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Bryophyte species assemblages in fire and clear-cut origin boreal forests

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ABSTRACT

Natural and anthropogenic disturbances could have different impacts on understory plant communities. Investigating these differences could help improve silvicultural and management practices in order to better achieve biodiversity protection objectives. Using post-fire (20–90 years) and post-clearcutting (20–70 years) forest chronosequences placed on similar sites, we examined which environmental factors are the main drivers of bryophyte community assembly in eastern Canadian boreal forests, using information on bryophyte life-history strategies (colonist: high reproductive effort but a short potential life span; perennial: low reproductive effort and a long potential life span) to interpret the resulting patterns. The fire origin stands were affected by high-severity fires followed by natural regeneration, whereas the clear-cut stands were regenerated through the advance regeneration present in the understory of the harvested stands. Our results indicate that by killing the existing mosses and baring the mineral soil, fire tends to decrease the cover of perennial species (such as *Pleurozium scherberii*) and increase the presence of colonist species compared with clear-cut. Overall species richness does not increase much in older stands, but some species that have been identified by previous studies as being more sensitive to management activities, such as liverworts, tend to be strongly associated with balsam fir basal area, which is higher in mature clear-cut origin stands. This tree species tends to be heavily affected by partial mortality events after >50 years (insect outbreaks, windthrow), which could accelerate the creation of heterogeneous canopy structure and generate a greater diversity of microhabitats suitable for sensitive bryophyte species. More research needs to be conducted to better understand the underlying functional relationships between overstory tree composition and bryophyte communities.

1. Introduction

In the last decades, the expansion and intensification of forest management activities have led to the replacement of fire by clear-cut logging as the most important disturbance in much of the boreal forest of North America (Cyr et al., 2009; Burton et al., 2010; Bouchard and Pothier, 2011). This represents a major concern from a conservation perspective because some species are suspected to be ill-adapted to maintain healthy populations in anthropogenized environments. Bryophytes, and particularly liverworts, are a good example of a species group that could be negatively affected by forest management (Fenton and Frego, 2005; Hylander et al., 2005; Arseneault et al., 2012; Caners et al., 2013). Bryophytes are a major component of boreal forest ecosystems, and higher bryophyte species richness has been reported in natural forests compared to forests affected by logging (Vanha-Majamaa et al., 2007; Hart and Chen, 2006, 2008; but see Schmalholz et al., 2011). This is often explained by a greater range of environmental conditions in natural forests, which translate in niches for a wider range of specialized organisms (Tilman and Pacala, 1993; Beatty, 2003; Tews et al., 2004). In particular, coarse woody debris (CWD) of variable quality is an important type of microhabitat for bryophyte species (Söderström, 1988; Andersson and Hytteborn, 1991; Rambo and Muir, 1998; Schmalholz et al., 2011), and the

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amount of CWD has been found to be a key factor influencing bryophyte species richness and composition in forest ecosystems (Rydgren et al., 1998; Mills and Macdonald, 2005; Fenton and Bergeron, 2008; Schmalholz et al., 2011).

Forest succession is an important process in natural or managed forest ecosystems, particularly in boreal forests where severe disturbances such as fire and clearcutting are common. Initial post-disturbance microhabitat characteristics and subsequent temporal changes in microhabitat availability are expected to differ following fire or clear-cutting. For example, fire is expected to remove an important part of the organic layer, thus creating a greater quantity of exposed mineral microhabitats compared with clearcutting (Nguyen-Xuan et al., 2000). These conditions favor the recolonization of fire-adapted species through regeneration from seed banks, underground plant structures that may have survived the fire, or from seeds from nearby unburnt stands (Dyrness, 1973). On the other hand, in North-American boreal conditions, clear-cut logging generally causes little direct disturbance to the organic layer outside skidding trails, and the vegetation generally includes a significant number of species that were present prior to disturbance (Timoney et al., 1997; Rees and Juday, 2002; Nguyen-Xuan et al., 2000). Temporal variations in CWD availability are also expected to differ between stand origins: in post-fire stands, CWD will be most abundant during the first few decades after disturbance, but they will decline afterwards and increase again in late successional stage (Brassard and Chen, 2006). By contrast, in clear-cut origin stands, CWD abundance tends to be low initially, and to increase progressively during the subsequent decades (Barrette et al., 2013). The effect of these temporal changes in microhabitat abundance on bryophyte communities has rarely been compared directly thus far, but Schmalholz et al. (2011) found that in mixed-wood forests of eastern Canada, young stands regenerating after natural disturbances were distinctly different from clear-cut origin stands in terms of woody debris flora.

