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Effects of variable retention harvesting on natural tree regeneration in *Pinus resinosa* (red pine) forests

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ABSTRACT

Concerns over loss of ecosystem function and biodiversity in managed forests have led to the development of silvicultural approaches that meet ecological goals as well as sustain timber production. Variable Retention Harvest (VRH) practices, which maintain mature overstory trees across harvested areas, have been suggested as an approach to balance these objectives; however, long-term evaluations of outcomes of VRH strategies do not exist for most forest types. The objective of this study was to determine the 11-year effects of overstory tree retention pattern and shrub removal on regeneration in *P. resinosa* forests in Minnesota, USA using a large-scale manipulative study in which four overstory (control, small gap-aggregated, large gap-aggregated, and dispersed) and two shrub (ambient and reduced shrubs) treatments were applied. Hardwood regeneration greatly outnumbered conifer regeneration and several mechanisms (disease, browse, and seedbed conditions) likely interacted to limit *P. resinosa* regeneration across treatments. The presence of recalcitrant shrub layers filtered response to retention with regeneration of *P. strobus* L. being greater under an intact *Corylus* layer irrespective of overstory conditions. This work reinforced the importance of accounting for shrub competition when designing VRH to secure natural regeneration.

1. 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). Retention of overstory trees following harvest is one approach that is increasingly being utilized to retain mature forest structures and conditions in post-harvest stands (Gustafsson et al., 2012). These structures were historically present under natural patterns of mixed severity disturbance; however, they have largely been lost or greatly reduced in many managed forests, particularly when using even-aged silviculture. The pattern of surviving trees following natural disturbances, particularly fire, was often spatially variable (Larson and Churchill, 2012) and variable retention harvest (VRH) practices 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, the concept is still relatively new, such that considerable knowledge gaps exist regarding the long-term impacts of these practices (and how they are implemented) on forest ecosystem structure and composition.

Given the underlying objectives of ecologically focused management much of the research to date examining VRH has focused on relationships between forest biodiversity and structure, (Gustafsson et al., 2012). Nonetheless, the establishment and growth of regeneration is an important goal in most if not all management settings (Franklin et al., 1997; Urgenson et al., 2013) and requires attention in VRH practices to ensure long-term sustainability. One of the key decisions when implementing VRH is the spatial pattern of retention (i.e., dispersed or aggregated), which has been shown to impact resource availability and competition (Boyden et al., 2012; Palik et al., 2003) and numerous studies have highlighted that overstory retention may delay regeneration establishment and growth, particularly for shade-intolerant species (Mitchell, 2001; Palik et al., 1997; Urgenson et al., 2013; Zenner et al., 1998). Retained trees also provide a source of seed and potential access to mycorrhizae (Luoma et al., 2006) and hence

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could enhance establishment and growth of regeneration. Given these effects, there is a need to investigate these aspects of tree regeneration across a range of spatial retention patterns and species groups.

One of the primary hypotheses behind VRH is that post-harvest retention of live trees in a range of spatial arrangements more closely approximates the post–disturbance structural conditions found under natural disturbance, such as mixed severity fire regimes (Franklin et al., 1997). These regimes 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; Larson and Churchill, 2012). This variation in conditions maintains a diversity of microhabitats, likely allowing various tree species to establish and persist. In *Pinus resinosa* ecosystems in the western Great Lakes region, fire and wind likely created this resource heterogeneity at a smaller scale than is traditionally thought for mixed severity fire and generated within-stand patchiness and variability in overstory tree and understory resource conditions over space and time (Fraver and Palik, 2012).

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 in many regions of the globe is the formation of a dense and persistent layer of one or several species of woody shrubs in the understory, often due to alterations in historic disturbance regimes in conjunction with elevated levels of herbivory (Royo and Carson, 2006). For example, dense understories of *Corylus americana* Walter and *C. cornuta* Marshall (American and beaked hazel, respectively) exist in forests in the western Great Lakes region, likely reflecting changes to the fire regimes in these forests, which historically included high frequency, low intensity surface fires that 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 ecosystems, affecting 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 understory layers on the efficacy of VRH in today's forests is important to achieving objectives associated with the establishment of new cohorts of trees.

This study aimed to examine the relationship between three spatial variants of residual trees in VRH and natural tree regeneration in *Pinus resinosa* (red pine) forests. The applied goal of this work is to evaluate the effectiveness of utilizing different retention patterns to establish mixed species stands while maintaining levels of structural complexity likely observed under natural disturbance regimes. To accomplish this, we used 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 medium-term evaluation of the effectiveness of VRH practices at regenerating forests that are more similar to historical conditions in terms of both increased structural complexity and tree species richness. More specifically, this study examined the impacts of a range of spatial patterns of retained trees on the 11-year dynamics of natural tree regeneration, while holding abundance of overstory retention constant (~45%). Additionally, the study provided an opportunity to examine the interaction between a recalcitrant shrub layer and retention pattern when regenerating mixed species stands in *P. resinosa* ecosystems. We hypothesized that the spatial pattern of retention would significantly impact long-term abundance and composition of tree regeneration, with the gap-based, aggregated retention resulting in greater densities of shade-intolerant *Pinus resinosa* (due to more open high light environments in gaps) than dispersed retention or unmanaged reference areas. In addition, we hypothesized that reducing shrub layer density would increase density of large (>1-m tall) tree regeneration (as this size class better represents regeneration that has successfully established) more than ambient (reference) shrub density.

2. Methods

2.1. 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 occurring primarily between April and October and mean annual temperature of 4 °C. The study sites occupy outwash and ice contact landforms, with deep sand parent material supporting excessively to well-drained, nutrient poor loamy sand soils. Overall, sites are low elevation (400–450 m) with little topographic relief.

At the time of initial treatment, stands in the study area were approximately 85 years old, broadly even-aged and dominated by *Pinus resinosa*. Stands had naturally regenerated between 1910 and 1912 following logging and wildfires. All of the stands had basal areas of approximately 32 m^2/ha prior to treatment with a moderately open canopy, and dominant trees averaging 27 m in height (Palik et al., 2014).

The study sites are classified as northern dry-mesic mixed forests, 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 (MN DNR, 2003). While dominated by *P. resinosa*, the overstory contained lesser amounts (~10% of basal area) of *Pinus strobus* L. (eastern white pine), *Acer rubrum* L. (red maple), *Populus tremuloides* Michx. (trembling aspen), *Populus grandidenta* Michx. (bigtooth aspen), *Betula papyrifera* Marshall. (paper birch), *Abies balsamea* L. (balsam fir), *Picea glauca* (Moench) Voss. (white spruce), *Quercus rubra* L. (northern red oak) and *Quercus macrocarpa* Michx. (bur oak) at the time of treatment.

