 (Bergeron et al. 2002; McRae et al. 2001). While creation of larger cutblocks might allow the forestry industry to decrease the "footprint" of roads and fragmentation (Delong 2002), other benefits have not been tested.

Greater ranges in variation of remaining structure are generally seen in larger natural disturbances (Bergeron et al. 2002; Schulte and Niemi 1999), and so larger cutblocks with residual patches may overlap with post-fire forests at least in terms of such structural attributes. Recent simulation studies suggest that harvest plans including retained linear strips and cutblock size restrictions generally lead to the weakest predictions in models of forest bird communities compared to other harvesting scenarios (Loehle et al. 2006; Rempel et al. 2007). In contrast, Rempel et al. (2007) found that harvesting plans that use larger harvest blocks and defer harvesting both spatially and temporally to produce large areas of similar aged forest show more similarity to simulated NRV. To my knowledge, no field study has directly tested the landscape-scale consequences of single-pass style harvests for boreal forest bird communities.

Research supporting the use of natural disturbance emulation approaches to forest harvesting in the boreal as a means of better conserving birds and other wildlife is still lacking. In particular, large landscape-scale studies that compare multiple disturbance types have rarely been conducted within industrial forests in general (Song 2002). To address these knowledge gaps, I focused on the effects of landscape-scale disturbance pattern on forest bird communities. Avian richness and abundance were contrasted between replicate landscapes of fire origin and single-pass (aggregated) harvesting with residuals; multi-pass harvesting with residuals; and salvage logged post-fire landscapes with variable harvest rates. Based on a prior analysis of spatial autocorrelation for several species within my study area, I considered "landscape" to encompass processes at the scale of >2.56 km^2, as this is approximately the scale over which most species showed autocorrelation in abundance. My specific objectives were to assess how bird communities are influenced by each harvest type relative to fire and how amount and composition of residuals mediate forest-bird community response to harvesting. I predicted that

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songbird community composition in treatments would be most similar to those in fire-generated landscapes in the following order: post-fire sites with salvage logging > single-pass post-harvest sites with residual standing structure left on sites > conventional multi-pass post-harvest sites. I hypothesized that single-pass harvesting and salvage logging would be more similar in avian composition and relative abundance to that in post-fire sites than in multi-pass harvesting due to greater variability in amount and composition of residual patches. Furthermore, I predicted that salvage logged sites would be most similar to NRV since in addition to having harvest, the chemical disturbance caused by fire was also present, and thus the landscapes would include substantial standing-dead material and different ground-layer vegetation, and therefore post-fire specialists should respond to any influx of deadwood associated arthropods and the foraging and nesting habitats created by fire (Imbeau and Desrochers 2002; Koivula and Schmiegelow 2007).

3.3 Methods

3.3.1 Study Area

The study area was located within the Boreal Plain Ecozone, a gently rolling plain, covered by boreal mixedwood forest including trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), white birch (*Betula papyrifera*), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), black spruce, balsam fir (*Abies balsamea*) and tamarack (*Larix laricinia*) (Acton et al. 1998; Rowe 1972). Within the Boreal Plain, my study area extended from Candle Lake, Saskatchewan in the east (53° 50' N; 105° 50' W) to the House River Fire in north-eastern Alberta (approximate location 56° 44' N; 111° 23' W; see Chapter 2, Figure 2.1). The frequency of stand-replacing disturbances and complexity of hydrologic regimes have led to complex successional patterns within the Boreal Plain. The resultant heterogeneous mosaic of habitats

created through multiple-stand disturbance patterns (Weir et al. 2000), have led to some of the richest and most diverse bird communities in North America (Kirk et al. 1996).

3.3.2 Study Design

Single-pass harvesting within the western Boreal Forest is a recent practice, and therefore site selection was limited by the number of existing aggregated harvests in my study area. I therefore attempted to select disturbances in the other treatments that were as similar as possible in pre-disturbance vegetation to single-pass harvests. To avoid bias associated with succession, I first selected areas containing recent (<5 y) disturbances. Using forest inventory data, a series of 400 ha overlays was used to select areas within recent disturbances having approximately 50% of the stands being rotation age (≥80 years old) and classified as hardwood- and/or hardwood- or softwood-dominated mixedwood stands. Since many of the recent fires within my study area had lower proportions of stands meeting my selection criteria, I selected sub-sample 1.6 x 1.6 km (256 ha) plots that had composition closest to my selection criteria. The 256ha plots were then treated as my sample units. The proportional area of the plots meeting the selection criteria above was reasonably similar between disturbance types (fires =0.43 ± 0.22 SD; salvage=0.41 ± 0.19 SD; single-pass=0.51 ± 0.22 SD; multi-pass=0.49 ± 0.29 SD). In addition, plots in the salvage logged, single-pass and multi-pass harvesting treatments were selected to encompass similar levels of forest harvest. For multi-pass harvests, sampling was restricted to areas that included a recent (<5 y) harvest; however, these included four sites that had only the first pass completed (median cutblock age= 2 years, min= 0 y, max= 6 y), 21 that had the second pass completed (median cutblock age= 2.5 years, min= 0 y, max= 17 y), and four that had the third pass completed (median cutblock age= 4 years, min= 0 y, max= 25 y). None of the multi-pass

harvests had the final pass completed. Attempts were also made to cover similar spatial gradients across all treatments (see Chapter 2, Figure 2.1).

3.3.3 Avian Sampling

Seventy two plots were surveyed over the summer breeding seasons (31 May -3 July) of 2003-2005 (see Chapter 2, Figure 2.1). These plots consisted of 12 post-fire, 15 post-salvage harvest, 16 single-pass, and 29 multi-pass harvest plots. Twelve post-fire control plots were located in areas burned in 1998 (Cobra Fire), 2002 (Chitek Fire, House River Fire, Timber Fire, Milo Fire) and 2003 (Pasture/Rawhide Fire). Fifteen post- fire salvage plots were surveyed in the eight separate fires (Chitek Fire, Dore Fire, House River Fire, Timber Fire, Milo Fire, Pasture/Rawhide Fire). Single-pass plots were distributed among three large-scale (1200-2700 ha) and five small-scale (250-400 ha) aggregated harvests.

Within each plot, a systematic grid of 16 sampling stations, each separated by 400m in a four by four station configuration, was established. In cases where there was a physical barrier or a station landed in water, a replacement station was selected outside of the square plot boundary (e.g., see inset of Figure 2.1). Systematic grids included both the disturbed and "green" island portions of the landscape as well as adjacent leave areas, and therefore covered any habitat type available within the plots.

Avian community composition and abundance was sampled at each station. Surveys were conducted using early morning point counts (~0400-0900h) at each station based on the Indice Ponctual D'Abondance technique of Blondel et al. (1970). At each station, all birds heard or seen during a ten-minute count period were recorded and coded to indicate whether they were detected visually or by song. To augment sample size, surveys were conducted using digital recordings made with a stereo configuration bio-acoustic monitoring kit (Hobson et al. 2002).

This technique allows sufficient spatial information for skilled observers to estimate abundance (Hobson et al. 2002). Digital recordings were later transcribed by three highly skilled observers, and data were coded for observer identity for subsequent comparison (see Appendix B). To allow comparison of field counts and digital recordings, counts were of unlimited distance. Ten-minute counts were coded into three subset time periods (first three, three to five, and the last five minutes), to allow modelling and correction for detection probabilities (Farnsworth et al. 2002).

3.3.4 Habitat Composition

To determine vegetation pattern and composition at the plot scale, I collated vegetation variables using GIS analysis of digital forest inventory maps. Forest inventory data were standardized into 12 cover types based on proportions of hardwood and softwood cover, as well as soil moisture (see Chapter 2, Table 2.1). Similarly, I reclassified estimated stand ages into seven age-classes. For each plot, I used ArcGIS v. 9.1 (ESRI, Redlands, CA), to generate estimates of pre-disturbance area covered by hardwood, softwood, hardwood-dominated mixedwood, softwood-dominated mixedwood and non-merchantable habitats.

All treatments in this study had remnant forest islands smaller than the minimum mapping of forest inventory data (~2-4ha depending on FMA). Therefore, I used Garmin 12XL handheld GPS receivers to map small (clusters of ≥15 trees) residual patches below the minimum mapping unit within an FMA. Apex co-ordinates of all residual patches were recorded using position-averaging. Data collection was limited to times when 3D navigation was available and the satellite constellation provided a (GPS) estimated horizontal accuracy of ≤ 7m (Holden et al. 2002). Indian Remote Sensing (IRS) satellite imagery (5m panchromatic) was used to digitize

residual patches in six disturbances. In the case of the House River Fire, however, a classified Landsat 7 image of burn intensity was used to categorize residual patches. The Landsat 7 image was classified by Ducks Unlimited Canada (Edmonton) into three burn intensity scores (high, medium, and low) based on ground survey data; however, we reclassified this into a binary variable, categorizing the low burn intensity cells (defined as >95% canopy survival) as residual, and all other cells were classified as destroyed by fire. GIS overlay procedures were used to generate total area of residuals per plot, and extract forest inventory variables associated with the residual patches.

3.3.5 Statistical Analysis

I used Principal Components Analysis (PCA) to create indices of habitat composition to use as covariates to control for differences in pre-disturbance vegetation in the analyses of bird abundance (Lichstein et al. 2002). A separate PCA was conducted on post-disturbance vegetation. PCA was conducted using PC-ORD v 4.0 (MjM Software, Glendon Beach, Oregon) and axes were selected based on the broken stick criterion.

Prior to analysis, point-count data were corrected for detection probabilities (Farnsworth et al. 2002). I used Huggins' closed-capture models in program MARK (White and Burnham 1999) via the RMark interface (Laake and Rexstad 2005) to estimate detection probabilities as a linear function of ln (effort), time of day, day of the month, proportion of the point-count station disturbed (within 100m), shrub cover (high vs. low), whether the count was done by point count or recording, and observer experience. Detailed explanation of detection probability estimation and species specific estimates of detection probability are given in Appendix B.

After correcting the avian data for differences in detection probabilities among species, I derived a data matrix consisting of 27,061 individuals representing 141 species (Appendix A). A

subset of 24 plots had repeat (between-year) visits. In order to treat all sites similarly (i.e. as single visit), I calculated maximum abundance across years for sites with repeat visit data, since maximum abundance tends to provide a better reflection of true abundance (Toms et al. 2006). To ensure this method did not influence my results, I used multivariate comparisons of community composition between community matrices calculated using maximum versus minimum counts; these analyses showed no difference in community composition as the two measures were highly correlated (Standardized Mantel Statistic = 0.98, p=0.001).

Prior to multivariate ordination of the avian data, all species occurring on fewer than 4 plots were removed from the data, leaving 26,939 birds representing 104 species. Plot-level bird abundance (i.e. sum of counts across 16 stations) was calculated for each species and used as the response variable. A preliminary ordination suggested a linear model was appropriate (ter Braak and Smilauer 2002), therefore I used redundancy analysis (RDA) to model species composition. Avian data were square-root transformed to decrease the influence of extremely abundant species and standardized to zero mean and unit variance. Symmetric scaling was used since this method provides a good portrayal of both species and samples (Gabriel 2002).

A preliminary RDA model with all explanatory variables was created and forward selection (tested using Monte Carlo permutations) was used to select explanatory variables and check for multi-collinearity. Non-significant or collinear variables were removed from the candidate set for subsequent models. Spatial trends in abundance of species across the study area were accounted for by including latitude and longitude coordinates in RDA analyses, with coordinates standardized to a mean of zero and unit variance (Legendre and Legendre 1998). Based on this analysis, I reduced the variables to include area harvested, area harvested squared, area harvested

cubed, area disturbed , area disturbed squared, area of residuals, RComp1, area of residuals *

RComp1, as well as X and Y coordinates with interactions up to the third order.

To separate effects due to disturbance versus those due to geographic trends, I created five

separate models using the reduced variable suite (above), and used variance partitioning to

examine relative contribution of spatial- versus disturbance-related effects on community

composition and abundance (Borcard et al. 1992). First, a model was created (hereafter the Full

model) using all explanatory variables and having none of the variables treated as covariates.

Four subsequent models were created, varying which factors were included or treated as

explanatory versus co-variables. In this fashion, it was possible to assign proportions of the

variance uniquely attributable to a particular suite of variables (Borcard et al. 1992).

Statistical comparison of community composition between pairwise combinations of

disturbance type was made via Monte Carlo permutations of ordination scores from partial

RDAs, using dummy variable coding for disturbance type, and treating pre-disturbance forest

composition as covariates. Ordinations were conducted using Canoco for Windows v 4.5 (ter

Braak and Smilauer, 2002). Ordinations were tested using Monte Carlo tests of significance

(499 permutations each). Statistical significance was assessed at $\alpha=0.1$ and corrections for

multiple comparisons were made using the False Discovery Rate control (Benjamini and

Hochberg, 1995).

3.3.6 Optimization of Community Similarity

To assess the range of habitat attributes that could minimize community dissimilarity of

harvest (excluding salvage) sites relative to NRV, I used Monte-Carlo simulations to create an

optimization routine using the YASAI add-in for Microsoft Excel[TM] (Eckstein and Riedmueller,

2002). I calculated Sorensen's Dissimilarity Index between all pairwise comparisons of post-fire

plots (unsalvaged) and the single-pass and multi-pass sites using PC-ORD (McCune and

Medford, 2006), and averaged these for each plot. I then used General Linear Models to create a

regression function to predict average community dissimilarity relative to post-fire plots. Prior to

analysis, the data were logit transformed to keep predicted values within a 0-1 range. Sixteen

models to explain community dissimilarity were considered, and I selected between competing

models using AICc (Burnham and Anderson, 1998). Monte Carlo simulations were then created

to seek the harvest type, and values for the proportion of landscape harvested, proportion of

harvest left as residuals, and proportion of hardwoods left in the post-harvest landscape that

minimized predicted community dissimilarity. I created 100,000 simulated landscapes to match

the means and approximate distributions of habitat variables determined from a GIS query of the

entire forest inventory for a 1,237,090 ha Forest Management Agreement Area (FMA) in our

study area. Based on these queries, proportion harvested was simulated with a normal

distribution (mean =0.41 and SD=0.17); proportion of the landscape composed of Hardwoods

was normally distributed (mean =0.47 and SD=0.23), proportion of the harvest left as residuals

was distributed as a combined Poisson/negative exponential random variable with mean

=0.0699, and area of hardwoods post-harvest was simulated as a negative-exponential variable

with a mean of 9.92ha. The resulting distribution for each of these variables in the 100,000

simulated landscapes are given in Appendix C.

From the 100,000 randomly simulated landscapes, I selected landscapes in the 5th percentile

of simulated community dissimilarity values (i.e. simulations with the lowest predicted

community dissimilarity relative to NRV). For simulated landscapes in the lowest percentile

group mentioned above, I then calculated percentiles for the simulated habitat attributes from

these simulations and report these harvest attributes that tend to minimize community

dissimilarity relative to NRV.

3.3.7 Species and Guild Responses

Differences in species frequency of occurrence and abundance were compared for all 104

species using Indicator Species Analysis (Dufrene and Legendre, 1997). Indicator values

combine both the species abundance and frequency of occurrence in each habitat and is a

"distribution-free" method relying on Monte Carlo permutations to determine if the indicator

value for a species is greater than expected by random occurrence between habitats. I conducted

pairwise comparisons between fire vs. salvage, fire vs. single-pass and fire vs. multi-pass

harvests. Statistical significance was assessed using 1000 permutations, and results were

considered significant at α=0.05. Indicator Species Analysis was conducted using PC-ORD v.

4.0.

I examined factors influencing the abundance of cavity, canopy, ground and shrub nesters

using General Linear Models (GLMs). Examination of correlations and scatter plots suggested

no relationship between abundance of the canopy nesting or cavity nesting guilds and spatial

variables or pre-disturbance vegetation and so those variables were not included in candidate

models. GLMs incorporated treatment, area harvested, area of residuals, area harvested squared

to account for potential non-linear responses to area harvested, and interactions between

treatment and area harvested as well as area of residuals and area harvested. Six candidate

models were considered and top models were selected using AICc (Burnham and Anderson,

1998). Scatter plots suggested both ground- and shrub-nester abundance was influenced by pre-

disturbance habitat; therefore all models included PC1, and an additional model that included a

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treatment by PC1 interaction. I only considered the models within four AIC units of the top

model as potentially useful (Burnham and Anderson, 1998).

3.4 Results

3.4.1 Habitat Composition

Habitat composition of pre-disturbance vegetation characteristics was reduced to a set of

simplified metrics using PCA. The first three axes explained 39.8% of the variation in the

vegetation variables, with axes 1-3 explaining 15.6, 13.2 and 11% of the variance, respectively.

Axis 2 did not differ between treatments and was therefore not retained. PC1 was negatively

associated with proportion of the plot dominated by hardwoods (factor loading= -0.487), and

positively associated with proportion of the plot dominated by other HS stands (factor loading=

0.300), other SH stands (factor loading= 0.312), and other Conifer stands (factor loading=

0.430). PC3 was negatively associated with HS stands (factor loading= -0.312), other HS stand

area (factor loading= -0.301) and positively associated with the shrubby swamps (factor

loading= 0.433), water (factor loading= 0.401), and meadows (factor loading= 0.169).

PCA was also used to summarize composition of residual patches. Based on the broken-stick

criterion, the first two axes were selected to represent residual-patch composition. These two

axes explained 44.6% of the variance in residual patch composition, with 26.9% and 17.7% of

the variation being captured by PC1 and PC2 respectively. Residual Composition PC1 (hereafter

RComp1) was negatively correlated with area of hardwoods (factor loading= -0.417), other

conifers (factor loading= -0.454), other HS mixedwoods (factor loading= -0.343) and other SH

mixedwoods (factor loading= -0.343). Residual composition PC2 (hereafter RComp2) was

positively associated with non-forested habitats such as meadow (factor loading= 0.323) and

water (factor loading= 0.355) and negatively associated with HS mixedwoods (factor loading= -0.437), SH mixedwoods (factor loading= -0.511) and softwood (factor loading= -0.455).