Species life-history strategies are increasingly recognized as good indicators of the functional diversity of an ecosystem. During (1992) has elaborated a classification for bryophytes that integrates reproductive effort, potential life span, size and number of spores. Species from different life-history strategies are expected to be impacted differently by fire and logging. For instance, colonist species with spores well adapted to colonize harsh environments might be more frequent after fire, while perennial species, which have a low reproductive output but long potential life span, could be more abundant in habitats that are relatively stable (see Table S1). By knowing which traits best explain community response to a given environmental modifications, it becomes feasible to expand the results of a study to other regions affected by similar disturbances, or other types of organisms that share similar traits.

In this study, our main objective is to examine bryophyte species assemblages in fire origin and clear-cut origin stands of different ages (ranging from 20 to 90 years), and to examine if these responses are associated with life-history strategies (colonist and perennial). We hypothesize that in young stands, colonist species richness will be higher in fire origin stands (because fire removes organic matter), but perennial species richness will be higher in clear-cut origin stands (because harvests cause little direct disturbance to the organic layer). In older stands, we expect that the closed canopy cover will translate into a higher cover of perennial species and mosses compared with younger stands. We also expect that the differences in species composition between fire origin and clear-cut origin stands will tend to decrease with time as the initial differences in microhabitat characteristics subside. Finally, we expect that coarse woody debris volume will be an important habitat variable to explain species richness and species composition, as suggested by previous studies (Fenton and Bergeron, 2008; Schmalholz et al., 2011; Arseneault et al., 2012).

2. Study area

The study area is located in a section of the boreal forest (49°N–50°N, 68°W–70°W), in the province of Québec, Canada. It is located on the Canadian shield (a granitic, acidic bedrock formation), and surficial deposits are mostly represented by glacial tills of various thicknesses and by fluvioglacial deposits (Bouchard et al., 2008). The study area is located at the interface between two bioclimatic domains, the balsam fir – white birch to the south and black spruce – feathermoss to the north, according to the provincial classification (Morneau and Landry, 2007). Mean annual temperature was 1.5 °C during the 1971–2000 period at the Baie-Comeau weather station, which is located to the south of the study area (Environnement Canada, 2009). Climatic conditions tend to get colder when latitude or elevation increase, approaching 0 °C in average in the northern part of the study region. Average annual rainfall is 684 mm, and average annual snowfall 362 cm (Environnement Canada, 2009). The length of the growing season is between 140 and 160 days, and extends from May to October (Morneau and Landry, 2007).

Large forest fires are an important natural disturbance in this region, with fire return intervals that vary between 250 and 500 years, a fire recurrence that can be considered as relatively long compared with what is generally observed elsewhere in the North American boreal forest (Cyr et al., 2007; Bouchard et al., 2008). The forests are overwhelmingly dominated by the two aforementioned coniferous species, *Picea mariana* (Mill.) (black spruce) and *Abies balsamea* (L.) Mill (balsam fir), with a relatively secondary occurrence of hardwoods such as *Betula papyrifera* (Marsh.) (white birch) and *Populus tremuloides* (Michx.) (trembling aspen), particularly in early successional forests (Bouchard and Pothier, 2011). Forest harvestings have been performed in the region since the 1930s (Bouchard and Pothier, 2011): while they were initially very limited in extent, they increased progressively in importance throughout the 20th century.

Forest stands that originate from two types of stand-origin disturbances were sampled in this study: fires and clearcuts. The fire origin stands that were sampled were affected by high-severity crown fires, regenerated naturally, and were not affected by salvage logging or thinnings during the course of post-fire stand dynamics. Post-clear-cut stands were primarily regenerated through the advanced regeneration (i.e. seedlings or trees <9 cm DBH) that was present in the understory of the harvested stands. Following clearcutting, the sampled stands were not treated with silvicultural treatments such as pre-commercial or commercial thinnings.

3. Methods

3.1. Sampling

A chronosequence of stands originating from fires and from clear-cut logging was established based on disturbance maps available for the study area (Bouchard and Pothier, 2011). These maps were built from the information available from government archives and old aerial photographs, and were validated systematically by using forest inventory plots (Bouchard et al., 2008; Bouchard and Pothier, 2011). The year of stand origin was further validated in this study by taking sample cores of dominant trees in each plot, particularly in older stands for which the year of disturbance was uncertain.

