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Combining aggregated and dispersed tree retention harvesting for conservation of vascular plant communities

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Abstract. Retention harvesting (also called tree retention or structural retention), in which live mature trees are selectively retained within harvested stands at different retention levels and in different patterns (aggregated to dispersed), is increasingly being used to mitigate the negative impacts of forest harvesting on biodiversity. However, the effectiveness of combining different patterns of retention harvesting for conservation and recovery of understory vascular plants in the long term is largely unknown. To address this gap, we compared understory vascular plant diversity, abundance, and composition between aggregated retention and five levels of surrounding dispersed retention (0% [clearcut], 10%, 20%, 50%, 75%) 15 yr postharvest. We also investigated the influence of dispersed retention on the ability of embedded retention patches to support plant communities characteristic of unharvested forests, and whether it varies by patch size of aggregated retention (0.20 ha or 0.46 ha) and position within patches (edge or interior). Species richness, diversity, and cover were higher in the dispersed retention than in the patch retention as the harvested areas favored early-seral plant species. Graminoid cover was greater at the edges than in the interior of large patches. Retention patches as small as 0.2 ha more effectively supported shade-tolerant (forest interior) plant communities when they were surrounded by higher levels of dispersed retention (as compared to patches retained within clearcuts). Overall, the combined use of both aggregated and dispersed retention within a given cutblock benefits both late- and early-seral plant species and thus could effectively conserve understory plant assemblages in harvested landscapes. Sustainable forest management should therefore consider using a range of retention patch sizes combined with varying levels of surrounding dispersed retention in harvest designs to achieve objectives for plant conservation.

Key words: aggregated retention; biodiversity conservation; boreal forest; dispersed retention; partial harvesting; understory vegetation; variable retention harvesting; vascular plant communities.

Introduction

Retention harvesting, whereby mature live trees are retained at the time of harvest, is used in sustainable forestry to enhance structural diversity, maintain ecosystem function, and conserve biodiversity (Franklin et al. 1997, Vanha-Majamaa and Jalonen 2001, Gustafsson et al. 2012, Lindenmayer et al. 2012, Fedrowitz et al. 2014, Mori and Kitagawa 2014). There are many options to consider in the application of retention harvesting, including retention level (proportion of the initial density, basal area, or volume that is retained) and pattern (spatial arrangement of retained trees). A primary function of aggregated retention (retained trees are grouped in patches) is to “lifeboat” forest-dependent species by providing habitat and microclimatic conditions that are relatively similar to unharvested forest (Franklin et al. 1997). On the other hand, dispersed retention, whereby retained trees are uniformly distributed, enhances landscape connectivity as the retained trees maintain structural complexity throughout the harvested area (Franklin et al. 1997). Thus, combining both spatial patterns in a single harvested area (i.e. variable retention harvesting) could represent a very effective strategy for conservation of biodiversity (Franklin et al. 1997, Rosenvald and Lõhmus 2008, Aubry et al. 2009). Unfortunately, we have limited evidence for effectiveness of such harvest prescriptions (but see Lencinas et al. 2011, Pinzon et al. 2012, Lee et al. 2017).

An important consideration in the effectiveness of retention patches as lifeboats will be the contrast between them and the surrounding matrix and how this changes over time postharvest. Dispersed retention surrounding aggregated patches should reduce the structural contrast between the patches and their surrounding matrix, as compared to if they were surrounded by a clearcut, and thus is expected to moderate microclimatic conditions and reduce edge effects (Bannerman 1998, Harper et al. 2005). Small aggregated retention patches experience increased blowdown (Jönsson et al. 2007, Steventon 2011), and the gradual conversion of retained trees to snags and downed logs will impact their effectiveness as lifeboats for forest-dependent species. Leaving dispersed retention surrounding retention patches could better protect them and preserve their lifeboat function in the longer term. Most studies on retention harvesting have occurred within 5 yr postharvest; hence, longer-term studies are needed to detect potential lag effects of biodiversity responses (Fedrowitz et al. 2014).

In boreal and temperate forests, the vast majority of plant diversity is found in the understory layer, which includes saplings, shrubs, forbs, and graminoids (De Grandpré et al. 2003, Gilliam 2007). Understory plant communities provide food and habitat for wildlife, play key roles in nutrient cycling, and affect tree regeneration, thereby influencing forest stand dynamics (Nilsson and Wardle 2005, Hart and Chen 2006, Gilliam 2007). Disturbances such as harvesting

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alter understory communities by creating favorable conditions for early-seral species (Pykälä 2004, Hart and Chen 2006). Higher dispersed retention levels result in fewer changes in plant species richness, cover, and composition, as compared to preharvest conditions (Bergstedt and Milberg 2008, Craig and Macdonald 2009, Halpern et al. 2012).

Previous studies on understory vegetation responses to retention patches only considered retention patches surrounded by clearcuts; thus, the effects of the adjacent cleared area negated the ecological benefits of the patch (Halpern et al. 2005, 2012, Roberts et al. 2016). Even in relatively large patches (>0.5 ha), plant communities can be substantially different than in unharvested forest when patches are surrounded by clearcut (Bradbury 2004). Lencinas et al. (2011) revealed that understory plant communities in combined aggregated patch and dispersed retention treatments were most similar to those in old-growth forest when compared to a single retention pattern; however, their study was short-term (4 yr postharvest) and limited to one patch size and one retention level. Higher levels of dispersed retention should better preserve the effectiveness of aggregated retention patches as lifeboats for understory plant communities. Furthermore, patches may not have to be as large to effectively maintain late-seral plant communities if they are surrounded by dispersed retention. Knowledge of the interactive effects of patch size, position within patch, and surrounding retention levels, particularly in the longer term, is needed to better inform forest management policies and harvest planning.

