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Retention level affects dynamics of understory plant community recovery in northern temperate hemlock-cedar forests☆

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ABSTRACT

Retention forestry is replacing clear-cutting as the dominant silvicultural practice in many parts of the world. Higher retention levels are thought to promote faster, more complete ecological recovery after logging, but this hypothesis is insufficiently tested. We compared plant community dynamics in 0%, 40% and 70% retention stands to unharvested stands for 24 years after logging at the Date Creek Research Forest near Kispiox, BC, Canada. The study has a before-after control-impact experimental design with four replicates of each treatment. For terricolous understory plants, we used the similarity of cover, species richness and composition to pre-harvest and unharvested conditions as indicators of ecological integrity. Changes in cover, richness and composition were greatest at 0% retention. For nonvascular plants, changes were generally intermediate at 40% retention and smallest at 70% retention, and recovery increased with retention. The dominant moss *Hylocomium splendens* responded negatively to harvest in proportion to retention level, while most other species responded positively, shifting community composition. Most vascular plants responded positively to harvest, especially at 0% retention, with the exception of two late seral species, *Platanthera orbiculata* and *Oplopanax horridus*. Generally, understory communities in these largely unfragmented northern cedar-hemlock forests displayed less sensitivity to low retention levels than studies conducted elsewhere. For some vascular plant indicators, changes at 70% retention were equal to or greater than those at 40%. Thus, most -but not all- vegetation responses supported the hypothesis that higher retention enhances ecological recovery after logging. The non-linear results were apparently driven by suppression of understory conifer growth in small gaps at 70% retention and illustrate that evaluating ecological integrity strictly in terms of departure from an un-impacted benchmark system risks oversimplifying complex forest dynamics.

1. Introduction

New conceptual and multidisciplinary approaches are proposed to manage the structure and dynamics of forest ecosystems to promote their long-term productivity, biodiversity and adaptability (Puettmann et al., 2009; Messier et al., 2013). Retention forestry is an approach that focuses on the type and quantity of forest structures left behind during logging operations to maintain identified ecological, social and economic values (Gustafsson et al., 2012; Lindenmayer et al., 2012; Fedrowitz et al., 2014). How forest ecosystem attributes and functions change and recover after different frequencies and intensities of canopy removal is still under investigation. Hypothesized benefits of retaining some canopy trees during logging are reduced negative effects of harvest on forest specialist species and faster ecological recovery after harvest compared to clear-cutting (Gustafsson et al., 2012; Fedrowitz et al., 2014), but few well-designed studies have existed for long enough to determine rates of recovery. In a recent meta-analysis of 78 studies, more than 70% were five years or less in duration (Fedrowitz et al., 2014).

The Date Creek Experimental Forest in northwestern British Columbia (BC), Canada (Coates and Burton, 1997) offers an excellent opportunity to test whether retention forestry lessens effects of harvest and hastens ecological recovery. Four replicates of three retention levels and an unharvested control (0%, 40%, 70% and 100% retention) were applied to ∼20 ha treatment units in 1992. Potentially confounding environmental effects (Lindenmayer and Laurance, 2012)

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were minimized using a randomized complete block design. The understory plant community was measured pre-harvest and regularly for 24 years post-harvest, creating a strong before-after control-impact (BACI) experimental design with one of the longest datasets in North America, including measurements of light availability over time. Here, we use the long-term response of the understory plant community as an indicator of ecological integrity, defined as departure from the condition of an un-impacted benchmark system (Haeussler and Kneeshaw, 2003). We compare the dynamics of understory tree, vascular and nonvascular plant functional groups and species at three retention levels and evaluate whether the vegetation remains closer to, and recovers more quickly to pre-harvest and unharvested conditions at higher levels of canopy retention.

Although few large scale forestry experiments have tracked the recovery of plant communities for as long as Date Creek, much knowledge about understory responses to logging has been acquired over shorter time frames or by using the chronosequence approach. Logging creates a stressful microclimate for understory plants acclimated to mature closed forest canopies, including higher understory light levels, greater air and soil temperature and moisture fluctuations (Heithecker and Halpern, 2006) and abrupt changes in soil nutrients and microbiota (Brundrett, 1991; Prescott, 2002). Higher levels of retention ameliorate these stresses (Heithecker and Halpern, 2006; Caners et al., 2013b), reducing the magnitude of understory change (Craig and Macdonald, 2009). As tree seedlings and saplings replace harvested trees, the microclimate approaches mature forest conditions and understory vascular plants recover to near undisturbed levels in some forests (Halpern and Spies, 1995). Although logging impacts are short-lived for many temperate forest plants and species richness is often higher in managed forests (Boch et al., 2013), species composition can be substantially or permanently altered by traditional clear-cut logging (Haeussler et al., 2002).

Life history or functional traits of plant species can help to predict their differing responses to harvest and recovery over time (Lavorel and Garnier, 2002). We expect early seral species with little or no presence in undisturbed forest to quickly increase after disturbance (Halpern, 1989), then to decline as light and nutrient availability decline. Most forest generalist species can survive disturbances ranging from 40% retention (Zenner et al., 2012) to full clear-cut logging and burning (Halpern 1989) and respond positively to the new environment (Bond and Midgley, 2001). We expect forest generalists to increase after harvest but to lag behind early seral species in recovery due to greater tolerance of diminishing resource availability. Sensitive late seral species are reduced in cover or extirpated in the first years after disturbance (Halpern et al., 2005), and we expect negligible to slow recovery over 24 years. Shifts in plant community composition can be expected when negative responses of slow growing late seral species are exacerbated by competition from early seral and generalist species that respond positively to increased light or to changes in soil chemistry, including invasive, non-native plants. Changes in community composition may be temporary, or may pass a threshold (Craig and Macdonald, 2009) and not return to unharvested forest conditions.

Shifts in composition can also occur between life forms that differ in response to disturbance. In the understory of northern temperate forests a carpet of feather moss impedes establishment of tree seedlings. Partial logging can reduce feather moss cover and allow tree seedling germination (LePage et al., 2000) because most bryophytes are more sensitive to overstory removal than most vascular plants (Frego, 2007). Within bryophytes, mosses are less sensitive than liverworts (Bartels et al., 2017), but both groups contain sensitive species that persist only in intact forests, as well as species that thrive after disturbance (Caners et al., 2013b). Based on the hypothesis that retention increases ecological integrity, we expect retention to have a stronger stabilizing effect on nonvascular plants than on vascular plants, and to have the strongest stabilizing effect on liverworts.

We used a conceptual model to simplify interpretations of plant community dynamics, identifying four alternative responses to harvest that support the hypothesis that retention maintains ecological integrity via a stabilizing effect (the retention-stability hypothesis; Fig. 1). A positive response to harvest with recovery occurs when an indicator increases as retention decreases, then returns to pre-harvest (or unharvested) levels over time (Fig. 1a). Retention has a stabilizing effect if the peak of change (largest departure from pre-harvest levels) or recovery time (length of time the indicator remains different from pre-harvest levels) are reduced at higher retention levels. A positive response to harvest without recovery occurs when an indicator increases with decreasing retention but remains at an elevated level (Fig. 1b). A negative response with recovery (Fig. 1c) and a negative response without recovery (Fig. 1d) occur when an indicator decreases with decreasing retention, but otherwise correspond to the respective positive responses. “Without recovery” scenarios (1b and 1d) could represent indicators that require more time to recover, or are irrevocably shifted because a threshold has been passed.

2. Methods

2.1. Study area

This study of understory plant community responses was a component of the larger 4000 ha Date Creek Silvicultural Systems Experiment (55°22′ N, 127°50′ W) located 21 km north of Hazelton in northwestern BC (Coates et al., 1997). It was established in 1992 to meet timber production goals while also retaining live trees, snags or logs that serve important ecological functions in post-harvest stands. The study area was located within the moist cold subzone of the Interior Cedar-Hemlock biogeoclimatic zone, a transitional zone between interior and coastal forest ecosystems lying at the northern temperate forest limit (Banner et al., 1993). Between 370 and 665 m in elevation, the area averages 535 mm annual precipitation (238 mm during the growing season) and has a mean annual temperature of 4.4 °C. Morainal parent materials with loamy sand to clay loam textures are dominant. Soils are Eluviated Dystric Brunisols, Orthic Dystric Brunisols and Orthic Humo-Ferric Podzols (Soi1 Classification Working Group, 1998) with 4–14 cm thick forest floors layers.

