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Assessing the single-tree and small group selection cutting system as intermediate disturbance to promote regeneration and diversity in temperate mixedwood stands

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ABSTRACT

Traditional silvicultural systems such as clearcutting and single-tree selection cutting are critiqued for their tendency to simplify forest complexity. By more closely emulating natural disturbance regimes and increasing the availability and heterogeneity in understory light levels, we pose that systems causing intermediate disturbances such as the single-tree and small group selection cutting system can promote tree regeneration, retain stand structural attributes, and maintain high understory plant diversity in temperate mixedwood stands. To assess this, we implemented a harvest intensity gradient experiment (residual basal area [BA], % removal) consisting of uncut control (26 m²/ha, 0%), light (21 m²/ha, 20%), moderate (18 m²/ha, 31%) and heavy (15 m²/ha, 42%) cutting with retention of legacy trees in uneven-aged yellow birch (*Betula alleghaniensis* Britton) – conifer stands. We evaluated the effects on gap size, light transmittance, abundance of living and dead trees, plant diversity, and regeneration of target species (i.e. yellow birch, red spruce [*Picea rubens* Sarg.] and balsam fir [*Abies balsamea* L.]), during the 8 years postcut. Moderate and heavy single-tree and small group selection cutting treatments triggered changes in microenvironments and in understory plant community. Moderate and heavy selection had greater yellow birch seedling density > 30 cm in height compared to the control. Cutting treatments did not significantly improve red spruce and balsam fir regeneration, despite favorable micro-environmental conditions (e.g. gaps averaging 200–350 m² and 15–40% transmitted light). The vascular plant community rebounded quickly after disturbance and harvesting did not depress any diversity metric or alter community composition beyond control levels. Tree species richness increased in moderate and heavy selection cuts, while vascular species diversity (H′) was greatest in the heavy selection cut. Observed richness and diversity gains were driven by augmented yellow birch and mountain maple (*Acer spicatum* Lam.) recruitment into larger classes as well as greater forb, tree, and shrub cover in response to greater cutting intensities. Species richness and diversity were positively correlated with increased light availability, but not with light heterogeneity. Our results show that this hybrid selection cutting system benefits yellow birch recruitment without negatively impacting plant diversity. However, because increasing harvest intensity simultaneously enhanced interfering non-commercial species abundance (e.g. mountain maple), failed to improve red spruce regeneration, and decreased the abundance of large trees (diameter at breast height > 29 cm), we caution to opt for moderate cutting intensity in this forest type. Additional treatments such as enrichment planting in harvest gaps might be necessary to maintain red spruce over time.

1. Introduction

Traditional silvicultural systems have long been critiqued for their tendency to simplify the complexity of natural forest stands (Puettmann et al., 2009). On one end of the harvest intensity spectrum, clearcutting greatly increases and homogenizes light availability creating conditions that favor the development of single-cohort stands dominated by shade-intolerant species (Archambault et al., 1998; De Grandpré et al., 2000; Laflèche et al., 2000). Although this system can reliably regenerate high-value timber, tradeoffs include decreases in structural complexity (Chaudhary et al., 2016; Gustafsson et al., 2012), alterations of wildlife habitat and taxa (Deal, 2007; Klimaszewski et al., 2005; Work et al.,

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2010), and shifts in plant community composition (Boucher et al., 2008; Duguid and Ashton, 2013). At the other end of the spectrum, less intensive uneven-aged systems that maintain continuous canopy cover generally exert fewer negative impacts (Falk et al., 2008; Kuuluvainen et al., 2012; Rogers et al., 2018). Indeed, recent reviews have found that selection cutting systems have neutral to positive effects on plants and wildlife (Duguid and Ashton, 2013; Chaudhary et al., 2016). Nevertheless, long term application of certain variants of selection systems can reduce structural complexity and the abundance of biological legacies that are key to maintaining biodiversity (e.g. large trees, snags, coarse woody debris) (McGee et al., 1999; Angers et al., 2005; Kenefic and Nyland, 2007; Mahon et al., 2008). Less intense silvicultural systems (e.g. single-tree selection) also tend to create homogenous low light environments that favor shade-tolerant species (e.g. sugar maple [*Acer saccharum* Marsh.]) but that fail to regenerate more light demanding species (e.g. yellow birch [*Betula alleghaniensis* Britton]) (Webster and Lorimer, 2005; Domke et al., 2007; Shields et al., 2007). Thus, silvicultural systems at both ends of the harvest spectrum promote homogeneous understory light patterns that favor a restricted set of species.

Alternatively, silvicultural systems causing intermediate levels of disturbances (*sensu* Connell, 1978) could enhance resource availability and heterogeneity, thereby diversifying the array of ecological niches that can promote plant diversity and mixed-species regeneration. For example, gap-based approaches (*sensu* Coates and Burton, 1997), such as group and patch selection systems, create medium to large gaps (e.g. 300–2000 m^2) to increase both resource availability and heterogeneity with the goal of diversifying tree species regeneration (Raymond et al., 2006; Beaudet et al., 2011; Poznanovic et al., 2014). Although these gap-based systems are hypothesized to promote species coexistence, the empirical evidence for this effect has been equivocal. Group and patch selection systems can regenerate mid-tolerant and shade-intolerant species (Leak and Filip, 1977; Prévost et al., 2010; Prévost and Charette, 2015), but often fail to regenerate slow-growing, shade-tolerant conifers (e.g. red spruce [*Picea rubens* Sarg.] and eastern hemlock [*Tsuga canadensis* (L.) Carrière]; Webster and Lorimer, 2002; Prévost et al., 2010). In addition, group and patch-selection systems using large gaps are criticized for their lack of flexibility to optimize wood production, especially when applied to stands with complex structures (Raymond et al., 2016). Indeed, these systems are too often uniformly, regularly dispersing gaps throughout a stand with little consideration to the existing structural or biological conditions that may influence regeneration and maintenance of biodiversity (Puettmann et al., 2009). This approach is risky because the application of silvicultural systems without explicit recognition of the disturbance and stand dynamics characteristic to a particular ecosystem may fail to meet management objectives (O'Hara, 2002; Puettmann et al., 2015).

In contrast, silvicultural systems that create irregularly dispersed harvest gaps of variable size could create heterogeneous understory conditions favorable to mixed-species regeneration and plant diversity (Fahey and Puettmann, 2007; Kern et al., 2017). This could be the case for the hybrid single-tree and small group selection cutting system (Nyland, 2002), in which gaps are haphazardly created throughout stands, depending on the location and pattern of mature trees to harvest. Such system establishes small gaps (< 300 m^2) of variable size, thereby expanding the variety of regeneration niches that can potentially satisfy the ecological requirements of multiple species (e.g. Dumais and Prévost, 2014). Additionally, this system increases age class interspersion and promotes heterogeneous spatial and vertical structures, thus perpetuating the heterogeneous character of the community (Nyland, 2002). Although a few studies have shown the merits of this approach on tree regeneration (e.g. Bédard et al., 2014; Prévost and Charette, 2015; Walters et al., 2016), the effects on stand structural attributes and plant community diversity still need to be assessed.

