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Long-term impacts of variable retention harvesting on ground-layer plant communities in *Pinus resinosa* forests

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Summary

1. Concerns about loss of biodiversity and structural complexity in managed forests have recently increased and led to the development of new management strategies focused on restoring or maintaining ecosystem functions while also providing wood outputs. Variable retention harvest (VRH) systems, in which mature overstorey trees are retained in various spatial arrangements across harvested areas, represent one potential approach to this problem. However, long-term evaluations of the effectiveness of this strategy at sustaining plant community composition are needed as this strategy is increasingly applied in managed forest landscapes throughout the world.

2. The forest ground layer plays a central role in forest ecosystem functioning, and we evaluated the long-term (11+ year) dynamics in ground-layer plant communities in response to VRH study in *Pinus resinosa* Aiton. forests. This large-scale, manipulative study included four overstorey (control, small gap-aggregated, large gap-aggregated and dispersed) and two understorey (ambient and reduced shrubs) treatments replicated four times in 16-ha stands.

3. Changes in ground-layer community composition were apparent 11 years following harvest, regardless of live-tree retention pattern. Richness and diversity increased and were driven by introduction and colonization of ruderal species, while forest interior species continued to persist across treatments. All life-forms responded positively to harvest with the exception of moss and clubmoss species.

4. The lack of effect of spatial pattern of retention on ground-layer plant communities was likely related to the presence of a dense and persistent shrub layer, a result of decades of fire suppression. In particular, the greatest responses to overstorey retention pattern occurred in areas receiving shrub reduction treatments, indicating this recalcitrant layer likely filtered response to retention pattern.

5. *Synthesis and applications*. Overall, this work highlights flexibility in choosing a variable retention harvest approach when sustaining ground-layer plant community diversity and composition are goals, but altered disturbance regimes (e.g. fire suppression, timber harvesting) that have facilitated the presence or formation of recalcitrant understories, need to be considered. The legacy effects of historical land use and alterations to natural disturbance regimes on the understorey in northern temperate forests are of equal, if not greater, importance to overstorey retention patterns in eliciting desired responses to variable retention harvest and need to be more carefully considered in future applications of this method.

Key-words: disturbance regimes, ecological forestry, herbaceous layer, recalcitrant understorey, silviculture, temperate forests

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Introduction

The forest ground layer plays an important role in the functioning of forest ecosystems (Whigham 2004; Elliott *et al.* 2015). Although often representing <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 (George & Bazzaz 1999a,b). 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 (Roberts 2004). This knowledge is particularly important considering recent evidence that human actions may be the most influential process determining levels of diversity in certain forest ecosystems (Schmiedinger *et al.* 2012).

Research examining the impacts of forest harvesting on the ground-layer plant community has indicated that certain species or functional guilds may be adversely impacted by conditions resulting from traditional management practices (Ramovs & Roberts 2003; Decocq *et al.* 2004; Halpern *et al.* 2012). Meier, Bratton & Duffy (1995) outlined five primary ecological mechanisms to explain the declines in many forest species often observed following harvesting. These mechanisms include initial damage during harvest, physiological stress and competition with exotic/ruderal species, limited growth/reproduction rates and dispersal methods, as well as the loss of canopy gaps and associated microhabitat conditions.

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 ground-layer 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, Palik & Strong 2006; Duguid & Ashton 2013). Despite this uncertainty, recent studies support the finding that late-successional and old-growth forests have significantly different understories from managed forests (Scheller & Mladenoff 2002; D'Amato, Orwig & Foster 2009; Bergeron & Fenton 2012). Given these recognized differences, forest managers are increasingly applying practices that reduce the impact of the mechanisms outlined by Meier, Bratton & Duffy (1995) and mimic natural disturbance as a means to safeguard species diversity and community composition (Franklin *et al.* 1997). These include maintaining and restoring a diversity of microhabitats, such as large dead wood on the forest floor, emulating historical disturbance regimes with silvicultural systems, and retaining aggregates of mature forest to serve as refugia.

Variable retention harvest (VRH) systems are one example of a management approach proposed to mitigate mechanisms adversely impacting the forest ground layer (Franklin *et al.* 1997). Maintenance and re-establishment of native forest biodiversity is one of the end goals of this system (Baker *et al.* 2013) in addition to growth and production of timber (Franklin *et al.* 1997; Urgenson, Halpern & Anderson 2013). In particular, VRH approaches focus 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 forests following meso- and stand-scale disturbances. As such, VRH 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 forests managed for wood products.