3.4.2 Avian Community Composition

An initial RDA model created using all explanatory variables accounted for 45% of the variance in the species data. After removing non–significant and collinear variables, the variation in the species matrix accounted for by the Full model was 37.6% (F=2.072, p=0.002). The first four axes accounted for 22.8% of the variance in the species data and 60.6% of the species-environment relationship. Pre-disturbance vegetation, spatial variables and treatment variables all influenced community structure (Figure 3.1). Green harvests (single- and multi-pass harvests) split from post-fire (salvaged and unsalvaged) plots primarily on Axis 1, which was strongly correlated with lowland habitats (PC3) and total area disturbed, and negatively associated with area harvested (Figure 3.1). Along Axis 2, samples split primarily based on spatial variables and amount of coniferous or mixedwood (i.e. PC1) habitat (Figure 3.1). Single-pass harvests showed slightly more convergence with NRV on Axis 3 and 4, which were positively correlated with area harvested.

Variance partitioning showed that the greatest proportion (19.7%) of the variation uniquely associated with the explanatory variables was associated with the disturbance variables. A significant proportion (11.8%) was also attributable to broad-scale spatial trends. Some variance (5.8%), was shared variance, not separable between spatial and disturbance variables.
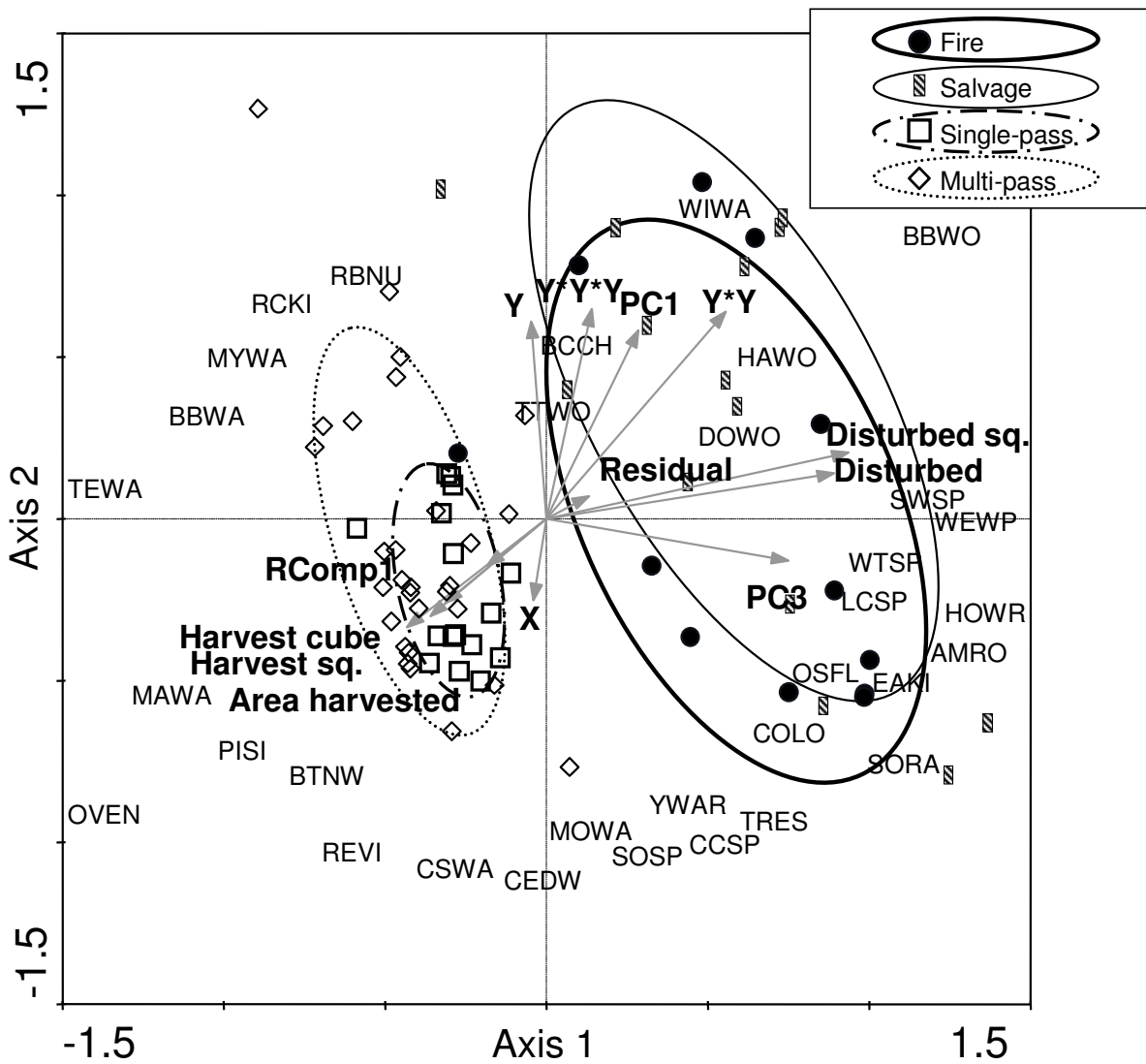
Figure 3.1. Site level community composition (sample scores) in fire, salvage logged, single-pass harvest and multi-pass harvest sites inferred by Redundancy Analysis axes 1 and 2 from the Full model. Grey vectors represent relative degree and direction of relationship with explanatory variables. 67% confidence ellipses are portrayed for each treatment. Four letter codes represent species (see Appendix A). PC1 and PC3 are multivariate metrics of predisturbance forest composition within the plots, RComp1 is a multivariate metric of residual patch composition, X is latitude, and Y is longitude, see text for details.

Of the 19.7% of variation attributable to disturbance-related environmental factors, 6.0% was related to the pre-disturbance vegetation. The remaining 13.7% was attributable to a quadratic response to total area disturbed (5.5%), a non-linear response to amount of area harvested (5.5%), and area and composition of residuals (2.7%). Increasing area of residual patches tended to increase similarity to NRV; however, interaction with RComp1 suggests residual patches composition influences the value of patch area. Re-running the analysis as a partial RDA, using spatial and pre-disturbance vegetation as covariates, suggested a slightly closer match of single-pass harvests than multi-pass harvest areas to post-fire sites, and greatest similarity between post-fire and post-fire salvage sites (Figures 3.2). Community composition differed between all treatments except fire versus salvage (Table 3.1). This same pattern is true after correcting for multiple comparisons (Table 3.1).

Table 3.1. Pairwise comparison of community composition between disturbance types. Comparisons were made using 499 Monte Carlo permutations of ordination scores from partial redundancy analysis controlling for pre-disturbance vegetation.

Comparison	n	Trace	F	p	FDR*
Fire vs. Salvage	27	0.043	1.159	0.254	0.100
Fire vs. Single-pass	28	0.079	2.322	0.002	0.017
Fire vs. Multi-pass	41	0.059	2.510	0.002	0.033
Salvage vs. Single-pass	31	0.079	2.636	0.002	0.050
Salvage vs. Multi-pass	44	0.057	2.666	0.002	0.067
Single-pass vs. Multi-pass	45	0.055	1.238	0.066	0.083

*FDR= False Discovery Rate correction for multiple comparisons, statistical significance was assessed at the FDR value
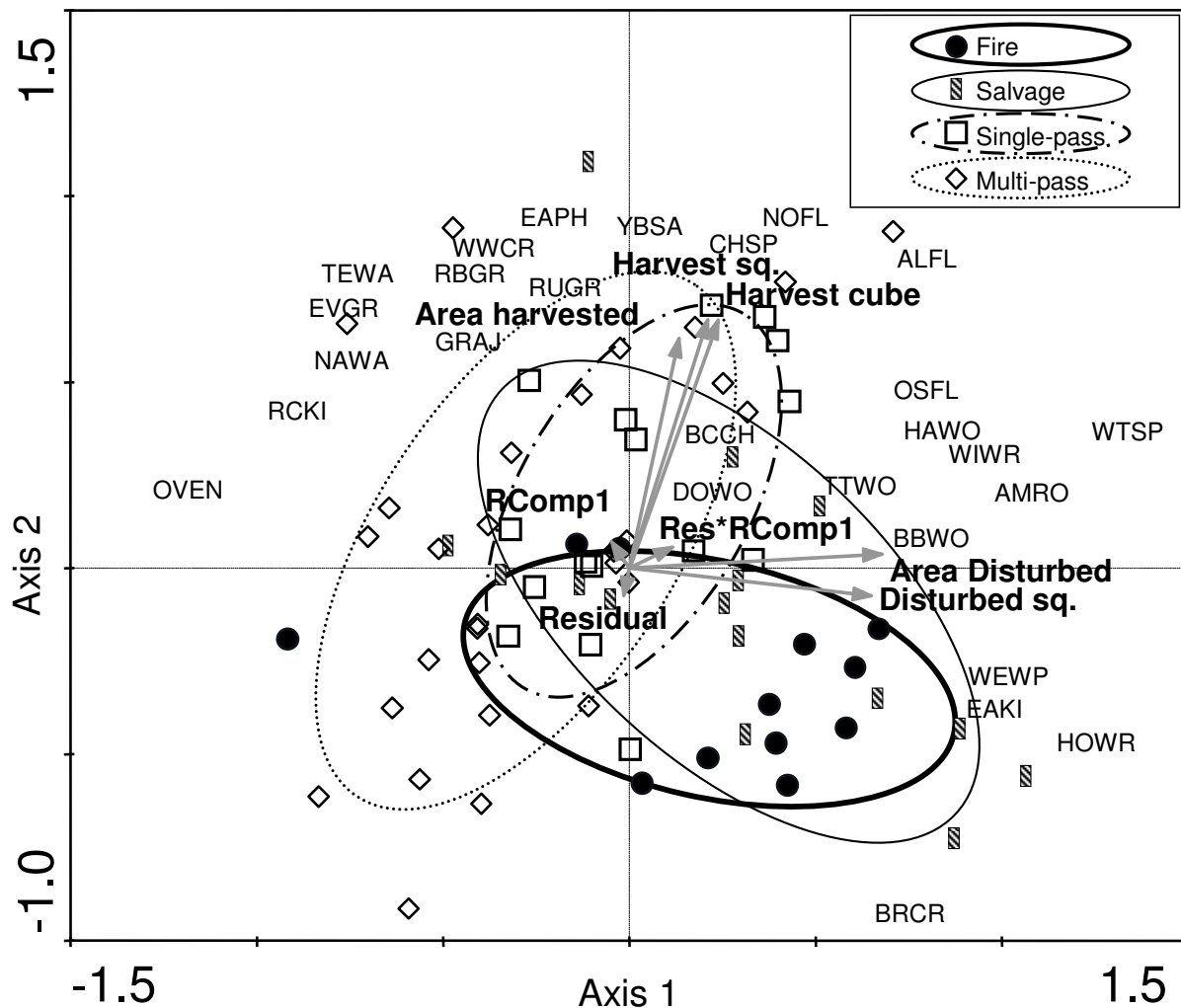
Figure 3.2. Site level community composition (sample scores) in fire, salvage logged, single-pass harvest and multi-pass harvest sites inferred from axes 1 and 2 from partial Redundancy Analysis controlling for pre-disturbance vegetation and spatial trends. Grey vectors represent relative degree and direction of relationship with explanatory variables. 67% confidence ellipses are portrayed for each treatment. Four letter codes represent species (see Appendix A). RComp1 is a multivariate metric of residual patch composition and Res*RComp1 represents an interaction between residual composition and area of residual patches.

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3.4.3 Optimization of Community Similarity

The General Linear Models of (logit transformed) community dissimilarity had substantial model uncertainty, with no clear top model (Table 3.2); therefore, I used model averaging to generate parameter estimates for my predictive equation (Burnham and Anderson 1998). The simulations suggested that community dissimilarity to NRV could best be minimized using single-pass harvests preferentially to multi-pass harvests, as 67% of the lowest dissimilarity simulations were classified as single-pass harvests. Furthermore, dissimilarity was minimized when 50 percent of simulated harvests removed 74% of the timber in the planning unit (range of 66-88% based on 5th-95th percentiles). In addition, leaving 5-19% of the disturbance area in live residual patches, with 50% having at least 9% of the area in residuals, and while 61-98% (median of 88%) of the pre-disturbance area of hardwoods were harvested also minimized community dissimilarity to NRV (Table 3.3).

Table 3.2. Candidate models and model selection statistics from General Linear Models predicting logit transformed Sorensen's Community Dissimilarity to NRV for single-pass and multi-pass harvest plots. RSS= residual sum of squares, k = number of parameters, AICc= Akaike's Information Criterion corrected for small sample size, and ωi = AIC weight. Sample size =44.

Model*	k	AICc	ΔAIC	ωi
Harv	3	-245.646	0.000	0.167
Harv+Resid+Harv*Resid	5	-245.301	0.345	0.140
Treat+PC1+Harv+Resid+Treat*Harv	7	-245.288	0.359	0.139
Treat+Harv+Resid+Harv*Resid+PC1	7	-244.535	1.111	0.096
Treat+Harv+Resid+PC1	6	-244.000	1.647	0.073
Treat+Harv	4	-243.966	1.680	0.072
Treat+Harv+Resid+Treat*Harv	6	-243.649	1.997	0.061
Treat+Harv+Resid+Harv*Resid	6	-243.649	1.997	0.061
Treat+Harv+PC1	6	-243.301	2.345	0.052
Treat+PC1+H+Harv+Resid+Treat*Harv	8	-243.288	2.359	0.051
Treat+Harv+Resid+Treat*Harv+Harv*Resid	7	-242.353	3.293	0.032
Treat+Harv+H+PC1	7	-241.649	3.997	0.023
Harv+Resid+H+H*Resid	6	-241.602	4.044	0.022
Treat+Harv+H	6	-239.966	5.680	0.010
Treat	3	-227.806	17.840	0.000
Treat+Resid	4	-225.806	19.840	0.000

*Treat=treatment (single-pass or multi-pass), Harv=area harvested, Resid= area of residuals, H= area of hardwoods post-harvest

Table 3.3. Habitat attributes of simulated landscapes with minimal (5th percentile of 100,000 simulations) predicted community dissimilarity relative to the Natural Range of Variation (NRV).

Harvest Variable	Percentile						
	5th	10th	25th	50th	75th	90th	95th
Proportion of Planning Unit Harvested	0.66	0.67	0.70	0.74	0.79	0.84	0.88
Proportion of Harvest Left as Residuals	0.05	0.05	0.07	0.09	0.12	0.16	0.19
Proportion of Hardwood Harvested	0.98	0.97	0.94	0.88	0.79	0.70	0.61

3.4.4 Species and Guild Responses

Indicator Species Analysis showed that 39 out of 104 species had greater abundance and frequency of occurrence in at least one of the disturbance types (p<0.05). Ten species had maximum indicator values in post-fire sites, eight in salvage logged sites, 13 in single-pass sites, and eight in multi-pass sites. The majority of species with maximum indicator values in post-fire sites also had high indicator values in post-salvage sites, with seven being cavity nesters (Black-capped Chickadee (for all scientific names, refer to Appendix A), Common Merganser, Downy Woodpecker, Hairy Woodpecker, House Wren, Three-toed Woodpecker, and woodpecker spp.) known to be associated with fire disturbed habitats (Figure 3.3A). Similarly, three species (American Robin, Black-backed Woodpecker and Swamp Sparrow) had their highest indicator values in salvage-logged sites and had similar indicator values in post-fire sites and are known to be associated with fires; the other (Lesser Yellow legs) had an indicator value of zero for fires, and is likely a statistical artefact (Figure 3.3B).

With the exception of Solitary Sandpiper, Spotted Sandpiper and Killdeer, the ten species with highest indicator values in single-pass harvest sites are typically associated with mature to late-seral aspen and white spruce stands (Figure 3.3C). Species showing maximum abundance within multi-pass harvests were mostly associated with mature to late-seral mixedwood forests (Figure 3.3D). Two species associated with shrubby growth, Nashville Warbler and Magnolia Warbler, also had their highest indicator values in multi-pass harvests (Figure 3.3D).

Cavity nester abundance differed between treatments with post-fire plots (both salvaged and unsalvaged) having roughly 1.5 times the abundance of cavity nesters compared to the green harvest treatments. Mean cavity nester abundance was 71.6 ± 11.7 (SE) birds/plot in post-fire, 68.8 ± 5.9 birds/plot in salvage logged, 44.8 ± 5.6 birds/plot in single-pass, and 41.7 ± 5.3

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birds/plot in multi-pass sites. The top two models received 99.8% of the support, with the top model having ~58.6% of the support and the second best model having ~41.1% of the support. The top model included treatment, area harvested and the interaction between treatment and area harvested, while the second-best model was identical except for the addition of area of residuals. Model parameters and examination of scatter plots suggest that the interaction between treatment and area harvested captured the tendency of primary cavity nesters to increase in abundance with area harvested in single-pass and multi-pass harvests while showing no trend in the post-fire treatments. Composition of this guild differed between treatments, with 5.5-17.3% of cavity nester abundance in post-fire and salvage-logged sites consisting of Black-backed and Three-toed woodpeckers, while these species made up 4.5-8.4% of cavity nester abundance in single-pass sites and only 0.8-4.3% of the cavity nester abundance in multi-pass harvests (see also Figure 3.3). Mean combined abundance for Black-backed and Three-toed woodpeckers was 7.9 $\pm$ 1.6(SE) birds in post-fire sites, 6.4 $\pm$ 1.3 in salvage logged sites, 2.8 $\pm$ 1.4 in single-pass sites, and 1.4 $\pm$ 0.5 in multi-pass sites.

Canopy nester abundance was highest in green-harvest sites, with 175.7 $\pm$ 16.3 birds/ plot in single-pass sites, and 147.3 $\pm$ 10.0 birds/plot in multi-pass sites, whereas there were 121.9 $\pm$ 12.8 and 118.1 $\pm$ 8.6 birds/plot in post-fire and salvage logged sites, respectively. All GLMs were within four AIC units.

All GLM models for ground nester abundance were within four AIC units. Due to vegetation bias influencing inference, I used model averaging to generate a predictive equation to estimate treatment effects while holding vegetation PC1 constant. The estimates suggest that ground-nester abundance was highest in single-pass harvests (172.1 $\pm$ 3.0 birds/plot), then multi-pass

harvests (154.7 ± 2.0 birds/plot), salvage logged sites (146.4 ± 1.1 birds/plot) and lowest in post-fire sites (139.8 ± 2.1 birds/plot).

