Effectiveness of Retention Harvesting for Biodiversity Conservation: Evidence for Understory Vegetation and Wildlife

by

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Abstract

Natural disturbance emulation is being used in forest management in an attempt to mitigate the negative effects of harvesting on biodiversity. In the western Canadian boreal forest where the predominant large-scale natural disturbance is wildfire, harvests that leave live mature trees behind at harvest retain some of the structural complexity characteristic of pyrogenic landscapes. Such ‘retention harvests’ are thought to emulate wildfire in a way that conserves biodiversity. Trees can be retained at different levels (percentage of initial basal area retained) and in different patterns (dispersed and aggregated). Although retention harvesting provides for greater structural diversity post-harvest, the forest floor is not burned as it is by wildfire. Therefore, prescribed burning may emulate the influence of wildfires more effectively than does retention harvesting alone. In this dissertation, I explored the effects of different retention levels and patterns, as well as post-harvest prescribed fire, on wildlife and understory vascular plants in the boreal mixedwood forests of northwestern Alberta, Canada. First, I used a combination of midden counts, scat surveys, and camera trapping to compare wildlife use of different stands harvested across a range of dispersed retention levels (0%, 10%, 20%, 50%, 75%, 100%) 15-18 years post-harvest. Second, I examined the effectiveness of combining two retention patch sizes (0.20 ha and 0.46 ha) with different dispersed retention levels (0%, 10%, 20%, 50%, 75%) for supporting understory vascular plant communities that are characteristic of unharvested forest 15 years post-harvest. Third, I investigated the effects of prescribed fire in post-retention harvested stands on understory vascular plant communities up to 12 years post-fire in three different forest cover types (conifer-dominated, mixedwood, deciduous-dominated). Use of harvest stands for late-seral wildlife species was highest in stands having higher retention levels (≥ 50% retention) characterized by high tree basal area and canopy cover. In contrast, lower retention levels (≤ 20% retention) having greater understory cover benefitted early-seral wildlife species. For vascular plants, different retention patch sizes supported distinct understory plant communities with both patch sizes being more effective at supporting late-seral plant communities when surrounded by higher levels of dispersed retention. Prescribed fire benefitted some fire-specialist plant species with the effects of prescribed fire on understory plant communities still evident more than a decade later. Overall, these results suggest that a variety of retention levels, combinations of retention patterns, and the appropriate application of prescribed fire would maintain the structural heterogeneity that supports a wide spectrum of species' habitats within harvested landscapes. These findings contribute to our understanding, development, and application of effective harvesting practices for sustainable forest management and biodiversity conservation.

Preface

Research related to the use of motion-triggered wildlife cameras as presented in Chapter 2 received ethics approval from the University of Alberta Research Ethics Board (study #AUP00001231 entitled “Effects of retention forestry on furbearers” approved June 9, 2014).

Dedication

For my grandfather, Dr. Joseph H. Leach

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Chapter 1: General introduction

1.1. The boreal forest

The boreal forest encompasses one-third of global forest cover, which accounts for approximately 30% of the terrestrial surface area (FAO 2001; Keenan et al. 2015). Constituting the circumpolar vegetated zone of northern latitudes, the boreal forest is characterized by cold-tolerant trees predominantly within the genera *Abies*, *Betula, Larix*, *Picea*, *Pinus*, and *Populus* (Brandt 2009). In addition to providing various socio-economical and cultural benefits (e.g., Uprety et al. 2012), the boreal forest provides numerous ecosystem services, including soil and water resource maintenance and carbon storage (Pan et al. 2011; Bradshaw and Warkentin 2015).

Natural disturbances in the boreal forest are critical processes that contribute to both spatial and temporal landscape heterogeneity (Kenkel et al. 1997). They range from small-scale gap dynamics to stand-replacing phenomena at large-scales (Kuuluvainen and Aakala 2011). Common stand-replacing disturbances in the boreal forest include wildfire and insect outbreaks, which drive ecosystem processes supporting a diversity of organisms partly by creating habitat heterogeneity (Attiwill 1994; Burton et al. 2008).

There are obvious differences between the influences of natural disturbances and those of anthropogenic activities, including forest harvesting, on biodiversity (McRae et al. 2001). Because of the ecological differences between the disturbance types, there has been increasing interest in forest management approaches that aim to reduce these differences by emulating natural disturbances in harvesting practices (Burton et al. 2006). In this thesis, I investigate the effects of such management practices on understory vascular plants and wildlife.

1.1.1. Flora and fauna

1.1.1.1. Understory vascular plants

Understory vascular plants, including shrubs, forbs, and graminoids, are an integral component of forest ecosystems (Gilliam 2007). They contribute more to boreal forest plant biodiversity than does the overstory (De Grandpré et al. 2014) and they provide food and shelter for species at higher trophic levels. Understory plants play other important ecological roles by influencing tree regeneration, as well as belowground processes such as decomposition and soil nutrient cycling (Nilsson and Wardle 2005). Plants are affected by changes in resource (e.g., light and nutrients) availability resulting from disturbances, which consequently promote heterogeneity of plant communities (White 1979; Bartels and Chen 2010). Although disturbances typically cause increases in vascular plant diversity, post-disturbance plant communities differ depending on disturbance type (Peltzer et al. 2000).

1.1.1.2. Wildlife

Boreal wildlife species are adapted to long annual periods of cold temperatures and snow cover (e.g., Telfer and Kelsall 1984). They represent multiple trophic levels and have different population dynamics (Clark and Fritzell 1992). In addition to their ecological value, many mammal and bird species are valued economically and culturally (Nelson et al. 2008). Individual species have different habitat requirements that structure their respective responses to large-scale disturbance (Telfer 1974; Bunnell 1995). While some species are habitat generalists, other species are specialists that rely either on late-successional forest or, conversely, on early-seral stands. Wildlife habitat requirements should therefore be considered in sustainable forest management planning, especially because human activity is associated with range contractions for some mammals (Laliberte and Ripple 2004) including species like woodland caribou that are of conservation concern (Hervieux et al. 2013).

1.1.2. Disturbance

Wildfire is the predominant stand-replacing natural disturbance in the boreal forest of western Canada (Payette 1992; Bergeron et al. 2004). The severity, frequency, and extent of wildfires affect forest dynamics (Eberhart and Woodard 1987; Johnstone and Chapin 2006a; Johnstone and Chapin 2006b). Wildfire effects are heterogeneous and, within the perimeter of any given burn, live trees are left either as single residuals or in unburned patches (Eberhart and Woodard 1987; Smyth et al. 2005). Consequently, wildfires cause changes in tree cover, composition, and regeneration (Lavoie and Sirois 1998), and wildfire residuals contribute to structural complexity that provides biological legacies in regenerating forest (Franklin et al. 2002). More specifically, unburned residuals support sources of propagules for forest regeneration, provide habitat for fauna post-fire, and affect nutrient cycling (Perera and Buse 2014). Wildfire also creates thin organic layers (Greene et al. 2007) that promote seedling recruitment (Purdy et al. 2002). Plants in the boreal forest have regeneration strategies that are adapted to fire, such as buried vegetative parts that escape heat or wind-dispersed propagules, to thrive post-fire (Rowe 1983). This has important implications for plant community composition in the immediate post-disturbance period and redevelopment of the plant community thereafter.

Forestry is associated with one of the main anthropogenic disturbances in Canada’s boreal forest (Pasher et al. 2013). It provides significant economic benefits (Whiteman et al. 2015) and affects forest dynamics and landscape patterns. The removal of canopy trees affects understory plant species composition (Haeussler et al. 2002) and influences wildlife distribution (Telfer 1974). There are significant ecological differences between harvesting and wildfire. For example, wildfire kills trees and leaves behind more deadwood, including snags and downed coarse woody debris, than does forest harvesting (McRae et al. 2001). Furthermore, wildfire causes combustion of the forest floor while harvesting creates mechanical damage. These important differences between wildfire and harvesting result in substantial variation in the responses of species to the two disturbance types (Zwolak 2009).

1.2. Natural disturbance emulation in forest management

1.2.1. Retention harvesting

Traditional even-aged harvesting practices, such as clearcutting, do not provide the complex structural development and spatial patterns caused by wildfire (Delong and Tanner 1996; Franklin et al. 2002; Kuuluvainen 2009). Structural features, such as snags and mature trees that remain on the landscape post-wildfire, are important for biodiversity (Nilsson et al. 2001). For example, they create structural complexity and provide habitat to ‘lifeboat’ species in the regenerating forest post-fire (Franklin et al. 2000). In recognition of the importance of residual structures post-wildfire, forest harvesting practices have evolved from clearcuts to carefully planned designs that involve structural retention. Retention harvesting, whereby live mature trees are retained at the time of harvest, is becoming widely used in sustainable forestry (Gustafsson et al. 2012) to mitigate negative effects of harvesting on biodiversity (Fedrowitz et al. 2014).

Retention harvesting can be applied at different levels based on the proportion of original basal area that is retained at the time of harvest (Franklin et al. 1997). Some researchers recommend a minimum of 5%-10% retention (Gustafsson et al. 2012), yet others argue that retention levels greater than 15% are needed to maintain biodiversity in the short term (one to seven years) (Aubry et al. 2009). Responses to retention level are species-specific and reflect habitat requirements (Vanderwel et al. 2009). In general, increases in the amount of retained trees positively affects forest-dependent small mammals, birds, plants, and invertebrates (Fedrowitz et al. 2014). Mammals that depend on large tracts of contiguous closed-canopy forest are expected to use stands harvested to high retention levels (70%); however, studies on large mammals are lacking (Vanderwel et al. 2009).

In addition to retention level, the pattern of retention (spatial arrangement of retained trees) is another important consideration in its design/application. Dispersed retention, whereby retained live trees are distributed uniformly in the harvested area, could enhance dispersal for many species by providing increased connectivity across harvested landscapes (Franklin et al. 1997). Conversely, aggregated retention, whereby retained trees are grouped together, provide patches of mature forest that will include remmnants of previous forest that may help lifeboat species more effectively than dispersed retention, assuming that these patches are not negatively affected by edge effects (Franklin et al. 1997). Thus far, research on the effects of combining aggregated and dispersed retention for plant conservation has been limited to short-term (four years post-harvest) studies on vascular plants (Lencinas et al. 2011). Longer-term studies are needed to assess lag effects in biodiversity responses, as it could take several years for sensitive species to disappear and/or re-occupy harvested sites.

1.2.2. Prescribed fire

Although retention harvesting may retain some structural features similar to wildfire, it cannot emulate all ecological processes typical of wildfire (Stockdale et al. 2016). Forest management should therefore incorporate practices that promote fire-related processes that are absent from harvested areas (Spence 2001). Prescribed fire could be an effective management practice that benefits fire-dependent plants that rely on heat for germination (Granström 2001). Thus, the application of retention harvesting followed by prescribed fire may emulate the influence of wildfires in managed forests more effectively than retention harvesting alone. Prior research examining aggregated retention harvesting with prescribed fire benefitted some understory plant species more effectively than harvesting alone (Johnson et al. 2014); however, the effects of prescribed fire combined with dispersed retention on understory vascular plants are unknown.

1.3. Research objectives

There are many options to consider in the design of retention harvesting including the amount and spatial pattern of retained trees, as well as post-harvest management tools such as prescribed fire. This thesis explores the effects of these forest management practices on boreal fauna and flora with the objective of improving the scientific foundation upon which to base forest management policies that are specifically aimed at mitigating the negative effects of harvesting on biodiversity. Data were collected at the Ecosystem Management Emulating Natural Disturbance (EMEND) project, which is a large-scale experiment located in the boreal mixedwood forest of northwestern Alberta, Canada. EMEND was established in 1998 to test the effects of five retention levels (0%, 10%, 20%, 50%, 75% retention), two retention patterns (dispersed and aggregated), and post-harvest prescribed burns on biodiversity over a full rotation age (80-100 years) in three different forest cover types representative of the boreal mixedwood forest (Spence et al. 1999).

Previous EMEND studies revealed that low levels of dispersed retention (≤ 20% retention) favoured more early-successional understory vascular plant species than did higher levels of retention up to two years post-harvest (Macdonald and Fenniak 2007) and eight years post-harvest (Craig and Macdonald 2009). Such studies also demonstrated that understory vascular plant communities vary by canopy composition (Macdonald and Fenniak 2007) and are different in the retention strips versus the machine corridors used by harvesting equipment eight years post-harvest (Craig and Macdonald 2009). These studies did not consider comparisons of understory vascular plant communities between retention patterns or between stands harvested to 10% retention with and without the application of prescribed fire post-harvest. Studies on EMEND wildlife are limited to bats (e.g., Hogberg et al. 2002; Patriquin and Barclay 2003), songbirds (e.g., Harrison et al. 2005), owls (Z. Domahidi, personal communication) and the wood frog (*Lithobates sylvaticus*) (Robinson 2017).

The following chapters each consider effects of different management practices on wildlife or understory vascular plants. In Chapter 2, I investigate the influence of different levels of dispersed retention on wildlife 15-18 years post-harvest and identify structural variables correlated with habitat use by wildlife. In Chapter 3, I examine the combined effects of retention level and pattern (dispersed versus aggregated) on understory vascular plants 15 years post-harvest to determine if different sizes of retention patches more effectively support plant communities characteristic of unharvested forest and how this is affected by different levels of surrounding dispersed retention. In Chapter 4, I consider the effectiveness of prescribed burning as a post-harvest management tool by comparing plant communities subjected to retention harvest with and without prescribed fire over time up to 12 years post-fire in three different forest cover types (conifer-dominated, mixedwood, deciduous-dominated). Chapter 5 summarizes the findings, highlights important management implications, and suggests potential areas of future research.

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Chapter 2: Wildlife responses to different levels of retention harvesting

2.1. Abstract

Retention harvesting, whereby live mature trees are retained in harvested forests, is used to mitigate undesirable effects of forest harvesting on biodiversity. However, responses of many vertebrates to variable retention harvesting are unknown. I investigated the influence of different levels of retention harvesting on habitat use by wildlife 15-18 years post-harvest using a combination of midden counts, scat surveys, and camera trapping. Site-level measures of forest structure, including canopy cover, horizontal cover, tree height, tree diameter, basal area, log cover, and understory cover, were used to document habitat differences post-harvest. Habitat use of six species (black bear, coyote, fisher, red squirrel, wolverine, woodland caribou) increased with increased levels of retention, while habitat use of two species (grouse, snowshoe hare) declined with increasing retention level. Five species (American marten, Canada lynx, deer, moose, gray wolf) did not significantly differ in their use of harvests by retention level. Higher levels of retention were associated with greater canopy cover, basal area, and deadwood abundance, which likely enhanced habitats for late-seral species. Woodland caribou, a species of conservation concern, was only detected in stands harvested to at least 20% retention. Lower levels of retention were characterized by greater understory and horizontal cover, which likely benefitted early-seral species. These findings demonstrate the value of retention harvesting for conservation of vertebrates in boreal forest, while highlighting the challenge of managing forests for multiple species with different habitat preferences.

2.2. Introduction

The traditional method of forest harvesting by clearcutting affects wildlife activity (Telfer 1974; Thompson 1988; Fisher and Wilkinson 2005). Retention harvesting, whereby live mature trees are retained at time of harvest, is an alternative to clearcutting and is widely used in sustainable forestry for biodiversity conservation (Gustafsson et al. 2012). Retention harvesting is thought to reduce the impacts of logging by increasing habitat connectivity, enhancing structural complexity, and facilitating recovery of forest species within harvested areas (Franklin et al. 1997). Retention harvesting could, therefore, mitigate the effects of forestry on wildlife by retaining habitat structure associated with late-successional forests used by canopy-dependent vertebrates.

Responses of wildlife to retention harvesting are species-specific and reflect habitat requirements (Rosenvald and Lõhmus 2008; Vanderwel et al. 2009). While early-successional species benefit from open areas created by harvesting, species dependent on closed-canopy forest are negatively affected by the removal of overstory trees (Fedrowitz et al. 2014). Species responses vary by level of retention (percent of original basal area retained), as the amount of residual trees will influence habitat characteristics, including forage/prey availability and protective cover post-harvest (Vanderwel et al. 2009). Furthermore, interactions between species could influence the effects of retention harvesting on vertebrate activity; for example, predator-prey relationships and competition for resources could dictate the use of different levels of retention harvesting by species.

In addition to harvesting level, time since logging is another important factor to consider when examining responses of wildlife to harvesting (Fisher and Wilkinson

2005). Residual live trees in retention harvests may not only provide greater canopy cover than clearcut stands immediately post-harvest, but they could also improve overall structural heterogeneity over time as standing trees eventually contribute to deadwood abundance (Hämäläinen et al. 2016). Retention level will also affect forest regeneration, which could influence habitat suitability. Recent clearcuts could be unsuitable habitat for some species while retention harvests may provide important structural elements that enable species to persist during the regenerating period or allow them to re-occupy harvested areas more quickly post-harvest. The majority of studies on retention harvesting and biodiversity have occurred at less than six years post-harvest (Fedrowitz et al. 2014). Long-term studies are needed to detect lag effects of wildlife responses, as it could take several years for sensitive species to re-occupy harvested sites.

While the majority of previous studies on retention harvesting and vertebrates focused on small forest-floor mammals (mice, voles, shrews) (e.g., Gitzen et al. 2007), bats (e.g., Patriquin and Barclay 2003), and passerine birds (e.g., LeBlanc et al. 2010), the effects of retention harvesting on larger mammals and game birds remain poorly understood (Vanderwel et al. 2009). Larger vertebrates including carnivores, ungulates, lagomorphs, and arboreal rodents, represent different trophic levels. Many of these species are also valued economically and culturally (Muth et al. 1996). A better understanding of responses to different levels of retention harvesting is needed to assess whether these alternative timber harvesting practices can be used to mitigate the negative effects of harvesting on these species.

The objective of this research was to determine the influence of retention harvesting on vertebrates by: 1) comparing wildlife use (activity) among different levels of retention harvesting 15-18 years post-harvest; and 2) identifying forest structural attributes most associated with the presence of individual species. If retention harvest mitigated the effects of clearcut harvesting, I expected habitat use of: 1) late-seral species to show increased use of areas with higher levels of retention (characterized by greater canopy cover, basal area, and deadwood abundance); 2) early-seral species to decline with increases in tree retention since they prefer low levels of canopy with high understory cover; and 3) habitat generalist species to be unaffected by retention level.

2.3. Methods

2.3.1. Study Site

Research was conducted at the large-scale Ecosystem Management Emulating Natural Disturbance (EMEND) experiment located approximately 90 km northwest of Peace River, Alberta, Canada (56° 46’ 13” N, -118° 22’ 28” W). Climate data from nearby Eureka River (56° 29’ 00” N, -118° 44’ 00” W) collected from 1981 to 2010 indicated mean temperatures of -16.9 °C and 15.0 °C for January and July, respectively (Environment Canada 2017). Mean annual snowfall and rainfall were 128.8 cm and 307.4 mm, respectively (Environment Canada 2017). The area is representative of the boreal mixedwood plains. Data were collected in the conifer-dominated stands at EMEND because this cover type represents typical old-growth forest on the landscape in which sensitive species are most likely to be affected by harvesting. The stands were dominated by conifers, predominantly white spruce (*Picea glauca*), prior to harvest and post-harvest regeneration mainly consisted of aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*).

Compartments (c. 10 ha each) were harvested in the winter of 1998-1999 across five harvest retention levels (treatments): 0% (clearcut), 10%, 20%, 50%, and 75% retention. Harvesting equipment was restricted to 5 m wide corridors, which were separated by 15 m wide areas where trees were removed or retained depending on the retention level. The only trees harvested in the 75% retention treatment were those removed in the 5 m wide corridor. The retention pattern was predominantly dispersed green-tree retention but each compartment contained two small (< 0.50 ha each) embedded retention patches. All sampling occurred in the dispersed retention areas. Unharvested compartments (c. 10 ha each) were used as controls (100% retention). There were three replicates of each treatment, including control stands without harvest, for a total of 18 compartments.

2.3.2. Data Collection

2.3.2.1. Transect Surveys

Belt transects (east-west orientation) totaling 1200 m^2 were randomly established in each 10-ha compartment in June 2015 (Appendix 2.1). The width of each transect was 4 m and the length varied depending on the shape of the compartment but the length of all transects in a compartment totaled 300 m. All transects were located > 40 m from each other and > 30 m from compartment edges. Within each belt transect, the number of red squirrel (*Tamiasciurus hudsonicus*) middens and cone shell piles were counted in June 2015. These have been considered suitable indicators of red squirrel feeding activity (Gurnell et al. 2009). Along these transects all fecal pellets were removed in June 2015. To obtain estimates of use I subsequently counted all fecal pellets along the transects and cleared them as I went; this was done prior to leaf fall in 2015 and 2016 and prior to leaf out in 2016 and 2017 for spring/summer and fall/winter use, respectively. Fecal pellets of black bear (*Ursus americanus*), coyote (*Canis latrans*), deer (*Odocoileus* spp.), gray wolf (*Canis lupus*), grouse (*Bonasa umbellus*/*Canachites canadensis*), moose (*Alces alces*), and snowshoe hare (*Lepus americanus*) were identified. Coyote and gray wolf were excluded from analyses due to insufficient observations.

2.3.2.2. Camera Traps

I used 35 motion-triggered wildlife cameras (Reconyx Hyperfire PC900, Holmen, WI, USA) to capture use of compartments (treatments) by wildlife species from October 31, 2014 until May 30, 2017. Cameras were randomly rotated around the compartments each spring and fall and programmed on the "normal" setting with trigger speed set to high sensitivity and five pictures per trigger with one-second delay between each photograph and no delay between consecutive triggers (Burton 2014). The cameras were set facing north to avoid sun glare and mounted to trees approximately 1 m from the ground in spring/summer or 1.5 m from the ground in winter/fall to account for snow accumulation. Light vegetation was removed from the area to avoid triggers from wind-induced vegetation movement. In the zone of detection, which here was approximately 3-5 m from the camera lens, I applied 10 mL of a scented lure (O'Gorman's Long Distance Call, Broadus, MT, USA) to a tree in view of the camera. The University of Alberta Research Ethics Office (Study ID: AUP00001231) as well as the Government of Alberta Environment and Sustainable Resource Development Fish and Wildlife Division (Permit #54605 and Collection Licence #54606) approved the research.