2.2. 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). Each of the four blocks was 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-aggregated, small gap-aggregated, and dispersed) was to reduce basal area to similar levels of approximately 17 m^2/ha but to vary spatial pattern of this retention. Each of the whole plots was further divided into two split-plots of approximately 8 ha each with shrub treatment (ambient or reduced shrubs) assigned randomly to the split-plots.

2.3. Variable retention harvest treatments

The VRH treatments tested a range of spatial openness and aggregation of retained trees. The control treatment received no overstory manipulation and had an average basal area of approximately 36 m^2/ha. The large gap-aggregated and small gap-aggregated treatments effectively created variability in open and closed forest conditions by the cutting of 0.3 ha and 0.1 ha gaps, respectively. These patterns were designed to emulate the live-tree patterns resulting from fine- and meso-scale disturbances historically affecting these systems, including surface and patchy canopy fires, wind, and root disease. Large gap centers were placed on an 83.8 m grid, while small gap centers were placed on a 76.2 m grid (for gap area details see Table A1). Both gap treatments included light thinning in the surrounding matrix in an attempt to achieve the desired final basal area of 17 m^2/ha (~45% retention), although the residual basal areas differed somewhat from the target (for details see Table B1). Residual trees were retained evenly throughout the dispersed retention treatment, resembling the initial harvest in a traditional, uniform shelterwood system. Large individuals of *P. resinosa*, and other species when they occurred, were retained in the dispersed treatment. Other species contributed approximately 10% of the basal area both before and after harvest. Harvests occurred over the fall and winter of 2002–2003 on largely frozen ground and snow cover.

2.4. Shrub treatments

The shrub treatments tested the effect of competing shrubs on tree regeneration in retention harvests. The ambient shrub treatment contained no manipulation. The shrub removal 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 ecosystem (Palik et al., 2014). The shrub removal treatment was implemented immediately following harvest, in the spring of 2003, to aid in planting seedlings (for a separate study) and to release natural regeneration of all tree species other than *Populus* spp. In all subsequent years, shrub removal was confined to the prescribed half of each stand and applied in the late spring of 2004, 2005, 2006 and 2011. In 2007 and 2008, due to funding limitations, only shrubs within 21 m of sample points of the prescribed halves were cut.

2.5. Data collection

Data were collected at study points placed evenly along transects located systematically within each stand (25–100 m apart). Transect length and number depended on the size and shape of the stand. Sample points were placed at least 50 m from treatment boundaries and throughout the stand to represent stand level conditions within each treatment. Sample points in the aggregate treatments were adjusted to represent matrix and gap plots proportional to those conditions presence in the stands, for details see Boyden et al. (2012). 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. At each sample point, two 1 m^2 quadrats were established opposite one another and perpendicular to the transect line. Within each quadrat, stems were counted for all woody species less than 1 m tall, including trees ("small regeneration" hereafter). Shrub and tree stems greater than 1 m tall and less than 2.54 cm diameter at breast height (DBH = 1.3 m; "large regeneration" hereafter) were counted in a circular 1.26 m radius plot centered on each study point. The data were sampled pre-harvest in 2000 and 2002, and following harvest in 2003, 2006 and 2013 between June and August of each year. Planted tree seedlings have been addressed elsewhere (Montgomery et al., 2013).

2.6. Data analysis

Immediate and long-term responses of natural regeneration to overstory retention pattern and shrub competition were analyzed using repeated measures generalized linear mixed-effects models with a zero-inflated Poisson distribution. Area (block) was considered a random factor while shrub treatment, overstory treatment, year (time) and their interactions were considered fixed factors. Pre-treatment stem counts were included as covariates. Analysis was done using the glmmADMB package in R (Fournier et al., 2012; R Development Core Team, 2015; Skaug et al., 2016). Tests were considered significant at the alpha = 0.05 level. Models were selected using likelihood ratio tests. Wald χ^2 tests were used to test the significance of treatment effects and their interactions in cases where they were included in the final model. When a significant interaction was included in the final model, sub-models were used to compare treatment effects within years or shrub treatment.

Pinus resinosa seedlings and *P. strobus* were analyzed separately given their ecological and economic importance in these ecosystems, while all other tree species were grouped by shade-tolerance and lifeform, including tolerant conifers (*Abies balsamea/Picea glauca*), mid-tolerant hardwoods (*Quercus rubra/Q. macrocarpa/Fraxinus* spp.), intolerant hardwoods (*Betula papyrifera/Prunus* spp./*Populus* spp. mainly *P. tremuloides* and occasionally *P. grandidenta*), and tolerant hardwoods (*Acer rubrum/A. saccharum* Marshall/ *A. spicatum* Lam./ *Tilia americana* L.). Large regeneration of *Pinus banksiana* Lambert and *P. resinosa* was not present in sufficient numbers to analyze statistically.

Tree regeneration and shrub community composition among treatments and over time were analyzed using nonmetric multidimensional scaling ordination (NMS) based on tree and shrub

Table 1
Selected models (lowest AIC) describing the effects of overstory treatment, shrub treatment, and year on small regeneration (less than 1 meter tall) densities (pretreatment densities included as a covariate) in *Pinus resinosa* forests, northern Minnesota, USA.

Response	Selected model	Df	χ^2	Pr (>χ^2)
Tolerant conifers	Pretreatment densities	1	62.4056	<0.0001
	Overstory	3	24.3479	<0.0001
	Shrub	1	3.7303	0.0534
	Year	1	0.0045	0.9462
	Overstory × shrub	3	16.1536	0.0010
	Overstory × year	3	10.9187	0.0121
	Shrub × year	1	4.5655	0.0326
P. resinosa	Pretreatment densities	1	11.7037	0.0006
	Overstory	3	5.658	0.1294
	Year	1	15.4745	<0.0001
	Shrub	1	0.7916	0.3736
	overstory × year	3	14.2977	0.0025
	Year × shrub	1	6.2499	0.0124
Intolerant hardwoods	Pretreatment densities	1	8.7421	0.0031
	Year	1	0.3995	0.5273
	Overstory	3	43.3973	<0.0001
	Shrub	1	2.6797	0.1016
	Year × overstory	3	7.2156	0.0653
	Overstory × shrub	3	16.9203	0.0007
P. strobus	Pretreatment densities	1	78.072	<0.0001
	Overstory	3	101.669	<0.0001
	Shrub	1	19.175	<0.0001
	Overstory × shrub	3	17.443	0.0005
Tolerant hardwoods	Pretreatment densities	1	632.1171	<0.0001
	Overstory	3	287.8887	<0.0001
	Shrub	1	7.2706	0.0070
Mid-tolerant hardwoods	Pretreatment densities	1	90.029	<0.0001
	Year	1	15.728	<0.0001
	Overstory	3	22.29	<0.0001
	Shrub	1	15.212	<0.0001

density. 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 (McCune et al., 2002; McCune and Mefford, 2011). Compositional differences between treatments were examined using distance-based multivariate analysis of variance (perMANOVA; McCune et al., 2002). 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 (McCune et al., 2002). 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, Sørensen'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.

