Effects of variable retention harvesting on ground-layer plant communities and natural regeneration in *Pinus resinosa* (red pine) forests in northern Minnesota, USA

A THESIS SUBMITTED TO THE FACULTY OF
UNIVERSITY OF MINNESOTA
BY

Margaret W. Roberts

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE

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August 2015

Acknowledgements

Working on this thesis has been a truly great opportunity because of the colleagues, family and friends who have supported me along the way. It would not have been possible without them. My graduate advisors, Drs. Anthony D'Amato and Christel Kern, entertained my questions with endless patience. Tony, thank you for always encouraging my questions and being dedicated to my success. Christel, thank you for your continued support and for always making me feel welcome in Grand Rapids. Both of you have helped me become a vastly improved researcher, writer and scientist. I have gained so much working with both of you on this project, and your input has made this work something I am truly proud of. I also want to thank my committee members, Drs. Brian Palik and Meredith Cornett, for your insight on this project and advice along the way.

This work is built upon the efforts of so many people, and I am thankful to have the opportunity to benefit from the foresight of researchers who appreciated the complex questions that are difficult, if not impossible, to answer without long term data. In particular, Brian Palik was instrumental in the design of the Red Pine Retention Study. I also want to thank everyone at the Chippewa National Forest for their contributions to the implementation of the study as well as the many people involved with the USFS Northern Research Station. Sawyer Scherer and Louise Potter worked with me over my first summer in Minnesota, and were patient as I learned the native species and the best way to combat mosquitoes.

A big thank you goes out to the University of Minnesota Silviculture and Applied Forest Ecology Lab. Lab meetings allowed me to learn from and interact with great students, faculty, and projects. In particular, Miranda Curzon, Sawyer Scherer, Jason Reinhardt, and Kyle Gill have been such a great sounding board for my ideas, questions about statistics, and life in general.

I am indebted to the University of Minnesota Natural Resources Science and Management (NRSM) graduate program, and particularly The Department of Forest Resources for awarding me the Hugo J. and Helen K. Pawek Fellowship in Forest Resources which provided the funding for my graduate studies. The USFS Northern Research Station also provided support for this project, without which this research would not have been possible.

My interactions with many people lead me to graduate school. In particular, my interest in forest ecology was encouraged by my undergraduate advisor, Dr. Zack Murrell, who has been instrumental in encouraging me to pursue my interests.

I am truly grateful to my family and friends for their support. My parents raised me to believe that I could do anything. They encouraged me to pursue my interests, whatever they might be, and worked so hard to give me opportunities to succeed. Lastly, I want to thank my husband, Chad. I can't thank him enough for making our life an adventure as I drag you around the country and for making dinner all those late nights I spent at the office. I owe so much to Chad, my parents, and my brother Henry; you have provided an unwavering support system that I am incredibly fortunate to have.

Abstract

Concerns about loss of biodiversity and ecosystem complexity in managed forests have recently increased and prompted the need for new management strategies that restore or maintain ecosystem functions and allow for wood production. Variable Retention Harvest (VRH) systems, in which mature overstory trees are retained in various spatial arrangements across harvested areas, represent one potential approach to this problem. In the Great Lakes Region, VRH has been suggested as a management approach for *Pinus resinosa* (red pine) forests given this may more closely mimic historical disturbance regimes that resulted in mixed-species, multi-cohort forests; however, long-term evaluations of the effectiveness of this strategy at sustaining and restoring plant community complexity and diverse tree species do not exist. The objective of this thesis was to determine the long-term (10+ year) effects of overstory tree retention pattern and shrub competition on ground-layer community composition and tree regeneration in *P. resinosa* forests in Minnesota, USA. Long-term data from a large-scale manipulative study in which four overstory (control, small gap-aggregated, large gap-aggregated and dispersed) and two understory (ambient and reduced shrubs) treatments were replicated four times in 16 ha stands were used to address this objective.

Changes in herbaceous community composition were apparent 11 years following harvest and increases in richness and diversity were driven by introduction and colonization of early successional species, while forest interior species continued to persist across treatments. Harvest resulted in immediate decreased cover by native forbs, but this result was not apparent in later sampling periods. All life forms responded positively to harvest with the exception of moss and clubmoss spp, which were more common in the control by the last sampling year. Retention harvests were successful at reintroducing hardwood species to the establishing cohort regardless of the spatial pattern of retention, and hardwood densities greatly outnumbered conifer regeneration in both regeneration size classes. Several mechanisms (disease, browse, and poor seedbed conditions) interacted to limit regeneration of *P. resinosa*. *P. strobus* densities were greater under an intact *Corylus* layer as well as in the large gap-aggregated treatment 11 years after harvest. In the case of both the herbaceous layer and natural tree regeneration, the presence of a dense and persistent shrub layer, likely a result of fire suppression, filtered the response to retention pattern. Overall, this work highlights the flexibility of VRH in attaining diversity goals in ground-layer plants but also reinforced the importance of understory competition control and seedbed preparation for ensuring natural regeneration of the dominant species in these systems.

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Chapter 1: Introduction

This thesis explores the immediate and long term (10+ years) response of the ground-layer and natural tree regeneration to Variable Retention Harvest (VRH), an ecological silvicultural system that retains mature trees in various spatial arrangements through the subsequent rotation. These structures were historically present following many natural, stand replacing disturbances; however, they have largely been lost or greatly reduced in many managed forests. The pattern of surviving trees following natural disturbances was often spatially variable and VRH were developed to approximate these patterns and maintain a diversity of microhabitats and forest structures (Franklin et al. 1997) that are otherwise lost under traditional management regimes. The Red Pine Retention Study, a large-scale VRH study in northern Minnesota, provides a unique opportunity to conduct a long-term evaluation of the effectiveness of these systems at regenerating forests more similar to historical conditions and sustaining native ground-layer communities. More specifically, this study examines the impacts of a range of spatial variability in retained trees on the long term dynamics of tree regeneration, while holding abundance of overstory retention constant. Additionally, stands contain shrub control treatments on half of the study plots providing an opportunity to examine the importance of shrub competition to regenerating mixed species stands and maintaining ground-layer composition.

The second chapter considers the role of retention pattern and shrub competition in shaping the response of ground-layer plant species to harvest. Nonmetric-multidimensional scaling was used to quantify treatment effects on ground-layer composition along with linear mixed effects models analyzing changes in cover, richness, Shannon's diversity and evenness of successional and life form groups. VRH changed the composition and richness of the ground-layer, mainly as a result of increases in early successional disturbance adapted species such as *Carex pensylvanica*, *Pteridium aquilinum* and *Rubus spp*. Release from the recalcitrant *Corylus* understory magnified these treatment effects and significantly increased ground-layer diversity in all treatments. Cover, richness and diversity of forest interior species were also maintained both immediately after treatment initiation and over the long term (11 years).

The third chapter examines the relationship between the spatial arrangement of residual trees and natural tree regeneration. Composition of woody species in addition to densities of small and large tree regeneration were analyzed. Retention harvests were successful at reintroducing tree species diversity to the establishing cohort regardless of the spatial pattern of retention, particularly various hardwood (mainly *A. rubrum/Q. rubra/B. papyrifera*) species. Several mechanisms including disease, browsing pressure and poor seedbed conditions, interacted to limit regeneration of *P. resinosa* despite a modest increase in densities of large regeneration in large gaps and small regeneration in stands where shrubs had been reduced in the final sampling year. *P. strobus* maintained greater densities than the dominant species, particularly under an intact shrub layer. Overall, treatments with greater spatial variation (large gap-aggregated) of retention and light environments did not result in increased diversity of composition, but the treatment creating the most uniform conditions (dispersed) did result in the greatest densities of large regeneration.

Finally, the fourth chapter offers a summation of the work outlined in the previous chapters. Overall conclusions and potential management strategies are outlined in the context of VRH as a tool to maintain ground-layer diversity and composition as well as promote regeneration of multi-cohort, mixed-species stands. Limitations of this project and potential future directions are also discussed.

Chapter 2: Effects of variable retention harvesting on ground-layer plant communities in *Pinus resinosa* (red pine) forests in northern Minnesota, USA

Introduction

The forest ground layer plays an important role in the functioning of forest ecosystems (Franklin et al. 1997, Gilliam 2002, Whigham 2004). Although often representing less than 1% of the biomass of a forest, this layer can make up 90% of the plant species in forests and influences the cycling of essential plant nutrients (Gilliam 2007). In addition, the ground layer exerts important controls on tree regeneration and development (Halpern and Lutz 2013). Therefore, an understanding of the relationships between ground layer dynamics and forest management practices is key for informing sustainable management regimes that maintain this and other important forest ecosystem components. This knowledge is particularly important considering recent evidence that human action may be the most influential process determining levels of diversity in certain forest systems (Schmiedinger et al. 2012).

Research examining the impacts of forest harvesting on the ground layer have indicated that certain species or functional guilds may be adversely impacted by conditions resulting from traditional management practices (Duffy and Meier 1992, Ramovs and Roberts 2003, Decocq et al. 2004, Fraterrigo et al. 2006, Halpern et al. 2012). Meier et al. (1995) outlined five primary ecological mechanisms to explain the declines in many forest species often observed following harvesting. First, harvesting may directly impact diversity by reducing populations of rare herbs during harvest. Second, already reduced herbaceous populations may also be excluded during successional response following harvesting, in particular due to physiological stress and competition with exotic or early successional species. Third, many vernal herbs exhibit slow growth and reproduction rates resulting in low alpha diversity years after harvest. Fourth, some herbaceous species have dispersal methods that limit population expansion, such as ant-mediated and clonal growth. Finally, the elimination of gaps in the canopy and loss of specific microhabitats may also impact levels of ground layer diversity. While the work forming the basis for these proposed mechanisms focused on ephemeral herbaceous species present in early spring, the outlined mechanisms have been attributed to the decline of many vulnerable ground-layer species (Kahmen and Jules 2005).

Many of the early works documenting the impacts of harvesting on ground-layer plant species looked primarily at clearcutting regeneration systems; however, studies focusing on the response of herbaceous diversity to a spectrum of management intensity, both immediately following the disturbance and many years later, have produced mixed results (Battles et al. 2001, Kern et al. 2006, Duguid and Ashton 2013). Despite this, recent studies support the finding that late-successional stands and old-growth forests have significantly different understories from managed areas (Scheller and Mladenoff 2002, D'Amato et al. 2009, Bergeron and Fenton 2012). Given these recognized differences, forest managers are increasingly applying practices that reduce the impact of the mechanisms outlined by Meier et al. (1995) and mimic natural disturbance as a means to safeguard species diversity (Gilliam 2007). These include maintaining and restoring a diversity of microhabitats through retention of mature forest structure, emulating historical disturbance regimes in management planning, and retaining aggregates of mature forest to serve as refugia for the conservation of species with limited dispersal methods or slow growth and reproduction rates.

Variable Retention Harvest (VRH) systems are one example of the management approaches that have been proposed to mitigate the above mentioned mechanisms adversely impacting the forest ground layer in managed forests (Franklin et al. 1997). These methods are novel relative to traditional forest management approaches in that maintenance and re-establishment of native forest biodiversity is an end goal (Baker et al. 2013), with growth of timber often serving as a secondary objective (Franklin et al. 1997, Urgenson et al. 2013). In particular, this approach focuses on retaining mature live trees in a range of spatial configurations across a harvested area in an attempt to emulate the post-disturbance legacies historically characterizing forest systems following meso- and stand-scale disturbances. As such, this approach is designed to create a diversity of microhabitats, including open habitat and mature forest structures, which presumably provide the range of conditions necessary to maintain ground layer biodiversity in areas managed for wood products.

Despite the theoretical basis that suggests VRH can sustain and restore native forest biodiversity, long-term studies are needed to evaluate the effectiveness of this approach at achieving this goal, particularly since legacy effects can continue decades to centuries after logging (Tester et al. 1997, Roberts 2004, D'Amato et al. 2009). One such legacy of historical land-use is the formation of a dense and persistent layer of one or several species in the ground of shrub layers often due to increased overstory disturbance in conjunction with elevated levels of herbivory (Royo and Carson 2006). For example, dense understories of *Corylus americana* and *C. cornuta* (American and beaked hazel) exist in some pine forests in the western Great Lakes region, likely reflecting an alteration in historical disturbance regimes, including the suppression of high frequency, low intensity surface fires, which historically limited the abundance of these species (Tappeiner 1979, Palik and Zasada 2003, Royo and Carson 2006). These shrub species, as well as *Rubus spp.,* are often abundant in pine-dominated systems affecting tree regeneration, altering successional pathways, and impacting forest diversity and composition (Royo and Carson 2006). Given these changes in shrub and ground layer conditions over the last century, it is important to understand the influence of recalcitrant layers on the efficacy of VRH at achieving objectives associated with restoring or maintaining the diversity and composition of the native ground layer.

The Red Pine Retention Study, a >12-year-old VRH study in northern Minnesota, provides a unique opportunity to conduct a long-term evaluation of the effectiveness of these systems at sustaining native ground-layer communities. Although *Pinus resinosa* (red pine) forests have traditionally been managed as single-cohort monocultures (Benzie 1977), the use of VRH may more closely mimic the historical, mixed severity disturbance regimes that resulted in mixed-species, multi-cohort forests (Palik and Zasada 2003, Fraver and Palik 2012). This research is particularly important considering most studies dealing with ground layer response to VRH have been short-term (North et al. 1996, Halpern et al. 2005, Nelson and Halpern 2005, Macdonald and Fenniak 2007, de Graaf and Roberts 2009, Lencinas et al. 2011). More specifically, the Red Pine Retention Study examines a different spatial configuration (dispersed, gap-aggregated) of retained trees on the long term dynamics of the ground layer, while holding abundance of retained basal area constant (16 m^2/ha, ~45%). Moreover, this study included shrub control treatments, providing an opportunity to examine the importance of shrub competition to maintaining native plant biodiversity in *P. resinosa* ecosystems.

We addressed several questions relating ground-layer response to variable retention pattern and shrub reduction to evaluate the short and long term effectiveness of these systems at sustaining native ground-layer communities in *P. resinosa* forests in northern Minnesota: (1) How does ground layer community composition change across a range of overstory retention patterns and shrub competition? (2) In what way do the range of life forms and successional groups respond to retention pattern in light of a recalcitrant understory layer?

Methods

Study Sites

This study was conducted on the Chippewa National Forest in north-central Minnesota, USA (47°24’45”– 47°32’53”N, 94°04’15”–94°08’45”W). The study area has a cold-temperate climate with mean annual precipitation of 70 cm and mean annual temperature of 4^{o}C. The study sites occupy outwash and ice contact landforms, with deep sand parent material and excessively to well drained, nutrient poor loamy sands. Overall, all sites are low elevation (400-450 m) with little topographic relief.

At the time of initial treatment, stands were approximately 85 years old, broadly even-aged and dominated by *P. resinosa.* The study area naturally regenerated between 1910 and 1912 following logging and wildfires. Basal area of the study area averaged 32 m^2/ha prior to treatment, with a moderately open canopy, and dominant trees averaged 27 m in height (Palik et al. 2014). Historically, fire was the primary natural disturbance in this ecosystem. The site is classified as a northern dry-mesic mixed forest, Red Pine-

White Pine Woodland (FDn33a) based on the Minnesota native plant community classification (MN DNR 2003).

Study Design

The Red Pine Retention Study is a split-plot, complete block design replicated four times. Four blocks were randomly selected from a group of eight within the greater study landscape (Palik et al. 2014). All four blocks are approximately 64 ha in size and four overstory retention treatments (unmanaged reference area, large gap-aggregated, small gap-aggregated, and dispersed), approximately 16 ha each, were randomly assigned within each block. The goal in treated stands (large gap-aggregate, small gap-aggregate and dispersed) was to reduce basal area to similar low levels of retention, approximately 17 m^2/ha (Figure 2.1). Each of the whole plots was further divided into split-plots of two woody shrub treatments, approximately 8 ha each, (ambient and reduced shrubs). The treatments are described in detail below.