   Three top models for shrub nester abundance received 95.1% of the support, with 55.1, 28.6 and 11.3% of the support coming from the first through third models respectively. The top model included treatment, area harvested, pre-disturbance vegetation composition (PC1), and a treatment by area harvested interaction, while the second best model was identical accept for also including area of residuals. The third best model included treatment, area harvested, area of residuals, pre-disturbance vegetation composition (PC1), and an interaction between area of residuals and area harvested. Estimated abundance from model averaged estimates holding PC1 constant suggest that Shrub nester abundance was highest in salvage logged sites (20.8 ± 1.2 birds/plot), followed by post-fire sites (19.0 ± 1.2 birds/plot), multi-pass sites (16.5 ± 1.3 birds/plot), and lowest in single-pass harvests (16.1 ± 0.6 birds/plot).
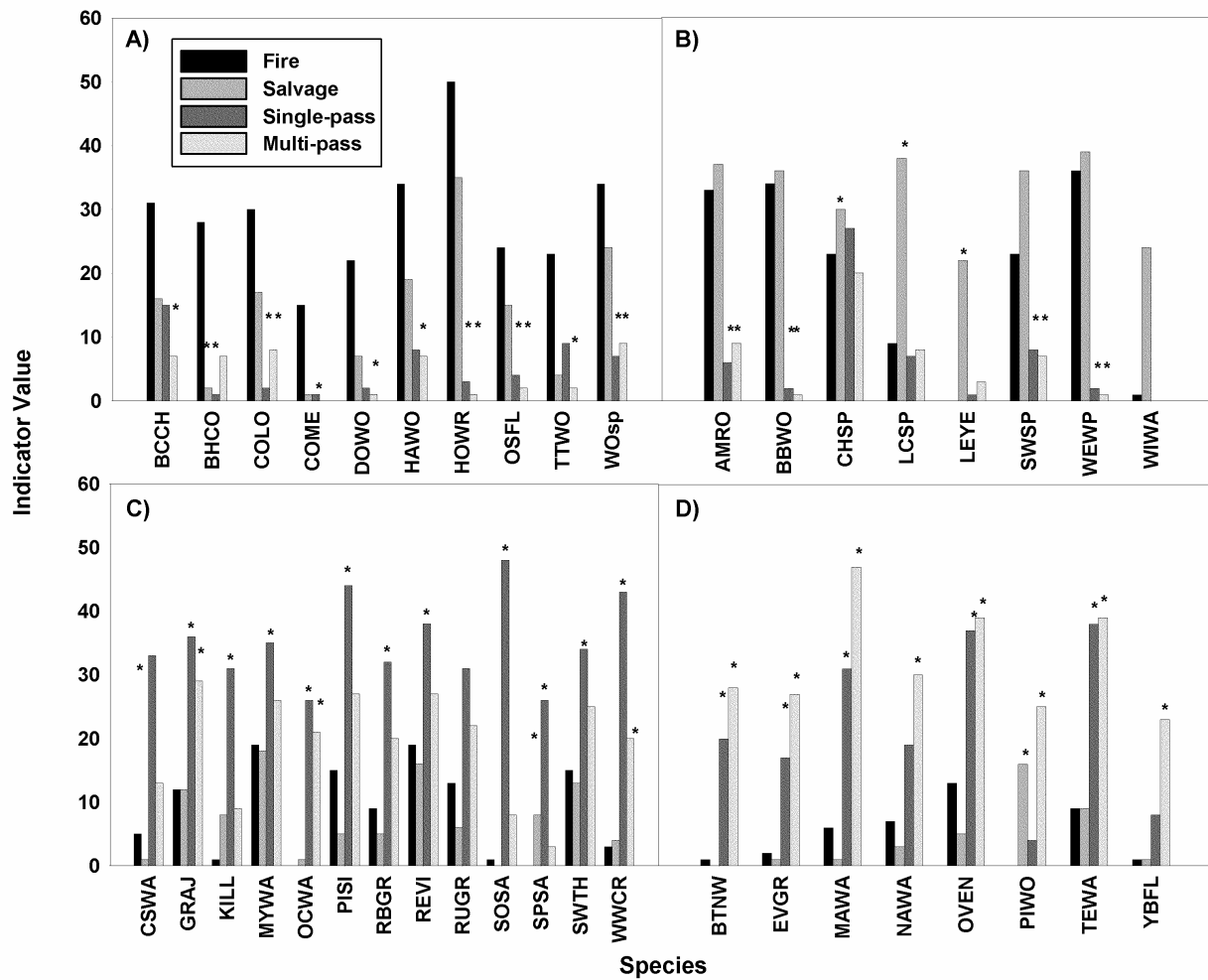
Figure 3.3. Indicator values by treatment for species with maximum indicator values within A) post-fire habitats, B) salvage logged habitats, C) single-pass harvests, and D) multi-pass harvests. *- indicates significant (p<0.05) pairwise planned contrast with post-fire habitats.

3.5 Discussion

Fire was the main driver of differences in avian community composition across the several disturbance types I examined. Avian community composition was most similar between single-pass and multi-pass sites (i.e. green sites) and differed considerably from salvaged and un-salvaged (post-fire) sites. Post-fire plots were primarily distinguished by cavity-nesting species, while single- and multi-pass harvests were more associated with open-habitat and shrub-nesting species. At a landscape level, single and multi-pass harvests tended to have more species associated with mixedwood and mature conifer habitats, due in part to leave blocks adjacent to cutblocks. Furthermore, single-pass harvests had greater area of HS and SH mixedwoods in residual patches compared to fires (see Chapter 2). These general patterns are similar to those found at stand scales by previous studies that suggest post-fire bird communities are dominated by cavity nesters while post-harvest communities are dominated by ground and shrub nesting species and habitat generalists (Hobson and Schieck 1999; Morissette et al. 2002; Schieck and Hobson 2000; Schieck and Song 2006; Simon et al. 2002) at least within 30 years of disturbance.

Previous research on avian communities in the boreal forest of western Canada suggests that species associated with late-seral and early post-fire habitats face the greatest conservation challenges related to forestry (Hobson and Schieck 1999; Hannon and Drapeau 2005; Morissette et al. 2002). This is due, in part, to targeted harvesting of post-rotation aged forest (Cumming and Diamond 2002; Hobson and Bayne 2000). However, several species inhabiting older age class stands also make use of early post-fire habitats (e.g. Black-backed and Three-toed Woodpeckers), to take advantage of the pulse of deadwood associated arthropods (Imbeau and Desrochers 2002; Koivula and Schmiegelow 2007). In addition, several species take advantage of the structural characteristics associated with early post-fire habitats (Hobson and Schieck 1999; Schieck and Hobson 2000; Schieck and Song 2006; Simon et al. 2002). Given that it may

take at least 30-60 years for harvested boreal forests to converge ecologically with post-fire

forests (Hobson and Schieck 1999; Schieck and Hobson 2000; Schieck and Song 2006), any

improvements to approximating NRV earlier in succession is expected to have significant

conservation value. My results suggest that avian community composition can be brought

somewhat closer to that occurring in natural disturbance by the spatial and temporal aggregation

of larger cutblocks with residuals than can be achieved by multi-pass harvesting with residuals.

Multivariate ordinations showed differences in community composition between fire and single-

pass harvests were less than between fire and multi-pass harvests, and pairwise comparison

suggested that community composition of single-pass harvests were not a simple subset of multi-

pass harvests. Similarly, results from my optimization favoured single-pass harvest over multi-

pass harvests in 67% of the top simulations. Furthermore, cavity-nester abundance was closer to

NRV in single-pass than multi-pass harvests. The cavity nesters guild is amongst those of most

concern where early post-disturbance is concerned, and several of these species are considered

post-fire specialists. Since primary cavity nesters serve a role in structuring subsequent bird

communities by creating nesting substrates (Martin and Eadie 1999; Martin et al. 2004), the

greater similarity in abundance of cavity nesters between fire and single-pass harvests may have

for consequences the future structure of the bird community.

   It remains unclear if the observed increase in similarity to NRV in single-pass harvests is

sufficiently large to translate into earlier convergence with NRV. Despite single-pass harvests

being slightly more similar to NRV than multi-pass harvests, the difference between community

composition and NRV was substantial. I expected greater effect sizes than observed, suggesting

that perhaps use of single-pass harvests might not lead to earlier ecological convergence with

NRV than might occur with multi-pass harvests. In multi-pass harvests, similarity to NRV will

change through time, as the leave blocks may serve, to some extent, as residual patches until they are finally harvested in later passes. Some might argue that leave blocks serve the same role as within cut-block residuals, and thus multi-pass harvests may be more similar to fire than single-pass harvests at specific points during the rotation. Leave blocks were included within my plots, but community similarity to NRV was still slightly higher in single-pass harvests. Multi-pass harvests did not have the final pass completed, and therefore the multiple age classes that occur after the final pass of a multi-pass system may serve to accentuate the dissimilarity to NRV at a landscape-scale. Future research following these or other disturbances through time would be beneficial to determine if single-pass harvests converge with NRV sooner than multi-pass harvests.

My data generally fit the hypothesized pattern of community similarity to NRV, with salvage-logged sites showing greatest ecological similarity, single-pass harvests being second most similar, and multi-pass harvests least similar to fire. This pattern generally fits at both the community and species levels, with more species showing greater similarity to NRV in salvage logged sites, single-pass harvests and multi-pass harvests in that general order. This, combined with the lack of overlap in community composition, suggests that while approximating disturbance patterns may bring harvests closer to NRV, pattern alone will not cause harvest to converge with NRV. That salvage logged sites were close to NRV, suggests that the standing dead material and proliferation of pyrophilous insects present post-fire are crucial to the conservation of early post-fire bird communities, a conclusion similarly reached in several recent studies (Hobson and Schieck 1999; Imbeau and Desrochers 2002; Koivula and Schmiegelow 2007; Schieck and Hobson, 2000; Schieck and Song 2006). In particular, the cavity nesting guild was generally most abundant and occurred most frequently in post-fire sites followed by

salvage logged sites, single-pass harvests, and were generally least abundant in multi-pass harvests, however, individual species of cavity nesters had disparate responses. Species of the genus Picoides (Black-backed, Three-toed, Downy and Hairy woodpeckers) were all most abundant in post-fire sites, particularly unsalvaged sites, while Yellow-bellied Sapsuckers and Northern flickers were most common in green harvests, particularly in single-pass harvests. Only Pileated Woodpeckers were most common in multi-pass harvests, likely due to patches of old forest to be harvested in later passes. Conservation of most cavity-nesting species will therefore require maintaining post-fire habitats protected from salvage, which are representative of a broad spectrum of burn severity. This result is consistent with those of other recent studies (Koivula and Schmiegelow 2007; Schmiegelow et al. 2006).

Community composition was strongly influenced by pre-disturbance vegetation. While I attempted to control these effects by site selection, post-fire landscapes tended to be wetter and have more softwoods than green-harvest landscape, as would be expected given the stand types targeted for forestry operations in my study area. Similarity to NRV in green harvest landscapes was driven, in part, by non-linear responses to area harvested. Cubic polynomial terms for area harvested suggest that intermediate to high proportions of planning units being in early succession increased similarity to NRV. This non-linearity was perhaps due to the trade off with residual retention, with larger disturbances tending to also contain more residuals. In my Full model, residual retention was positively correlated with Axis 1 of the bird community ordination. This relationship was supported by my optimization models, which suggested community similarity was greatest when 66-88% of the planning unit was harvested with 5-19% of the area as residuals. To a lesser extent, greater proportions of the residual patches comprised of hardwoods and other mixedwood stand types contributed to green harvest similarity with NRV,

as Axis 1 was negatively associated with RComp1 which was in turn negatively associated with those habitats. Green harvests also tended to be most similar to post-fire landscapes that had less area disturbed by fire. While area disturbed is not necessarily a measure of fire severity, it would seem reasonable that green-harvests are more similar to less severely disturbed landscapes. Little is currently known about the influence of burn severity on avian community composition, however, recent work suggests abundance of woodpeckers generally increase with fire severity (Koivula and Schmiegelow 2007; Schmiegelow et al. 2006). If area disturbed by fire can be considered a surrogate for fire severity, then my results suggest green harvests are more similar to less-severe fire.

One proposed benefit of spatial and temporal aggregation of forest harvesting is the potential to decrease the density of roads necessary to access timber. Logging road density is related to fragmentation of the regenerating landscape and previous simulation studies have shown that the spatio-temporal aggregation of cutblocks can reduce the footprint of roads (Delong 2002). However, this might not be the case in mountainous terrain or where older harvests may not have constrained road networks (D'Eon 2007). Forest bird abundance has previously been shown to display threshold responses to linear disturbances (Bayne et al. 2005). Future research quantifying differences in logging road densities between single-pass versus multi-pass harvesting scenarios and their influence on forest biota is encouraged.

Broader scale (>2.56 km^2) differences in community composition and avian abundance could not be investigated with my current study design since several of the single-pass harvests were adjacent to planning units previously harvested in a multi-pass fashion. In theory, forest harvesting within a planning unit may influence the abundance and population dynamics of forest biota in adjacent planning units, particularly for forest interior specialists. Broad-scale

aggregation of harvest units might decrease fragmentation effects on forest interior specialists in adjacent leave areas and planning units (e.g. Rempel et al. 2007). Replicated, adaptive management experiments where new planning units of similar forest composition and adjacent to un-harvested planning units assigned to either single or multi-pass harvest would be useful to determine the influence of harvest pattern on adjacent planning units and on bird abundance at planning unit or regional scales (>50 km^2). Similarly, analyses at the stand scale using individual point-count stations would allow the examination and partitioning of variance related to leave blocks as well as distance to disturbance.

My comparisons of how bird communities differ from patterns expected with NRV suggest that approximating disturbance pattern is insufficient to bring about ecological convergence with NRV in the early post-disturbance phase. Regardless of whether single- or multi-pass harvesting was used, community composition differed substantially between post-fire and green harvest landscapes. Salvage logged areas were ecologically more similar to fire than single-pass harvests, highlighting the role of the disturbances caused by fire that are above and beyond the effects of the mechanical harvesting (e.g. standing dead material etc.). If the natural disturbance approximation paradigm is to be taken any further as a means of preserving representative biodiversity and ecological function where harvesting occurs, the most fruitful avenue would therefore be experimentation with prescribed burning as a method of post-harvest site treatment, or some other means of approximating the chemical disturbance caused by fire. Future research should attempt to examine this as a potential management tool from both ecological and economic perspectives. However, my results suggest that moving toward single-pass, aggregated harvest plans in the boreal forest will provide a better fit with NRV than multi-pass harvests. Furthermore, my optimization routine provides the first quantitative targets for residual retention

based on data other than landscape patterns. Aggregated harvest systems are often considered

more cost effective due to harvesting and transportation efficiencies (Delong 2002; D'Eon 2007).

Given the slight improvement in approximating NRV and increased efficiencies, I suggest forest

managers in the Boreal plain preferentially use single-pass harvests instead of multi-pass

harvests, and use the percentiles from my optimization to set targets for and relative proportions

of harvests receiving these attributes. Results of the optimization routine however, may be most

appropriately applied to planning units with high (>50%) mature deciduous forest. Similar

efforts might be fruitful in landscapes dominated by greater proportions of coniferous forest.

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CHAPTER 4. GENERAL CONCLUSIONS, IMPLICATIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

4.1 General Conclusions

Forest management practices in the boreal forest of western Canada have traditionally sought to maximize the immediate economic return from forest harvesting practices. Typically, this approach employed multi-pass clear-cut harvesting with cut-and-leave blocks, designed to provide a continuous supply of timber with minimal harvesting costs. Forests created in this fashion would typically approach monocultures of even-aged stands, with age structure truncated at the age where stands typically are a maximum growth rate (i.e. maximum sustained yield). A consequence of this approach is forest structure and composition dramatically simplified relative to the complex forest mosaics created by natural disturbances, particularly fire (Schieck and Hobson 2000). This raises concern that biodiversity would be negatively influenced by forestry practices, and thus foresters and ecologists have sought a new paradigm for management of harvesting in the boreal forest (Delong and Tanner 1996).

The prevalence of natural disturbances in shaping the structure and composition of plant communities of the boreal forest, and the presumed adaptation of boreal wildlife to these habitats (Hunter 1993), have led to the idea of the use of natural disturbance as a template for forestry operations (Delong and Tanner 1996; Delong 2002). Initially, this involved the idea of retaining single or multi-tree islands of residuals within cutblocks, cutting to natural boundaries, and occasionally changing rotation lengths to match fire return intervals. More recently, foresters have experimented with the spatio-temporal aggregation of cutblocks into single-pass harvests and it was this aspect of the natural disturbance paradigm that I investigated. Specifically, the objectives of this thesis were to assess; 1) how bird communities are influenced by anthropogenic disturbances relative to natural disturbance (fire); and 2) which attributes (residual

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composition, configuration and pattern) of these landscapes are key to the maintenance of forest-bird communities. Some of the key findings from my research are outlined below.

While many previous studies have investigated within-cutblock residual retention as a means of maintaining boreal forest bird communities (Schieck and Song 2006), all have done so at the stand scale. Furthermore, no previous study has explicitly contrasted bird communities in single-pass harvests to the similarly aged post-fire origin forests that they are designed to approximate. Due to the large-scale of these disturbances, the number and types of habitats involved are highly variable, necessitating landscape-scale approaches. In addition, bird communities show strong structure related to forest composition and age (Cumming and Diamond 2002; Hobson and Bayne 2000a; Hobson and Bayne 2000b; Kirk et al. 1996; Kirk et al. 1997). Therefore, I began in Chapter 2 by identifying differences in vegetation between plots selected in each of my four treatments, and examined how structure and composition changed after disturbance.