3. Results

3.1. Regeneration densities

3.1.1. Small regeneration

Small regeneration (less than one m tall) density of many tree species and lifeform groups was significantly related to VRH treatment, shrub treatment, time, and their interactions (Table 1). Overall, densities of *P. resinosa* were lower relative to other species and species groups and were too low following harvest to compare in sub-models in subsequent years (Figs. 1 and 2). Densities of *P. strobus* and tolerant conifers (*A. balsamea* and *P. glauca*) were several times greater than *P. resinosa* in all sample years following harvest and their response to shrub removal varied by VRH treatment (Fig. 3). *P. strobus* seedling were generally more abundant at ambient shrub levels and in the overstory control treatment, but were greater in the large gap-aggregated treatment than the control when shrubs were reduced (Fig. 3). Tolerant conifers were less dense in the dispersed treatment compared to the control, but response to gaps differed between ambient and reduced shrub treatments (Fig. 3). Densities in the small-gap aggregated treatment were greater than the control when shrubs were left intact, but were significantly lower when shrubs were reduced (Fig. 3). Additionally, tolerant conifers were greater in the large-gap aggregated treatment when shrubs were reduced (Fig. 3).

Densities of hardwood species groups were significantly impacted by VRH and shrub treatment (Table 1). Densities of tolerant hardwoods (mainly *A. rubrum*) were higher in the control (Fig. 1) and at ambient shrub levels (Fig. 2). Densities of mid-tolerant hardwoods (mainly *Q. rubra*) were generally lower than tolerant hardwood densities (Figs. 1 and 2). Mid-tolerant densities were high in the control treatment and after the first year following harvest when shrubs were reduced (Figs. 1 and 2). The gap-aggregated treatments maintained greater densities of intolerant hardwoods regardless of shrub treatment, but the dispersed treatment only maintained greater densities when shrubs were at ambient levels (Fig. 3).

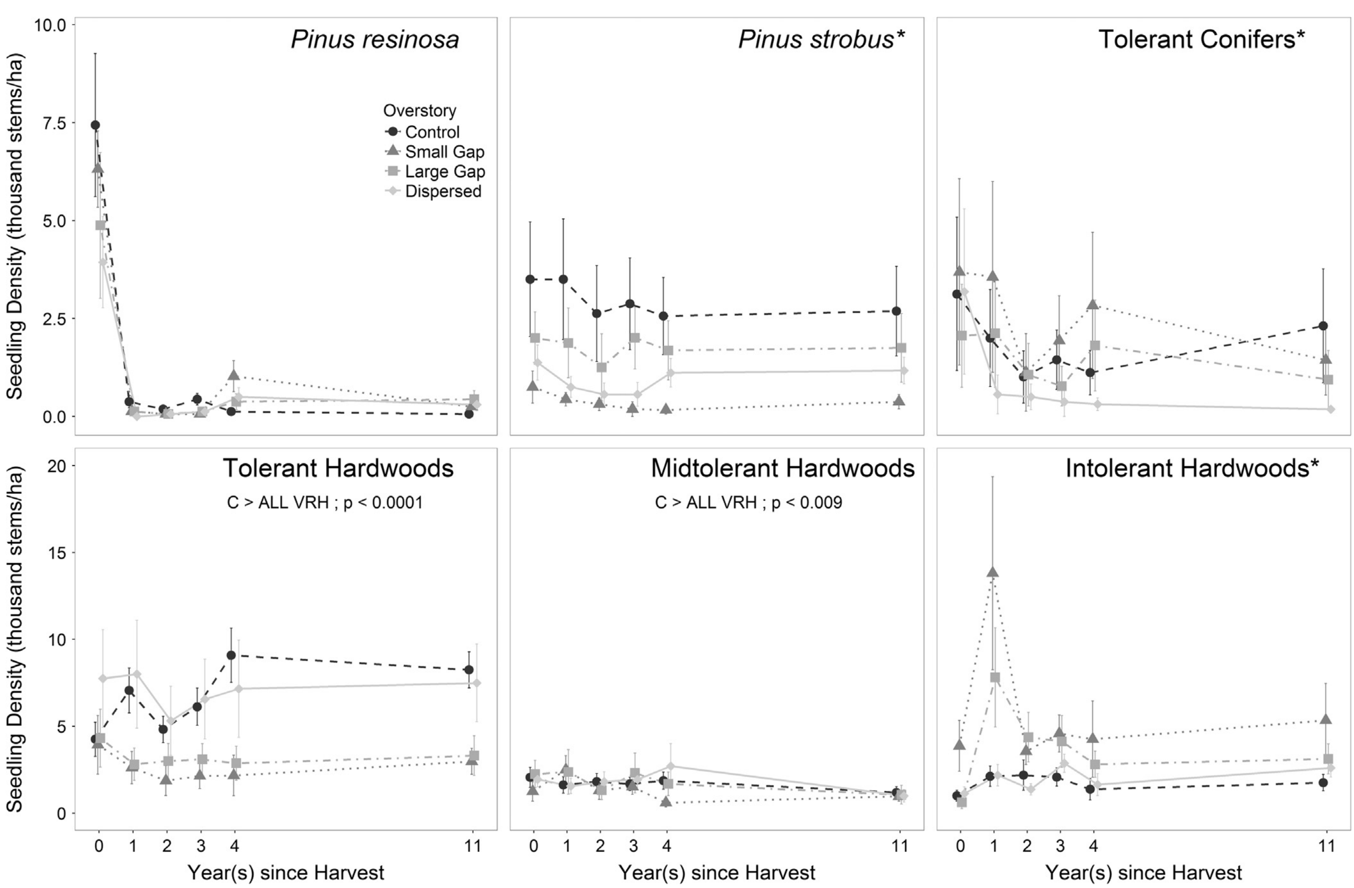

Fig. 1. Unadjusted mean and standard error of densities of small regeneration (<1 m height) prior to treatment (year 0), immediately following harvest (year 1, 2, 3 and 4) and 11 years later. Species/groups are presented separately by variable retention (overstory) treatment (Treatment labels: Control (C), Small Gap-Aggregated (SG), Large Gap-Aggregated (LG), Dispersed (D)). Asterisk denotes significant treatment interaction.