Overall, 30 stands distributed along a gradient of time since fire and time since logging were selected for this study. For the post-fire chronosequence, six young stands (range 20–50 yr) and six mature stands (range 51–90 yr) were selected. For the post-clear-cut chronosequence, nine young stands (range 20–50 yr) and nine mature stands (range 51–70 yr) were selected. Clear-cut origin stands >70 years could not be sampled because logging history is too recent in this region (c.f. Section 2). We made sure that the severity of the stand-origin disturbance was homogeneous across age-classes, notably by discarding stands that were not regenerated through the advance regeneration that was present in the understory before harvesting (c.f. Fourrier et al., 2013). The sampled stands were distributed randomly in the landscapes along the main access roads, by respecting a minimal distance of 500 m between each site. One sample plot (400 m^2) was placed in each stand, by respecting the following conditions: minimum distance of 100 m from the nearest road access or nearest recent harvested area, on tills with a thickness >50 cm with mesic drainage. Within each plot, we measured the diameter at breast-height (DBH) of all trees (DBH $\geqslant$ 9.1 cm) to calculate basal area (BA). We measured the length and the diameter at the base and at the upper end of all CWDs >1 m in length and with at least one extremity with a diameter $\geqslant$9.1 cm. A decay class was assigned to each woody debris (adapted from Hunter, 1990): (1) presence of branches; (2) absence of branches; (3) no bark remaining; (4) wood is decayed; and (5) log is buried. We then used the conical-paraboloid formula to calculate the volume of CWDs (Fraver et al., 2007). At four locations within the plot (4 m from the center in each cardinal direction and at 50 cm from any rock or stump), we measured organic layer depth and bryophyte layer depth, and the four data for each variable were averaged.

Within each 400-m^2 sample plot, 20 quadrats of 4 m^2 were established to evaluate sapling and regeneration abundance. Five quadrats were located at 4-m intervals along four transects that went from the center to each cardinal direction. All saplings were counted in each quadrat; a sapling was defined as a small tree that had a height >1.3 m and a DBH <9.1 cm. Regeneration abundance (trees $\leqslant$1.3 m in height) was also evaluated in a 1-m^2 sub-quadrat located in the upper left corner of each quadrat, with the observer's back oriented toward the center of the plot.

Within each plot, we sampled bryophytes within 20 1-m^2 microquadrats located at 4-m intervals along four transects along the cardinal directions (five microquadrats per direction). Within each microquadrat, we evaluated the cover of each bryophyte species. The inventory included bryophytes on the ground, on woody debris, on tree bases (up to 30 cm), on snag bases (up to 1 m), and on rocks. We also estimated the cover of needles, leaves, lichens, vascular plants, pits, mounds, and rocks. We gathered bryophyte specimens from each micohabitat for subsequent laboratory identification. Nomenclature follows Ireland (1982) and Faubert (2012).

3.2. Life history strategies

Four classes of life-history strategies were defined (*sensu* During, 1992): colonist, shuttle, dominant, and perennial species. Life-history strategies are described in Table S1, and the life-history strategies associated with each bryophyte species are listed in Table S2. In the context of this study, we decided to combine, on the basis of their reproduction effort, colonist and shuttle species (high vegetative and sexual reproduction effort), and perennial and dominant species (low reproduction effort).

3.3. Data analyses

3.3.1. Site characteristics

We used ANOVAs to test differences between classes for environmental variables (fire origin and clear-cut origin stands) at the plot level ($n = 30$) (see Table 1 for the variable list). Age class (young and old), disturbance type class (fire and cut) and the interaction age x disturbance type (young-fire (YF), mature-fire (MF), young-cut (YC) and mature-cut (MC)) were fixed factors.

3.3.2. Species richness and abundance

With respect to species richness and abundance, the analyses were conducted on mosses (including *Sphagnum*) and liverworts (taxonomic groups), and on colonists and perennial groups (life history strategy groups). To test the hypotheses of higher colonist species richness in young fire origin stands, higher species richness of perennial in young clear-cut origin, and higher cover of perennial species and mosses in older stands, we used nested ANOVAs. Data were analyzed at the subplot level ($n = 120$). Age class, disturbance type and the interaction were fixed factors, and subplot nested within plot, and plot nested within age class were random factors. Richness data were analyzed with the GLIMMIXED procedure of SAS (SAS Institute 2002) and denominator degrees-of-freedom were calculated using the method of Kenward-Roger. The richness variable corresponded to the total number of species per subplot (within the 5 microquadrats (5 m^2)). Cover data were analyzed with the MIXED procedure of SAS and denominator degrees-of-freedom were calculated using Satterthwaite's approximation (Littell et al., 1996). The cover variable corresponded to the mean cover per subplot (average of the 5 microquadrats) and they were log transformed ($\log x$) to conform to the normality and homoscedasticity assumptions of ANOVA. Significant differences ($p \leqslant 0.05$) between classes in all ANOVAs were detected with LSmeans Tukey HSD tests.