Treatment units were located in mature stands dating from an 1885 fire and in old-growth stands aged ≥350 years. The ~140 year old mature stands were dominated by western hemlock (*Tsuga heterophylla*, 65% of stand basal area), western red-cedar (*Thuja plicata*, 18% basal area) and hybrid spruce (a complex of *Picea glauca, Picea sitchensis* and *Picea engelmannii*, 8% basal area) with six minor tree species: subalpine fir (*Abies lasiocarpa*), amabilis fir (*Abies amabilis*), lodgepole pine (*Pinus contorta* var. *latifolia*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*) and black cottonwood (*Populus balsamifera* ssp. *trichocarpa*) (plant nomenclature follows MacKenzie et al. 2016; authorities are in Appendix A). Old growth stands lacked pine, birch, aspen and cottonwood, and were dominated by western hemlock (81% basal area), with minor western red-cedar, amabilis fir, subalpine fir and hybrid spruce. Understories had a thick growth of feather mosses (80% cover), *Pleurozium schreberi*, *Hylocomium splendens*, *Ptilium crista-castrensis* and *Rhytidiadelphus* spp. The sparse shrub and herb layers (4–8% cover) had scattered oval-leaved blueberry (*Vaccinium ovalifolium*), Alaskan blueberry (*V. alaskaense*), black huckleberry (*V. membranaceum*), bunchberry (*Cornus canadensis*), five-leaved bramble (*Rubus pedatus*), one-sided wintergreen (*Orthilia secunda*) and prince's pine (*Chimaphila umbellata*). Wetter sites had devil's club (*Oplopanax horridus*), black gooseberry (*Ribes lacustre*), highbush-cranberry (*Viburnum edule*), oak fern (*Gymnocarpium dryopteris*), lady fern (*Athyrium filix-femina*) and leafy mosses (*Mniaceae* spp.).

2.2. Experimental design and treatments

Three logging treatments were applied at Date Creek and compared to unharvested forest: 0% (clear-cut) retention, 40% retention and 70% retention (Table 1). All conifer trees were removed in the 0% retention

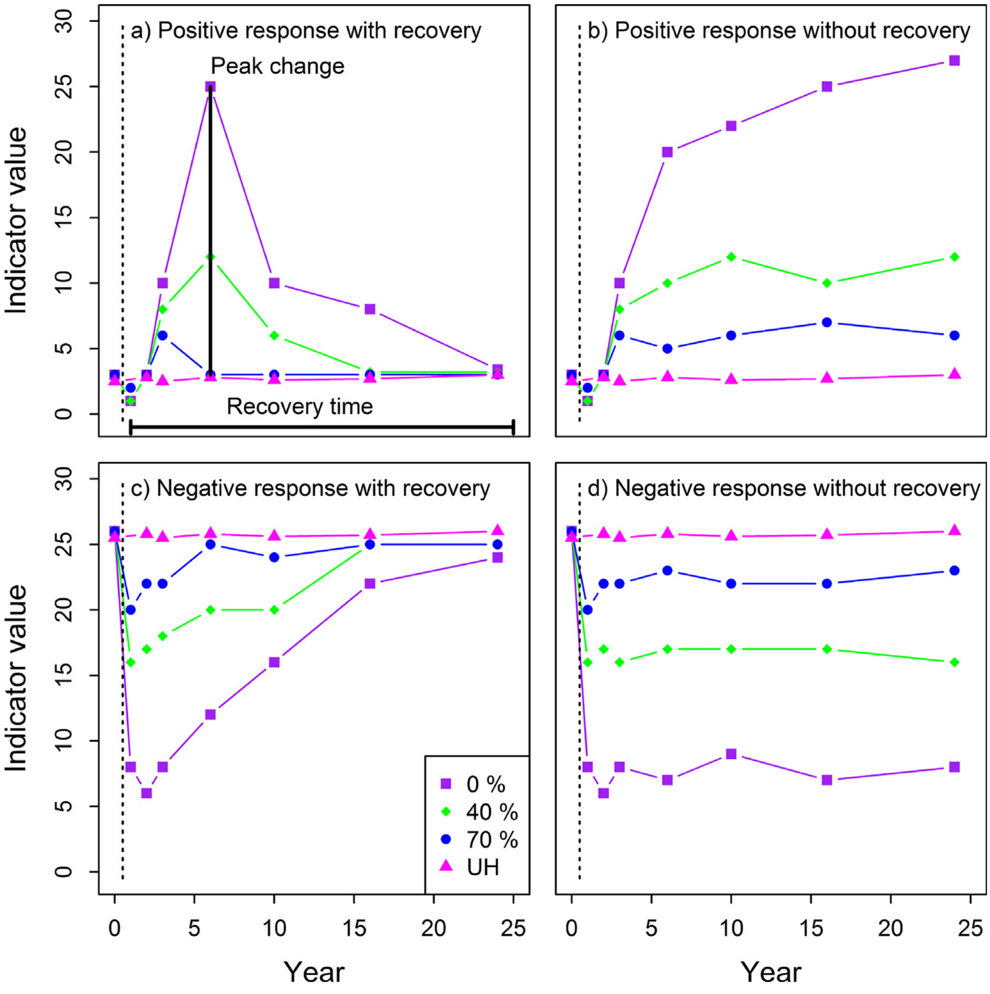

Fig. 1. Four hypothesized trajectories for forest ecosystem indicator response at three levels of retention (0%, 40% and 70%) and unharvested (UH) conditions: (a) positive response with recovery to UH; (b) positive response without recovery, (c) negative response with recovery and (d) negative response without recovery. Dotted vertical lines indicate timing of harvest, solid vertical line in (a) illustrates peak change (maximum change from pre-harvest) and solid horizontal line in (a) illustrates recovery time (length of time until the indicator is no longer significantly different from UH).

treatment. A few scattered aspen and birch were retained, and very few understory trees survived after logging. The 40% retention treatment included large gaps (500–5000 m^2 in size) evenly distributed across the stand, and single tree or small gap (< 300 m^2) removal in the forest matrix between the large gaps. The 70% retention treatment included infrequent large gaps and frequent single tree or small gaps. Experimental treatment units were ~20 ha and replicated four times (16 total) in a randomized block design, with blocking based on ecological site type and forest age (mesic 350 yr; mesic 140 yr; mesic-submesic 140 yr; mesic-subhygric 140 yr; Table 1).

Table 1
Date Creek silvicultural systems study treatment unit description.

Block, site type and stand age at establishment	Treatment (% retention)	Elevation (m)	Area (ha)	Stand density (stems ha^{-1})[1]		Stand basal area (m^2 ha^{-1})[1]		No. of understory plots
				Pre-harvest (1991)	Post-harvest (1992)	Pre-harvest (1991)	Post-harvest (1992)	
1. Mesic, old growth (350 + yr)	Unharvested	470–630	24.4	414.4	414.5	63.6	63.6	12
	70%	610–665	17.4	458.6	285.1	69.1	47.6	12
	40%	470–505	18.9	389.4	156.1	56.7	28.7	12
	0%	600–630	16.0	1121.1	–	74.5	–	12
2. Mesic to submesic (~140 yr)	Unharvested	370–440	20.1	841.7	841.7	55.5	55.5	12
	70%	435–450	18.5	881.3	683.3	65.6	39.9	12
	40%	440–480	22.0	701.9	448.5	55.7	28.1	12
	0%	420–440	11.5	1030.2	–	56.7	–	8
3. Mesic (~140 yr)	Unharvested	480–590	21.6	957.4	957.4	64.1	64.1	12
	70%	400–440	17.8	687.5	596.4	63.5	40.6	12
	40%	480–590	20.6	819.9	406.6	71.2	34.3	12
	0%	430–460	18.5	1183.0	–	52.2	–	12
4. Mesic to subhygric (~140 yr)	Unharvested	400–440	38.2	677.2	677.2	55.4	55.4	12
	70%	455–480	22.9	731.7	616.2	69.1	46.4	12
	40%	410–480	25.2	814.9	417.5	70.3	30.6	12
	0%	400–440	25.3	1825.1	–	71.4	–	12

[1] Pre and post treatment density and basal area based on trees ≥17.5 cm DBH.

All treatment units were logged in summer-winter 1992/3 and planted in spring 1993. The 0% retention units were fully planted with conifer seedlings: mesic and drier sites with an equal mixture of western hemlock, interior spruce and lodgepole pine, with some subalpine fir; wetter sites with an equal mix of spruce and western red-cedar. In the 40% retention units, gaps were planted with the above prescription with pine concentrated in the middle of gaps. In the matrix of 40% retention units and throughout the 70% retention units, spruce and cedar were planted wherever stumps were present, but no closer than 2 m from a standing tree to achieve 300 stems ha^{-1} total stocking. No further silviculture activities were planned, but in three of the 0% retention units, deciduous trees surrounding conifer seedlings were unintentionally cut 8 years post-harvest.