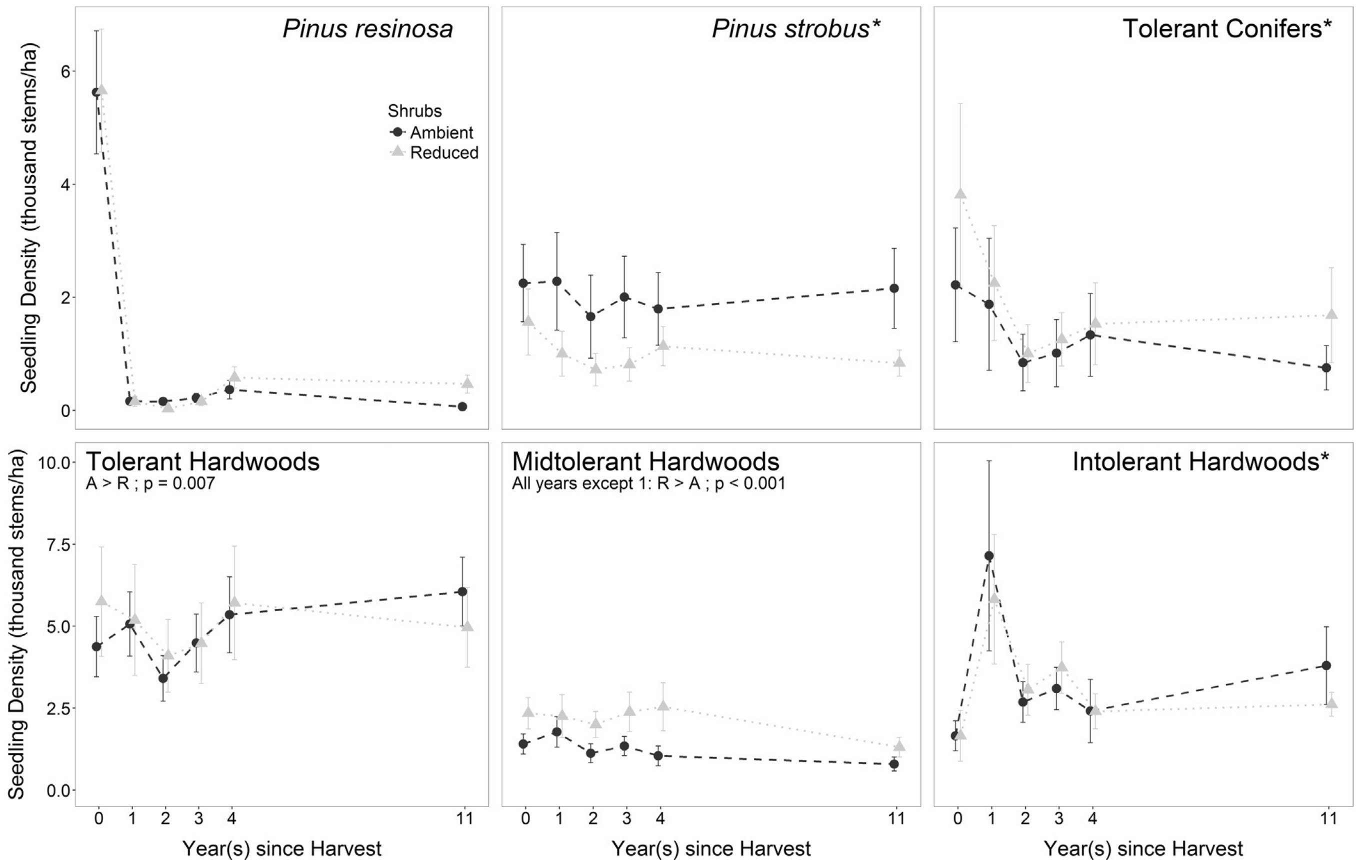

Fig. 2. Unadjusted mean and standard error of densities of small regeneration (<1 m height) prior to treatment (year 0), immediately following harvest (year 1, 2, 3 and 4) and 11 years later. Species/groups are presented separately by shrub (shrubs Ambient (A)/Reduced (R)) treatment. Asterisk denotes significant treatment interaction.

3.1.2. Large regeneration

Overall, large regeneration densities of *Pinus* species were lower than regeneration of hardwood species in all retention harvest treatments (average density of all *Pinus* spp. ranged from 182 ± 60 to 627 ± 175, hardwood species from 2054 ± 476 to 3099 ± 471 stems ha^{-1}; Table C1 & Fig. D1). Unlike small regeneration, we found no significant interactions between retention pattern and shrub treatment on density of large regeneration (greater than 1 m tall and less than 2.54 cm dbh; Table 2). Large regeneration of the dominant species in this system, *P. resinosa*, was not found in sufficient densities to analyze statistically. Densities of *P. strobus* were affected by shrub and overstory treatment (Table 2). *P. strobus* densities were greater when shrubs were ambient, but less dense in the small gap-aggregated treatment (Fig. 4 and 5). Densities of 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 (Fig. 4).

The density of tolerant hardwoods was primarily affected by retention pattern with increased densities in the dispersed treatment (Fig. 4). Mid-tolerant hardwood densities were not significantly different until year 11, when all overstory treatments were greater than the control (Fig. 4). Additionally, densities of mid-tolerant hardwoods were greater in the reduced shrub treatment the second and all subsequent years following harvest (Fig. 5). Intolerant hardwood densities were affected by the interaction between shrub treatment and year and VRH treatment (Table 2). This group was significantly greater in the large gap treatment (Fig. 4).

3.2. Community composition of natural regeneration

The application of VRH and shrub removal treatments resulted in distinct patterns in woody species community composition over the 11-year period examined, as evident in the NMS ordination, which included both size classes combined. The final result was a 2-dimensional solution explaining 91.3% of the variation in woody composition (Fig. 6). Little separation between the pre-harvest and final sample periods or among treatments was observed along Axis 1, which explained 65% of the variation, but several tree species, including *P. resinosa* (Kendall's τ: Axis 1–0.319), were associated with this axis. Most of the temporal and treatment variation was found along Axis 2, which explained 24.5% of the total 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. This suggests an increase in *Rubus strigosus* (Kendall's τ: Axis 2–0.589; Axis 1 0.341), as well as the tree species *B. papyrifera* (Kendall's τ: Axis 2–0.185; see also Table E1). The dispersed and large gap-aggregated ambient shrub treatments occupied similar portions of ordination space compared to pre-treatment results, whereas the ambient and reduced shrub control treatments moved slightly towards the more positive portions of Axis 2 over time.