Despite my initial selection criteria being reasonably similar between treatments, there remained some difference in vegetation community composition between treatments. Salvage and unsalvaged post-fire plots tended to have more area of lowland and/or black spruce or jack pine habitats than the green harvest treatments, which had more hardwood and mixedwood habitats. Though this could have been due, in part, to a selection process that was not random, it was more likely due to fires acting in a more stochastic fashion than the targeted harvesting of the most commercially viable forest stands in green harvests. Due to these differences, I included pre-disturbance vegetation as covariates for analyses of bird community composition in Chapter 3.

Comparison of residual patch area, size class distribution, fragmentation metrics, and residual patch composition relative to pre-disturbance conditions all suggested that treatments differed in

how they disturbed the landscape. Comparison of the vegetation composition of live stands pre-
and post-disturbance at the landscape and residual patch scales, suggest that fires were relatively
stochastic, leaving live stands roughly in proportion to pre-disturbance composition, with a
tendency for less hardwood to be disturbed. However, both unharvested and salvage-logged post-
fire plots differed in that salvage logged plots had significantly less other conifer habitat retained
than predicted and a trend toward less area surviving as residual patches. Differences between
unharvested and salvage-logged post-fire areas were likely attributable to the role played by fire
severity in determining where salvage logging operations can occur. Single-pass harvests tended
to be structurally similar to the post-fire treatments with high residual retention, similar
fragmentation metrics to post-fire residual patches, similar size-class distribution of residual
patches, and having more hardwoods in the retained residuals than expected based on pre-
disturbance composition.

In general, the greatest differences between the characteristics of post-fire and post-harvest
landscapes occurred when forests were harvested using multi-pass harvests. Multi-pass harvests
had significantly less area retained as within cut-block residual patches than in all of the other
disturbances, and patches that were uniformly smaller, more isolated, less complex and less
variably sized and shaped than the other disturbances. In addition, unlike the other treatments,
there was a bias toward less softwood dominated mixedwood habitat in post-harvest residuals
than expected. Given these differences, multi-pass harvests are less likely to maintain bird
communities that overlap with the Natural Range of Variation (NRV), particularly through time.
Previous research suggests that old-growth forest bird communities may only occur in patches
>5 ha (Schieck and Hobson 2000), and that 5 ha patches might not be sufficiently large for the
long-term persistence of this community (Schmiegelow et al. 1997; Schmiegelow and

Mönkkönen 2002). Therefore, the relative paucity (14% by area) of large (>5 ha) residual patches in multi-pass harvests suggests that bird communities might be less likely to persist within NRV through time than in single-pass harvests, which had 57% of the residual patch area in patches >5ha in size. However, the interaction between residual patch area and composition in maintaining bird communities similar to NRV has received little attention in the literature, and was therefore part of the focus in Chapter 3.

To determine the value of single-pass harvesting in approximating NRV as a means maintaining biodiversity where forest harvesting occurs, I examined abundance and community composition of the forest bird community across treatments. Due to the paucity of studies conducted at the landscape-scale, I chose to represent species abundances by summation of their point-scale abundances across all 16 point-count stations within 2.56 km^2 plots (i.e. 1.6 x 1.6 km), thus reflecting avian abundance across the breadth of niches within a plot. Multivariate ordination using redundancy analysis revealed that species composition and abundance split primarily on the basis of burned versus unburned habitats. Of 37.6% of the variance in the community data that could be explained, variance partitioning showed the majority (19.7%) was attributable to disturbance related variables, 6% of which was associated with the pre-disturbance differences in vegetation described in Chapter 2. Only 2.7% of the variance was associated with amount and composition of residual patches, whereas non-linear responses to area disturbed by fire and area harvested each accounted for 5.5% of the variance. Given the high proportions of the plots disturbed, and the relatively low areas of residual patches, it is not entirely surprising that plot-level community composition was not more affected by residual patches, as community composition would be dominated by the effect of early successional environments. Graphical examination of sample scores as well as pairwise statistical

comparisons of the treatments suggested that community composition of single-pass harvests was closer to NRV than was achieved in multi-pass harvests, though effect size was not as great as I originally predicted. Unlike the single- and multi-pass harvests (green harvests), salvage harvested plots generally showed substantial overlap in community composition with NRV. Since salvage-logged landscapes contained harvests yet did not overlap with green harvests, I interpreted overlap with NRV as being attributable, in part, to the role of the chemical disturbance created by fire, and the preponderance of unharvested snags that remain on the landscape that can act as foraging and nesting substrates for the cavity-nesting guild. In general, trends in community composition fit my *a priori* hypothesis that community similarity to NRV would occur in the following order: post-fire sites with salvage logging > single-pass post-harvest sites > conventional multi-pass post-harvest sites.

Results of my community level comparison between various harvesting strategies and NRV are not directly comparable to other studies due to the lack of previous studies involving single-pass harvest, and the lack of studies comparing harvest to NRV at a landscape-scale. Post-fire plots were primarily distinguished by cavity-nesting species, while single- and multi-pass harvests were more associated with open-habitat and shrub-nesting species. Single- and multi-pass harvests also tended to have greater abundance of species associated with mixedwood and mature conifer habitats. While this was due in part to adjacent leave blocks (particularly for multi-pass harvests), it can also be attributed to residual patches in green harvests having slightly more mixedwood habitat maintained in residual patches, though this is complicated by differences in pre-disturbance vegetation between treatments. Previous stand-scale studies have shown these same general patterns, with post-fire bird communities dominated by cavity nesters while post-harvest communities are dominated by ground and shrub nesting species and habitat

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generalists (Hobson and Schieck 1999; Morissette et al. 2002; Schieck and Hobson 2000; Schieck and Song 2006; Simon et al. 2002) at least within 30 years of disturbance.

Application of a Monte-Carlo simulation model that sought to minimize a regression function relating community dissimilarity (Sorensen's dissimilarity coefficient) relative to NRV, to harvest type and landscape composition, generally supported the results of community ordinations. Of 100,000 simulations, 67% were minimized where single-pass harvesting was simulated. Furthermore, dissimilarity was minimized when harvests removed 66-88% of the area of a planning unit, and 5-19% was left as residual patches. This is similar to the nonlinear responses selected in ordination models, that suggested harvest were most similar to fire when intermediate to high proportions of the plots were harvested.

4.2 Implications

The relative improvements in similarity of single-pass harvested landscapes to NRV with respect to both vegetation structure and to a lesser extent the avian community, suggest that it is preferable to conventional multi-pass harvesting plans. Application of single-pass harvests is not only more efficient for foresters, but will maintain avian communities that are at least, if not more similar to NRV than multi-pass harvests. If the underlying premise of the Natural Disturbance Paradigm holds true, then single-pass harvests should be more sustainable in the long-term. However, until the unlikely event of forest harvests showing complete overlap with NRV, maintenance of early-post disturbance bird communities will require retaining early post-fire habitats of both live and fire killed residual stands (Hobson and Schieck 1999; Koivula and Schmiegelow 2007; Morissette et al. 2002; Schieck and Hobson 2000; Schieck and Song 2006; Schmiegelow et al. 2006).

Several aspects of the data presented herein suggest that the benefits of single-pass harvests could extend into longer time frames, and possibly result in early ecological convergence between harvest and NRV. With respect to residual patches, high levels of residual retention tended to increase community similarity to NRV and total area of residual patches was substantially higher in single-pass harvests. In addition, residual patches in both harvest and post-fire sites act to maintain components of the old-growth community. The distribution of patch size classes within the single-pass harvests had proportionally greater area (57% vs. 14%) in patches >5ha in size in which old-growth associated species are more likely to occur and persist (Schieck and Hobson 2000; Schmiegelow et al. 1997; Schmiegelow and Mönkkönen 2002).

In addition to the role of residual patches, the surrounding matrix of re-growing forest will continue to play a role. Much like the forest fires that they are designed to approximate, single-pass harvests have a large area of relatively similarly aged forest re-growing, whereas multi-pass harvests will in most circumstances have a new age cohort imposed when the final pass is completed. Therefore, while single-pass harvests will contain a more-or-less bimodal age class structure, multi-pass harvests will have at least three age classes within the landscape. Given the strong influence of forest age in structuring bird communities (Cumming and Diamond 2002; Hobson and Bayne 2000a; Schieck et al. 1995; Schieck and Song 2006; Westworth and Telfer 1993) this may serve to accentuate landscape-scale differences between single- and multi-pass harvests when the final pass occurs. The greatest divergence between harvest and NRV occurs in the early post-disturbance period, and bird communities begin to converge approximately 14 years post-disturbance as snags in post-fire landscapes begin to fall (Hobson and Schieck 1999; Schieck and Hobson 2000). Therefore reintroducing a new disturbance (final-pass) in ~10 years

into multi-pass landscapes might set back ecological convergence at the landscape-scale, by re-introducing an early post-harvest bird community.

4.3 Recommendations for future research

Although the key question in my study involves whether or not avian communities in harvested landscapes overlap with NRV, it would be useful to assess the fitness consequences of various disturbances on boreal bird populations. While species' abundances are often considered good proxies for habitat quality, occasionally abundance provides inferences that are opposite to the true fitness consequences (Bock and Jones 2004). A recent study by King and DeGraaf (2004), suggested birds in smaller group- selection cuts had later clutch initiation dates than birds in larger openings, potentially highlighting a role of disturbance size in population dynamics. Future studies contrasting nest success, fledging success, survival, or behaviour (e.g. movements, placement of territories relative to roads, etc.) are necessary to assess the population consequences of approximating natural disturbance in all treatments.

Simulation studies suggest that the spatio-temporal aggregation of cutblocks can reduce the footprint of roads (Delong, 2002), though this might not be the case in mountainous terrain (D'Eon, 2007). Aggregated plans can result in as little as one third of those in multi-pass systems (Andison 2003). Quantification of the area and length of roads in single-pass versus multi-pass harvests as well as habitat fragmentation is therefore needed. The distribution, density and longevity of logging roads within the forest landscape have implications for long-term ecological sustainability. Roads that are relatively permanent cause not only habitat loss, but also serve to fragment the landscape. Linear disturbances such as roads can impact forest birds by acting as territorial boundaries, or through edge effects in sensitive species (Bayne et al. 2005). Furthermore, at high densities, linear disturbances can cause non-linear responses in forest bird

abundance (Bayne et al. 2005). Therefore, studies examining the influence of logging road density on forest bird abundance, behaviour (e.g. willingness to cross roads, whether roads are treated as territory boundaries or are avoided), and demography are needed. Furthermore, data from such studies should be used in spatially explicit simulation models to assess the consequences of aggregated versus multi-pass harvests for forest birds across entire forest management areas.

Given the greatest ecological similarity to NRV was seen in salvage-logged landscapes shortly after disturbance, the most fruitful avenue for further experimentation would be application of single-pass harvest with prescribed burning as a post-harvest site treatment. In addition to the abundance of cavity nesters already being higher in single- than multi-pass harvests, the potential for fire to act as an attractant for pyrophilous insects (e.g. Cobb et al. 2007) and create standing dead trees within the landscape might enhance habitat for early post-fire specialist birds such as Black-backed and Three-toed Woodpeckers. Since these species are primary cavity nesters, elevated populations of these species after harvest could cause a response in the cavity nest-web (Martin and Eadie 1999; Martin et al. 2004), through greater abundance of nest cavities which could be subsequently inhabited by secondary cavity nesters. Although it remains to be seen, it is unlikely that even single-pass harvests that received prescribed burning could converge with NRV in the early (1-5 yrs) post-disturbance phase, given recent research suggesting salvage logging does not completely overlap with NRV for cavity nesters (Koivula and Schmiegelow 2007) or in both vascular and non-vascular plant community composition (Bradbury 2006; Macdonald 2007). However, it would be fruitful to examine if earlier ecological convergence with NRV could be brought about via prescribed fire.

Hobson and Schieck (1999) and Schieck and Hobson (2000), examined ecological convergence of bird communities with NRV in post-harvest residual patches of similar age (1, 15,30, and 60 years post-disturbance) in a retrospective study. A similar study examining temporal convergence of single-pass and multi-pass harvest with NRV at the landscape-scale by either revisiting the sites used in this study or finding new disturbances would be useful. In particular, future research should test whether the age class differences created by the final pass in multi-pass harvests will accentuate the minor differences between single and multi-pass harvests. Due to this potential effect, I would hypothesize that at a landscape-scale, single-pass harvests will be closer to NRV than multi-pass harvests in a time frame of ~10-15 years post-disturbance. Similarly, at the stand scale, it would be useful to create a stratified selection of residual patches and create a balanced design based on patch size and composition in a study contrasting avian communities. In this fashion, it would be possible to examine the interactions of harvest type, patch size and patch composition on convergence of bird communities with NRV through time. Ultimately it must be recognized however, that as found in previous comparisons with NRV through a chronosequence of up to 60 years (Hobson and Schieck 1999; Schieck and Hobson 2000), managing live residuals and harvest pattern will, at best, have limited success at making harvest more similar to NRV. Thus, while Natural Disturbance Emulation may currently be a better paradigm than maximum sustained-yield forestry for incorporating values beyond timber, additionally limiting the extent of forestry activities and/or finding alternate management strategies may assist in maintaining boreal forest songbird communities.

The difficultly I had in fully replicating pre-disturbance vegetation composition between treatments highlights several avenues for future research. Pre-disturbance vegetation played a

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role in the structure of forest bird communities, as 6% of the explained variance was attributed to this variable. It would be useful to assess whether single-pass harvesting is most appropriately applied in hardwood, mixedwood or softwood habitats. The best approach to accomplishing this would be to conduct replicated experiments with more coniferous dominated management units randomly assigned to single-and multi-pass style harvests. Further experiments are made more difficult however, by both the difficulty of co-ordination with forestry companies, and the likelihood of having similar habitats burned in a similar time frame. Alternatively, the data presented herein could be re-examined using stratified randomized sampling from with the data set to create balanced designs. This approach has the disadvantage however, of being applicable at a point scale and being influenced by the surrounding landscape. Given the lower abundance and frequency of occurrence of Neotropical migrants associated with mixedwood and coniferous habitats, as well as the greater occurrence of post-fire specialists in mature black spruce and jack pine habitats, I would hypothesize that single-pass harvesting in these habitat types would results in greater convergence with NRV than seen in aspen or mixedwood habitats.

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APPENDIX A. SPECIES NAMES AND AOU CODES

AOU code	Common Name	Latin name
RNGR	Red-necked Grebe	*Podiceps grisegena*
PBGR	Pied-billed Grebe	*Podilymbus podiceps*
COLO	Common Loon	*Gavia immer*
RBGU	Ring-billed Gull	*Larus delawarensis*
FRGU	Franklin's Gull	*Larus pipixcan*
BLTE	Black Tern	*Chlidonias niger*
COME	Common Merganser	*Mergus merganser*
MALL	Mallard	*Anas platyrhynchos*
AMWI	American Wigeon	*Anas americana*
AGWT	Green-winged Teal	*Anas crecca*
BWTE	Blue-winged Teal	*Anas discors*
REDH	Redhead	*Aythya americana*
RNDU	Ring-necked Duck	*Aythya collaris*
COGO	Common Goldeneye	*Bucephala clangula*
BUFF	Bufflehead	*Bucephala albeola*
CAGO	Canada Goose	*Branta canadensis*
AMBI	American Bittern	*Botaurus lentiginosus*
SACR	Sandhill Crane	*Grus canadensis*
SORA	Sora	*Porzana carolina*
AMCO	American Coot	*Fulica americana*
COSN	Common Snipe	*Gallinago delicata*
GRYE	Greater Yellowlegs	*Tringa melanoleuca*
LEYE	Lesser Yellowlegs	*Tringa flavipes*
SOSA	Solitary Sandpiper	*Tringa solitaria*
SPSA	Spotted Sandpiper	*Actitis macularia*
KILL	Killdeer	*Charadrius vociferus*
SPGR	Spruce Grouse	*Falcipennis canadensis*
RUGR	Ruffed Grouse	*Bonasa umbellus*
MODO	Mourning Dove	*Zenaida macroura*
SSHA	Sharp-shinned Hawk	*Accipiter striatus*
COHA	Cooper's Hawk	*Accipiter cooperii*
RTHA	Red-tailed Hawk	*Buteo jamaicensis*
BWHA	Broad-winged Hawk	*Buteo platypterus*
BAEA	Bald Eagle	*Haliaeetus leucocephalus*
MERL	Merlin	*Falco columbarius*
AMKE	American Kestrel	*Falco sparverius*
OSPR	Osprey	*Pandion haliaetus*
LEOW	Long-eared Owl	*Asio otus*

BAOW	Barred Owl	*Strix varia*
GGOW	Great Gray Owl	*Strix nebulosa*
NOHO	Northern Hawk Owl	*Surnia ulula*
BEKI	Belted Kingfisher	*Ceryle alcyon*
HAWO	Hairy Woodpecker	*Picoides villosus*
DOWO	Downy Woodpecker	*Picoides pubescens*
BBWO	Black-backed Woodpecker	*Picoides arcticus*
TTWO	Three-toed Woodpecker	*Picoides dorsalis*
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius*
PIWO	Pileated Woodpecker	*Dryocopus pileatus*
NOFL	Northern Flicker	*Colaptes auratus*
CONI	Common Nighthawk	*Chordeiles minor*
RTHU	Ruby-throated Hummingbird	*Archilochus colubris*
EAKI	Eastern Kingbird	*Tyrannus tyrannus*
GCFL	Great Crested Flycatcher	*Myiarchus crinitus*
EAPH	Eastern Phoebe	*Sayornis phoebe*
OSFL	Olive-sided Flycatcher	*Contopus cooperi*
WEWP	Western Wood-Pewee	*Contopus sordidulus*
YBFL	Yellow-bellied Flycatcher	*Empidonax flaviventris*
WIFL	Willow Flycatcher	*Empidonax traillii*
ALFL	Alder Flycatcher	*Empidonax alnorum*
LEFL	Least Flycatcher	*Empidonax minimus*
BLJA	Blue Jay	*Cyanocitta cristata*
GRAJ	Gray Jay	*Perisoreus canadensis*
CORA	Common Raven	*Corvus corax*
AMCR	American Crow	*Corvus brachyrhynchos*
BHCO	Brown-headed Cowbird	*Molothrus ater*
YHBL	Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*
RWBL	Red-winged Blackbird	*Agelaius phoeniceus*
WEME	Western Meadowlark	*Sturnella neglecta*
BAOR	Baltimore Oriole	*Icterus galbula*
RUBL	Rusty Blackbird	*Euphagus carolinus*
COGR	Common Grackle	*Quiscalus quiscula*
EVGR	Evening Grosbeak	*Coccothraustes vespertinus*
PIGR	Pine Grosbeak	*Pinicola enucleator*
PUFI	Purple Finch	*Carpodacus purpureus*
RECR	Red Crossbill	*Loxia curvirostra*
WWCR	White-winged Crossbill	*Loxia leucoptera*
AMGO	American Goldfinch	*Carduelis tristis*
PISI	Pine Siskin	*Carduelis pinus*
SAVS	Savannah Sparrow	*Passerculus sandwichensis*