A total of 18 species, excluding passerine birds, were detected and identified throughout the sampling period (American marten (*Martes americana*), black bear, Canada lynx (*Lynx canadensis*), coyote, fisher (*Martes pennanti*), gray wolf, moose, mule deer (*Odocoileus hemionus*), red squirrel, river otter (*Lutra canadensis*), ruffed grouse (*Bonasa umbellus*), short-tailed weasel (*Mustela erminea*), snowshoe hare, spruce grouse (*Canachites canadensis*), white-tailed deer (*Odocoileus virginianus*), wolverine (*Gulo gulo*), woodchuck (*Marmota monax*), woodland caribou (*Rangifer tarandus*)). Mule deer and white-tailed deer were combined (hereafter referred to as 'deer') and ruffed grouse and spruce grouse were combined (hereafter referred to as 'grouse') for the purpose of analysis. River otter, short-tailed weasel, and woodchuck were excluded from analysis due to low total detections. Based on scientific literature related to habitat preferences, I made predictions for responses of individual species to increased levels of retention (Table 2.1).

At each camera station, I measured the following variables of forest structure: canopy cover, horizontal vegetation cover, tree height, tree diameter at breast height (DBH), basal area of live trees, basal area of snags, downed woody debris (log) cover, and understory cover. Canopy cover and horizontal cover were measured in both spring and fall to account for seasonal changes in leaf cover. Average canopy cover was calculated from four measurements each taken along cardinal directions using a convex spherical densiometer. Average horizontal vegetation cover was calculated from estimates in the 0-1 m and 1-2 m height from ground strata using a Robel pole placed 10 m and 20 m from the camera lens. Basal area of live trees and snags was measured using a prism with a basal area factor of 3. Average tree height was calculated by measuring height of the three tallest trees considered ‘in’ by the prism using a clinometer. Maximum tree DBH was determined for the largest trees considered ‘in’ by the prism as measured by diameter at breast height (1.37 m from the ground). Log cover was calculated by measuring the diameter at point of transect intersection of all logs (diameter ≥ 5 cm at largest point) bisecting a transect that extended 10 m in front of the camera and 10 m behind the camera. Understory vegetation cover (total of all vascular plants and by group: saplings, shrubs, forbs, graminoids) was visually estimated in a 10 m^2 circular plot (camera in centre) and placed in a cover class with the following percent cover midpoints: 1 (0.5%), 2 (2%), 3 (7%), 4 (18%), 5 (38%), 6 (63%), and 7 (87.5%).

2.3.3. Data Analysis

All analyses were performed in the R statistics programming environment version 3.4.1 (R Development Core Team 2017). Response variables were tested for nonlinearity using generalized additive mixed models and by comparing Akaike Information Criterion (AIC) values between linear and nonlinear models. Linear model responses were more supported than nonlinear models, having the lowest AIC value for all response variables, and so only linear models are presented here. Diagnostic plots were used to assess normality and homoscedasticity of the residuals for all models.

Transect data for red squirrels were based on number of feeding sites/1200 m^2 (count data) and were analyzed using a negative binomial generalized linear model with the *glm.nb* function in the *MASS* package (Ripley et al. 2017). Number of feeding sites and retention level (0%, 10%, 20%, 50%, 75%, 100%) were the response and continuous predictor variables, respectively. Transect data for pellet counts were analyzed using the *lmer* function in the *lme4* package (Bates et al. 2017). Models for pellet data (number of pellet groups standardized for number of accumulation days) included retention level (0%, 10%, 20%, 50%, 75%, 100%) and season (spring/summer, fall/winter) as continuous and categorical fixed independent variables, respectively. Compartment and year were random variables. The interaction between retention level and season (retention level × season) was never significant so all models included retention level and season as main effects (retention level + season). Fall/winter season was excluded for black bear due to hibernation.

Photographs from the motion-triggered cameras were examined to determine number of detections for individual species standardized by number of trapping nights. Detections for a given species were considered independent after a 30-minute time period or if individuals were distinctly different (i.e., multiple individuals of the same species captured in a single photo). Photographs taken April-September and October-March were classified as spring/summer and fall/winter, respectively. Data were zero-inflated (Appendix 2.2) and analyzed using zero-inflated negative binomial models using the *glmmTMB* package (Magnusson et al. 2017). Number of detections for individual species was the response, number of trap nights was an offset, retention level (0%, 10%, 20%, 50%, 75%, 100%) was a continuous variable and season (spring/summer, fall/winter) was a categorical variable. Compartment and year were, again, included as random variables with the interaction between retention level and season (retention level × season) never significant so all models were fit with retention level and season as main effects (retention level + season). Likewise, fall/winter season was excluded for black bear due to hibernation.

Forest structure variables were analyzed using the *lmer* function in the *lme4* package (Bates et al. 2017). Mixed-effects models included retention level (0%, 10%, 20%, 50%, 75%, 100%) and season (spring/summer, fall/winter) as continuous and categorical fixed independent variables, respectively, with an interaction tested between retention level by season for canopy cover and horizontal cover. Models for the remaining forest structure variables (tree height, tree DBH, basal area of live trees, basal area of snags, log cover, total understory cover, sapling cover, shrub cover, forb cover, and graminoid cover) only included retention level as a main effect. Compartment and year were included as random variables.

2.4. Results

2.4.1. Wildlife responses to retention harvesting

Activity of red squirrel, fisher, coyote, wolverine, black bear, and caribou increased with retention harvest level (Table 2.2). Red squirrel use increased dramatically with retention level as the median number of red squirrel feeding sites was 0/1200 m^2 in the clearcut and increased to 18/1200 m^2 in both 75% and 100% retention harvests (Figure 2.1a). This trend was supported by the camera data, which also revealed a notable increase in red squirrel activity from 10% retention to 20% retention (Figure 2.2a). Although the camera data did not reveal a significant effect of retention level on habitat use of black bear (Table 2.2), the number of black bear scats increased with retention level and no black bear scat was found in clearcuts (Table 2.2; Figure 2.1b). Habitat use of fisher increased with retention level and was notably higher at 50% retention and above (Figure 2.2b). The maximum number of coyote detections was highest in the 75%

retention harvest and unharvested control (Figure 2.2c). Retention level had a significant positive effect on habitat use of wolverine (Figure 2.2d). Effect of season on coyote and wolverine was marginally significant with a higher number of detections in fall/winter than spring/summer (Table 2.2). Woodland caribou were never detected in harvested stands with less than 20% retention with the number of detections increasing with retention levels above that (Figure 2.2e).

Snowshoe hare and grouse use declined with increasing retention level reaching quite low values at retention levels of ≥ 50% (Table 2.2, Figure 2.1c, 1d). The median number of snowshoe hare pellet groups was over twice as high in clearcuts than in retention harvested stands, and was higher in fall/winter compared to spring/summer (Figure 2.1c). Number of snowshoe hare detections, as captured by the motion-triggered cameras, also declined with increasing retention level; however, detections were higher in spring/summer compared to fall/winter (Figure 2.2f). Similar to snowshoe hare, grouse activity was higher in fall/winter according to pellet counts but in spring/summer according to photographs (Figures 2.1d, 2g).

American marten, Canada lynx, gray wolf, deer, and moose showed no significant differences related to retention level (Table 2.2). Deer activity was higher in all compartments in spring/summer than in fall/winter for both pellet counts and photographs (Table 2.2). Pellet group counts also revealed greater use of compartments by moose in spring/summer compared to fall/winter (Table 2.2).

2.4.2. Forest structure responses to retention forestry

There was a significant interaction between retention level and season on canopy cover (Table 2.3). While canopy cover was higher in spring/summer and did not change with retention level, it was lower in fall/winter and increased with retention level so differences in canopy cover between seasons attenuated as retention level increased (Figure 2.3a). Field observations revealed that differences in canopy cover between low and high retention levels in fall/winter resulted from differences in canopy composition as canopy trees were predominantly early-successional deciduous species and conifer species in low and high retention levels, respectively. Horizontal cover was also significantly lower in fall/winter compared to spring/summer, but it declined with increasing retention level in both seasons (Table 2.3; Figure 2.3b). Average tree height, maximum live tree DBH, live tree basal area, dead tree basal area, and log cover all increased with retention level (Table 2.3; Figure 2.3c-g). Conversely, total understory cover, sapling cover, and graminoid cover declined with increasing retention level (Table 2.3; Figure 2.3h-j). Shrub cover and forb cover were not significantly affected by retention level (Table 2.3).

2.5. Discussion

These findings reveal different responses of multiple wildlife species to varying retention levels 15-18 years post-harvest. The responses of habitat use to retention level were as predicted for all vertebrates except for American marten, black bear, and coyote. Six species (red squirrel, fisher, coyote, black bear, wolverine, woodland caribou) showed increased activity with increasing retention level, for two species (snowshoe hare, grouse) activity declined with increasing retention level, and five species (American marten, Canada lynx, gray wolf, moose, deer) did not significantly vary with retention level. Stands harvested to different retention levels were characterized by different structural attributes, which likely explain the wildlife responses.

2.5.1. Positive responses of habitat use to increasing retention harvest levels

As predicted, red squirrel activity increased with retention level and this corresponded to higher canopy cover, greater basal area, and larger trees that could better support both feeding and nesting sites for red squirrels, as compared to lower retention levels. The median maximum live tree DBH in stands harvested to ≥ 20% retention was over 30 cm, which is a preferred tree size for nesting (Fancy 1980). Mature seed-producing conifers also provide a reliable food source for red squirrels (Kemp and Keith 1970; Rusch and Reeder 1978). My findings conform to other studies that revealed that red squirrels preferred unharvested stands with high densities of large spruce trees and snags, as compared to more recent partially harvested stands (≤ 10 years post-harvest) (Holloway and Malcolm 2006; Herbers and Klenner 2007). The complete lack of red squirrel activity in clearcut stands more than 15 years post-harvest highlights the importance of retention harvesting for these arboreal rodents. Moreover, the presence of red squirrel middens benefits other species, including martens (Ruggiero et al. 1998) and toads (Browne and Paszkowski 2010).

Fishers select habitats with complex vertical forest structure that includes large trees, deadwood, and high canopy cover (Carroll et al. 1999; Raley et al. 2012; Schwartz et al. 2013; Lewis et al. 2016). These structural attributes, which were most prevalent in areas of high retention, are important for fisher denning and resting sites (Aubry and

Raley 2006; Aubry et al. 2013). Activity of fishers was lowest in stands harvested to 0% and 10% retention, where canopy cover was lower than the minimum threshold (56%) for suitable fisher habitat (Purcell et al. 2009). Fishers also avoid recently logged stands (< 10 years post-harvest) (Weir and Corbould 2010). My results suggest that residual trees in retention harvests ≥ 20% could promote structural heterogeneity and therefore offer more suitable habitat than could clearcut areas (Sauder and Rachlow 2015).

Coyotes were predicted to be neutral to retention harvesting because they are generalist predators (Thurber et al. 1992; Bekoff and Gese 2003) but my results showed that their activity increased with increasing retention. Although coyotes have been found to select clearcuts 5-20 years old due to availability of moose carcasses and berries (Boisjoly et al. 2010) they also use mature conifer forest to avoid deep snow that hampers mobility (Parker and Maxwell 1989; Thibault and Ouellet 2005). I found no evidence that moose activity or shrub cover were greater in areas with higher levels of retention; thus the observation of apparent preferred habitat use of higher retention levels by coyotes must correspond to other factors, such as snow depth.

Black bear was also predicted to exhibit a neutral response to retention harvesting; however, I found that habitat use increased with retention level. Several studies have provided evidence that recent clearcuts are a preferred habitat for black bears due to forage availability (Lindzey and Meslow 1977; Mitchell and Powell 2003; Brodeur et al. 2008; Mosnier et al. 2008). In my study, shrub and forb cover did not vary significantly with retention level, which suggests that food availability may not have been greater at lower retention levels 15 years post-harvest. High levels of retention could provide both forage and cover, two important factors in habitat selection of black bears (Young and

Beecham 1986). Other studies revealed that black bears use mature forests, which are valuable for den sites (Tietje and Ruff 1980; Boileau et al. 1994). Mature residual trees with large diameters in retention harvests may also be important for climbing (Herrero 1972) and rubbing (Green and Mattson 2003).

As predicted, wolverine habitat use increased with increasing retention level. Wolverines have been shown to avoid logged areas in British Columbia (Krebs et al. 2007), Ontario (Bowman et al. 2010), and in the Rocky Mountains of Alberta (Fisher et al. 2013). Scrafford et al. (2017) considered wolverine occurrence in successional stages post-harvest demonstrating that wolverines avoided the interior of cutblocks at 11-25 years. Greater log cover in high levels of retention compared to lower retention levels could benefit wolverines by providing den sites (Dawson et al. 2010).

My results conform to previous studies that revealed caribou preference for mature coniferous forest and avoidance of clearcuts and low retention cutovers at least up to 12 years post-harvest (Chubbs et al. 1993; Rettie and Messier 2000; Smith et al. 2000; Bowman et al 2010). Logging not only alters caribou distribution but has also been positively associated with chronic stress, as measured by cortisol concentrations (Ewacha et al. 2017). Servheen and Lyon (1989) stated that canopy cover > 50% and tree diameter > 20 cm were important for caribou habitat. These thresholds were observed in harvested stands with at least 20% retention, below which caribou were not detected. Caribou may prefer the low horizontal cover in high retention levels because it better enables them to visually detect predators (Pinard et al. 2012). Furthermore, retention trees and snags may support arboreal lichen, an important winter food source for caribou.

2.5.2. Negative responses of habitat use to increasing retention harvest levels

As expected, snowshoe hare preferred low levels of retention, especially clearcuts. Higher levels of activity in low retention levels than in retention of 50% or above could be attributed to suitable habitat as determined by availability of food and cover (Wolff 1980; Pietz and Tester 1983). Low retention harvests were characterized by high sapling cover, total understory cover, and horizontal cover, which provide snowshoe hares with food resources and protection from predators (Dodds 1960; Wolfe et al. 1982; Litvaitis et al. 1985; Ferron and Ouellet 1992; Holbrook et al. 2017). Previous studies demonstrated that regeneration in clearcut stands less than 10 years post-harvest failed to provide adequate protective cover (Thompson et al. 1989; de Bellefeuille et al. 2001; Potvin et al. 2005). Retention harvests could be beneficial for snowshoe hare in sites younger than the ones investigated in this study because retention harvest areas would provide structural elements important for cover as well as food (Ferron et al. 1998).

As predicted, habitat use by grouse was greatest in stands harvested with low levels of retention where understory vegetation cover was high and the canopy was dominated by trembling aspen, which is a prevalent tree species characterizing preferred habitat by grouse (Stauffer and Peterson 1985a; Stauffer and Peterson 1985b). The higher levels of horizontal cover that were associated with low retention levels may provide protective cover from predators (Boag and Sumanik 1969). Throughout the regeneration period post-harvest, retention harvests may be important as they provide logs, which are used by drumming males (Rusch and Keith 1971).

2.5.3. Neutral responses of habitat use to retention harvesting

Contrary to expectation, American marten habitat use did not exhibit a significant positive response to retention level. I predicted that habitat use of American marten would increase with increasing retention level because this species has been associated with high abundance of coarse woody debris, high basal area, and mature forests (Hargis and McCullough 1984; Sturtevant et al. 1996; Proulx 2006; Andruskiw et al. 2008). While previous research considered clearcuts up to 15 years old as poor marten habitat (Soutiere 1979), regenerating stands of aspen that are 15 years post-harvest may provide adequate habitat (Poole et al. 2004). Suitable habitat for marten includes canopy cover of at least 50%, average tree height over 6 m, tree diameter over 7.6 cm, and live tree basal area over 18 m^2/ha (Chapin et al. 1998; Payer and Harrison 2003; Bull et al. 2005). More than 15 years post-harvest, the regenerating stands for all levels of retention in this study supported these minimum requirements. Marten have also been shown to use partially harvested stands in Quebec (Godbout and Ouellet 2008) and Maine (Soutiere 1979; Steventon and Major 1982; Fuller and Harrison 2005). In Newfoundland, marten used a variety of habitat types, including recent clearcuts, mature forest, and regenerating stands (Hearn et al. 2010). Forest structural attributes may be a more important factor than successional stage in determining marten habitat (Chapin et al. 1997). More than 15 years post-harvest, retention level may not influence American marten activity as all retention levels could potentially provide adequate structural complexity for marten habitat (Payer and Harrison 2000; Godbout and Ouellet 2010).

The neutral response of Canada lynx to retention harvesting was as predicted and reflects the use of various structural attributes for different habitat needs. Lynx have been reported to use both regenerating post-disturbance forest and mature conifer forest

(Vashon et al. 2008; Simons-Legaard et al. 2013). Regenerating harvested areas supported abundant snowshoe hares that would have served as prey (Mowat and Slough 2003; Holbrook et al. 2017); however, higher levels of retention had reduced understory cover and that could facilitate prey accessibility (Fuller et al. 2007; Fuller and Harrison 2010; Ivan and Shenk 2016). Furthermore, retention harvesting, as compared to clearcutting, provides greater basal area and deadwood abundance, which provide den sites for lynx (Slough 1999; Gilbert and Pierce 2005). Thus all levels of retention harvesting, as well as unharvested forest, could be useful habitat for lynx.

As a generalist predator, wolves occupy various habitats (Mladenoff et al. 1995; Houle et al. 2010). Similar to my findings, wolf habitat use did not significantly vary between cutblocks and unharvested forests in west-central Alberta (Kuzyk et al. 2004). Wolf prey such as moose also exhibited a neutral response to retention harvesting, which may partly explain the lack of response in wolves as they select areas based on prey availability (Lesmerises et al. 2012).

Both moose and deer benefit from the higher forage availability in early-seral stands and the higher hiding and thermal cover in late-seral stands; this could explain the lack of response to different levels of retention harvest. Moose habitat is characterized by closed-canopy forest for shelter from extreme temperatures and predators, as well as more recently disturbed areas for food availability (Timmermann and McNicol 1988; Forbes and Theberge 1993). Browse availability for moose has been reported to be greater in regenerating stands more than 10 years old post-harvest (Potvin et al. 2005; Newbury et al. 2007). Retention harvests could, therefore, be more valuable moose habitat as compared to clearcut in the shorter-term, when moose habitat quality is reduced immediately post-harvest (Dodds 1960; Potvin et al. 1999). Large mature trees in retention harvests could provide thermal cover as well as cover from predators (Mastenbrook and Cumming 1989; Kunkel and Pletscher 2000). Similar to moose, deer could benefit from superior forage availability in stands harvested to lower retention levels (Lyon and Jensen 1980). Nevertheless, deer could select stands harvested to high retention levels with greater canopy cover to facilitate movement in snow (Armleder et al. 1994), or to avoid temperature extremes (Schmitz 1991).

2.5.4. Management implications

This study highlights the importance of retention harvesting for conserving faunal biodiversity while revealing challenges associated with managing forest landscapes for multiple species. Over half of the species investigated exhibited a significant response to retention harvesting more than 15 years post-harvest. While responses of individual species could have differed immediately post-harvest, retention harvesting may enable closed-canopy species to use cutblocks earlier than if they had been clearcut (Fisher and Wilkinson 2005).

This study demonstrates the value of retention harvests for sensitive species such as woodland caribou, which was not detected in stands harvested to less than 20% retention and is a species of conservation concern with rapid population declines (Hervieux et al. 2013). Canada has been criticized for neglect of habitat protection (Hebblewhite and Fortin 2017) and industrial activities, such as forestry, are a dominant cause of caribou habitat degradation (Festa-Bianchet et al. 2011). Courtois et al. (2008) suggested amalgamating forest harvesting in localized areas to preserve large areas of intact habitat in the landscape; retention harvests could facilitate habitat connectivity between areas of intact forests (Courtois et al. 2004). Knowing that woodland caribou use retention harvest cutblocks, forestry companies could consider other management strategies to enhance habitat quality, such as terrestrial lichen transplants or seeding (Government of Alberta 2017).

Responses to different retention levels varied by species and reflected different habitat requirements. Many late-seral species revealed notable differences in activity between 20% and 50% retention, and habitat use of stands harvested to at least 50% retention was comparable to use of unharvested stands. Additional research is required to determine whether or not harvesting multiple small areas using a wide range of retention levels is more advantageous than harvesting a single large area to low retention while preserving a large area of unharvested forest (St-Laurent et al. 2007; Lindenmayer et al. 2015). When comparing these different harvesting designs, the amount of edge creation and consequent effects of fragmentation on vertebrates should also be considered to better accommodate habitat preferences of numerous species and ultimately maintain vertebrate diversity in harvested landscapes.

I recognize the limitations in this study related to both transect surveys (Keiter et al. 2016) and camera trapping (Burton et al. 2015). I do not assume that 1) treatments were devoid of a particular species when not detected (MacKenzie et al. 2002; MacKenzie et al. 2005), and 2) there was equal detectability for all species because detection rates may vary by animal behaviour (MacKenzie et al. 2004). My results should therefore be interpreted with caution; especially since treated compartment sizes (~ 10 ha) were smaller than the home ranges for several of the species examined. Despite these study limitations, the findings contribute to a better understanding of multi-species wildlife responses to retention harvesting for the boreal forest.

2.6. Literature cited

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Table 2.1. Predicted responses of species habitat use to increasing retention levels (0% to 100%) 15-18 years post-harvest indicated as positive (habitat use increases with increasing retention level), negative (habitat use declines with increasing retention level), or neutral (habitat use is not affected by retention level) with the rationale for predictions and supporting references.