To verify the importance of habitat variables in explaining species richness (colonist, perennial, mosses, and liverworts), we used model selection, using Akaike's information criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002). Sixteen models were tested in the model selection analyses for species richness and cover (Table S3). Environmental variables were divided in three groups that could have an effect on bryophytes communities: age, ground variables, and canopy variables. Ground variables describe colonization substrates and were represented by volume of CWD, cover of needles, cover of leaves, and cover of pits. Canopy structure variables influence bryophytes mainly through their effect on factors such as light and microclimate and also affect litter fall quality and abundance and were represented by black spruce BA, balsam fir BA, hardwood BA, and vascular plant cover. Model averaging (Burnham and Anderson, 2002) was used when the AIC weight of the top-ranking model was <0.95. Average parameter estimates and unconditional standard errors were calculated from all candidate models. Analyses were conducted with the AICcmodavg package (Mazerolle, 2012) in R (vers. 2.15.3). Multicollinearity between the environmental variables was assessed using variance inflation factors (VIF > 5 indicating collinear variables). Black spruce BA was excluded from model that already contained age (VIF > 5, models 1 and 2, Table S3). All variables were standardized before the analyses to facilitate assessment of their relative contribution in the models (Gelman, 2008).

3.3.3. Bryophyte species composition

To test the hypothesis that differences in species composition between fire origin and clear-cut logging stands will tend to decrease with time, we used permutational manova (McArdle and Anderson, 2001) with the function adonis of the vegan package

Table 1
Mean (±SD) of environmental variables for each class. ANOVAs were used to compare means between different classes (age class and type of disturbance class as main factors and the interaction between age and type of disturbances). Significant p values ($p \leqslant 0.05$) are given in bold type and means with different letters differed significantly (F = fire, C = clear-cut logging, Y = young, M = mature).