The PerMANOVA results indicated VRH treatments interacted with shrub treatments to affect woody species composition (p value 0.001; Table F1). Given this interaction, community composition was analyzed for each VRH treatment separately and the effect of shrub abundance was significant in all cases except within the large gap-aggregated treatment. Several species

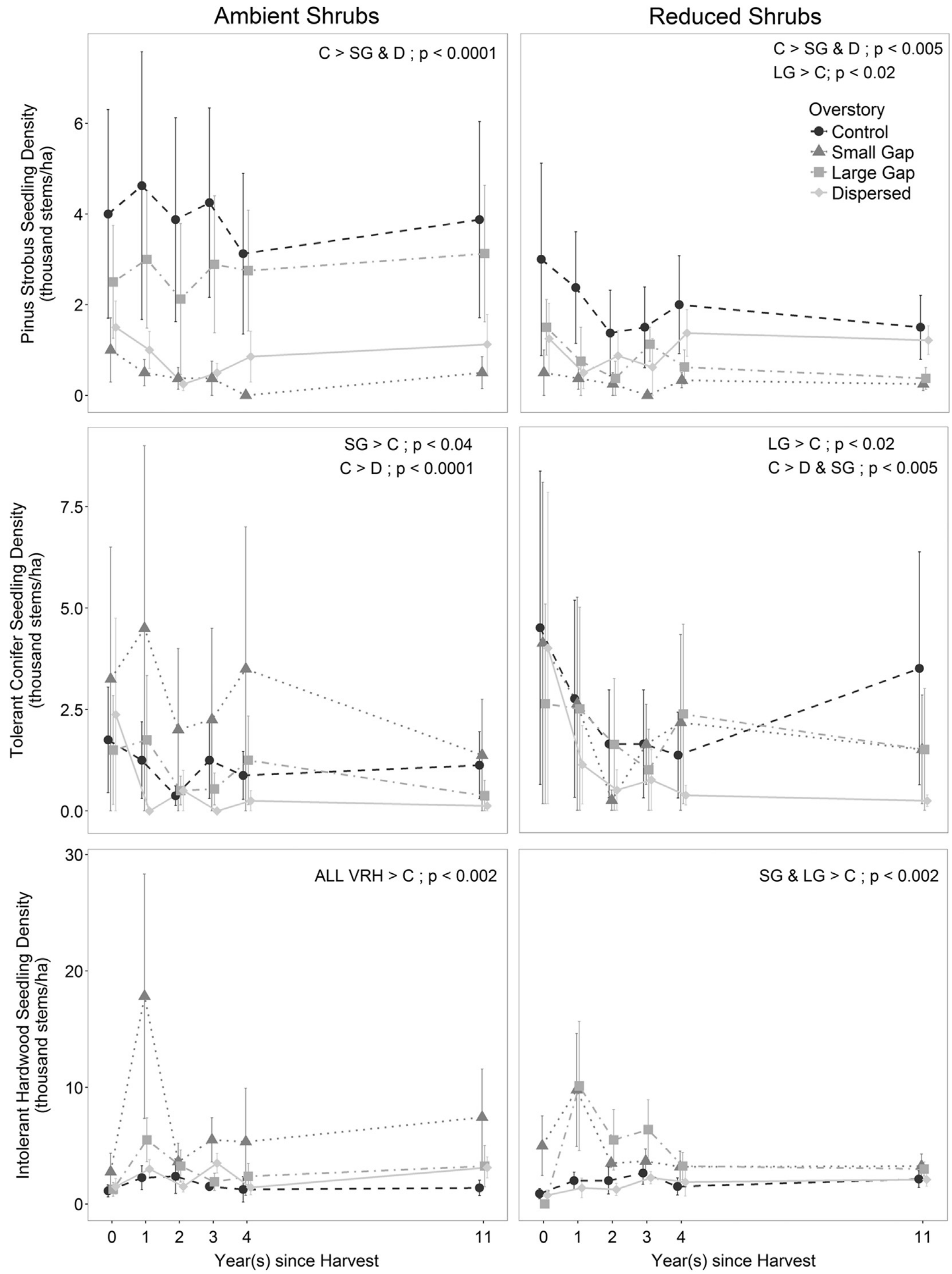

Fig. 3. Unadjusted means and standard errors of densities of small regeneration (>1 m height, <4 in. dbh) that showed a significant treatment (overstory by shrub) interaction. Densities prior to treatment (year 0), immediately following harvest (year 1, 2, 3 and 4) and 11 years later are displayed. Species/groups are presented separately by shrub (shrubs ambient/reduced) treatment by columns.

were significant indicators of VRH and shrub treatments (based on Indicator Species Analysis, $p < 0.05$). *A. rubrum* (Indicator value = 21.3, p = 0.0004) and *P. strobus* (IV = 22.3, p = 0.0022) were significant indicators in the control treatment. The dispersed treatment was associated with *Corylus* spp. (IV = 16.7, p = 0.026), and *P. glauca* (IV = 10.8, p = 0.0318) when shrub abundance was reduced. *Q. rubra* (IV = 23.6, p = 0.001) *and P. virginiana* (IV = 22.9, p = 0.0036) were significant indicators of the small gap-aggregated treatment. *B. papyrifera* (IV = 25.7, p = 0.0034) indicated the small gap-aggregated treatment when shrubs were reduced. *Populus* spp., (IV = 20.8, p = 0.0024) mainly *P. tremuloides*, were found more often in the large gap-aggregated ambient shrub treatment (the shrub removal treatment prescribed removal of *Populus* spp. root suckers).

Table 2
Selected models (lowest AIC) describing the effects of overstory treatment, shrub treatment, and year on large regeneration densities (pretreatment densities included as a covariate) in *Pinus resinosa* forests, northern Minnesota, USA.

Response	Selected model	*Df*	χ^2	*Pr* (>χ^2)
P. strobus	Pretreatment densities	1	68.8141	<0.0001
	Year	1	23.9349	<0.0001
	Shrub	1	13.8434	0.0001
	Overstory	3	9.0751	0.0283
	Year × shrub	1	5.8721	0.0153
Tolerant conifers	Pretreatment densities	1	72.755	<0.0001
	Overstory	3	28.675	<0.0001
Tolerant hardwoods	Pretreatment densities	1	47.6531	<0.0001
	Year	1	50.1422	<0.0001
	Shrub	1	11.2738	0.0007
	Overstory	3	19.644	0.0002
	Year × shrub	1	7.6471	0.0056
Midtolerant hardwoods	Pretreatment densities	1	35.2674	<0.0001
	Year	1	8.0776	0.0044
	Shrub	1	7.7166	0.0054
	Overstory	3	11.7798	0.0081
	Year × shrub	1	16.0006	<0.0001
	Year × overstory	3	42.0543	<0.0001
Intolerant hardwoods	Pretreatment densities	1	9.5032	0.0020
	Year	1	1.6592	0.1977
	Overstory	3	24.4201	<0.0001
	Shrub	1	87.7376	<0.0001
	Year × overstory	3	5.0639	0.1671
	Overstory × shrub	3	3.3041	0.3470
	Year × shrub	1	22.6292	<0.0001