Species	Predicted response	Rationale	References
American marten	Positive	Late-seral specialist	Hargis and McCullough 1984; Buskirk et al. 1989; Ruggiero et al. 1998; Bull and Heater 2000; Payer and Harrison 2003; Bull et al. 2005; Proulx 2006
Black bear	Neutral	Habitat generalist	Jonkel and Cowan 1971; Lindzey and Meslow 1977; Young and Beecham 1986; Boileau et al. 1994; Mitchell and Powell 2003
Canada lynx	Neutral	Habitat generalist	Koehler and Brittell 1990; Slough 1999; Gilbert and Pierce 2005; Fuller et al. 2007; Simons-Legaard et al. 2013; Holbrook et al. 2017
Coyote	Neutral	Habitat generalist	Bekoff and Gese 2003; Thibault and Ouellet 2005; Boisjoly et al. 2010
Deer	Neutral	Habitat generalist	Lyon and Jensen 1980; Tomm et al. 1981; Beier and McCullough 1990; Armleder et al. 1994; Sullivan et al. 2008
Fisher	Positive	Late-seral specialist	Carroll et al. 1999; Aubry and Raley 2006; Purcell et al. 2009; Raley et al. 2012; Aubry et al. 2013; Schwartz et al. 2013
Gray wolf	Neutral	Habitat generalist	Mladenoff et al. 1995; Kuzyk et al. 2004; Houle et al. 2010; Lesmerises et al. 2012; Ehlers et al. 2016
Grouse	Negative	Early-seral specialist	Boag and Sumanik 1969; Stauffer and Peterson 1985a; Stauffer and Peterson 1985b
Moose	Neutral	Habitat generalist	Tomm et al. 1981; Timmermann and McNicol 1988; Forbes and Theberge 1993; Courtois et al. 2002
Red squirrel	Positive	Late-seral specialist	Kemp and Keith 1970; Rusch and Reeder 1978; Fancy 1980; Thompson et al. 1989; Holloway and Malcolm 2006
Snowshoe hare	Negative	Early-seral specialist	Monthey 1986; Ferron and Ouellet 1992; Hodson et al. 2011
Wolverine	Positive	Late-seral specialist	Krebs et al. 2007; Bowman et al. 2010; Dawson et al. 2010; Fisher et al. 2013
Woodland caribou	Positive	Late-seral specialist	Chubbs et al. 1993; Rettie and Messier 2000; Smith et al. 2000; Courtois et al. 2004; Bowman et al. 2010

Table 2.2. Results of regression models [beta coefficient with standard error (β (SE)) and *P* values (*P*)] examining the influence of retention level (0%, 10%, 20%, 50%, 75%, 100%) and season (spring/summer, fall/winter) on wildlife activity. Data from transects (# of pellet groups/100 days) for all species, except red squirrel, were analyzed using Gaussian distribution. Transect data for red squirrel were based on number of feeding sites/1200 m^2 and were analyzed using negative binomial distribution. Transect data for other species were from counts of pellet groups. Data from photographs were analyzed using zero-inflated negative binomial models. Reference category for season was spring/summer. *P* values in bold were considered significant at α = 0.05.

	Transects				***Photos***			
	Retention		Season		Retention		Season	
	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*
American marten	-	-	-	-	0.008 (0.008)	0.283	0.090 (0.493)	0.856
Black bear*	**0.010 (0.004)**	**0.036**	-	-	-0.003 (0.003)	0.285	-	-
Canada lynx	-	-	-	-	-0.005 (0.005)	0.322	-0.188 (0.324)	0.562
Coyote	-	-	-	-	**0.021 (0.009)**	**0.022**	0.606 (0.310)	0.051
Deer	-0.009 (0.009)	0.342	**-0.948 (0.319)**	**0.004**	-0.006 (0.005)	0.267	**-4.574 (1.016)**	**< 0.001**
Fisher	-	-	-	-	**0.029 (0.010)**	**0.003**	0.320 (0.568)	0.572
Gray wolf	-	-	-	-	0.004 (0.006)	0.470	0.361 (0.392)	0.357
Grouse	**-0.116 (0.027)**	**0.001**	**2.712 (1.195)**	**0.027**	**-0.043 (0.014)**	**0.002**	**-1.643 (0.620)**	**0.008**
Moose	-0.014 (0.012)	0.250	**-1.187 (0.436)**	**0.009**	-0.005 (0.003)	0.127	0.156 (0.187)	0.405
Red squirrel	**0.037 (0.005)**	**< 0.001**	-	-	**0.011 (0.006)**	**0.041**	0.219 (0.257)	0.395
Snowshoe hare	**-1.340 (0.302)**	**< 0.001**	**20.405 (8.016)**	**0.014**	**-0.021 (0.006)**	**< 0.001**	**-0.671 (0.206)**	**0.001**
Wolverine	-	-	-	-	**0.022 (0.011)**	**0.047**	1.835 (1.103)	0.096
Woodland caribou	-	-	-	-	**0.025 (0.010)**	**0.013**	0.871 (0.641)	0.174

Table 2.3. Results of regression models [beta coefficient and standard error, (β (SE)), and *P* values (*P*)] examining the influence of retention level (0%, 10%, 20%, 50%, 75%, 100%) and season (spring/summer, fall/winter) on measures of forest structure. Data were analyzed using Gaussian distribution and the reference for season was spring/summer. *P* values in bold were considered significant at α = 0.05.

	Retention		Season		Retention × Season	
	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*
Canopy cover	**0.077 (0.064)**	**< 0.001**	**-58.441 (3.573)**	**< 0.001**	**0.580 (0.064)**	**< 0.001**
Horizontal cover	**-0.211 (0.072)**	**0.005**	**-10.398 (4.289)**	**0.017**	0.046 (0.075)	0.538
Tree height	**0.200 (0.026)**	**< 0.001**	-	-	-	-
Tree DBH	**0.377 (0.052)**	**< 0.001**	-	-	-	-
Live basal area	**0.303 (0.048)**	**< 0.001**	-	-	-	-
Dead basal area	**0.065 (0.011)**	**< 0.001**	-	-	-	-
Log cover	**0.055 (0.022)**	**0.021**	-	-	-	-
Understory cover	**-0.630 (0.147)**	**0.001**	-	-	-	-
Sapling cover	**-0.196 (0.055)**	**0.003**	-	-	-	-
Shrub cover	-0.093 (0.071)	0.208	-	-	-	-
Forb cover	0.026 (0.065)	0.698	-	-	-	-
Graminoid cover	**-0.363 (0.087)**	**0.001**	-	-	-	-

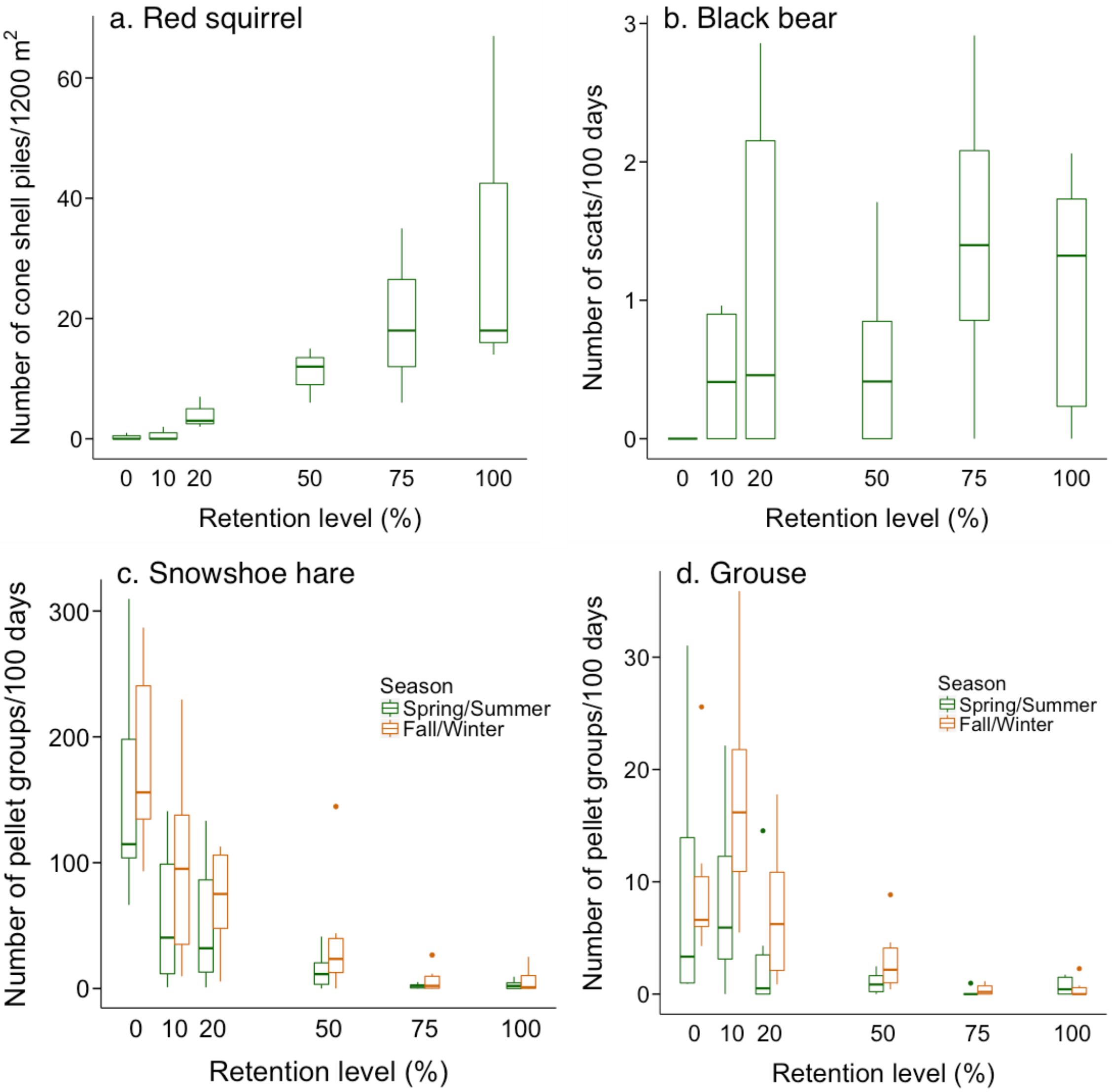

Figure 2.1. Box plots of a) red squirrel, b) black bear, c) snowshoe hare, and d) grouse activity based on number of feeding sites (a) and number of pellet groups (b-d) from surveys along transects in 0%, 10%, 20%, 50%, 75%, and 100% retention. Horizontal lines within the boxes indicate the medians, box boundaries represent the 25th and 75th percentiles; dots outside the box-whiskers are outliers.

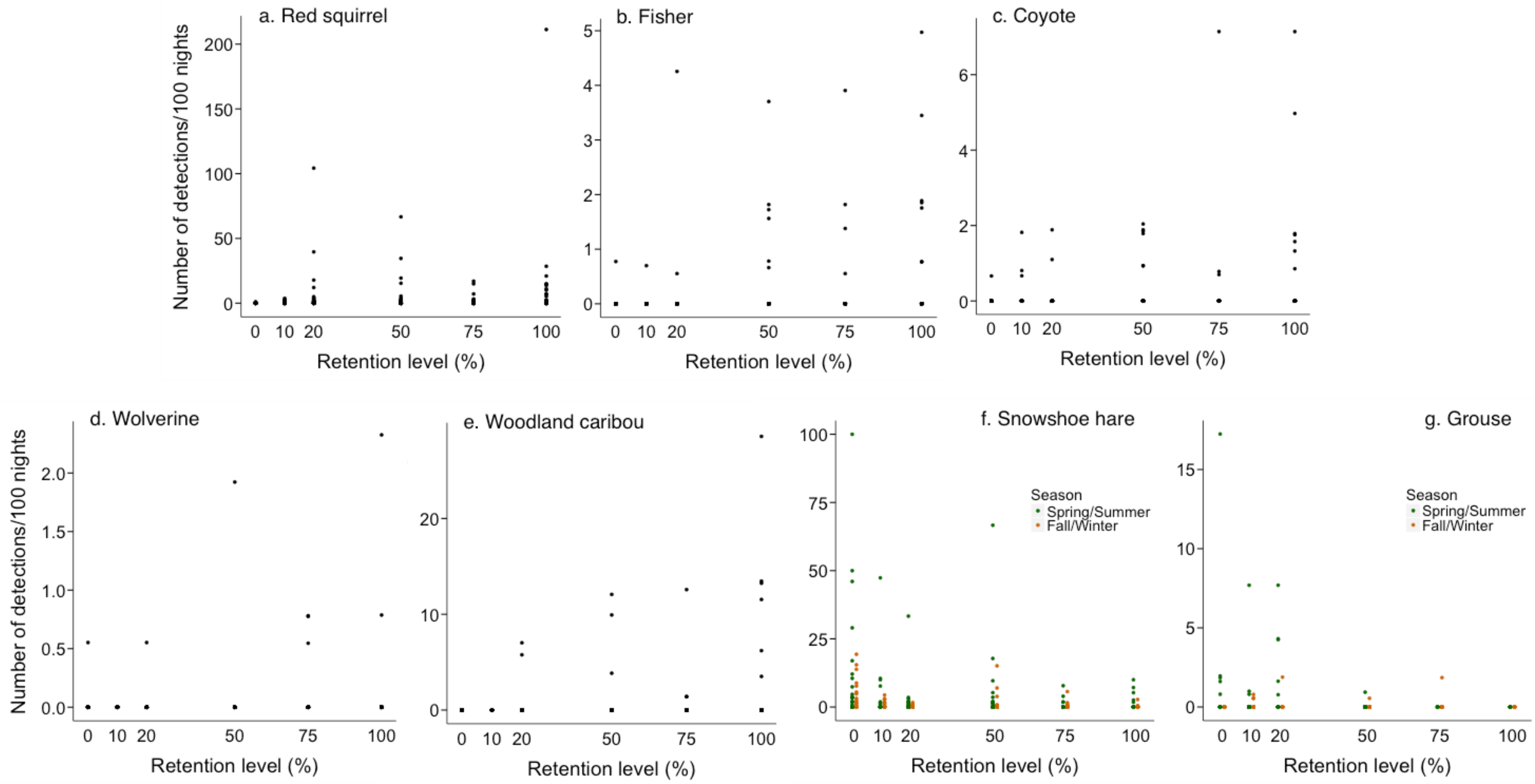

Figure 2.2. Scatterplots of number of detections/100 nights for a) red squirrel, b) fisher, c) coyote, d) wolverine, e) woodland caribou, f) snowshoe hare, and g) grouse based on photographs captured by motion-triggered cameras deployed in 0%, 10%, 20%, 50%, 75%, and 100% retention harvest treatments from 2014-2017.

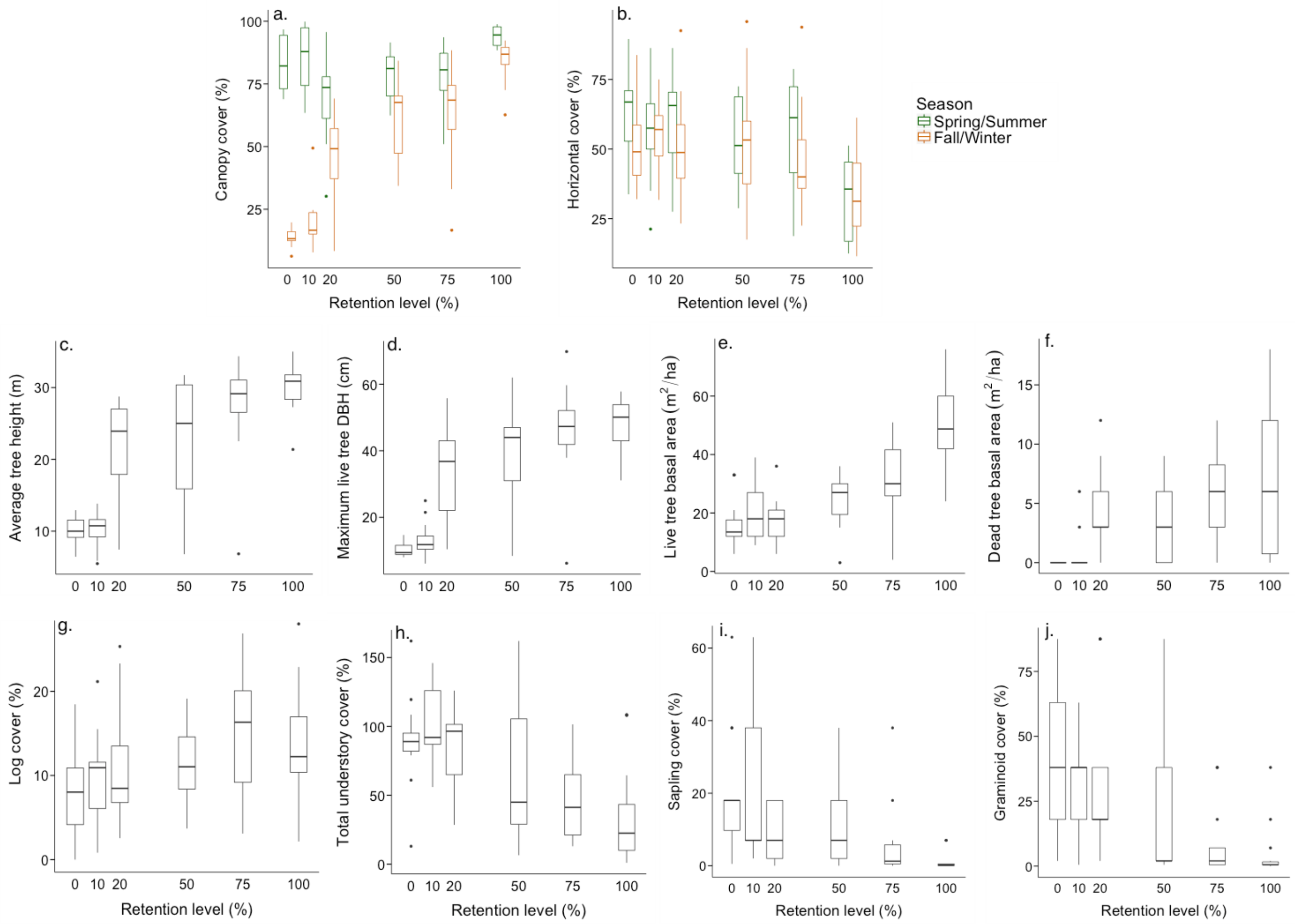

Figure 2.3. Box plots of a) canopy cover, b) horizontal cover, c) average tree height, d) maximum live tree DBH, e) live tree basal area, f) dead tree basal area, g) log cover, h) total understory cover, i) sapling cover, and j) graminoid cover in 0%, 10%, 20%, 50%, 75%, and 100% retention. Horizontal lines within the boxes indicate the medians, box boundaries represent the 25th and 75th percentiles, and dots outside the box-whiskers are outliers.

Appendix 2.1. Universal Transverse Mercator coordinates (zone = 11, datum = NAD83) for belt transects used for counts of feeding activity sites and fecal pellet groups.

Retention level (%)	Compartment identification number	Transect number	Transect length (m)	Transect start		Transect end	
				Easting	Northing	Easting	Northing
0	892	1	200	0414487	6290540	0414297	6290550
0	892	2	100	0414521	6290452	0414617	6290435
0	922	1	150	0416252	6295557	0416099	6295563
0	922	2	50	0416076	6295616	0416026	6295622
0	922	3	100	0416014	6295718	0415915	6295734
0	932	1	300	0418787	6296663	0419081	6296633
10	895	1	300	0413974	6291036	0414269	6291004
10	917	1	100	0416662	6294671	0416561	6294676
10	917	2	100	0416614	6294621	0416715	6294605
10	917	3	100	0416649	6294528	0416743	6294521
10	934	1	50	0418484	6296562	0418439	6296566
10	934	2	200	0418413	6296445	0418217	6296455
10	934	3	50	0418286	6296394	0418240	6296392
20	896	1	100	0414570	6291287	0414654	6291276
20	896	2	100	0414619	6291152	0414722	6291134
20	896	3	100	0414637	6291103	0414733	6291088
20	919	1	50	0416921	6295388	0416873	6295395
20	919	2	100	0416901	6295309	0416803	6295310
20	919	3	150	0416843	6295265	0416697	6295268
20	933	1	100	0418665	6296610	0418570	6296623
20	933	2	50	0418641	6296312	0418592	6296316

20	933	3	150	0418640	6296237	0418493	6296245
50	898	1	50	0414453	6291482	0414495	6291483
50	898	2	100	0414449	6291408	0414348	6291420
50	898	3	150	0414480	6291377	0414334	6291385
50	920	1	100	0416227	6294902	0416132	6294908
50	920	2	100	0416225	6294959	0416127	6294961
50	920	3	100	0415966	6295073	0416066	6295058
50	929	1	150	0419118	6296052	0419266	6296028
50	929	2	150	0419126	6295983	0419274	6295969
75	890	1	150	0413562	6290541	0413415	6290546
75	890	2	100	0413516	6290493	0413418	6290500
75	890	3	50	0413488	6290455	0413438	6290457
75	921	1	150	0415905	6295281	0416045	6295259
75	921	2	150	0415898	6295335	0416043	6295325
75	931	1	200	0418993	6295997	0418789	6296009
75	931	2	100	0418922	6295944	0419026	6295932
100	889	1	150	0413343	6290615	0413188	6290630
100	889	2	150	0413309	6290478	0413168	6290500
100	918	1	200	0416759	6295116	0416564	6295132
100	918	2	100	0416811	6294989	0416715	6294994
100	930	1	50	0419046	6296248	0418993	6296245
100	930	2	50	0419078	6296319	0419029	6296323
100	930	3	150	0419187	6296383	0419038	6296396
100	930	4	50	0419231	6296440	0419192	6296438

Appendix 2.2. Total number of camera deployment nights and wildlife detections for each replicate (n = 3) of different retention levels (0%, 10%, 20%, 50%, 75%, 100%).

Retention level (%)	0	0	0	10	10	10	20	20	20	50	50	50	75	75	75	100	100	100
Replicate	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Number of nights	1285	1431	1083	1156	1340	1224	1341	1503	1077	1338	1583	1223	1323	1592	1138	891	1664	1557
Number of detections																		
American marten	1	3	0	2	6	0	4	3	0	1	0	1	2	3	1	13	2	1
Black bear	18	21	4	15	14	15	14	26	21	21	17	34	16	19	23	8	6	19
Canada lynx	9	4	4	2	1	4	2	8	8	7	1	1	1	1	1	10	4	7
Coyote	0	1	0	1	1	1	1	0	2	1	4	1	1	1	1	11	5	1
Deer	35	15	2	7	13	1	12	2	9	14	4	6	3	21	3	7	13	10
Fisher	0	0	1	0	0	1	3	0	0	0	8	0	0	6	3	10	2	4
Gray wolf	7	5	0	2	2	0	2	6	1	0	2	1	5	2	0	2	44	4
Grouse	3	5	2	2	3	1	9	2	1	1	1	0	0	1	0	0	0	0
Moose	29	6	12	33	17	7	15	12	23	17	57	11	20	11	26	9	13	5
Red squirrel	1	1	2	5	4	4	114	8	12	33	81	6	22	11	2	170	10	64
Snowshoe hare	129	116	38	28	21	14	8	3	11	56	5	6	14	9	1	9	0	10
Wolverine	1	0	0	0	0	0	1	0	0	1	0	0	1	2	0	3	1	0
Woodland caribou	0	0	0	0	0	0	0	0	7	0	22	2	4	19	0	0	24	24

Chapter 3: Combining aggregated and dispersed retention harvesting for conservation of vascular plant communities

3.1. Abstract

Retention harvesting (also called tree retention), in which a portion of live mature trees are left behind at forest harvest is increasingly used to mitigate negative impacts of harvesting on biodiversity. Retention is left at different levels and in different patterns, that have been described as ‘aggregated’ or ‘dispersed’; however, the effectiveness of combining patterns of retention on conservation and recovery of understory vascular plants in the long-term is largely unknown. To address this gap, I compared understory vascular plant diversity, abundance, and composition between aggregated retention and five levels of surrounding dispersed retention (0% = clearcut, 10%, 20%, 50%, 75%) 15 years post-harvest. I also investigated whether dispersed retention influenced the ability of embedded retention patches to support plant communities characteristic of unharvested forests, and whether the effect varies with patch size (0.20 ha or 0.46 ha) or position within patches (edge or interior). Species richness, diversity, and cover were higher in dispersed retention than in patches as harvested areas favoured early-seral plants. Graminoid cover was greater at the edges than in the interior of large patches. Even retention patches of 0.2 ha surrounded by dispersed retention more effectively supported shade-tolerant (forest interior) plant communities than those surrounded by clearcuts, and the effect was stronger when they were surrounded by higher levels (densities) of dispersed retention. Overall, combining aggregated and dispersed retention within a single cutblock benefitted both late- and early-seral plant species, and thus should more effectively conserve understory plant assemblages in harvested landscapes than use of

only a single retention pattern. Therefore, harvest prescriptions that deploy a range of retention patch sizes combined with varying levels of surrounding dispersed retention should better achieve the plant conservation objectives of sustainable forest management.