Variable	Young-Cut ($n = 9$)		Young-Fire ($n = 6$)		Mature-Cut ($n = 9$)		Mature-Fire ($n = 6$)		Age		Type		Age ∗ Type		Significant differences between main factors
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	F	p	F	p	F	p	
Mean diameter at breast height (cm)	12.03a	1.57	6.98b	5.44	13.91a	0.87	14.17a	1.55	20.76	**<0.001**	5.76	**0.024**	7.09	**0.013**	
Number of regenerating trees	9.56b	8.03	3.50b	3.56	36.56a	29.06	3.50b	3.89	4.60	**0.041**	9.66	**0.005**	4.60	**0.041**	
Hardwood basal area (m^2/ha)	0.54	1.39	0.12	0.16	0.74	2.14	2.61	3.83	2.68	0.114	0.79	0.383	1.94	0.175	
Balsam fir basal area (m^2/ha)	5.02	7.08	0.10	0.24	12.69	7.77	0.93	1.18	3.79	0.062	14.62	**<0.001**	2.46	0.129	F < C
Black spruce basal area (m^2/ha)	4.12	4.28	0.25	0.44	14.29	7.42	21.56	16.01	24.81	**<0.001**	0.29	0.596	3.11	0.090	Y < M
Number of saplings	63.89	36.12	84.67	37.52	29.11	23.32	14.67	14.35	22.48	**<0.001**	0.08	0.777	2.54	0.123	Y > M
CWD-1 (m^3/ha)	1.86b	5.40	30.66a	30.01	4.16b	3.70	8.56ab	9.34	3.47	**0.074**	9.77	**0.004**	5.28	**0.030**	
CWD-2 (m^3/ha)	0.61	1.08	5.85	5.62	1.40	2.28	2.55	3.35	1.11	0.302	7.23	**0.012**	2.97	0.097	F > C
CWD-3 (m^3/ha)	0.54b	1.27	23.19a	20.39	1.56b	3.23	2.50b	4.82	7.90	**0.009**	11.37	**0.002**	9.63	**0.005**	
CWD-4 (m^3/ha)	3.31b	3.68	42.81a	47.43	11.81ab	13.62	5.08b	4.65	3.09	0.091	3.88	0.060	7.72	**0.010**	
CWD-5 (m^3/ha)	11.78	14.14	2.69	6.09	29.47	15.86	10.01	13.34	6.24	**0.019**	8.13	**0.008**	1.07	0.310	Y < M; F < C
Organic layer depth (mm)	220.69	94.53	156.58	55.46	203.75	103.01	198.10	42.49	0.13	0.719	1.07	0.312	0.75	0.395	
Bryophyte layer (mm)	19.44	14.29	4.00	4.03	28.42	20.10	22.70	7.27	6.88	**0.014**	4.02	**0.050**	0.85	0.365	Y < M; F < C
Cover of rocks (%)	1.15	2.50	0.52	0.52	0.02	0.05	0.44	1.01	1.22	**0.280**	0.03	0.854	0.92	0.346	
Cover of vascular plants (%)^A	22.57	16.62	26.69	14.39	14.94	4.27	14.03	14.92	4.28	**0.049**	0.11	0.746	0.26	0.612	Y > M
Cover of ericaceous (%)	15.38	15.94	10.16	8.52	6.19	3.32	8.69	10.10	1.78	0.194	0.12	0.737	0.93	0.343	
Cover of needles (%)	16.93	9.45	45.16	12.05	26.13	12.17	5.79	4.27	1.23	0.278	17.93	**<0.001**	2.17	0.153	F < C
Cover of leaves (%)	27.71	15.77	7.09	8.80	11.06	10.44	10.55	12.45	28.18	**<0.001**	3.08	0.091	3.46	0.074	Y > M
Cover of pits (%)	11.62	4.52	13.81	8.29	12.52	4.18	11.63	3.62	0.11	0.745	0.11	0.742	0.62	0.437	
Cover of lichen (%)	1.79	2.76	2.46	1.05	0.91	0.30	6.73	14.01	0.51	0.480	1.88	0.183	1.19	0.286	
Cover of exposed soil (%)	0.00	0.00	0.20	0.31	0.00	0.00	0.00	0.00	–	–	–	–	–	–	

^{A} Including ericaceous species.

(Oksanen et al., 2008) in R (vers. 2.15.3). We performed the analysis on species frequency data at the plot level ($n = 30$) with all species included in the analyses. The Bray and Curtis distance measure was used in the analyses. Multiple pair-wise comparisons were also performed to test compositional differences between classes (YC, MC, YF and MF).

Multivariate regression trees (MRT, De'ath, 2002) were used to test the hypothesis that CWD will be an influent variable for bryophyte species composition. MRT permits the analysis of an entire community of species and multiple explanatory variables within one model or tree, and is a form of constrained clustering where the data are recursively partitioned to minimize the dissimilarity within the resulting groups using different levels of the explanatory variables. MRT is a robust method that makes no assumptions as to the form of the relationship between species and the explanatory variables. Bray–Curtis distance was used in these analyses. The size of the tree was assessed by its predictive error, which is estimated from the cross-validated relative error (CVRE). A CVRE of 0 indicates a perfect predictor and a CVRE close to 1, a poor predictor. The analyses were conducted with the function mvpart of the vegan Package (Oksanen et al., 2008) in R (vers. 2.15.3). Explanatory variables considered were: cover of vascular plants, black spruce BA, balsam fir BA, hardwood BA, organic layer depth, cover of needles, cover of leaves, cover of pits, CWD volume, cover of exposed mineral soil, and cover of lichen. The analysis was

Table 2
ANOVA summaries for the effects of age (young and mature stands), disturbance type (fire origin and clear-cut origin stands) and the interaction between age and disturbance type. Perennials are species with a low reproductive effort and a long potential life span and colonists are species with a high reproductive effort and a short potential life span. Significant p values ($p \leqslant 0.05$) are given in bold type.