LCSP	Le Conte's Sparrow	*Ammodramus leconteii*
STSP	Saltmarsh Sharp-tailed Sparrow	*Ammodramus caudacutus*
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*
WTSP	White-throated Sparrow	*Zonotrichia albicollis*
CHSP	Chipping Sparrow	*Spizella passerina*
CCSP	Clay-colored Sparrow	*Spizella pallida*
DEJU	Dark-eyed Junco	*Junco hyemalis*
SOSP	Song Sparrow	*Melospiza melodia*
LISP	Lincoln's Sparrow	*Melospiza lincolnii*
SWSP	Swamp Sparrow	*Melospiza georgiana*
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*
WETA	Western Tanager	*Piranga ludoviciana*
BARS	Barn Swallow	*Hirundo rustica*
TRES	Tree Swallow	*Tachycineta bicolor*
CEDW	Cedar Waxwing	*Bombycilla cedrorum*
REVI	Red-eyed Vireo	*Vireo olivaceus*
PHVI	Philadelphia Vireo	*Vireo philadelphicus*
WAVI	Warbling Vireo	*Vireo gilvus*
BHVI	Blue-headed Vireo	*Vireo solitarius*
BAWW	Black-and-white Warbler	*Mniotilta varia*
NAWA	Nashville Warbler	*Vermivora ruficapilla*
OCWA	Orange-crowned Warbler	*Vermivora celata*
TEWA	Tennessee Warbler	*Vermivora peregrina*
CMWA	Cape May Warbler	*Dendroica tigrina*
YWAR	Yellow Warbler	*Dendroica petechia*
MYWA	Yellow-rumped Warbler	*Dendroica coronata*
MAWA	Magnolia Warbler	*Dendroica magnolia*
CSWA	Chestnut-sided Warbler	*Dendroica pensylvanica*
BBWA	Bay-breasted Warbler	*Dendroica castanea*
BLBW	Blackburnian Warbler	*Dendroica fusca*
BTNW	Black-throated Green Warbler	*Dendroica virens*
WPWA	Palm Warbler	*Dendroica palmarum*
OVEN	Ovenbird	*Seiurus aurocapillus*
NOWA	Northern Waterthrush	*Seiurus noveboracensis*
CONW	Connecticut Warbler	*Oporornis agilis*
MOWA	Mourning Warbler	*Oporornis philadelphia*
COYE	Common Yellowthroat	*Geothlypis trichas*
WIWA	Wilson's Warbler	*Wilsonia pusilla*
CAWA	Canada Warbler	*Wilsonia canadensis*
AMRE	American Redstart	*Setophaga ruticilla*
HOWR	House Wren	*Troglodytes aedon*

WIWR	Winter Wren	*Troglodytes troglodytes*
MAWR	Marsh Wren	*Cistothorus palustris*
BRCR	Brown Creeper	*Certhia americana*
WBNU	White-breasted Nuthatch	*Sitta carolinensis*
RBNU	Red-breasted Nuthatch	*Sitta canadensis*
BCCH	Black-capped Chickadee	*Poecile atricapillus*
BOCH	Boreal Chickadee	*Poecile hudsonicus*
GCKI	Golden-crowned Kinglet	*Regulus satrapa*
RCKI	Ruby-crowned Kinglet	*Regulus calendula*
VEER	Veery	*Catharus fuscescens*
SWTH	Swainson's Thrush	*Catharus ustulatus*
HETH	Hermit Thrush	*Catharus guttatus*
AMRO	American Robin	*Turdus migratorius*
MOBL	Mountain Bluebird	*Sialia currucoides*
BBsp	un-identified blackbird	
THsp	un-identified thrush	
VIsp	un-identified vireo	
Gull	un-identified gull	
Dusp	un-identified duck	
MERG	un-identified merganser	
WOsp	un-identified woodpecker	

APPENDIX B. HABITAT CHARACTERISTICS, TEMPORAL TRENDS, AND OBSERVER EFFECTS ON DETECTION FOR POINT-COUNT SURVEYS IN BOREAL FOREST HABITATS.

Introduction

Point-count sampling is a widely used technique to examine trends in avian abundance spatially, temporally or with respect to experimental treatments (Simons et al. 2007). Typically, indices of relative abundance (as opposed to densities) are generated from such surveys. Comparison of abundance indices has been called into question, however, since they require the assumption that rates of detection do not differ between sampling units or species to be compared (Bart et al. 2004; Farnsworth et al. 2002). Any source of bias must therefore be consistent and linearly related to true abundance (Pollock et al. 2002; Toms et al. 2006). Many factors may influence detection rates, including time of day, season, attenuation of calls due to habitat, and ambient noise, to name a few (Farnsworth et al. 2002; Rosenstock et al. 2002; Schieck 1997; Simons et al. 2007; Waide and Nairns 1988).

Recent advances in statistical modeling have allowed for estimation of biases in detection, allowing data to be corrected for biases in detectability prior to subsequent analyses. Several alternatives have been proposed, including double sampling; where large samples are taken, such as point counts, and an intensive survey method (e.g. territory mapping) is used on a subset of the sample units to model the relationship between the point-count estimate of abundance and "true" abundance measured in the intensive survey (Bart et al. 2004). Such a method is impractical for large-scale studies. Alternatively, detectability can be modeled as a function of distance from the cue (e.g. bird song) of the observer (Bart et al. 2004; Rosenstock et al. 2002). While this method is appealing in that it allows direct modeling of densities, it only models one component of detectability (i.e. the probability that a bird is detected given that it sings,

Farnsworth et al. 2002). Furthermore, distance sampling assumes that distances are estimated accurately, an assumption that does not hold for even small distances within forested habitats (Simons et al. 2007).

An appealing alternative for large landscape-scale studies is the count-removal method which treats a point count as a closed-population removal experiment in which all "captured" individuals are removed from the population before the next sampling interval (Farnsworth et al. 2002). This method has the advantage of being easily applied to field surveys and models two components of detectability; both the probability that a bird is detected given that it sings and the probability that a bird sings during a count (Farnsworth et al. 2002). However, the count-removal method assumes that detection rates do not vary within the survey period, an assumption that may be violated by species that sing in bouts or that move during the count period (Bart et al. 2004; Farnsworth et al. 2002). Since landscape-scale studies require sampling of multiple habitats and may involve numerous species (>100) and often preclude the use of double-sampling and distance-estimation methods, the count-removal method seems most amenable to estimating sources of bias for large-scale studies involving numerous species.

The extent to which factors such as habitat, landscape fragmentation, temporal trends in singing rates, and ambient conditions affect detection probabilities for point-count surveys in the boreal forest have not been previously reported. My objectives were to assess how landscape composition and structure, community complexity and temporal trends in singing patterns can propagate bias in abundance estimates. In addition, I assessed the relative importance of observer affects on detection probability. I hypothesized that increasing area of tree and dense shrub cover would reduce detection probability due to increased sound attenuation. Conversely, I hypothesized that detection probability will be greater around point counts with greater degrees

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of forest removal. Across species, I postulated that estimated detection probabilities would by positively related to song frequency. Observer effects are thought to have the most influence on detectability of neotropical migrants or residents due to their more generally complex and/or hard-to-hear songs or calls. Support for temporal models of detection probability are likely related to migratory strategy since timing of breeding and hence song frequency of residents and short-distance migrants differ temporally. Finally, I assessed the relative bias in detectability between four major disturbance types within the boreal forest: fire, post-fire salvage harvesting, multi-pass harvests with residual retention, and single-pass harvests with retention.

Methods
Study Area

The study area extended from Candle Lake, Saskatchewan in the east (53° 50' N; 105° 50' W) to the House River Fire in northeastern Alberta (approximate location 56° 44' N; 111° 23' W). The study area was located within the Boreal Plain Ecozone (Acton et al. 1998). This ecozone extends across Prairie Canada from southeastern Manitoba to northwestern Alberta and is bounded by the Precambrian Shield to the north and Aspen Parkland to the south. The Boreal Plain Ecozone is a gently rolling plain, covered by boreal mixedwood forest. The forest is composed of both deciduous- and coniferous-dominated forests, comprised of varying amounts of trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), and white birch (*Betula papyrifera*), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), black spruce (*P. mariana*) and balsam fir (*Abies balsamea*) (Rowe 1972; Kabzems et al. 1986). The successional patterns within the Boreal Plain are complex, with a heterogeneous mosaic of habitats created through multiple stand-disturbance patterns (Weir et al. 2000), which have led to some of the richest and most diverse bird communities in North America (Kirk et al. 1996).

Field methods

Breeding bird surveys were conducted using early morning point counts (~0400-0900h) at each station within each site based on the Indice Ponctual D'Abondance technique of Blondel et al. (1970). A total of 3547 points counts surveyed between 28 May and 1 July each breeding season from 2003-2005. All point counts were conducted using unlimited-distance point counts, where all birds seen or heard during 10 minutes were recorded. Point counts were conducted in a broad variety of habitats, including areas from zero to 100% disturbed by forest fire or clear-cut forest harvesting and were placed 400m apart to avoid acoustic overlap between stations. To augment sample size, staff also conducted surveys using digital recordings made with a stereo configuration bio-acoustic monitoring kit (Hobson et al. 2002). This technique allows sufficient spatial information for skilled observers to estimate abundance (Hobson et al. 2002). Digital recordings were transcribed by SVW and two other skilled observers (Rob Wapple and Enid Cumming) to avoid inter-observer biases. To allow comparison of field counts and digital recordings, counts were of unlimited distance.

Data collection and transcription (recordings) was designed to allow for estimation of detection probabilities using the count-removal model of Farnsworth et al. (2002). Therefore all observers coded detections according to whether a bird was first detected in the first three minutes, between three and five minutes, or in the last five minutes of a 10 minute point count.

Quantifying habitat

Primary vegetation variables were collated using GIS analysis of digital-cover maps. Since data came from three forest management areas in two provinces, I standardized forest inventory data into a few ecologically meaningful species associations. Estimates of pre-disturbance area

covered by hardwood (>75%), softwood (>75%), hardwood-dominated mixedwood (50-75% hardwood), and softwood-dominated mixedwood (50-75% softwood), forest types dominated by black spruce or jack pine, and non-forested habitats were generated for a 100m radius buffer around points using ArcGIS v9.1 (ESRI, Redlands, CA). I also quantified area of early seral habitat (5-30 years old) since high stem densities during this phase could impede sound transmission. Area in disturbance burned and/or harvested was also quantified as more open habitats may allow greater sound transmission.

In addition to vegetation data from forest inventories, I quantified shrub cover around point-count stations. Since my data came from several sources, more than one method of quantifying shrub cover was used. Shrub cover data for 600 point counts were stem counts of shrubs and saplings averaged from 10x10m square samples done 60m to the north, southeast and southwest of each point-count stations. Shrub cover for 1530 point counts were collected using cover abundance categories for each shrub species (0, 1-<1%, 2- 1-5%, 3- 5-15%, 4- 15-25, 5-25-50%, 6- 50-75%, 7- >75%), except in 2003 when shrub cover was estimated for 643 point counts using subjective categorizations of scattered, low, medium, and high total shrub cover. Due to this inconsistency, I used a subset of 329 point counts for which both the subjective and cover abundance codes were available, to create a binary model of high (1) versus scattered to moderate (0) shrub cover using Classification Tree analysis (Breiman et al. 1984). This categorization was used as I felt that high shrub cover was most likely to impede sound transmission, and was therefore most biologically relevant to detection probability. Classification Trees were constructed using the recursive partitioning library, rpart in R v. 2.3.1, (R Development Core Team, 2006). To avoid overfitting, classification trees were pruned using a minimal deviance complexity cross-validation (Breiman et al. 1984). High shrub cover was

predicted by beaked hazelnut (*Corylus cornuta*) cover of >15%, or by alder (*Alnus rugosa*) cover >25%. The Classification Tree resulted in a cross-validated error rate of approximately 17% (83% correct). The model was then used to predict shrub cover for 860 point counts left out of the original model creation set, and resulted in 81% correct classification for 419 samples with known shrub cover categories. Data from the 600 point counts using stem counts were categorized into the same binary classification by selecting data from the 80th percentile (≥100 stems/100m2) and above as high shrub cover. This decision was subjective, but appeared to fit with average stem counts for 57 plots for which I also had categorized shrub cover from scattered to high.

Estimation of Detection Probability

I used Huggins' closed-capture models implemented in program MARK (White and Burnham 1999) to estimate detection probabilities (Moore et al. 2004). Since I expected *a priori* that species would differ in their detectability, I ran separate analyses for each species, except for species with small sample sizes which were grouped with species I suspected should have similar detectabilities based on call characteristics and habitats used (MacKenzie et al. 2005).

The count-removal method treats a point count as a removal experiment, counting individuals only the first time they are detected (Farnsworth et al. 2002). I therefore fixed recapture probability (*c*) to zero for each time interval. Since I originally designed the survey to estimate detection probabilities using the method and software code of Farnsworth et al. (2002), I had unequal sampling effort between sampling intervals. Therefore, all models included a time-specific measure of effort as a covariate in the design matrix. I expected that the relationship between effort and detection rates would not be linear due to observer effects and the removal

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process biasing in favour of early portions of a count. Therefore, I first used a subset of 73 point counts divided into ten equal one minute count intervals to model detection rates as a function of cumulative effort using Huggins' closed captures in program MARK. Interval specific estimates of detectability for three separate groups of species categorized *a priori* high detectability species (n= 421, e.g. Ovenbird, Red-eyed Vireo), moderate detectability species (n= 479, e.g. Thrushes, Mourning Warbler), and low detectability species (n= 216, e.g. Golden-crowned Kinglet, Cape May Warbler) were estimated. Since the removal process alters the probability of capturing a new individual in subsequent sampling intervals (Farnsworth et al. 2002), I calculated cumulative detection probabilities from the derived, interval specific estimates of the Huggins' models. Cumulative detection probabilities were calculated using the formula $1-((1-p_1)*(1-p_2)*(1-p_x))$, where *p* refers to detection probability estimates for intervals 1 through x. Cumulative detection probabilities were fit with non-linear regressions, to determine the appropriate measure to include as a measure of effort in subsequent Huggins' models, and also to determine approximate lengths of surveys required to approach a detectability of one.

Detectability of individual species were estimated using Huggins' closed capture models in program MARK (White and Burnham 1999), via the RMark interface (Laake and Rexstad 2005) in R v. 2.3.1 (R Development Core Team 2006). The least parameterized model only included *p* as a function of effort. A total of 22 models were run per species (Table B.1). Shrub cover was included as a categorical dummy variable for high versus low shrub cover. In addition, I included observer experience (hereafter Experience), and whether the count was a field point-count or transcription of a digital recording (Mic) as a categorical dummy variables. Observers with ≥ seven years of experience were coded as experienced (1), observers with less experience were coded as inexperienced (0). Linear covariates including time of day (Hour), time of season

(Day), proportion of the buffer harvested by variable retention logging (Harvest), proportion of the buffer killed by fire (Burn), and species richness at the station were also included among candidate models. Time of day was standardized to hours after 03:00 h whereas time of season was standardized relative to 15 May. In addition, I fit up to the third-order polynomial for time of day and time of season as I expected detectability would not fit linearly with these variables.

Table B.1. *A priori* candidate models for Huggins' closed-capture models.

Model Name	Parameters included
Observer Perception models	
Effort	Effort
Experience	Effort + Observer Experience (dummy)
Mic	Effort + Microphone use (dummy)
Richness	Effort + Species Richness
Mic*Experience	Effort + Experience + Microphone + Experience*Microphone
Observer	Effort + Experience + Microphone + Species Richness
Mic*Richness	Effort + Microphone + Microphone*Species Richness
Temporal Effects models	
Time of day	Effort + Hour
Quadratic time of day	Effort + Hour + Hour^2
Cubic time of Day	Effort + Hour + Hour^2 + Hour^3
Date	Effort + Day
Quadratic date	Effort + Day + Day^2
Cubic Date	Effort + Day + Day^2 + Day^3
Time	Effort + Day + Hour + Day*Hour
Habitat models	
Harvest	Effort + Harvest
Burn	Effort + Burn
Harvest + Burn	Effort + Harvest + Burn
Harvest*Burned	Effort + Harvest + Burn + Harvest* Burn
Shrub cover	Effort + Shrub Cover (dummy)
Habitat	Effort + Harvest + Burn + Shrub
Early Seral	Effort + Area of Early Seral Habitat
Disturbance + shrub	Effort + Harvest+ Area of Early Seral Habitat + Shrub

Comparison of factors influencing Detection Probability and model types

I examined natural history characteristics influencing estimates of detection probability using General Linear Models (GLMs) on logit-transformed average estimates of detection probability. Four candidate models were considered including migratory guild, song rate (calls per minute), migratory guild + song rate, and a model including the interaction between guild and song rate. Song rate data were obtained from Borror and Gunn (1985), or from individual species accounts in the Birds of North America. (American Ornithologists' Union 2002) I selected amongst models using AICc (Akaike's Information Criterion corrected for small samples).

To examine what natural history characteristics influenced how much support each class of detectability model received, I analyzed Logit transformed model weights for the three model classes (Observer, Temporal and Habitat) using GLMs. Models included migratory guild, nesting guild, and primary habitat type (hardwood, softwood, mixedwood or open) as factors. Only main effects models were considered and model selection was via AICc.