3.2. Introduction

Retention harvests that leave mature live trees behind at harvest are used in sustainable forestry to enhance structural diversity, maintain ecosystem function, and conserve biodiversity (Franklin et al. 1997; Vanha-Majamaa and Jalonen 2001; Gustafsson et al. 2012; Lindenmayer et al. 2012; Fedrowitz et al. 2014; Mori and Kitagawa 2014). Many options may be considered in application of retention harvesting, including retention level (proportion of the initial density, basal area, or volume that is retained) and pattern (spatial arrangement of retained trees). A primary function of aggregated retention (or retention ‘patches’) is to ‘lifeboat’ forest-dependent species through disturbance by providing habitat and microclimatic conditions that are relatively similar to unharvested forest (Franklin et al. 1997). In contrast, a more uniform dispersion of retained trees (dispersed retention) on cutblocks, enhances landscape connectivity by maintaining structural complexity throughout the harvested area (Franklin et al. 1997). Thus, combining both spatial patterns in a single harvested area (i.e., variable retention harvesting) represents an attractive strategy for conservation of biodiversity (Franklin et al. 1997; Rosenvald and Lõhmus 2008; Aubry et al. 2009). Unfortunately, there is only limited evidence about the effectiveness of such harvest prescriptions (but see Lencinas et al. 2011; Pinzon et al. 2012; Lee et al. 2017).

Contrast between retained patches and the surrounding matrix and how this changes over time post-harvest may influence the effectiveness of retention patches as lifeboats. Dispersed retention around patches should reduce their structural contrast with the surrounding matrix over that of a clearcut, and such effects are expected to moderate microclimatic conditions and reduce edge effects (Bannerman 1998; Harper et al. 2005). Small retention patches experience increased blowdown (Jönsson et al. 2007; Steventon 2011) and this gradual conversion of retained trees to snags and downed logs could impact their effectiveness of patches as lifeboats for forest-dependent species. Dispersed retention around retention patches could better protect them and conserve their lifeboat function over a longer-term. Few studies of retention harvests have addressed effects more than five years post-harvest, and thus longer-term studies are needed to detect potential lag effects in biodiversity responses (Fedrowitz et al. 2014).

In boreal and temperate forests, the vast majority of plant diversity is in the understory layer, which includes saplings, shrubs, forbs, and graminoids (De Grandpré et al. 2003; Gilliam 2007). These plant communities provide food and habitat for wildlife, play key roles in nutrient cycling, and affect tree regeneration, thereby influencing forest stand dynamics (Nilsson and Wardle 2005; Hart and Chen 2006; Gilliam 2007). Disturbances such as forest harvest alter understory communities by creating favourable conditions for early-seral species (Pykälä 2004; Hart and Chen 2006). Fewer changes result with higher levels of dispersed retention as more residual material is associated with fewer changes in plant species richness, cover, and composition, as compared to pre-harvest conditions (Bergstedt and Milberg 2008; Craig and Macdonald 2009; Halpern et al. 2012).

Previous studies on understory responses to harvest in retention patches have considered mainly retention patches surrounded by clearcuts, and these studies suggest that vegetation in patches is negatively affected by surrounding clearcuts (e.g., Halpern et al. 2005; Halpern et al. 2012; Roberts et al. 2016). Even in relatively large patches (> 0.5 ha), plant communities can be substantially different than in unharvested forest when patches are surrounded by clearcuts (Bradbury 2004). In southern temperate forest, understory plant communities were more similar to uncut forest in harvest designs that combined aggregated and dispersed retention treatments than when a single retention pattern was used (Lencinas et al. 2011); however, their study was short-term (four years post-harvest) and limited to a single patch size and retention level. I suggest that higher levels of dispersed retention should better preserve the effectiveness of retention patches as lifeboats for understory plant communities as seen for saproxylic beetles (Lee et al. 2017). Furthermore, smaller patches may more effectively maintain late-seral plant communities if surrounded by dispersed retention. Knowledge of the interactive effects of patch size, position within patch, and surrounding retention levels, particularly in the longer term, promise to better inform harvest planning to meet conservation goals in sustainable forest management.

I examined the effects of combinations of aggregated and dispersed retention on understory vascular plant diversity, abundance, and composition 15 years post-harvest. Specifically, I tested four hypotheses that were related to either the retention pattern for comparisons between retention patches and surrounding harvested areas (H1), retention level surrounding retention patches (H2), patch size (H3), or position within patches (H4) as follows. H1: species richness, diversity, cover, and sapling density is lower in retention patches than in a surrounding matrix of dispersed retention, because the harvested area supports both early-seral species and more shade-tolerant species that are resilient to harvesting; furthermore, these differences between patches and the surrounding harvested areas attenuate with increasing levels of dispersed retention. H2: higher levels of surrounding dispersed retention will improve retention of plant communities characteristic of unharvested forest in retained patches. H3: larger retained patches will support late-seral plant communities better than smaller patches. H4: species diversity, cover, and sapling density will be higher at the edge than in the interior of patches because shade-intolerant species will be favoured at the edge.

3.3. Methods

3.3.1. Study Site

Research was conducted at the large-scale Ecosystem Management Emulating Natural Disturbance (EMEND) experiment located approximately 90 km northwest of Peace River, Alberta, Canada (56° 46’ 13” N, -118° 22’ 28” W). The area is representative of the boreal mixedwood plains and forests are dominated by white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). Mean annual precipitation is 436 mm and mean temperatures are -16.9°C and 15.0°C for January and July, respectively (“Government of Canada: 1981-2010 climate normals and averages” accessed 16 January 2017 from www.climate.weather.gc.ca). Soils are well-drained and primarily Luvisolic (Kishchuk 2004).

I studied a subset of the experimentally harvested compartments (c. 10 ha each) at EMEND. These were dominated by conifers, mainly white spruce, and had been harvested in the winter of 1998-1999 using one of five different retention levels (treatments) based on the percentage of the initial density retained in particular compartments: 0% (clearcut), 10%, 20%, 50%, and 75% retention. Each compartment was cut to retain one large (c. 0.46 ha) and one small (c. 0.20 ha) elliptical retention patch surrounded by clearcut or dispersed retention (Figure 3.1; see Spence et al. 1999 for details of design). The two patches within each compartment were at least 80 m apart. Unharvested compartments were used as controls. There were three replicates of each treatment giving a total of 18 experimental compartments in this study.

3.3.2. Data Collection

During June-August 2014, samples were collected from eight 1-m^2 quadrats that were placed in each harvested compartment, and another eight quadrats placed in each large and small embedded retention patch. Craig and Macdonald (2009) demonstrated that eight quadrats in an area less than 0.5 ha provides sufficient sampling intensity to well represent the understory vascular plant community, including shrubs, forbs, graminoids, and tree saplings. Quadrats in the harvested area were randomly established in an area no larger than the size of a large patch (< 0.46 ha). Quadrats within patches were placed as follows: four quadrats were placed at the edge of the patch, one in each cardinal direction, and the remaining four quadrats were placed randomly at least 5 m apart in the patch interior. Eight quadrats were also placed randomly in unharvested control compartments in an area of between 0.20 and 0.46 ha.

Percent cover of all individual shrub, forb, and graminoid species were visually estimated in each quadrat for each species to the nearest 0.5% from 0% to 1%, to the nearest 1% from 1% to 10%, and to the nearest 5% from 10% to 100%. Sapling (> 10 cm in height; ≤5 cm diameter at breast height) densities (for tree species) were also quantified within a 2-m radius of each quadrat center. Specimens that could not be identified in the field were collected for identification in the laboratory. Specimens unidentifiable at the species level were identified to genus and treated separately from identified species of the same genus for the purpose of analysis (Appendix 3.1).

3.3.3. Data Analysis

Species richness was expressed as the total number of species per quadrat (1 m^2). Vascular plant diversity was calculated using Hill numbers to obtain the effective number of species (Hill 1973). Shannon diversity was considered Hill number of order 1, which is the exponential of Shannon's entropy and weights each species relative to their respective abundance (Jost 2006). Response variables included: vascular plant species richness, diversity, and percent cover (total and by vegetation type: shrubs, forbs (including prostrate/trailing woody species), and graminoids), and sapling density to quantify forest regeneration.

Mixed-effects models of variance were produced in the R statistics programming environment version 3.2.1 (R Development Core Team 2015) with the *lme* function in the *nlme* package (Pinheiro et al. 2017). Response variables were tested for nonlinearity using generalized additive mixed models and by comparing Akaike information criterion (AIC) values between linear and nonlinear models. Linear model responses were more supported than nonlinear models, having the lowest AIC value for all response variables, and so only linear models are presented here.

For examining the influence of retention pattern (H1) and patch size (H3) on species richness, diversity, cover, and sapling density, the mixed-effects model included retention level (0%, 10%, 20%, 50%, 75%) and spatial pattern (harvest area, small patch, large patch) as continuous and categorical fixed independent variables, respectively, and the interaction between retention level and spatial pattern. Compartment was included as a random variable. Data from the unharvested compartments could not be included in these analyses since unharvested forest had nothing comparable to the retention pattern categories. I therefore present means and standard errors from the unharvested compartments with the results from the mixed models for comparative purposes with the other treatments. To determine the influence of surrounding dispersed retention level on the lifeboating function of retention patches (H2), mixed-effects models were conducted for each patch size separately and included retention level (0%, 10%, 20%, 50%, 75%, 100%) and compartment as a continuous and random variable, respectively. To compare responses between the edge and interior of retention patches (H4), I used a split-split plot design. Retention level (0%, 10%, 20%, 50%, 75%) was the main plot, patch size (small, large) was the split-plot, position within patch (edge, interior) was the split-split plot, and compartment was a random variable.

Diagnostic plots were used to assess normality and homoscedasticity of the residuals for all of the mixed models. Assumptions of normality were not met for graminoid cover and those data were log-transformed. When there was a significant main effect from the mixed-effects models, pairwise comparisons ($\alpha = 0.05$) of least-squares means were made using the *lsmeans* package (Lenth 2016). When the interaction between patch size and position within patch was significant, pairwise comparisons (α = 0.05) between positions were made for each patch size.

To examine the effect of variable retention harvesting on understory species composition, I conducted distance-based redundancy analyses (db-RDA) following the mixed models described above in R version 3.2.1 (R Development Core Team 2015) using the *capscale* function in the *vegan* package (Oksanen et al. 2017). I performed db-RDA using the Bray-Curtis distance measure because this analysis tests the significance of individual independent variables and their interactions for multispecies response variables (Legendre and Anderson 1999). Statistical significance of the db-RDA model terms was determined using 999 permutations. Species data were represented by percent cover and were Hellinger-transformed to reduce the value of abundant species (Legendre and Gallagher 2001). The Hellinger transformation converts each abundance value to the proportion of total sum of values (relative abundance) and subsequently calculates the square root each proportion (Legendre and Gallagher 2001).

For examining the influence of retention pattern (H1) and patch size (H3) on species composition, the primary matrix of the db-RDA was the species data for each 1-m^2 sampling quadrat while the secondary matrix consisted of retention level (0%, 10%, 20%, 50%, 75%) and retention pattern (harvest area, small patch, large patch) as a continuous and categorical variable, respectively. I used the *ordisurf* function to fit smooth surfaces for retention level onto the ordination plot using thinplate splines with generalized cross-validation for selection of smoothness (Oksanen et al. 2017). Species displayed in the plot were selected using the circle of equilibrium method, which chooses species that make above average contributions to the ordination plot (Legendre and Legendre 1998). The interaction between retention pattern and level was significant so I performed additional db-RDAs that examined the differences in species composition between retention patterns for individual retention levels. I used the *ordiellipse* function to add dispersion ellipses (95% confidence regions) based on standard errors of the weighted average of scores around the centroids of each retention pattern (Oksanen et al. 2017).

To investigate the ability of the retention patch to support plant communities similar to intact forest (H2), I conducted db-RDA that included retention harvest treatments and unharvested control for the small patch and large patch separately. I did not explore differences among retention levels for the dispersed retention only because others are examining these comparisons with a larger data set. To determine whether or not there were differences in responses between the edge and interior of retention patches (H4), the primary matrix of the db-RDA was the species data for each 1-m^2 sampling quadrat while the secondary matrix consisted of position within patch (edge, interior), patch size (small, large), and retention level (0%, 10%, 20%, 50%, 75%). In all db-RDA models, compartment was a conditional variable to remove its random effect before constraining the other variables (Oksanen et al. 2017).

3.4. Results

3.4.1. Responses to retention pattern and level

In total, 18 shrub, 59 forb, and 10 graminoid species were found (Appendix 3.1). Retention pattern significantly affected species richness, Shannon diversity, total cover, and graminoid cover (Table 3.1). The interaction between retention level and pattern was significant for forb cover, sapling density, and composition, while shrub cover did not vary significantly with retention level or pattern (Table 3.1). The level of surrounding dispersed retention did not significantly affect species richness, Shannon diversity, total cover, shrub cover, and forb cover in the retention patches; however, as the level of surrounding dispersed retention increased, graminoid cover, sapling density, and species composition in the small and large patches were more similar to the unharvested control (Table 3.2; Figure 3.6).

3.4.2. Understory vegetation diversity and cover

Vascular plant species richness per quadrat was higher in the harvested area than in either the small ($p < 0.001$) or the large ($p = 0.002$) embedded patches, and was lower in small than in large patches ($p = 0.017$). Species richness in the retention patches was more similar to that in unharvested control compartments than to the harvested areas regardless of dispersed retention level (Figure 3.2A).

Shannon diversity was higher in the harvested areas compared to both the small ($p < 0.001$) and large ($p = 0.004$) patches with no significant difference in species diversity between patch sizes ($p = 0.194$). Species diversity of the patches was also more similar to that of the unharvested control compartments than the surrounding harvested area (Figure 3.2B).

Total understory cover was significantly higher in harvested areas than in small patches ($p = 0.007$), while cover in large patches was intermediate and did not differ from either that in small patches ($p = 0.106$) or harvested areas ($p = 0.277$). As with the results for species diversity and richness, total cover was more similar to unharvested controls in retention patches than in harvested areas (Figure 3.2C).

Graminoid cover in harvested areas was significantly higher than in both the small ($p = 0.019$) and large ($p = 0.037$, Figure 3.2D) patches, which did not differ from one another in this respect ($p = 0.790$). When both patch sizes were surrounded by higher amounts of dispersed retention, graminoid cover was more similar to that in the unharvested control (Table 3.2). The significant interaction between retention level and pattern for forb cover was due to the fact that in both patch sizes forb cover decreased with increasing retention level in the surrounding retention (small patches: $\beta = -0.08 \pm 0.16$; large patches: $\beta = -0.07 \pm 0.16$), whereas in harvested areas forb cover was positively related to retention level ($\beta = 0.18 \pm 0.16$) (Figure 3.3A).

3.4.3. Saplings

Populus balsamifera and *P. tremuloides* accounted for the majority of saplings. Sapling density decreased under higher retention level but the effect was stronger in the harvested areas ($\beta = -0.91 \pm 0.21$) than patches of either size (small: $\beta = -0.07 \pm 0.21$; large: $\beta = -0.36 \pm 0.21$). Sapling density was lowest in unharvested controls and was twice as high in the harvested areas as in the patches when dispersed retention level was $\leq 20\%$ (Figure 3.3B). There was less variation in sapling density between harvested areas and retention patches when higher levels of dispersed retention surrounded the patches (Figure 3.3B). Moreover, sapling densities in patches of both sizes were more similar to the unharvested controls with increasing amounts of dispersed retention surrounding patches (Table 3.2).

3.4.4. Composition

Vascular plant species composition varied among small patches, large patches, and harvested areas and was influenced by amount of dispersed retention (Figure 3.4A). The different retention patterns (patch vs. distributed retention) separated mostly on axis 2 of the RDA, while variation related to amount of dispersed retention was distributed along axis 1 (Figure 3.4A). Species such as *Aster ciliolatus*, *Calamagrostis canadensis*, and *Epilobium angustifolium* were associated with lower amounts of dispersed retention, while *Cornus canadensis* was characteristic of high retention (Figure 3.4B). *Linnaea borealis* and *Geocaulon lividum* characterized small patches, while *Vaccinium vitis-idaea* and *Ledum groenlandicum* were more associated with large patches (Figure 3.4B). Distinct plant communities characterized the harvested areas, small patches, and large patches for each level of dispersed retention (0%, 10%, 20%, 50%, 75%) (Figure 3.5). As surrounding dispersed retention increased, species composition in both small and large patches became more similar to those in unharvested forest, as compared to patches surrounded by clearcut (Figure 3.6).

3.4.5. Responses to position within retention patches

Position within the retention patches did not affect species richness, Shannon diversity, total cover, shrub cover, forb cover, and composition, but did significantly influence graminoid cover (Table 3.3). Median graminoid cover was higher at patch edges than in patch interiors for both patch sizes, but this difference was greater for large than small patches (Figure 3.7). In large patches graminoid cover was significantly greater at the edge than in the interior ($p < 0.001$) but in small patches there was no difference in graminoid cover between the interior and edge ($p = 0.991$).

3.5. Discussion

My results demonstrate that combining dispersed and aggregated retention in a single harvested area is beneficial for conservation of understory vegetation 15 years post-harvest. Compared to areas harvested to dispersed retention prescriptions, patch retention was more effective at supporting plant communities similar to unharvested forest, particularly when these patches were surrounded by higher amounts of dispersed retention. Small (0.20 ha) and large (0.46 ha) patches supported different understory plant communities and large patches had higher gramionoid cover at the edges compared to the interiors of the patches.

3.5.1. Responses to retention pattern and level

My results supported my first hypothesis (H1), which predicted more increased species richness, diversity, cover, and sapling density in dispersed retention than in retention patches. Harvested areas were characterized by early-seral vegetation, whereas embedded retention patches more effectively supported late-successional species associated with the unharvested control compartments. Higher species richness, diversity, and cover, and presence of more shade-intolerant species, in harvested areas can be explained by greater light availability resulting from reduced canopy, as compared to conditions in the patches (Battles et al. 2001; Heithecker and Halpern 2007). Reduced canopy cover in harvested areas benefitted species that prosper under higher light transmission such as *E. angustifolium* (Lieffers and Stadt 1994). My findings are similar to those of Soler et al. (2016) in showing that unharvested patches in a temperate forest contained more native forest specialists than did dispersed retention.

As amount of retention increased, sapling density in harvested areas became more similar to that in retention patches, as I expected to follow as a function of fewer structural differences between the surrounding harvested area and patches. The significant combined effects of retention pattern and amount on forb cover and sapling density could reflect the potential interactions between canopy closure, regeneration, and understory vegetation cover. Shade intolerant sapling species, such as *P. tremuloides* and *P. balsamifera*, are favoured by high light environments associated with low retention levels (Frey et al. 2003; Heithecker and Halpern 2006; Gradowski et al. 2010). Presence of high sapling densities in areas with low retention likely contributed to reducing forb cover by shading the understory, thus explaining the contrasting responses of these two vegetation components (Wagner et al. 2011). I did not observe such differences in retention patches; both sapling density and forb cover were relatively low, likely as a result of greater canopy cover. Somewhat higher forb cover in patches could have resulted from greater light availability resulting from more blowdown in patches surrounded by lower retention (Scott and Mitchell 2005; Lee et al. 2017).

In accordance with my second hypothesis (H2), patches surrounded by dispersed retention were more effective as local refugia for forest-dependent species than were patches surrounded by clearcuts. My results showed that, as dispersed retention level increased, retention patches better supported more shade-tolerant species such as *V. vitis-idaea* (Väisänen et al. 1977) and *L. borealis* (Eriksson 1988). Lencinas et al. (2011) also showed that aggregated retention combined with dispersed retention (40%-50% retention) more effectively conserved understory plant communities in the short term (four years post-harvest), as compared to only dispersed retention (20%-30%) or one small (~ 0.28 ha) patch per hectare within a clearcut. The positive influence of dispersed retention on faunal conservation in embedded retention patches also has been recorded for arthropods (Pinzon et al. 2012; Lee et al. 2017). Retained trees surrounding retention patches reduce environmental extremes between regenerating and unlogged patches, decreasing blowdown rates in patches (Lee et al. 2017). Consequently, embedding them in dispersed retention enhances the ability of retention patches to support species composition characteristic of unharvested forest. Even though retention patches < 1 ha can provide habitat for some forest-dependent species when surrounded by clearcuts (Baker et al. 2015), my findings indicate that the conservation effect increases when patches are surrounded by higher amounts of dispersed retention.

3.5.2. Responses to retention patch size and position within patches

Although I expected larger patches to better support late-seral plant communities than smaller patches under my third hypothesis (H3), there was no evidence to support this prediction. Nevertheless, plant communities differed between large and small patches, which suggests that both sizes are ecologically valuable. Bradbury (2004) observed differences in understory plant communities between retention patch sizes two years after harvest, my findings generalize this effect to 15 years post-harvest. More importantly, my findings indicate that the level of dispersed retention surrounding retention patches affects individual patch sizes differently. By reducing the structural contrast between the harvested area and large patches, sapling densities in patches surrounded by more dispersed retention were more comparable to unharvested forest than those surrounded by lower amounts. Athough Lee et al. (2015) suggest that patches larger than 0.50 ha would have higher conservation value for saproxylic beetles, my findings suggest that patches as small as 0.20 ha were able to support some late-seral plant species more effectively than the surrounding harvested areas.