Variable Retention Harvest Treatments

The variable retention harvest treatments tested the response of plant communities to spatial pattern of retained trees. The control treatment contained no overstory manipulation and had an average basal area of approximately 32 m^2/ha. The large gap-aggregated and small gap-aggregated treatments effectively created variability in openness and canopy cover by the creation of 0.3 ha and 0.1 ha gaps, respectively. These patterns were meant to emulate the live-tree patterns resulting from fine- and meso-scale disturbances historically affecting these systems, including surface fires, wind, and root disease. Large gap centers were placed on an 83.8 meter grid, while small gap centers were placed on a 76.2 meter grid. The number of gaps varied depending on stand size. Both gap-aggregate treatments included light thinning in the surrounding matrix to achieve the desired final basal area, although the small gap-aggregated treatment ultimately resulted in slightly higher basal area than the other harvest treatments (Palik et al. 2014). Residual trees were retained evenly throughout the dispersed retention treatment, resembling a traditional, uniform shelterwood harvest. The treatments were implemented through timber-harvesting over the fall and winter of 2002/2003.

The dispersed treatment resulted in a uniform distribution of retained trees, and therefore a more uniformly distributed disturbance. Along a gradient of disturbance distribution, the small gap-aggregated treatment introduced more spatial variability to the disturbance. The large gap-aggregated treatment resulted in large harvest gaps, and the most spatially variable disturbance. All treatments held level of retention relatively constant, focusing effect of harvest on spatial pattern as opposed to level of retention (~45% retention).

Shrub Treatments

The shrub treatment tested the effect of competing shrubs on natural regeneration and herbaceous communities in retention harvests. The shrub reference treatment involved no manipulation, hereafter called the 'ambient' levels of shrub density treatment. The reduced shrub treatment included the reduction of all woody shrubs, as well as *Populus* spp. suckers, greater than 0.3 m in height and less than 6.4 cm dbh; hereafter called the 'reduced' shrub density treatment. All other tree species were left intact. In particular, the reduced treatment targeted *Corylus* and *Rubus* spp. which can become prolific in this community (Palik et al. 2014). The shrub reduction treatment was implemented using handheld gas-powered brush cutters to the entirety of each stand immediately following harvest in the spring of 2003, to aid in planting. In all subsequent years the shrub treatment was confined to the prescribed half of each stand and applied in the late spring. Treatment occurred annually from 2004 to 2006 and in 2011. In 2007 and 2008 only shrubs within 21 meters of sample points (see below) were cut.

Data Collection

The forest ground layer data was collected at study points placed evenly along transects that crossed each stand (25 to 50 m apart). Transect length and number depended on the shape and size of the treatment stand. Study points were placed at least 50 m apart from each other and from treatment boundaries. Each stand contained 20 study points, equally divided between the ambient and reduced shrub treatments (10 study points per split plot). In all, 320 study points were established. To sample ground layer composition, two quadrats were established at each point. Each quadrat was 0.25 m^2, and were established at each sample point opposite one another and perpendicular to the transect line, two meters from the sample point. Within each quadrat, all herbaceous vascular plant species and woody species less than a meter tall were categorized within one of six cover classes (<1%, 1-5%, 6-15%, 16-30%, 31-60%, 61-100%). Additionally, stems were counted for all woody species less than one meter tall, including trees. Sampling was done before harvest in 2002 (year 0 hereafter), and following harvest in 2003 (year 1), 2006 (year 4) and 2013 (year 11), from mid-June to mid-August each year.

Data Analysis

Ground layer community composition patterns among treatments and over time were analyzed using nonmetric multidimensional scaling ordination (NMS). For all analyses, cover classes of each species in a plot were converted to the midpoint of their range (<1%, 1-5%, 6-15%, 16-30%, 31-60%, 61-100% became 0.5%, 3%, etc.) and were averaged to the split-plot level within each block. Sørenson's distance measure was used and only common species (species that occurred in greater than 5% of plots) were included. NMS was performed using PC-ORD 6.0 with 250 runs with real data, 250 runs with randomized data, and a maximum of 500 iterations per run. The data matrix consisted of species (columns) and split-plots (rows). Kendall rank correlation coefficients were calculated between species abundance and their NMS axis scores. Compositional differences between treatments were examined using distance-based multivariate analysis of variance (perMANOVA). Permutations were constrained within Area (i.e., block), which was considered a random factor. Variable retention harvest treatment, shrub treatment and year were considered fixed factors. In addition, Blocked Indicator Species Analysis (ISA) was used to identify species that differentiated treatments. Indicator values represent percent of perfect indication. Both perMANOVA and Indicator Species Analysis were run in PC-ORD 6.0. Diagnostic plots were used to confirm appropriate multivariate spread.

Immediate and long term effects of overstory retention patterns and shrub competition on change in ground layer richness, Shannon's diversity and evenness were evaluated using linear mixed-effects models. Richness, Shannon's diversity and evenness were calculated per square meter in PC-ORD. Change in percent cover relative to pre-harvest conditions by growth form (graminoids, ferns and allies, native forbs, subshrubs, exotic species, moss species) as well as successional role was also analyzed. Successional role was determined based on Coefficient of Conservatism values (c), resulting in 74 species being characterized as early successional (c 1-4), 63 as mid-successional species(c 5-6) and 35 as later successional (c 7-10) (12 species c value was unknown) (Bernthal 2003, Milburn et al. 2007, Mortellaro et al. 2012, Matthews et al. 2015). When values specific to Minnesota were not available, we used values developed for similar settings in an adjacent state (Wisconsin). Area (block) was considered a random factor while shrub treatment, VRH treatment, year, and their two-way and three-way interactions were considered fixed factors. In instances where a significant interaction term was identified, models were run separately for each time period or treatment type to assess differences among different levels of the main effect(s). Analysis was done using the 'lme' command in the R package nlme. Diagnostic plots were used to assess model assumptions and basic transformations were applied when necessary.

Results

Community Composition

The NMS ordination of ground layer community composition had a three-dimensional solution with the first axis explaining 37.5% of the variation, followed by the second axis at 30.5% and the third at 16.2% (Figure 2.2). Most of the temporal and treatment variation was found along axis 1. Sample units in the negative portion of axis 1 included the three VRH treatments in year 11. Control and pre-treatment ordination points fell close to zero on axis 1 and moved towards the more negative ordination space along axis 1 and more positive ordination space along axis 2 (the exception being the overstory control). This suggests an increase in many early and mid-successional species in treatments plots based on the species correlations with each axes (Table 2.1). While the VRH treatments occupied different portions of ordination space relative to the controls, large separation according to retention pattern was not apparent along either of the first two axes. Additionally, the distance separating shrub treatments in ordination space suggests shrub reduction increased the magnitude of compositional change when applied in conjunction with harvest treatments.

PerMANOVA results indicated that ground-layer community composition was affected by VRH treatment, shrub treatment, year, and the interaction between VRH treatment and year as well as VRH and shrub treatment (Table 2.2). Given this interaction, community composition was analyzed for each year separately, revealing that the VRH effect was not significant prior to treatment, but had a significant effect 1 ($p = 0.029$), 4 ($p = 0.001$) and 11 ($p = 0.001$) years following harvest.

Several species were significant indicators of VRH and shrub treatments (based on Indicator Species Analysis, $p < 0.05$; (Table 2.3). Species with strong affinities for undisturbed forests (*Goodyera pubescens* (Coefficient of Conservatism [c] = 8), *Chimaphila umbellata* (c = 8), *Gaultheria procumbens* (c = 6), *Pyrola rotundifolia* (c = 8) and *Clintonia borealis* (c = 7)) were significant indicators of the VRH control treatment. Overall, indicators of the control treatment had higher coefficient of conservatism values compared to other treatments.

Coefficient of Conservatism values were more variable for indicators of the other VRH treatments. Both early (*Rubus strigosus* (c = 3), *Galium triflorum* (c = 4), *Thalictrum dioicum* (c = 5)) and later (*Viola spp* (c = 7), *Dryopteris spinulosa* (c = 6), *Rhus radicans* (c = 7)) successional species were indicators for the small gap-aggregated treatment. Neither gap aggregate treatment resulted in significant indicators when shrubs were left at ambient levels. The dispersed treatment was also associated with a wide range of Coefficient of Conservatism values, including *Aster macrophyllus* (c = 4), *Rubus pubescens* (c = 6), *Vaccinium angustifolium* (c = 5), *Rubus alleghaniensis* (c = 2) and *Arctostaphylos uva-ursi* (c = 7). The disturbance-adapted species *Rubus alleghaniensis* (c = 2) responded well to shrub reduction in the dispersed treatment.

Richness, Diversity and Evenness

Ground layer species cover, richness, Shannon's diversity and evenness changed significantly in response to VRH and shrub treatments over time (Figure 2.3). All VRH treatments increased total cover of ground layer species in year 4 (p = 0.0147; Figure 2.3) and VRH (p = 0.0003) as well as shrub treatment (p = 0.0012) in year 11 compared to the control. The reduced shrub treatment (p = 0.0032) and all VRH treatments (p = 0.0060; Figure 2.3) had significantly greater increase in species richness than the control. Small gap-aggregated ($p < 0.0001$) and dispersed (p = 0.0025) treatments had significantly lower evenness than the control (Figure 2.3) compared to pretreatment values, while shrub treatment had no significant effect on this measure. There was a significant positive shrub treatment effect on diversity (p = 0.0091).

Successional Groups

Richness, Shannon's diversity, evenness, and cover were then broken down by species association with or without disturbance (early and later successional species). Overall, no significant changes were associated with treatment for late successional species ($n = 35$) (Figures 2.3). Change in total cover by early successional species ($n = 74$), and early successional richness, evenness and diversity did show a treatment effect. Early successional cover response depended on year (significant interaction $p = 0.0001$). Starting in year 4, early successional species showed significant increases in cover in all VRH treatments ($p = 0.0002$). This trend continued in year 11 ($p = 0.0002$), and early successional species also increased by year 11 in the reduced shrub treatments ($p = 0.0043$). Increased richness ($p < 0.0001$, $p = 0.0217$) and diversity ($p < 0.0001$, $p = 0.0141$) of early successional species were also associated with VRH (Figure 2.3) and shrub treatments compared to the control. There was a significant interaction between treatments types for evenness of early successional species ($p = 0.0283$, Figure 2.3). The small gap-aggregated reduced shrub treatment was associated with increased evenness in this group ($p = 0.0265$), while the large gap-aggregated ($p = 0.0009$) and dispersed ($p = 0.0175$) treatments at ambient shrub levels were associated with increased evenness.

Life Forms

Change in cover by ground layer species showed significant interactions between year and VRH/shrub treatments ($p < 0.0001$, $p = 0.0017$) and many lifeforms responded positively to harvest (Figure 4). By year 11, all VRH and shrub reduction resulted in a significant increase in cover by subshrub ($p = 0.0025$, $p = 0.0144$) species. Pattern of retention interacted with shrub treatment and year in its effect on ground layer shrub cover. The large gap-aggregated ambient shrub treatment resulted in increased shrub cover (p = 0.0163). Cover by native forbs/herbs was not significantly impacted by treatment despite lower densities in harvested areas in year 1 (Figure 5).

The reduced shrub treatment was associated with increased total cover of ground layer species in year 11 (p = 0.0012) and had a significant effect on various lifeforms. In particular, this treatment was associated with increased cover by graminoids 11 years after harvest (p = 0.0015) compared to the control. Subshrub species responded positively to reduced shrub treatment in the small gap-aggregated treatment (p = 0.0012) and ambient shrub treatment regardless of retention pattern (p = 0.0015).

Large gap-aggregated (p = 0.0238) and dispersed (p = 0.0181) treatments resulted in a decrease in total cover of moss and clubmosses compared to the control (Figure 5). Exotic species increased significantly in the small gap-aggregated treatment (p = 0.0010) in shrub reduction treatment (p = 0.0205).

Discussion

Our findings suggest that VRH, regardless of the spatial distribution of retention, shifted the composition and diversity of the herbaceous ground layer of *P. resinosa* forests to include a mixture of early, mid and late successional species. While harvest did result in changes in richness, diversity, and evenness, effects of retention pattern on the magnitude and direction of compositional change were not apparent. The primary driver of changes in herbaceous community composition was the harvest disturbance itself, and observed trends 11 years after treatment suggest that ground layer composition continues to move further from unharvested controls, regardless of VRH treatment. Changes in richness and diversity were driven by the introduction and colonization of early successional species, while forest interior species continued to persist across treatments. Reduced shrub competition did not have a drastic impact on composition of the herbaceous layer immediately following treatment; however, the difference between ambient and reduced shrubs plots appears to be increasing the magnitude of compositional change as time since harvest increases.

Retention harvest with high spatial variability (e.g. large gap-aggregated) are expected to result in greater levels of compositional change relative to unharvested forests due to the decreased presence of interior habitat in these systems (Franklin et al. 1997, Halpern et al. 2012) as well as the increase in edge habitat. Contrary to these expectations, an increased magnitude of compositional change in retention harvests with high spatial variability (large gap-aggregated) relative to those with low levels (dispersed) was not observed. This result would have been expected if aggregates of retained trees provided refuge for late successional species, compared to evenly dispersed retention, which has been related to declines in late successional species abundance (Halpern et al. 2012). The relatively high retention level (~45% BA retained) examined in this study may provide adequate structural elements to fulfill habitat and microclimatic condition requirements of the current ground-layer species regardless of spatial distribution (Franklin et al. 1997, Boyden et al. 2012).

Beyond providing refugia and contrasting levels of harvesting disturbance, the gap and matrix environments created by harvests are expected to increase heterogeneity in resource availability, particularly in the large gap-aggregated treatment (Palik et al.

2003) potentially allowing for a greater range of ground-layer plant species. The distribution of species abundance was impacted by VRH treatment, but not shrub treatment and the small gap-aggregated and dispersed treatments (the two treatments with lower spatial variation of retention) had decreased levels of evenness. This herbaceous species response may be driven by changes in light availability, whereas changes in woody ground layer species may be related to different drivers, including patterns in below-ground resources and competition (Coomes and Grubb 2000, Boyden et al. 2012). In particular, moisture availability and fine-scale differences in soil characteristics and nutrient availability have been shown to impact the distribution of ground layer species (Mitchell et al. 1999, Galhidy et al. 2006, Fahey and Puettmann 2007).

In a companion study conducted on this site, Boyden et al. (2012) found significantly greater light availability in all VRH treatments, as well as greater heterogeneity of light availability in the gap treatments. Dispersed canopy openings will likely close more rapidly as a result of canopy expansion than those gap-aggregated treatments (Webster and Lorimer 2005), presumably resulting in greater differences in light availability between more spatially variable treatments and the control over time. However, the relationship between canopy closure on ground layer species is complex (Halpern and Lutz 2013).

The primary focus of past work examining VRH has been on the role of overstory trees in structuring understory resource environments and microclimatic conditions; however, an important aspect of the systems examined in this work is the role of the dense understory layer composed of rhizomatous *Corylus* species. Related work from the study examining planted seedling growth in these systems indicated that shrub competition may be just as important as overstory competition in influencing resource availability (Montgomery et al. 2013). This influence was also apparent in the treatments we examined where beaked and American hazel often formed a dense and persistent understory layer following harvest and impacted ground-layer diversity more than overstory treatments. Although these shrub species were common historical components of this forest, their current abundance has been enhanced by past land use and alterations to historical disturbance regimes (Tappeiner 1979, Royo and Carson 2006). Given that a primary objective of VRH is to emulate the structural outcomes of natural disturbance, these results underscore the importance of applying treatments to reduce the impact of these recalcitrant shrub layers if competitive environments for ground-layer communities are to truly reflect conditions generated by natural disturbance.

Significant changes in total cover by ground-layer species were observed following harvesting with cover increasing over time for all treatments; a trend documented in other forest types (Beese and Bryant 1999, Fredericksen et al. 1999, Scheller and Mladenoff 2002). This suggests that the initial decreases in cover observed immediately following harvest in this and other VRH studies (Macdonald and Fenniak 2007) is transient. Cover by exotic species increased significantly in the small gap-aggregated and shrub reduction treatments and has been associated with increasing levels of harvest disturbance in other work (Buckley et al. 2003, Shields and Webster 2007). This increase was largely driven by *G. tetrahit* (brittlestem hempnettle), which was not found in the study until year 11. While the average increase in cover of exotic species is increasing with time, the increase is low (approximately 1%) and not likely driving overall increases in cover.

Our result suggests VRH remediated several mechanisms responsible for decreases in vernal herbs outlined by Meier (1995), including the loss of populations of rare herbs as a direct result of harvest, as well as physiological stress due to successional response. Protection from snow pack during the majority of harvest may have minimized direct damage to forest floor species, particularly in the dispersed treatment, where harvest occurred throughout the stand. Season of harvest can significantly impact ground-layer vegetation (Wolf et al. 2008) and may partially explain the differences in our findings relative to studies in which harvests occurred under snow-free, unfrozen ground conditions.