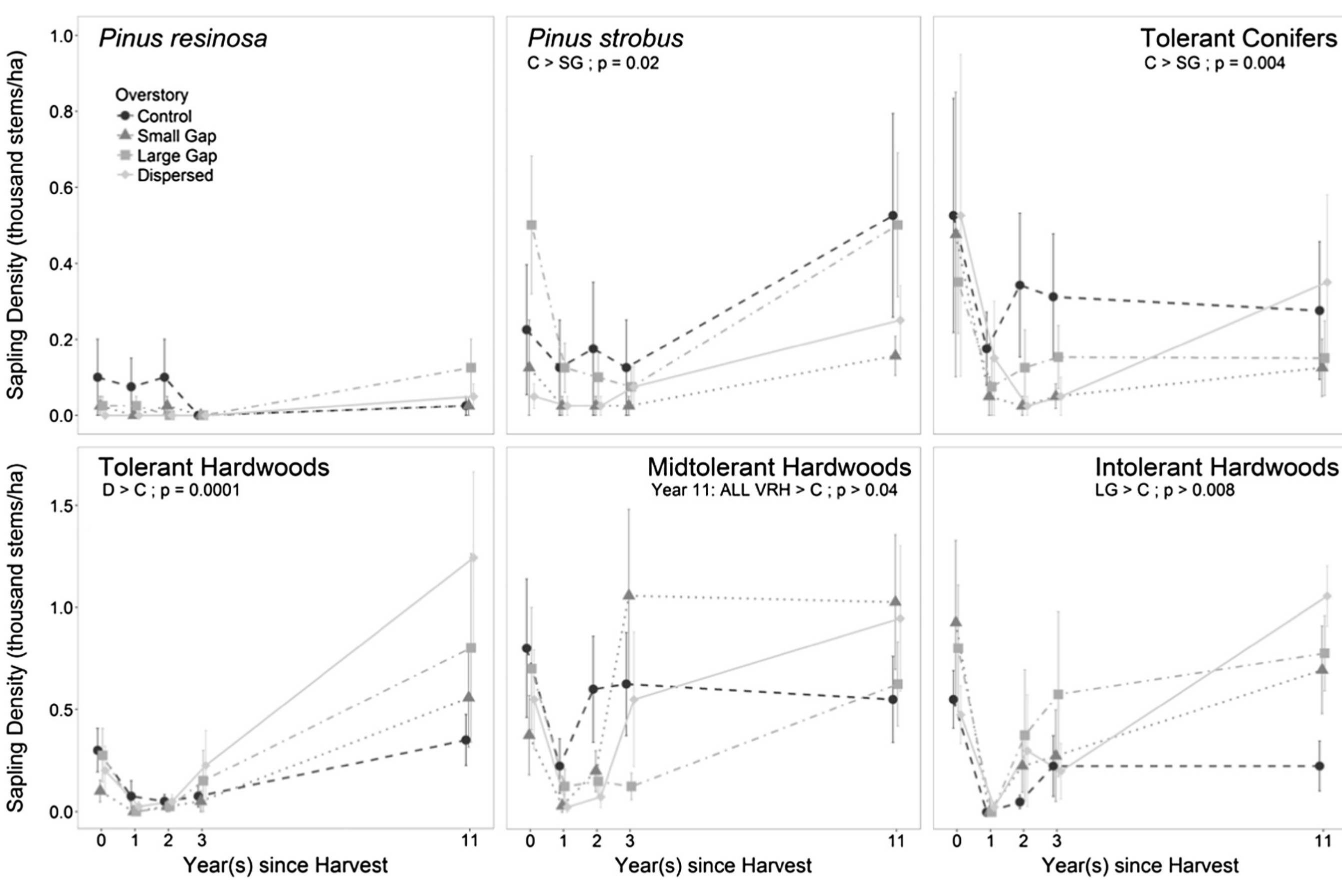

Fig. 4. Unadjusted means and standard errors of densities of large regeneration (>1 m height, <2.54 cm dbh) prior to treatment (year 0), immediately following harvest (year 1, 2 and 3) and 11 years later. Species/groups are presented separately by overstory (variable retention harvest) treatment (Treatment labels: Control (C), Small Gap-Aggregated (SG), Large Gap-Aggregated (LG), Dispersed (D)).