	dfn, dfd	F	p
Moss richness			
Age	1, 23.9	3.14	0.089
Type	1, 23.9	0	0.983
Age ∗ Type	1, 23.9	8.53	**0.008**
Liverwort richness			
Age	1, 21.4	1.74	0.201
Type	1, 21.4	0	0.986
Age ∗ Type	1, 21.4	7.08	**0.015**
Colonist species richness			
Age	1, 22.6	0.75	0.395
Type	1, 22.6	0.45	0.510
Age ∗ Type	1, 22.6	10.8	**0.003**
Perennial species richness			
Age	1, 23.9	2.89	0.102
Type	1, 23.9	0.21	0.654
Age ∗ Type	1, 23.9	7.03	**0.014**
Moss cover			
Age	1, 26	8.02	**0.009**
Type	1, 26	0.01	0.937
Age ∗ Type	1, 26	1.81	0.190
Liverwort cover			
Age	1, 25.6	2.30	0.141
Type	1, 25.6	5.60	**0.026**
Age ∗ Type	1, 25.6	4.68	**0.040**
Colonist species cover			
Age	1, 26	0	0.954
Type	1, 26	0.14	0.709
Age ∗ Type	1, 26	32.39	**<0.001**
Perennial species cover			
Age	1, 26	8.36	**0.008**
Type	1, 26	0.01	0.938
Age ∗ Type	1, 26	2.27	0.144
Sphagnum cover			
Age	1, 25	1.45	0.240
Type	1, 25	0.99	0.330
Age ∗ Type	1, 25	0.25	0.622

performed on species frequency data at the plot level and all species were included ($n = 30$); because number of regenerating trees was correlated with balsam fir BA, the number of regenerating trees was not considered in the models.

We identified indicator species for each node of the MRT and for each combination of age class and disturbance type class with the method of Dufresne and Legendre (1997) with the labdsv function of the vegan package (Oksanen et al., 2008) in R (vers. 2.15.3). The indicator values were calculated using the relative abundance and percent cover of species for each plot. Significance of these indicator values was assessed by Monte Carlo tests (1000 permutations). To be considered as an indicator species, a species should be present in more than 10% of the plots.

4. Results

4.1. Site characteristics

Balsam fir BA and cover of needles on the ground were higher in clear-cut origin stands than in fire origin stands while CWD-2 volume was higher in fire origin stands than in clear-cut origin stands (Table 1). Black spruce BA was higher in mature stands than in young stands, and number of saplings, cover of leaves on the ground and cover of vascular plants were higher in young stands than in mature stands (Table 1). Volume of CWD-5 and bryophyte layer depth were highest in mature stands than in young stand and in clear-cut origin stands than in fire origin stands. The number of regenerating trees was highest in MC, and volume of CWD-1, CWD-3, and CWD-4 were highest in YF. Mean tree DBH was lowest in YF (Table 1). Hardwood BA, organic layer depth, cover of ericaceous, cover of pits, and cover of lichen did not differ significantly among classes. Exposed soil was only observed in young fire origin stands.

4.2. Species richness and abundance

A total of 94 species (Table S2) were found in this study: 34 liverworts, 50 mosses, and 10 *Sphagnum*. 76.5% of the liverworts were colonist species and 76% of the mosses were perennial. *Sphagnum* spp. were classified as dominant species and shuttle species can be found among liverworts and mosses. Exclusive species, those only found in one forest type, were more numerous in YF (9 species). Four exclusive species were found in MF but none were found in YC nor in MC sites. *Anastrophyllum minutum* and *Platygyrium repens* were only found after fire (YF and MF) while *Lophozia ascendens* and *Brotherella recurvans* were only found after cut (YC and MC).

The interaction between age and type were significant for all richness variables (Table 2). Moss richness in YF was significantly higher than in MF and liverwort richness in MC was significantly higher than in YC (Fig. 1). Perennial species richness was lower in MF and differ significantly from YF, and colonist species richness was higher in YF and in MC but did not differ significantly from MF (Fig. 1).

The effect of forest type and the interaction between age and forest type were not significant for the cover of mosses and cover of perennial species: these two groups were significantly higher in mature forests than in young forests (Table 2). Cover of colonist species was significantly higher in YF and MC compared with YC and MF (Table 2, Fig. 2). Cover of liverworts was significantly higher in MC than in the other classes (Table 2, Fig. 2). Cover of *Sphagnum* did not vary according to age and forest type (Table 2).