One of the main concerns with loss of vernal herb diversity is competition with exotic or early successional species, both of which exhibited statistically significant increases in cover following harvest. Despite this, it does not appear that competition from these groups is driving decreases in later successional species, at least the first 11 years following harvest, and increases in exotic cover were very low. There was no treatment effect for late successional species, in contrast to other studies documenting loss of shade tolerant species following partial harvest (North et al. 1996, Fredericksen et al. 1999, Scheller and Mladenoff 2002). We found that forest species persisted regardless of the spatial pattern of retention. This result was observed throughout the sampling period and interior forest species may be insensitive to change following VRH in *P. resinosa*. No treatment effects on late- successional species were observed during any sampling period, and disturbance resistance rather than recovery is likely the mechanism responsible for presence of late successional species in later years.

Overall, VRH was an effective management method to maintaining existing late successional ground-layer species in this system. This may be driven by certain characteristics of the system itself. The historical disturbance regimes, including mixed severity fire, likely favored ground layer communities dominated by species naturally adapted to overstory, as well as understory disturbance. In particular, these disturbance regimes favored reproductive strategies, such as rhizomatous growth and seed banking, able to cope with disturbance compared to species found in more mesic forest types (Rowe 1983, Halpern 1989). For example, the species likely responsible for increasing overall fern cover, *Pteridium aquilinium*, re-sprouts from rhizomes following even severe fire, and other common species found on site (*Rubus ideaus, Epilobium angustifolium, Aster macrophyllus, Apocynum androsefolium, Solidago canadensis*) have been observed one year following moderate severity fire (Skutch 1929, Roberts and Dong 1993). Several species common in this study with high affinities for undisturbed conditions (high coefficient of conservatism values) were also documented three years after fire (*Clintonia borealis, Cornus canadensis, Cypripedium acuale, Mianthemum canadense*) (Skutch 1929). Historical disturbance regimes may also have excluded herbaceous species displaying dispersal methods that limit population expansion following disturbance.

Maintaining adequate retention of overstory trees can sustain late successional species in the ground-layer (North et al. 1996, Hannerz and Hanell 1997, Beese and Bryant 1999, Battles et al. 2001), while simultaneously supporting increased cover by early successional species, at least in this system. While our study stands were not in an old-growth state when treatments occurred, there were at least 35 species with high affinities for undisturbed conditions (Coefficient of Conservatism > 6), which is indicative of mature forest conditions. The slow growth and reproductive rates/methods that may limit recovery of late successional ground-layer species in other systems are either not present in the species in this study, or were not revealed in our study given the levels of ground layer disturbance severity and associated changes in the resource environment. The latter is more likely considering the lack of treatment effect in year 1 and 4.

Conclusions & Management Implications

Long term data is needed to evaluate ecological response to management, particularly when immediate response is not always reflective of long term impact (Halpern et al. 2005, Halpern et al. 2012). Cover by early successional species continued to show significant increases in year 11 in all harvest treatments, suggesting long term dynamics of ground layer response. In many cases, initial ground layer response (1 year after harvest) differed from later years (year 4 and 11). Certain trends appear to be increasing in time, such as the increase in cover by graminoids and early successional species in harvested treatments, while other trends appear to be transient. Overall, changes in composition, richness and diversity appear to be driven by the introduction and increase in cover by early successional species. This shift does not appear to be at the expense of the richness, diversity or cover of late successional species. These observations confirm the dynamic nature of the forest ground layer and the need for long term data when evaluating the impact of management decisions.

Our results are important for future consideration of VRH in *P. resinosa* and perhaps other pine ecosystems adapted to similar disturbance regimes. These findings suggest greater flexibility in choosing retention pattern when maintenance of herbaceous biodiversity is a concern. All treatments maintained forest interior species already present in these second growth stands, even 11 years after harvest. However, colonization or increase in abundance of many disturbance-adapted species continues to occur by year 11, suggesting the increase in early successional cover (Abrams and Dickmann 1983, 1984) and richness may not be transient, a finding observed in other studies (Metzger and Schultz 1984, Jenkins and Parker 2000, Gilliam 2002). This appears to be driven in part by graminoid and shrub species, more specifically *Carex pensylvanica* and *Rubus spp.,* which are indicators of the large and small gap-aggregated treatments, respectively. Additionally, the continued increase and persistence of these species may be perpetuated by elevated deer population density relative to historical levels. Pre-fawn deer densities in the study area were estimated between approximately 4.25 and 5 deer per square km since 2007 (MN DNR 2007, 2011). This is a sharp contrast to the very low/absent numbers thought to have occurred prior to European settlement, a result of northern Minnesota's severe winters and historical forest conditions (White 2012).

There may be particular tradeoffs in diversity-related objectives when implementing different spatial arrangements of VRH. The small gap-aggregated treatment did result in greater cover by exotic species, particularly in conjunction with shrub reduction. One particular species of concern, *Galeopsis tetrahit*, was first observed in 2010, and may have been introduced along logging road and skid trails (Buckley et al.

2003). Both gap treatments resulted in lower cover of moss and clubmosses, consistent with other partial harvest results (Shields et al. 2007, Halpern et al. 2012) compared to the control, but cover still increased compared to pre-harvest levels.

Ideally, variation in spatial arrangement of retention across the landscape would ensure a range of conditions are created to maintain richness and diversity. The gap-based retention treatments utilized in this study may help enhance connectivity in the managed landscape, increasing the value of retention as habitat and maintaining wildlife corridors (Franklin et al. 1997). Overall, at this retention level, various spatial arrangements of retention appear to maintain ground layer biodiversity goals concerning a range of successional groups and growth forms, particularly in terms of maintaining species observed in the control.

Despite these findings, utilizing management practices that mimic historical disturbance regimes need to be considered in the context of altered forest understory conditions. The formation of a dense hazel layer following harvest had an impact on many of the diversity and composition measures analyzed in this study, in many cases more so than VRH treatment. The prolific response by hazel to harvest may not have occurred historically, considering the drastic change in historical disturbance regimes found in this, and many, forest systems following European settlement (Nyland et al. 2006b, D'Amato et al. 2015). This is particularly important as alternative silvicultural strategies are increasingly utilized to mimic natural disturbance. In order to effectively shift stands towards historical composition, conditions in the ground layer need to be considered. Overall, emphasis has been placed on overstory disturbance pattern and severity, while altered understory conditions may have a greater impact on ground-layer and regeneration response to overstory disturbance (Kern et al. 2012). Even in cases where management goals do not emphasize ground-layer response to harvest, shrub competition can negate the effects of varying retention pattern and negatively impact growth of regeneration (Montgomery et al. 2013).

Table 2.1. Species with significant correlations with the first two axes of the NMS ordination of ground-layer community composition of *Pinus resinosa* forests in northern Minnesota. Listed species had correlation *p*-values <0.0001. Coefficient of Conservatism values indicate species affinity for disturbance.

Axis	relationship	Species	Kendall's τ	Coefficient of Conservatism
1	negative	*Anemone quinquefolia*	-0.26029	5
		Pteridium aquilinum	-0.6838	3
		Vaccinium angustifolium	-0.45978	5
		Maianthemum canadense	-0.4332	5
		Carex pensylvanica	-0.35319	3
		Diervilla lonicera	-0.32599	6
		Lathyrus venosus	-0.32298	6
		Moss *spp*	-0.31275	-
		Comandra umbellata	-0.30493	4
		Danthonia spicata	-0.28883	4
		Vicia spp	-0.28378	-
		Rubus strigosus	-0.27643	3
2	positive	*Aster macrophyllus*	0.43043	4
		Cornus canadensis	0.23251	6
		Linnaea borealis	0.24903	7
		Rubus pubescens	0.25193	6
		Galeopsis tetrahit	0.27851	Exotic
		Rubus strigosus	0.34067	3
		Lycopodium clavatum	0.34305	6
		Galium boreale	0.36539	4
		Galium triflorum	0.40092	4
		Grass clade	0.41719	4
	negative	*Chimaphila umbellata*	-0.32036	8
		Gaultheria procumbens	-0.44631	6
		Vaccinium angustifolium	-0.28913	5

Table 2.2. Results of perMANOVA examining the influence of VRH and shrub treatments as well as time on the ground-layer plant composition of *Pinus resinosa* forests in northern Minnesota.

Main effect	Df	*F*	Pr(>*F*)
VRH	3	3.29	0.001
Shrub	1	1.39	0.068
Year	3	7.49	0.001
VRH x shrub	3	2.13	0.001
VRH x year	9	1.16	0.008
shrub x year	3	0.49	0.979
VRH x shrub x year	9	0.35	1

Table 2.3. Significant indicator species of VRH and shrub treatments by indicator value and Coefficient of Conservatism (c) in *Pinus resinosa* forests in northern Minnesota.

VRH	Shrub	Species	IV	*p* -value	c
Control	Ambient	*Goodyera pubescens*	28.9	0.0024	8
		Chimaphila umbellata	24.8	0.0282	8
		Gaultheria procumbens	19.3	0.019	6
		Pyrola rotundifolia	28.9	0.0024	8
	Reduced	*Clintonia borealis*	27	0.0142	7
Small Gap-Aggregated	Ambient	-	-	-	-
	Reduced	*Rubus strigosus*	36.4	0.0142	3
		Dryopteris spinulosa	20	0.0126	6
		Galium triflorum	27.2	0.0226	4
		Rhus radicans	20.4	0.0498	7
		Viola spp	20.8	0.0476	7
Large Gap-Aggregated	Ambient	-	-	-	-
	Reduced	*Thalictrum dioicum*	21.2	0.0304	5
Dispersed	Ambient	*Aster macrophyllus*	37.6	0.0004	4
		Rubus pubescens	24.7	0.007	6
	Reduced	*Vaccinium angustifolium*	19.7	0.0004	5
		Arctostaphylos uva-ursi	21.8	0.0088	7
		Rubus alleghaniensis	18.3	0.0202	2

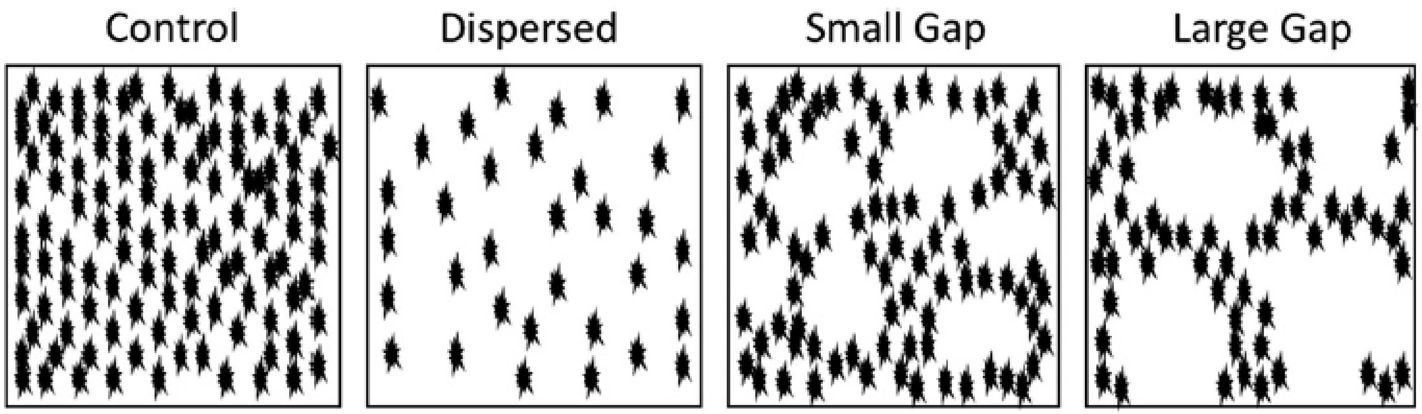

Figure 2.1. Representation of variable retention harvest treatments at the Red Pine Retention Study (from Ostry et al. (2012)). The control is uncut forest while the dispersed, small gap-aggregated and large gap-aggregated treatments are variable retention harvest treatments with variations of spatial retention pattern. Trees were retained uniformly in the dispersed treatment, while 0.1 hectare groups were harvested in the small gap-aggregated treatment and 0.3 ha gaps in the large gap-aggregated treatment.

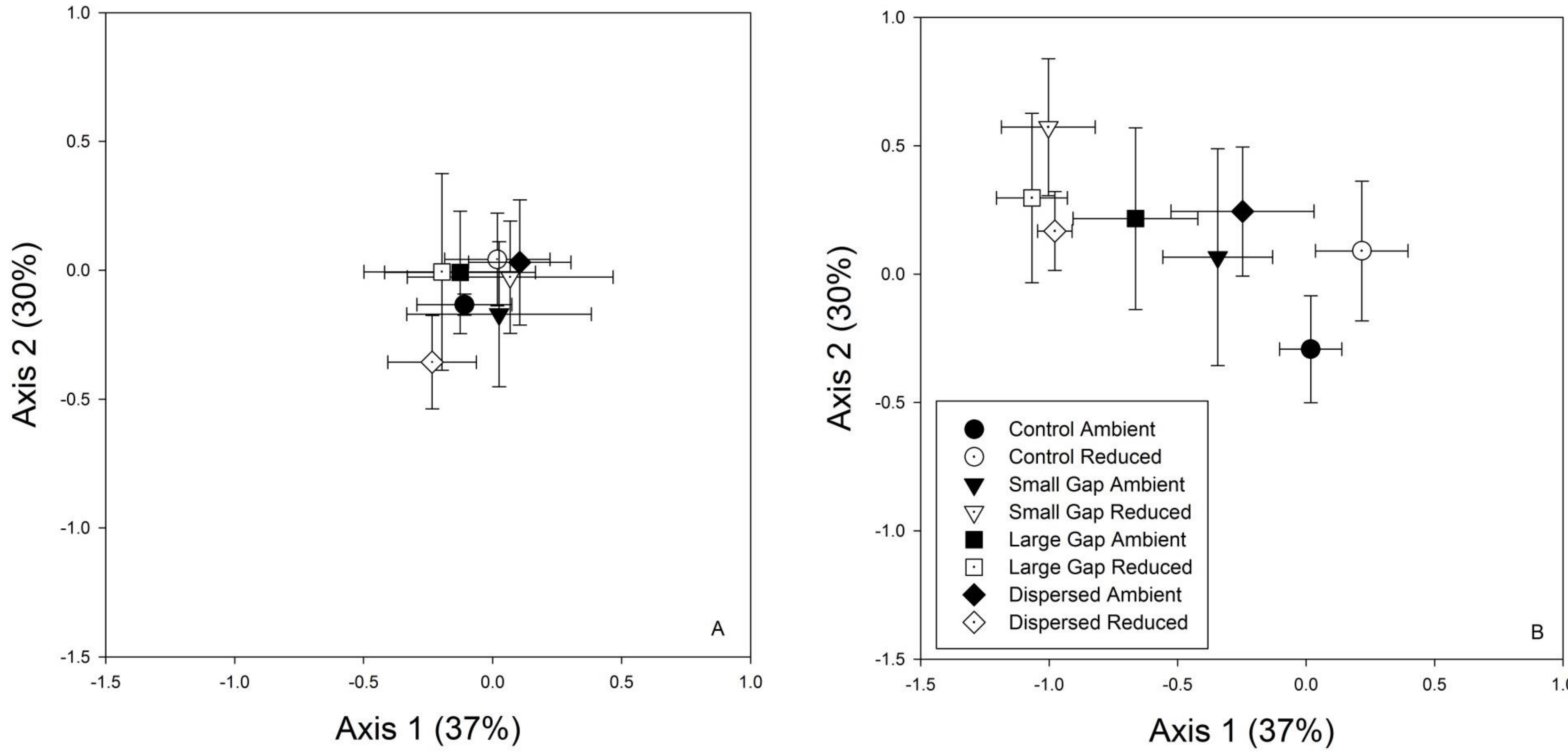

Figure 2.2. NMS ordination of ground-layer community composition (mean of four replicates +/- standard error) before treatment (A) and 11 years after treatment (B) in *Pinus resinosa* forests in northern Minnesota.