Results

Detection rates as a function of cumulative effort

Cumulative detection probability increased nonlinearly with cumulative effort (Figure B.1). Detectability of species classified *a priori* as highly detectable was described by the function y= $0.171*Ln(x) + 0.621$ ($r^2 = 0.99$, p<0.001), moderately detectable species by the function y = $0.286*Ln(x) + 0.332$ ($r^2 = 0.99$, p<0.001), and low detectability species by the function y = $0.296*Ln(x) + 0.273$ ($r^2 = 0.98$, p<0.001). Solving for the length of survey required on average to reach 100% detectability suggests that 9.12, 10.34 and 11.62 minutes of survey effort are required for highly, moderately and low detectability species respectively.   Alternatively, to

reach 95% detectability, on average it would take 6.81, 8.71 and 9.84 minutes respectively for highly, moderately and low detectability species.

Estimated detection probabilities based on the natural logarithm of cumulative effort were very similar to estimates calculated using the original method of Farnsworth *et al.* (2002) Mc estimator for heterogeneous detection probabilities calculated using program SURVIV (Table B2). For nine species with detectability estimate calculated using both methods, estimates were significantly correlated (r= 0.682, p<0.05). When model-averaged estimates from the 22 candidate models are contrasted to the Farnsworth estimator (Mc), the correlation is stronger (r=0.817, p<0.01).
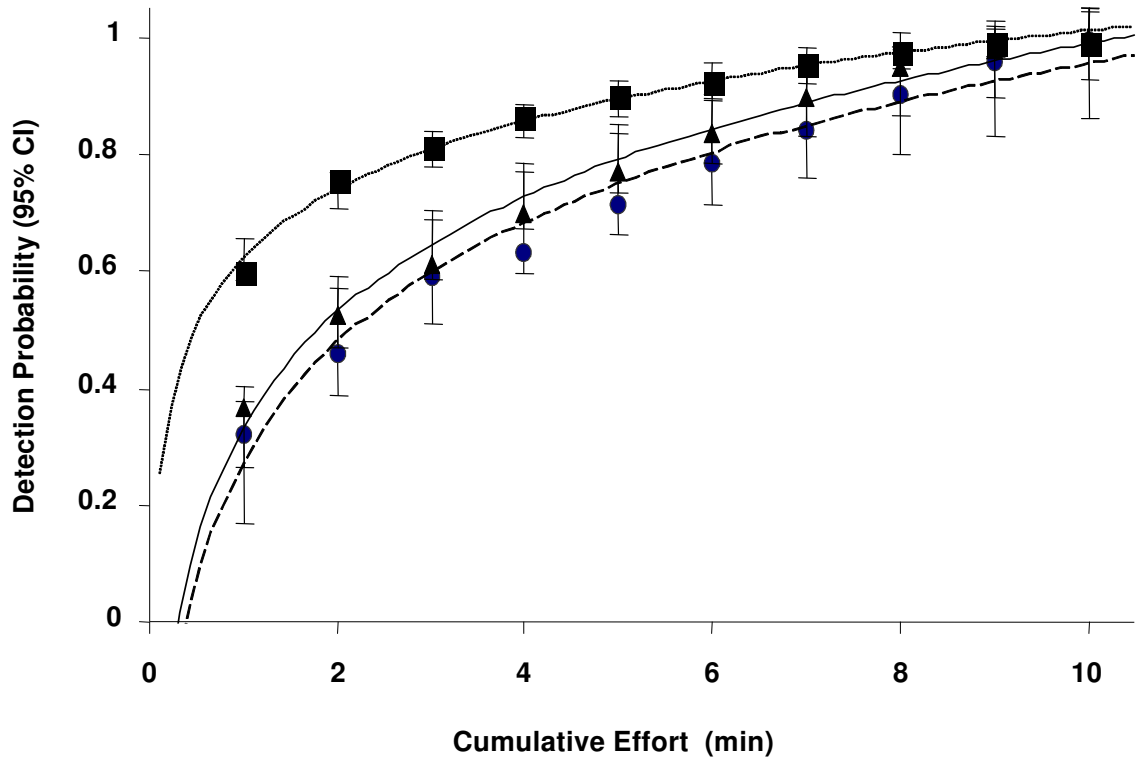
Figure B.1. Cumulative probability of detection for species grouped *a priori* as highly detectable (squares), moderately detectable (triangles), and low detectability (round) species. Detection probabilities were estimated as a function of interval (time) and group (detectability grouping) using Huggins' closed captures models. Non-linear regressions were fit separately to High (y= $0.171*Ln(x) + 0.621$; r^2= 0.99), Medium (y = $0.286*Ln(x) + 0.332$; r^2= 0.99), and Low (= $0.296*Ln(x) + 0.273$; r^2= 0.98) detectability groups.

Table B.2. Comparison of Farnsworth (Mc) estimator of detection probability with estimates derived using Huggins' closed capture models accounting for cumulative effort, and models including observer, temporal or habitat effects.

Species	Farnsworth estimate (Mc)	Ln(Cumulative Effort) estimate	Model Avg. estimate
AMRE	0.710	0.762	0.731
AMRO	0.785	0.850	0.796
BAWW	0.827	0.690	0.727
OVEN	0.919	0.928	0.922
RCKI	0.904	0.859	0.843
REVI	0.906	0.932	0.909
SWTH	0.812	0.875	0.857
WEWP	0.894	0.898	0.847
WTSP	0.952	0.929	0.914
Pearson Correlation		0.682	0.817
p		0.04	0.007

Estimated Detection probabilities

In total, there were 52774 encounter histories from which to create detectability models. However, 4223 detections were of species not appropriate for modeling because they were expected *a priori* to violate the assumption of closure, hence modeling was done on 48551 encounter histories. Detectability was modeled for 72 detectability groups. Eleven detectability groups (AMGO, BBsp, BCCH, BHCO, COSN, GCKI, KILL, OSFL, PIWO, WIWA and YBSA) had models that failed to converge due to sample size or violation of the closure assumption. Species violating the closure assumption were subsequently assumed to have detectability of 1. Detectability equations from similar species were used for species with models that failed to converge due to sample size. Detectability estimates across all 59 detection groups successfully analyzed averaged 76% ±14 (SD), but ranged from a low of 38% ±23 for Blue Jay to a high of 97% ±1 for Tennessee Warbler (Table B3).

Table B.3. Estimated species detection probabilities from Huggins' closed capture models.

Group	n	Average Mean (±SD)	Contiguous Mean (±SD)	Fire Mean (±SD)	Green Harvest Mean (±SD)	Salvage Mean (±SD)
ALFL	1500	0.88 (0.09)	0.90 (0.08)	0.90 (0.05)	0.86 (0.12)	0.90 (0.05)
AMRE	236	0.73 (0.07)	0.76 (0.05)	0.80 (0.03)	0.69 (0.06)	0.70 (0.17)
AMRO	816	0.79 (0.17)	0.84 (0.16)	0.80 (0.18)	0.68 (0.16)	0.83 (0.13)
BAWW[1]	148	0.72 (0.17)	0.72 (0.17)	0.91 (0.08)	0.64 (0.14)	0.90 (0.04)
BBWA	149	0.87 (0.01)	0.87 (0.01)	0.88 (0.02)	0.87 (0.01)	0.91
BBWO	405	0.79 (0.18)	0.71 (0.25)	0.83 (0.15)	0.50 (0.17)	0.81 (0.13)
BHVI	393	0.79 (0.04)	0.76 (0.02)	0.77 (0.01)	0.81 (0.03)	0.82 (0.02)
BLBW	54	0.72 (0.18)	0.59 (0.00)	0.59 (0.00)	0.90 (0.14)	
BLJA	201	0.38 (0.22)	0.41 (0.30)	0.30 (0.16)	0.36 (0.17)	0.50 (0.27)
BOCH	222	0.68 (0.28)	0.61 (0.29)	0.74 (0.23)	0.68 (0.29)	0.72 (0.26)
BRCR	246	0.59 (0.28)	0.63 (0.28)	0.66 (0.28)	0.48 (0.28)	0.51 (0.22)
BTNW	197	0.54 (0.19)	0.56 (0.22)	0.50 (0.05)	0.53 (0.16)	0.43
CAWA	150	0.79 (0.26)	0.83 (0.25)	0.47 (0.18)	0.80 (0.26)	0.77 (0.34)
CCSP[2]	619	0.82 (0.08)	0.85 (0.06)	0.83 (0.09)	0.81 (0.08)	0.80 (0.10)
CEDW	611	0.40 (0.22)	0.44 (0.23)	0.51 (0.25)	0.34 (0.17)	0.54 (0.29)
CHSP	2910	0.83 (0.07)	0.83 (0.07)	0.85 (0.07)	0.82 (0.06)	0.84 (0.06)
CMWA	93	0.70 (0.15)	0.73 (0.13)	0.56 (0.16)	0.72 (0.14)	
CONW	514	0.90 (0.03)	0.91 (0.03)	0.90 (0.02)	0.90 (0.03)	0.90 (0.03)
COYE	536	0.86 (0.08)	0.86 (0.08)	0.91 (0.06)	0.83 (0.07)	0.89 (0.06)
CSWA	329	0.87 (0.05)	0.91 (0.00)	0.90 (0.01)	0.83 (0.04)	0.84 (0.04)
DEJU	1768	0.81 (0.09)	0.82 (0.09)	0.83 (0.10)	0.79 (0.07)	0.82 (0.10)
EAKI	59	0.75 (0.21)	0.86 (0.20)	0.67 (0.23)	0.67 (0.22)	0.78 (0.11)
FLSP[3]	86	0.44 (0.15)	0.47 (0.15)	0.38 (0.08)	0.42 (0.16)	0.44 (0.14)
GRAJ	779	0.52 (0.28)	0.37 (0.23)	0.81 (0.15)	0.36 (0.17)	0.75 (0.21)
GRYE[4]	412	0.67 (0.24)	0.58 (0.22)	0.82 (0.17)	0.58 (0.25)	0.78 (0.17)
HAWO	246	0.66 (0.14)	0.56 (0.13)	0.73 (0.11)	0.60 (0.08)	0.83 (0.08)
HETH[5]	1778	0.89 (0.06)	0.88 (0.06)	0.89 (0.07)	0.88 (0.06)	0.89 (0.07)
HOWR[6]	751	0.87 (0.13)	0.90 (0.12)	0.87 (0.15)	0.85 (0.15)	0.87 (0.11)
LCSP	324	0.89 (0.08)	0.83 (0.11)	0.91 (0.06)	0.88 (0.10)	0.92 (0.07)
LEFL	492	0.84 (0.08)	0.86 (0.03)	0.96 (0.01)	0.77 (0.05)	0.88 (0.07)
LISP[7]	1186	0.86 (0.08)	0.86 (0.08)	0.89 (0.08)	0.83 (0.07)	0.88 (0.08)
MAWA	525	0.75 (0.17)	0.73 (0.14)	0.76 (0.07)	0.76 (0.18)	0.93 (0.01)
MOWA	1567	0.92 (0.01)	0.92 (0.01)	0.92 (0.01)	0.92 (0.01)	0.93 (0.02)
MYWA	2145	0.78 (0.07)	0.78 (0.07)	0.8 (0.09)	0.77 (0.06)	0.79 (0.08)
NAWA	401	0.68 (0.11)	0.72 (0.13)	0.64 (0.06)	0.64 (0.08)	0.61 (0.05)
NOFL	540	0.49 (0.28)	0.27 (0.20)	0.71 (0.22)	0.30 (0.09)	0.70 (0.22)
NOWA	84	0.82 (0.10)	0.71 (0.06)	0.93 (0.04)	0.77 (0.05)	0.89 (0.03)
OCWA	185	0.80 (0.05)	0.79 (0.05)	0.76 (0.02)	0.80 (0.05)	0.78 (0.02)
OVEN	2410	0.92 (0.04)	0.93 (0.04)	0.93 (0.04)	0.91 (0.04)	0.94 (0.04)

PHVI[8]	247	0.87 (0.11)	0.88 (0.09)	0.93 (0.10)	0.85 (0.11)	0.93 (0.10)
RBGR[9]	401	0.85 (0.02)	0.86 (0.03)	0.85 (0.02)	0.84 (0.01)	0.78 (0.04)
RBNU	527	0.65 (0.07)	0.67 (0.06)	0.64 (0.08)	0.65 (0.06)	0.64 (0.07)
RCKI	1698	0.84 (0.09)	0.84 (0.08)	0.83 (0.10)	0.85 (0.08)	0.82 (0.09)
REVI	1858	0.82 (0.08)	0.81 (0.09)	0.83 (0.09)	0.83 (0.08)	0.83 (0.09)
RUGR	572	0.83 (0.09)	0.82 (0.12)	0.83 (0.07)	0.84 (0.08)	0.83 (0.06)
SOSA	155	0.49 (0.25)	0.69 (0.02)	0.89 (0.06)	0.33 (0.18)	0.63 (0.20)
SOSP	408	0.85 (0.03)	0.88 (0.04)	0.85 (0.03)	0.84 (0.03)	0.83 (0.03)
SWSP	578	0.76 (0.16)	0.75 (0.14)	0.78 (0.17)	0.75 (0.16)	0.68 (0.14)
SWTH	1048	0.86 (0.05)	0.86 (0.05)	0.88 (0.06)	0.85 (0.05)	0.86 (0.04)
TEWA	3267	0.97 (0.01)	0.97 (0.00)	0.95 (0.00)	0.97 (0.00)	0.96 (0.00)
TRES[10]	290	0.57 (0.25)	0.43 (0.17)	0.79 (0.19)	0.40 (0.18)	0.66 (0.21)
TTWO	108	0.67 (0.31)	0.62 (0.40)	0.69 (0.25)	0.63 (0.41)	0.77 (0.18)
WETA	173	0.79 (0.19)	0.81 (0.16)	0.75 (0.17)	0.77 (0.22)	0.85 (0.09)
WEWP[11]	411	0.84 (0.14)	0.90 (0.05)	0.83 (0.15)	0.81 (0.18)	0.86 (0.10)
WIWR	604	0.90 (0.04)	0.90 (0.04)	0.92 (0.05)	0.89 (0.04)	0.90 (0.05)
WOsp[12]	346	0.69 (0.14)	0.57 (0.14)	0.75 (0.11)	0.60 (0.10)	0.81 (0.10)
WPWA	196	0.72 (0.26)	0.64 (0.26)	0.85 (0.18)	0.52 (0.26)	0.79 (0.21)
WTSP	7582	0.91 (0.04)	0.92 (0.04)	0.92 (0.04)	0.90 (0.03)	0.92 (0.04)
YWAR	202	0.71 (0.08)	0.71 (0.12)	0.70 (0.08)	0.72 (0.05)	0.71 (0.09)

[1] group includes BAWW (145) and BLPW (3)

[2] group includes CCSP(614), SAVS(3), VESP(2)

[3] group includes FLSP(1),GCFL(11), YBFL(73), WIFL(1)

[4] group includes GRYE(360), LEYE(56)

[5] group includes HETH(1766), THsp(1), VEER(11)

[6] group includes HOWR(726), MAWR(23), SEWR(2)

[7] group includes LISP(1185), FOSP(1)

[8] group includes PHVI(215), VIsp(25), WAVI(7)

[9] group includes RBGR(399), BAOR(2)

[10] group includes TRES(256), BARS(16), MOBL(18)

[11] group includes WEWP(388), SAPH(1), EAPH(22)

[12] group includes WOsp(301), DOWO(45)

Of 59 detection groups successfully analyzed, only 15 had model certainty (minimum model weight of 0.87). Of the species with model certainty, only three did not have Temporal models as their top model; Blackburnian Warbler had the Harvest model as the top model, Cedar Waxwing had Mic*Experience as the top model and Red-eyed Vireo the Observer model as top model. Nine species had the cubic date model as their top model (Alder Flycatcher, Chipping Sparrow, Dark-eyed Junco, Hermit Thrush, House Wren, Le Conte's Sparrow, Myrtle Warbler, Ruby-crowned Kinglet, Swainson's Thrush, and White-throated Sparrow). In addition Western Wood-peewee and Lincoln's Sparrow had the Time model as the top model.