Despite theoretical underpinnings that suggest VRH can sustain later successional species at the stand-scale, long-term studies are needed to evaluate the effectiveness of this approach at achieving this goal (Gustafsson, Kouki & Sverdrup-Thygeson 2010), particularly since legacy effects of past management can continue decades to centuries after logging (D'Amato, Orwig & Foster 2009; Schmiedinger *et al.* 2012). One such legacy of historical land use is the formation of a dense and persistent layer of one or several species in the understorey (Royo & Carson 2006). For example, dense understories of American hazel *Corylus americana* (Walt.) and beaked hazel *Corylus cornuta* (Marsh.) exist in many *Pinus* forests in the western Great Lakes region, USA, likely reflecting an alteration in historical disturbance regimes, including the suppression of high frequency, low-intensity surface fires, which limited the abundance of these species (Tappeiner 1979; Palik & Zasada 2003; Royo & Carson 2006). These shrub species, as well as *Rubus* spp., are often abundant in *Pinus*-dominated systems, affecting tree regeneration, altering successional pathways, and impacting forest diversity and composition (Royo & Carson 2006). Given these changes in shrub and ground-layer conditions over the last century, and the presence of recalcitrant understories throughout the world (Royo & Carson 2006; Young & Peffer 2010), it is important to understand the influence of recalcitrant layers on the efficacy of VRH at achieving objectives of maintaining the diversity and composition of the ground layer.

The Red Pine Retention Study, a >12-year-old VRH study in northern Minnesota, USA, provides a unique opportunity to conduct a long-term evaluation of the effectiveness of these systems at sustaining native ground-layer communities. *Pinus resinosa* Aiton. red pine forests have traditionally been managed as single-cohort near-monocultures (Benzie 1977) either through the application of even-aged silvicultural methods to natural origin stands or through the establishment of red pine plantations; however, the use of VRH may more closely mimic historical, mixed severity disturbance regimes that resulted in mixed-species, multicohort forests (Palik & Zasada 2003; Fraver & 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; Macdonald & Fenniak 2007; de Graaf & Roberts 2009; Lencinas *et al.* 2011; but see Halpern *et al.* 2012). The Red Pine Retention Study examines different spatial configurations of retained trees on the long-term dynamics of the ground layer, while holding abundance of retained basal area relatively constant. In addition, this study includes a shrub reduction treatment, providing an opportunity to examine the importance of shrub competition in maintaining native plant biodiversity in the application of VRH.

We addressed two primary questions relating ground-layer plant response to variable retention harvesting spatial pattern interacting with shrub reduction: (i) how effective are VRH systems patterned after natural disturbances at maintaining native biodiversity in ground-layer plant communities with and without dense shrub competition; and (ii) in what way does the abundance of a range of life-forms and successional groups respond to various patterns in post-harvest live-tree legacies in the light of a recalcitrant understorey layer.

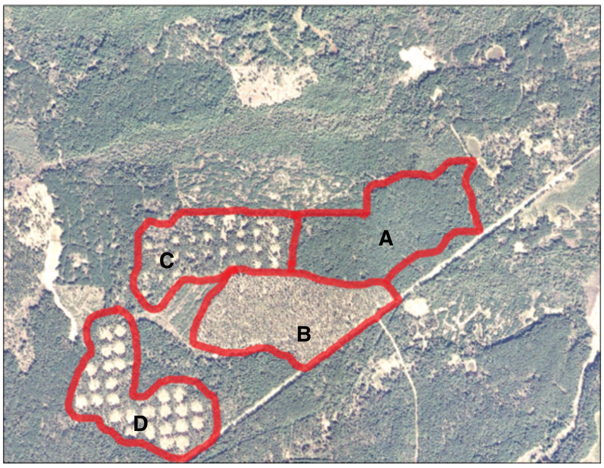

Fig. 1. Aerial view of variable retention harvest (VRH) treatments at the Red Pine Retention Study (one of four blocks). The (A) reference is uncut forest while the (B) dispersed, (C) small gap-aggregated and (D) large gap-aggregated are VRH treatments with variations of spatial retention pattern. Trees were retained uniformly in the dispersed treatment, while 0·1-ha groups were harvested in the small gap-aggregated and 0·3-ha gaps in the large gap-aggregated treatments.

Materials and 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. 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 wildfires associated with widespread logging in the region, and there was no prior management of these areas prior to application of the experimental treatments. Basal area of the study area averaged 32 m^2 ha^{-1} prior to harvest, with a moderately open canopy, and dominant trees averaging 27 m in height (Palik *et al.* 2014). Historically, fire was the primary natural disturbance in this ecosystem; however, fire has been excluded from these areas resulting in greater levels of understorey shrubs than documented in natural forest systems. All stands are classified as northern dry-mesic mixed forest, Red Pine–White Pine Woodlands (FDn33a), based on regional native plant community classification (MN DNR 2003).