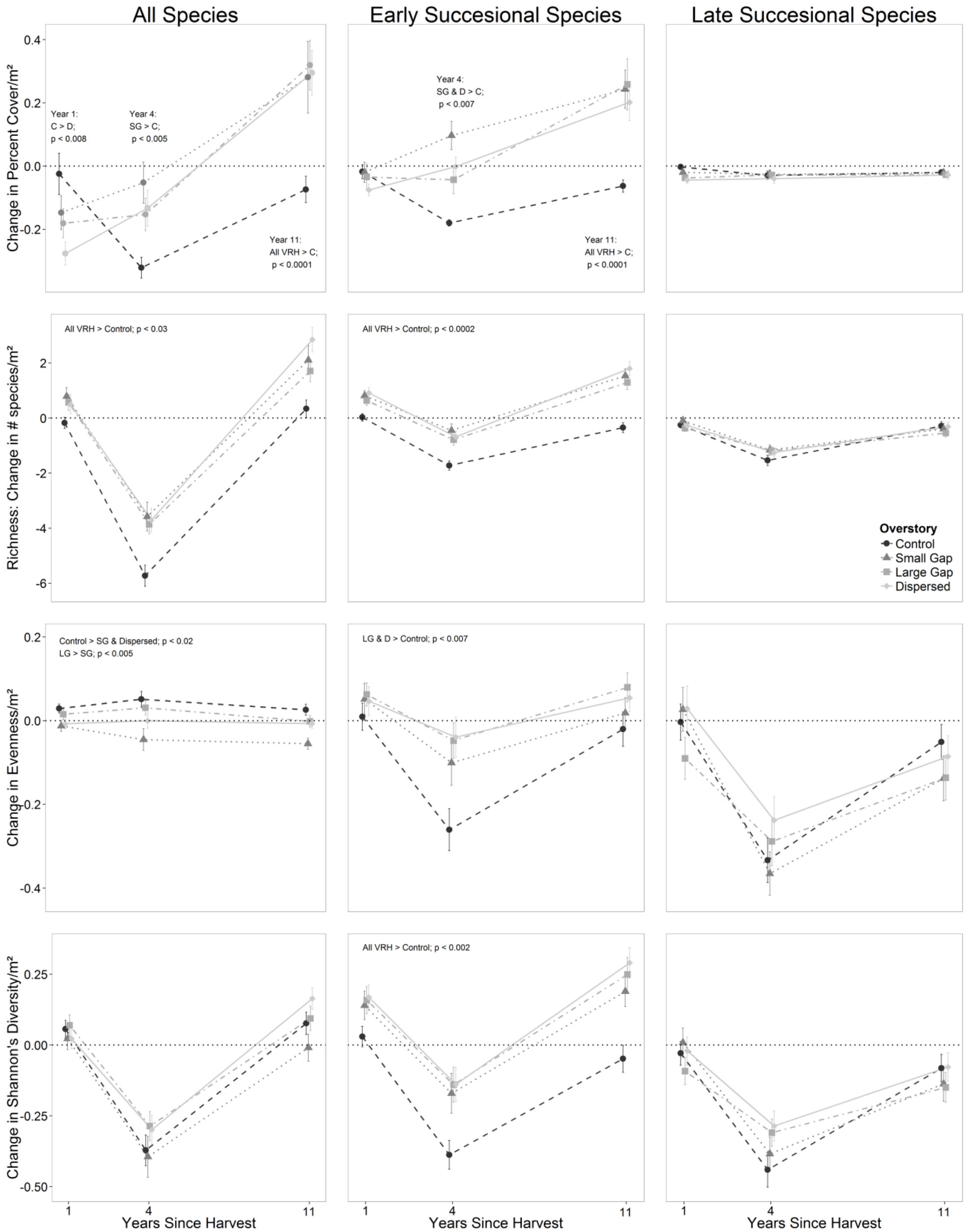

Figure 2.3. Change in cover, richness, Shannon's diversity and evenness relative to pre-treatment conditions 1, 4 and 11 years following harvest. Treatment is broken down by variable retention harvest treatment. The second column shows treatment effects on early successional species, while column three shows the late successional species.

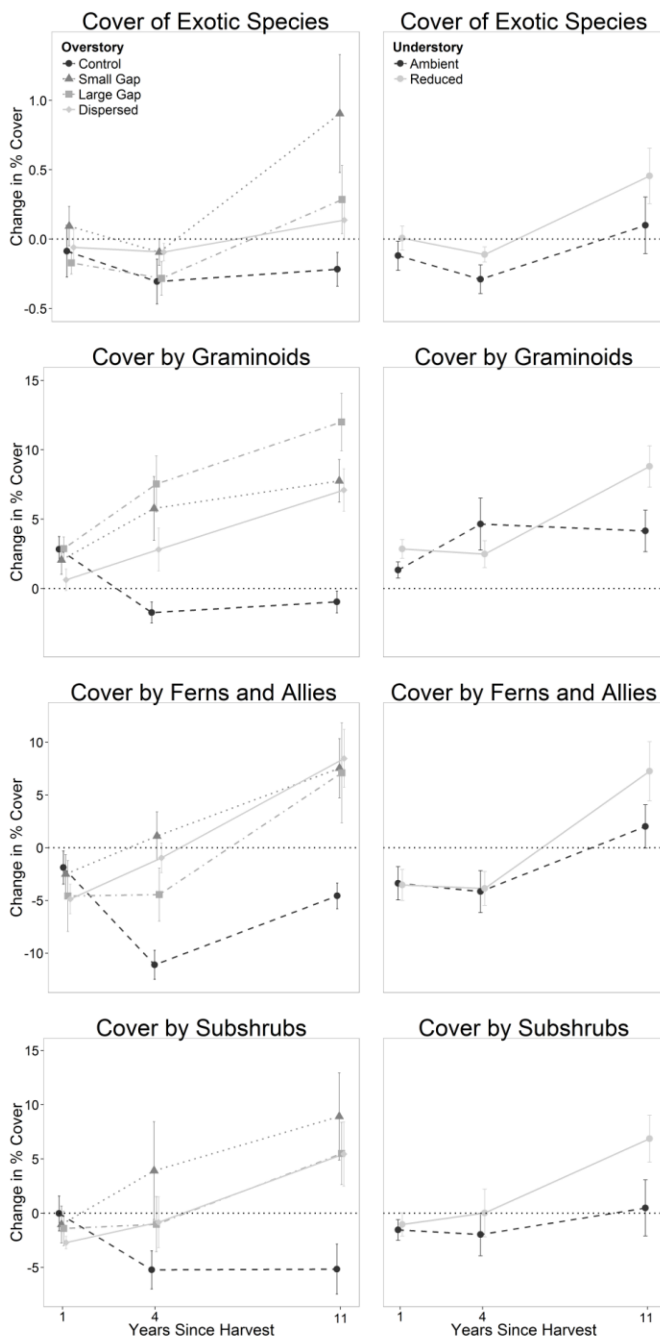

Figure 2.4. Change in percent cover of ground-layer plant life forms relative to pre-treatment values 1, 4 and 11 years following harvest in *Pinus resinosa* forests in northern Minnesota. Treatment is broken down by VRH treatment in the first column and shrub treatment in the second. Response to harvest and shrub reduction was positive for all groups.

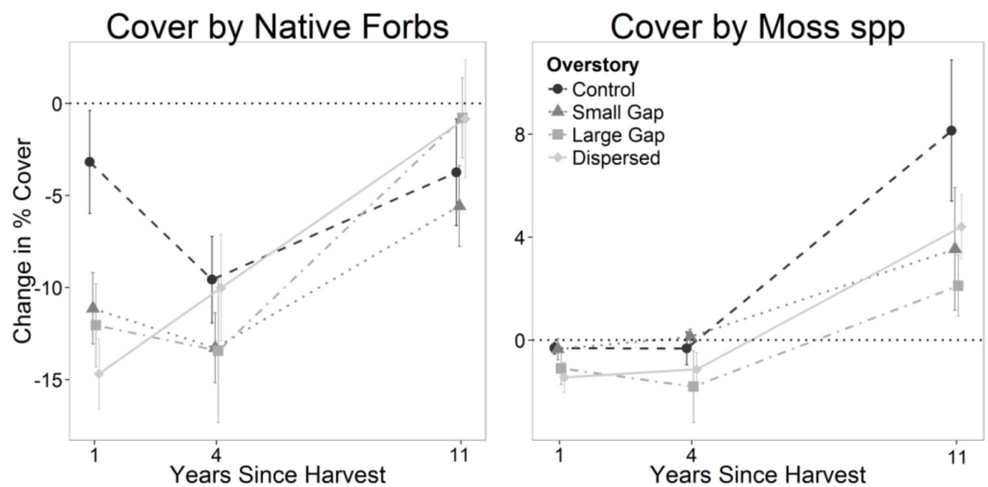

Figure 2.5. Change in percent cover of native forbs (A) and moss/clubmoss spp. (B) relative to pre-treatment values 1, 4 and 11 years following harvest in *Pinus resinosa* forests in northern Minnesota. These life forms either did not exhibit significant treatment effects (A) or were negatively impacted by harvest (B)

Chapter 3: Effects of variable retention harvests on natural tree regeneration in Pinus resinosa (red pine) forests in northern Minnesota, USA

Introduction

Management for biodiversity conservation and ecosystem resilience in forests managed for wood products has become a common goal in many areas of the world (Franklin et al. 1997, Lindenmayer et al. 2012). Integration of permanent overstory tree retention into traditional even-aged management regimes is one approach that is increasingly being utilized to retain mature forest structures and conditions in post-harvest stands in attempts to meet this management goal (Gustafsson et al. 2012). These structures were historically present following natural disturbances and under mixed severity fire regimes; however, they have largely been lost or greatly reduced in many forests managed using even-aged silvicultural systems. The pattern of surviving trees following natural disturbances was often spatially variable and variable retention harvest (VRH) systems were developed to approximate these patterns and maintain a diversity of microhabitats and forest structures (Franklin et al. 1997). Despite the widespread application of VRH in many regions of the globe, considerable knowledge gaps currently exist regarding the long-term impacts of these practices on forest ecosystem structure and composition given their relatively recent development.

To date, much of the research examining VRH has focused on forest biodiversity and structure given the underlying objectives of these management regimes. Nonetheless, the establishment and growth of regeneration is undoubtedly an important goal in all management settings (Franklin et al. 1997, Urgenson et al. 2013) and requires equal attention in VRH to ensure their long-term sustainability. Retention pattern has also been shown to impact competition and resource availability even at uniform retention levels (Palik et al. 2003, Boyden et al. 2012) and numerous studies have highlighted that overstory retention may delay regeneration development, particularly for shade-intolerant species (Hansen et al. 1995, Palik et al. 1997, Zenner et al. 1998, Mitchell 2001, Urgenson et al. 2013). Retained trees also provide a source of seed and potential access to mycorrhizae (Luoma et al. 2006, Boyden et al. 2012). Given these effects, there is a need to investigate the development of tree regeneration across a range of spatial retention patterns and species groups.

Mixed severity fire regimes historically created a range of light and resource conditions in north temperate forest ecosystems through creation of variable densities of mature, surviving trees across an area resulting in diverse vertical and horizontal structure across stands and landscapes (Collins and Stephens 2010, Kane et al. 2013). This variation in conditions maintained a diversity of microhabitats, likely allowing various tree species to establish and persist (Chappell and Agee 1996, Turner et al. 1997, Halofsky et al. 2011). Chappell and Agee (1996) found that recruitment of *Abies magnifica* was much more successful on burned than unburned sites, and mixed-severity fire resulted in variation in structure, patch size and shape, and tree species composition. A similar response was observed in *Pinus ponderosa* in South Dakota, where mixed-severity fire created an assortment of disturbance severities and facilitated the establishment of multi-cohort stands (Lentile et al. 2005).

While overstory competition is a primary driver of resource availability and regeneration success, altered disturbance regimes may also interact to confound the establishment of certain tree species. One legacy of historical land-use is the formation of a dense and persistent layer of one or several species in the understory, often due to increased overstory disturbance in conjunction with elevated levels of herbivory (Royo and Carson 2006). For example, dense understories of American and beaked hazel (*Corylus americana* and *C. cornuta*) exist in forests in the western Great Lakes region, likely reflecting an alteration in historic disturbance regimes, including the suppression of high frequency, low intensity surface fires, which historically limited the abundance of these species (Tappeiner 1979, Palik and Zasada 2003, Royo and Carson 2006). These shrubs, as well as *Rubus spp.,* are often abundant in pine-dominated systems affecting patterns in tree regeneration, altering successional pathways, and impacting forest diversity and composition (Royo and Carson 2006). Given these changes in understory conditions over the last century, understanding the influence of recalcitrant layers on the efficacy of VRH is important to achieving objectives associated with the establishment of new cohorts.

This study aims to examine the relationship between the spatial arrangement of residual trees and regeneration of woody species in *P. resinosa* VRH. Ultimately, our goal is to evaluate the effectiveness of utilizing a patchwork of dispersed and aggregated retention as a management approach to establish a mixed species forests while maintaining levels of structural complexity likely observed following natural disturbance in these systems. To accomplish this, we took advantage of a large-scale 12-year-old VRH study in northern Minnesota (hereafter referred to as the "Red Pine Retention Study"). This study provides a unique opportunity to conduct a long-term evaluation of the effectiveness of these systems at regenerating forests more similar to historical conditions. More specifically, this study examines a range of spatial variability of retained trees on the long term dynamics of tree regeneration, while holding abundance of overstory retention constant (~45%). Additionally, the study examined the interaction of a recalcitrant shrub reduction treatment providing an opportunity to examine the importance of shrub competition to regenerating mixed species stands in *P. resinosa* systems. We hypothesized that VRH creating the greatest levels of spatial variation in live tree structure will provide for the greatest diversity in tree regeneration, whereas those creating the most uniform resource conditions will have the greatest site-level densities. In addition, we predict that shrub density reduction will be of equal if not greater importance than overstory retention pattern in affecting post-harvest recruitment and development of tree regeneration.

Methods

Study Sites

This study was conducted on the Chippewa National Forest in north-central Minnesota, USA (47°24’45”– 47°32’53”N, 94°04’15”–94°08’45”W). The study area has a cold-temperate climate with mean annual precipitation of 70 cm and mean annual temperature of 4°C. The study sites occupy outwash and ice contact landforms, with deep sand parent material and excessively to well drained, nutrient poor loamy sands. Overall, all sites are low elevation (400-450 m) with little topographic relief.

At the time of initial treatment, stands were approximately 85 years old, broadly even-aged and dominated by *P. resinosa.* Stands naturally regenerated between 1910 and 1912 following logging and wildfires. All of the sites were stocked approximately at 32 m^2/ha basal area prior to treatment with a moderately open canopy, and dominant trees averaged 27 m in height (Palik et al. 2014). The site is classified as a northern dry-mesic mixed forest, Red Pine-White Pine Woodland type (FDn33a) based on the Minnesota native plant community classification system (MN DNR 2003). Historically, fire was the primary natural disturbance in this ecosystem.

While dominated by *P. resinosa*, the overstory contained lesser amounts of *Pinus strobus* (eastern white pine), *Acer rubrum* (red maple*), Populus tremuloides* (trembling aspen), *Populus grandidenta (bigtooth aspen), Betula papyrifera* (paper birch), *Abies balsamea* (balsam fir), *Picea glauca* (white spruce), *Quercus rubra* (northern red oak) and *Quercus macrocarpa* (bur oak) at the time of treatment.

Study Design

The Red Pine Retention Study is a split-plot, complete block design replicated four times. Four blocks were randomly selected from a group of eight within the greater study landscape (Palik et al. 2014). All four blocks are approximately 64 ha and four overstory retention treatments (unmanaged reference area, large gap-aggregated, small gap-aggregated and dispersed) were randomly assigned to whole plots (stands), approximately 16 ha each, within each block. The goal in treated stands (large gap-aggregate, small gap-aggregate and dispersed) was to reduce basal area to similar low levels of approximately 17 m^2/ha but to vary spatial pattern of this retention (Figure 1). Each of the whole plots was further divided into two split-plots or approximately 8 ha each with shrub treatment (ambient or reduced shrubs) assigned randomly to the split-plots.

Variable Retention Harvest Treatments

The VRH treatments tested a range of spatial openness and aggregation of retained trees. The control treatment contains no overstory manipulation and had an average basal area of approximately 32 m^2/ha. The large gap-aggregated and small gap-aggregated treatments effectively created variability in openness and aggregates by the cutting of 0.3 ha and 0.1 ha gaps, respectively. These patterns were meant to emulate the live-tree patterns resulting from fine- and meso-scale disturbances historically affecting these systems, including surface fires, wind, and root disease. Large gap centers were placed on an 83.8 meter grid, while small gap centers were placed on a 76.2 meter grid. The number of gaps varied depending on stand size (See Figure 3). Both gap treatments included light thinning in the surrounding matrix to achieve the desired final basal area of ~16 m^2/ha (~45% retention), although the small gap-aggregated treatment ultimately resulted in slightly higher basal area (Palik et al. 2014). Residual trees were retained evenly throughout the dispersed retention treatment, resembling a traditional, uniform shelterwood regeneration harvest. Harvested occurred over the fall and winter of 2002/2003.