Across the 44 species with model uncertainty, Observer models received an average of 42.4% of the support, Temporal models received 35.8% of the support, and habitat models received only 21.8% of the support. Observer models received the majority (≥50%) of the support in 16 species, while Temporal models received the majority of the support in 14 species, and Observer models only received ≥50% of the support in six species (Figure B.2).
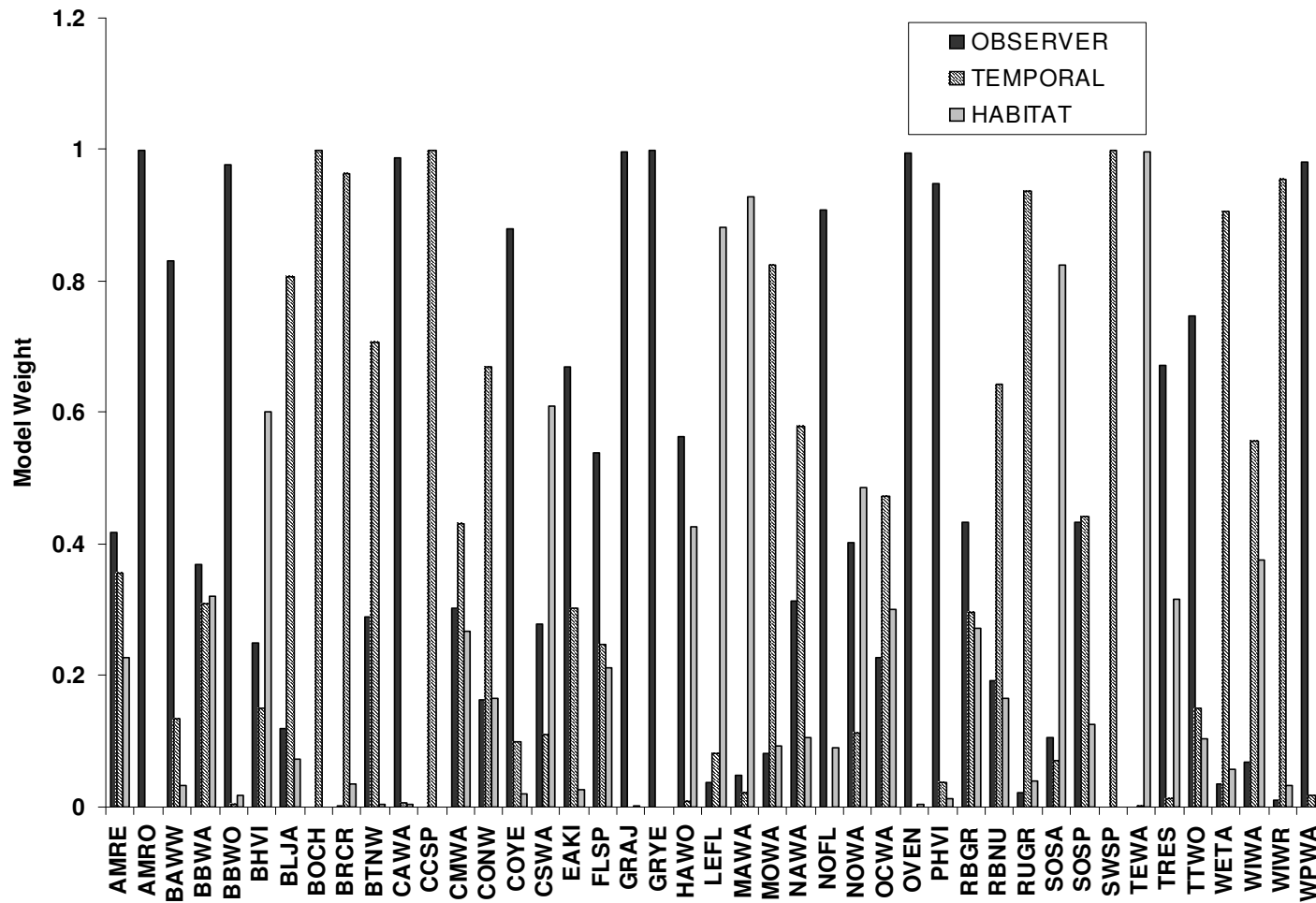
Figure B.2. Relative support (Model Averaged AICc weights) for Observer, Temporal and Habitat models of detection probability for 44 species with model uncertainty.

Factors influencing Detection Probability and model types

Detection probability appears to be related to several life history characteristics as there was substantial model uncertainty (Table B.4), and graphical examination of detectability versus song rate and migratory guild suggested both variables appeared to influence detectability estimates. The migratory guild model received the greatest support (38%) while the additive song rate plus migratory guild received similar support (37%). Due to the model uncertainty, I chose to generate predicted values from the interaction model to illustrate the relationship between detection probability and both song rate and migratory guild. The model predictions suggest species that sing more frequently are more likely to be detected, with Neotropical migrants being the most easily detected and residents the most difficult to detect (Figure B.3).

Table B.4. Model selection statistics from General Linear Models contrasting logit transformed detection probability estimates based. RSS= residual sum of squares, k = number of parameters, AICc= Akaike's Information Criterion corrected for small sample size, and ωi = AIC weight.

Model	n	RSS	k	AICc	ΔAIC	ωi
Migratory guild	57	28.78	3	-32.49	0.00	0.38
Song rate+Migratory guild	42	15.63	4	-32.43	0.06	0.37
Song rate	42	17.41	3	-30.36	2.13	0.13
Song rate+Migratory guild+Song rate*Migratory guild	42	15.49	5	-30.22	2.27	0.12
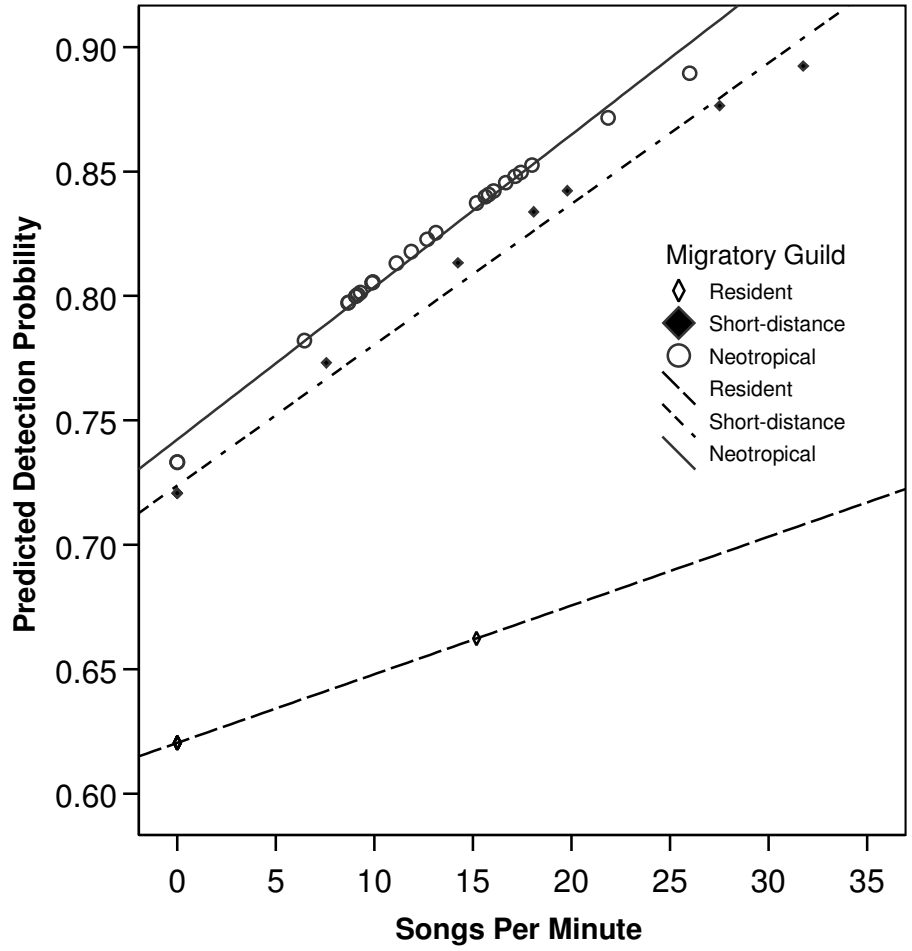
Figure B.3. Illustration of the relationship between frequency of singing and migratory guild and species average probability of detection estimates from Huggins' closed capture models.

Support for observer models was related to migratory strategy, as the GLM based on

migratory guild received 92.8% of the support. Resident species were more likely to have

detectability models supported than Neotropical or short-distance migrants (Figure B.4).

The relationship between support for temporal models of detection probability and life-history

characteristics was equivocal. All three GLMs were within four AIC units, though the habitat

type model received 59% of the support and the migratory guild model received 31% of the

support. Confidence intervals suggest no clear pattern in the data for either habitat type (Figure

B.5) or migratory guild (Figure B.6).

Of the three main effects GLMs explored for model weights for habitat detectability models,

the most parsimonious model was based on migratory strategy, receiving 99.9% of the support.

Detection functions based on habitat characteristics were more likely to be selected for

Neotropical migrants and residents than for short distance migrants (Figure B.7).
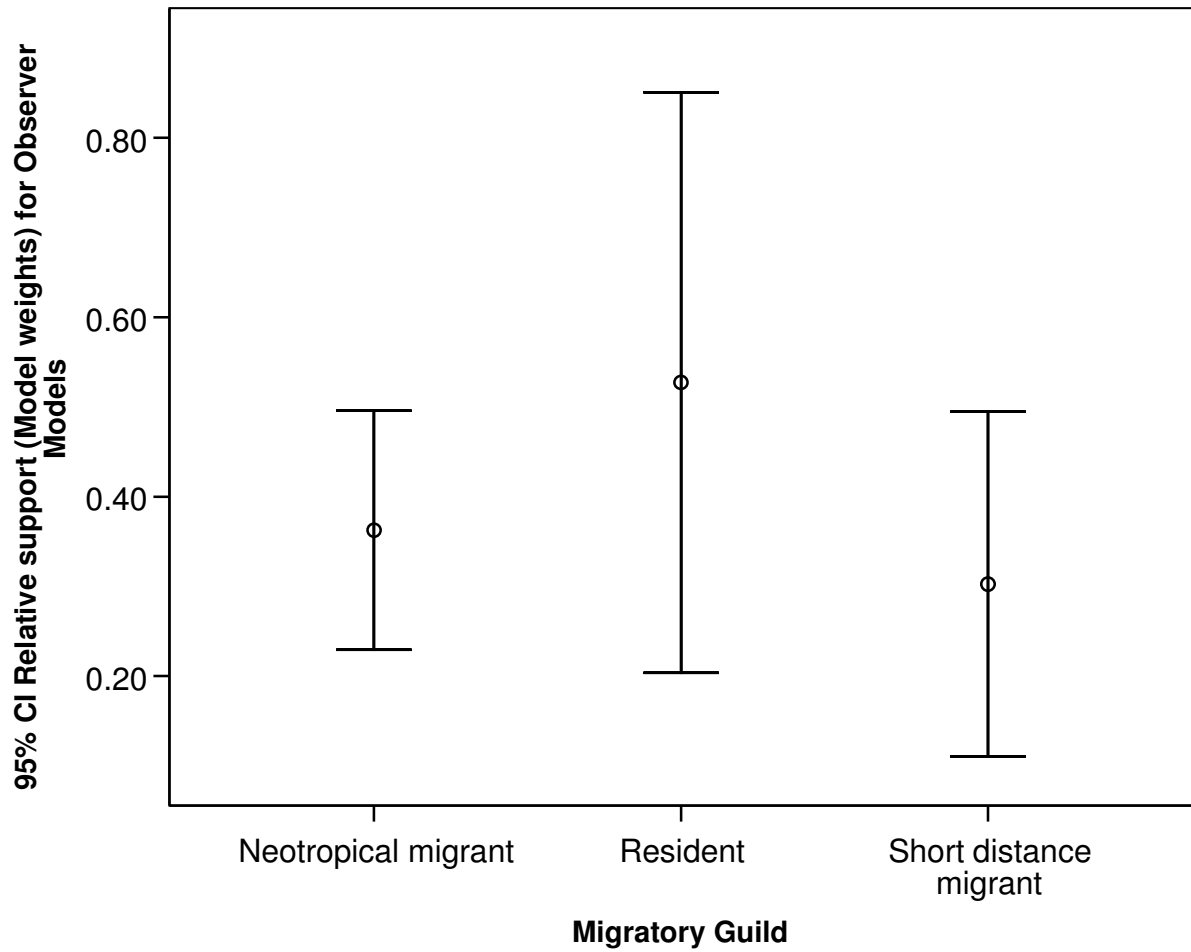
Figure B.4. Relative support for observer models of detection probability by migratory guild.
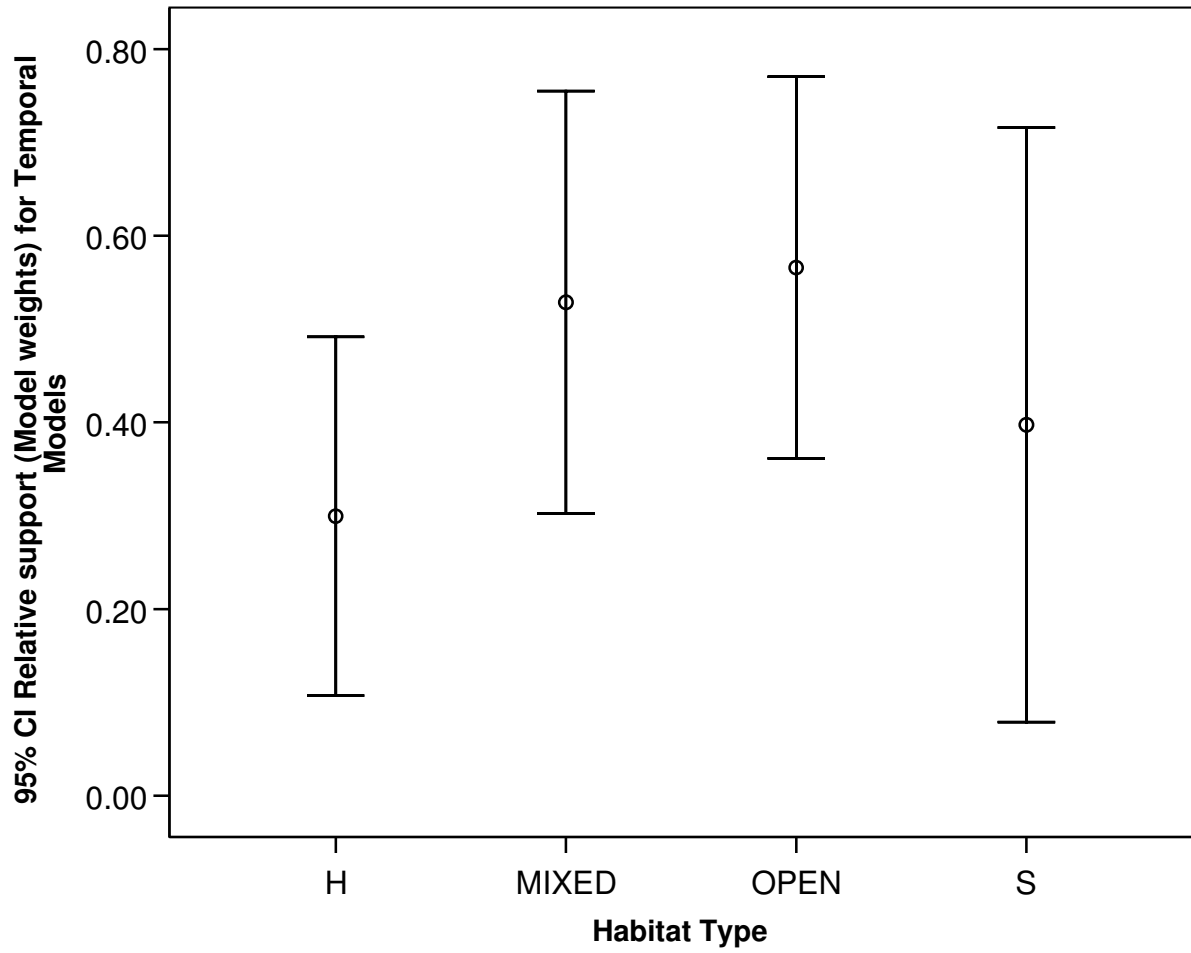
Figure B.5. Relative support for temporal models of detection probability by primary habitat types used by 59 species.
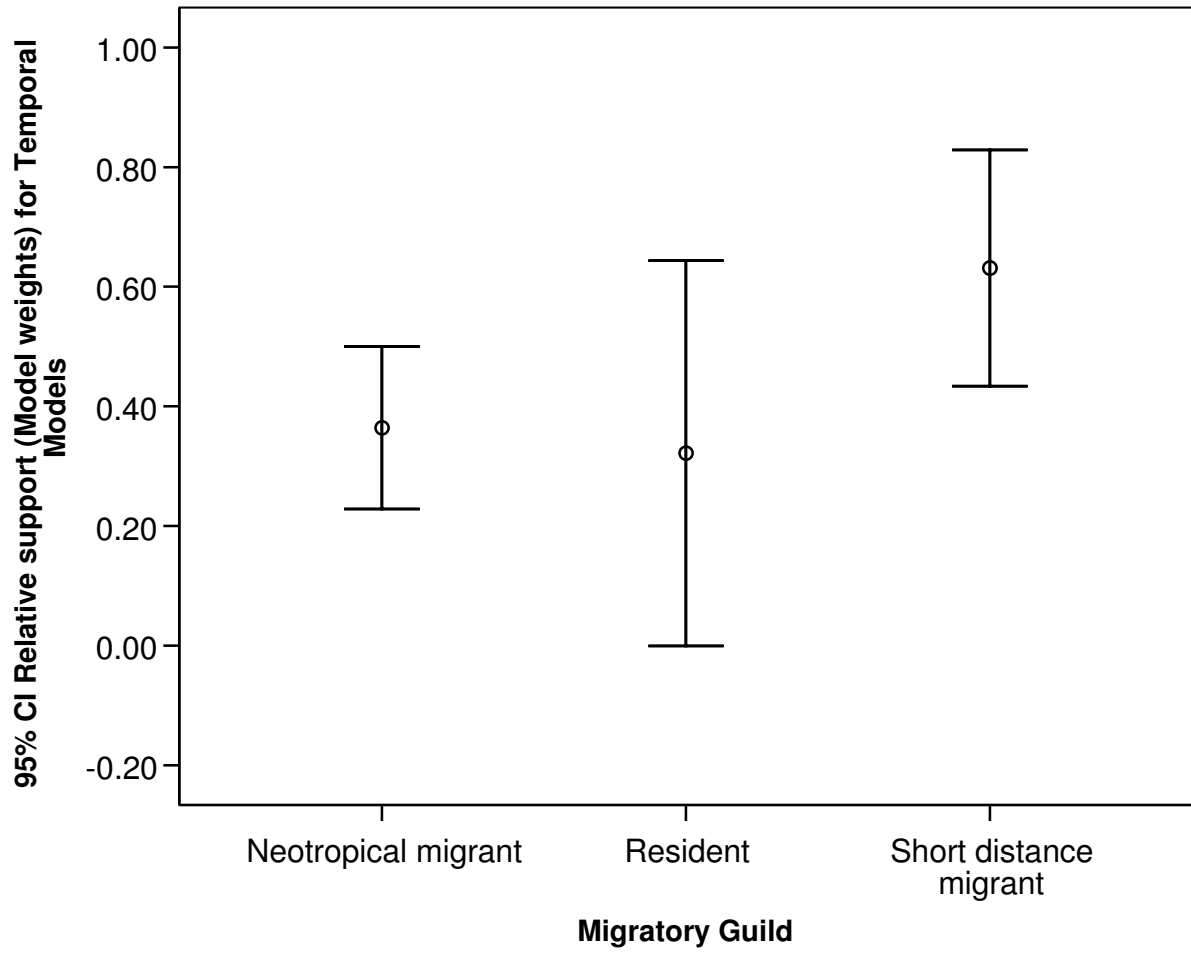
Figure B.6. Relative support for temporal models of detection probability by migratory guild.
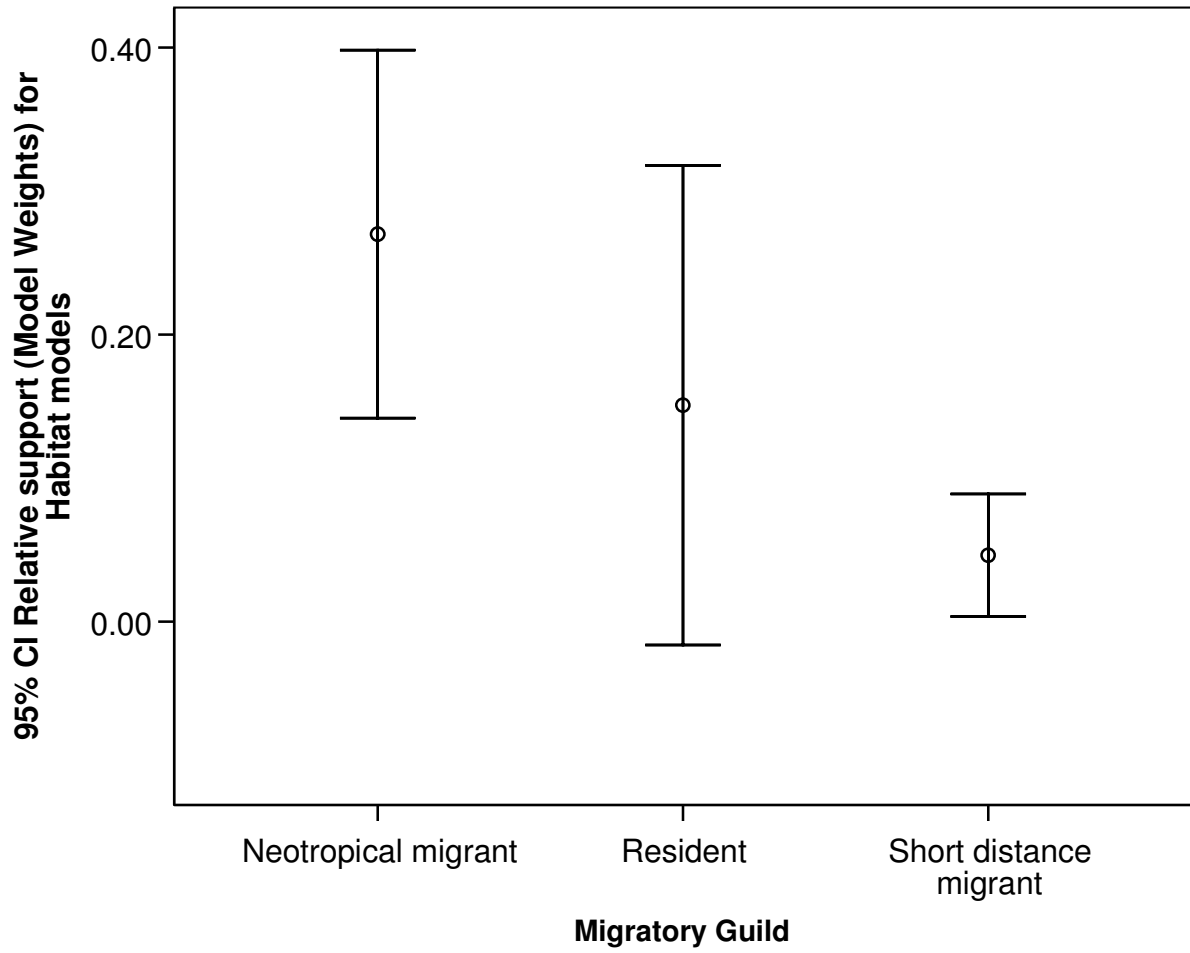
Figure B.7. Relative support for habitat models of detection probability by migratory guild.