With a diversity of co-occurring species from the boreal and temperate forests, late-successional yellow birch – conifer stands provide an ideal setting to assess the hybrid single-tree and small group selection cutting system. Yellow birch – conifer is the most widespread and economically important forest type in Quebec's temperate mixedwood forest, a boreal-temperate forest ecotone that extends roughly between the 47°N and 48°N parallels (Saucier et al., 2009). Similar to spruce-fir-hardwood in USA (Kabrick et al., 2017), these stands grow on rich sites where several tree species with contrasting traits coexist as a result of a long successional process characterized by frequent, yet relatively low-severity gap-phase disturbances rather than infrequent, high severity stand-replacing disturbances (Seymour et al., 2002; Duchesne and Prévost, 2012). Gap regimes in this forest type are highly variable in size and spatial distribution ($\overline{X}$ = 270 m^2, stdev = 314 m^2, range: 20–2100 m^2; Kneeshaw and Prévost, 2007). Moreover, the mixture of tree species of varying crown geometries, phenologies, and shade tolerances generates structurally complex stands that often exhibit greater heterogeneity in understory light conditions than in hardwood or conifer stands (Brown and Parker, 1994; Bartels and Chen, 2010; Macdonald and Fenniak, 2007). Indeed, Bartels and Chen (2010) hypothesized that in mixedwood stands, heterogeneity of light conditions may be more important than light availability itself for regulating understory plant species diversity and coexistence, relative to hardwood or conifer stands.

Here, we test the hypothesis that a hybrid single-tree and small group selection system, by more closely emulating natural disturbance regimes and increasing the availability and heterogeneity in understory light levels, will promote regeneration of target species (i.e. yellow birch, red spruce and balsam fir [*Abies balsamea* L.]), retain stand structural attributes, and maintain high understory plant diversity. Furthermore, by implementing this variable harvesting regimen across a range of cutting intensities we explore whether an optimal harvest intensity exists to achieve desired regeneration outcomes and retain structural and biological legacies.

2. Materials and methods

2.1. Site description

We conducted this study north of Saint-Raymond (46°58′N, 72°02′E), approximately 80 km northwest of Quebec City, Canada. The region is characterized by a high-hill topography with rounded summits and the prevalence of glacial tills (Robitaille and Saucier, 1998). Mean monthly temperatures (1981–2010) vary from –14.6 °C in January to 17.3 °C in July (using BioSIM; Régnière and Bolstad, 1994). On average, the region receives 1253 mm of precipitation annually, with 31% falling as snow. The experiment was established in late-successional uneven-aged yellow birch – conifer stands, at the margins of the balsam fir – yellow birch and the sugar maple – yellow birch bioclimatic domains (Saucier et al., 2009). The natural disturbance regime is characterized by light to moderate partial disturbances occurring between stand-replacing disturbances (fire at 200–400 year return) (Boucher et al., 2011). Background mortality and insect outbreaks (e.g. spruce budworm [*Choristoneura fumiferana* (Clemens)], hemlock looper [*Lambdina fiscellaria* (Guenée)]) cause partial mortality that induces gap regeneration (Bouchard et al., 2006; Barrette and Bélanger, 2007; Kneeshaw and Prévost, 2007).

Before the cut, stand merchantable basal area (BA of trees > 9 cm dbh [diameter at breast height]) averaged 25.7 m^2/ha (± 3.6 m^2/ha SD, n = 20) and was composed of 42% yellow birch, 20% red spruce, 16% balsam fir, 12% sugar maple, and 6% red maple (*Acer rubrum* L.). Companion species including paper birch (*Betula papyrifera* Marsh.), American beech (*Fagus grandifolia* Ehrh.), American mountain ash (*Sorbus americana* Marsh.), pin cherry (*Prunus pensylvanica* L.f.), striped maple (*Acer pensylvanicum* L.), and mountain maple (*Acer spicatum* Lam.) constituted the remaining 4%. Dendrochronological analyses of trees sampled at 1 m-height indicated the mature canopy trees had attained ages of up to 100, 140, and 200+ years for balsam fir, yellow

birch, and red spruce, respectively. Standing dead trees represented $6.2 \pm 2.5 \, \text{m}^2/\text{ha}$ and coarse woody debris ($> 9 \, \text{cm dbh}$) $90.9 \pm 44.1 \, \text{m}^3/\text{ha}$. Regeneration of desirable species was largely restricted to smaller ($< 30 \, \text{cm tall}$) height classes. This included balsam fir ($50\,690 \, \text{stems/ha}$, $95\% < 30 \, \text{cm}$), yellow birch ($35\,270 \, \text{stems/ha}$, $98\% < 30 \, \text{cm}$), red maple ($6220 \, \text{stems/ha}$, $80\% < 30 \, \text{cm}$), and sugar maple ($6110 \, \text{stems/ha}$, $86\% < 30 \, \text{cm}$), with sparse red spruce seedlings ($2150 \, \text{stems/ha}$, $77\% < 30 \, \text{cm}$). Non-commercial species (mountain maple, striped maple, American mountain ash) were dominant in larger height classes ($12\,130 \, \text{stems/ha}$, $58\% > 30 \, \text{cm}$).

2.2. Experimental design

We established a split-plot design with five complete randomized blocks of four cutting treatments (residual BA) in main plot (20 experimental units [EU]) in 2007. Given the variability of precut conditions in mixedwood stands, we blocked the stands based on hardwood/softwood proportions. The design compares three intensities of the hybrid single-tree and small group selection cutting corresponding to light ($21 \, \text{m}^2/\text{ha}$ residual BA, 20% removal), moderate ($18 \, \text{m}^2/\text{ha}$, 31%) and heavy ($15 \, \text{m}^2/\text{ha}$, 42%) cutting intensities to an uncut control ($26 \, \text{m}^2/\text{ha}$, 0%). These treatments were applied on $80 \, \text{m} \times 80 \, \text{m}$ and the surrounding $10 \, \text{m}$ buffer. Each EU was split in two regeneration treatments (natural and planted halves of $40 \, \text{m} \times 80 \, \text{m}$). For the purposes of this study we restricted our analyses to the halves under natural regeneration as the enrichment planting with red spruce and release treatments utilized in the planted halves confound interpretation of plant community dynamics to overstory treatments.

We marked trees to harvest as single and small groups of trees according to priorities based on tree vigor ("MSCR" method; see Boulet, 2005 for complete classification), species (balsam fir $> 20 \, \text{cm dbh}$ and paper birch $> 32 \, \text{cm dbh}$ first) and quality (defective trees first). We employed "adapted silviculture practices" (*sensu* Déry and Leblanc, 2005) that retained legacy trees including a minimum of 10 snags and 6 living trees/ha, all of which $> 19 \, \text{cm dbh}$, but also all vigorous red spruces $< 35 \, \text{cm dbh}$ to maintain this declining species, as recommended by Fortin et al. (2003). Harvests were conducted during October-December 2008. Trees were felled by chainsaw, and then skidded with a cable Timberjack 240E, with the instruction to disrupt the forest floor within harvested areas (i.e. passive scarification, *sensu* Nyland, 2002), while avoiding damage to roots of living trees and spruce saplings. Hardwoods were delimbed on site and skidded tree-length to the landings, whereas softwoods were skidded full-tree to the landings.

2.3. Data collection

Each EU contained a $40 \times 40 \, \text{m}$ central plot ($1600 \, \text{m}^2$) for precut and postcut mensuration inventories. We numbered and measured all living and dead standing trees $> 9 \, \text{cm dbh}$ for diameter, total height, defects and tree vigor. We used a network of 420 circular microplots ($4 \, \text{m}^2$) with $10 \, \text{m}$ spacing to tally the understory vegetation ($< 3 \, \text{m}$). We monitored the density of commercial and non-commercial tree species in the regenerating layer by recording each stem by height class (≤ 5, 6–30, 31–60, 61–100, 101–200 and 201–300 m) before the cut (2007), and 1, 3, 5 and 8 years after the cut (2009, 2011, 2013 and 2016). We censused understory plant cover, by species, at 1, 3, 5 and 8 years after the cut. The first year postcut, we estimated canopy gap size (*sensu* Runkle, 1992) by mapping the boundaries of projected crowns on graph paper and later calculated polygon size with a point grid. Additionally, we characterized summer light transmittance with hemispherical photographs (Coolpix 4500 digital camera and FC-E88-mm fisheye lens, Nikon, Tokyo, Japan) taken $1.3 \, \text{m}$ above vegetation plots centers (9 microplots/EU) under overcast sky or before sunrise. We analyzed all photographs with the gap light analyzer (GLA) software to calculate % of total transmitted light (Frazer et al., 1999).