Shrub Treatments

The shrub treatments tested the effect of competing shrubs on tree regeneration in retention harvests. The shrub control (ambient levels of woody shrubs) treatment contained no manipulation. The shrub removal (woody shrubs reduced) treatment prescribed removal of all woody shrubs, as well as *Populus* spp. root suckers, greater than 0.3 m in height and less than 6.4 cm dbh. All other tree species were left intact.

This treatment specifically targeted *Corylus* and *Rubus* spp. which can become prolific in this community (Palik et al. 2014). The shrub reduction treatment was implemented immediately following harvest, in the spring of 2003, to the entire study site to aid in planting and release of natural regeneration of desired tree species (i.e., non-*Populus spp.*) (Appendix A). In all subsequent years the shrub reduction was confined to the prescribed half of each stand and applied in the late spring. Treatment occurred annually from 2004 to 2006 and in 2011. In 2007 and 2008 only shrubs within 21 meters of sample points were cut.

Data Collection

Data were collected at study points placed evenly along transects that crossed each stand (25 to 100 m apart). Transect length and number depended on the shape of the block. Study points were placed at least 50 m apart and from treatment boundaries. Each stand contained 20 study points, equally divided between the shrub treatments (10 study points per split plot). In all, 320 study points were established. Two one by one meter square quadrats were established opposite one another and perpendicular to the transect line, two meters from the sample point. Within each quadrat, stems were counted for all woody species less than one meter tall, including trees. At each study point, shrub and tree stem counts were collected on species greater than 1 m tall and less than 2.54 cm dbh. This data was collected on a circular 1.26 m radius plot centered on the study plot. Sampling was done before harvest in 2000 and 2002, and following harvest in 2003, 2006 and 2013 between June and August each year.

Data Analysis

Immediate and long term responses of natural regeneration to overstory retention pattern and shrub competition were analyzed using linear mixed-effects models. Pre-treatment stem counts were used as covariates in all analyses. Area (block) was considered a random factor while shrub, overstory treatment, year and their interactions were considered fixed factors. Analysis was done using the 'lme' command in the R package nlme. Diagnostic plots were used to examine residuals and basic transformations were applied when the assumptions of analysis of variance were not met. In cases where there was a significant fixed effect**,** Tukey's test, using the 'lsmeans' command in R, was used to identify where differences existed between factor levels. *P. resinosa* and *P. strobus* were analyzed individually with these models given their ecological and economic importance in these communities. All other tree species were grouped by shade-tolerance and lifeform, including tolerant conifers (*A. balsamea/ P. glauca)*, mid-tolerant hardwoods (*Q. rubra/Quercus macrocarpa/Fraxinus spp*), intolerant hardwoods (*B.papyrifera/Prunus spp/Populus spp, mainly P. tremuloides and occasionally P. grandidenta)*, and tolerant hardwoods (*A. rubrum/A. saccharum/ A.spicatum/ Tilia americana. P. banksiana* was not present in the regeneration layer in sufficient numbers to analyze statistically.

Tree regeneration and shrub community composition patterns among treatments and over time were analyzed using nonmetric multidimensional scaling ordination (NMS). NMS was performed using PC-ORD 6.0 with 250 runs with real data, 250 runs with randomized data and a maximum of 500 iterations per run. Compositional differences between treatments were examined using distance-based multivariate analysis of variance (perMANOVA). Permutations were constrained within Area (block), which was considered a random factor. VRH treatment, shrub treatment, year, and their interactions were considered fixed factors. In addition, Blocked Indicator Species Analysis was used to examine species differentiating between treatment combination, as well as VRH and shrub treatments independently. These were run at the VRH treatment level, the shrub treatment level and within each VRH treatment level to test the effect of treatment interactions. Both perMANOVA and Indicator Species Analysis were run in PC-ORD 6.0. For the analyses listed above, Sørenson's distance measure was used and only common species (species that occurred in greater than 5% of plots) were included. For all analyses, stem counts were averaged to the split-plot level within each block. Diagnostic plots were used to confirm appropriate multivariate spread.

Results

Regeneration Densities

Small Regeneration

Many tree species and lifeform groups were significantly impacted by VRH treatment, shrub treatment, time, and their interactions (Table 1 & 2). Small regeneration *P. resinosa* densities varied among treatment depending on year since harvest (significant VRH by year and shrub by year interactions; Table 1). Four years after harvest the small gap-aggregated treatment had greater densities than either the control or large gap-aggregated treatments (Figure 2). This trend was not observed in the most recent sampling year, but there were significantly greater densities in the reduced shrub compared to ambient shrub treatment during this time period (11 years after harvest; Figure 3).

Small regeneration of *P. strobus* was affected by shrub treatment and the interaction between shrub and VRH treatment (Table 1). Densities were greater in the ambient shrub treatment for all years (Figure 3). The small regeneration class of *P. strobus* also responded to shrub reduction differently depending on retention pattern. When shrubs were at ambient levels, densities were greater in the control and large gap-aggregated than either the small gap-aggregated or dispersed treatments. In contrast, small regeneration of tolerant conifers responded to retention pattern, but not shrub reduction (Table 1). This group (*A. balsamea* and *P. glauca*) was less dense in the dispersed treatment compared to all VRH treatments, including the control (Figure 2). Tolerant hardwoods (mainly *A. rubrum*) were significantly impacted by VRH treatment and shrub treatment. Additionally, small regeneration of tolerant hardwoods varied within shrub treatment depending on retention pattern (significant VRH by shrub interactions; Table 1). Small regeneration of tolerant hardwood was more common in the dispersed treatment compared to either gap treatment, but only when shrubs were reduced. Overall, there were greater numbers of tolerant hardwoods in the control compared to harvested stands (Figure 2) and when shrubs were ambient (Figure 3). Time since harvest also impacted small regeneration of tolerant hardwoods, with greater densities of this species group at the final sampling year (year 11) compared to 2 years after harvest.

Small regeneration densities of mid-tolerant hardwoods (mainly *Q. rubra*) were affected by the interaction between VRH and shrub treatments (Table 1). Densities did not vary significantly between VRH treatments when shrubs were reduced, but the large gap-aggregated treatment resulted in greater numbers compared to the small gap-aggregated treatment when shrubs were ambient.

VRH treatment and the interaction between VRH and shrub treatment had a significant effect on small regeneration of intolerant hardwoods (Table 1). The small gap-aggregated treatment maintained higher densities compared to the control and dispersed treatments (Figure 2) overall, but densities also varied within retention pattern depending on shrub treatment. The small gap-aggregated treatment maintained greater densities than all other treatments when shrubs were ambient. When shrubs were reduced, the large gap-aggregated treatment had greater numbers of small regeneration intolerant hardwoods compared to the dispersed treatment.

Large Regeneration

There were fewer significant treatment effects on large regeneration (Tables 5). Notably, large regeneration of the dominant species in this system, *P. resinosa*, was not significantly impacted by treatment or year for the duration of this study (Table 2). *P. strobus* densities were affected by shrub treatment, year and the interaction between VRH and shrub treatment (Table 2). *P. strobus* responded to shrub reduction differently depending on harvest. Densities were greater under an intact shrub layer in the control compared to the small gap-aggregated. This difference in retention pattern was not present when shrubs were reduced. Overall, large regeneration of *P. strobus* was present in greater densities in the ambient shrub treatment (Figure 5). Year also significantly affected large regeneration of *P. strobus* with greater densities in the final sampling year (year 11) compared to all earlier sampling years. Large regeneration densities for tolerant (year 11) compared to all earlier sampling years. Large regeneration densities for tolerant conifer species (*A. balsamea* & *P. glauca*) were solely affected by spatial pattern of retention (Table 2) with significantly lower densities of this group in the small gap-aggregated treatment compared to the control (Figure 4).

Large regeneration densities of tolerant hardwoods were primarily affected by time since harvest (Table 2). This group increased in the final sampling year (year 11) compared to earlier years. Mid-tolerant hardwood densities were affected by VRH treatment and year (Table 2). The small gap-aggregated treatment maintained greater densities compared to large gap-aggregated treatment, but no treatments were significantly different from the control (Table 4). Mid-tolerant hardwood large regeneration densities also increased significantly by year 3 compared to immediately following harvest (year 1) and this increase was maintained over the remainder of the study (year 11). Intolerant hardwood densities were affected by shrub treatment and year, but not VRH treatment (Table 2). This group was significantly less dense in the reduced shrub treatment and increased in the final sampling year (year 11) compared to earlier years.

Community Composition of Regeneration

The application of VRH and shrub reduction treatments resulted in distinct patterns in woody species community composition over the 11-year period examined, as evident in the NMS ordination, which analyzed regeneration from both size classes. The final result was a 2-dimensional solution explaining 91.3% of the variation in woody plant composition (Figure 6). Very little separation between the pre-harvest and final sample periods was observed along Axis 1, which explained 65% of the variation, but several tree species were associated with this axis (Table 3) including *P. resinosa,* which was negatively correlated. Most of the temporal and treatment variation was found along axis 2, which explained 24.5% of the variation. By year 11, the small gap-aggregated treatments, as well as the other harvest treatments where shrubs were reduced, had moved towards the more negative portion of axis 2, particularly the small gap-aggregated reduced treatment. This suggests an increase in shrub species, particularly *Rubus strigosus*, as well as the tree species, *B. papyrifera* (Table 3). The dispersed and large gap-aggregated ambient treatments occupied similar portions of ordination space compared to pre-treatment results whereas the ambient and reduced control treatments moved slightly towards the more positive portions of axis 2 over time.

The distance separating treatments in ordination space suggests reduced shrub competition increased the magnitude of compositional change when applied in conjunction with the small gap-aggregated treatment and to a lesser extent the large gap-aggregated and dispersed treatments. This was confirmed by the PerMANOVA results, which indicated VRH treatments interacted with shrub control to affect woody species composition (Appendix B). Given this interaction, community composition was analyzed for each VRH treatment separately and the effect of shrub competition was significant in all cases except within the large gap-aggregated treatment.

Several species were significant indicators of VRH and shrub treatments (based on Indicator Species Analysis, $p < 0.05$; (Table 3.4). *A. rubrum* and *P. strobus* were significant indicators in the untreated stands. The dispersed treatment was associated with *Corylus spp.*, and *Vaccinium spp.* and *P. glauca* when shrub competition was reduced. *Q. rubra, P. virginiana* and the shrubs, *Amelanchier spp.* and *D. lonicera,* were significant indicators of the small gap-aggregated treatment. *B. papyrifera*, as well as the shrubs *R. strigosus* and *L. canadensis*, responded to small gaps when shrubs were reduced. *Populus spp.*, mainly *P. tremuloides*, was found more often in the large gap-aggregated ambient shrub treatment.

Discussion

A central goal of traditional silvicultural systems is ensuring regeneration of desired tree species following harvest (Baker et al. 2013); however, little is known about natural regeneration response to VRH methods (Peck et al. 2012, Scott et al. 2013). Most long term studies examining regeneration development in VRH have focused on planted seedlings (Mitchell et al. 2007, Montgomery et al. 2010, Peck et al. 2012) and this study addresses the relationship with natural regeneration, which is particularly important as variable retention methods are increasingly utilized in places where planting is less common (Newsome et al. 2010).

Regeneration Response to Variable Retention Harvests

Although the overstory tree spatial patterns in our study areas resembled those found in some unmanaged *P. resinosa* forests in the region prior to harvest , we saw little evidence of *P. resinosa* recruitment, contrary to what would have been expected in historical multi-cohort systems (Fraver and Palik 2012). This result may be driven by several mechanisms. Prolonged periods of fire suppression have likely increased competition from fire-intolerant species and increased depth of the litter layer/organic matter (Nyamai et al. 2014) decreasing the suitability of seedbed conditions for *P. resinosa.* Further, while the overstory tree patterns in the present study may reflect natural disturbance patterns, the failure to emulate other important aspects of mixed severity fire regimes, namely reduced litter layer thickness, is likely limiting *P. resinosa* recruitment.

In addition to altered disturbance regimes, widespread establishment of fungal shoot blight diseases (*Sirococcus* and *Diplodia*) confounds management in *Pinus* systems in the western Great Lakes region in both planted and naturally regenerated stands (Haugen and Ostry 2013, Oblinger et al. 2013). Large regeneration densities of *P. resinosa* were greater in the large gap-aggregated treatments compared to other retention patterns by year 11, suggesting growth into the larger size class may be less impacted by disease in larger openings. This is supported by the work of Albers (2014) which showed that large gap-aggregated may decrease infection by shoot blight diseases by removing the main inoculum source from directly above or adjacent to seedlings. Large gaps also may have increased resource availability (Palik et al. 2003, Boyden et al. 2012), which may allow regeneration to reach size classes where shoot blight infection is less lethal. Therefore, in stands such as ours where fungal shoot blight diseases play a role in establishment, large gaps may provide opportunities for successful regeneration this species.

Contrary to our hypothesis, we did not find spatial variation of retention to be associated with greater variability of composition of regeneration. In particular, retention harvests were successful at reintroducing diversity to the establishing cohort regardless of the spatial pattern of retention, as we found few significant effects of retention pattern on large regeneration densities over the sampling period and no species or lifeform groups were significantly greater in the large gap-aggregated treatment. This result may be driven by a lack of spatial variability in key, limiting resources within treatments. Boyden et al. (2012) found that gap treatments in this study maintained greater variation in light environments, but spatial variability in soil nutrients were not as clearly related to the spatial variation of retention. Mean stand level light availability was greater in the gap treatments, and variability of soil nutrients may be limiting for some species. Although light may be a critical resource for the establishment of the tree species examined in this study, the lack of spatial structure in below ground resources may have prevented niche differentiation and greater levels of compositional diversity as would be expected in large gaps based on the gap partitioning hypothesis (Ricklefs 1977, Denslow 1980).

Lack of greater diversity of regeneration in large gaps compared to other treatments could also be a result of altered disturbance regimes, as discussed earlier, and species that would be expected to do well in large gaps (e.g. *P. resinosa* and intolerant hardwoods) may be inhibited by unsuitable seedbed conditions and competition. Interestingly, large regeneration densities of mid-tolerant hardwoods were greatest in the small gap-aggregated treatment and generally the lowest in large gaps. Other studies have found that response to increasing gap size may be dampened by shrub species and herbivory (Kern et al. 2012, Kern et al. 2013) and that regeneration response may be greatest in small/moderate gaps under these conditions. This may be the case here, as colonization of many disturbance-adapted herbaceous species, specifically *Carex pensylvanica and Rubus spp.,* which are indicators of the large and small gap-aggregated treatments, continued to occur in later years in these stands (Chapter 2). These species can form dense and persistent mats in the understory (Metzger and Schultz 1984, Jenkins and

Parker 2000, Royo and Carson 2006) and have been associated with decreased regeneration of tree species (Johnson 1992, Powers and Nagel 2009) and alterations of the successional trajectory of forest gaps. Influx of aggressive early successional species in the gaps was associated with reduced shrub competition, suggesting hazel removal may be releasing other competitors and creating challenging seedbed conditions for the establishment of tree seedlings.

Consistent with our hypothesis, the dispersed treatment maintained the greatest site level densities of large regeneration, particularly of hardwoods, by year 11 (Appendix C & D). This trend likely reflected the greater uniformity in light availability across this treatment, which allowed for treatment-level advancement from small to large regeneration stages across the entire treatment area (Boyden et al. 2012). Tolerant hardwood and tolerant conifer large regeneration increased in the dispersed treatment between the latest sampling years reflecting the ability of these species to establish and develop under the partially shaded microclimate conditions created by this treatment. This finding is consistent with other work examining long-term natural regeneration responses to VRH in which tolerant, late- successional species dominated the regeneration layer in dispersed retention treatments 11 years after treatment (Urgenson et al. 2013).

Overall, densities of hardwood large regeneration were much greater than any conifer or *Pinus* group in all treatments (Appendix C & D). This difference in density may be due to sprouting response following initial shrub reduction in year 1, as well as a greater tolerance of browsing damage relative to conifer species. An increase in hardwood species in the understory of *P. resinosa* dominated forests has been documented elsewhere in the Great Lakes region and has been attributed to long-term fire suppression (Nyamai et al. 2014). Competition from the disproportionately high density of hardwood species may increase the challenges associated with establishing conifer species in these forest types (Carleton et al. 1996, Nyamai et al. 2014), particularly in the absence of periodic surface fires to reduce their abundance.