STUDY DESIGN

The Red Pine Retention Study is a split-plot, complete block design replicated four times. All four blocks were approximately 64 ha in size, and four overstorey retention treatments (unmanaged control, large gap-aggregated, small gap-aggregated and dispersed) of approximately 16 ha each were randomly assigned within each block (Fig. 1). Each whole plot 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 VRH treatments tested the response of plant communities to difference in spatial pattern of retained trees. The control treatment contained no overstorey manipulation. All VRH treatments held amount of retention relatively constant (*c.* 45% retention), focusing effect of harvest on spatial pattern as opposed to level of retention. This retention level was chosen to allow comparison with other VRH experiments, such as the DEMO study (Halpern *et al.* 1999), in addition to being consistent with the disturbance dynamics and resultant structure of red pine forests in Minnesota (Fraver & Palik 2012). The large gap-aggregated and small gap-aggregated treatments created 0·3 ha and 0·1 ha gaps, respectively. Large gap centres were placed on an 83·8-m grid, while the small gap centres were placed on a 76·2-m grid. The number of gaps varied depending on stand size. Both gap-aggregated 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 (*c.* 17 vs. *c.* 19 m^2 ha^{-1}) than the other harvest treatments (Palik *et al.* 2014). Residual trees were retained evenly throughout the dispersed retention treatment. Harvest, including thinning between the gaps, was implemented over the autumn and winter of 2002/2003, largely on frozen soil and a snow pack limiting the level of ground disturbance across the study areas.

SHRUB TREATMENTS

The shrub treatment tested the effect of competing shrubs on natural regeneration and herbaceous communities in retention harvests. The reference treatment involved no manipulation, hereafter the ‘ambient’ shrub density treatment. The reduced shrub treatment included the reduction in all woody shrubs, as well as *Populus* spp. suckers, >0·3 m in height and <6·4-cm d.b.h., hereafter called the ‘reduced’ shrub density treatment. In particular, the reduced shrub treatment targeted *Corylus* and

Rubus spp. The shrub reduction treatment was implemented using handheld gas-powered brush cutters. In the initial application, the entirety of each stand was treated following harvest in the spring of 2003, to aid in planting. There were no other site preparation treatments applied to any of the areas to improve planting conditions. In all subsequent years, the shrub treatment was confined to the prescribed half of each stand and applied in the late spring. Shrub treatment occurred annually from 2004 to 2006 and in 2011. In 2007 and 2008, only shrubs within 21 m of sample points (see below) were cut.

DATA COLLECTION

The forest ground-layer data were collected at study points placed evenly along transects that crossed each stand (25–50 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 1 m^2 and was established at each sample point opposite one another and perpendicular to the transect line, 2 m from the sample point. Within each quadrat, all herbaceous vascular plant species and woody species <1-m tall were categorized within one of six cover classes (<1%, 1–5%, 6–15%, 16–30%, 31–60%, 61–100%). Cover by non-vascular plant species was pooled in a single category. Additionally, stems were counted for all woody species <1-m tall. 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 analysed using non-metric multidimensional scaling ordination (NMS). For all analyses, cover classes of each species in a plot were converted to the mid-point 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. Two species, *Oryzopsis asperifolia* Michx. and *Piptatheropsis pungens* (Torr.) Romasch., P.M. Peterson & R.J. Soreng, were not differentiated during the pre-treatment field season and were therefore combined for analysis (noted as Grass clade). Sørensen's distance measure was used, and only common species (species that occurred in >5% of plots) were included. NMS was performed using PC-ORD 6.0 (MjM Software, Gleneden Beach, OR, USA) with 250 runs with real data, 250 runs with randomized data and a maximum of 500 iterations per run (McCune & Mefford 2011). 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 among treatments were examined using distance-based multivariate analysis of variance (PERMANOVA) in R (Oksanen *et al.* 2015; R Development Core Team 2015). Permutations were constrained within Area (i.e. block), which was considered a random factor. VRH treatment, shrub treatment and year were considered fixed factors. In addition, blocked indicator species analysis (ISA) was performed in PC-ORD 6.0 to identify species that differentiated treatments. Indicator values represent percentage of perfect indication. Diagnostic plots were used to confirm appropriate multivariate spread for all analyses.

Immediate and long-term effects of overstorey retention patterns and shrub competition on change in ground-layer richness, Shannon's diversity and evenness were evaluated using linear mixed-effects models. Change in percentage 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 analysed. Successional role was determined based on Coefficient of Conservatism values specific to the study region (*c*), resulting in 74 species, being characterized as early successional (*c* 1–4), 63 as mid successional (*c* 5–6) and 35 as later successional (*c* 7–10) (12 species *c* values were unknown) (Bernthal 2003; Milburn, Bourdaghs & Husveth 2007; Mortellaro *et al.* 2012; Matthews, Spyreas & Long 2015). 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 (Pinheiro *et al.*; R Development Core Team 2015). Diagnostic plots were used to assess model assumptions.