2.4. Statistical analysis

We utilized analyses of variance (ANOVAs) or covariance (ANCOVAs) to assess treatment effects on stand structural attributes, understory plant community and tree regeneration using general linear mixed models (Proc GLIMMIX; SAS 9.4, SAS Institute, Inc., Cary, NC). All analyses considered block as a random effect, treatment and year as fixed effects, and a 0.05 significance level (α). Treatment effects on year 1 postcut (2009) stand structural response variables were analyzed using the pretreatment data (2007) as a covariate to help adjust for precut differences among stands (Milliken and Johnson, 2002). Stand structural attributes included overstory stand BA, overstory tree density of dead and living individuals, and four stand structural diversity indices. Stand structural diversity indices of living trees used the Shannon index (H'; Magurran, 2004) extended to diameter (H_d'), height (H_h') and tree species (H_s') and a mean structural diversity (MSD) index using these three components of structural diversity ($H_{sdh} = (H_s + H_d + H_h)/3$) following Staudhammer and Le May (2001). We used $2 \, \text{cm dbh}$ classes to evaluate H_d and Kraft crown classification classes (Smith et al., 1997) as proxy to tree height classes. We compiled distribution of frequencies by $10 \, \text{cm dbh}$ class to compare diameter distributions of standing living and dead trees among treatments.

We tested treatment effects on gap fraction (%), gap size (m^2) and on total light transmittance (% of total transmitted light) to determine how treatments altered canopy openness and resource availability using ANOVAs. Additionally, we performed a Levene's test (i.e. equality of variances) to determine whether variation in light availability (i.e. light heterogeneity) differed across treatments by conducting an ANOVA on the absolute value of the residuals ($|e|$; Levene, 1960).

We used repeated measures analyses of variance rmANOVAs to examine understory plant dynamics in response to treatments over time (2009, 2011, 2013, 2016). For the regenerating tree community we examined changes in seedling density (individuals $> 30 \, \text{cm}$ in height) using the pre-treatment (2007) values as a covariate to control for initial differences in seedling densities across plots. Understory plant dynamics analyses examined overall vascular species abundance (% cover), richness, and diversity (H') as well as richness and abundance of five vascular species groups: trees, forbs, ferns, shrubs, graminoids and bryophytes (e.g. mosses, liverworts; see Appendix A). Analyses on graminoids were restricted to changes in cover as taxa were simply tallied as *Carex* spp. or unknown grasses. Bryophytes analyses were restricted to 2016. We also examined whether treatments shifted the vascular community composition using a permutational multivariate analysis of variance (*adonis* function in R; Oksanen et al., 2018). For these analyses, permutations were constrained to each block using the *strata*. Analyses were run on year 1 and 8 species abundance matrices wherein rare species ($\leq 5\%$ of plots) were deleted and standardized using the Hellinger metric (Legendre and Gallagher, 2001). Else, we tested the direct effects of average light availability and heterogeneity by regressing vascular species richness and diversity (H') on average percent light transmittance and its standard deviation (Stevens and Carson, 2002). Finally, we analyzed changes in tree seedling density (individuals $> 30 \, \text{cm}$ in height) in response to treatment over time (2009, 2011, 2013, 2016) using repeated measures analyses of covariance (rmANCOVA) with pre-treatment (2007) values as a covariate.

We checked the homogeneity of slopes assumption by testing the interaction between the covariate and the main effect (Milliken and Johnson, 2002). This interaction was removed from the full model when not significant, resulting in an equal slopes model testing only the covariate. When data distributions were non-normal, we used a Gamma distribution and a log-link function, except for richness data for which we used a Poisson distribution and a log-link function. For all analyses, when random effects were near zero, we removed these from the model to avoid convergence problems (Milliken and Johnson, 1984). We estimated the treatments and year parameters effects with the LSMEAN function statement, the Tukey-Kramer adjustment for multiple
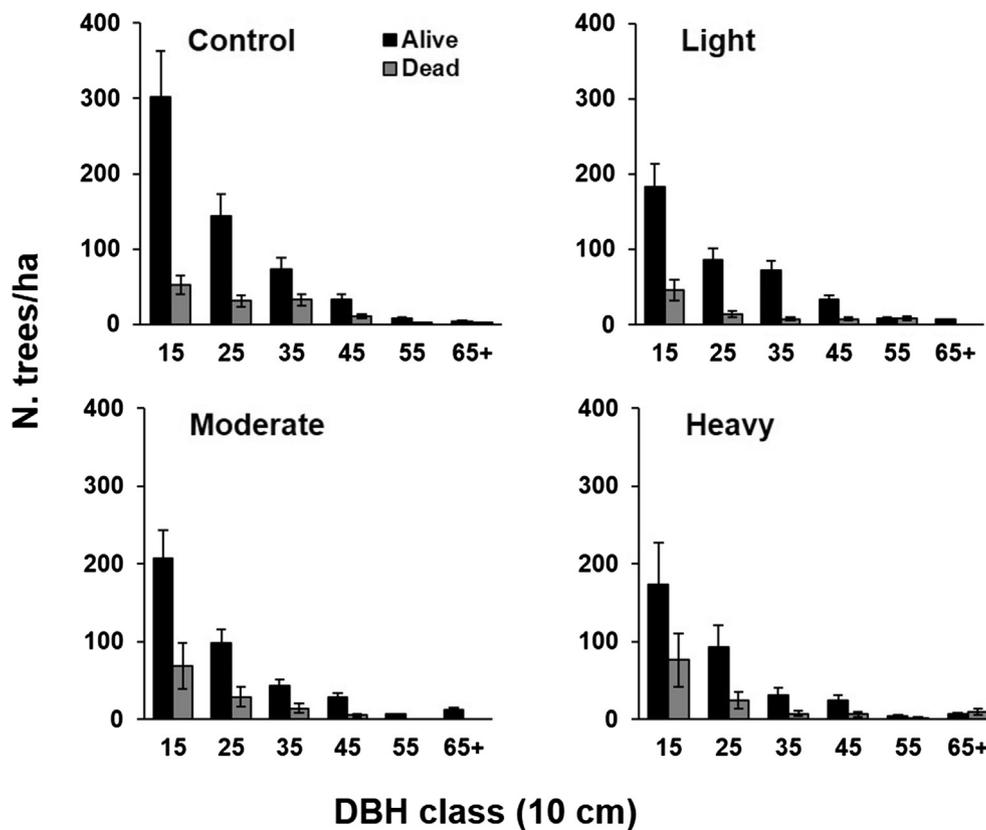
Fig. 1. Diameter distributions assessed in each treatment immediately after the cut.

comparisons and the ILINK option. We compared treatments within significant years (SLICE option) with polynomial contrasts using the LSMESTIMATE function statement and the SIMULATE option. Homogeneity of the variance and normality of residuals were graphically checked beforehand.

3. Results

3.1. Postcut stand characteristics

Following treatment, diameter distributions of living trees retained the uneven, reverse-J distribution found in the control plots; albeit with a smaller number of stems, particularly in the larger size classes (Fig. 1; Table 1). Cutting treatments did not affect significantly gap size but increased the gap fraction (P = 0.002, Table 1). Gap fraction increased five-fold in the moderate cut (25%) relative to the control (5%) and eight-fold in the heavy cut (40%) relative to the control and light cut. As a result, resource availability, as assessed by average percent transmitted light levels, varied by treatment immediately after harvest (P = 0.002), where it was greater in the moderate cut than in the control (19.8 vs 13.3%) and greatest in the heavy cut (33.2%) than in all other treatments. Similarly, resource heterogeneity, as assessed by the Levene's test on the residuals of light transmittance, differed among treatments with the heavy cut exhibiting significantly more variability ($\bar{e}$ = 1.0) than the control ($\bar{e}$ = 0.3) (Table 1).