Here, we examined the effects of combined aggregated and dispersed retention on understory vascular plant diversity, abundance, and composition 15 yr postharvest. Specifically, we tested four hypotheses that were related to either the retention pattern for comparisons between retention patches and surrounding harvested areas (H_1), retention level surrounding retention patches (H_2), patch size (H_3), or position within patches (H_4) as follows. H_1: Species richness, diversity, cover, and sapling density would be lower in retention patches than in a surrounding matrix of dispersed retention, because the harvested area would favor early-seral species; these differences between patches and the surrounding harvested areas would attenuate with increasing levels of dispersed retention. H_2: Higher levels of surrounding dispersed retention will result in improved ability of embedded retention patches to support plant communities characteristic of unharvested forest because the harvested area provides additional retained structure. H_3: Larger aggregated patches will better support late-seral plant communities than smaller patches, because of reduced edge effects. H_4: Species diversity, cover, and sapling density will be higher at the edge than in the interior of patches because shade-intolerant species will be favored at the edge.

METHODS

Study site

Research was conducted at the large-scale Ecosystem Management Emulating Natural Disturbance (EMEND) experiment located approximately 90 km northwest of Peace River, Alberta, Canada (56°46′13″ N, 118°22′28″ W). The area is representative of the boreal mixedwood plains and forests are dominated by white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). The mean annual precipitation is 436 mm, and the mean temperatures are −16.9°C and 15.0°C for January and July, respectively (Government of Canada: 1981–2010 climate normals and averages; *available online*).[2] Soils are well-drained and primarily Luvisolic (Kishchuk 2004).

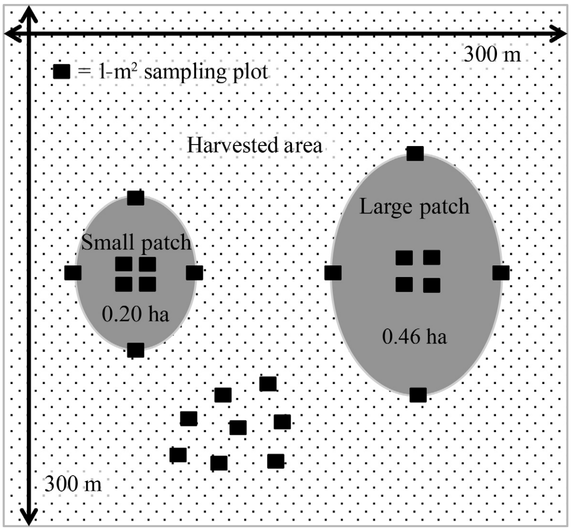

FIG. 1. Schematic diagram illustrating the experimental design of a 10-ha compartment that contains two sizes of aggregated retention patches (0.20 and 0.46 ha) embedded in a harvested matrix. The dotted background represents the area harvested to 0% (clear cut), 10%, 20%, 50%, or 75% of the original stand volume using dispersed retention. Compartments for each harvest level and for unharvested control were replicated three times. Illustration is not to scale.

Conifer-dominated compartments (~10 ha each) were harvested in the winter of 1998–1999 across five harvest retention levels (treatments): 0% (clearcut), 10%, 20%, 50%, and 75% retention. Each compartment contained a large (~0.46 ha) and small (~0.20 ha) elliptical retention patch surrounded by clearcut or dispersed retention (Fig. 1). The two patches within each compartment were at least 80 m apart. Unharvested compartments (~10 ha each) were used as controls. There were three replicates of each treatment, including control stands without harvest, for a total of 18 experimental compartments.

Data collection

Sampling occurred from June until August 2014. In each harvested compartment, eight 1-m^2 quadrats were placed in the harvested area; similarly, eight quadrats were placed in each of the large and small retention patches. A previous study at EMEND revealed that eight quadrats in an area <0.5 ha would provide sufficient sampling intensity to well represent the understory vascular plant community, which included shrubs, forbs, graminoids, and tree saplings (Craig and Macdonald 2009). In the harvested area, quadrats were randomly established in an area no larger than the size of

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[2] www.climate.weather.gc.ca

the large patch (<0.46 ha). Within each patch, a quadrat was placed in each cardinal direction on the edge of the patch with the remaining four quadrats placed at least 5 m apart in the patch interior. In the unharvested control compartments, eight quadrats were randomly placed in an area between 0.20 and 0.46 ha.

Percent cover of shrubs, forbs, and graminoids was visually estimated in each quadrat for each species to the nearest 0.5% from 0% to 1%, to the nearest 1% from 1% to 10%, and to the nearest 5% from 10% to 100%. Sapling (>10 cm in height; ≤5 cm diameter at breast height) densities (for tree species) were also quantified within a 2-m radius of each quadrat center. Tree seedlings (≤10 cm in height) were counted in the quadrats but were excluded from analyses due to insufficient observations. Specimens that could not be identified in the field were collected for identification in the laboratory. Specimens unidentifiable at the species level were identified to genus and treated separately from identified species of the same genus for the purpose of analysis (Appendix S1).