2.3. Understory plant community data collection

Understory vegetation was sampled prior to logging (1992) and at 1, 2, 3, 6, 10, 16 and 24 years post-harvest (except unharvested units were not sampled at year 1). In each treatment unit, three hub points were randomly located. Four understory vegetation sample plots were clustered at random bearings and distances (< 30 m) around each hub for a total of 12 plots per treatment unit. Four plots were left unharvested in one 0% retention unit and were excluded from analysis. Each plot was 5 × 5 m, with 3 × 3 m and 1 × 1 m subplots nested within. Understory trees and shrubs 2–10 m in height (including planted trees) were sampled in 5 × 5 m plots. Trees and shrubs < 2 m in height (including planted trees) were sampled in 3 × 3 m subplots. Herbs, bryophytes and lichens were sampled in 1 × 1 m subplots. Only bryophytes and lichens growing directly on the forest floor (terricolous species) were recorded. Samples of unfamiliar species were collected adjacent to the plot for expert identification with a microscope, when possible. Before analysis, genera with inconsistent identification across the sampling years were lumped.

Percent cover by species was estimated in each plot in late summer of each sampling year and a mean cover was calculated for each treatment unit. The cover of individual species was summed by understory vegetation layer: trees, vascular plants (herbs and shrubs) and nonvascular plants (mosses, liverworts and lichens) and functional group: early seral shrubs, forest generalist shrubs, early seral herbs (including invasive non-native species), forest generalist herbs, late seral shrubs and herbs, early seral mosses, feather mosses, other mosses, liverworts (excluding early seral liverworts) and lichens based on our experience and the literature (Caners et al., 2013a; Halpern et al., 2012; Appendix A). Invasive herbs and early seral mosses were not frequent enough to analyze statistically. The high frequency and abundance of the feather mosses *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis* and *Rhytidiadelphus* spp. allowed their cover to be examined individually. Low frequency and abundance of late seral species limited our confidence in analysis of their cover responses to logging using the permanent sample plots. At year 24, we surveyed late seral herbs in the *Ericaceae*, *Liliaceae* and *Orchidaceae* families and the late seral shrub *Oplopanax horridus* by randomly locating four 200 × 4 m transects in each treatment unit and counting individual stems or ramets of each late seral species along each transect.

2.4. Understory light data collection

Hemispherical canopy photographs were taken 1.3 m above the forest floor at a fixed location in each 1 × 1 m subplot. At year 3 (1995) photos were taken with a Nikkor 8-mm true fisheye lens mounted on a Nikon F (Mississauga, Ontario, Canada) camera and analyzed using GLI/C software following Canham (1988). At years 14 and 24–25, photos were taken again using a Nikon FC-E8 fisheye lens converter mounted on a Nikon Coolpix 5000 digital camera and analyzed using Gap Light Analyzer software (GLA 2.0) (Frazer et al., 2000). Percent light from these analyses was considered to be the total light transmitted to the understory relative to the light available above the canopy.

2.5. Data analysis

From 2 years post-harvest and onward, we examined the effect of retention treatment and time on understory plant percent cover, species richness and species composition (percent dissimilarity) using linear mixed effects modeling (with the “nlme” package v. 3.1 in R version 3.1.2; R Core Team 2014; Pinheiro et al., 2016). The fixed effects were treatment, year and their interaction and the random effect was block. Repeated measures of plots over the years were modelled using a continuous autoregressive correlation matrix. Visual inspection of residuals revealed heteroscedasticity among treatments (with the smallest variance in the unharvested treatment), which was accounted for with an additional variance term in the model (Pinheiro et al., 2016). It was not possible to fit models with the variance term for early seral shrubs and herbs (and for some individual year comparisons for other groups). Data from the late seral species transects were analyzed with a negative binomial mixed effects model (GLIMMIX procedure, SAS Institute Inc. 2011). Species richness and percent dissimilarity were computed for tree species, vascular and non-vascular plants, using the “vegan” package v. 2.2-1 (Oksanen et al., 2015) in R. Percent dissimilarity was based on the Bray-Curtis distance between pre-harvest and post-harvest composition in each year for each treatment unit.

When the treatment or treatment × year interaction was significant in the overall model and treatment also had a significant effect in a reduced model for an individual year, the R package “multcomp” (Hothorn et al., 2008) was used to compare the 0%, 40% and 70% retention treatments to the unharvested treatment. “Multcomp” was also used to estimate means and standard errors for fitted models.

The effect of treatment and time on percent light were tested with the same linear mixed effects model used for understory plants for year 3 and year 24–25 measurements, and the same multiple comparisons were made if the model indicated a significant effect of treatment. Year 14 measurements were excluded from the overall model because no photos were taken at 0% retention, but within year multiple comparisons were made between 40% and 70% retention and unharvested. At year 3, three 0% retention units had one or fewer photos taken, so the sample size was low for this treatment, but we are confident that the 89% light estimated by the model for these stands is a conservative estimate of light availability 3 years after clear-cutting.

For each response variable significantly affected by treatment or treatment × year, we quantified peak change as the largest magnitude of pre-harvest-to-post-harvest difference in that variable, and relative peak change as the ratio of the peak change for each treatment and the largest peak change for any treatment. We used multiple comparison *p*-values to determine which response variables departed significantly from unharvested conditions and quantified recovery time as the number of years until the *p*-value was no longer significant. For variables that remained significantly different from the unharvested treatment at year 24, we used a recovery time of 24+ years.

3. Results

3.1. Percent light

Understory light availability increased after harvest compared to light in the unharvested forest (Table 2; Fig. 2). Light measurements in the unharvested forest were stable between sampling years despite equipment changes between 1995 and 2016 and several windthrow events (Coates, 1997). At 0% retention, nearly full light was available to the understory three years after harvest, but by year 24, light availability had dropped to 20%, because of the new canopy created by regenerating trees. Although 60% of the basal area was removed in the 40% retention treatment, average light availability after harvest was only 30%, which dropped to 15% by year 24 (Fig. 2).

Table 2

Results of linear mixed model testing (including numerator (ndf) and denominator (ddf) degrees of freedom) for Treatment or Year × Treatment effects of harvest on understory light and vegetation. Stars indicate treatments that are significantly different from unharvested forest at α = 0.05 (*), α = 0.01 (**) and α = 0.001 (***).

Category	Variable	Effect[1]	F stat	ndf	ddf	*p*-value	Sig. level
Understory light	Percent of total transmitted	Yr × Trt	66.74	3	10	< .0001	***
Understory trees	Percent cover	Yr × Trt	13.26	15	60	< .0001	***
	Species richness[1]	Trt	10.27	3	9	.0029	**
	Percent dissimilarity	Yr × Trt	3.23	15	60	.0006	***
Vascular plants	Percent cover	Yr × Trt	6.65	15	60	< .0001	***
(shrubs and herbs)	Species richness[1]	Trt	4.82	3	9	.0287	*
	Percent dissimilarity	Yr × Trt	2.18	15	60	.0171	*
Nonvascular plants	Percent cover	Yr × Trt	6.07	15	60	< .0001	***
	Species richness	Yr × Trt	1.14	15	60	0.3457	
	Percent dissimilarity	Yr × Trt	2.00	15	60	.0306	*
Early seral shrubs	Percent cover	Yr × Trt	2.50	15	60	.0063	**
Early seral herbs	Percent cover	Yr × Trt	6.05	15	60	< .0001	***
Generalist shrubs	Percent cover	Yr × Trt	2.36	15	60	.0099	**
Generalist herbs	Percent cover	Yr × Trt	3.17	15	60	.0007	***
Late seral herbs and shrubs	Percent cover	Yr × Trt	3.94	15	60	.0001	***
Chimaphila umbellata	Frequency	Trt	1.52	3	9	.2761	
Clintonia uniflora	Frequency	Trt	3.56	3	9	.0603	
Oplopanax horridus	Frequency	Trt	7.79	3	9	.0072	**
Orthilia secunda	Frequency	Trt	2.44	3	9	.131	
Pyrola asarifolia	Frequency	Trt	1.97	3	9	.1893	
Pyrola chlorantha	Frequency	Trt	2.28	3	9	.1485	
Platanthera orbiculata	Frequency	Trt	5.27	3	9	.0226	*
Streptopus amplexifolius	Frequency	Trt	0.74	3	9	.556	
Feather mosses	Percent cover	Yr × Trt	4.68	15	60	< .0001	***
Hylocomium splendens	Percent cover	Yr × Trt	2.15	15	60	.0188	*
Pleurozium schreberi	Percent cover	Yr × Trt	7.85	15	60	< .0001	***
Ptilium crista-castrensis	Percent cover	Yr × Trt	2.63	15	60	.0041	**
Rhytidiadelphus spp.	Percent cover	Yr × Trt	0.84	15	60	.6308	
Other mosses	Percent cover	Yr × Trt	2.22	15	60	.02	*
Lichens	Percent cover	Yr × Trt	2.03	15	60	.028	*
Liverworts	Percent cover	Yr × Trt	1.26	15	60	.2547	

[1] Treatment effects (Trt) are presented when Year × Treatment effects (Yr × Trt) effects were non-significant ($p > .05$).