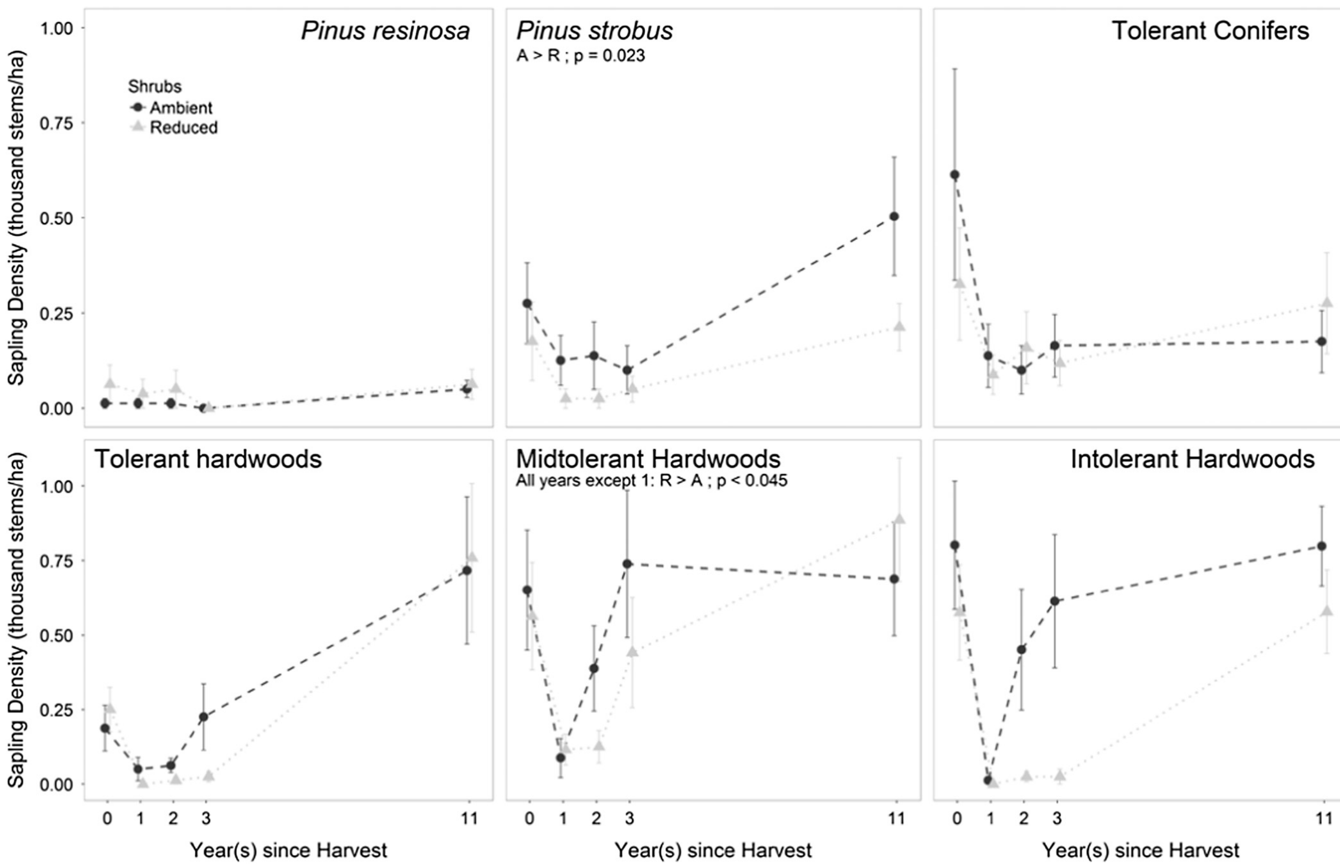

Fig. 5. Unadjusted means and standard errors of densities of large regeneration (>1 m height, <4 in. dbh) prior to treatment (year 0), immediately following harvest (year 1, 2 and 3) and 11 years later. Species/groups are presented separately by shrub (shrubs ambient/reduced) treatment.

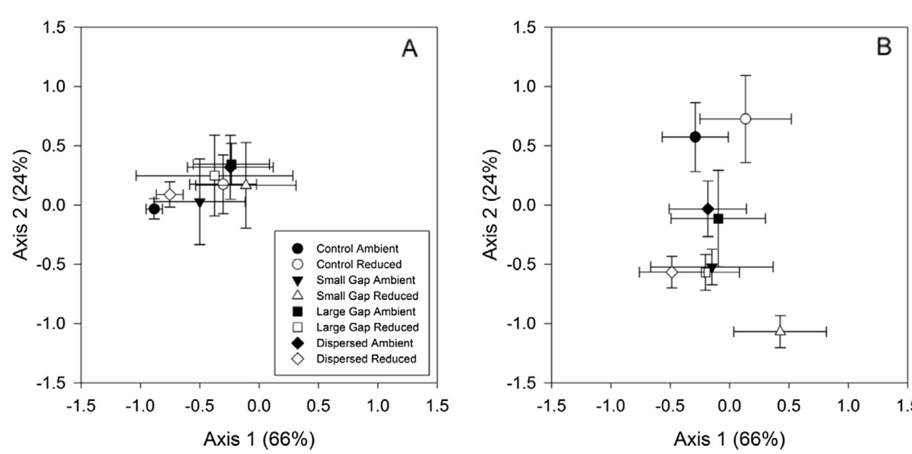

Fig. 6. Non-metric multidimensional scaling ordination of community composition of woody regeneration (averaged with standard error bars) pre-treatment (A) and 11 years post-treatment (B) are presented separately by overstory (variable retention harvest) and shrub (shrubs ambient/reduced) treatment in *Pinus resinosa* forests in northern Minnesota.

4. Discussion

4.1. Regeneration response to variable retention harvests

The spatial patterns of retention used in our study areas were designed to emulate the structural conditions after disturbance in some old-growth *P. resinosa* forests in the region (Fraver and Palik, 2012); however, we saw little evidence of *P. resinosa* recruitment in the openings created by harvest, contrary to our first hypothesis, and what has been reported to occur after natural disturbance in multi-cohort old-growth forests of the region. This suggests that the trajectory of these stands following harvest tends towards hardwood dominance, regardless of retention pattern. An important element of disturbance regimes in these forests historically were the increases in exposed mineral soil seedbeds following fire events (Turner et al., 1997). While retention patterns in the present study may reflect patterns that occurred following natural disturbance (Fraver and Palik 2012), the failure to emulate other important aspects of disturbance regimes, namely reduced litter layer thickness, may limit *P. resinosa* establishment. However, an initial pulse of *P. resinosa* germinants was documented immediately following harvests, and prolonged periods of fire suppression may have increased competition from fire-intolerant species (Nyamai et al., 2014), suggesting more work is required to fully understand this lack of *P. resinosa* regeneration.

In addition to altered disturbance regimes, widespread establishment of fungal shoot blight diseases (*Diplodia pinea* and *Sirococcus conigenus*) negatively impacts regeneration in *Pinus resinosa* systems in the western Great Lakes region in both planted and naturally regenerated stands (Haugen and Ostry, 2013; Oblinger et al., 2013), including our study site (Ostry et al., 2012). Other work has indicated that large gaps may decrease infection by shoot blight diseases by removing the main inoculum source from directly above or adjacent to seedlings (Albers, 2008); however, we found no evidence for such an effect in the present study with *P. resinosa* densities in large gap-aggregated treatments being similar to other retention patterns.

The low regeneration densities observed in *P. resinosa* did not extend to the other species and groups. Regeneration of large intolerant hardwoods was greatest in the large-gap aggregated treatment and regeneration of large midtolerant species were greater in all VRH treatments regardless of retention pattern while *P. strobus* and tolerant hardwood densities were lower in the small-gap aggregated treatments than the control. Other studies have found that regeneration response to gap size may be dampened by shrub competition and herbivory, with *Rubus ideaus* densities serving as significant covariates in models of height growth of regeneration for several tree species (Kern et al., 2013). This may be the case in our study, as many disturbance-adapted herbaceous species, specifically *Carex pensylvanica and Rubus* spp., were indicators of the large and small gap-aggregated treatments (Roberts et al., 2016). These species, which can form dense and persistent mats in the understory (Royo and Carson, 2006), have been associated with decreased regeneration of certain tree species (Powers and Nagel, 2009) and alterations of the successional trajectory of forest gaps. Influx of aggressive early successional ground-layer species in the gaps was associated with reduced shrub competition (Roberts et al., 2016) suggesting *Corylus* spp. removal may be releasing other competitors.

The dispersed treatment maintained the greatest treatment level densities of large regeneration, particularly of hardwoods, by year 11 (Table C1 & Fig. D1). 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). Midtolerant hardwood large regeneration was greatest in the dispersed treatment, reflecting the ability of these species to establish and develop under partially-shaded conditions. This finding is consistent with other work examining long-term natural regeneration responses to VRH in which dispersed retention favored tolerant, late-successional saplings (Urgenson et al., 2013).

Overall, densities of larger hardwood regeneration were much greater than any conifer or *Pinus* group in all treatments (Tables B1 & C1). Sprouting response of hardwood species following initial shrub removal in year 1 may be driving this difference in density, as well as a greater tolerance of browsing damage relative to conifer species, considering increased estimated deer densities compared to historical conditions (MN DNR, 2011; USDA FS, 2004). 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 (Nyamai et al., 2014), particularly in the absence of periodic surface fires or other understory treatments to reduce their abundance.