Shrub Competition Effects on Regeneration Response

Consistent with our hypothesis, amount of shrub competition was in many cases as important as retention pattern in shaping natural regeneration. Even in the absence of canopy disturbance, dense understory layers can limit the growth, survival, density, and composition of regeneration (George and Bazzaz 1999a, b). Previous work examining planted tree regeneration from this study indicated that shrub treatment often had a greater impact on growth and survival of several species relative to retention pattern (Montgomery et al. 2013). Our results with natural regeneration also support this assertion; however, the influence of the shrub layer (positive, negative, or neutral) varied between species. Most notably, *P. strobus* densities were greater under an intact shrub layer, which is consistent with work from these sites that indicated survival of planted *P. strobus* was facilitated by shade from an understory shrub canopy (Montgomery et al. 2010). Results from other studies across the region examining *P. strobus* have been mixed, with some indicating a negative competitive effect of this layer (Cornett et al. 1998, Saunders and Puettmann 1999a) and others pointing to a positive effect of understory shrubs (Krueger and Puettmann 2004). The latter response can partially be attributed to protection from browsing pressure (Saunders and Puettmann 1999b) as well as suppressing competition from ground-layer early successional species (previous chapter). A positive effect of shrub competition on intolerant hardwoods was also observed, but is likely explained by cutting of *Populus spp*. stems during shrub reduction. In contrast, densities of small regeneration of *P. resinosa* were greater in stands where shrubs had been reduced 11 years following harvest. This delayed response to treatment suggests shrub reduction may provide conditions more conducive to germination, but browsing pressure remains a concern, particularly since this effect has not been observed in the larger size class. Continued measurement is needed to determine if decreased shrub competition results in increased survival and growth into the larger regeneration layer in later years, as smaller regeneration may be more vulnerable to browsing and lethal *Diplodia* infection.

Pattern and size of overstory disturbance and shade tolerance of regenerating species may not interact as expected in areas where dense and persistent understory shrub canopies are present (Royo and Carson 2006). As mentioned earlier, many species and life-form groups did not always respond as would be predicted by the gap partitioning hypothesis (Ricklefs 1977, Denslow 1980). More specifically, tolerant and intolerant hardwood small regeneration response to retention pattern may have been masked by the impacts of the shrub canopy on resource availability. Tolerant hardwoods did well in the dispersed treatment compared to the gap treatments, as would be expected, when shrubs were reduced. Intolerant hardwoods in the smaller regeneration class were more common in the large gap-aggregated treatment, but only if shrubs were reduced. In these cases, proliferation of *Corylus* and *Rubus* spp. may be negating increases in light and below-ground resources that drive treatment effects that would otherwise be created at the ground-layer following harvest. In contrast, mid-tolerant species (*P. strobus* small and large regeneration as well as small regeneration of mid-tolerant hardwoods) only differed between retention treatments when the recalcitrant understory was left intact. This may reflect greater browse protection, but hardwood stems could also potentially have been inadvertently cut during initial shrub reduction.

Conclusions & Management Implications

Roberts (2004) outlined three axes of severity for evaluating how anthropogenic disturbance relates to natural disturbance, specifically in terms of the forest ground-layer, which is intimately associated with regeneration. Namely, the axes are represented by the major vertical layers in forest systems: the canopy, understory vegetation, and the forest floor/soil. Two of these axes, canopy and understory vegetation, were addressed in the Red Pine Retention Study. Retention harvest created differing mosaics of overstory structure that might be expected following mixed-severity fire. Reduction of shrubs emulated disturbance impacts on the understory vegetation layer, at least in terms of one of the principle understory layers (*Corylus spp/Rubus spp*) impacting regeneration. Despite these two axes being addressed, forest floor and soil disturbances were lacking, and likely had a substantial impact on regeneration dynamics. Mixed severity fire regimes are heterogeneous, and can result in decreases in organic material and duff (Christensen et al. 1989). Consequently, these decreases in organic material can create patches of exposed mineral soil, which are essential to regeneration of *P. resinosa* and *P. strobus* (Turner et al. 1997). These patches of exposed mineral soil were minimal in our treatment stands.

This work suggests that variation in retention pattern, cohort-structure, and species makeup observed in this study is only partially consistent with pre-European *P. resinosa* forests in the western Great Lakes region. The use of VRH may more closely mimic the canopy disturbance of mixed severity disturbance regimes compared to *P. resinosa* managed in single-cohort monocultures. That being said, the desired result of mixed-species, multi-cohort forests may be co-dependent on other disturbance mechanisms associated with mixed-severity fire. This argues for addressing all three axes of severity either through fully reintroducing the natural disturbance regime or, alternatively, by circumventing the bottleneck of germination and early survival through planting. This may only be required for species that depend on resource and seedbed conditions not found as a result of prescribed canopy and understory disturbance. These mechanisms are important to consider when functional emulation of the natural disturbance regime is a goal.

Natural regeneration of *P. resinosa* was limited compared to other species/successional groups. Additional treatments, including altering the seed bed (e.g. exposing mineral soil) and supplemental planting, may remove barriers to successful regeneration in the absence of fire. The presence of shoot blight diseases such as *Diplodia* and *Sirococcus* must be considered when regenerating *P. resinosa* beneath or adjacent to mature trees. *P. strobus* was an important component of this forest type, and has historically been significant throughout the Great Lakes region. As such, there is interest in increasing this species on the landscape (Frelich 1995, Peck and Zenner 2009). Separating cohorts in time, as opposed to space, could provide an alternative to by-pass difficulties with *P. resinosa* regeneration; a long lived species which would persist on the landscape regardless of the composition of the new cohort. Focusing regeneration on *P. strobus* would maintain canopy dominance with a conifer species historically abundant in this forest type. Additionally, focusing regeneration on *P. strobus* would allow opportunities for future regeneration of *P. resinosa* below a canopy dominated by species less prone to *Sirococcus* and *Diplodia* (Ostry et al. 2012).

Objectives are the primary driver behind management decisions and in many cases goals have shifted towards diversifying composition. In light of this, the VRH treatments we examined were very successful, and managers have flexibility in utilizing various retention patterns across harvested areas. Retention pattern can be utilized to shift forest succession through introduction of a range of hardwood and conifer species. Shifting succession towards *P. strobus* dominance may provide more opportunities for facilitating *P. resinosa* regeneration in the future. These forests may shift, however, towards mixed hardwood stands if alternative treatments or planting are not employed to ensure adequate and successful conifer regeneration.

Table 3.1. Results of ANOVA examining the impacts of VRH and shrub treatments as well as time on natural small tree regeneration densities in *Pinus resinosa* forests in northern Minnesota

		P. resinosa		*P. strobus*		tolerant conifers		tolerant hardwoods		mid-tolerant hardwoods		intolerant hardwoods	
Main effect	df	*F* stat	*p* value	*F* stat	*p* value	*F* stat	*p* value	*F* stat	*p* value	*F* stat	*p* value	*F* stat	*p* value
VRH	3	0.094	0.9634	1.914	0.1313	4.952	0.0029*	29.170	<.0001*	0.681	0.5655	7.461	0.0001*
shrub	1	1.899	0.1709	7.989	0.0056*	0.829	0.3645	5.620	0.0194*	2.453	0.1201	0.262	0.6096
year	4	2.935	0.0237*	0.476	0.7534	1.029	0.3955	2.762	0.031*	2.246	0.0684	1.831	0.1276
VRH x shrub	3	0.030	0.9931	5.890	0.0009*	2.194	0.0926	3.648	0.0148*	3.707	0.0137*	3.221	0.0254*
VRH x year	12	2.027	0.0279*	0.316	0.9853	0.617	0.8237	1.045	0.4131	0.801	0.6486	1.541	0.1198
shrub x year	4	2.789	0.0297*	0.454	0.7691	0.383	0.8207	0.613	0.6542	0.742	0.5655	0.466	0.7608
VRH x shrub x year	12	0.641	0.8031	0.177	0.9991	0.294	0.9892	0.316	0.9853	0.984	0.4687	0.421	0.9526

Table 3.2. Results of ANOVA examining the impacts of VRH and shrub treatments as well as time on natural large regeneration in *Pinus resinosa* forests in northern Minnesota

		P. resinosa		*P. strobus*		tolerant conifers		tolerant hardwoods		mid-tolerant hardwoods		intolerant hardwoods	
Main effect	df	*F* stat	*p* value	*F* stat	*p* value	*F* stat	*p* value	*F* stat	*p* value	*F* stat	*p* value	*F* stat	*p* value
VRH	3	0.691	0.5601	2.259	0.0868	3.783	0.0131*	0.822	0.4848	2.713	0.0494*	2.379	0.0748
shrub	1	0.230	0.6327	7.993	0.0058*	1.387	0.242	3.079	0.0826	0.730	0.3952	11.531	0.001*
year	3	2.512	0.0634	7.436	0.0002*	1.247	0.2972	6.910	0.0003*	6.510	0.0005*	10.582	<.0001*
VRH x shrub	3	0.185	0.9063	3.620	0.016*	0.084	0.9687	0.225	0.8791	1.128	0.3418	0.667	0.5747
VRH x year	9	1.730	0.0932	0.532	0.8479	0.839	0.582	0.560	0.8264	1.313	0.2411	1.031	0.4214
shrub x year	3	0.322	0.8091	1.919	0.132	0.757	0.521	0.732	0.5357	1.964	0.1249	2.062	0.1106
VRH x shrub x year	9	1.873	0.0658	0.674	0.7305	0.559	0.827	0.231	0.9892	0.413	0.9255	0.954	0.4832

Table 3.3. Species with significant correlations with the first two axes of the NMS ordination of woody regeneration in *Pinus resinosa* forests in northern Minnesota (Figure 2). All axes correlation *p-values* <0.0008 (Significant following Bonferroni correction)

Axis	Relationship	Species	Kendall's τ
1	positive	*Abies balsamea*	0.413
		Rubus strigosus	0.341
		Corylus spp	0.229
	negative	*Quercus rubra*	-0.297
		Vaccinium spp	-0.793
		Pinus resinosa	-0.319
		Diervilla lonicera	-0.202
		Amelanchier spp	-0.223
2	negative	*Rubus strigosus*	-0.589
		Vaccinium spp	-0.223
		Diervilla lonicera	-0.197
		Betula papyrifera	-0.185

Table 3.4. Significant indicator species of VRH and shrub treatments by indicator for woody regeneration in *Pinus resinosa* forests in northern Minnesota

VRH	Shrub	Species	IV	*p* -value
Control	Ambient	*Acer rubrum*	21.3	0.0004
		Pinus strobus	22.3	0.0022
	Reduced	-	-	-
Small Gap-Aggregated	Ambient	*Quercus rubra*	23.6	0.001
		Amelanchier spp.	20.1	0.0026
		Prunus virginiana	22.9	0.0036
		Diervilla lonicera	17.3	0.046
	Reduced	*Rubus strigosus*	31.1	0.0004
		Betula papyrifera	25.7	0.0034
		Lonicera canadensis	18.6	0.0478
Large Gap-Aggregated	Ambient	*Populus spp.*	20.8	0.0024
	Reduced	-	-	-
Dispersed	Ambient	*Corylus spp.*	16.7	0.0266
	Reduced	*Vaccinium spp.*	19.3	0.0012
		Picea glauca	10.8	0.0318

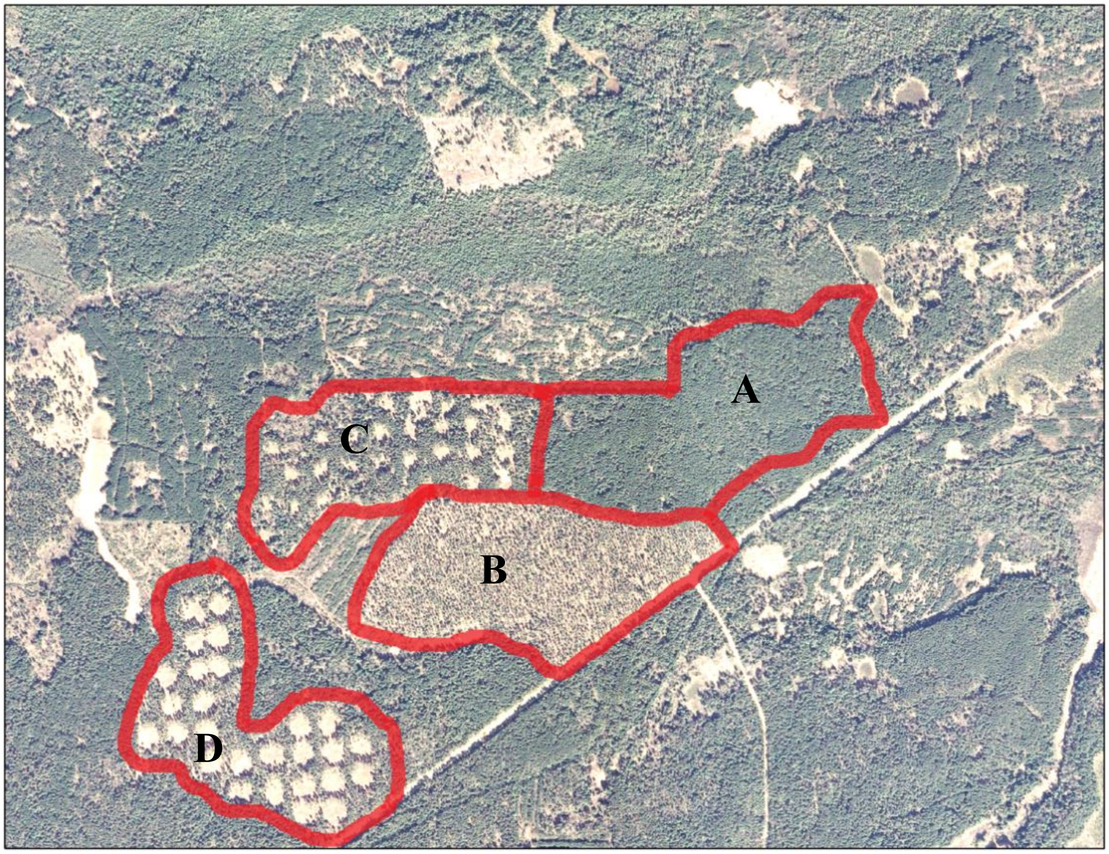

Figure 3.1. Aerial view of variable retention harvest treatments at the Red Pine Retention Study (One of four blocks). The (A) reference is uncut forest while the (B) dispersed, (C) small gap-aggregated and (D) large gap-aggregated are variable retention harvest treatments with variations of spatial retention pattern. Trees were retained uniformly in the dispersed treatment, while 0.1 hectare groups were harvested in the small gap-aggregated and 0.3 ha gaps in the large gap-aggregated treatments. All variable retention treatments represent a common level of live-tree retention (~45%).