Data analysis

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

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

For examining the influence of retention pattern (H_1) and patch size (H_3) on species richness, diversity, cover, and sapling density, the mixed-effects model included retention level (0%, 10%, 20%, 50%, 75%) and spatial pattern (harvest area, small patch, large patch) as continuous and categorical fixed independent variables, respectively, and the interaction between retention level and spatial pattern. Compartment was included as a random variable. Data from the unharvested compartments could not be included in these analyses since unharvested forest had nothing comparable to the retention pattern categories. We therefore present means and standard errors from the unharvested compartments with the results from the mixed models for comparative purposes with the other treatments. To determine the influence of surrounding dispersed retention level on the lifeboating function of retention patches (H_2), mixed-effects models were conducted for each patch size separately and included retention level (0%, 10%, 20%, 50%, 75%, 100%) and compartment as a continuous and random variable, respectively. To compare responses between the edge and interior of retention patches (H_4), we used a split–split-plot design. Retention level (0%, 10%, 20%, 50%, 75%) was the main plot, patch size (small, large) was the split–plot, position within patch (edge, interior) was the split–split plot, and compartment was a random variable.

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

To examine the effect of variable retention harvesting on understory species composition, we conducted distance-based redundancy analyses (db-RDA) following the mixed models described above in R version 3.2.1 (R Development Core Team 2015) using the capscale function in the vegan package (Oksanen et al. 2017). We performed db-RDA using the Bray-Curtis distance measure because this analysis tests the significance of individual independent variables and their interactions for multispecies response variables (Legendre and Anderson 1999). Statistical significance of the db-RDA model terms was determined using 999 permutations. Species data were represented by percent cover and were Hellinger-transformed (Legendre and Gallagher 2001).

For examining the influence of retention pattern (H_1) and patch size (H_3) on species composition, the primary matrix of the db-RDA was the species data for each 1-m^2 sampling quadrat while the secondary matrix consisted of retention level (0%, 10%, 20%, 50%, 75%) and retention pattern (harvest area, small patch, large patch) as a continuous and categorical variable, respectively. We used the ordisurf function to fit smooth surfaces for retention level onto the ordination plot using thin-plate splines with generalized cross-validation for selection of smoothness (Oksanen et al. 2017). Species displayed in the plot were selected using the circle of equilibrium method, which chooses species that make above average contributions to the ordination plot (Legendre and Legendre 1998). The interaction between retention pattern and level was significant so we performed additional db-RDAs that examined the differences in species composition between retention patterns for individual retention levels. We used the ordiellipse function to add dispersion ellipses (95% confidence regions) based on standard errors of the weighted average of scores around the centroids of each retention pattern (Oksanen et al. 2017).

To investigate the ability of the retention patch to support plant communities similar to intact forest (H_2), we conducted db-RDA that included retention harvest treatments and unharvested control for the small patch and large patch separately. We did not explore differences among retention levels for the dispersed retention only because others are examining these comparisons with a larger data set. To determine whether or not there were differences in responses between the edge and interior of retention patches (H_4), the primary matrix of the db-RDA was the species data for each 1-m^2 sampling quadrat while the secondary matrix consisted of position within patch (edge, interior), patch size (small, large), and retention level (0%, 10%, 20%, 50%, 75%). In all db-RDA models, compartment was a conditioned variable to remove its random effect before constraining the other variables (Oksanen et al. 2017).

RESULTS

Responses to retention pattern and level

In total, 18 shrubs, 59 forbs, and 10 graminoid species were found (Appendix S1). Retention pattern had a significant effect on species richness, Shannon diversity, total cover, and graminoid cover (Table 1). The interaction between retention level and pattern was significant for forb cover, sapling density, and composition, while shrub cover did not vary significantly with retention level or pattern (Table 1). The level of surrounding dispersed retention did not significantly affect species richness, Shannon diversity, total cover, shrub cover, and forb cover in the retention patches; however, as the level of surrounding dispersed retention increased, graminoid cover, sapling density, and species composition in the small and large patches were more similar to the unharvested control (Table 2; Fig. 6).

Understory vegetation diversity and cover.—Vascular plant species richness per quadrat was higher in the harvested area compared with both the small ($P < 0.001$) and the large ($P = 0.002$) embedded patches and was lowest overall in the small patch when compared to the large retention patch ($P = 0.017$). Species richness in the retention patches was more similar to that in the unharvested control than was the harvested treatment (Fig. 2A).

Shannon diversity was higher in the harvested area compared with both the small ($P < 0.001$) and large ($P = 0.004$) patches with no significant difference in species diversity between patch sizes ($P = 0.194$). Species diversity of the patches was also more similar to the unharvested control than the surrounding harvested area (Fig. 2B).

Total understory cover was significantly higher in the harvested area than in the small patch ($P = 0.007$), while cover in the large patch was intermediate and did not differ from the small patch ($P = 0.106$) or from the harvested area ($P = 0.277$). Similar to species diversity and richness, total cover in the retention patches was more similar to the unharvested control than to the harvested area (Fig. 2C).

Graminoid cover in the harvested area was significantly higher than in both the small ($P = 0.019$) and large ($P = 0.037$, Fig. 2D) patches, which did not differ from one another ($P = 0.790$). When both patch sizes were surrounded by higher levels of dispersed retention, graminoid cover was

TABLE 1. Results of mixed models examining the influence of pattern (harvest area/small patch/large patch), retention level surrounding patches (0%, 10%, 20%, 50%, 75%), and retention pattern × level interaction on understory vascular plant vegetation.