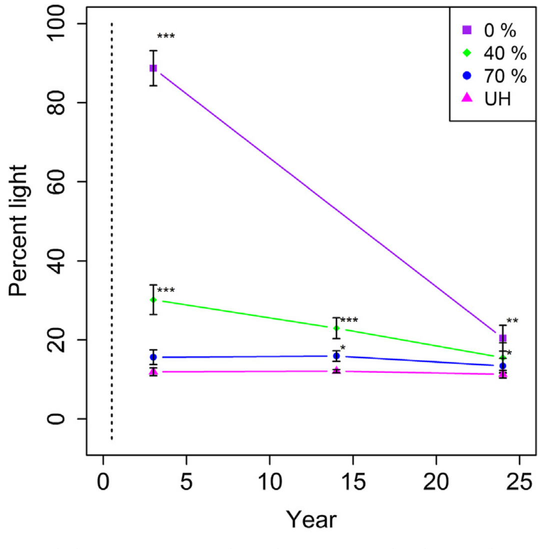

Fig. 2. Percent light (mean ± SE) in the understory (1.3 m height) after harvest at three levels of retention (0%, 40% and 70%) and in unharvested (UH) forest. The data point at year 3 in 0% retention represents data from three stands only. Stars indicate treatments that are significantly different from UH at α = 0.05 (*), α = 0.01 (**) and α = 0.001 (***).

3.2. Percent cover

The percent cover of understory trees, vascular plants and nonvascular plants responded significantly to logging (Table 2) and response trajectories varied with the level of retention and among indicator groups (Fig. 3). Understory tree cover (including advanced regeneration, natural and planted seedlings < 10 m tall) had a negative response to harvest but recovered to unharvested levels by six years (as in Fig. 1c) and subsequently had a positive response to harvest that corresponded to retention level but did not recover by year 24 (Fig. 3a and as in Fig. 1b).

Vascular understory plant cover responded positively to logging (after a brief delay) and did not recover to unharvested levels by year 24 (Table 2; Fig. 3b), even though light availability in the understory decreased substantially over time at 0% and 40% retention (Fig. 2). A positive response with recovery to unharvested levels (as in Fig. 1a) was demonstrated in part by early seral shrubs and herbs which displayed greater peak change at lower retention (Fig. 4a and b). Early seral herbs also demonstrated a shorter recovery time at higher retention and had fully recovered (i.e., mostly disappeared) by year 24 (Fig. 4b). Recovery of early seral shrubs was delayed compared to herbs, but did show a trajectory of recovery at 0% and 40% retention by year 24. At 70% retention, early seral shrubs continued on an increasing trajectory (Fig. 4a).

Generalist shrubs, like understory trees, initially responded negatively to harvest, then recovered and responded positively (corresponding to retention level but not significantly different from unharvested forest in any single year; Table 2; Fig. 4c). By contrast, generalist herbs showed a positive response to logging without recovery (dramatically so at 0% retention), but the relationship did not correspond to retention level. Generalist herb cover was somewhat higher at 70% retention than at 40% retention starting at year 10 (Fig. 4d).

Contrary to expectations, late seral shrub and herb cover showed a slow positive response to logging without recovery to unharvested levels, with the largest gain in cover between years 16 and 24 at 0% retention (Fig. 4e). Although late seral species responded significantly to year × treatment (Table 2), the largest contrast (year 24 at 0% retention) was only marginally significant ($p = 0.057$). Data from the late seral species transects at year 24 indicated that several species (*Chimaphila umbellata*, *Pyrola asarifolia*, *P. chlorantha* and *Clintonia uniflora*)

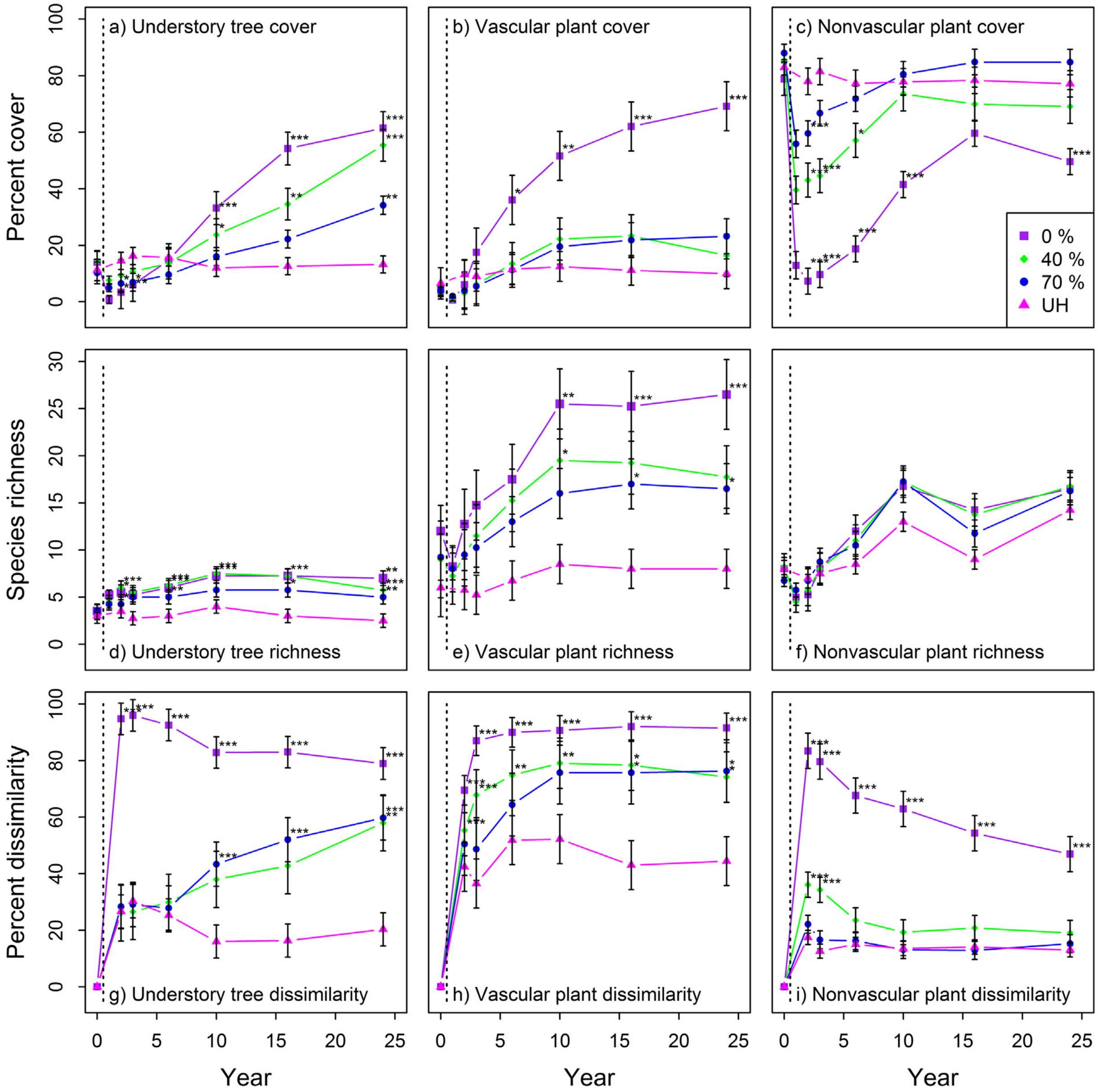

Fig. 3. Percent cover, species richness and percent dissimilarity pre-harvest and over 24 years post-harvest at three levels of retention (0%, 40% and 70%) and in the unharvested (UH) forest, for: (a), (d), (g) understory trees < 10 m tall; (b), (e), (h) vascular plants (herbs and shrubs); and (c), (f),(i) non-vascular plants (forest floor bryophytes and lichens). Values are mean ± SE. Stars indicate treatments that are significantly different from UH at $\alpha = 0.05$ (*), $\alpha = 0.01$ (**) and $\alpha = 0.001$ (***). Dotted vertical lines indicate timing of harvest.

considered late seral actually had higher cover with lower retention, although not significantly so (Table 2; Fig. 5). Only *Platanthera orbiculata* and *O horridus* had significant declines in frequency with harvest and persistent negative effects of the 0% retention treatment at year 24 (Fig. 5). The ericads *Moneses uniflora, Monotropa uniflora* and *Hypopitys monotropa*, the lilies *Maianthemum racemosum*, *M. stellatum* and *Streptopus streptopoides* and the orchids *Calypso bulbosa*, *Corrallorhiza* spp., *Goodyera* spp. and *Listera* spp. were not sufficiently frequent to investigate their response to retention.