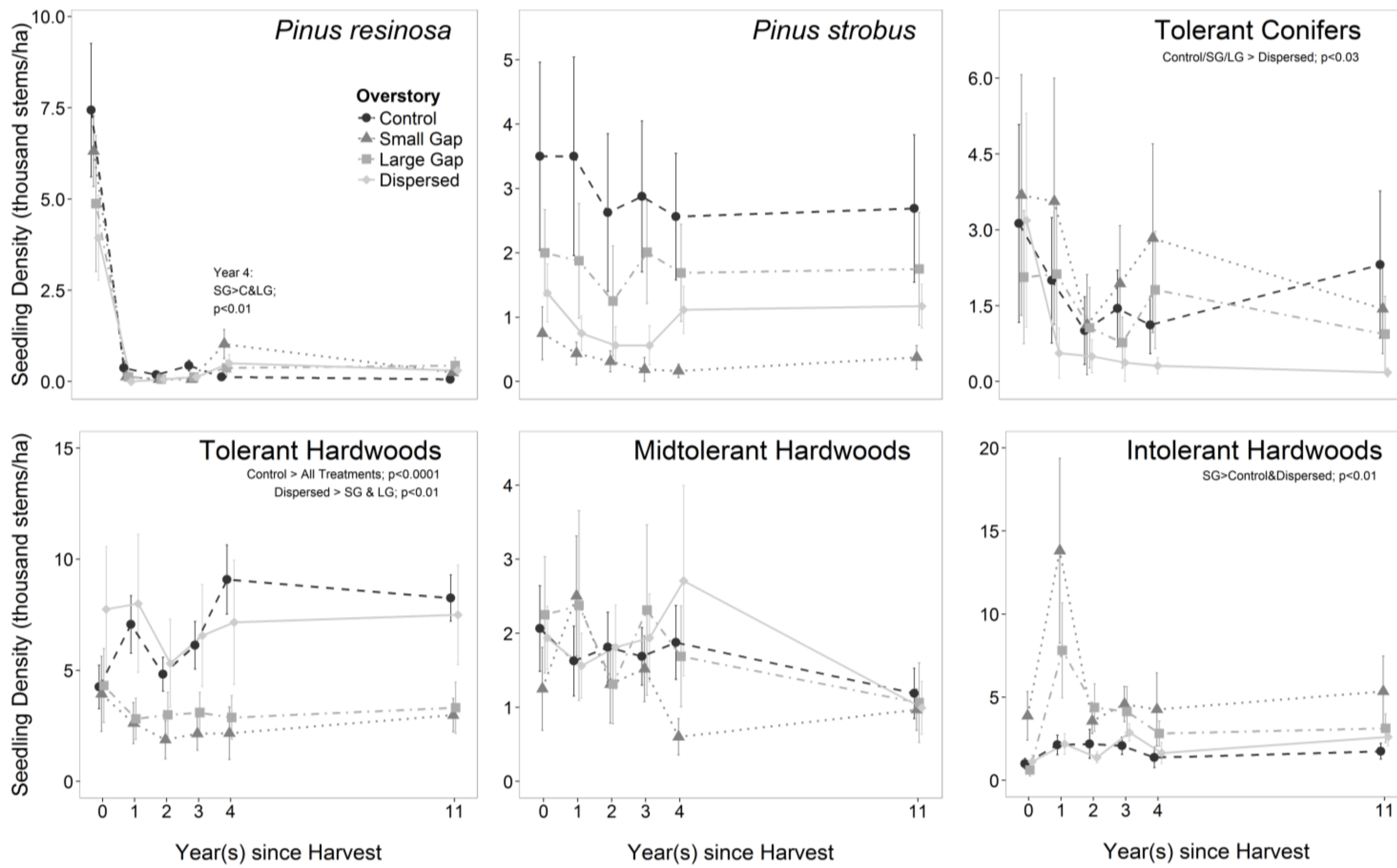

Figure 3.2. Unadjusted mean and standard error of densities of small regeneration (<1m height) prior to treatment (year 0), immediately following harvest and 11 years later. Species/groups are separated by variable retention (overstory) treatment (Treatment labels: Control (C), Small Gap-Aggregated (SG), Large Gap-Aggregated (LG), Dispersed (D)).

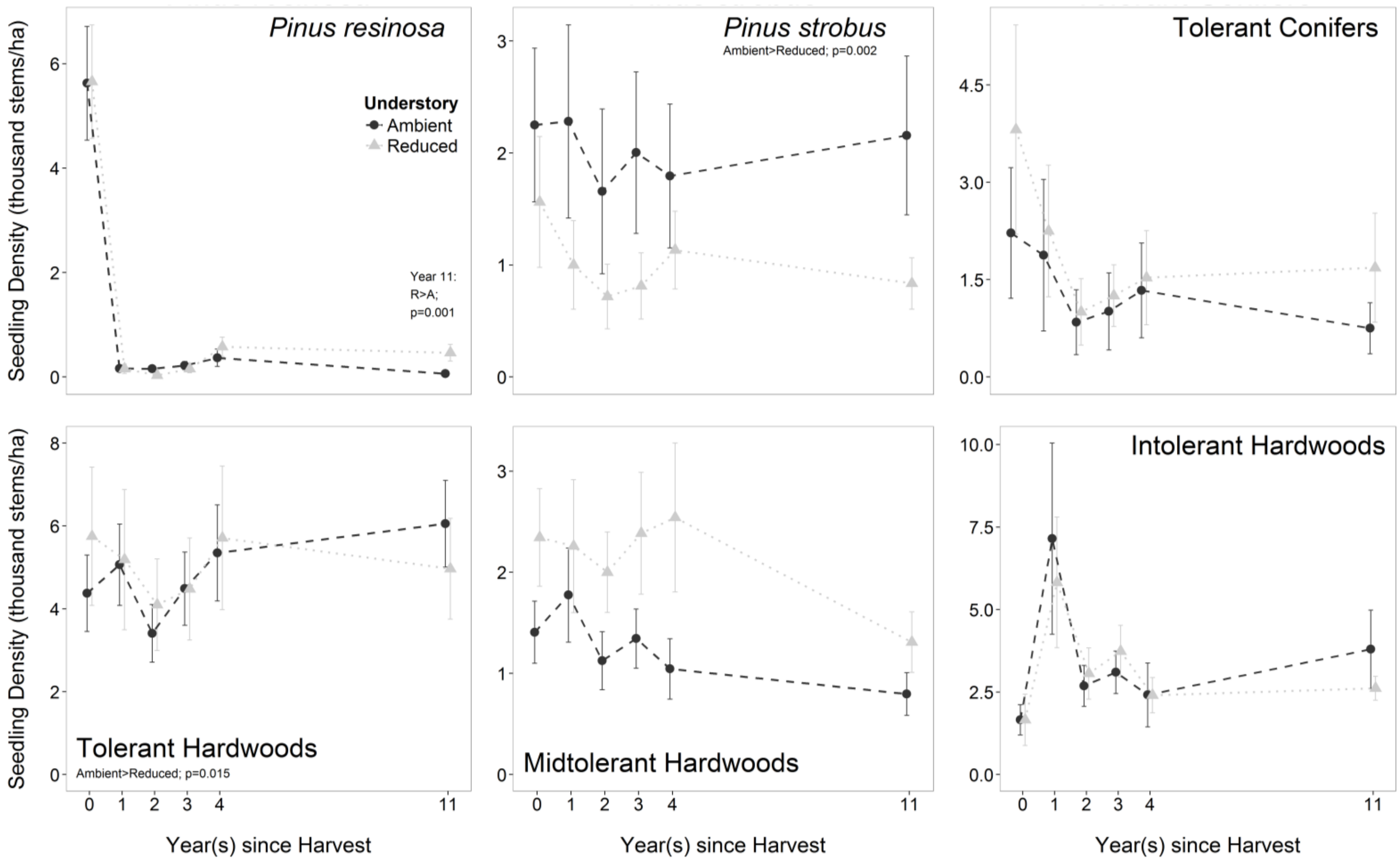

Figure 3.3. Unadjusted mean and standard error of densities of small regeneration (<1m height) prior to treatment (year 0), immediately following harvest and 11 years later. Species/groups are separated by shrub (shrubs Ambient (A) / Reduced (R)) treatment

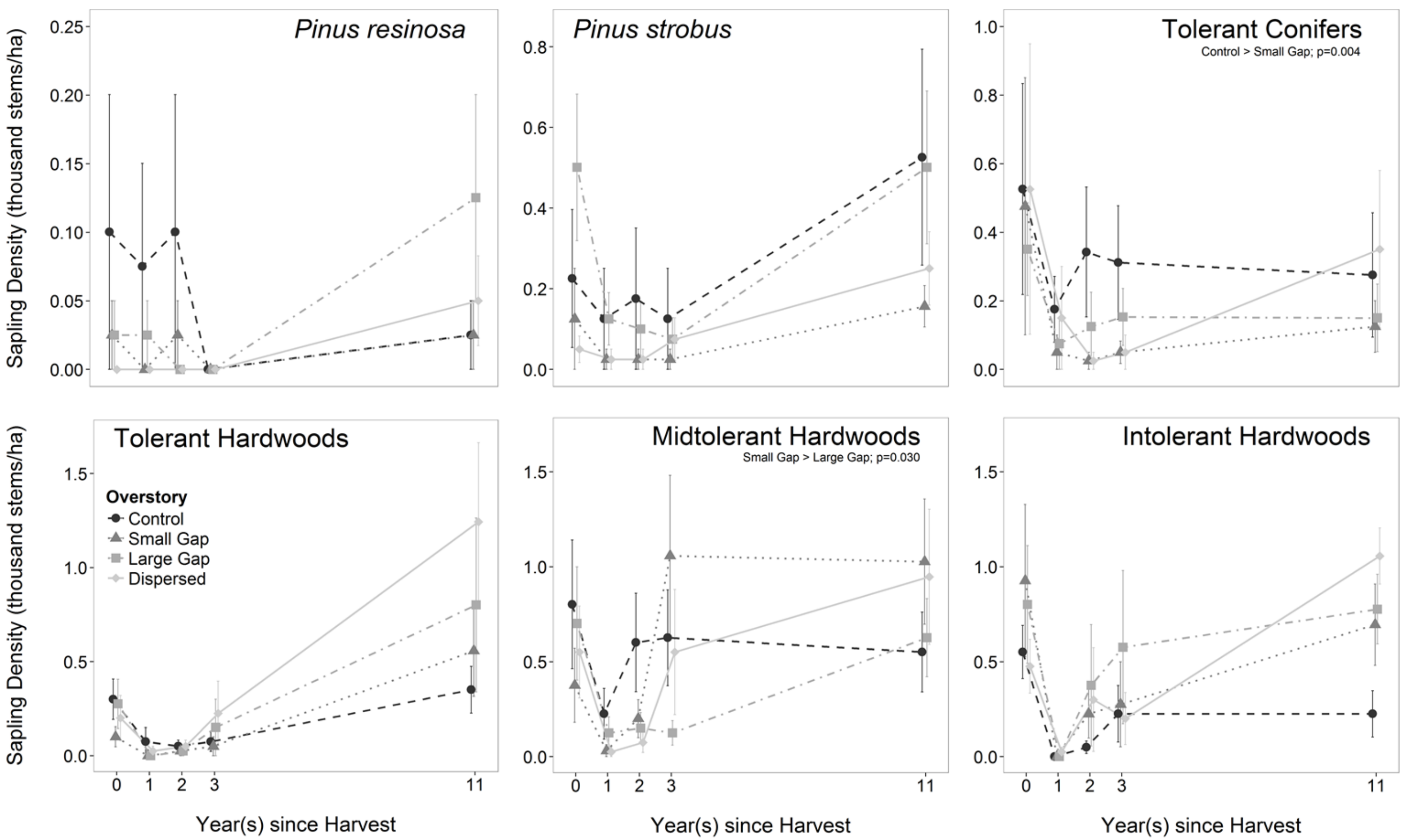

Figure 3.4. Unadjusted means and standard errors of densities of large regeneration (>1m height, < 2.54 cm dbh) prior to treatment (year 0), immediately following harvest and 11 years later. Species/groups are separated by overstory (variable retention harvest) treatment (Treatment labels: Control (C), Small Gap-Aggregated (SG), Large Gap-Aggregated (LG), Dispersed (D))

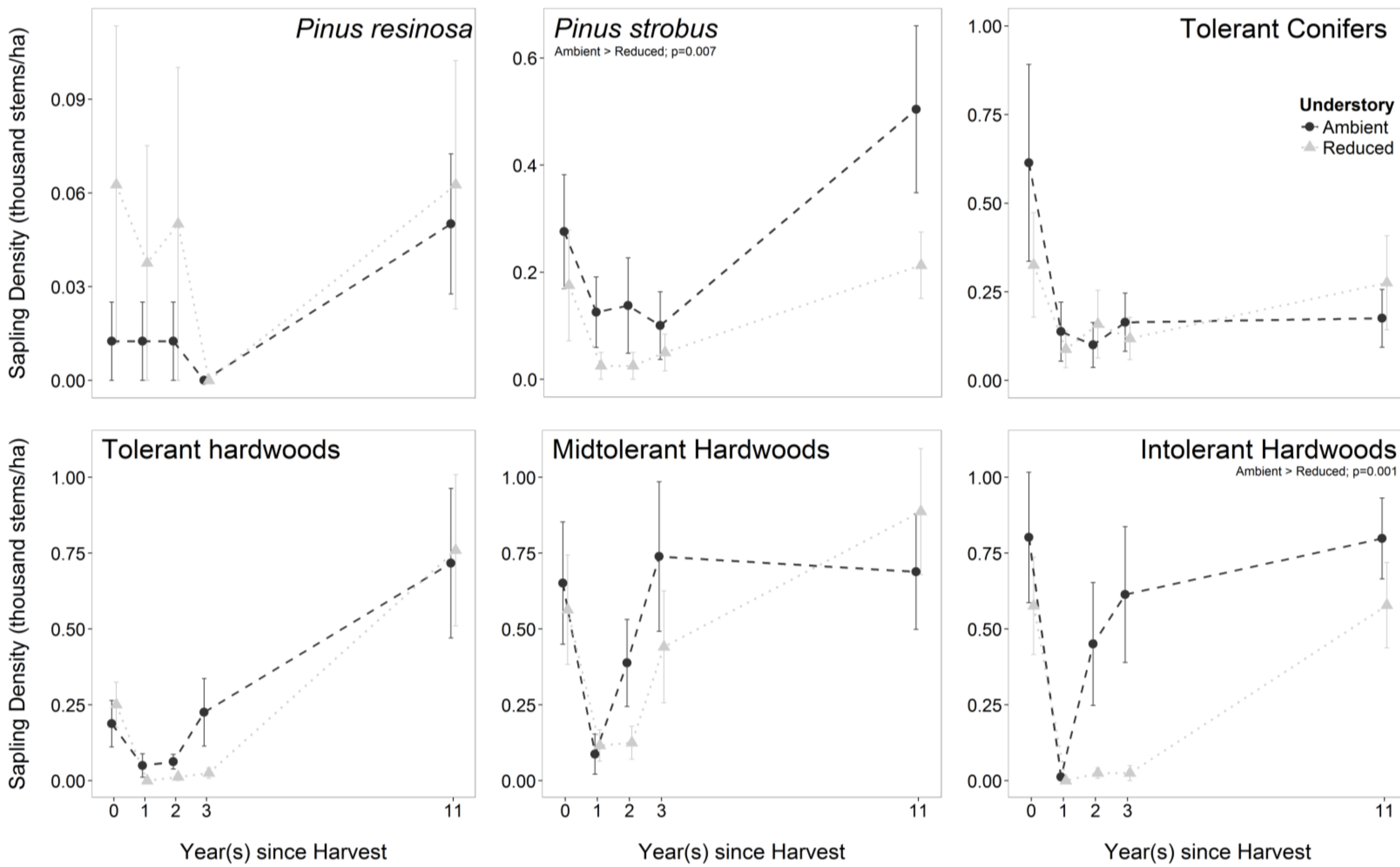

Figure 3.5. Unadjusted means and standard errors of densities of large regeneration (>1m height, < 4 in. dbh) prior to treatment (year 0), immediately following harvest and 11 years later. Species/groups are separated by shrub (shrubs ambient/reduced) treatment