Cutting treatments had a significant influence on stem density of living trees > 9 cm and > 29 cm dbh (both P < 0.001, Table 1) and only trends of effects for standing dead trees (P = 0.085 and P = 0.075 for > 9 cm and > 29 cm dbh, respectively). All cutting treatments significantly reduced the number of living trees > 9 cm dbh compared to the control (381, 384 and 326 vs 561 trees/ha), and in the heavy cut compared to the lighter cut (326 vs 381 trees/ha). The density of large living trees (> 29 cm dbh) was significantly lower in the heavy cut (60 trees/ha) than in all the others (78–115 trees/ha). There was a

marginally significant effect (P = 0.057) of treatments on the BA of merchantable living trees and the effects were similar to those of the total density of living trees > 9 cm dbh. Structural diversity indices were largely unaffected by the cutting intensity gradient. Only diameter diversity index (H'_d) was marginally lower (P = 0.072) in the heavy cut relative to the control (2.57 vs 2.81).

3.2. Understory plant community diversity and composition

Across all areas and census periods, we documented 91 species or taxa in the herbaceous layer: 14 tree species, 14 shrub species, 42 forb species, 12 fern species, 9 bryophyte species, and graminoids (Appendix A). Cutting treatments did not affect overall vascular species richness (Table 2), however it was significantly lower in the first year postcut than in all other years (Fig. 2a). In contrast, cutting intensity changed overall vascular plant cover patterns over time (i.e. significant Trt × Year interaction P = 0.029, Fig. 3a). Specifically, vascular plant cover was similar across treatments in the first year post-harvest, increased over time, and by year 8 was 69% greater in the heavy cut compared to the uncut controls. Species diversity increased with cutting intensity (P = 0.002) and was significantly greater in the heaviest cut than the control (H'_C = 2.21, H'_L = 2.26, H'_M = 2.26, H'_H = 2.52). Additionally, pooled across treatments, diversity peaked 3 years postcut (P < 0.001, Table 2, H'_1 = 2.21, H'_3 = 2.41, H'_5 = 2.36, H'_8 = 2.27, not shown).

Across the study period, tree species richness peaked in year 3 although it is worth noting that average difference among years is less than one species (Fig. 2a). Tree richness also increased in response to cutting intensity with the two heaviest cuts having significantly greater species richness than the control (9.6 and 9.7 species/4 m^2 in moderate and heavy cuts, respectively, versus 8.5 species/4 m^2 in uncut control; Fig. 4). Cutting intensity did not alter tree cover; however, tree cover immediately postcut was 44–48% lower than in subsequent years (Fig. 2b). Similarly, cutting effects on shrubs were restricted to the first

Table 1
ANOVAs of response variables measured immediately after cutting to assess stand structural attributes (number of living and dead trees > 9 cm dbh and > 29 cm dbh, gap fraction and size), light transmittance (availability [%] and variability [|e|]), as well as stand structural diversity using Shannon's diversity index extended to tree species (H′$_s$), diameter (H′$_d$), height (H′$_h$) and mean structural diversity (MSD H′$_{sdh}$).

Response variables	Effects (P > F)		Control	Light	Moderate	Heavy
	Trt	Cov				
Gap size m^2	0.122	N/A	103(26)	217(91)	266(1 2 3)	342(85)
Gap fraction %	0.002	N/A	5.2 (2.0)a	19.1 (6.7)ab	25.0(5.7)bc	40.1(7.1)c
Light % transmittance	0.002	N/A	13.3 (0.5)a	17.6 (1.9)ab	19.8 (1.7)b	33.2 (4.4)c
Light variability |e|	0.027	N/A	0.3(0.1)a	0.6(0.1)ab	0.7(0.1)ab	1.0(0.1)b
Living trees MBA	*0.057*	*0.023*	*25.7 (1.2)a*	*20.8 (1.0)b*	*17.8 (1.0)bc*	*14.9 (1.0)c*
N. tree/ha > 9 cm	< 0.001	< 0.001	561 (85)a	381 (36)b	384 (17)bc	326 (58)c
N. tree/ha > 29 cm	< 0.001	< 0.001	115 (11)a	113 (2)a	78 (11)a	60 (17)b
Dead trees MBA	0.087	0.005	8.0 (0.7)	4.5 (0.7)	4.4 (1.2)	5.8(1.2)
N. snags/ha > 9 cm	0.085	< 0.001	130 (18)	80(17)	116(39)	119(46)
N. snags/ha > 29 cm	0.075	0.001	46 (5)	20 (5)	19 (6)	19 (3)
Tree species H′$_s$	0.202	< 0.001	1.29 (0.11)	1.04 (0.5)	1.12 (0.06)	0.94 (0.15)
Tree diameter H′$_d$	0.072	NS	2.81 (0.03)*a*	2.70 (0.07)*ab*	2.71 (0.05)*ab*	2.57 (0.07)*b*
Tree height H′$_h$	0.615	< 0.001	1.24 (0.10)	1.00 (0.06)	1.12 (0.05)	1.13 (0.09)
MSD H′$_{sdh}$	0.334	< 0.001	1.78 (0.07)	1.58 (0.08)	1.65 (0.03)	1.55 (0.05)

Note: Trt = treatment (cutting intensity); Cov = covariate; MBA = merchantable basal area (m2/ha); N/A = non-applicable (no precut measurement); NS = Non significant (excluded from the model). We used Gamma distribution in PROC GLIMMIX when it was not normal (i.e. for % light transmittance, densities of living trees, MBA of dead trees, tree height H′$_h$ and MSD H′$_{sdh}$). We performed a Tukey-Kramer multiple comparisons test (α = 0.05) for significant treatment effects. Differing letters indicate differences among treatments for a given variable (trends of effects are shown in italic). Values in parenthesis are standard errors.

Table 2
ANOVAs of richness, diversity and cover response variables assessed at the community level and by species group 8 years after cutting.

Response	Trt	Year	Trt * Year			
Community						
Vascular Richness	0.359	< 0.001	0.142			
Overall Cover (%)	0.043	< 0.001	0.029			
Overall Diversity (H′)	0.002	< 0.001	0.451			

Species group	Richness			Cover (%)		
	Trt	Year	Trt * Year	Trt	Year	Trt * Year
Tree	0.005	0.048	0.621	0.502	< 0.001	0.089
Shrub	0.175	< 0.001	0.440	0.641	< 0.001	0.063
Forb	0.465	0.008	0.183	0.058	< 0.001	0.007
Fern	0.149	< 0.001	0.972	0.942	< 0.001	0.513
Graminoid	N/A	N/A	N/A	0.564	< 0.001	< 0.001
Bryophytes	0.855	N/A	N/A	0.158	N/A	N/A

Note: Trt = treatment (cutting intensity); N/A = non-applicable. Diversity (H′) was modelled using a normal distribution, richness values were modelled using a Poisson distribution, and percent cover was modelled using a Gamma distribution in PROC GLIMMIX. Analyses on graminoids were restricted to percent cover and data on bryophytes (i.e. mosses) were only available for 2016 (year 8).