Away from roadsides, there were few invasive non-native plant species at Date Creek; no non-native plants were found pre-harvest or in unharvested units. *Taraxacum officinale*, *Cirsium arvense* and *Poa pratensis* invaded at 0% retention. *T. officinale* and *C. arvense* also invaded at 40% retention and only *T. officinale* invaded at 70% retention. Although their occurrences were too few to test statistically, total invasive species cover displayed a positive response to harvest that recovered by year 24, when invasives were nearly extirpated from the permanent sample plots, with only one occurrence remaining at 0% retention (Fig. 4f).

Nonvascular plant cover had an immediate, strong negative response to logging and significantly decreased in proportion to retention treatment, then recovered (Fig. 3c), fully conforming to the negative response with recovery trajectory (Fig. 1c). Peak changes were greater and recovery times were longer with less retention (Fig. 3c).

Feather mosses dominated the nonvascular layer and their combined response to retention level paralleled that of total nonvascular cover (Fig. 3c and a). Other mosses (including *Sphagnum* spp., *Dicranum* spp., *Polytrichum* spp. and *Brachythecium* spp.; Appendices A and B) had a delayed positive response to harvest, with greater increases in cover at lower retention and a slight trajectory of recovery by year 24 (Fig. 6b). Early seral moss species were too small in number to analyze statistically, but did establish at all three retention levels, showing a positive response to harvest with recovery (Fig. 6c).

Individual feather moss species diverged in response to retention level. *Hylocomium splendens* responded like a prototypical late seral

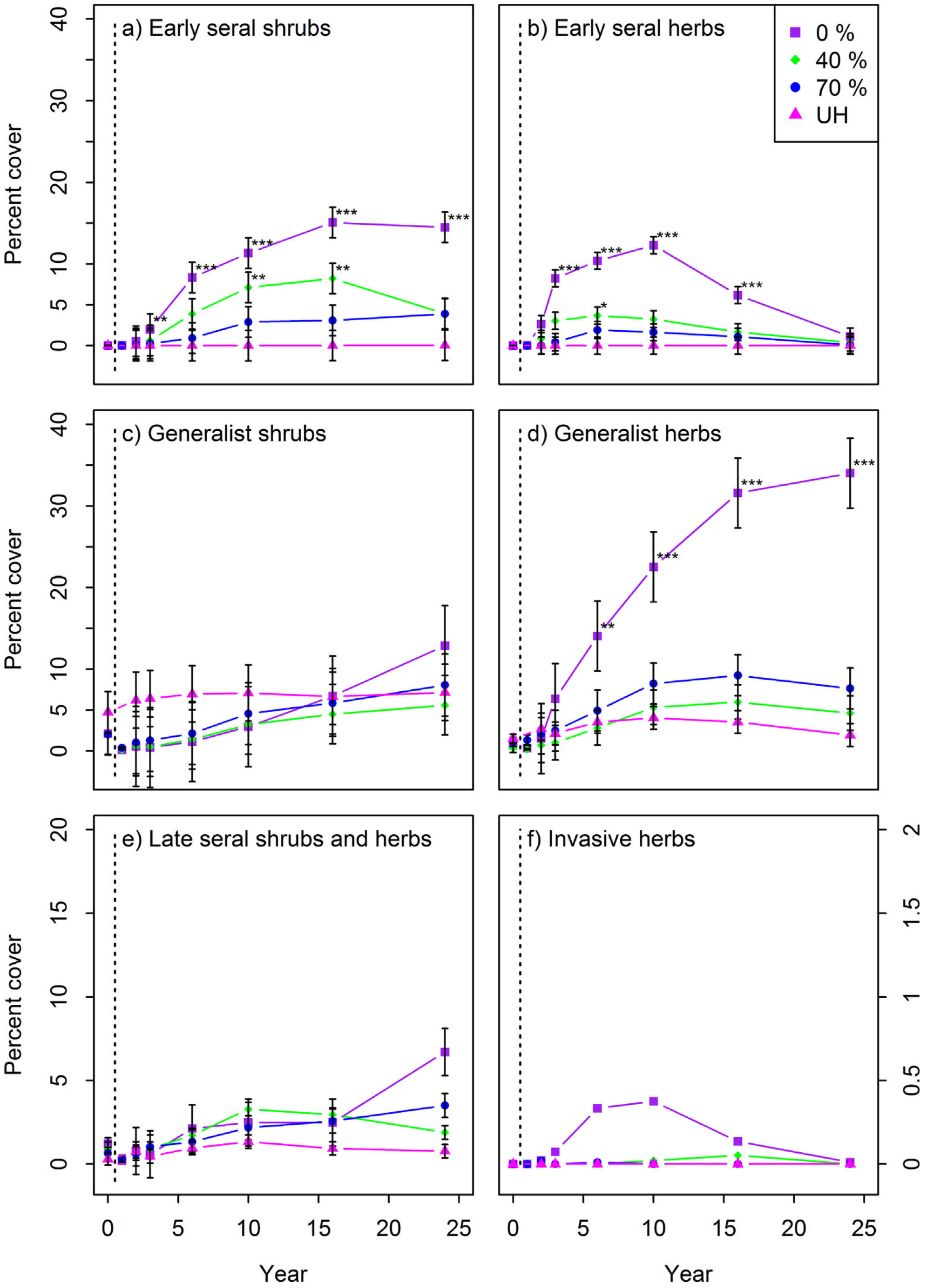

Fig. 4. Percent cover pre-harvest and over 24 years post-harvest at three levels of retention (0%, 40% and 70%) and in the unharvested (UH) forest for (a) early seral shrubs, (b) early seral herbs, (c) generalist shrubs, (d) generalist herbs, (e) late seral shrubs and herbs and (f) invasive herbs. Values are mean ± SE. Stars indicate treatments that are significantly different from UH at $\alpha = 0.05$ (*), $\alpha = 0.01$ (**) and $\alpha = 0.001$ (***). Dotted vertical lines indicate timing of harvest.

species, with cover decreases and recovery times in proportion to retention (Fig. 6d). *Pleurozium schreberi* was more resilient to harvest than *H. splendens*: at 0% retention it declined significantly in cover, but then more than quadrupled its cover by year 16 (Fig. 6e). *Ptilium crista-castrensis* had a slight negative response to 0% retention but recovered by year 10 (Fig. 6f). Lichens, dominated by *Cladonia* and *Peltigera* spp., had a delayed positive response to harvest, but only at 0% and 40% retention (Fig. 6g). Neither *Rhytidiadelphus* spp. nor total liverworts (excluding early seral *Marchantia polymorpha* which established in two plots after harvest but disappeared by year 16) responded significantly to harvest (Table 2, Fig. 6h). Although their occurrences were too few to test statistically, *Barbilophozia* spp. appeared to be the least sensitive and *Plagiochila* spp. most sensitive to harvest (Appendix B).

3.3. *Species richness*

Species richness of understory trees and vascular plants generally responded positively to harvest, remaining elevated at year 24 (Table 2, Fig. 3d and e). Understory tree richness reached an asymptote at 7 species per treatment unit at 0% and 40% retention and at 5 species at 70% retention from a pool of 10 tree species in the study area. Slightly lower richness at 70% retention was due to fewer shade intolerant species (birch, aspen, cottonwood and pine). Vascular plant richness at 40% retention did show a slight hump and trajectory towards recovery (Fig. 3e) due to decreased frequency of early seral shrubs and herbs at year 24 (especially *Chamerion angustifolium*, *Hieracium albiflorum*, *Rubus parviflorus* and *R. idaeus*; Appendix B).