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

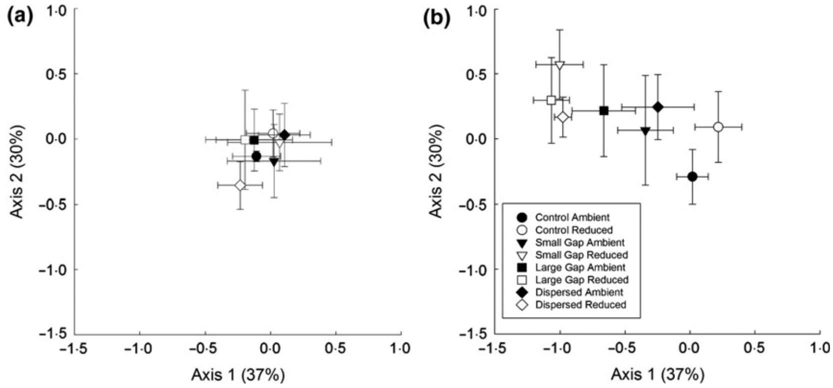

Fig. 2. Non-metric multidimensional scaling ordination of ground-layer community composition (mean of four replicates ± standard error) before treatment (a) and 11 years after treatment (b) in *Pinus resinosa* forests in northern Minnesota.

Table 1. Species with significant correlations with the first two axes of the non-metric multidimensional scaling 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 with higher values indicating greater disturbance sensitivity

Axis	Relationship	Species	Kendall's τ	Coefficient of conservatism
1	Negative	*Anemone quinquefolia* L.	−0·26029	5
		Pteridium aquilinum (L.) Kuhn	−0·6838	3
		Vaccinium angustifolium Aiton.	−0·45978	5
		Maianthemum canadense Desf.	−0·4332	5
		Carex pensylvanica Lam.	−0·35319	3
		Diervilla lonicera Miller	−0·32599	6
		Lathyrus venosus Muhl.	−0·32298	6
		Moss spp.	−0·31275	–
		Comandra umbellata (L.) Nuttall.	−0·30493	4
		Danthonia spicata (L.) F. Beauv.	−0·28883	4
		Vicia spp.	−0·28378	–
		Rubus idaeus L.	−0·27643	3
2	Positive	*Aster macrophyllus* L.	0·43043	4
		Cornus canadensis L.	0·23251	6
		Linnaea borealis L.	0·24903	7
		Rubus pubescens Raf.	0·25193	6
		Galeopsis tetrahit L.	0·27851	Exotic
		Rubus idaeus var. strigosus Michx.	0·34067	3
		Lycopodium clavatum L.	0·34305	6
		Galium boreale L.	0·36539	4
		Galium triflorum Michx.	0·40092	4
		Grass clade	0·41719	4
	Negative	*Chimaphila umbellata* (L.) Barton.	−0·32036	8
		Gaultheria procumbens L.	−0·44631	6
		Vaccinium angustifolium Aiton.	−0·28913	5

Table 2. Results of PERMANOVA examining the influence of variable retention harvest (VRH) and shrub treatments as well as time on the ground-layer plant composition of *Pinus resinosa* forests in northern Minnesota

Main effect	d.f.	*F*	Pr(>*F*)
VRH	3	3·29	0·001
Shrub	1	1·39	0·068
Year	3	7·49	0·001
VRH × SHRUB	3	2·13	0·001
VRH × Year	9	1·16	0·008
Shrub × Year	3	0·49	0·979
VRH × Shrub × Year	9	0·35	1

axis at 30·5% and the third at 16·2% (Fig. 2). Most of the temporal and treatment variation was found along axis 1. Control and pre-treatment ordination points fell close to zero on axis 1, while the three VRH treatments moved towards the more negative ordination space along axis 1 and more positive ordination space along axis 2 in year 11. This pattern reflects an increase in many early and mid-successional species in VRH treatment stands based on the species correlations with each axes (Table 1). While the VRH treatments occupied different portions of ordination space relative to the controls, large separation related 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). Given this interaction, community composition was analysed for each year separately, revealing that the VRH effect was not significant prior to treatment, but had a significant effect 1 ($P = 0{\cdot}029$), 4 ($P = 0{\cdot}001$) and 11 ($P = 0{\cdot}001$) years following harvest.

Several species were significant indicators of VRH and shrub treatments (based on ISA ($P < 0{\cdot}05$; Table 3). Species with strong affinities for undisturbed forests [*Goodyera pubescens* (Willd.) R. Br. (Coefficient of Conservatism (c) = 8), *Chimaphila umbellata* (L.) Barton. ($c = 8$), *Gaultheria procumbens* L. ($c = 6$), *Pyrola rotundifolia* L. ($c = 8$) and *Clintonia borealis* (Aiton.) Raf. ($c = 7$)] were significant indicators of the control treatment. Overall, indicators of the control treatment had higher Coefficient of Conservatism values compared to other treatments [mean c values ± SE = 7·4 ± 0·4, 5·4 ± 0·8, 5 (only one indicator), and 4·8 ± 0·9, for the control, small gap-aggregated, large gap-aggregated and dispersed treatments, respectively].