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

Notes: Species richness, Shannon diversity, cover, and sapling density were analyzed using mixed model regression. Composition was analyzed using distance-based redundancy analysis. *P* values in boldface type were considered significant at α = 0.05. Residual df were as follows: 341 for “Pattern” and “Pattern × Level”, 13 for "Level" for each univariate response variable and 353 for composition.

†Data were log-transformed for analysis.

TABLE 2. Results of regression models examining the influence of surrounding level of dispersed retention (0%, 10%, 20%, 50%, 75%) on understory vascular plant vegetation in small and large retention patches.

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

Notes: Unharvested forest (100% retention) was included in the analyses. β is the regression slope. *P* values in bold were considered significant at α = 0.05. Degrees of freedom = 1 and residual degrees of freedom = 16 for all response variables.

†Data were log-transformed for analysis.

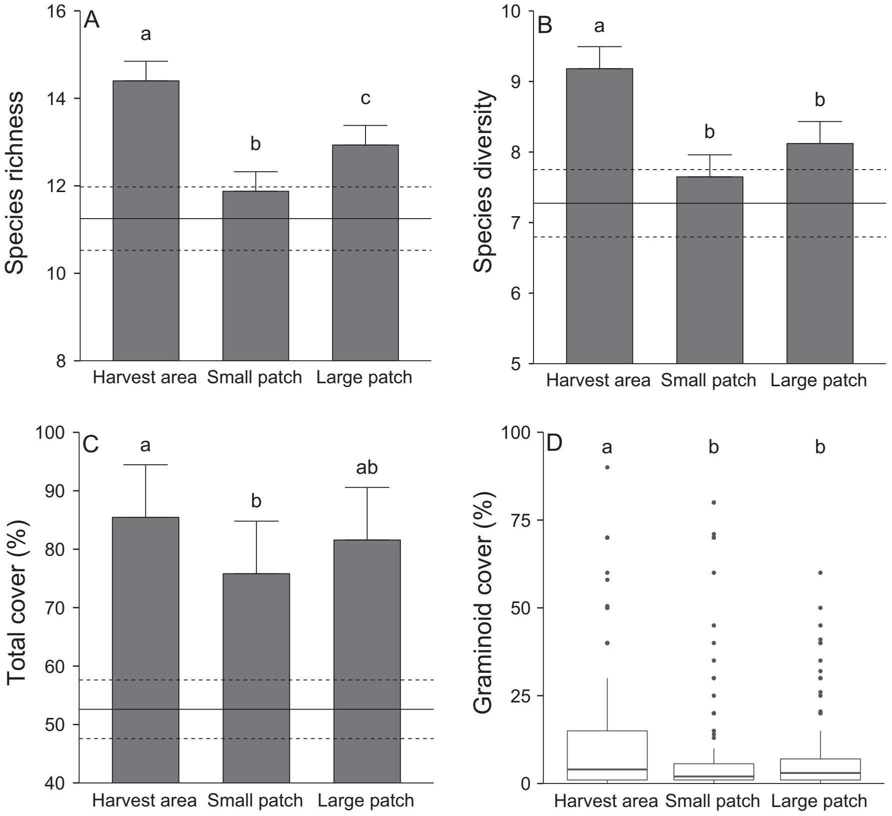

FIG. 2. Least-square mean and SE of (A) species richness, (B) Shannon diversity, and (C) total cover, and median, 25th, and 75th percentiles of (D) graminoid cover in harvest area, small patch, and large patch retention. Horizontal lines in panels A–C represent mean (solid line) and standard error (dashed lines) of unharvested control. (D) Dots outside the box-whiskers represent outlier values, and graminoid cover in unharvested control was 0.4% ± 4.9%. Means with different letters are significantly different (pairwise comparison of least-squares means; $P < 0.05$).

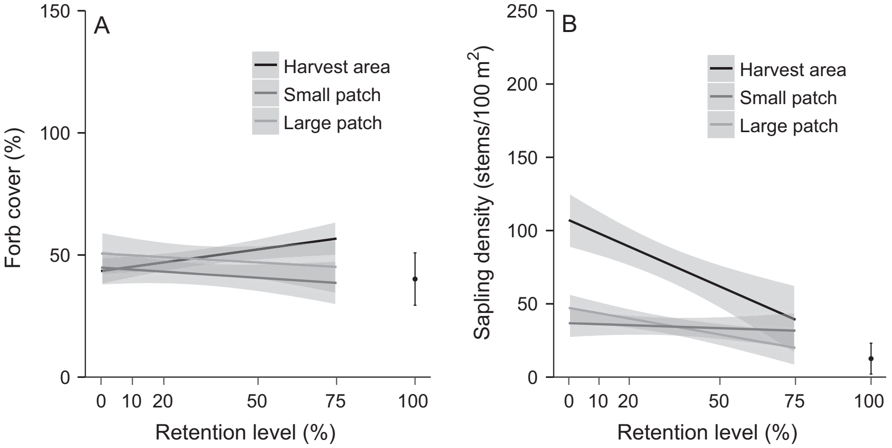

FIG. 3. Fitted linear regression with 95% CI for (A) forb cover and (B) sapling density, for harvest area, small patch, and large patch across different retention levels. Least-square mean ± SE for unharvested control (100% retention) is shown for reference.

more similar to the unharvested control (Table 2). The significant interaction between retention level and pattern on forb cover was due to the fact that in both patch sizes, forb cover decreased with increasing retention level (small patch, $\beta = -0.08 \pm 0.16$; large patch, $\beta = -0.07 \pm 0.16$; mean ± SE), whereas in the harvested area, forb cover was positively related to retention level ($\beta = 0.18 \pm 0.16$; Fig. 3A).