The best model (structure + ground) explaining moss richness was 2.2 times (i.e. 0.69/0.31) better than the second best model (age + structure + ground) (Table 3). Moss richness decreased with age, black spruce BA and cover of vascular plants, and increased with volume of CWD, cover of leaves, and balsam fir BA (Table 4). The top-ranking model explaining liverwort richness (structure; $\text{AIC}_{\text{cw}} = 0.43$) was mostly equivalent to the second best model (age + structure, $\text{AIC}_{\text{cw}} = 0.38$) (Table 3). Liverwort richness increased with CWD volume and balsam fir BA, and decreased with vascular plant cover (Table 4). The top-ranking model explaining perennial species richness (structure + ground) was 2 times (i.e. 0.65/0.33) better than the second one (age + structure and ground) (Table 3). CWD volume and cover of leaves increased perennial

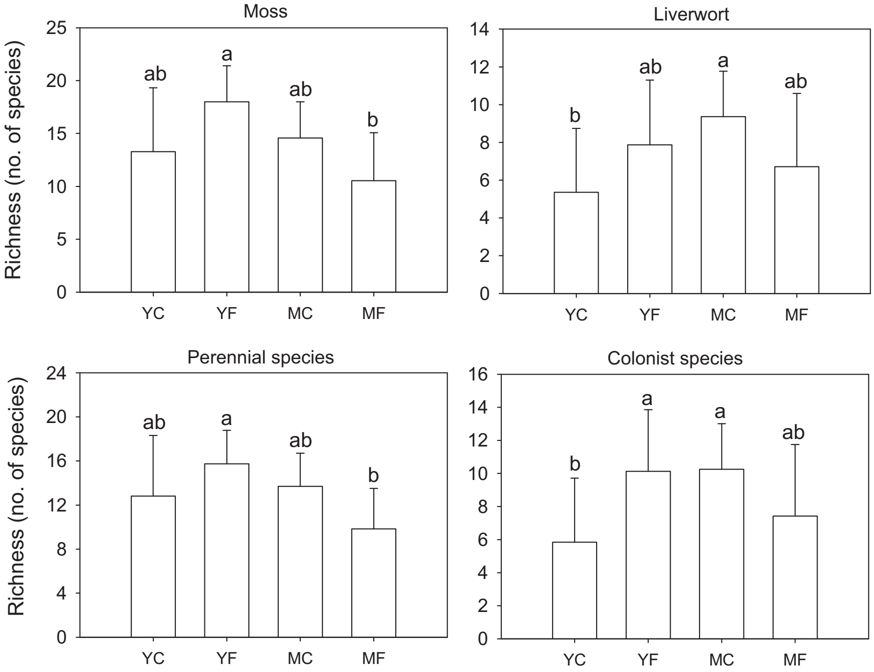

Fig. 1. Richness (±SD) of bryophytes. Richness corresponds to the total number of species per subplot (5 m^2). Perennials are species with a low reproductive effort and a long potential life span and colonists are species with a high reproductive effort and a short potential life span. ANOVA models were used to compare means. Differences that were significant ($p \leqslant 0.05$) are indicated by different letters ($n = 120$, YC = Young-Cut, YF = Young-Fire, MC = Mature-Cut, MF = Mature-Fire).