Coefficient of Conservatism values were more variable for indicators of the VRH treatments. Both early [*Rubus idaeus var. strigosus* Michx. ($c = 3$), *Galium triflorum* Michx. ($c = 4$), *Thalictrum dioicum* L. ($c = 5$)] and later [*Viola* spp. ($c = 7$), *Dryopteris carthusiana* (Villars) H.P. Fuchs ($c = 6$), *Rhus radicans* (L.) Kuntze ($c = 7$)] succes-

Table 3. Significant indicator species of variable retention harvest (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* (Willd.) R. Br.	28·9	0·0024	8
		Chimaphila umbellata (L.) Barton.	24·8	0·0282	8
		Gaultheria procumbens L.	19·3	0·019	6
		Pyrola rotundifolia L.	28·9	0·0024	8
	Reduced	*Clintonia borealis* (Aiton.) Raf.	27	0·0142	7
Small gap-aggregated	Ambient	–	–	–	–
	Reduced	*Rubus idaeus var. strigosus* Michx.	36·4	0·0142	3
		Dryopteris carthusiana (Villars) H.P. Fuchs	20	0·0126	6
		Galium triflorum Michx.	27·2	0·0226	4
		Rhus radicans (L.) Kuntze	20·4	0·0498	7
		Viola spp.	20·8	0·0476	7
Large gap-aggregated	Ambient	–	–	–	–
	Reduced	*Thalictrum dioicum* L.	21·2	0·0304	5
Dispersed	Ambient	*Aster macrophyllus* L.	37·6	0·0004	4
		Rubus pubescens Raf.	24·7	0·007	6
	Reduced	*Vaccinium angustifolium* Aiton.	19·7	0·0004	5
		Arctostaphylos uva-ursi (L.) Sprengel	21·8	0·0088	7
		Rubus alleghaniensis T. C. Porter	18·3	0·0202	2

sional species were indicators for the small gap-aggregated treatment. Neither gap-aggregated treatment resulted in significant indicators when shrubs were left at ambient levels. The dispersed treatment resulted in a wide range of Coefficient of Conservatism values, including *Aster macrophyllus* L. ($c = 4$), *Rubus pubescens* Raf. ($c = 6$), *Vaccinium angustifolium* Aiton. ($c = 5$), *Rubus alleghaniensis* T. C. Porter ($c = 2$) and *Arctostaphylos uva-ursi* (L.) Sprengel ($c = 7$). The disturbance-adapted species, *R. alleghaniensis* ($c = 2$), responded positively 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 (Fig. 3). All VRH treatments increased total cover of ground-layer species in year 4 ($P = 0·0147$; Fig. 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 ($P = 0·0060$; Fig. 3) had significantly greater increases 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 (Fig. 3) compared to pre-treatment 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 broken down by species association with or without disturbance (early, mid and later successional species). Overall, we found no significant treatment effects for mid- ($n = 63$) or late-successional species ($n = 35$, Fig. 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 ($P = 0·0043$). VRH (Fig. 3) and shrub treatments increased richness ($P < 0·0001$, $P = 0·0217$) and diversity ($P < 0·0001$, $P = 0·0141$) of early successional species compared to the control. There was a significant interaction between treatment types for evenness of early successional species ($P = 0·0283$, Fig. 3). The small gap-aggregated treatment with reduced shrub levels had 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 had increased evenness.

LIFE-FORMS

Change in cover of different life-forms of ground-layer species showed significant interactions between year and VRH/shrub treatments ($P < 0·0001$, $P = 0·0017$) and many life-forms responded positively to harvest (Fig. 4). By year 11, all VRH treatments and the shrub reduction treatment resulted in a significant increase in cover of sub-shrub species ($P = 0·0025$, $P = 0·0144$) 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 influenced by treatment despite lower densities in harvested areas in year 1 (Fig. 5).