Saplings.—*Populus balsamifera* and *Populus tremuloides* accounted for the majority of saplings. Sapling density was always negatively related to retention level but the effect was stronger in the harvested area ($\beta = -0.91 \pm 0.21$) than in either patch size (small patch, $\beta = -0.07 \pm 0.21$; large patch, $\beta = -0.36 \pm 0.21$). Sapling density was lowest in the unharvested control and was twice as high in the harvested area as in the patches when dispersed retention level was lower than 20% (Fig. 3B). There was less variation in sapling density between harvested area and retention patches when higher levels of dispersed retention surrounded the patches (Fig. 3B). Moreover, sapling densities in both patch sizes were more similar to the unharvested control with increasing dispersed retention level surrounding patches (Table 2).

Composition.—Vascular plant species composition varied between small patch, large patch, and harvested area and were influenced by dispersed retention level (Fig. 4A). The different retention patterns separated mostly on axis 2, while variation related to level of dispersed retention was distributed along axis 1 (Fig. 4A). Species such as *Aster ciliolatus*, *Calamagrostis canadensis*, and *Epilobium angustifolium* were associated with lower levels of dispersed retention, while *Cornus canadensis* was characteristic of high retention (Fig. 4B). *Linnaea borealis* and *Geocaulon lividum* characterized small patches, while *Vaccinium vitis-idaea* and *Ledum groenlandicum* were more associated with large patches (Fig. 4B). Distinct plant communities characterized the harvested areas, small patches, and large patches for each level of dispersed retention (0%, 10%, 20%, 50%, 75%; Fig. 5). As surrounding dispersed retention level increased, species composition in both small and large patches became more similar to those in unharvested forest, as compared to patches surrounded by clearcut (Fig. 6).

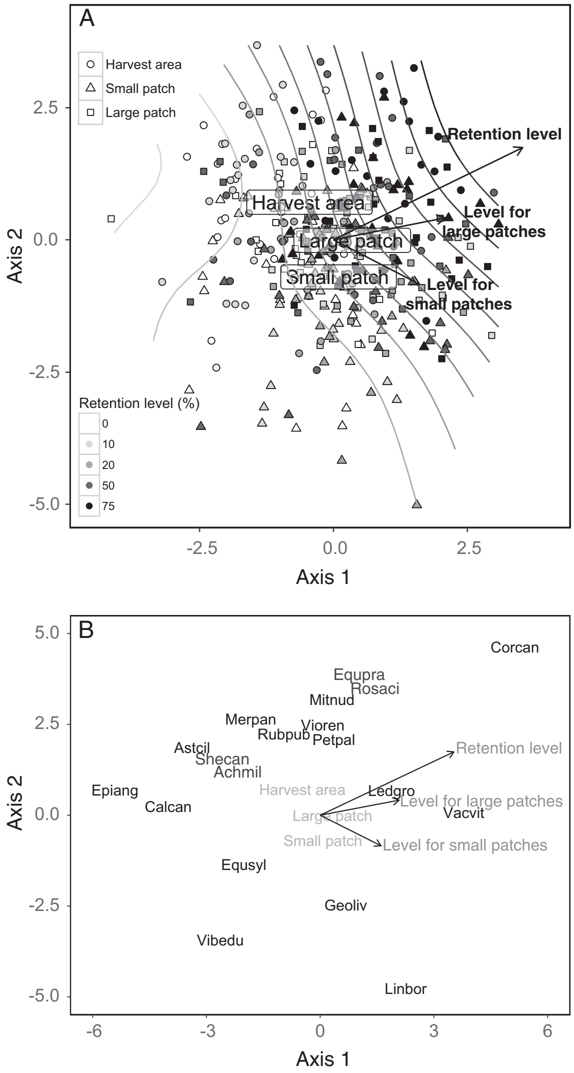

FIG. 4. Results of distance-based redundancy analysis testing the influence of dispersed retention level (0%, 10%, 20%, 50%, 75%) surrounding small patch and large patch retention on understory vascular plant species composition. (A) Symbols represent the plant community in a 1-m^2 sampling quadrat coded by harvested/unharvested area (harvest area/small patch/large patch) and retention level. (B) Species that made above average contributions to the ordination analysis (circle of equilibrium). Labels for harvest area, small patch, and large patch represent middle of centroids based on standard errors of the weighted average of scores. Vectors for retention level indicate the direction of retention level that surrounded large patches ("Level for Large Patches") and small patches ("Level for Small Patches"). See Appendix S1 for definition of species codes.

Responses to position within retention patches

Measured understory vegetation variables were not influenced by the position within the retention patches, except for graminoid cover (Table 3). Median graminoid cover was higher at patch edges than in patch interiors for both patch sizes, but this difference was greater for large than small patches (Fig. 7). In large patches, graminoid cover was significantly greater at the edge than in the interior ($P < 0.001$), but in small patches, there was no difference in graminoid cover between the interior and edge ($P = 0.991$). The db-RDA did not detect a significant effect of position within patch on overall species composition (Table 3).

Discussion

Our results demonstrate that combining dispersed and aggregated retention in a single harvested area will benefit understory vegetation 15 yr postharvest. Compared to harvested areas, patch retention was more effective at supporting plant communities similar to unharvested forest, particularly when these patches were surrounded by higher levels of dispersed retention. Both patch sizes were valuable in supporting different understory plant communities, and there were few differences in understory vegetation between the interiors and edges of the patches.