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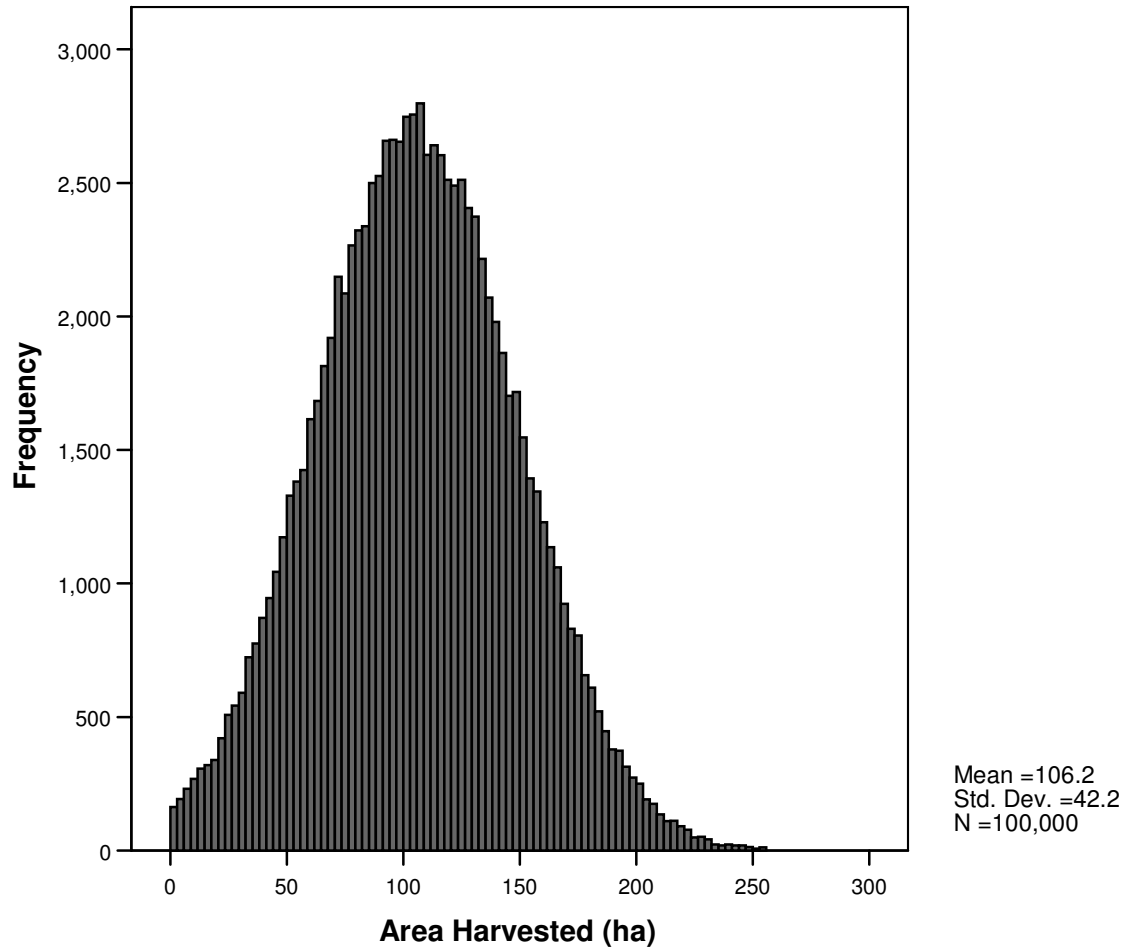
APPENDIX C. SIMULATED DISTRIBUTION OF VARIABLES IN MONTE-CARLO
OPTIMIZATION MODEL

Figure C.1. Distribution of simulated values for area harvested (ha).
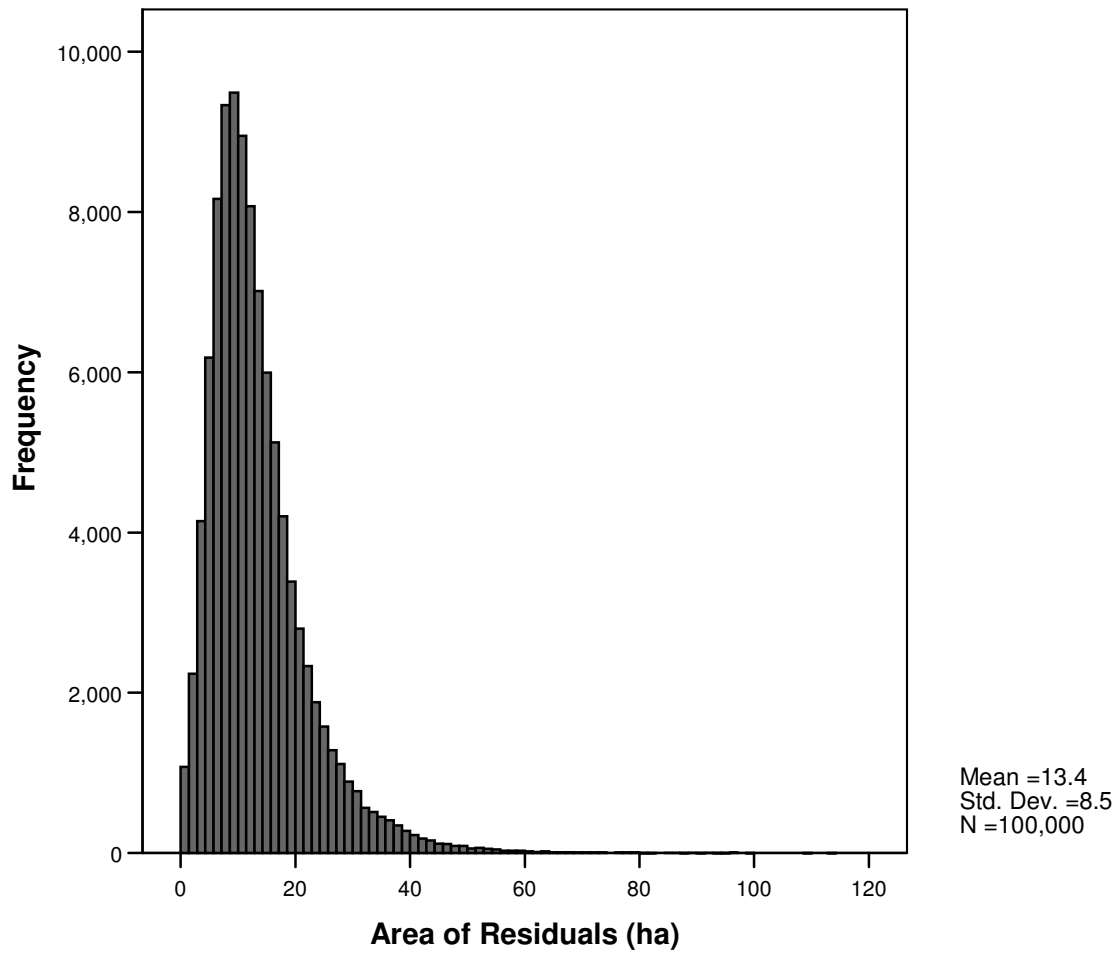
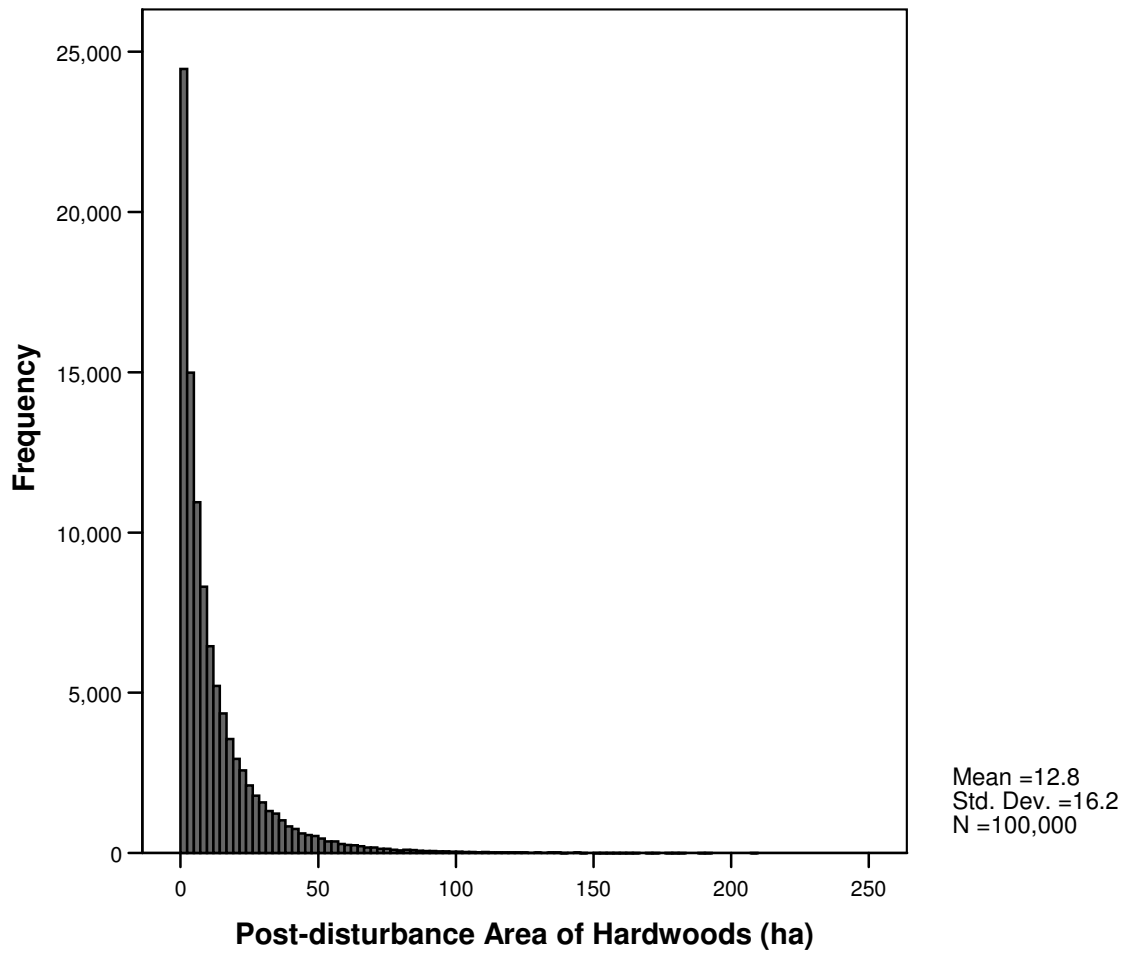Figure C.2. Distribution of simulated values for area of residuals (ha).

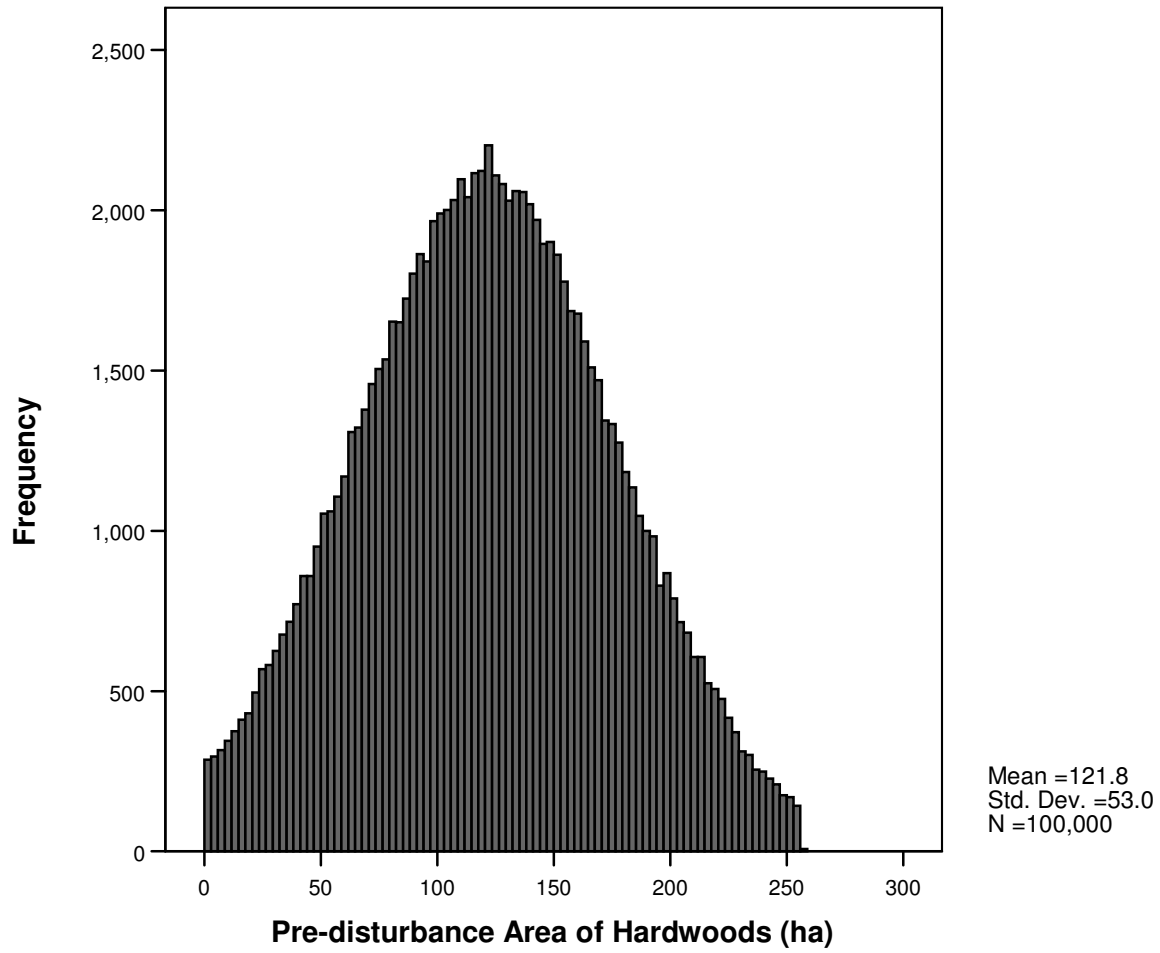Figure C.3. Distribution of simulated values for post-disturbance area of hardwood (ha)

Figure C. 4. Distribution of simulated values for pre-disturbance area of hardwoods (ha).