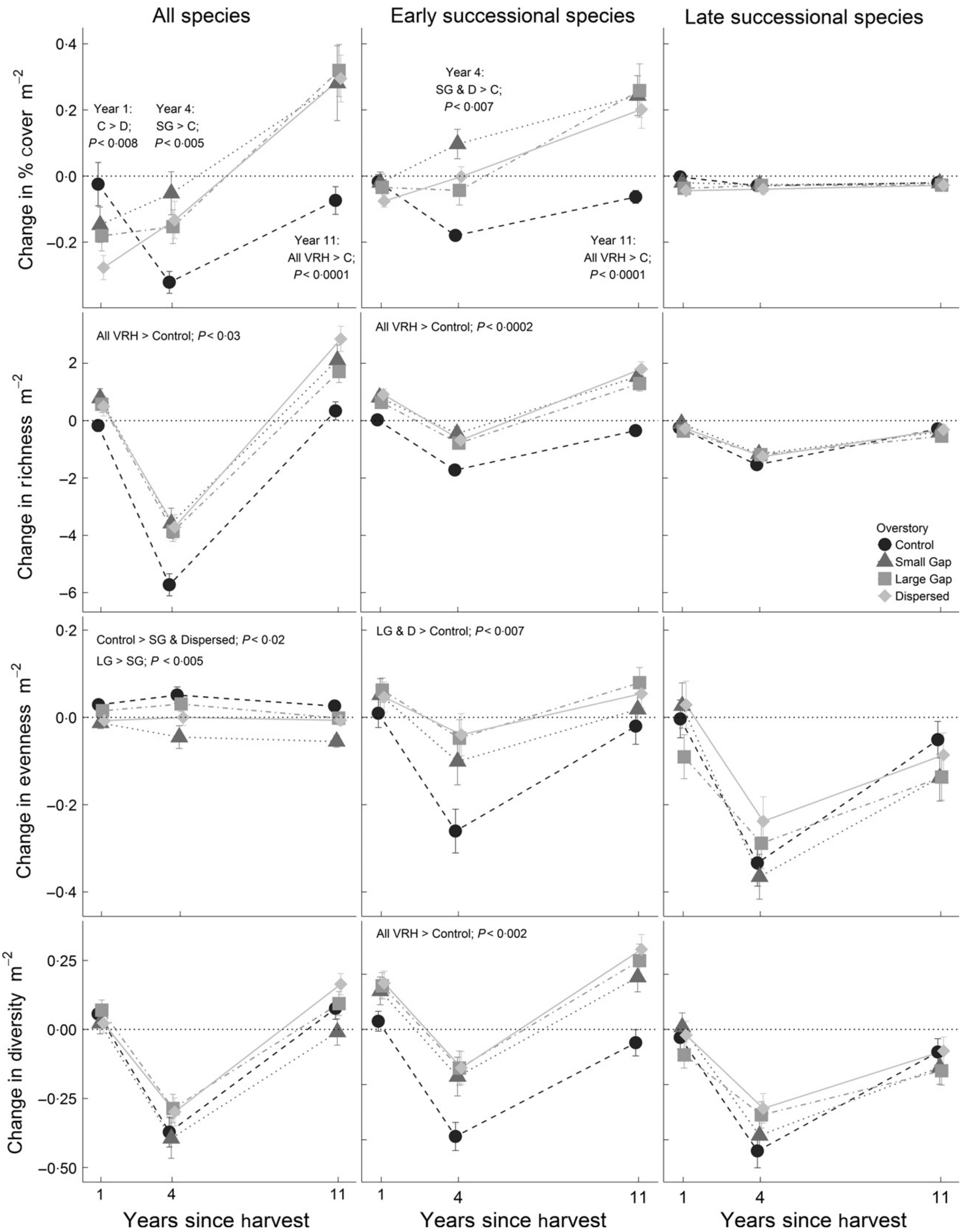

Fig. 3. Change in cover, richness, Shannon's diversity and evenness relative to pre-treatment conditions 1, 4 and 11 years following harvest. Treatment is broken down by variable retention harvest treatment. The second column shows treatment effects on early successional species, while column three shows the late-successional species.