My fouth hypothesis (H4) predicted that patch edges would favour more shade-intolerant species than patch interiors and be associated with differences in species diversity and composition between patch edges and interiors. However, understory vegetation was generally similar between the edge and interior of patches, and different from that of the unharvested control compartments. Thus, edge effects on understory vascular plants could have extended the entirety of the patches. Hautala et al. (2011) concluded that edge effects influenced epixylic plant species throughout retention areas that averaged 0.2 ha in size. Furthermore, understories at the interiors and edges of 0.12-2.6 ha retention patches surrounded by clearcuts did not differ in temperate forests over five years post-harvest (Baker et al. 2016). Although I expected dispersed retention to minimize edge effects by reducing the contrast between harvested and retained areas (Bannerman 1998), the retention patches were likely too small to foster differences in understory vegetation between patch interiors and edges. Alternatively, considering the study was conducted 15 years post-harvest, edge effects on understory vegetation could have diminished over time (Harper et al. 2015).

Graminoid cover, the only variable that responded to position within patch, was higher at the edge than in the interior of large patches, perhaps reflecting lower light availability and temperatures at the patch centers than at the edges (Heithecker and Halpern 2007). In a study of 1 ha patches within clearcuts in temperate forests, Nelson and Halpern (2005) found that canopy cover was reduced at edges, as compared to patch interiors, and early-seral plant species were restricted to within 10 m of the edge two years after harvest. Differences in graminoid cover between the interior and edge of small patches may have been attenuated as a result of the shorter distance between the edge and center, as compared to large patches. The distance between the interiors and edges of small patches was approximately 25 m, thus the entire patch was likely influenced by edge effects on microclimatic variables such as light availability (Heithecker and Halpern 2007; Harper et al. 2015).

3.5.3. Management implications

My findings suggest that a strategy of variable retention harvesting incorporating a variety of harvest patterns and amount of residual will best benefit understory vascular plants on harvested landscapes. Notably, combining patch and dispersed retention in harvested areas is a better alternative to meet conservation goals than leaving patches within clearcuts. Areas harvested by dispersed retention were characterized by early-successional communities, and thus can play a valuable role on the forested landscapes by providing high plant productivity and spatial complexity (Swanson et al. 2011). Meanwhile, aggregated retention promoted maintenance of late-seral species, partly because they maintained structural complexity (Moussaoui et al. 2016) and microclimatic conditions characteristic of unharvested stands (Baker et al. 2016).

My results also highlight the importance of incorporating a variety of patch sizes in retention harvest designs to support various vascular plant species. Even the small patches (0.20 ha) were beneficial for some late-seral plant species and, in fact, both patch sizes supported understory communities more similar to unharvested forests than did harvested areas; this was particularly true when patches were surrounded by higher levels of dispersed retention. Thus, the amount of dispersed retention surrounding patches interacts with patch characteristics to affect species composition and should be considered in harvest designs.

In addition to providing ecological benefits, combining patterns of retention harvest may confer benefits in terms of improving the aesthetics of harvested areas, as compared to the pattern of leaving unharvested patches within clearcuts, which was found to have low aesthetic value (Ribe 2005). Future studies should consider a greater variety of retention patch sizes as well as the location of retention patches within harvested areas of different forest types.

3.6. Literature cited

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Table 3.1. Results of mixed models [F values (*F*), degrees of freedom (*df*), and *P* values (*P*)] examining the influence of pattern (harvest area/small patch/large patch), retention level surrounding patches (0%, 10%, 20%, 50%, 75%), and retention pattern × level interaction on understory vascular plant vegetation. Species richness, Shannon diversity, cover, and sapling density were analyzed using mixed model regression. Composition was analyzed using distance-based redundancy analysis. *P* values in bold were considered significant at $\alpha = 0.05$.

	Pattern			Level			Pattern x Level		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Species richness	**16.51**	**2**	**<0.001**	1.23	1	0.288	2.30	2	0.102
Species diversity	**9.36**	**2**	**<0.001**	0.12	1	0.737	3.01	2	0.051
Total cover	**3.72**	**2**	**0.025**	0.10	1	0.759	1.19	2	0.305
Shrub cover	0.06	2	0.943	0.01	1	0.939	0.73	2	0.485
Forb cover	2.84	2	0.060	0.00	1	0.962	**3.47**	**2**	**0.032**
Graminoid cover*	**3.34**	**2**	**0.037**	1.70	1	0.214	1.77	2	0.173
Sapling density	**32.28**	**2**	**<0.001**	**7.52**	**1**	**0.017**	**6.98**	**2**	**0.001**
Composition	**3.37**	**2**	**0.001**	**7.69**	**1**	**0.001**	**1.88**	**2**	**0.009**

*Data were log-transformed for analysis.

Table 3.2. Results of regression models [beta coefficient and standard error, (β (SE)), F values (*F*), and *P* values (*P*)] examining the influence of surrounding level of dispersed retention (0%, 10%, 20%, 50%, 75%) on understory vascular plant vegetation in small and large retention patches. Unharvested forest (100% retention) was included in the analyses. *P* values in bold were considered significant at α = 0.05. Degrees of freedom = 1 for all response variables.

	Small Patch			Large Patch		
	β (SE)	*F*	*P*	β (SE)	*F*	*P*
Species richness	-0.01 (0.02)	0.17	0.684	-0.02 (0.01)	2.95	0.105
Species diversity	-0.00 (0.01)	0.14	0.714	-0.01 (0.01)	1.02	0.328
Total cover	-0.24 (0.22)	1.19	0.291	-0.25 (0.25)	1.00	0.332
Shrub cover	-0.14 (0.12)	1.34	0.264	-0.08 (0.12)	0.49	0.493
Forb cover	-0.02 (0.10)	0.05	0.827	-0.10 (0.14)	0.49	0.495
Graminoid cover*	**-0.01 (0.00)**	**13.38**	**0.002**	**-0.01 (0.00)**	**10.55**	**0.005**
Sapling density	**-0.03 (0.01)**	**5.33**	**0.035**	**-0.04 (0.01)**	**15.56**	**0.001**

*Data were log-transformed for analysis.

Table 3.3. Results of split-split-plot analyses [F values (*F*), and *P* values (*P*)] used to examine the influence of position within patch (edge, interior), patch size (small, large), and level of retention surrounding patch (0%, 10%, 20%, 50%, 75%) on understory vascular plant vegetation. Species richness, Shannon diversity, cover, and sapling density were analyzed using mixed model regression. Composition was analyzed using distance-based redundancy analysis. *P* values in bold were considered significant at α = 0.05. Degrees of freedom = 1 for all response variables.

	Position		Size		Level		Position × Size		Position × Level		Size × Level		Position × Size × Level	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Species richness	0.00	0.983	1.63	0.224	0.20	0.662	0.32	0.575	0.40	0.530	0.55	0.471	0.91	0.341
Species diversity	0.00	0.991	0.75	0.401	0.20	0.665	0.07	0.791	2.84	0.093	1.06	0.322	0.03	0.856
Total cover	1.35	0.246	1.21	0.291	0.14	0.710	2.50	0.116	2.98	0.086	0.52	0.482	1.68	0.197
Shrub cover	0.02	0.896	0.04	0.843	0.00	0.958	1.22	0.272	1.12	0.291	0.36	0.559	0.04	0.852
Forb cover	0.02	0.899	2.44	0.142	0.20	0.662	1.79	0.182	0.01	0.947	0.01	0.941	0.96	0.328
Graminoid cover*	**7.39**	**0.007**	0.05	0.836	0.60	0.453	**7.31**	**0.007**	2.23	0.137	0.02	0.881	1.24	0.266
Sapling density	1.88	0.172	0.05	0.828	4.40	0.056	0.22	0.642	1.43	0.233	2.06	0.175	0.50	0.481
Composition	1.18	0.276	1.33	0.153	**3.48**	**0.001**	0.64	0.886	1.11	0.303	**4.14**	**0.001**	0.81	0.710

*Data were log-transformed for analysis.

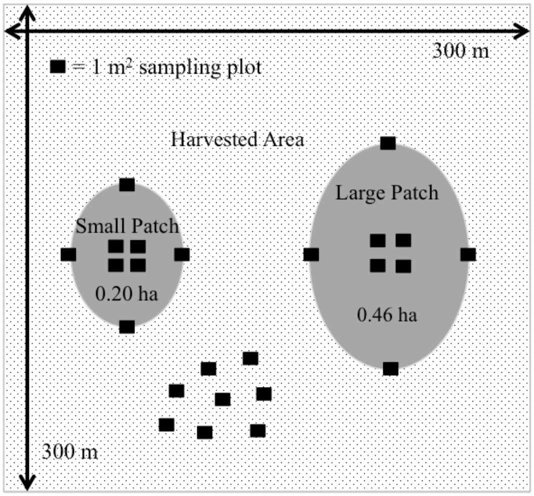

Figure 3.1. Schematic diagram illustrating the experimental design of a 10 ha compartment that contains two sizes of aggregated retention patches (0.20 ha and 0.46 ha) embedded in a harvested matrix. The dotted background represents the area harvested to 0% (clearcut), 10%, 20%, 50%, or 75% of the original stand volume using dispersed retention. Compartments for each harvest level and for unharvested control were replicated three times. Illustration is not to scale.

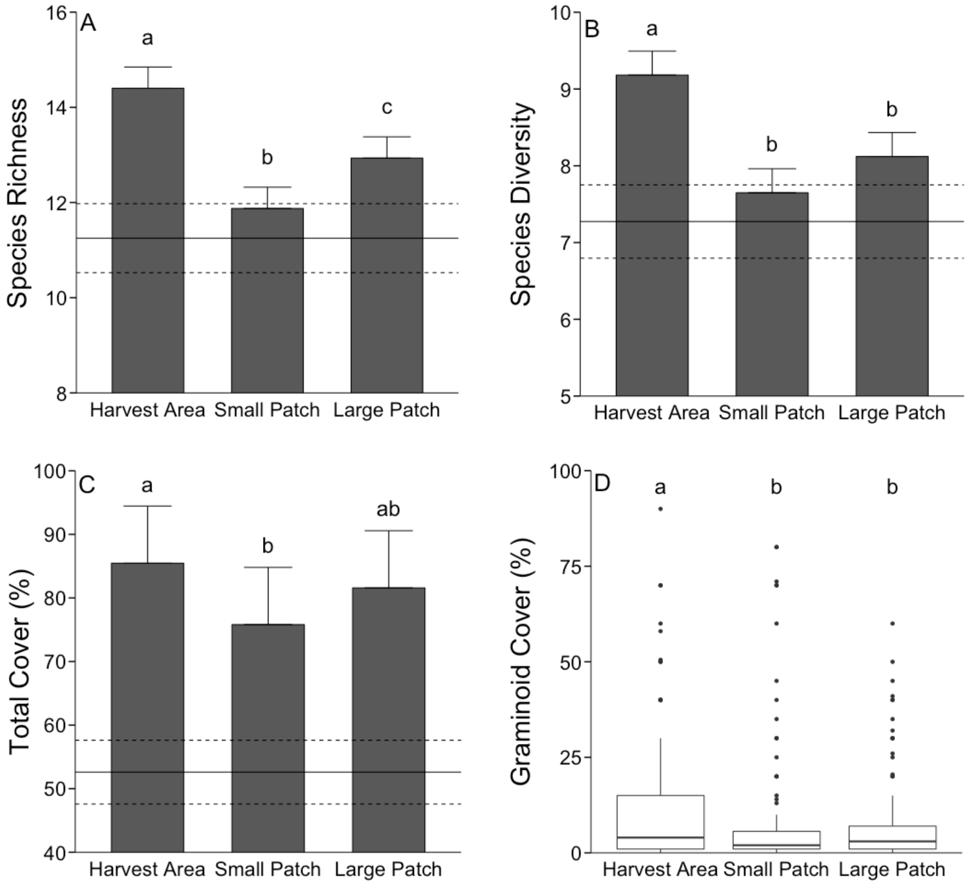

Figure 3.2. Least-square mean ± SE of: A) species richness, B) Shannon diversity, and C) total cover, and median, 25th, and 75th percentiles of D) graminoid cover in harvest area, small patch, and large patch retention. Horizontal lines in A)-C) represent mean (solid line) and standard error (dashed lines) of unharvested control. D) Dots outside the box-whiskers represent outlier values and graminoid cover in unharvested control was 0.4 ± 4.9%. Means with different letters are significantly different (pairwise comparison of least-squares means; $P < 0.05$).

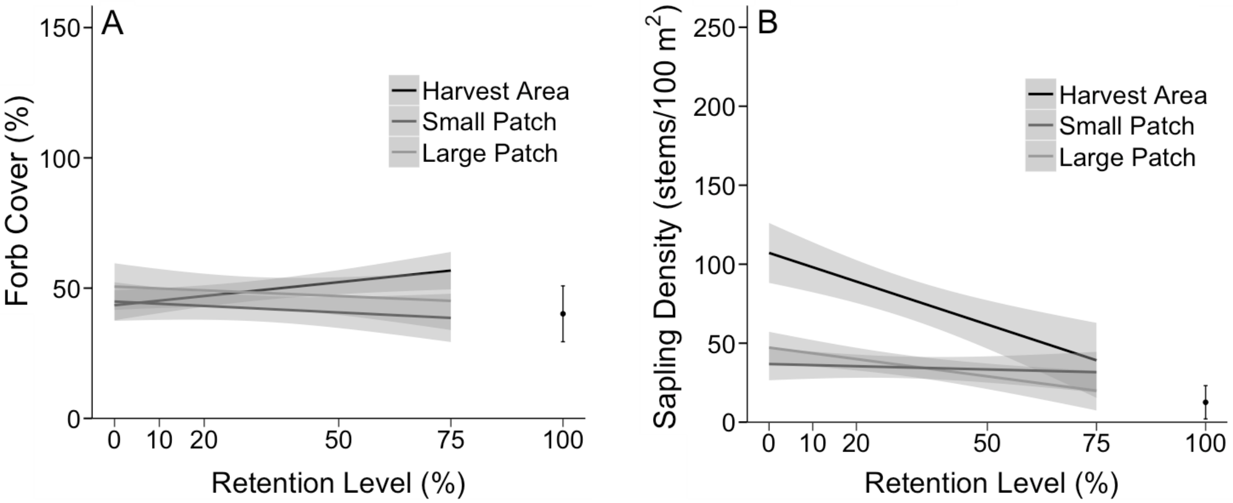

Figure 3.3. Fitted linear regression with 95% CI for: A) forb cover; and B) sapling density, for harvest area, small patch, and large patch across different retention levels. Least-square mean ± SE for unharvested control (100% retention) is shown for reference. Sampling plot size was 1.00 m^2 for forb cover (A) and 12.57 m^2 for sapling density (B).

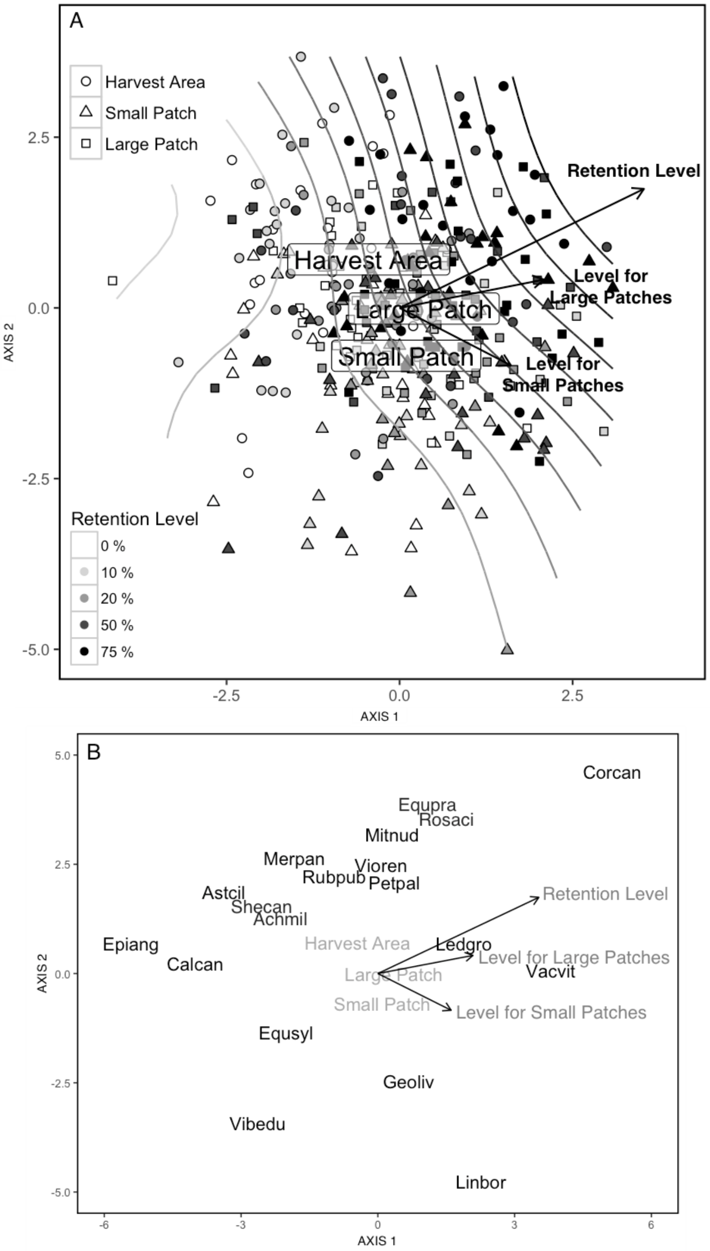

Figure 3.4. Results of distance-based redundancy analysis testing the influence of dispersed retention level (0%, 10%, 20%, 50%, 75%) surrounding small patch and large patch retention on understory vascular plant species composition. Symbols in A) represent the plant community in a 1-m^2 sampling quadrat coded by harvested/unharvested area (harvest area/small patch/large patch) and retention level. Shown in B) are species that made above average contributions to the ordination analysis (circle of equilibrium). Labels for harvest area, small patch, and large patch represent middle of centroids based on standard errors of the weighted average of scores. Vectors for retention level indicate the direction of retention level that surrounded large patches ("Level for Large Patches") and small patches ("Level for Small Patches"). See Appendix 3.1 for definition of species codes.

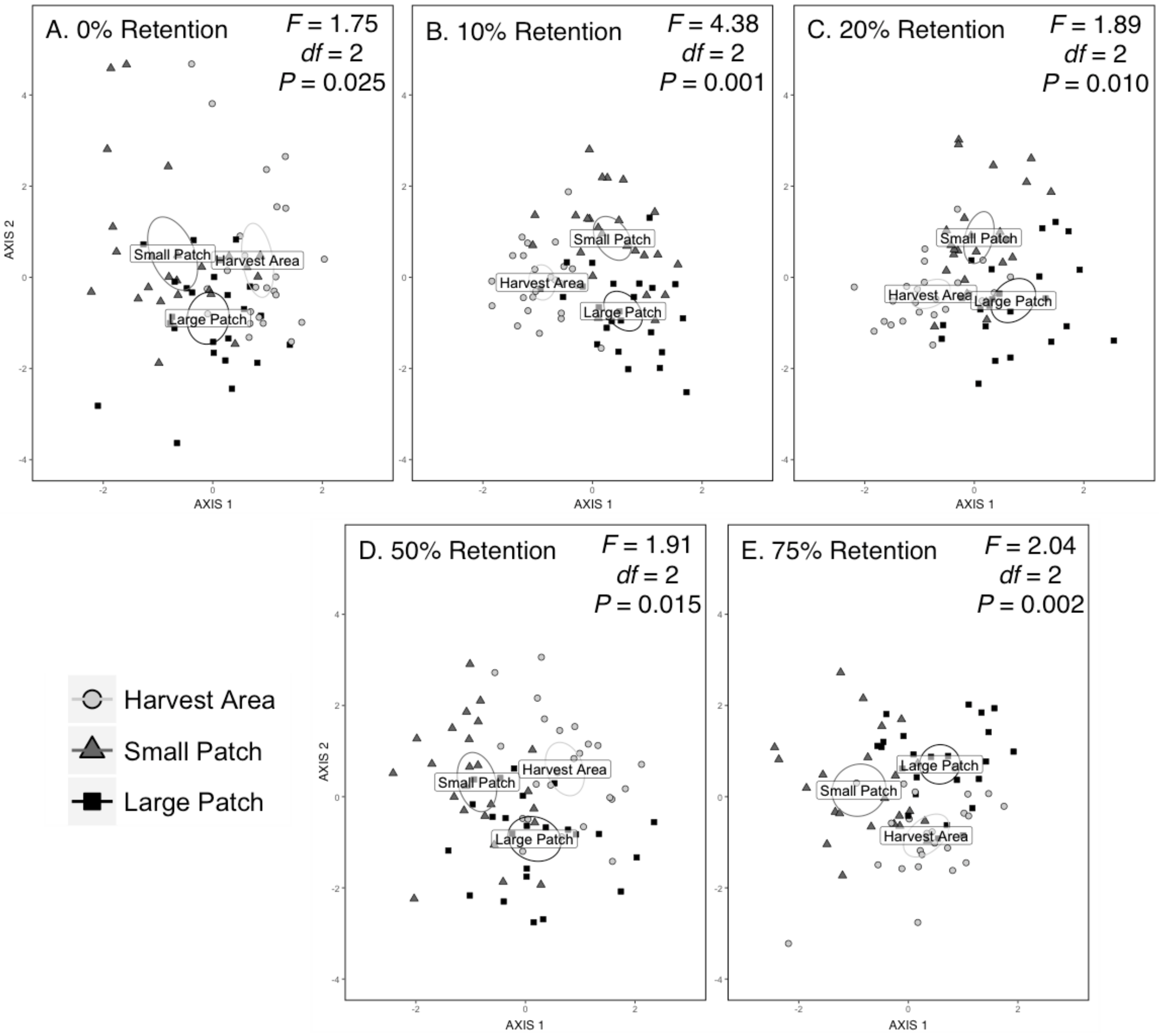

Figure 3.5. Results of distance-based redundancy analyses testing the influence of harvest area, small patch, and large patch on understory vascular plant species composition for: A) 0%, B) 10%, C) 20%, D) 50%, and E) 75% dispersed retention. Each symbol represents the plant community in a 1-m^2 sampling quadrat coded by harvested/unharvested area (harvest area/small patch/large patch). Ellipses show 95% confidence intervals around treatment centroids.