year postcut. Shrub richness and cover were reduced by as much as 28% and 57%, respectively, at year 1, relative to subsequent years (Fig. 2). Cutting intensity did not affect shrub richness or cover. Forb richness peaked in year 3 and was significantly greater (9.7 species/4 m^2) than in either year 1 or year 8 (8.6 and 8.7 species/4 m^2, respectively; Fig. 2). Forb cover varied in response to cutting intensity over time (Trt × Year interaction: P = 0.007, Table 2). Forb cover was equivalent across all cutting intensities in the first year postcut (~1.0%) and increased over time, peaking in year 3 (6.2%, averaged across treatments). Differences grew increasingly pronounced at the two extremes of the harvest gradient with average forb cover in the heavy treatment nearly three-fold greater than the uncut control by year 8 (Fig. 3b). Postcut fern richness and abundance were reduced by 38–45% and 36–59%, respectively, following the cut compared to subsequent years (Fig. 2). Graminoid cover was in general low (i.e. ~1%), exhibiting only a slight increase in abundance in year 3 postcut
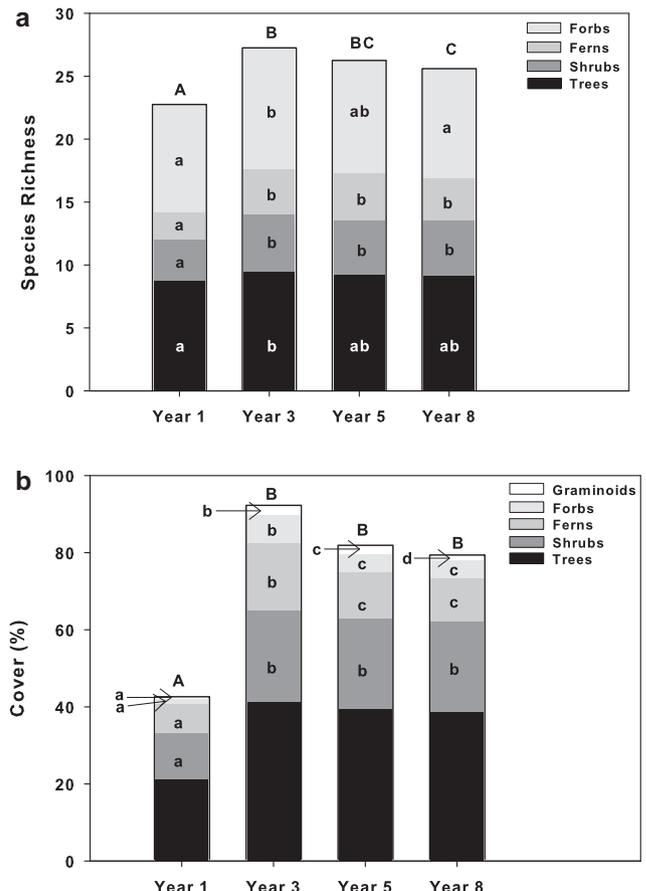
Fig. 2. Overall and within group species richness (a) and % cover (b) across years. Differing letters indicate significant differences among years (uppercase: overall; lowercase: within group).

(Fig. 3). While the analyses found a significant treatment*year effect, further investigation revealed no differences among treatments within years. No analyses were conducted on graminoid richness as data was collected at genus (e.g. *Carex*) or morphospecies (i.e. grass) level. Finally, bryophyte (i.e. moss) richness and density at year 8 were
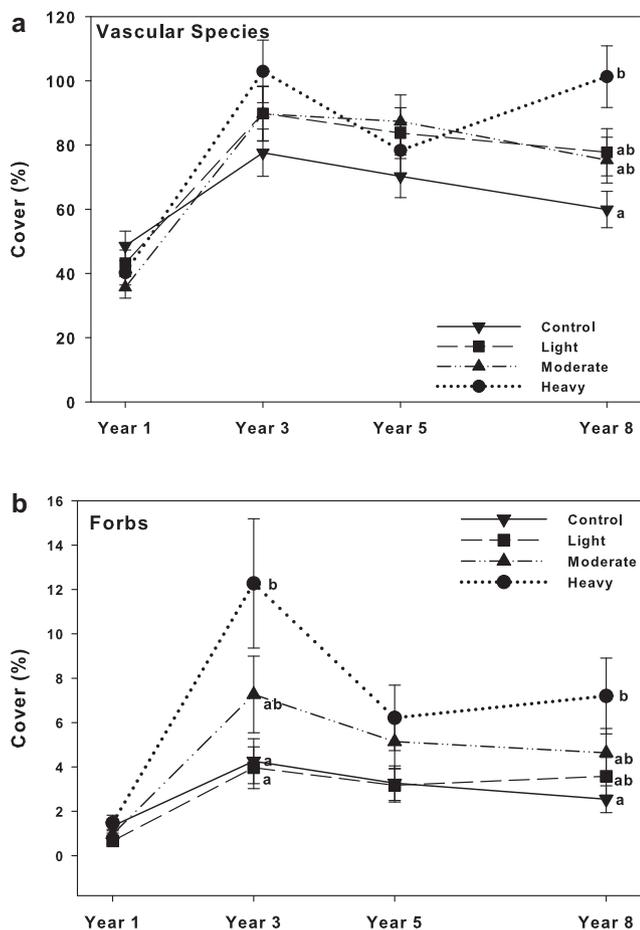
Fig. 3. Interaction between cutting intensity and time for overall vascular species and forbs. Differing letter indicate significant differences among treatments for a given year.
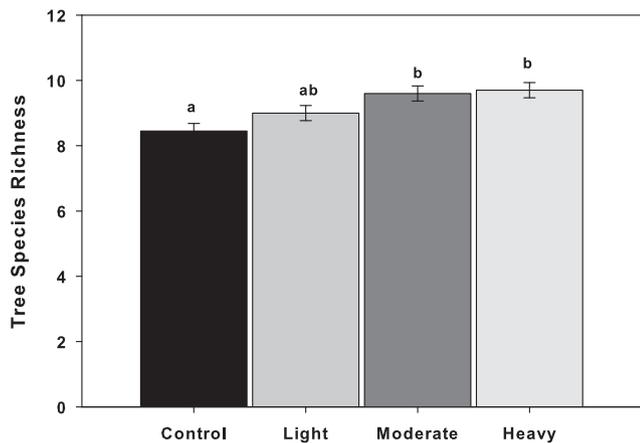

Fig. 4. Cutting intensity effect on tree species richness. Differing letters indicate significant differences among treaments.

Fig. 5. Correlation of vascular species richness and diversity (H′) with initial post-treatment % of total transmitted light.

unaffected by variation in cutting intensity.