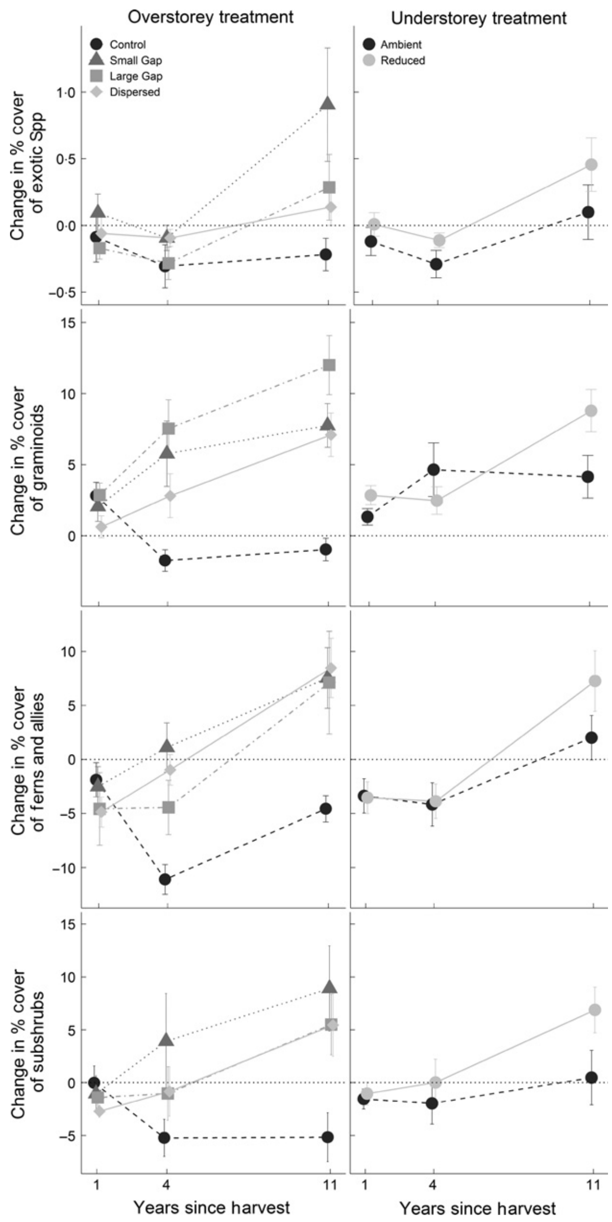

Fig. 4. Change in percentage cover of ground-layer plant life-forms relative to pre-treatment values 1, 4 and 11 years following harvest in *Pinus resinosa* forests in northern Minnesota. Treatment is broken down by variable retention harvest (VRH) treatment in the first column and shrub treatment in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

The reduced shrub treatment resulted in increased total cover of ground-layer species in year 11 ($P = 0{\cdot}0012$) and had a significant effect on various life-forms. In particular, this treatment had increased cover by graminoids 11 years after harvest ($P = 0{\cdot}0015$) compared to the control. Subshrub species responded positively to reduced shrub treatment in the small gap-aggregated treatment ($P = 0{\cdot}0012$) and ambient shrub treatment regardless of retention pattern ($P = 0{\cdot}0015$).

Large gap-aggregated ($P = 0{\cdot}0238$) and dispersed ($P = 0{\cdot}0181$) treatments resulted in a decrease in total cover of moss and clubmosses compared to the control (Fig. 5). Exotic species increased significantly in the small gap-aggregated treatment ($P = 0{\cdot}0010$) and in the shrub reduction treatment ($P = 0{\cdot}0205$).

Discussion

Our findings suggest that VRH, regardless of the spatial pattern of retention, shifted the composition and diversity of the ground layer of *P. resinosa* forests. 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 drivers of changes in ground-layer community composition were the harvest disturbance and shrub treatment. Observed trends 11 years after treatment suggest that ground-layer composition continues to move further from unharvested controls, regardless of retention pattern. 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. The reduced shrub treatments increased the magnitude of compositional change as time since harvest increased. The temporal fluctuations observed throughout the study area, particularly in diversity and richness (Fig. 3), likely were a result of differences between sampling crews in estimating cover and/or environmental/climatic factors.

A primary focus of past work examining VRH has been on the role of overstorey trees in structuring resource environments and microclimatic conditions (Palik *et al.* 2003; Boyden *et al.* 2012; Halpern *et al.* 2012); however, an important aspect examined in our work, that has been rarely included in other studies, is the role of recalcitrant understorey layers in affecting ground-layer response. Related work from our study examining planted seedling growth indicated that shrub competition may be just as important as overstorey competition in influencing resource availability (Montgomery *et al.* 2013). This influence was also apparent in our work where rhizomatous *Corylus* spp. impacted ground-layer diversity more than overstorey treatments. Although these shrub species were common historical components of this forest, their current abundance has been enhanced by alterations to historical disturbance regimes (Tappeiner 1979; Royo & Carson 2006). These results underscore the importance of applying treatments to reduce the impact of these recalcitrant shrub layers if understorey environments for ground-layer communities are to truly reflect conditions generated by historical natural disturbance.

Our result suggests VRH remediated several mechanisms responsible for decreases in vernal herbs outlined by Meier, Bratton & Duffy (1995) including the loss of populations of rare herbs as a direct result of harvest. Season of harvest can significantly impact ground-layer vegetation (Wolf *et al.* 2008). Protection from snow pack during the majority of harvest may have minimized direct damage to ground-layer species, particularly in the

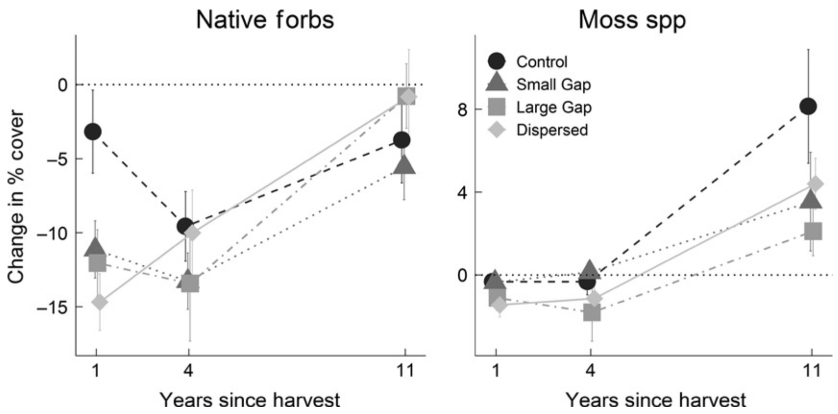

Fig. 5. Change in percentage cover of native forbs and moss/clubmoss spp. by overstorey treatment relative to pre-treatment values 1, 4 and 11 years following harvest in *Pinus resinosa* forests in northern Minnesota. These life-forms either did not exhibit significant treatment effects (native forbs) or were negatively impacted by harvest (moss spp.).

dispersed retention treatment, where harvest occurred throughout the stand.