Nonvascular plant richness did not vary significantly with retention

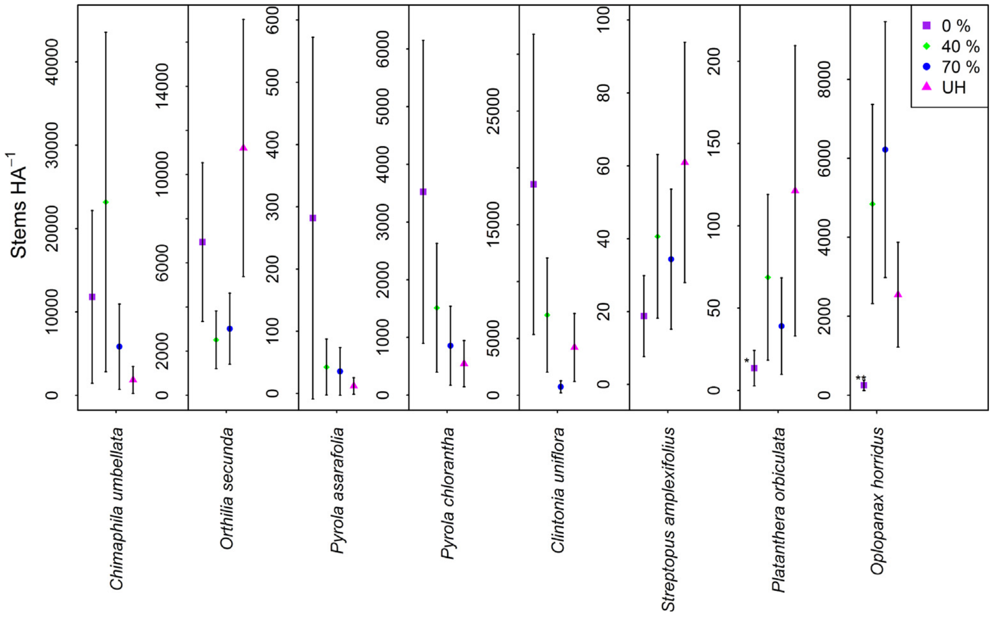

Fig. 5. Frequency of late seral shrub and herb species (that occurred frequently enough to analyze) 24 years post-harvest at three levels of retention (0%, 40% and 70%) and in unharvested (UH) forest. Values are mean ± SE. Stars indicate treatments that are significantly different from UH at $\alpha = 0.05$ (*), $\alpha = 0.01$ (**) and $\alpha = 0.001$ (***).

in any year (Table 2), but did vary significantly by year across the spectrum of retention (data not shown). Observer inconsistency is the most likely cause of the temporal response as surveyors became more adept at recognizing scarcer bryophyte species, particularly liverworts, over time. At year 10 (the peak of nonvascular richness) a bryophyte specialist was on the survey crew and 15 more liverwort species were observed compared to the previous measurement. The survey crew at year 24 followed her method of searching between feather moss stems for liverworts, causing another peak in nonvascular species richness at year 24.

3.4. Species composition

All treatments, including unharvested forest, experienced changes in species composition relative to the year 0 benchmark (Table 2, Fig. 3g–i). Changes in plant community composition in the unharvested forest were likely a consequence of the dynamic equilibrium among species in time and space (Fenton et al., 2003), as well as observer inconsistency. This dissimilarity levelled out near 20% for understory trees, 40% for vascular plants and 10% for nonvascular plants; so although their communities were not static over time, the unharvested treatment units were still able to serve as controls against which to compare the dissimilarities among harvested treatments (Fig. 3g–i).

Species composition of understory trees and vascular plants responded strongly to harvest remaining dissimilar at year 24 (Fig. 3g and h). Dissimilarity was not consistently higher with lower retention, because changes in community compositions were equal or greater at 70% retention than at 40% retention treatment starting at year 10 for understory trees and year 24 for shrubs and herbs. Nonvascular plant community composition responded strongly to harvest, recovering at 40% retention but not at 0% retention by year 24 (Fig. 3i). The lack of treatment differences in nonvascular species richness (Fig. 3f) indicates that shifts in relative abundances of common species rather than shifts in species presence generated the compositional change.

3.5. Peak change and recovery time

Most understory plant response variables had a smaller peak change after harvest with more retention, whether their response was positive or negative (Fig. 7a.i). However, generalist and late seral shrubs and herbs had larger peak changes at 70% retention than at 40% retention and tree composition peak change was slightly higher at 70% retention (Fig. 7a.ii). For two variables (lichen cover and tree richness), peak change was higher at 40% retention than at 0% retention (Fig. 7a.iii). Vascular plant richness was the only variable for which recovery time was longer at 70% than at 40% retention (Fig. 7b).

4. Discussion

Retention forestry is an important approach for balancing ecological, social and economic goals in forest management (Lindenmayer and Laurance, 2012). We used one of the longest available plant community datasets to examine if higher retention maintains and hastens recovery of ecological integrity. Nonvascular plants best demonstrated the stabilizing effects of retention: for most species and groups, changes from pre-harvest cover were smaller and recovery was faster at higher retention, although full recovery occurred only at 70% retention. Early seral and invasive herbs also changed less from pre-harvest cover at higher retention levels and were mostly extirpated at 24 years, supporting our retention-stability hypothesis. Cover of semi- and shade-tolerant trees, shrubs and herbs did not necessarily change less with more retention, nor did they recover to pre-harvest levels within 24 years. Percent cover and species composition for several understory groups had greater amplitudes of changes and slower recovery trajectories at 70% retention than at 40% retention.

4.1. Retention evaluation

Achieving continuity of habitats for both early and late successional species is an important goal of retention forestry (Gustafsson et al., 2012) that was met by the 40% retention treatment at Date Creek. Compared to 0% retention, the 40% treatment provided > 30 times more natural regeneration (at 3 years post-harvest; LePage et al., 2000), maintained two sensitive late seral species and reduced establishment of invasive herbs. Compared to 70%, 40% retention created higher light habitats for shade intolerant tree species and allowed more early seral shrubs and herbs to establish. Likewise for vertebrates at Date Creek, forest dwelling bird and small mammal species were maintained at 40% retention at Date Creek but declined immediately after harvest at 0% retention, while open-habitat species colonized stands at 40% retention, but not at 70% retention (Steventon et al., 1998). Several retention forestry experiments that include retention treatments below 40% have suggested that 10–15% retention is too little to mitigate negative effects of logging (Craig and Macdonald, 2009; Halpern et al., 2012; Johnson

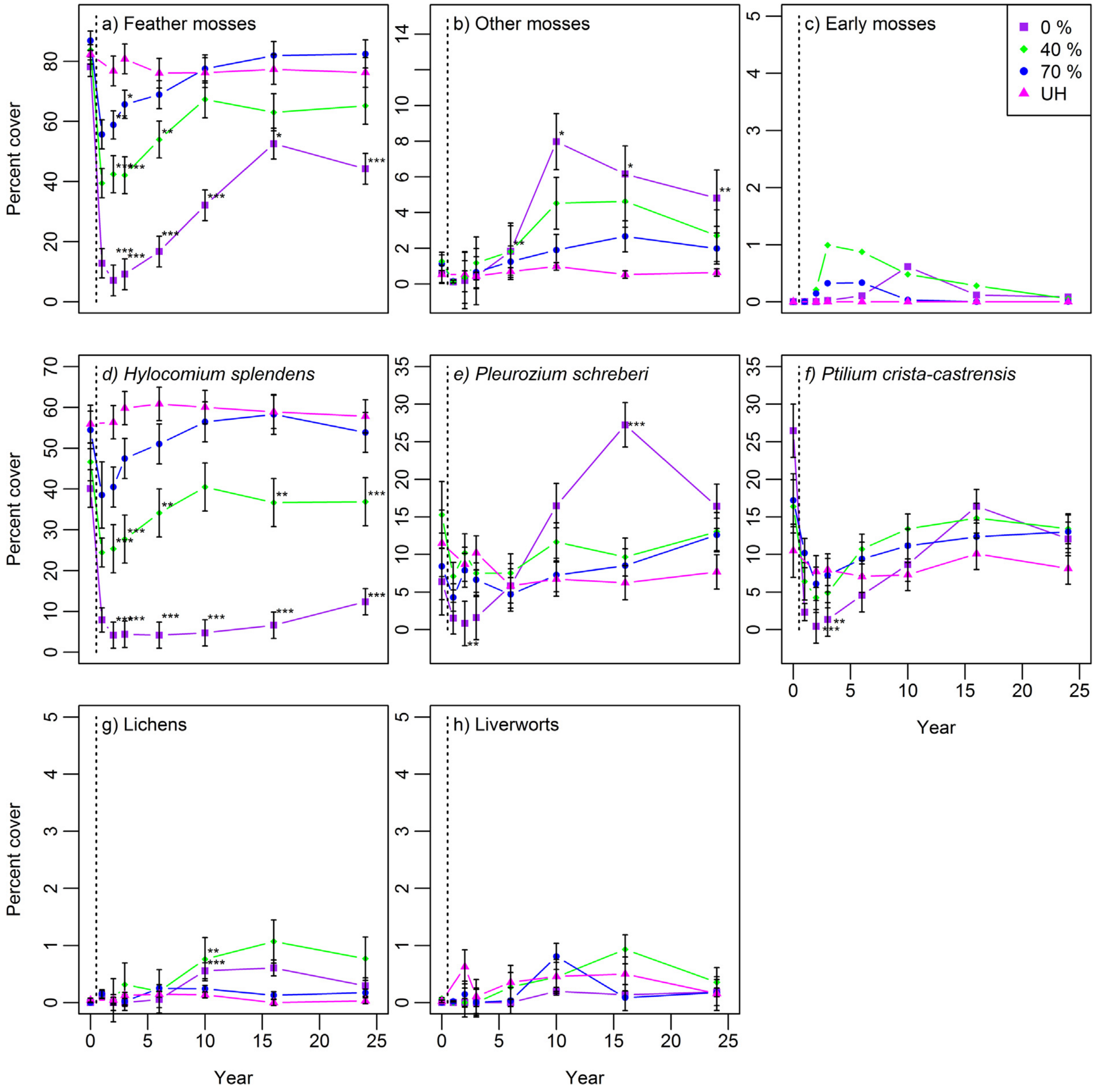

Fig. 6. Percent cover pre-harvest and over 24 years post-harvest at three levels of retention (0%, 40% and 70%) and in unharvested (UH) forest of (a) all feather mosses, (b) other mosses, (c) early seral mosses, (d) *Hylocomium splendens*, (e) *Pleurozium schreberi*, (f) *Ptilium crista-castrensis*, (g) lichens and (h) liverworts (excluding one early seral liverwort). Values are mean ± SE for summed covers within each group. Stars indicate treatments that are significantly different from UH at $\alpha = 0.05$ (*), $\alpha = 0.01$ (**) and $\alpha = 0.001$ (***). Dotted vertical lines indicate timing of harvest.