Harvest treatments did not significantly alter vascular plant community composition in either year 1 or 8 postcut (Trt_{2009}: $F = 0.602$, $P = 0.929$ and Trt_{2016}: $F = 0.679$, $P = 0.892$). Increases in % transmitted light increased species richness ($R^2 = 0.22$, $P = 0.05$, Fig. 5a) and diversity ($R^2 = 0.49$, $P < 0.001$, Fig. 5b). In contrast, there was no evidence light heterogeneity altered either richness ($R^2 = 0.00$, $P = 0.96$) or diversity ($R^2 = 0.13$, $P = 0.13$).
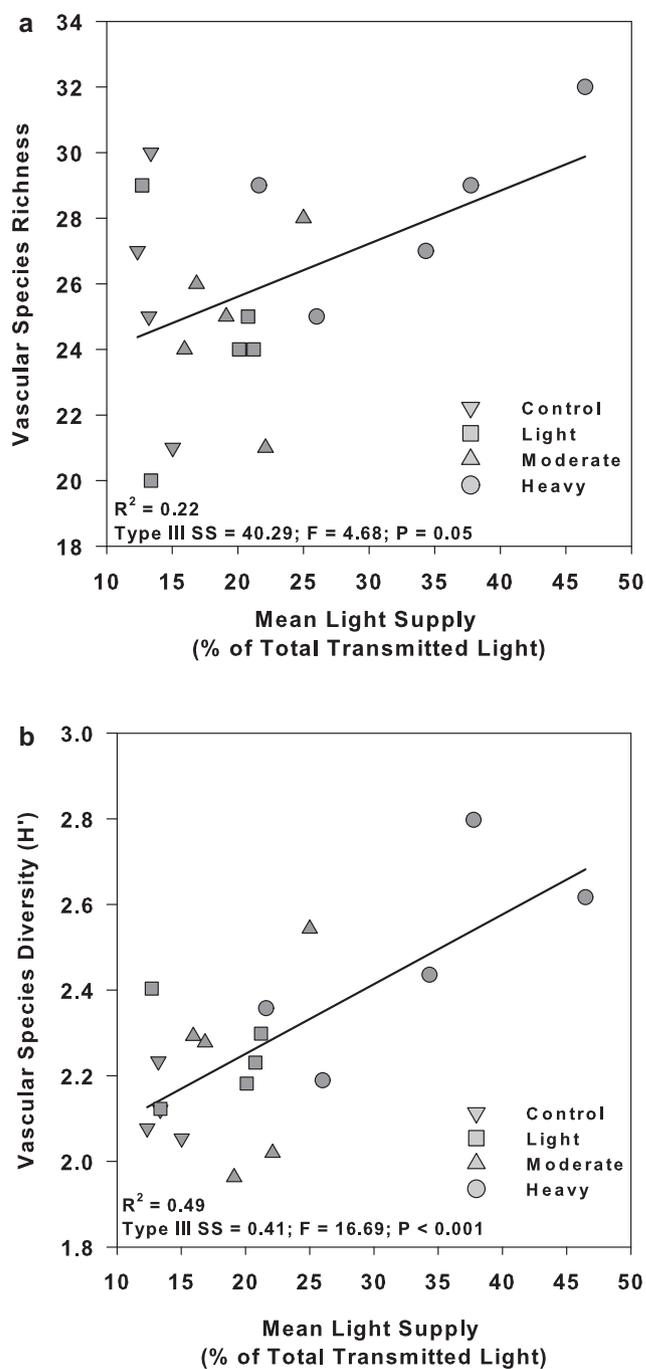
3.3. Tree regeneration density > 30 cm in height

The single-tree and small group selection cutting treatments increased yellow birch and mountain maple seedling (> 30 cm in height) density over time (Trt × Year interaction: $P < 0.001$ for both, Table 3). After 5 years, yellow birch density was greater in the heavy cut (14 200 seedlings/ha) than in the control (2200 seedlings/ha). After 8 years, both moderate and heavy cuts (10 600 and 16 000 seedlings/ha, respectively) had greater seedling density than the control (2100 seedlings/ha), while the lightest cut did not trigger significant seedling recruitment with 4900 seedlings/ha (Fig. 6). Difference in mountain maple density among treatments also varied with time, but density was higher in all cutting treatments than in the control after 8 years

Table 3
ANOVA of commercial and non-commercial tree seedlings density > 30 cm in height 8 years after treatment.

Species	Trt	Year	Trt * Year	Cov
Commercial				
Yellow birch	0.007	< 0.001	< 0.001	NS
Balsam fir	0.042	0.005	0.034	< 0.001
Red spruce	0.161	< 0.001	0.331	NS
Red maple	0.673	< 0.001	0.318	< 0.001
Non-commercial				
Mountain maple	0.053	0.761	0.001	< 0.001
Striped maple	0.752	< 0.001	0.733	< 0.001
Pin cherry	0.051	< 0.001	0.035	NS

Note: Trt = treatment (cutting intensity); Cov = covariate (precut value); NS = Non-significant (excluded from the model). Sugar maple, American mountain ash, paper birch, trembling aspen, American beech, beaked hazelnut, red elderberry, Alleghany serviceberry and speckled alder were tallied but in insufficient number to permit individual analysis. We used Gamma distribution in PROC GLIMMIX when it was not normal (i.e. for yellow birch, balsam fir and red spruce) and Ar(1) covariance structure when possible (arh(1) for pin cherry, sugar, mountain and striped maples).
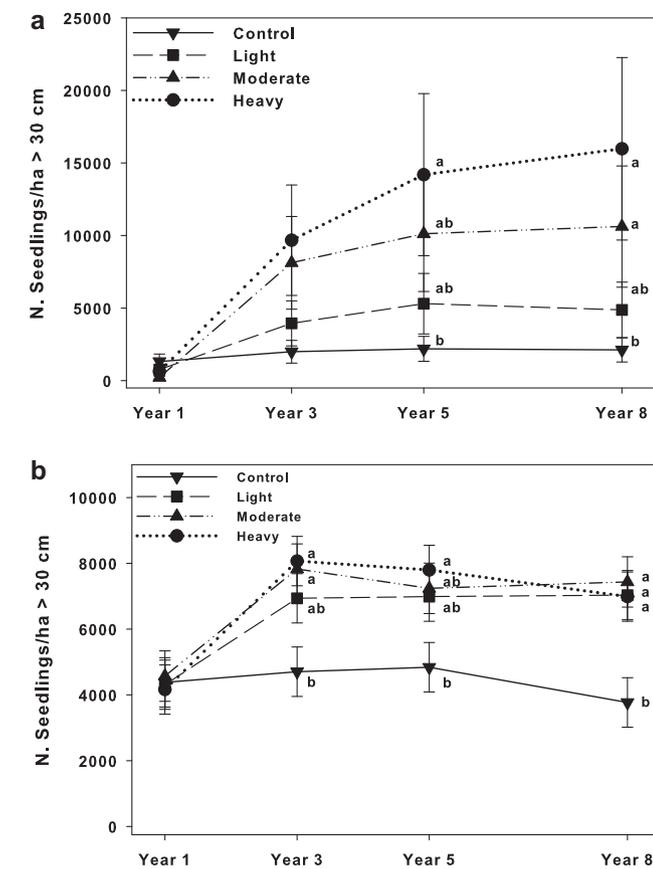
Fig. 6. Interaction between cutting intensity and time for yellow birch (a) and mountain maple (b) density of seedlings > 30 cm in height. Differing letter indicate significant differences among treatments for a given year.

(7000–7400 vs 3800 seedlings/ha, respectively). We also detected significant interactions for balsam fir (P = 0.034) and pin cherry (P = 0.035), but further analysis revealed no differences among treatments within years and only single effects of time were considered (Table 3). The time effect was significant for five species: balsam fir, red spruce, red maple, striped maple and pin cherry (Fig. 7). Balsam fir, red spruce and red maple density increased over time, independently of cutting intensity and averaged respectively 2700, 750 and 4800
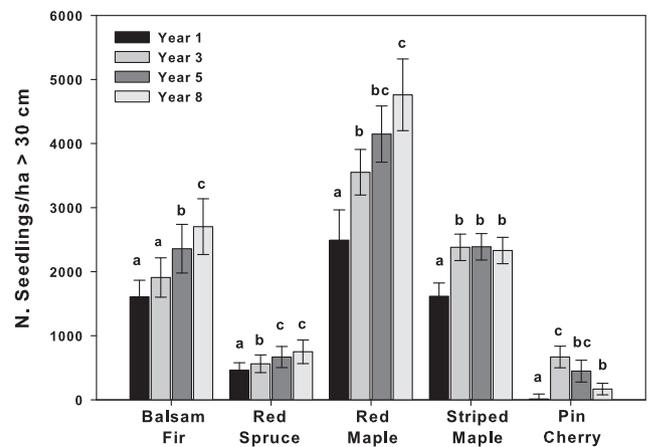
Fig. 7. Time effect on balsam fir, red spruce, red maple, striped maple and pin cherry density of seedlings > 30 cm in height. Differing letters indicate significant differences among years for a species.

seedlings/ha after 8 years. Striped maple increased after 3 years but its density remained stable afterwards (2300 seedlings/ha). Pin cherry increased at year 3 (670 seedlings/ha) but decreased at year 8 (170 seedlings/ha).