Responses to retention pattern and level

Our results supported our first hypothesis (H_1), which predicted increased species richness, diversity, cover, and sapling density in dispersed retention than in retention patches. Harvested areas were characterized by early-seral vegetation, whereas embedded retention patches more effectively supported late-successional species associated with unharvested forest. Higher species richness, diversity, and cover, and more shade-intolerant species, in harvested areas can be explained by greater light availability resulting from reduced canopy, as compared to patch retention (Battles et al. 2001, Heithecker and Halpern 2007). Reduced canopy cover in harvested areas benefitted species that prefer higher light transmission such as *Epilobium angustifolium* (Lieffers and Stadt 1994). Our findings conform to the study by Soler et al. (2016) in temperate forests where patch retention

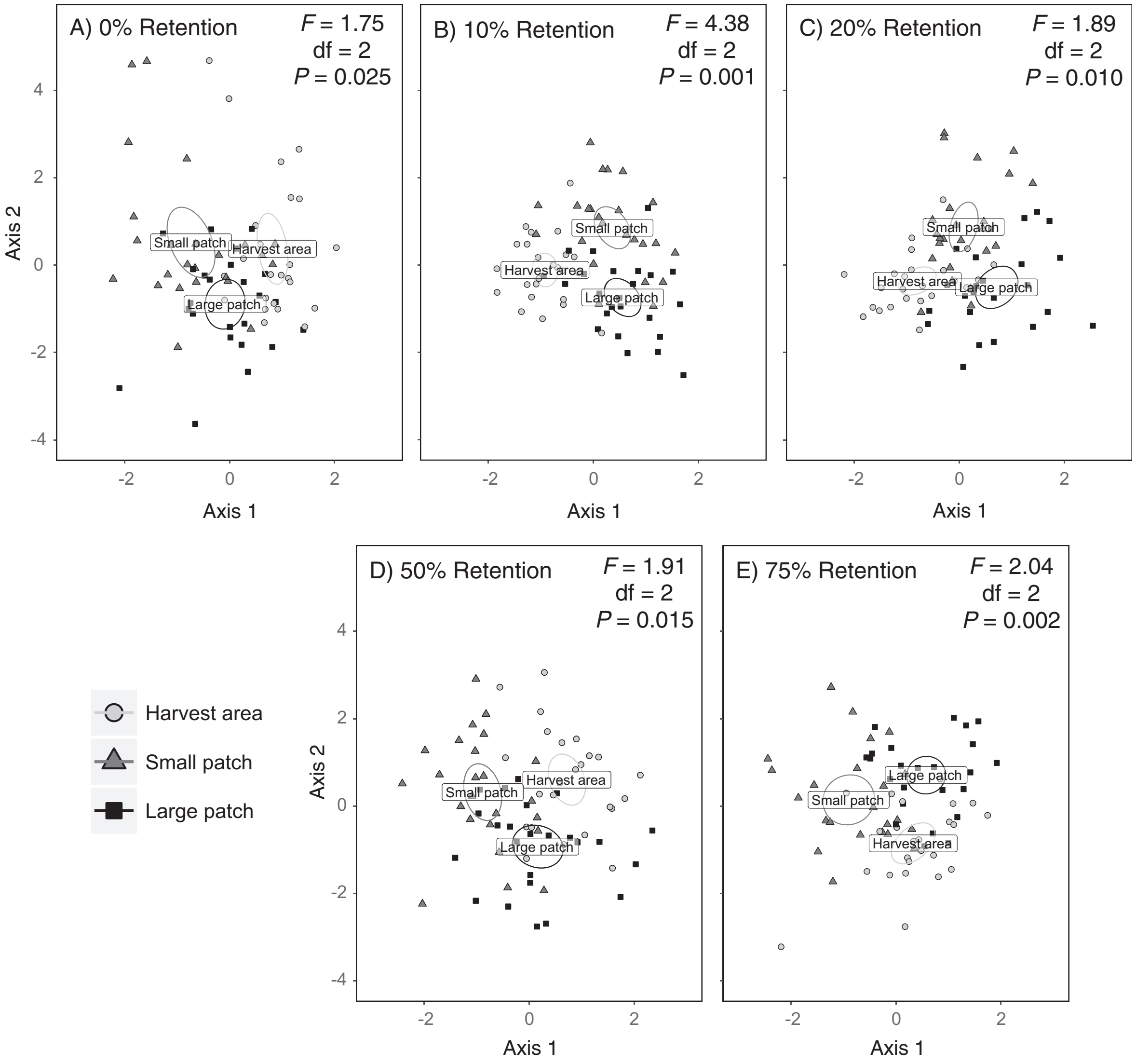

FIG. 5. Results of distance-based redundancy analyses testing the influence of harvest area, small patch, and large patch on understory vascular plant species composition for (A) 0%, (B) 10%, (C) 20%, (D) 50%, and (E) 75% dispersed retention. Each symbol represents the plant community in a 1-m^2 sampling quadrat coded by harvested/unharvested area (harvest area/small patch/large patch). Ellipses show 95% confidence intervals around treatment centroids. Residual df = 68 for (A)–(E).

contained more native forest specialists than did dispersed retention.