One of the main concerns with loss of 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 for the first 11 years following harvest, and increases in exotic cover were low (approximately 1%). One particular species of concern, *Galeopsis tetrahit*, was first observed in 2010 and may have been introduced along logging roads and skid trails (Buckley *et al.* 2003); however, many of the exotic species present were found in stands prior to treatment. There was no treatment effect for late-successional species, in contrast to results from the Pacific Northwest documenting loss of shade-tolerant species following partial harvest (Halpern *et al.* 2005). This result was observed throughout the sampling period, suggesting that 'interior forest' species may be insensitive to change following VRH at this retention level in these historically open woodland-like *P. resinosa* ecosystems.

Overall, VRH was an effective management method for maintaining existing late-successional ground-layer species in this ecosystem. This may be driven by the historical processes affecting the development of plant communities in *P. resinosa* forests. In particular, the historical disturbance regimes, including mixed severity fire, likely favoured ground-layer communities dominated by species naturally adapted to overstorey, as well as understorey, disturbance. These disturbance regimes likely favoured reproductive strategies, such as rhizomatous growth and seed banking, adapted to persist and respond to disturbance (Rowe 1983) compared to those characterizing species found in more mesic forest types. Several species common in this study, including *C. borealis, Cornus canadensis* L., *Cypripedium acuale* Aiton. and *Maianthemum canadense* Desf., have high affinities for undisturbed conditions (high Coefficient of Conservatism values) yet have been observed 3 years after fire in other forest types (Skutch 1929) underscoring the range in late-seral species responses to disturbance depending on demographic and physiological characteristics (Nelson, Halpern & Antos 2007). Historical disturbance regimes may have also excluded herbaceous species displaying dispersal methods that limit population expansion following disturbance.

It has been demonstrated elsewhere that maintaining adequate retention of overstorey trees can sustain shade-tolerant species in the ground layer (North *et al.* 1996; Hannerz & Hanell 1997; Battles *et al.* 2001) while simultaneously supporting increased cover by early successional species. The high level of retention maintained in this study likely contributed significantly to the observed ground-layer response. In addition, the slow growth and reproductive rates and methods that may limit recovery of late-successional ground-layer species in other forests may not be 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.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our findings suggest greater flexibility in choosing retention pattern when maintenance of ground-layer 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 and richness may not be transient, at least within the time frame examined. This appears to be driven in part by graminoid and shrub species, more specifically *Carex pensylvanica* Lam. 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. Note the levels of retention are greater than those generally recommended by guidelines in many regions of the world (Gustafsson *et al.* 2012), and we would expect even greater departures from ground-layer conditions found in intact stands if such lower levels were employed in these systems. As such, managers aiming to minimize diversity losses may want to employ retention levels above those generally recommended by site-level guidelines.

Our results are important for future consideration of VRH in north temperate ecosystems, and potentially across the world. Alterations to natural disturbance regimes have occurred in many other regions, and as a result response to harvesting disturbance may not be straightforward, even when canopy disturbance mimics natural processes. For example, in lowland wet Eucalyptus forests in Tasmania, variable retention systems and low-intensity burns are being utilized in systems once perpetuated by infrequent, high-intensity fires (Baker & Read 2011). In Finland, loss of fire interacts with land-use history to determine restoration success when the natural disturbance is restored (Kouki *et al.* 2012).

The recalcitrant layer had an impact on many of the diversity and composition measures analysed in this study, in many cases more so than VRH treatment. The prolific response by *Corylus* species to harvest likely did not occur historically, considering the drastic change in historical disturbance regimes found in this, and many, forest systems following European settlement (Spurr 1954; Tappeiner 1979). Consideration of the understorey is particularly important as alternative silvicultural strategies are increasingly utilized to mimic natural disturbance in order to maintain or restore historical conditions to the ground layer. Overall, emphasis has been placed on overstorey disturbance pattern and severity, while altered understorey conditions may have a greater impact on ground-layer response to overstorey disturbance (Kern *et al.* 2012). Even in cases where management goals do not emphasize ground-layer response to harvest, interactions with the recalcitrant understorey can filter response to varying retention pattern and negatively impact growth of regeneration (Montgomery *et al.* 2013).

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Data accessibility

Ground-layer species data are available from Dryad Digital Repository doi: 10.5061/dryad.fj4f2 (Roberts *et al.* 2016).

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