et al., 2014). Given the success of 40% retention in maintaining ecosystem integrity and enhancing species richness, and relatively strong recovery at 0% compared to studies cited above, we suggest the threshold to avoid persistent negative consequences for Date Creek understory plant communities probably lies between 15 and 40%.

Unexpectedly, we found non-linear responses between retention level and recovery dynamics of Date Creek understory plant communities. These were likely due to the spatial pattern of harvest. Some changes from pre-harvest and differences from unharvested forest were greater at higher retention, and some signs of recovery appeared sooner with less retention. Whereas the 40% retention treatment mimicked a stand replacing disturbance with a substantial amount of surviving overstory, the closest analog for 70% retention (in forests as initially dense as at Date Creek) is gap phase dynamics (Coates and Burton, 1997). Understory light measurements illustrate the difference: at 40% retention, light was initially higher but decreased over time, showing a trajectory of recovery; at 70% retention, although light levels were barely higher than in unharvested forest, they were stable over time at this elevated level. Rather than growing into the canopy, regenerating trees at 70% retention stagnate in small gaps until another disturbance allows more light penetration. We believe the removal of single and small groups of trees in the 70% retention treatment accelerated vascular plant community succession towards an old growth forest. We predict that the understory tree, shrub and herb layers will remain distinct from those of unharvested forest because of the marginally higher, yet stable, light availability.

Retention treatments above 70% are also described as heavy thinning, single tree or group selection, or structural complexity enhancement (SCE), and can be implemented with the goal of accelerating late successional forest development (Keeton, 2006; Anderson, 2008). In mature mixed forests of Vermont, SCE with 80% retention better enhanced late successional species than ~67% retention within 4 years (Smith et al., 2008). A similar experiment in 30–40 year old Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), found little effect of 67–79%

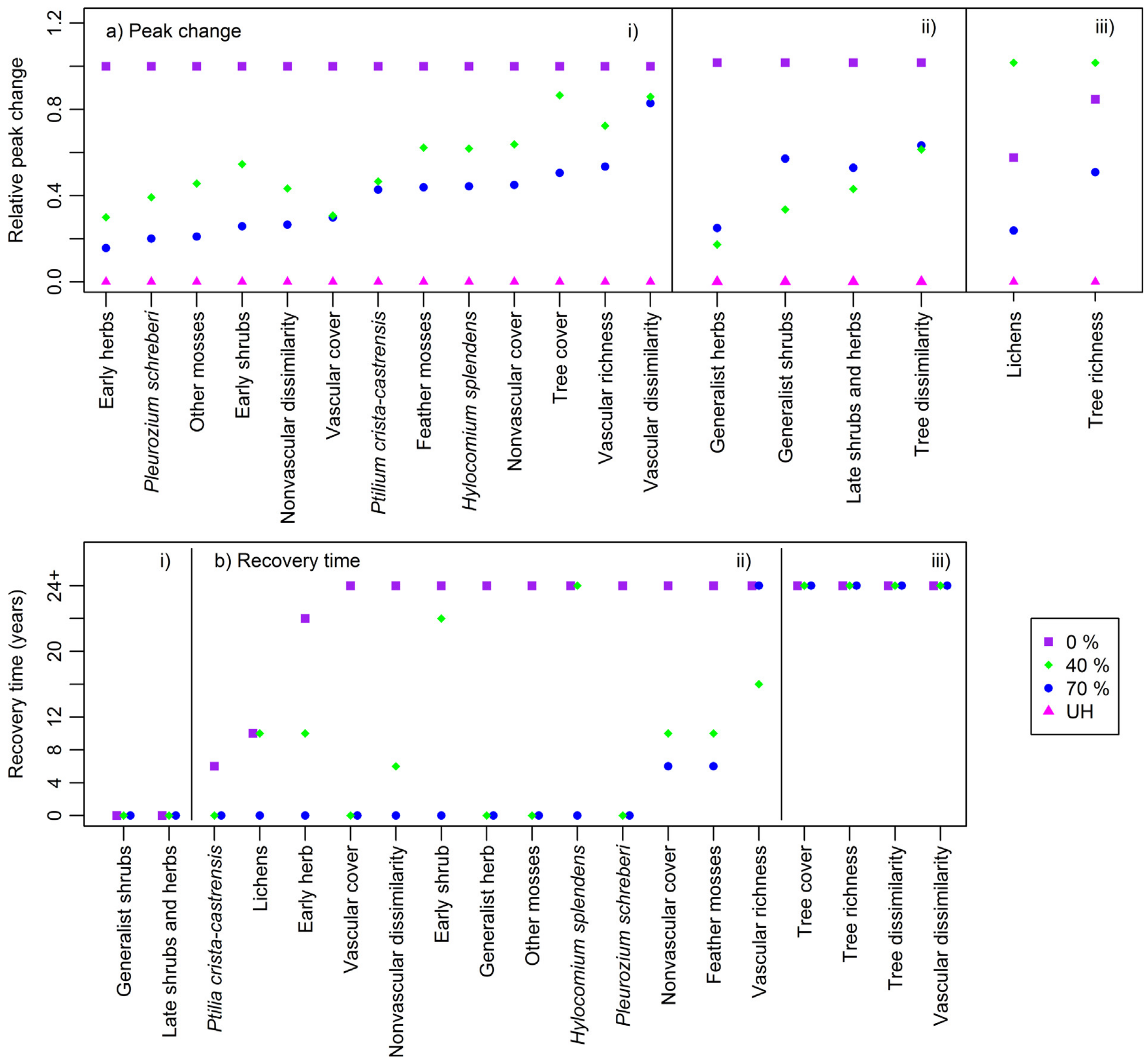

Fig. 7. Relative peak changes (a) and recovery times (b) of understory plant response variables at three levels of retention (0%, 40% and 70%) and in the unharvested (UH) forest for variables with a significant effect of Treatment or Treatment × Year within 24 years post-harvest. In (a) variables are ranked within three groups: i. Peak change increases as retention level decreases; ii. Peak change is highest at 0% retention but 70% retention ranks higher than 40% retention; and iii. Peak change is highest at 40% retention. In (b), recovery times are ranked within three groups: i. Variables that did not show significant effects of treatments in any year; ii. Variables with recovery times that varied by retention level; and iii. Variables that did not yet show recovery at any level of retention.

retention treatments on the understory at year 5 (Anderson, 2008), suggesting that stand type and age influence understory responses. Retention of 75% in Alberta mixedwoods did not cause greater understory changes than lower retention levels after 8 years (Craig and Macdonald, 2009), but neither did 8-yr results at Date Creek, so there is still time for different dynamics to develop in the Alberta stands.

4.2. Vascular plant dynamics

Our study confirms patterns of understory plant secondary succession well documented by chronosequence studies. Early seral herb cover (including invasive herbs) peaked at 10 years post-harvest and had almost disappeared by 24 years, whereas early seral shrub cover responded more slowly, consistent with findings of Schoonmaker and McKee (1988) and Schmiedinger et al. (2012). Short-term declines in generalist shrubs followed by increases at 0% retention are also well documented, as is the expansion of generalist herbs (Schoonmaker and McKee, 1988). Early seral and generalist species most likely responded to increased light availability that gradually declined over time at 0% and 40% retention, because soil nutrients were stable at Date Creek after 10 years (Kranabetter and Coates, 2004). Chronosequence studies have shown that when trees reach the stem exclusion stage (~40 yr in temperate forests), understory layers that flourished after harvest decrease sharply (Alaback, 1982; Schoonmaker and McKee, 1988), and we expect the vascular plant communities at Date Creek to recover to pre-harvest and unharvested cover, richness and composition over the next few decades.