As the retention level in the harvested area increased, sapling density in harvested areas became more similar to that in patch retention, which we expected as structural differences between the surrounding harvested area and patches diminished. The significant combined effects of retention pattern and level on forb cover and sapling density could reflect the potential interactions between canopy closure, regeneration, and understory vegetation cover. Shade-intolerant sapling species, such as *Populus tremuloides* and *Populus balsamifera*, favor high light environments associated with low retention levels (Frey et al. 2003, Heithecker and Halpern 2006, Gradowski et al. 2010). In the harvested area, high sapling densities at low retention levels likely contributed to reduced forb cover by shading the understory and consequently hindering forb growth, thus explaining the contrasting responses of these two vegetation components (Wagner et al. 2011). In retention patches, we did not observe these differences in response between sapling density and forb cover; both sapling density and forb cover were relatively low, likely as a result of greater canopy cover. Forb cover in patch retention could have been slightly higher when patches were surrounded by lower retention levels because of greater light availability resulting from more blowdown (Scott and Mitchell 2005, Lee et al. 2017).

In accordance with our second hypothesis (H_2), patches surrounded by dispersed retention were more effective as local refugia for forest-dependent species than were patches surrounded by clearcuts. Our results showed that, as dispersed retention level increased, retention patches better supported more shade-tolerant species such as *Vaccinium vitis-idaea* (Väisänen et al. 1977) and *Linnaea borealis* (Eriksson 1988). This elaborates on the findings of Lencinas

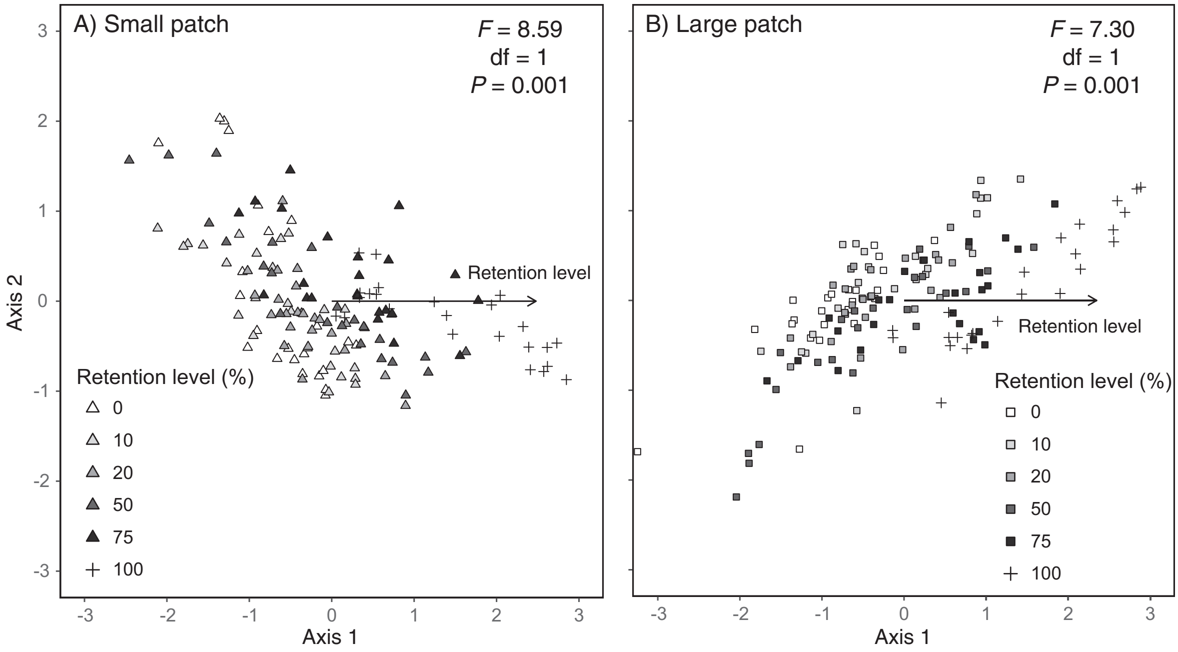

FIG. 6. Results of distance-based redundancy analyses investigating the influence of surrounding dispersed retention level on (A) small patches and (B) large patches. Each symbol represents the plant community in a 1-m^2 sampling quadrat coded by retention level (where 100% is unharvested forest). Vectors indicate the direction of increasing dispersed retention level surrounding retention patches. Residual df = 141 for (A) and (B).

TABLE 3. Results of split–split-plot analyses used to examine the influence of position within patch (edge, interior), patch size (small, large), and level of retention surrounding patch (0%, 10%, 20%, 50%, 75%) on understory vascular plant vegetation.

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

Notes: Species richness, Shannon diversity, cover, and sapling density were analyzed using mixed model regression. Composition was analyzed using distance-based redundancy analysis. *P* values in boldface type were considered significant at α = 0.05. Degrees of freedom = 1 for all response variables. Residual degrees of freedom were as follows: 206 for "Position", "Position × Size", "Position × Level", and "Position × Size × Level", 13 for "Size", "Level", and "Size × Level" for each univariate response variable and 229 for composition.