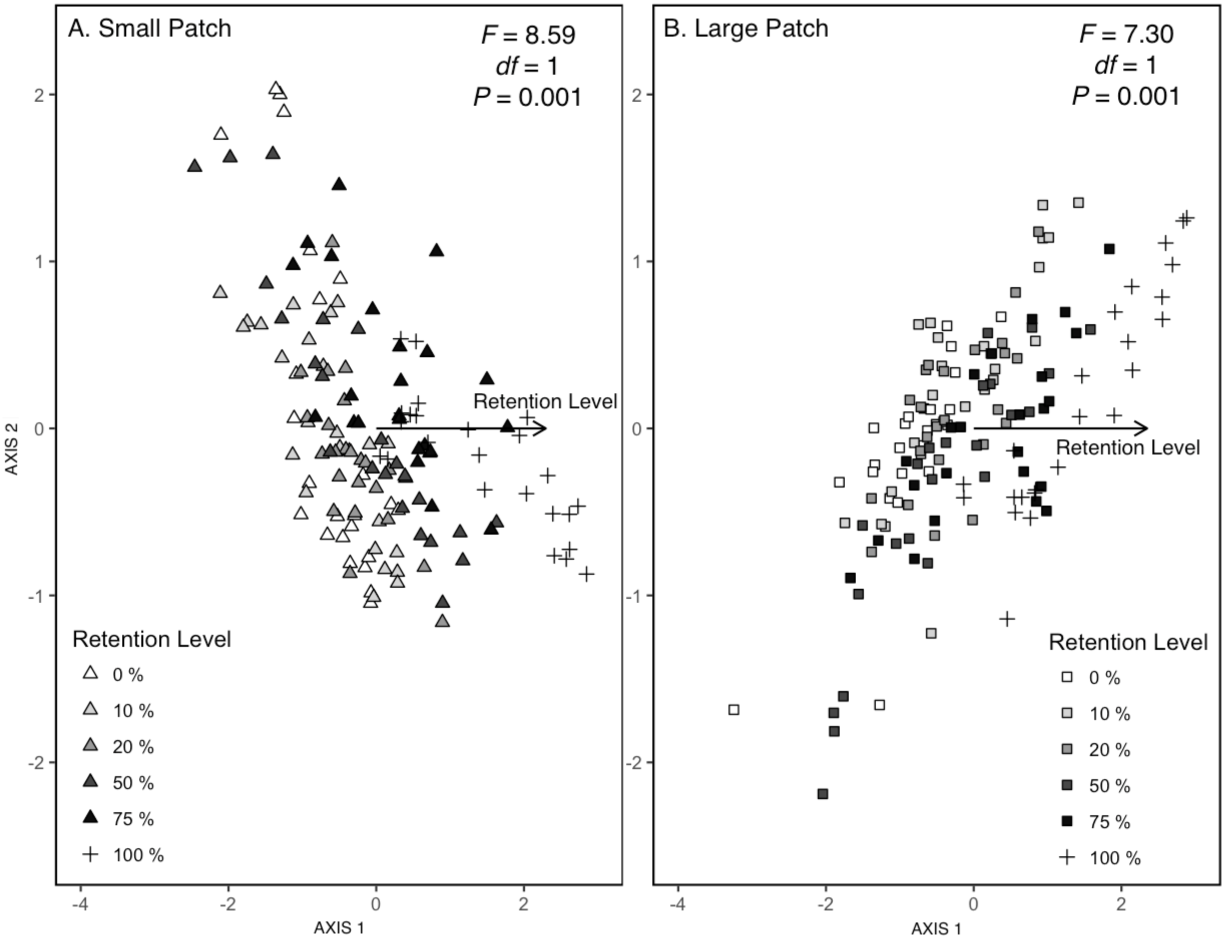

Figure 3.6. Results of distance-based redundancy analyses investigating the influence of surrounding dispersed retention level on A) small patches and B) large patches. Each symbol represents the plant community in a 1-m^2 sampling quadrat coded by retention level (100% = unharvested forest). Vectors indicate the direction of increasing dispersed retention level surrounding retention patches.

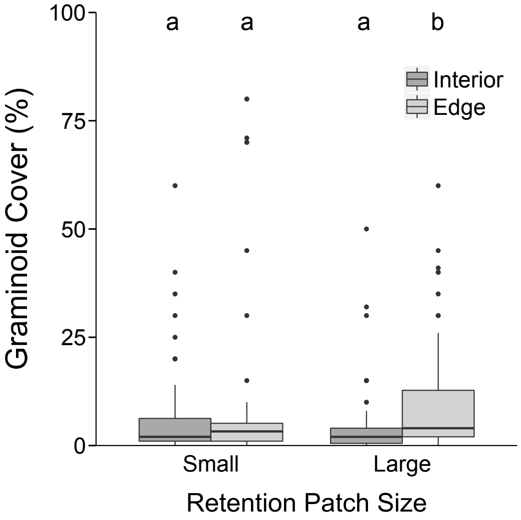

Figure 3.7. Median, 25th, and 75th percentiles of percent graminoid cover in the interior and edge of small and large patches. Dots outside the box-whiskers represent outlier values and different letters represent significant differences (pairwise comparison of least-squares means; $P < 0.05$) between positions within each patch size.

Appendix 3.1. List of vascular plant species identified in sampling quadrats and their six letter codes (see Figure 4B). Nomenclature follows Moss (1983).

Shrubs			
Alnten	*Alnus tenuifolia*	Amealn	*Amelanchier alnifolia*
Ledgro	*Ledum groenlandicum*	Londio	*Lonicera dioica*
Ribgla	*Ribes glandulosum*	Riblac	*Ribes lacustre*
Riboxy	*Ribes oxyacanthoides*	Ribtri	*Ribes triste*
Rosaci	*Rosa acicularis*	Rubida	*Rubus idaeus*
Salbeb	*Salix bebbiana*	Salmyr	*Salix myrtillifolia*
Salunk	*Salix unknown*	Shecan	*Shepherdia canadensis*
Symalb	*Symphoricarpos albus*	Vaccae	*Vaccinium caespitosum*
Vacmyr	*Vaccinium myrtilloides*	Vibedu	*Viburnum edule*
Forbs			
Achmil	*Achillea millefolium*	Actrub	*Actaea rubra*
Adomos	*Adoxa moschatellina*	Aranud	*Aralia nudicaulis*
Arncha	*Arnica chamissonis*	Arncor	*Arnica cordifolia*
Astame	*Astragalus americanus*	Astcil	*Aster ciliolatus*
Astcon	*Aster conspicuus*	Calbul	*Calypso bulbosa*
Ciralp	*Circaea alpina*	Corcan	*Cornus canadensis*
Delgla	*Delphinium glaucum*	Drycar	*Dryopteris carthusiana*
Epiang	*Epilobium angustifolium*	Epipal	*Epilobium palustre*
Equarv	*Equisetum arvense*	Equpra	*Equisetum pratense*
Equsci	*Equisetum scirpoides*	Equsyl	*Equisetum sylvaticum*
Fravir	*Fragaria virginiana*	Galbor	*Galium boreale*
Galtri	*Galium triflorum*	Geoliv	*Geocaulon lividum*
Geumac	*Geum macrophyllum*	Goorep	*Goodyera repens*
Gymdry	*Gymnocarpium dryopteris*	Habobt	*Habenaria obtusata*
Haborb	*Habenaria orbiculata*	Herlan	*Heracleum lanatum*
Latoch	*Lathyrus ochroleucus*	Linbor	*Linnaea borealis*
Lycann	*Lycopodium annotinum*	Lyccom	*Lycopodium complanatum*
Maican	*Maianthemum canadense*	Merpan	*Mertensia paniculata*
Mitnud	*Mitella nuda*	Moelat	*Moehringia lateriflora*
Monuni	*Moneses uniflora*	Petpal	*Petasites palmatus*
Petsag	*Petasites sagittatus*	Pyrasa	*Pyrola asarifolia*
Pyrmin	*Pyrola minor*	Pyrsec	*Pyrola secunda*
Pyrvir	*Pyrola virens*	Rubcha	*Rubus chamaemorus*
Rubpub	*Rubus pubescens*	Spirom	*Spiranthes romanzoffiana*
Stecal	*Stellaria calycantha*	Stecra	*Stellaria crassifolia*
Stelon	*Stellaria longifolia*	Taroff	*Taraxacum officinale*
Trieur	*Trientalis europaea*	Trihyb	*Trifolium hybridum*
Urtdio	*Urtica dioica*	Vacvit	*Vaccinium vitis-idaea*
Vicame	*Vicia americana*	Viocan	*Viola canadensis*
Vioren	*Viola renifolia*		
Graminoids			
Agrsca	*Agrostis scabra*	Agrtra	*Agropyron trachycaulum*
Brocil	*Bromus ciliatus*	Calcan	*Calamagrostis canadensis*
Cardis	*Carex disperma*	Carvag	*Carex vaginata*
Carunk	*Carex unknown*	Elyinn	*Elymus innovatus*
Graunk	*Grass unknown*	Poaunk	*Poa unknown*

Chapter 4: Understory vascular plant responses to retention harvesting with and without prescribed fire

4.1. Abstract

Natural disturbance emulation is increasingly being used in sustainable forestry to mitigate the negative effects of clearcutting on biodiversity. In the boreal forests of western Canada, wildfire is the predominant natural disturbance. Tree retention harvesting is a partial harvesting technique used in sustainable forest management to retain stand structural diversity post-harvest, but does not cause combustion of the forest floor. The application of prescribed burning to areas treated with retention harvesting may emulate the influence of wildfires more effectively than harvesting alone. Here I compared understory vascular plant diversity, abundance, and composition between forest stands subjected to retention harvesting (10% retention) with and without prescribed burning one year, six years, and 11/12 years post-burn. Untreated forest was also included as a reference. Research was conducted in three different boreal forest stand types (conifer-dominated, mixedwood, deciduous-dominated) in northwestern Alberta, Canada. In deciduous-dominated stands, burned areas of dispersed tree retention had higher species richness and greater cover compared to unburned areas of retention. Graminoid cover was higher in the harvest + burn treatment than in either the harvested treatment or unharvested control in mixed and deciduous forest. Effects of harvest with and without burn on richness, cover, and composition were still evident a decade after disturbance. Fire-adapted species benefited most from the prescribed burn treatment. The combination of prescribed burning with retention harvesting could be considered a useful option in forest management that aims to emulate natural disturbance.

4.2. Introduction

Wildfire is the predominant stand-replacing natural disturbance in the boreal forest driving vegetation dynamics (Johnson 1992; Payette 1992). In the boreal forest, the understory vegetation layer hosts the vast majority of plant diversity and plays many important roles in forest ecosystem function (Nilsson and Wardle 2005; De Grandpré et al. 2014). This layer is strongly influenced by fire and many boreal species show adaptations to a disturbance regime dominated by relatively frequent, severe, wildfire (Rowe and Scotter 1973; White 1979). Fire reduces organic layer depth (Greene et al. 2007) and exposes mineral soil, which is an important seedbed for plants (Charron and Greene 2002). Deposition of charcoal (Wardle et al. 1998), addition of nutrients in the form of ash (Noble et al. 1977; Lui et al. 2017), and increases in resource availability (light, soil moisture and nutrients) post-fire are important factors determining early post-fire vegetation dynamics. Plant adaptations to wildfire in the boreal include the ability to survive and resprout after fire; deeply buried, long-lived seed banks; aerial seedbanks (with serotinous cones); and the ability to disperse into recently disturbed sites (Rowe 1983; Greene et al. 1999; Allen 2008; Donato et al. 2009). After wildfire, plant species richness and abundance tends to be high due to rapid establishment of disturbance-adapted species combined with residual species that survived the fire (Lui et al. 2017).

Forest harvesting represents another large-scale disturbance in the boreal forest that has important ecological differences as compared to wildfire (McRae et al. 2001). Burned stands have lower decomposition rates (Wei et al. 1997), but thinner organic layers, higher pH levels, and greater short-term nutrient availability compared to harvested stands (Simard et al. 2001; Rees and Juday 2002; Thiffault et al. 2007).

Further, wildfire creates more coarse woody debris, particularly snags, than does harvesting (McRae et al. 2001; Pedlar et al. 2002). Regeneration patterns post-disturbance differ between wildfire and harvest with the latter supporting fewer pioneer species than post-fire sites where mineral soil is exposed (Nguyen-Xuan et al. 2000). The presence of fire-specialist species contributes to higher species richness in stands subjected to wildfire as compared to logging (Rees and Juday 2002).

Sustainable forest management incorporates, among other things, knowledge of natural disturbance patterns and processes as a basis for approaches to maintain biodiversity following anthropogenic disturbance (Attiwill 1994). Retention harvesting is an approach that aims to emulate natural disturbance by retaining biological legacies and maintaining forest structural diversity (Franklin et al. 1997). Retention harvesting, which involves leaving patches of live, mature trees standing in patches (aggregated retention) or dispersed across the block at time of harvest, has become an increasingly popular component of ecosystem-based forest management (Gustafsson et al. 2012). A minimum of 10% retention has been recommended for ameliorating disturbance effects on understory plant communities (Craig and Macdonald 2009). However, retention harvesting may not adequately emulate the effects of wildfire on understory vegetation, as there is no combustion of the forest floor and no heat to promote germination of fire-adapted species in the seed bank. Combining retention harvesting with prescribed burning could potentially attenuate the ecological differences between harvesting and wildfire.

Early post-fire plant communities are of conservation concern (Kurulok and Macdonald 2007) as stands affected by wildfires are often salvage logged (Nappi et al. 2004; Schmiegelow et al. 2006). Managed forests should contain early-successional forests, which are critical for habitat specialists and disturbance-adapted species (Swanson et al. 2011; Fedrowitz et al. 2014). Prescribed burning after harvest has been suggested as a tool for promoting unique substrates and habitats for fire-specialized species (McRae et al. 2001; Hart and Chen 2006; Vanha-Majamaa et al. 2007; Brassard and Chen 2010; Halpern et al. 2012; Faivre et al. 2016). When combined with aggregated tree retention, prescribed fire promoted the recovery of some plant species with wind-dispersed seeds (Johnson et al. 2014). There are notable differences between aggregated and dispersed retention patterns in terms of their effects on understory vegetation (Lencinas et al. 2011; Chapter 3); the responses of understory plant communities to prescribed burning after dispersed retention harvesting are unknown.

The objective of this study was to document the effects of prescribed burning after dispersed retention harvesting on understory vegetation. Specifically, I compared vascular understory plant diversity, abundance, and composition between forest stands subjected to 10% tree retention harvesting with and without prescribed burn post-harvest. I sampled three different forest cover types pre-harvest and at three separate time periods up to 12 years post-burn. I predicted that plant communities would differ between stands subjected to retention harvesting that were then treated with a prescribed burn versus those that were left unburned. More specifically, I expected understory species richness and abundance to increase with disturbance and for these effects to be greater in stands burned after harvesting because of increased release of resources, creation of a diversity of establishment microsites, and greater opportunities for establishment of fire-adapted species, such as those with deep rhizomes, buried seed banks, or those capable of wind dispersal. I also expected that differences between burned and unburned sites would be greatest immediately after disturbance and that these differences would diminish over time.

4.3. Methods

4.3.1. Study Site

Research was conducted at the large-scale Ecosystem Management Emulating Natural Disturbance (EMEND) experiment located approximately 90 km northwest of Peace River, Alberta, Canada (56° 46’ 13” N, -118° 22’ 28” W). The area was representative of the boreal mixedwood plains. Climate data collected at nearby Eureka River (56° 29’ 00” N, -118° 44’ 00” W) from 1981 to 2010 indicated a mean annual precipitation of 436 mm and mean temperatures of -16.9 °C and 15.0 °C for January and July, respectively (Environment Canada 2017). The study included three different forest stand types based on canopy composition prior to disturbance: 1) conifer-dominated (canopy > 70% coniferous trees); 2) mixed (conifer and deciduous (i.e., broadleaf) each 35%-65% of canopy); and 3) deciduous-dominated (canopy > 70% deciduous trees) (Spence et al. 1999). Cutblocks (~ 10 ha each) were harvested to 10% tree retention in the fall of 2002. Specifically, a standard feller-buncher cut 5-m wide machine corridors with centres spaced 20 m apart. Partial harvesting occurred in the 15-m wide retention strips between the machine corridors with the removal of seven out of every eight trees to obtain 10% level of retention distributed uniformly throughout the cutover area. Logging slash was left on the ground to cure for 1-2.5 years prior to burn treatments. There were four replicate harvested cutblocks for each of the conifer-dominated and mixed forest types and three replicates for deciduous-dominated. Each harvested cutblock was divided into two equal parts (hereafter referred to as ‘compartments’), one of which was burned in October 2003 (conifer-dominated and mixed) or May 2005 (deciduous-dominated), hereafter known as ‘harvest + burn’ treatment. The prescribed burns were low severity ground fires. The other part was left unburned and will hereafter be noted as ‘harvest’ treatment. I also include three replicate unharvested compartments (~10 ha each) per forest type for comparison purposes (hereafter referred to as ‘control’). No appropriate wildfire stands were available for comparison.

4.3.2. Data Collection

Sampling occurred in the summers of 1998 (pre-harvest), 2004 (first growing season post-burn for conifer and mixed forest types only), 2009 (mixed and conifer-dominated stands; sixth growing season post-burn), 2010 (deciduous-dominated stands; sixth growing season post-burn), and 2015 (11th growing season post-burn for deciduous-dominated stands; 12th growing season post-burn for mixed and conifer-dominated stands). Data from 1998, 2004, 2009, and 2010 were collected by EMEND Core Crews. There were six and three randomly distributed sampling points in the control and treated compartments, respectively, except in 2015 when all compartments had six sampling points. At each sampling point, understory vascular plant species presence in a 5 m × 5 m plot was recorded. Tree species were included if they were saplings (≤ 5 cm diameter at breast height; ≥ 10 cm tall). Percent cover was visually estimated for each species of understory vascular plant in embedded 2 m × 2 m quadrats to the nearest 0.5% from 0% to 1%, to the nearest 1% from 1% to 10%, and to the nearest 5% from 10% to 100%. Specimens that could not be identified in the field were collected for identification in the laboratory. Specimens unidentifiable at the species level were identified to genus and treated as species for the purpose of analysis.

4.3.3. Data Analysis

Species richness was expressed as the total number of species per 5 m × 5 m plot. Vascular plant diversity, at the scale of the 2m × 2m quadrat, was calculated using Hill numbers to obtain the effective number of species (Hill 1973). Shannon diversity was considered Hill number of order 1, which is the exponential of Shannon's entropy and weights each species relative to their respective abundance (Jost 2006). Response variables included: vascular plant species richness, diversity, and percent cover (total and by vegetation type: shrubs (including saplings), forbs (including prostrate/trailing woody species), graminoids). Response variables were compared among treatments (harvest + burn, harvest, control) and among years (pre-harvest, 1st post-burn growing season (hereafter noted as '1 year post-burn'), 6th post-burn growing season (hereafter noted as '6 years post-burn), 11th /12th post-burn growing season (hereafter noted as '11/12 years post-burn')) for each forest type separately. Data were analyzed using the R statistics programming environment version 3.2.3 (R Development Core Team 2015).

The mixed-effects models were developed using the *nlme* package (Pinheiro et al. 2014) and included disturbance type (harvest + burn, harvest, control) and time (pre-harvest (1998), one year post-burn (2004), six years post-burn (2009/2010), 11/12 years post-burn (2015)) as categorical fixed independent variables, the interaction between disturbance type and time, and compartment as a random variable to account for the fact that sampling points are sub-samples. Diagnostic plots were used to assess normality and homoscedasticity of the residuals for all of the mixed models. Assumptions of normality were not met for graminoid cover in conifer-dominated forest so those data were log-transformed. When only the treatment effect was significant, pairwise comparisons (α = 0.05) of least-squares means were made between treatments, ignoring time. When the treatment term (α = 0.05) or the interaction between treatment and time terms (α = 0.10) were significant in the mixed-effects models, pairwise comparisons (α = 0.05) of least-squares means were made between treatments for individual time periods separately. These analyses were completed using the *lsmeans* package (Lenth 2016).

To examine the effect of treatment and time on understory species composition, I conducted distance-based redundancy analyses (db-RDA) using the *capscale* function with the Bray-Curtis distance measure (Legendre and Anderson 1999) in the *vegan* package (Oksanen et al. 2017). Species data were represented by percent cover and were Hellinger-transformed (Legendre and Gallagher 2001). The primary matrix of the db-RDA was the species data for each 2-m^2 sampling quadrat while the secondary matrix consisted of treatment (harvest + burn, harvest, control) and time (pre-harvest, one year post-burn, six years post-burn, 11/12 years post-burn) as categorical variables. Compartment was included as a conditional variable. Forest types (conifer-dominated, mixed, deciduous-dominated) were examined separately. Statistical significance of the distance-based redundancy analysis model terms was determined using 999 permutations. I performed additional db-RDAs that examined the differences in species composition between treatments for each sample year post-burn. The *ordiellipse* function was used to add dispersion ellipses (95% confidence regions) based on standard errors of the weighted average of scores around the centroids (Oksanen et al. 2017).

Indicator species analyses were performed with the *indicspecies* package (De Cáceres and Jensen 2016) for individual forest types (conifer-dominated, mixed, deciduous-dominated) to identify species showing an association with specific treatments (harvest + burn, harvest, control) or combinations of treatments. The point biserial correlation coefficient analysis, which uses abundance values (percent cover) to determine the associations between species and disturbance types, was conducted with unlimited grouping variables (De Cáceres 2013). Significant indicator species ($\alpha = 0.05$) were identified after 999 permutations.

4.4. Results

4.4.1. Species richness and abundance

In total, eight sapling, 34 shrub, 115 forb, and 36 graminoid species were found (Appendix 4.1). The interactive effects of treatment and time influenced species richness (not significant for deciduous forest), total cover (marginally significant ($p = 0.057$) for conifer forest), and graminoid cover (Table 4.1). Forb cover was affected by the interaction between disturbance type and time only in mixed forest, while only time had a significant influence on species diversity (not significant for deciduous forest) and shrub cover (Table 4.1; Appendix 4.2).