4.3. Invasive non-native species

Invasion by non-native species is globally recognized as a threat to the ecological integrity of plant communities in managed forests (Kohli et al., 2008). At Date Creek, few non-native species established in the interior of forest stands; those that did were almost gone at 24 years. This was a faster recovery for presence, but slower recovery for cover than in Oregon Douglas-fir forests (Halpern and Spies, 1995). The peak change in invasive species cover was similar to 2–5% values recorded in disturbed Douglas-fir and Ponderosa pine (*Pinus ponderosa* Dougl. ex P.

& C. Lawson) stands (Schoonmaker and McKee, 1988; Nelson et al., 2008; Ares et al., 2009). Non-native species at Date Creek were mostly confined to roadsides (personal observation; cf. Nelson et al., 2008), and the remote location probably reduced the probability of establishment for many of the problematic invasive species common in northern BC. Stands closer to sources of invasive seeds are at higher risk for invasion, as are stands experiencing greater soil disturbance (Kranabetter et al., 2017; Haeussler et al., in press).

4.4. Late seral species

Surprisingly, most late seral shrub and herb species at Date Creek survived and thrived after harvest, even at 0% retention. We found evidence for declines at 0% retention only for *Platanthera orbiculata*, a heterotrophic (putatively mixotrophic) orchid, and *O. horridus*, a spiny clonal shrub with high cultural and medicinal value for the local Gitxsan First Nation (Burton and Burton, 2015). The sensitivity of *O. horridus* to disturbance is well known and of concern, but it can re-grow from clonal fragments after logging and even reach large sizes within 10 years on some sites (Lantz and Antos, 2002; Burton and Burton, 2015). *P. orbiculata* is also known to be disturbance sensitive and is listed in five USA states; its delicate carbon balance and limited recruitment of new adults hamper recovery (Cleavitt et al., 2017). Our data show that retention levels ≥40% avoided declines in these two species.

Four other herbs (*Chimaphila umbellata*, *Pyrola asarifolia*, *P. chlorantha* and *Clintonia uniflora*) that showed persistent negative responses to harvest in Oregon (Halpern and Spies, 1995), were more frequent in harvested than unharvested stands at Date Creek suggesting that they are more resilient to disturbance in these northern cedar-hemlock forests. The short summers and frequent cool, cloudy weather may provide a milder post-harvest environment for ericaceous, mixotrophic and mycoheterotrophic plants compared to forests further south (Halpern and Spies, 1995; Beese and Bryant, 1999) or east (Smith et al., 2008; Roberts et al., 2016). Little prior management at Date Creek probably also contributed to healthy late seral herb populations. Landscapes with long histories of management, such as in Europe, lack the suite of late seral species still present in western North America (Schmiedinger et al., 2012).

4.5. Nonvascular dynamics

Although our study lacked consistent bryophyte surveyors over time and radically underestimated bryophyte richness by sampling only the forest floor rather than all substrates (Caners et al., 2013a), impacts of retention level on recovery were detectable for common species and groups. Generally, nonvascular plant dynamics conformed to the competitive exclusion principle (Hardin, 1960). *Hylocomium splendens*, dominant in unharvested stands, responded negatively to harvest in proportion to retention level with recovery evident only at 70% retention. Ten years after its decline, a major shift to *Pleurozium schreberi*, other moss species and lichens had occurred. Even some liverworts (e.g. *Barbilophozia* spp.), which we expected to be very sensitive to harvest, may have benefitted from its decline. Across Canada, others have also reported decreases in *H. splendens* accompanied by increases in other generalist and pioneering bryophytes after harvest (Fenton et al., 2003; Baldwin and Bradfield, 2010; Caners et al., 2013b).

Both *H. splendens* and *P. schreberi* associate with cyanobacteria and fix nitrogen (Zackrisson et al., 2009), contributing substantially to N budgets in nutrient-poor forests (DeLuca et al., 2002). However, *H. splendens* fixes 50% less N than *P. schreberi*, and shifts in abundance between those two species at varying levels of canopy retention could affect N dynamics after harvest. While the effect of feather mosses on nutrient cycling in our study area is poorly understood, their influence on tree germination is well documented. In addition to suppressing other mosses, shrubs and herbs (including invasive non-native herbs), an undisturbed carpet of *H. splendens,* in combination with *P. schreberi*, suppresses tree germination (LePage et al., 2000; Astrup et al., 2008). The window of time for natural regeneration after disturbance, before recovery of the feather moss carpet, was only 6 years at 70% retention and 10 years at 40% retention. The functional roles of these two dominant mosses in sustaining conifer-dominated forests warrants further investigation across gradients of both retention and climate.

4.6. Recovery re-defined

Defining ecological integrity as departure from an unimpacted, benchmark system (Haeussler and Kneeshaw, 2003), was useful for generating our conceptual model and convenient for statistical analysis, but lacks the complexity to explain our results. By this definition, we would conclude that the 70% retention treatment has lower ecological integrity than 0% retention if its understory remains divergent from the unharvested forest for the next 200 years while the latter becomes identical to the unharvested forest within 50 years. An alternative definition of ecological integrity that explicitly accommodates complex forest dynamics and multiple successional pathways is *the absence of degradation* where degradation is “an event or process that reduces the productivity or value of an ecosystem, or that delays or prevents an ecosystem, from recovering from disturbance through normal successional processes” (Haeussler et al., 2002). With this alternative definition, we could even conclude that by accelerating the succession toward an old growth forest, the 70% retention treatment has enhanced the ecological integrity of the vascular plant community. Evaluation of the merits of differing levels of retention will depend on how we define ecological integrity, the indicators used to measure success and ultimately, the goals of forest management.

At the stand scale, we found little evidence that understory plant communities were degraded at Date Creek, and abundant evidence that successional pathways were proceeding normally. Retention effectively protected the most sensitive vascular species, but would probably provide wider benefits in a more fragmented forest (Mori et al., 2017) and with short rotation forestry. Currently in our northwest BC study region, negative consequences of forest management are more likely to be evident at the landscape scale with, for example, fragmentation and road building, which will not be solved by stand-scale retention practices.

4.7. Management implications

Forest understory plants have intrinsic (biodiversity) value and supply important ecosystem services such as berries, medicinals, animal forage, nitrogen fixation and erosion control. At Date Creek, 24 years of monitoring has shown the vast majority of understory plants, including most (not all) late seral herbs, do not require tree retention to survive and grow. This result from these perennially cool and moist northern temperate forests contradicts results from warmer, drier US temperate forests where some of the same late seral species require many decades to recover from logging or thinning. It supports recent work on epiphytic lichens (Arsenault and Goward, 2016) showing that highly sensitive species are more tolerant of forest disturbance in humid climates than in drier climates. Date Creek forests lie in a mostly unfragmented forest landscape. It is unlikely that the high resilience and resistance to non-native species invasion demonstrated by the Date Creek plant communities will continue through future forest harvest rotations, and unrealistic to expect similar outcomes in landscapes with greater urban, agricultural or industrial footprints. Practitioners of retention forestry must be aware that results are context-specific.

In environmental monitoring, understory vegetation often acts as a surrogate for other components or attributes of forest ecosystems that are more difficult to study. In the quarter century since the Date Creek study was initiated, it has become evident that plants rooted in the forest floor, especially vascular plants, are among the least sensitive indicators of the environmental impacts of logging. It is important to monitor organisms more directly dependent upon live, dead and downed wood (e.g., birds, saproxylic arthropods, epiphytic lichens, epixylic liverworts) to evaluate how the stand structural retention influences ecosystem function and integrity. The study nonetheless highlighted major differences in the response and recovery trajectories of vascular plants compared to bryophytes and confirmed that devil's-club, the most important medicinal plant for many Pacific Northwest indigenous peoples, is intolerant of clear-cutting even in these cool, northern forests. This large, charismatic shrub is an excellent focal and umbrella species for environmental monitoring programs in the region. By maintaining this high-value species, retention forestry achieved an important goal of providing habitat for both early and late successional species.

For some Date Creek plant indicators, outcomes at 70% retention were intermediate between those at 0% and 40% retention, apparently due to effects of gap dynamics on competition among trees, shrubs and herbs. These non-linear results highlight how difficult it is to define a "best" level of retention to meet forest management goals.

While 24 years is longer than most longitudinal datasets in retention forestry experiments, it is a short time frame to measure forest dynamics. We support Halpern et al.'s (2012) call for even longer measurements. Further monitoring at Date Creek will establish peaks of change and recovery times for species and groups that had not yet recovered at year 24. As the climate changes (Foord 2016), these permanent plots may also shed light on "without recovery" scenarios if indicators do not return to initial conditions, or if equilibrium dynamics in unharvested plant communities become directional (Damschen et al., 2010).

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Appendices A and B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.12.033.

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