4. Discussion

Our field assessment of the hybrid single-tree and small group selection cutting system as intermediate disturbance to promote regeneration and diversity in yellow birch – conifer stands generally supported the predicted responses. Stand structural attributes were largely retained, light availability and heterogeneity were increased, yellow birch regeneration was improved and plant diversity was maintained or enhanced. However, contrary to the predictions, this approach failed to augment red spruce or balsam fir regeneration. The mechanisms underlying the continued conifer regeneration challenges, in particular red spruce, remain unclear, but increased interference with non-commercial species could be a main factor.

4.1. The challenge of establishing natural mixed hardwood-conifer regeneration

Maintaining the mixedwood character of a forest community in boreal-temperate ecotones is challenging because hardwood species tend to regenerate more easily and to be more competitive than conifers (Greene et al., 1999; Evans and Brown, 2017; Kabrick et al., 2017). In silviculture, natural regeneration methods count on canopy manipulations to achieve light levels that can satisfy requirements of target species. Our results showed that light cutting intensity (e.g. leaving high residual BA of 21 m²/ha or 20% removal) was not intense enough to trigger significant changes in micro-environmental conditions and understory community. In contrast, moderate intensity treatments reducing BA to 18 m²/ha BA (31% harvest) or less caused sufficient environmental changes to prompt a regeneration phase. The magnitude of yellow birch response to treatments increased with cutting intensity, a typical behavior for this species that rapidly takes advantage of newly available resources after disturbance (Webster and Lorimer, 2005; Kneeshaw and Prévost, 2007; Prévost and Charette, 2015). Unfortunately, cutting treatments were not as positive for balsam fir and red spruce. We expected that partial shade conditions and small group openings (< 300 m²) would favor their regeneration (Dumais and Prévost, 2014; Prévost and Charette, 2015; Kern et al., 2017), but other factors interfered in the process. Scarce advance regeneration, along with slow initial growth contrasting with rapid expansion of non-commercial species (e.g. mountain maple) can explain these difficulties

(Dietze and Clark, 2008). The existing seedling densities may be sufficient to perpetuate balsam fir, but are likely insufficient for red spruce. In general, red spruce is more difficult to regenerate than balsam fir because of its infrequent good seed crops (Blum, 1990), its more specific germination and growth requirements (reviewed by Dumais and Prévost, 2007), and the long recruitment process involving multiple release events to access the canopy (Fraver and White, 2005). Historical overexploitation of red spruce further reduced the relative abundance of seed trees within stands (Fortin et al., 2003; Barrette and Bélanger, 2007). Hence, the current failure of natural red spruce regeneration in yellow birch – conifer stands is a concern because the species could continue to decline over time. Even the retention of mature red spruce seed trees (e.g. vigorous trees < 35 cm dhb) did not help to improve red spruce regeneration.

Undeniably, the current management context of herbicide ban on Quebec's public land (Thiffault and Roy, 2011) limits the capacity to control competitive non-commercial species. Our study demonstrated that after 8 years, all selection cutting treatments doubled the density of mountain maple compared to the control. This represents a dilemma for the "preventive silviculture approach" (*sensu* Thiffault and Roy, 2011) that relies primarily on canopy manipulation to reduce the abundance of non-commercial competing species. Although this approach can work with shade-intolerant species such as pin cherry, it has not proved to be very helpful with competing species that tolerate partial shade (e.g. mountain, striped and red maple; Raymond and Bédard, 2017). Mountain maple is an aggressive mid-tolerant species that benefits from partial canopy opening with vigorous vegetative reproduction and growth (Aubin et al., 2005). As for red maple, a commercial species considered as non-target in Quebec because of its poor value and competitive character, it did not respond to cutting treatments but continued to increase with time at a faster pace than all the other species. This generalist species has broad resource requirements and can grow in a variety of ecological conditions (Abrams, 1998). The presence of recalcitrant, non-commercial species in regenerating layers is common in forests worldwide and greatly influences the outcome of silvicultural treatments (Royo and Carson, 2006; Dietze and Clark, 2008; Kern et al., 2012).

4.2. Maintaining stand structural and plant diversity

Given that regeneration of only one of the three target species responded positively to treatments, one can ask what is the benefit of using the single-tree and small group selection system if it does not regenerate better the conifers than regular gap-based approaches. We argue that the hybrid selection system we used increased both light availability and heterogeneity, and revealed helpful to maintain overall structural and plant diversity. Our results showed that all selection treatments maintained uneven distributions of tree diameters and created multiple gaps of variable size (averaging 217–342 m^2). Furthermore, mean gap size and gap fraction in light and moderate cuts matched those found in unmanaged natural yellow birch – conifer stands (e.g. mean gap size 270 m^2, gap fraction of 19% in Kneeshaw and Prévost, 2007). Light transmittance was also significantly increased in moderate and heavy cuts compared to the control. The patchy character of these hybrid selection cuts could contribute to increase light transmittance and variability, which are generally favorable to species diversity (Beaudet et al., 2011).

Our study also showed that retaining large living and dead trees during the harvest operations helped maintain these attributes to similar levels than in uncut stands in the light and moderate treatments. In contrast, the heaviest cutting treatment reduced the number of large living trees (> 29 cm dbh) to nearly the half and tended to lower diameter diversity H′$_d$. Many wildlife species rely on large living trees as ecological resource for denning, perching, sheltering, breeding and foraging (Harmon et al., 1986; Poulin et al., 2008). Large living trees also contribute to the flow of coarse woody debris key to wildlife and

plant diversity (Fraver et al., 2002; Vanderwel et al., 2006; Angers et al., 2010). Silvicultural interventions designed to promote old-growth attributes in late-successional stands usually include retention modalities to help maintain ecological functions and non-plant species (Hansen et al., 1991; Bauhus et al., 2009).

Overall, we observed no negative impacts of cutting treatments on understory plant diversity or composition. Indeed, we observed enhanced tree richness after 8 years in the moderate and heavy cuts, whereas vascular species diversity (H′) was only increased in heavy cuts. Observed richness and diversity gains were driven by augmented yellow birch and mountain maple recruitment into larger classes as well as greater forb, tree and shrub cover in response to greater cutting intensity. The quick postcut recovery of richness and cover, and subsequent observed enhancement concur with other selection cutting studies showing initial increases with augmented cutting intensity (Duguid and Ashton, 2013; Kern et al., 2014; Falk et al., 2008). Moreover, unlike the pattern often observed following more intensive silvicultural practices (reviewed by Hart and Chen, 2007), plant community composition was unaffected across our range of single-tree and small group selection cutting intensity gradient.

Despite significant differences in light variability, we detected no correlation between light heterogeneity and diversity. Instead, we found that light availability was the key driver of species richness and diversity. Although we expected increasing light heterogeneity would enhance plant diversity in these mixed stands (e.g. Macdonald and Fenniak, 2007), our results are consistent with Bartels and Chen's (2010) conclusion that the immediate increase in understory light availability following canopy disturbances has an equal, if not stronger, structuring effect on plant diversity (see also Stevens and Carson, 2002). We cannot rule out the possibility that light heterogeneity may co-regulate diversity given that our sampling scheme (9 readings/EU) may inadequately capture the fine-scale variability in light throughout the plots.