Species richness in conifer-dominated forest was significantly higher in the harvest + burn than in the control six years and 12 years post-burn while the harvest treatment was intermediate (Figure 4.1A). Species richness in mixed forest was significantly lower in the harvest + burn treatment compared to the control one year post-burn while the harvest treatment was intermediate (Figure 4.1B). By six years and 12 years post-burn, however, species richness was significantly higher in both harvest + burn and harvest stands compared to the control (Figure 4.1B). In deciduous-dominated forest, the harvest + burn compartments had higher species richness than either harvested or the control six and 11 years post-burn; the latter two did not differ from one another (Figure 4.1C).

Total understory plant cover in conifer-dominated forest changed little from pre-harvest to one year post-burn, but had more than doubled by six years after disturbance in both harvest + burn and harvest stands; however, there were no significant differences among treatments (Figure 4.1D). In mixed forest, total cover was significantly lower in the harvest + burn treatment compared to the control one year post-burn while the harvest treatment was intermediate (Figure 4.1E). Total cover in both disturbance treatments increased dramatically from pre-harvest to 12 years post-burn, when cover in either disturbance treatment was significantly higher than the control (Figure 4.1E). Total cover in deciduous-dominated forest six years post-burn was similar in the two disturbance treatments and both were significantly higher as compared to the control (Figure 4.1F). By 11 years post-burn, however, the harvest + burn treatment had significantly higher cover than both the control and harvested forest, which did not differ from one another (Figure 4.1F).

Forb cover in mixed forest 12 years post-burn was significantly higher in the harvest treatment compared to either the control ($p = 0.028$) or the harvest + burn treatment ($p = 0.047$); the latter two did not differ from one another and there were no significant differences among treatments for the other time periods (not shown, see Appendix 4.2). In deciduous-dominated stands, the effect of treatment, but not time or the treatment and time interaction, had a significant effect on forb cover (Table 4.1). Overall, forb cover was significantly higher in the harvest + burn treatment (lsmean = 31.7 ± 2.9% over all sample times) compared to the harvest treatment (lsmean = 24.5 ± 2.7%) (p = 0.033) but there were no significant differences in forb cover between either disturbance treatment and the control (lsmean = 26.4 ± 2.4%).

In conifer forest, graminoid cover was significantly higher in the harvest treatment compared to the harvest + burn treatment and control one year post-burn (Figure 4.1G). By six and 12 years post-burn, graminoid cover did not vary between the two disturbance treatments, but was significantly higher in either disturbance treatment than in the control (Figure 4.1G). In mixed stands, graminoid cover in both harvest + burn and harvest treatments was higher than in the control six and 12 years post-burn; by 12 years post-burn the harvest + burn treatment also had significantly higher graminoid cover compared to the harvest treatment (Figure 4.1H). In deciduous-dominated stands, graminoid cover was significantly higher in the harvest + burn treatment than in either the harvest treatment or control 11 years post-burn (Figure 4.1I).

4.4.2. Community composition and indicator species

There was a significant interactive effect between treatment (harvest + burn, harvest, control) and time on understory plant composition in conifer-dominated and mixed but not in deciduous-dominated stands (Table 4.1; Figure 4.2). For conifer-dominated and mixed forests, the first axis of the distance-based redundancy analyses separated communities in the control and pre-harvest sampling periods on the left from communities in the two disturbance treatments on the right (Figure 4.2). The second axis revealed changes in communities over time as pre-harvest communities were in the middle, one year post-burn communities were towards the upper end of the axis, while six and 12 years post-burn communities were towards the lower end of the axis (Figure 4.2).

Vascular plant community composition differed between treatments (harvest + burn, harvest, control) at all post-burn time periods in all three forest types (based on non-overlapping 95% confidence interval ellipses; Figure 4.3). For all years and forest types, the first axis of the distance-based redundancy analyses separated plant communities between the treatments (harvest, harvest + burn, control) while the second axis separated plant communities between the two disturbance treatments (harvest, harvest + burn) (Figure 4.3).

Indicator species varied among harvest + burn, harvest, and control treatments (Table 4.2). In total, 15, seven, and 22 species were significant indicators for the harvest + burn, harvest, and control treatments, respectively (Table 4.2). Further, seven species were significant indicators of both the harvest and the harvest + burn treatment (Table 4.2). *Geranium bicknellii,* which is a well-known fire specialist species in the boreal, along with other species including *Achillea millefolium*, *Aquilegia brevistyla*, and *Calamagrostis canadensis*, were exclusively indicators of the harvest + burn treatments. Two indicator species of only the harvest treatment in the conifer and mixed forest types were *Actaea rubra* and *Delphinium glaucum*, both of which are associated with moist, open conifer forest. Several disturbance-adapted/early successional species (e.g., *Chamerion angustifolium*, *Populus tremuloides*, and *Petasites frigidus*) were indicators of both harvest + burn and harvest treatments (Table 4.2). Meanwhile, shade-tolerant species such as *Cornus canadensis*, *Goodyera repens*, *Lycopodium annotinum*, *Mertensia paniculata*, and *Pyrola asarifolia* were indicator species for the control (Table 4.2).

4.5. Discussion

My results reveal that the application of prescribed fire after retention harvesting affects understory vascular plant communities immediately post-treatment and that effects are still evident 12 years post-burn. While there was a lag effect of disturbance on species richness and abundance, differences in species composition between burned and unburned forest stands were apparent within one year post-burn. The harvest + burn treatment promoted fire-adapted species supporting the idea that prescribed fire combined with retention harvesting can be a useful management option in forests historically influenced by wildfire.

Species richness and abundance were higher in disturbed treatments compared to the control, which was expected due to increased availability of above- and below-ground resources for understory vegetation that accompanied removal of the canopy (Hart and Chen 2006). Graminoid cover increases post-treatment were an important component of the response of overall cover and this concurs with prior studies of disturbance effects on boreal understory vegetation (Craig and Macdonald 2009; Økland et al. 2016). In mixed and deciduous forests, the harvest + burn treatment resulted in greater increases in graminoid cover than did harvesting alone. For mixed forest, higher graminoid cover and lower forb cover in the harvest + burn treatment versus the harvest treatment could result from competition between the understory plant growth forms (Dwyer 1958). Meanwhile, higher cover for both forbs and graminoids in the harvest + burn treatment compared to the harvest treatment in deciduous forest could be attributed to reduced organic layer depths in burned sites that supported the growth of fire-specialist species (Rees and Juday 2002).

Deciduous forest could have been the only forest type with notable differences in richness and total understory cover between the harvest and the harvest + burn treatments because of differences in the time of prescribed fire application among forest cover types. The conifer-dominated and mixed stands were subjected to prescribed fire one year post-harvest while prescribed fire was applied to the deciduous-dominated stands three years post-harvest. Consequently, greater differences in species richness and cover between the harvest and harvest + burn treatments in deciduous-dominated stands as compared to the other forest cover types could be attributed to the longer elapsed time between the application of the two disturbance treatments in the deciduous-dominated stands. Future studies should apply prescribed fire the same year in all forest cover types to gain a better understanding of comparisons between harvesting treatments with and without prescribed burns in different forest cover types.

High graminoid cover dominated by *Calamagrostis canadensis*, as revealed in the indicator species analysis, in the harvest + burn treatment for mixed and deciduous forest types 11/12 years post-burn could be problematic for forest regeneration. *Calamagrostis canadensis* is a shade-intolerant species (Lieffers and Stadt 1994) that can reduce the number and growth of *P. tremuloides* suckers (Landhäusser and Lieffers 1998; Landhäusser et al. 2007). The growth of conifer tree seedlings could also be hindered by decreased soil temperatures caused by the presence of *Calamagrostis canadensis* (Hogg and Lieffers 1991). Severe fire typically kills belowground rhizomes; however, sprouting

Calamagrostis canadensis can increase in abundance after light burns (Smith and James 1978; Dyrness and Norum 1983). Therefore, *Calamagrostis canadensis* most likely would not be associated with more intense burns that would better mimic wildfire (Lieffers et al. 1993).

Substantial differences in understory community composition between the two disturbance treatments in all three forest types could be attributable to the different effects of the two disturbance types and particularly to the presence of fire-tolerant species, which were indicators of the harvest + burn treatment. Burned stands have higher nutrient availability and thinner humus layers compared to harvested stands (Simard et al. 2001). Rees and Juday (2002) revealed that harvested stands initiate forest succession with more species that characterized the stand pre-harvest while burned stands contain more specialized species. Čugunovs et al. (2017) found that vegetation in sites affected by both harvesting and prescribed burn were more severely disturbed than that in sites subjected only to harvesting.

Indicator species of the harvest + burn treatment included *G. bicknellii*, a fire-specialist that regenerates from buried seed banks (Rowe 1983; Haeussler and Bergeron 2004; Reeves 2007), and *P. frigidus*, which has been associated with forests that were clearcut post-wildfire (Ton and Krawchuk 2016). Other indicator species for burned sites were fire-adapted rhizomatous forbs, such as *A. millefolium* (Merrill et al. 1980; Aleksoff 1999), *Vicia americana* (McLean 1969; Coladonato 1993), and *A. brevistyla* (Ladyman 2006). Graminoids characteristic of burned sites, including *Agrostis scabra* and *Calamagrostis canadensis*, were shade-intolerant species with wind-disseminated seeds (Rowe 1983). Meanwhile, indicator species exclusive to the harvest treatment were fewer than those exclusive to the burn treatment and included *A. rubra* and *D. glaucum*, which prosper in moist, open areas (Moss 1983). *C. angustifolium*, an indicator species of both disturbance treatments, was previously found to be associated with aggregated retention harvesting followed by prescribed burn (Johnson et al. 2014). Similar to my study, Pidgen and Mallik (2013) found indicator plants for prescribed burns post-clearcut to be early successional ruderals with wind-dispersed seeds and/or seedbanks. Indicator plants for prescribed burned sites in my study were characteristic of those that persist after wildfire (Donato et al. 2009).

Responses of vascular plants to disturbance varied with time, which was expected since recovery over time is an important factor influencing plant communities affected by wildfire (Lui et al. 2017). I expected, but did not find, an initial increase in species richness and abundance one year post-burn, but the effects of disturbance on species composition were immediate. During the first year post-burn, the replacement of shade-tolerant species with shade-intolerant species could have masked the differences in species richness and cover compared to those pre-harvest. For instance, Lindholm and Vasander (1987) found species richness to be lowest immediately after prescribed burning and to increase post-burn for 15 years. Another study found no differences in species richness between clearcut with prescribed burn, clearcut, and wildfire more than 15 years after disturbance (Pidgen and Mallik 2013). In my study, species richness in both disturbance types had started to decline by 11/12 years post-burn, yet cover was still increasing (mixed and deciduous forest) despite substantial regrowth of deciduous tree species and differences in understory plant community composition were still quite apparent at that time. Indicator species changed from a fire-specialist that regenerates from buried seed banks immediately after the burn to fire-adapted rhizomatous forbs and graminoids with wind-dispersed seeds. Over time, I expect the cover of shade-intolerant forbs and graminoids to decrease, similar to the typical progression of forest succession after wildfire (Rees and Juday 2002; Lui et al. 2017).

The prescribed burns under investigation were low severity ground fires applied to areas that had been harvested to a relatively low retention level. I would expect greater differences in understory vegetation between the harvested sites with and without prescribed burns if the fires were more severe since vegetation dynamics are known to be strongly affected by burn severity (Schimmel and Granström 1996; Whittle et al. 1997; Ryan 2002; Lecomte et al. 2005; Wang and Kemball 2005). If the prescribed burns had been more severe and consequently consumed more of the forest floor, plants with buried viable seeds may not have been as abundant post-fire. When combined with retention harvests, effects of prescribed fire on vegetation dynamics also depend on retention level (Heikkala et al. 2014; Johnson et al. 2014). At higher retention levels, I would expect greater abundance of shade-tolerant species characteristic of intact forest (Johnson et al. 2014).

In conclusion, my findings suggest that the application of prescribed burns after retention harvests could potentially be used in boreal forest management to increase the ecological value of retention harvesting by creating conditions that are favourable for fire-adapted species. Stronger effects of the harvest + burn treatment than retention harvesting alone on richness (deciduous forest), total understory cover (deciduous forest), and graminoid cover (mixed and deciduous forest) suggests there were synergistic effects resulting from compounding disturbances (Paine et al. 1998; Pidgen and Mallik 2013).

The harvest + burn treatment was associated with the presence of plant species that have traits adapted to thrive after wildfire, the major natural disturbance in boreal forest. Retention harvesting could therefore better emulate the effects of wildfire on understory vascular plant communities when combined with prescribed burns. However, the dominance of *Calamagrostis canadensis* in harvest + burn treatments could be a concern, especially to forestry companies relying on tree species regeneration. Prescribed fire does not entirely emulate wildfire (Pastro et al. 2011) and future research should directly compare the effects of wildfire and prescribed burns on understory plants. Early-successional plant communities play important ecological roles and thus should be maintained (Swanson et al. 2011; Fedrowitz et al. 2014); the application of prescribed fire post-retention harvest could be a beneficial option for sustainable forest management.

4.6. Literature cited

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Table 4.1. Results of mixed models [F values (*F*), degrees of freedom (*df*), and *P* values (*P*)] examining the influence of treatment (harvest + burn, harvest, control), time (pre-harvest, one year post-burn, six years post-burn, 11/12 years post-burn), and treatment × time interaction on understory vegetation. *P* values in bold were considered significant (individual terms: α = 0.05; interaction between terms: α = 0.10).

	Forest type[1]	Treatment			Time			Treatment × Time		
		F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Richness	CD	1.33	2	0.268	**29.56**	**3**	**< 0.001**	**3.30**	**6**	**0.004**
	MX	1.19	2	0.307	**55.39**	**3**	**< 0.001**	**7.57**	**6**	**< 0.001**
	DD	**13.07**	**2**	**< 0.001**	**8.14**	**2**	**< 0.001**	1.60	4	0.179
Diversity	CD	1.08	2	0.344	**10.57**	**3**	**< 0.001**	0.91	6	0.487
	MX	0.50	2	0.607	**9.01**	**3**	**< 0.001**	0.27	6	0.952
	DD	1.55	2	0.217	0.49	2	0.608	0.70	4	0.593
Total cover	CD	0.90	2	0.409	**38.21**	**3**	**< 0.001**	**2.09**	**6**	**0.057**
	MX	1.45	2	0.238	**71.49**	**3**	**< 0.001**	**7.92**	**6**	**< 0.001**
	DD	**14.87**	**2**	**< 0.001**	**46.20**	**2**	**< 0.001**	**5.28**	**4**	**< 0.001**
Shrub cover	CD	0.05	2	0.952	**11.33**	**3**	**< 0.001**	1.33	6	0.249
	MX	0.82	2	0.443	**20.70**	**3**	**< 0.001**	1.25	6	0.283
	DD	1.22	2	0.299	**23.93**	**2**	**< 0.001**	1.98	4	0.103
Forb cover	CD	0.25	2	0.776	**19.84**	**3**	**< 0.001**	0.08	6	0.998
	MX	1.04	2	0.355	**27.24**	**3**	**< 0.001**	**3.16**	**6**	**0.006**
	DD	**4.36**	**2**	**0.015**	2.69	2	0.072	0.41	4	0.799
Graminoid cover	CD*	**7.30**	**2**	**0.001**	**21.11**	**3**	**< 0.001**	**3.59**	**6**	**0.002**
(*log-transformed)	MX	**10.77**	**2**	**< 0.001**	**21.20**	**3**	**< 0.001**	**5.18**	**6**	**< 0.001**
	DD	**6.60**	**2**	**0.002**	**9.29**	**2**	**< 0.001**	**2.56**	**4**	**0.043**
Composition	CD	**12.61**	**2**	**0.001**	**4.48**	**3**	**0.001**	**1.44**	**6**	**0.012**
	MX	**7.90**	**2**	**0.001**	**4.71**	**3**	**0.001**	**1.788**	**6**	**0.001**
	DD	**4.53**	**2**	**0.001**	**4.13**	**2**	**0.001**	1.02	4	0.407

[1] Forest type based on canopy composition prior to disturbance: CD = conifer-dominated (canopy > 70% coniferous trees); MX = mixed (conifer and deciduous (i.e., broadleaf) each 35%-65% of canopy); and DD = deciduous-dominated (canopy > 70% deciduous trees)

Table 4.2. Results of indicator species analysis (correlation coefficients of indicator species) for different forest types (conifer-dominated, mixed, deciduous-dominated) and number of years post-burn (one year, six years, 11/12 years). Only species with $P < 0.05$ in at least one forest type and time period are listed ('-' = not significant).

	Conifer			Mixed			Deciduous	
	1	6	12	1	6	12	6	11
Harvest + Burn								
Achillea millefolium	-	0.44	0.45	-	-	-	-	-
Agrostis scabra	-	0.28	-	-	-	-	-	-
Aquilegia brevistyla	-	-	-	-	-	-	-	0.39
Arnica cordifolia	-	-	-	-	0.34	-	-	-
Calamagrostis canadensis	-	-	-	-	-	0.41	-	0.49
Chamerion angustifolium	-	-	-	-	-	-	-	0.34
Eurybia conspicua	-	-	-	-	-	-	0.38	-
Geranium bicknellii	0.40	-	-	-	-	-	-	-
Petasites frigidus	0.42	-	-	-	-	-	-	-
Ribes oxyacanthoides	-	-	-	-	0.32	0.28	-	-
Rubus idaeus	-	-	-	-	0.37	-	-	-
Symphyotrichum ciliolatum	-	-	0.31	-	-	0.33	-	-
Taraxacum officinale	-	0.51	0.54	-	-	-	-	-
Trifolium hybridum	-	-	-	-	-	0.34	-	-
Vicia americana	-	0.54	0.58	-	-	0.47	-	-
Harvest								
Actaea rubra	-	0.26	-	0.35	0.35	-	-	-
Delphinium glaucum	-	-	0.33	0.37	-	-	-	-
Epilobium ciliatum	0.45	-	-	-	-	-	-	-
Heracleum maximum	-	-	-	-	-	-	0.43	-
Linnaea borealis	-	-	-	-	-	0.34	-	-
Petasites frigidus	-	0.38	-	-	-	-	-	-
Populus tremuloides	-	-	-	0.42	-	-	-	-
Harvest + Burn/Harvest								
Chamerion angustifolium	-	0.51	0.47	-	0.42	0.47	-	-
Fragaria virginiana	-	-	-	-	-	0.32	-	-
Lathyrus ochroleucus	-	-	-	-	-	0.32	-	-
Leymus innovatus	-	-	-	-	-	0.36	-	-
Petasites frigidus	-	-	-	-	-	0.38	-	-
Populus tremuloides	-	-	-	-	0.39	-	-	-
Symphyotrichum ciliolatum	-	-	-	-	0.38	-	-	-
Control								
Alnus viridis	-	-	-	-	0.39	0.38	-	0.30
Aralia nudicaulis	-	-	-	0.39	0.40	0.42	-	-
Arnica cordifolia	-	-	-	-	-	-	-	0.32
Circaea alpina	-	-	0.34	-	-	-	-	-
Cornus canadensis	0.51	0.54	0.51	0.56	0.48	0.46	-	-

Equisetum arvense	0.37	0.36	-	-	-	-	-	-
Equisetum pratense	-	-	0.31	-	-	-	-	-
Goodyera repens	-	-	0.45	0.45	0.40	0.45	-	-
Ledum groenlandicum	-	0.33	0.29	-	-	-	-	-
Linnaea borealis	0.51	0.33	-	0.46	-	-	-	-
Lycopodium annotinum	-	-	-	0.37	0.33	0.34	-	-
Mertensia paniculata	-	0.35	0.30	-	-	-	0.49	-
Mitella nuda	-	-	0.35	-	-	-	-	-
Moneses uniflora	-	-	0.33	-	-	-	-	-
Orthilia secunda	-	-	-	0.55	-	-	-	-
Osmorhiza depauperata	-	-	-	-	-	-	0.44	-
Pyrola asarifolia	-	-	-	0.36	-	-	-	0.38
Rosa acicularis	0.49	-	-	0.39	-	-	-	-
Vaccinium cespitosum	-	-	-	0.40	-	-	-	-
Vaccinium vitis-idaea	-	0.31	0.38	-	-	-	-	-
Viburnum edule	-	-	-	0.42	-	-	-	-
Viola renifolia	-	-	-	0.43	0.40	-	-	-

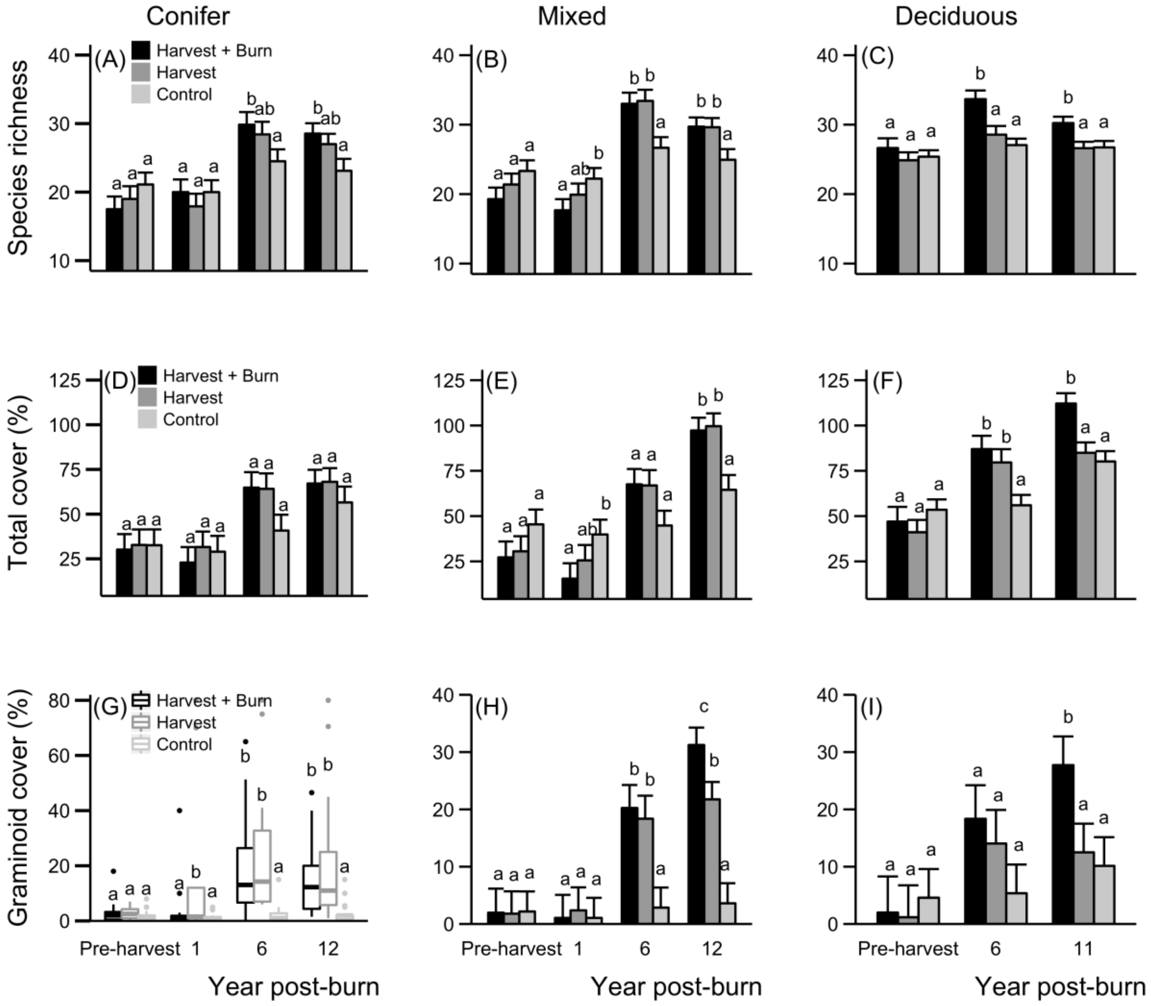

Figure 4.1. Least-square means ± SE of: species richness (A-C), total cover (D-F), and graminoid cover (H-I) in conifer-dominated (A, D), mixed (B, E, H), and deciduous-dominated (C, F, I) forest types, and median, 25th, and 75th percentiles of graminoid cover in conifer-dominated forest (G) for different treatments (harvest + burn, harvest, control) pre-harvest, one year, six years, and 11/12 years post-burn. G) Dots outside the box-whiskers represent outlier values. Means with different letters are significantly different within a given time period (pairwise comparison of least-squares means; $P < 0.05$).