†Data were log-transformed for analysis.

et al. (2011) who showed that aggregated retention combined with dispersed retention (40–50% retention) more effectively conserved understory plant communities in the short term (4 yr postharvest), as compared to only dispersed retention (20–30%) or one small (~0.28 ha) aggregated patch per hectare within a clearcut. The positive influence of

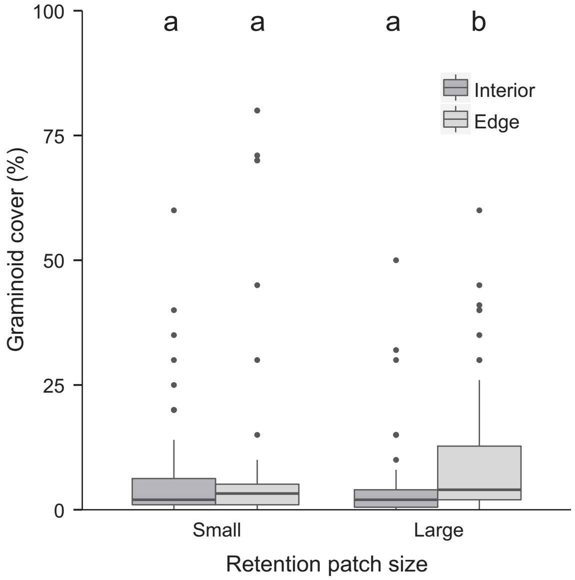

FIG. 7. Median, 25th, and 75th percentiles of percent graminoid cover in the interior and edge of small and large patches. Dots outside the box-whiskers represent outlier values, and different letters represent significant differences (pairwise comparison of least-squares means; $P < 0.05$) between positions within each patch size.

dispersed retention on embedded retention patches was also recorded for arthropods (Pinzon et al. 2012, Lee et al. 2017). Retained trees surrounding retention patches reduce environmental extremes between regenerating and unlogged patches and decrease blowdown rates in patches (Lee et al. 2017). Consequently, dispersed retention enhances the ability of retention patches to support species composition characteristic of unharvested forest. Even though retention patches <1 ha can provide habitat for some forest-dependent species when surrounded by clearcuts (Baker et al. 2015), our findings indicate that the effectiveness increases when higher levels of dispersed retention surround the patches and therefore reduce the structural contrast between patches and adjacent harvested areas.

Responses to retention patch size and position within patches

Although we expected larger patches to better support late-seral plant communities than smaller patches under our third hypothesis (H_3), there was no evidence to support this prediction. Nevertheless, plant communities differed between large and small patches, which suggest that both sizes are ecologically valuable. While Bradbury (2004) observed differences in understory plant communities between retention patch sizes 2 yr after harvest, our findings demonstrate differences in species composition 15 yr postharvest. Importantly, our findings indicate that the level of dispersed retention surrounding retention patches affects individual patch sizes differently. By reducing the structural contrast between the harvested area and large patches, higher levels of dispersed retention enabled large patches to support sapling densities comparable to unharvested forest. It seems likely that patches larger than 0.5 ha would have higher conservation value (Lee et al. 2015); however, our findings suggest that patches as small as 0.20 ha can have ecological value, as they were able to support some late-seral plant species more effectively than the surrounding harvested area.

Our fourth hypothesis (H_4) predicted that patch edges would favor more shade-intolerant species than patch interiors; this would cause differences in species diversity and composition between patch edges and interiors. However, understory vegetation was generally similar between the edge and interior of the patches, which were different from the unharvested forest; this suggests that edge effects extended through the entirety of both patch sizes. Hautala et al. (2011) concluded that edge effects on epixylic plant species influenced whole retention areas averaging 0.2 ha in size. The lack of differences between the interiors and edges of 0.12–2.6 ha retention patches when surrounded by clearcuts has also been documented in temperate forests over 5 yr postharvest (Baker et al. 2016). Although we expected dispersed retention to minimize edge effects by reducing the contrast between harvested and retained areas (Bannerman 1998), the retention patches under investigation were likely too small to result in differences in understory vegetation between patch interiors and edges. The distances between the edge and interior of the small and large patch were approximately 25 and 40 m, respectively. In boreal forests, Harper et al. (2015) found that edge effects on understory vegetation usually extend up to approximately 20 m from the edge into the forest and diminish over time.

Graminoid cover, the only variable that responded to position within patch, was higher at the edge than the interior of large patches, and this is perhaps due to lower light availability and temperatures at the patch centers as compared to the edges (Heithecker and Halpern 2007). In a study of 1 ha aggregated patches within clearcuts in temperate forests, Nelson and Halpern (2005) found that canopy cover was reduced at edges, as compared to patch interiors, and early-seral plant species were restricted to within 10 m of the edge 2 yr after harvest. The differences in graminoid cover between the interior and edge of small patches may have been attenuated as a result of the shorter distance between the edge and center, as compared to large patches. The distance between the interiors and edges of small patches was <30 m; thus, the entire patch was likely influenced by edge effects on microclimatic variables such as light availability (Heithecker and Halpern 2007).

Management implications

Our results suggest that a strategy of variable retention harvesting incorporating a variety of harvest patterns and amount of residual will best benefit understory vascular plants on harvested landscapes. Notably, we demonstrate the important ecological benefits of combining dispersed and aggregated retention within a single cutover area and that these benefits are still apparent 15 yr postharvest. Thus, combining patch and dispersed retention in harvested areas is a better alternative to meet conservation goals than leaving patches within clearcuts. The harvested area was characterized by early-successional communities and thus plays a valuable role in the forest landscape by providing high plant productivity and spatial complexity (Swanson et al. 2011). Meanwhile, aggregated retention promoted maintenance of late-seral species, partly reflecting their ability to maintain the structural complexity (Moussaoui et al. 2016) and microclimatic conditions characteristic of unharvested stands (Baker et al. 2016).

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

In addition to ecological benefits, combined patterns of retention harvesting could also potentially confer benefits in terms of the aesthetics of harvested areas, as compared to aggregated retention within clearcuts, which was found to have low aesthetic value (Ribe 2005). Future studies should consider a greater variety of retention patch sizes as well as the location of retention patches within harvested areas of different forest types.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.d545d55