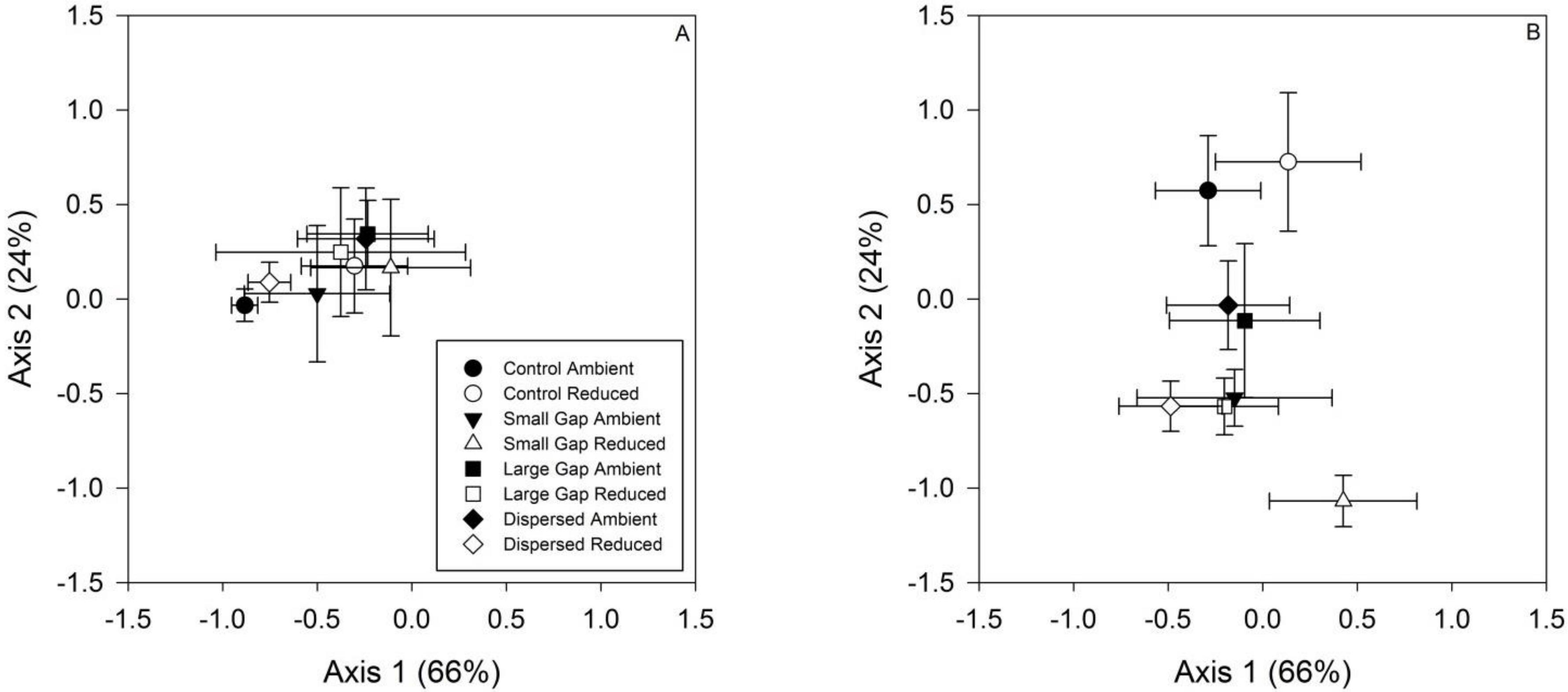

Figure 3.6. NMS ordination of community composition of woody regeneration (averaged with standard error bars) pre-treatment (A) and 11 years post-treatment (B) in *Pinus resinosa* forests in northern Minnesota

Chapter 4: Conclusions

This thesis highlights responses of the ground layer and natural regeneration to variable retention harvest (VRH) that have important implications for management practices that emulate natural disturbance patterns. In the second chapter, we found that interior species were resistant to canopy disturbance and continued to persist across treatments regardless of retention pattern. The regeneration response in the third chapter suggests VRH did not fully emulate the natural disturbances that historically occurred in these communities, particularly the levels of understory and ground layer disturbance that likely occurred with mixed severity fire. This lack of disturbance likely allowed for the maintenance and increase in ground-layer richness and diversity observed in this thesis yet also contributed to the limited recruitment of the dominant species, namely *P. resinosa*, following these harvests. Beyond lack of ground layer and soil disturbance, the singular and interactive effects of other factors, including shoot blight diseases, shrub competition, and deer herbivory also affected recruitment response to VRH.

Retaining mature tree structures may only partially address the mechanisms driving the diverse and complex forests that resulted from mixed-severity fire. Silvicultural systems aimed at restoration face multiple stressors that likely were not present prior to European settlement, including fire suppression, the formation of recalcitrant understory layers (Royo and Carson 2006) and increased browsing pressure. Additionally, shoot blight diseases have been introduced becoming a common component in once relatively disease free *P. resinosa* stands in the western Great Lakes (Albers 2014). These stressors alter response to anthropogenic and natural disturbance. Because of this, the ground layer and natural regeneration may not respond to disturbance in the same way they did historically. Management expectations and goals may need to be adjusted to account for these current dynamics.

Management Implications

Overall, the emphasis of natural disturbance-based silvicultural regimes, such as VRH, has been on emulating overstory disturbance pattern and severity (Franklin et al. 1997). However, altered understory and soil conditions may have a greater impact on ground-layer and regeneration response to overstory disturbance (Roberts 2004, Bolton and D'Amato 2011, Kern et al. 2012). Implementing VRH will likely require planting to ensure adequate regeneration of *Pinus* spp. unless other measures are taken to more closely mimic natural disturbance. Treatment options could include reintroducing fire or deliberate treatment of the soil, such as mechanical mulching, which has been shown to result in high *P. resinosa* regeneration densities in a partial harvest setting (D'Amato et al. 2012). Even with planting, release treatments may be necessary to ensure these species maintain a competitive advantage, both in terms of the *Corylus* layer and high densities of hardwood small and large regeneration.

Results from both chapters highlight the importance of the recalcitrant understory layer in this system. Even in cases where management goals do not emphasize ground-layer response to harvest, shrub competition can negate the effects of retention pattern and negatively impact growth of regeneration (Montgomery et al. 2013). If other treatments were prescribed to address seedbed conditions, they would have to be done so with shrub competition in mind. Fire would need to be applied repeatedly to effectively reduce *Corylus spp*. as this species re-sprouts prolifically following a single burn (Buckman 1964) and a single prescribed fire does not appear to increase *P. resinosa* regeneration, likely a result of maintained or increased shrub competition (D'Amato et al. 2012).

Herbivory and disease are also important factors to consider. Understory treatment effects on small and large regeneration are likely partly due to deer herbivory. Treatments to limit browsing, particularly of *P. resinosa* and *P. strobus*, key species in this system, may be particularly important in conjunction with treatments that reduce competitive conditions around seedlings. Planted seedlings (all *Pinus spp*) were treated with Plantskydd, a browse repellent, throughout the sampling period to reduce the effects of browse and VRH and shrub-layer treatment effects may be driven by other factors in those cases (Montgomery et al. 2013). Large gaps may be beneficial in decreasing *Diplodia* and *Sirococcus* infection, which has been shown to significantly impact growth and survival of *Pinus spp* on these sites (Ostry et al. 2012). Focusing regeneration on *P. strobus* could provide an alternative to by-pass difficulties with regenerating *P. resinosa* beneath retained trees. This approach would maintain canopy dominance with a conifer species historically abundant in this forest type and allow opportunities for future regeneration of *P. resinosa* below a canopy dominated by species less prone to *Sirococcus* and *Diplodia* (Ostry et al. 2012).

Emerging Issues

Introducing functional diversity to the stand allows for future adaptive capacity that may be important in light of global change (Puettmann 2011). If management objectives call for diversifying tree composition, managers have flexibility in utilizing various retention patterns across harvested areas to increase the presence of hardwoods and tolerant conifers, achieving composition likely more consistent with historical stands (Fraver and Palik 2012). However, these forests may shift towards mixed hardwood stands if alternative treatments or planting are not employed to ensure successful conifer regeneration. Additionally, not all of the species introduced are predicted to do well in these systems in the future, and increasing species diversity may not translate to increased functional and response-type diversity.

Heterogeneity was an important driver of resilience to disturbance in fire adapted forests historically (Churchill et al. 2013). The spatial pattern of retention is related to important aspects of ecological resilience and ecosystem function (Churchill et al. 2013) and VRH creates different elements of adaptive capacity within a stand. The gap-based retention treatments utilized in this study may help enhance resilience of these stands through maintenance of a variety of functional traits, but we did not find that this treatment resulted in the greatest diversity in tree regeneration.

To encourage functional diversity of tree species, seedbed conditions and the recalcitrant understory will need to be addressed to allow tree regeneration to respond to varying spatial patterns of resource availability. In this study, large regeneration densities of the future adapted species *P. strobus* are increasing in the large gap-aggregated treatments (Prasad et al. 2007-ongoing). This species may be an ideal alternative to the dominant species, which is also increasing in this treatment, but is projected to decline in suitability [at least in north central MN;(Prasad et al. 2007-ongoing)].

Uniform treatments implemented over large areas may result in decreased resilience at the landscape level and limit management opportunities (Churchill et al. 2013). Dispersed retention shifted the balance towards a greater component of shade tolerant tree species and large regeneration recruitment densities are greatest in this treatment. While the increased component of tolerant conifer species (*A. balsamea* and *P. glauca*) is a concern given the projected declines in suitable habitat for these species under climate change*, A. rubra* also maintained even greater densities in this treatment, and is projected to have increased habitat suitability (Prasad et al. 2007-ongoing).

Ideally, variation in spatial arrangement of retention across the landscape, with a mix of dispersed and gap/aggregate treatments, would ensure a range of conditions are created to maintain stand and landscape resilience to global change and future disturbance. Managing forests as complex adaptive systems suggests that increasing a stands ability to adapt to disturbance likely means increasing the diversity of response-type and functional traits (Puettmann 2011). The treatments outlined in this thesis either encouraged or allowed for planting of a species mixture that includes various response-types (hardwoods via sprouting, *Pinus banksiana* via serotinous cones, etc.) that increase the range of disturbances where natural regeneration could successfully occur. Increases in richness, diversity, and cover of the ground-layer created as a result of VRH may also provide key ecosystem services in the wake of disturbance. Finally, retention is likely a crucial structural aspect of forests facilitating restructuring following disturbance, and reintroducing or emulating the other aspects of disturbance severity capitalize on adaptation to historic disturbance regimes to generate resilient responses (Puettmann 2011).

Study Limitations

Addressing all three axes of disturbance severity (Roberts 2004) is likely an important part of management practices designed to emulate natural disturbance regimes. Two of these axes, canopy and understory vegetation, were addressed in the Red Pine Retention Study. Shrub reduction emulated disturbance impacts on the understory vegetation layer, at least in terms of one of the principle understory layers (*Corylus spp/Rubus spp*) impacting regeneration, if not ground-layer herbaceous species. However, shrub reduction likely resulted in other species being cut in addition to the targeted species (woody shrubs and *Populus spp*) which may have impacted treatment effects. Additionally, forest floor and soil disturbance was lacking, and likely had a substantial impact on regeneration dynamics. Mixed severity fire regimes are heterogeneous, and can result in decreases in organic material and duff (Christensen et al. 1989). These patches of exposed mineral soil, which are essential to regeneration of *P. resinosa*, were lacking in our stands.

We examined the impact of retention harvest on maintaining ground-layer species present in our study stands. While these stands maintained many herbaceous forest interior species, they were not old-growth stands. Studies have shown that forest understories may take prolonged periods of time to revert to old-growth conditions

(D'Amato et al. 2009). Late-successional species currently present in stands were maintained, but we did not determine if treatments had an impact on delaying the successional trajectory of ground-layer communities by increased representation of early successional species.

The observed responses may not be as applicable in more mesic systems, where canopy disturbance was less common historically, as the regeneration and ground-layer response we observed is likely a result of adaptation to mixed-severity fire regimes. Our results are important for future consideration of VRH in *P. resinosa* and perhaps other fire-dependent ecosystems having a similar natural disturbance history.

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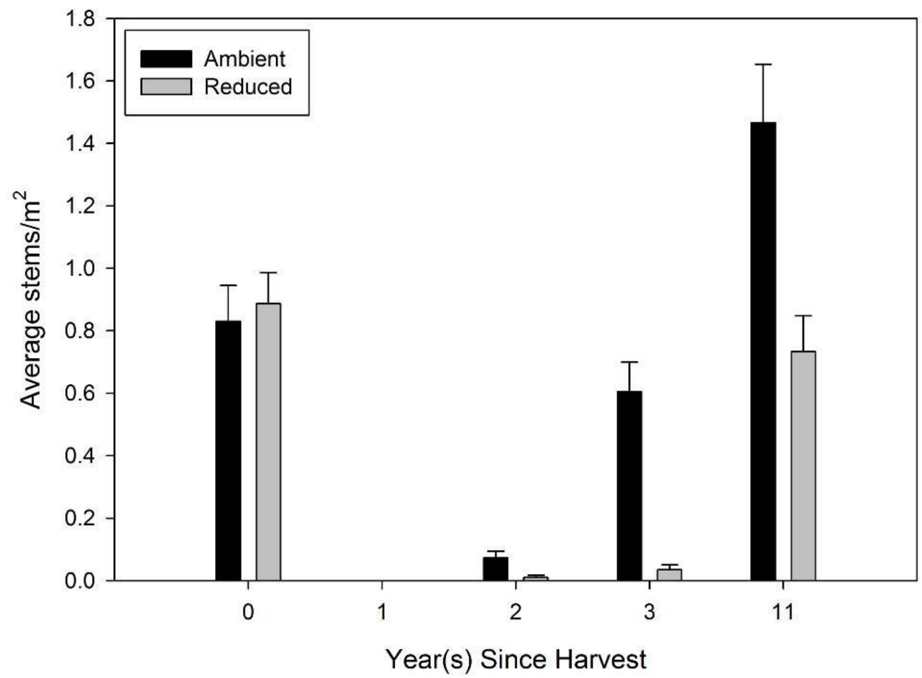
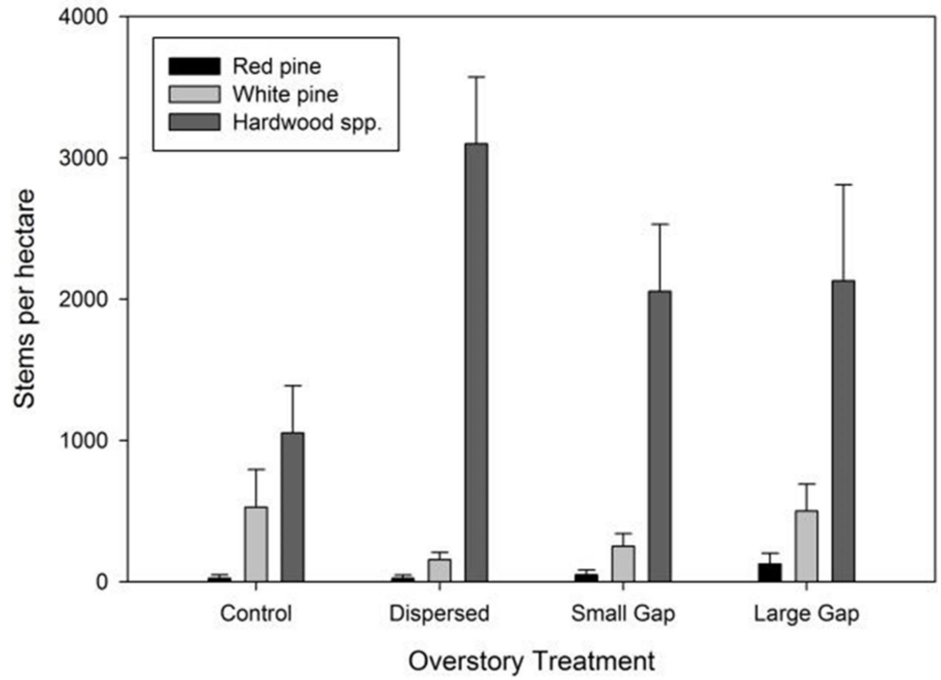
Appendices

Appendix A. Average densities of large regeneration *Corylus* stems in ambient and reduced shrub treatments throughout the sampling period



Appendix B. Results of perMANOVA examining the impacts of overstory and understory treatments as well as time on the composition of woody regeneration in red pine forests in northern Minnesota

Main effect	Df	*F*	Pr(>*F*)
VRH	3	5.925	0.001
shrub	1	1.168	0.113
year	4	5.393	0.001
VRH x shrub	3	2.622	0.001
VRH x year	12	0.595	0.673
shrub x year	4	0.327	0.963
VRH x shrub x year	12	0.295	1.000



Appendix C. Unadjusted mean and standard error of large regeneration densities 11 years following harvest. Minimum trees per hectare at five years of age necessary to adequately restock forests after tree harvest (conifers = 988 trees/ha) (USDA Forest Service 2004)

Appendix D. Unadjusted mean and standard error of large regeneration densities 11 years following harvest. Minimum trees per hectare at five years of age necessary to adequately restock forests after tree harvest (conifers = 988 trees/ha) (USDA Forest Service 2004)

VRH Treatment	Hardwoods	*Pinus spp*
Control	1052.1±333.9	551.1±261.7
Dispersed	3099.3±471.4	300.6±84.6
Small Gap-Aggregated	2054.1±475.6	181.6±59.8
Large Gap-Aggregated	2129.2±680.5	626.2±175.3

Appendix E . Unadjusted mean and standard error of large regeneration densities 11 years following harvest. Minimum trees per hectare at five years of age necessary to adequately restock forests after tree harvest (conifers=988 trees/ha) (USDA Forest Service 2004)

Shrub Treatment	Hardwoods	*Pinus spp*
Ambient	1978.9±334.2	554.2±148.7
Reduced	2188.4±442.1	275.5±72.8