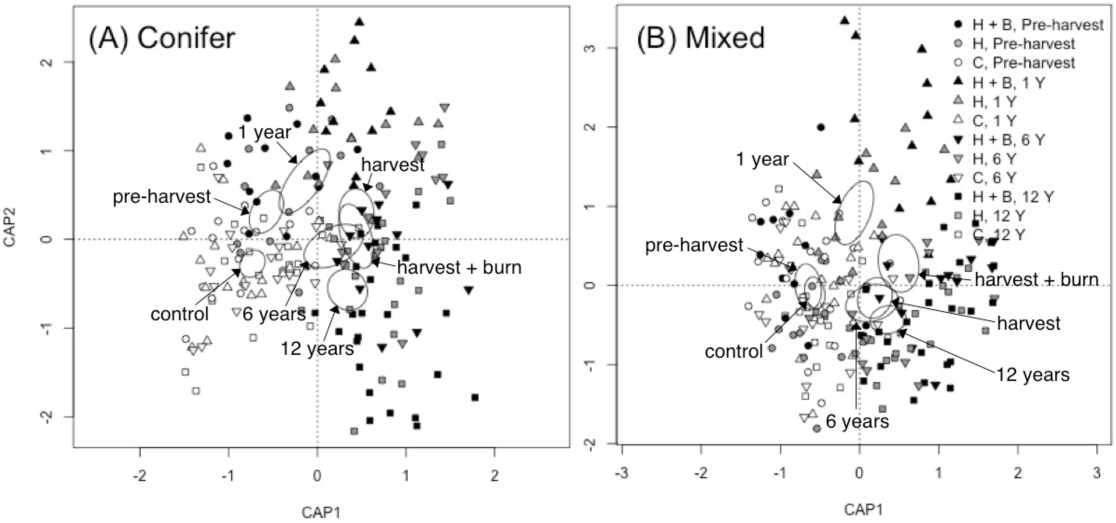

Figure 4.2. Results of distance-based redundancy analysis for the influence of the interaction between disturbance type (H + B = harvest + burn, H = harvest, C = control) and time (pre-harvest, 1 Y = one year post-burn, 6 Y = six years post-burn, 12 Y = 12 years post-burn) on understory vascular plant species composition for (A) conifer-dominated and (B) mixed forests. Ellipses represent 95% confidence intervals.

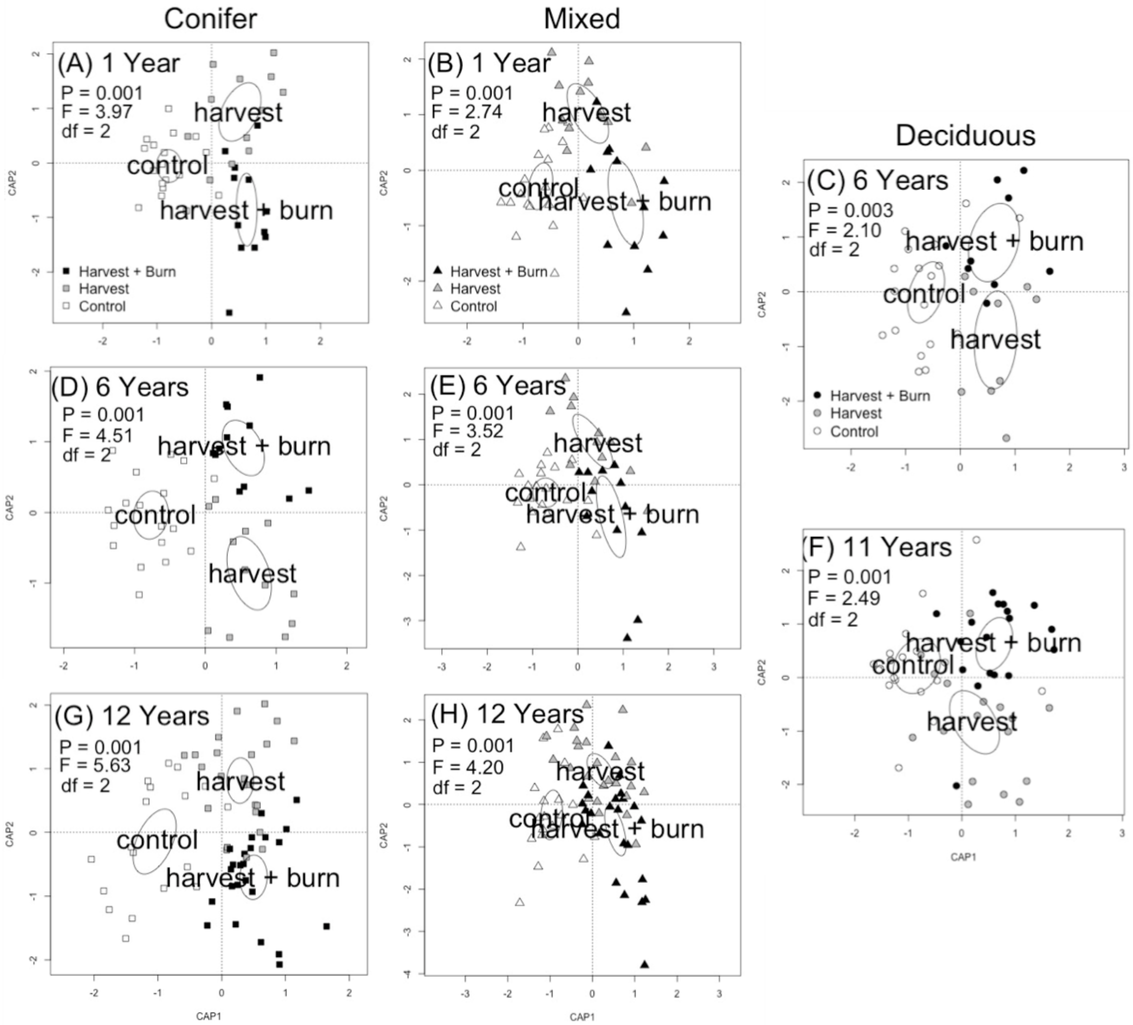

Figure 4.3. Results of distance-based redundancy analysis testing the influence of disturbance type (harvest + burn, harvest, control) on understory vascular plant species composition one year, six years, and 11/12 years post-burn. Ellipses represent 95% confidence intervals for the different treatments (harvest + burn, harvest, control).

Appendix 4.1. List of vascular plant species identified in sampling plots. Nomenclature follows USDA, NRCS (2017).

Saplings

Abies balsamea
Betula papyrifera
Larix laricina
Picea glauca
Picea mariana
Pinus contorta
Populus balsamifera
Populus tremuloides

Shrubs

Alnus incana
Alnus viridis
Amelanchier alnifolia
Betula occidentalis
Betula pumila
Betula sp.
Cornus sericea
Ledum groenlandicum
Lonicera dioica
Ribes glandulosum
Ribes hudsonianum
Ribes lacustre
Ribes oxyacanthoides
Ribes triste
Ribes sp.
Rosa acicularis
Rubus idaeus
Salix arbusculoides
Salix bebbiana
Salix discolor
Salix maccalliana
Salix myrtillifolia
Salix petiolaris
Salix planifolia
Salix pseudomonticola
Salix pyrifolia
Salix scouleriana
Salix sp.
Shepherdia canadensis
Shrub unknown
Sorbus scopulina
Symphoricarpos albus
Vaccinium cespitosum
Viburnum edule

Forbs

Achillea alpina
Achillea millefolium
Actaea rubra
Adoxa moschatellina
Aquilegia brevistyla
Aralia nudicaulis
Arctostaphylos uva-ursi
Arnica chamissonis
Arnica cordifolia
Aster unknown
Astragalus alpinus
Astragalus americanus
Botrychium virginianum
Botrychium sp.
Calypso bulbosa
Cardamine pensylvanica
Carum carvi
Chamerion angustifolium
Chrysosplenium alternifolium
Circaea alpina
Cirsium arvense
Coptis trifolia
Corallorhiza maculata
Corallorhiza trifida
Cornus canadensis
Corydalis aurea
Crepis tectorum
Cystopteris fragilis
Dactylorhiza viridis
Delphinium glaucum
Dracocephalum parviflorum
Dryopteris carthusiana
Epilobium ciliatum
Epilobium palustre
Epilobium sp.
Equisetum arvense
Equisetum pratense
Equisetum scirpoides
Equisetum sylvaticum
Eurybia conspicua
Forb unknown
Fragaria vesca
Fragaria virginiana
Galium boreale
Galium trifidum
Galium triflorum
Gentianella amarella
Geocaulon lividum
Geranium bicknellii
Geum aleppicum
Geum macrophyllum
Goodyera repens
Gymnocarpium dryopteris
Halenia deflexa
Heracleum maximum
Hieracium umbellatum
Impatiens noli-tangere
Lathyrus ochroleucus
Lathyrus venosus
Linnaea borealis
Lycopodium annotinum
Lycopodium complanatum
Maianthemum canadense
Maianthemum trifolium
Mentha arvensis
Mertensia paniculata
Mitella nuda
Moehringia lateriflora
Moneses uniflora
Orthilia secunda
Osmorhiza depauperata
Packera indecora
Packera paupercula
Parnassia palustris
Pedicularis labradorica

Petasites frigidus	*Phacelia franklinii*	*Plantago major*
Platanthera huronensis	*Platanthera obtusata*	*Platanthera orbiculata*
Polemonium acutiflorum	*Polygonum arenastrum*	*Potentilla norvegica*
Prosartes trachycarpa	*Pyrola asarifolia*	*Pyrola chlorantha*
Ranunculus abortivus	*Ranunculus sceleratus*	*Rhinanthus minor*
Rubus arcticus	*Rubus pubescens*	*Rumex aquaticus*
Senecio vulgaris	*Solidago canadensis*	*Spiranthes romanzoffiana*
Stellaria calycantha	*Stellaria crassifolia*	*Stellaria longifolia*
Symphyotrichum ciliolatum	*Symphyotrichum puniceum*	*Taraxacum officinale*
Thalictrum sparsiflorum	*Thalictrum venulosum*	*Trientalis borealis*
Trientalis europaea	*Trifolium hybridum*	*Trifolium pratense*
Urtica dioica	*Vaccinium vitis-idaea*	*Vicia americana*
Viola adunca	*Viola canadensis*	*Viola palustris*
Viola renifolia		
Graminoids		
Agrostis scabra	*Alopecurus pratensis*	*Beckmannia syzigachne*
Bromus ciliatus	*Bromus inermis*	*Calamagrostis canadensis*
Carex aquatilis	*Carex aurea*	*Carex brunnescens*
Carex canescens	*Carex concinna*	*Carex deweyana*
Carex disperma	*Carex interior*	*Carex norvegica*
Carex peckii	*Carex praticola*	*Carex raymondii*
Carex sect. Montanae	*Carex siccata*	*Carex sp.*
Carex vaginata	*Cinna latifolia*	*Elymus sp.*
Elymus trachycaulus	*Grass unknown*	*Hordeum jubatum*
Juncus bufonius	*Leymus innovatus*	*Luzula multiflora*
Phleum pratense	*Poa palustris*	*Poa pratensis*
Poa sp.	*Schizachne purpurascens*	*Trisetum spicatum*

Appendix 4.2. Least-square means (SE) of species diversity, shrub cover, and forb cover pre-harvest, one year post-burn, six years post-burn, and 11/12 years post-burn for conifer-dominated (n = 4), mixed (n = 4), and deciduous-dominated (n = 3) forest cover types in three different treatments (H + B = harvest + burn; H = harvest; C = control).

	Conifer-dominated			Mixed			Deciduous-dominated		
	Species diversity	Shrub cover (%)	Forb cover (%)	Species diversity	Shrub cover (%)	Forb cover (%)	Species diversity	Shrub cover (%)	Forb cover (%)
Pre-harvest									
H + B	7.1 (1.0)	9.5 (3.2)	16.8 (5.7)	7.8 (0.9)	8.3 (5.7)	16.5 (5.0)	10.6 (1.1)	20.5 (6.4)	24.5 (5.3)
H	8.1 (1.0)	13.7 (3.2)	16.4 (5.7)	8.1 (0.9)	13.8 (5.4)	15.4 (4.7)	8.8 (0.9)	18.3 (5.4)	21.6 (4.3)
C	7.0 (0.9)	11.4 (2.9)	19.3 (5.7)	8.7 (0.8)	16.9 (5.4)	26.4 (4.5)	9.5 (0.8)	24.8 (4.6)	24.1 (3.5)
1 year post-burn									
H + B	6.6 (1.0)	5.3 (3.2)	12.7 (5.7)	6.0 (0.9)	4.6 (5.5)	9.9 (4.8)	-	-	-
H	7.3 (1.0)	6.6 (3.2)	9.7 (5.7)	7.1 (0.9)	9.5 (5.5)	13.7 (4.8)	-	-	-
C	6.4 (0.9)	11.7 (2.9)	16.2 (5.7)	7.8 (0.8)	16.9 (5.4)	21.9 (4.5)	-	-	-
6 years post-burn									
H + B	7.9 (1.0)	18.5 (3.2)	25.2 (5.7)	8.4 (0.9)	19.5 (5.5)	27.7 (4.8)	9.8 (1.0)	35.5 (5.8)	33.1 (4.7)
H	7.2 (1.0)	15.6 (3.2)	22.1 (5.7)	8.1 (0.9)	19.5 (5.5)	29.1 (4.8)	7.9 (1.0)	39.8 (5.8)	25.8 (4.7)
C	8.0 (0.9)	12.9 (2.9)	25.7 (5.7)	8.6 (0.8)	15.0 (5.4)	27.0 (4.5)	10.1 (0.8)	24.4 (4.6)	26.2 (3.5)
11 (deciduous-dominated) or 12 (conifer-dominated, mixed) years post-burn									
H + B	11.2 (0.8)	19.6 (2.5)	33.1 (4.9)	9.4 (0.7)	29.1 (4.7)	36.9 (3.9)	8.8 (0.8)	46.9 (4.6)	37.5 (3.5)
H	9.8 (0.8)	17.4 (2.5)	31.8 (4.9)	9.9 (0.7)	33.0 (4.7)	44.9 (3.9)	8.6 (0.8)	46.3 (4.6)	26.1 (3.5)
C	8.8 (0.9)	19.1 (2.9)	34.5 (5.7)	10.1 (0.8)	29.2 (5.4)	31.7 (4.5)	9.4 (0.8)	41.0 (4.6)	29.0 (3.5)

Chapter 5: General conclusions

5.1. Summary of findings

The research presented in this thesis provides insights into the effects of different retention harvesting practices on wildlife and understory vascular plants up to 18 years post-harvest. Overall findings conform to a growing body of literature that supports the use of retention harvests as alternatives to clearcuts. Responses of common wildlife and understory vascular plants to retention harvesting, as examined by different retention levels, patterns, and prescribed fire as a post-harvest practice, varied by species and forest cover. These results contribute to a better understanding of the harvesting effects on the biota with the goal of informing the development of effective forest management practices for biodiversity conservation.

Research in Chapter 2 demonstrated that wildlife responses to different retention levels were species-specific and reflected individual habitat requirements. Results provide evidence for the value of retention harvesting when compared to traditional clearcuts with use of retention blocks for nearly half of the species investigated increasing with increasing levels of retention. In contrast to species that increased with retention level, two species declined with increasing retention level illustrating the importance of early-seral habitat for these species and predators that may rely on them. Here I demonstrate that the effects of retention level on wildlife were still evident more than 15 years post-harvest, but these effects are likely to change as the forest matures.

In addition to dispersed retention, spatial patterns of retention 15 years post-harvest were also examined for vascular plants. Chapter 3 demonstrated that dispersed retention benefitted early-seral plants, while aggregated patch retention favoured more late-seral plants characteristic of unharvested forest. Most importantly, results demonstrated that retention patches more effectively supported understory vascular plant communities when surrounded by increased levels of dispersed retention. Different patch sizes (0.46 ha and 0.20 ha) supported distinct plant communities. These findings demonstrate the value of combining both dispersed retention and patch retention using variable patch sizes in a harvested landscape to promote understory vascular plant diversity.

Research in Chapter 4 considered the ecological value of prescribed fire as a post-harvest management tool. The temporal component of this study was critical to evaluating changes in understory vascular plant communities from pre-harvest conditions to up to 12 years post-burn. There were differences in post-harvest plant communities with and without prescribed fire and among different forest types. For example, *Geranium bicknellii*, a fire-specialist was an indicator species for conifer-dominated forest immediately post-harvest, but was never an indicator of the mixedwood and deciduous-dominated forest. All burned forest types contained fire-adapted plants, which suggests that prescribed fire could better emulate wildfire than retention harvesting alone. Thus, the combination of retention harvesting and prescribed fire could be an effective strategy in natural disturbance emulation.

5.2. Management implications

My findings reveal the challenge in choosing an optimum retention level for biodiversity conservation as responses to retention level varied by species. Late-seral mammals were detected in retention harvest levels as low as 20%, but detections increased substantially in stands harvested to ≥ 50%. Early-seral species preferred levels lower than 50% retention. Thus, retention levels between 20% and 50% could benefit both early- and late-seral species. Variability in retention levels across the harvested landscape would benefit species with different habitat requirements. All successional stages have ecological value that should be considered in harvest designs.

The research presented in Chapter 3 reveals the ecological value of combining retention patterns in a single cutblock. Instead of surrounding retention patches with clearcut, whereby the negative effects of the clearcut negate the positive effects of the retention patch, retention patches could be surrounded by dispersed retention. The size of retention patch will depend on the size of the cutblock. Nevertheless, my results demonstrated that retention patches as small as 0.20 ha support late-seral species 15 years post-harvest. Thus, it is probably better to retain at least a small patch of trees instead of leaving no trees when feasible.

There are many challenges associated with the integration of biodiversity conservation with timber production in management objectives. Although my results suggest prescribed fire as a potential post-harvest management tool beneficial for fire-adapted plant species, I recognize that post-harvesting practices, such as prescribed fire, involve many considerations that were beyond the scope of this study. For example, controlled burns require appropriate weather conditions and fuel loads. The feasibility of incorporating controlled burns into management plans may also depend on financial costs incurred by the forestry companies. Cost-benefit analyses for all of the retention harvesting methods examined in this thesis are required to determine cost-efficiency associated with the implementation of biodiversity conservation objectives in forest management.

Given a fixed area of land, is it better to harvest a single large area to a low retention level and leave a single large tract of land unharvested or is it better to have a mosaic of small areas harvested to a range of retention levels (0% – 100%)? The former method could result in less fragmentation and disturbance caused by roads while the latter enables habitat variability across the landscape. Economic costs, landscape characteristics, and management objectives will ultimately dictate harvesting plans. Future research is required to determine appropriate retention prescriptions that meet societal objectives for maintaining economic, social, and ecological values.

5.3. Future research

Future studies should make direct comparisons of wildlife and vascular plant responses between retention harvesting and wildfire. In recognition of the complexity of wildfire processes, additional research could also consider varying prescribed burn severities. Such studies will give us a better understanding of the similarities and differences between the effects of wildfire and prescribed fire on biota to ultimately determine the effectiveness of prescribed burns at emulating wildfire.

More research is needed on elusive, threatened, or endangered species. Using a combination of midden counts, scat surveys, and camera trapping with a general scent lure, I was not deliberately excluding any wildlife species; however, I recognize that more elusive or uncommon species, such as the cougar (*Felis concolor*), were missing. Future studies should use field methods targeted for specific species, such as the use of radiotelemetry on an individual species, to collect habitat use and behaviour data on species difficult to study. Alternatively, researchers could consider camera traps with more elaborate baiting stations that target a particular species instead of using camera traps with a general scent. In addition to specific taxa, future research should also consider the effects of retention harvesting practices on ecological functions and direct plant-mammal interactions (e.g., herbivory, predator-prey dynamics).

The shortage of long-term studies on retention harvesting is understandable considering retention forestry emerged within the last four decades. My research provides relatively long-term findings compared to previous studies, but future research will be able to more easily study the effects of retention harvesting over longer time periods. Such research will be critical for enhanced knowledge of the temporal dynamics associated with retention harvesting.

Collaborations are necessary for effective implementation of research findings in harvesting practices and policies. I was fortunate to collaborate with the federal and provincial governments, forestry companies, as well as academic colleagues throughout the progression of my research project. Discussions provided valuable insight into my research questions and the feasibility of incorporating my research findings into harvest designs. I encourage future researchers to engage in such collaborations to foster innovation and improvement in forest harvesting. As research on retention forestry continues, adaptive management enables research findings to materialize into optimal harvesting guidelines for sustainable forest management that prioritizes the conservation of flora and fauna.

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