4.2. Shrub competition effects on regeneration response

Shrub competition, as inferred by shrub abundance, significantly impacted natural regeneration responses in addition to interacting with retention pattern. Even in the absence of canopy disturbance, dense understory layers can limit the survival, growth, density, and composition of tree regeneration (George and Bazzaz, 1999a,b). Previous work examining planted tree regeneration from our study indicated that shrub treatment often had a greater impact on survival and growth than retention pattern (Montgomery et al., 2013). Our results with natural regeneration also support the importance of shrubs; however, the influence of the shrub layer (positive, negative, or neutral) varied among species. Most notably, regeneration densities of large *P. strobus* 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) and counter to our second hypothesis regarding the benefits of shrub removal to large regeneration. Results from other studies across the region examining *P. strobus* have been mixed, with some indicating a negative effect of shrubs/positive effect of shrub control (Burgess and Wetzel, 2002; Cornett et al., 1998; Fahey and Lorimer, 2013; Saunders and Puettmann, 1999a) and others pointing to a positive effect (Krueger and Puettmann, 2004). The latter response may be partially attributed to protection from browsing pressure (Saunders and Puettmann, 1999b), as well as suppressing competition from species in the ground layer (Roberts et al., 2016). In contrast, densities of large midtolerant hardwood regeneration were greater following harvest in stands where shrubs had been reduced. While the negative effects of shrub competition on establishment of *P. resinosa* has been documented, the shrub removal treatment did not result in increased regeneration, suggesting the recalcitrant understory is not the only factor limiting establishment and growth of the dominant species in these ecosystems (D'Amato et al., 2012).

5. Conclusions

The primary focus of retention in VRH practices has been on the distribution and abundance of large, live-tree legacies across harvested areas to emulate natural, post-disturbance structural conditions (Franklin et al., 1997). The results of this study highlight the importance of considering the impacts these historical disturbances also had on understory vegetation and forest floor conditions (Roberts, 2004) and subsequent impacts on regeneration patterns. For most tree species and species groups, shrub competition was as, or more, important as overstory retention pattern in affecting abundance and composition of natural tree regeneration, suggesting that VRH approaches may need to incorporate treatments that alter the shrub layer.

Additionally, an initial pulse of *P. resinosa* germinants was documented immediately following harvests, suggesting seed bed conditions may not be limiting. Site preparation treatments focused on seedbed conditions should be integrated into future applications of VRH in these ecosystems to more closely approximate the processes giving rise to, or preventing, the structural and compositional conditions characterizing pre-European *P. resinosa* forests in the western Great Lakes region (Fraver and Palik, 2012). Relative growth and survival of planted *Pinus resinosa*, *P. strobus* and *P. banksiana* on our study sites were relatively high (see Montgomery et al. (2013)) and planting, in conjunction with shrub treatments, may be necessary to meet long-term management objectives.

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Appendix A

See Table A1.

Table A1
Summary of gap cutting in both the large gap-aggregated and the small gap-aggregated variable retention harvest treatments in the Red Pine Retention Study.

Block	Treatment	Gaps/ha	Gap area (ha)/ha
1	Large Gap-Aggregated	1.1	0.33
	Small Gap-Aggregated	1.2	0.12
2	Large Gap-Aggregated	1.2	0.36
	Small Gap-Aggregated	1.2	0.12
3	Large Gap-Aggregated	0.9	0.27
	Small Gap-Aggregated	1.3	0.13
5	Large Gap-Aggregated	1	0.3
	Small Gap-Aggregated	1.2	0.12

Appendix B

See Table B1.

Table B1
Treatment averages and standard deviations for residual basal areas remaining following tree removal from Boyden et al. (2012). Matrix is the portion of the stand falling outside any gap cuts. Total is the entire stand, including the matrix and any gaps. Gaps had 100% tree removal.

Treatment	Residual basal area (m^2 ha^{-1})	
	Matrix	Total
Control	36.2 (8.9)	36.2 (8.9)
Dispersed	14.4 (3.5)	14.4 (3.5)
Large Gap-Aggregated	22.9 (5.6)	17.7 (7.5)
Small Gap-Aggregated	23.0 (5.5)	15.2 (9.2)

Appendix C

See Table C1.

Table C1
Unadjusted mean and standard error of large regeneration (>1 m height and < 4 in. dbh) densities per hectare 11 years following harvest.

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 D

See Fig. D1.

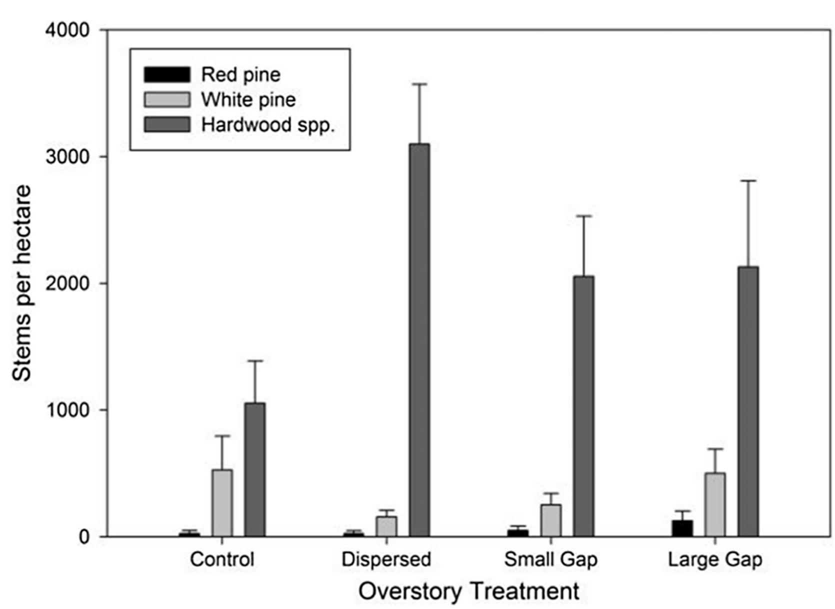

Fig. D1. Unadjusted mean and standard error of large regeneration (>1 m height, <4 in. dbh) densities 11 years following harvest.

Appendix E

See Table E1.

Table E1
Species with significant correlations with the first two axes of the NMS ordination of woody regeneration in *Pinus resinosa* forests in northern Minnesota (Fig. 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

Appendix F

See Table F1.

Table F1
Results of perMANOVA examining the impacts of overstory and shrub 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 × shrub	3	2.622	0.001
VRH × year	12	0.595	0.673
Shrub × year	4	0.327	0.963
VRH × shrub × year	12	0.295	1.000

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