4.3. Implications for management

This study aimed at assessing the single-tree and small group selection cutting system with retention as intermediate disturbance to promote natural regeneration, structural and species diversity in yellow birch – conifer stands located in the boreal-temperate forest ecotone of North America. Our experiment's explicit use of a gradient in cutting intensity found that the magnitude of the observed responses grew as cutting intensity increased. Nevertheless, our results suggest tradeoffs exist wherein the highest cutting intensity (42% or below 15 m^2/ha in residual BA) gains in understory plant diversity and yellow birch regeneration success are coupled with declines in overstory tree structural diversity and intensified understory competition by non-target tree species. Indeed, many of the predicted responses attained with the heavy selection cut were also achieved with the moderate cuts. Thus, we suggest moderate intensity treatments can achieve both regeneration and diversity goals in this forest type. For these reasons, we recommend to not reduce the BA below 15 m^2/ha (> 40% removal) in yellow birch – conifer stands, if the maintenance of structural attributes is a goal. Heavy partial cuts have proven to reduce the abundance of large trees useful to wildlife species in forested ecosystems, in particular when cuts are associated with diameter limits of harvesting (McGee et al., 1999; Angers et al., 2005).

Nevertheless, none of the cutting treatments improved conifer species regeneration, a key component of mixedwood stands (Kabrick et al., 2017). Given the persisting difficulties to regenerate naturally red spruce with silvicultural methods and the historical context of red spruce decline, we suggest to opt for supplementary actions beyond retaining seed trees and protecting advance regeneration. Others silvicultural options including artificial regeneration should be considered to supplement natural regeneration when advance regeneration of this species is lacking and understories harbor a dense layer of non-

commercial species (Dumais et al., in review). For example, planting large stock seedlings in harvest gaps combined to mechanized release with brush saws could help maintaining this signature species in the ecosystem over the long term. In this respect, the hybrid single-tree and small group selection cutting system with retention of biological legacies could be considered as coarse filter approach (*sensu* Hunter, 1999) to maintain the structure and disturbance intensity characteristic of this late-successional mixedwood forest. In addition, fine filter approaches such as enrichment planting of red spruce followed by tending (e.g., control of competing vegetation) may be necessary. Even though the composition and extent of mixedwood stands growing in boreal-temperate forest ecotones vary worldwide (Evans and Brown, 2017), such approaches combining natural and artificial regeneration methods could apply to other forest types to achieve diversity objectives (Greene et al., 1999). Sustaining mixed stand compositions constitutes a safer approach than monocultures in the current context of global changes, in particular because it confers a greater resistance and resilience to

disturbances (reviewed by Knoke et al., 2008; Coll et al., 2018).

Appendix A

List of species sorted by group. Values represent mean % cover, by treatment, in 2016. Asterisks (*) denote species which were found in one of the treatment areas in at least once of the prior censuses (2009, 2011, or 2013). A dash (–) denotes that species was not found in a particular treatment in any year.

Species	Treatment			
Ferns and Lycopods	Control 2016	Light 2016	Moderate 2016	Heavy 2016
Athyrium filix-femina	*	–	–	*
Dennstaedtia punctilobula	*	0.30	–	1.36
Dryopteris campyloptera	8.90	9.19	11.18	7.44
Huperzia lucidula	0.16	0.35	0.07	0.30
Lycopodium obscurum	–	–	0.00	*
Lycopodium spp.	*	*	*	*
Onoclea sensibilis	0.03	–	*	0.33
Osmunda cinnamomea	–	*	*	0.70
Osmunda claytoniana	–	*	*	*
Phegopteris connectilis	0.12	0.69	0.15	0.36
Polypodium virginianum	0.06	0.03	*	0.91
Thelypteris noveboracensis	0.03	0.58	0.06	1.04
Forbs				
Actaea spp.	*	–	–	–
Aralia nudicaulis	0.59	0.74	0.86	0.88
Asarum canadense	–	–	–	0.08
Aster spp.	0.03	0.00	*	0.15
Chamerion angustifolium	–	–	–	0.03
Circaea alpina	*	0.03	–	–
Circaea lutetiana	–	*	–	–
Clintonia borealis	0.48	1.18	1.40	1.31
Coptis trifolia	0.13	*	0.09	0.16
Cornus canadensis	0.32	0.00	0.65	0.92
Cypripedium acaule	0.03	*	0.03	0.00
Dalibarda repens	–	–	0.00	–
Equisetum spp.	–	–	–	*
Erythronium americanum	–	*	–	–
Eurybia macrophylla	0.00	0.03	–	–
Galium spp.	–	–	–	*
Hepatica nobilis var. acuta	*	*	*	*
Impatiens capensis	–	–	–	1.15
Impatiens spp.	–	–	–	*
Linnaea borealis	–	–	*	–
Maianthemum canadense	0.29	0.11	1.25	1.02
Maianthemum racemosum ssp. racemosum	0.06	0.03	–	0.06
Medeola virginiana	0.00	0.00	0.03	0.03

Mentha arvensis	–	–	–	0.00
Mitchella repens	–	–	–	0.00
Monotropa uniflora	*	*	*	*
Oclemena acuminata	*	0.03	0.00	0.12
Osmorhiza claytonii	–	0.03	–	*
Oxalis montana	0.41	0.57	0.63	0.79
Polygonatum pubescens	–	*	*	*
Prenanthes spp.	0.00	–	*	–
Pyrola elliptica	–	–	*	*
Solidago macrophylla	–	*	–	*
Solidago spp.	*	–	–	–
Streptopus amplexifolius	*	*	*	*
Streptopus lanceolatus var. roseus	0.06	0.06	0.06	0.03
Thalictrum dioicum	0.03	0.08	*	0.03
Thalictrum pubescens	–	–	0.00	-
Trientalis borealis	0.13	0.19	0.30	0.19
Trillium erectum	0.24	0.47	0.18	0.27
Viola macloskeyi ssp. pallens	–	0.03	*	–
Viola spp.	0.03	–	–	*
Shrubs				
Diervilla lonicera	–	*	–	0.03
Gaultheria humifusa	–	–	–	*
Ilex mucronata	*	–	*	–
Lonicera canadensis	*	0.00	*	–
Ribes glandulosum	0.10	0.12	0.10	0.08
Ribes spp.	*	*	*	*
Ribes triste	–	–	–	0.03
Rubus idaeus	0.06	2.42	1.70	3.74
Rubus pubescens	0.21	0.85	0.27	0.35
Sambucus racemosa var. racemosa	0.08	0.64	0.20	0.21
Taxus canadensis	2.31	4.02	4.06	4.80
Viburnum lantanoides	16.59	18.04	14.22	18.58
Viburnum nudum var. cassinoides	–	–	*	*
Viburnum opulus var. americanum	–	0.03	–	–
Trees				
Abies balsamea	6.19	4.43	5.17	6.88
Acer pensylvanicum	2.53	3.91	4.64	3.94
Acer rubrum	2.42	1.92	2.53	4.46
Acer saccharum	3.07	5.95	1.70	2.28
Acer spicatum	3.76	9.74	13.50	13.49
Amelanchier spp.	0.06	0.31	0.10	0.18
Betula alleghaniensis	4.24	6.22	6.79	12.62
Betula papyrifera	*	0.03	0.03	0.14
Corylus cornuta	–	0.97	0.00	0.30
Fagus grandifolia	0.03	0.03	0.18	1.23
Picea rubens	5.78	2.92	1.84	5.46
Populus tremuloides	–	*	–	*
Prunus virginiana	*	0.06	0.55	0.48
Sorbus americana	0.23	0.36	0.29	1.19
Bryophytes				
Bazzania trilobata	0.56	0.45	0.09	1.06
Dicranum spp.	2.31	1.39	0.89	1.27
Hylocomium splendens	0.28	0.00	0.03	0.03
Mnium spp.	*	0.03	0.00	0.00
Pleurozium schreberi	2.94	2.24	2.37	2.61
Polytrichum spp.	0.62	0.63	0.96	1.06
Ptilium crista-castrensis	0.08	0.00	*	0.03
Rhytidiadelphus triquetrus	*	*	*	*
Sphagnum spp.	0.33	1.75	0.85	7.81
Graminoids				
Various species	*	0.39	1.16	1.94

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