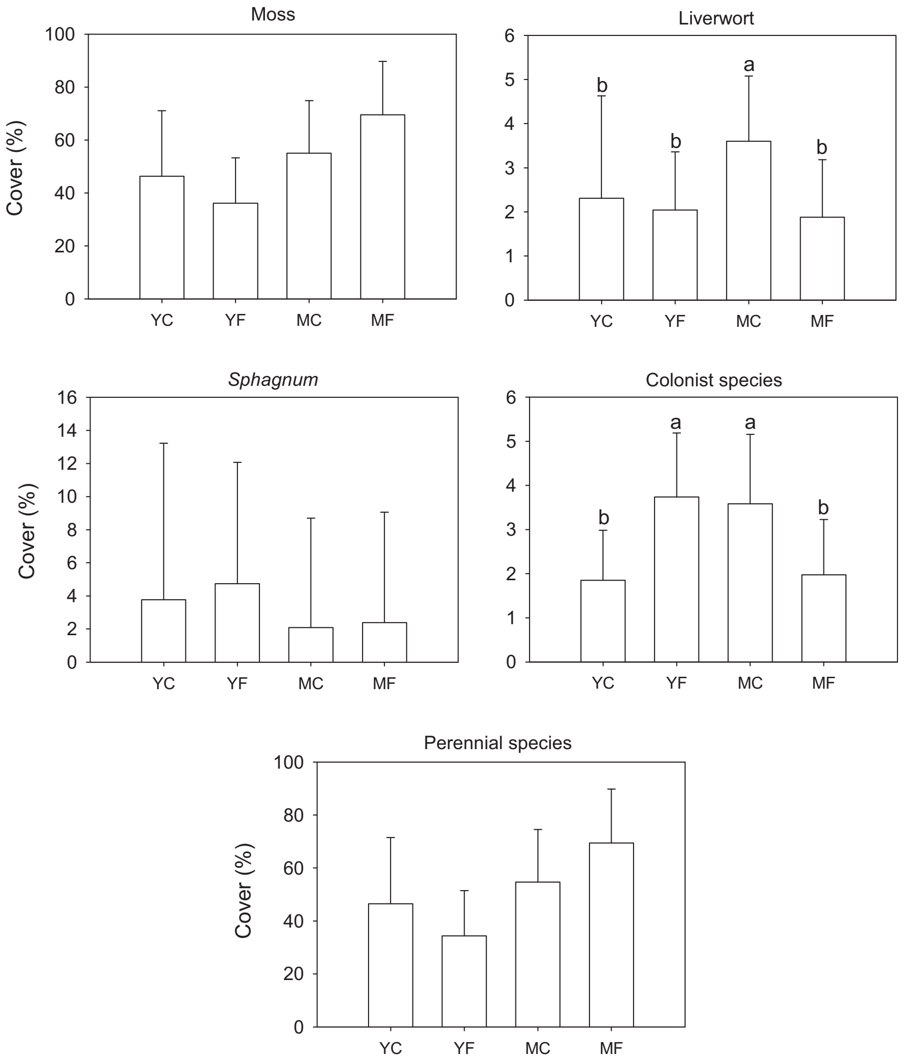

Fig. 2. Cover (±SD) of bryophytes. Cover corresponds to the mean cover per subplot (average of the 5 microquadrats). Perennials are species with a low reproductive effort and a long potential life span and colonists are species with a high reproductive effort and a short potential life span. ANOVA models were used to compare means. Differences that were significant ($p \leqslant 0.05$) are indicated by different letters ($n = 120$, YC = Young-Cut, YF = Young-Fire, MC = Mature-Cut, MF = Mature-Fire).

species richness, and age, black spruce BA, and cover of vascular plants decreased perennial species richness (Table 4). For colonist species richness, the top-ranking model (structure + ground) was 1.5 times (i.e. 0.56/0.37) better than the second one (age + structure + ground) (Table 3). Balsam fir BA and CWD volume increased colonist species richness, and vascular plant cover decreased colonist species richness (Table 4). The most important variables explaining species richness were CWD volume for moss species, balsam fir basal area for liverwort and colonist species, and cover of leaves for perennial species (Table 4). R^2 of the models with average estimates explaining richness of mosses, liverworts, perennial species, and colonist species were 53.1%, 28.8%, 47.6%, and 35.7%, respectively.

Table 3
Models selection results for moss, liverwort, perennial, and colonist species richness. Models are classified using Akaike's information criterion (AICc), including difference in AICc (ΔAICc), AICc weight (AICc$_w$), and the number of parameters included (K). Perennials are species with a low reproductive effort and a long potential life span and colonists are species with a high reproductive effort and a short potential life span.

	K	AICc	ΔAICc	AICc$_w$
Moss richness				
Structure + ground	10	625.00	0	0.69
Age + structure + ground	10	626.57	1.57	0.31
Liverwort richness				
Structure	6	567.90	0	0.43
Age + structure	6	569.14	0.24	0.38
Structure + ground	10	570.88	2.98	0.10
Age + structure + ground	10	571.31	3.42	0.08
Perennial species richness				
Structure + ground	10	604.40	0	0.65
Age + structure + ground	10	605.75	1.35	0.33
Colonist species richness				
Structure + ground	10	595.12	0	0.56
Age + structure + ground	10	595.98	0.86	0.37
Structure	10	586.46	4.90	0.05

4.3. Bryophyte species composition

Species composition varied significantly among age classes, disturbance type classes, and the interaction between age classes and disturbance type classes (Age: $F = 2.85$, $p = 0.008$; Type: $F = 3.38$, $p = 0.001$; Age × Type: $F = 3.50$, $p = 0.003$, $R^2 = 10.0$). We found significant differences between classes except for YC and MF ($R^2 = 9.0$, $p = 0.233$). The highest R^2 was found for comparisons between YF

Table 4
Average estimates (Estim.) unconditional standard errors (SE), and confidence intervals (CI) for each variable predicting richness of perennial species, colonist species, mosses, and liverworts included in the models for which the sum of AICc weights reached ⩾0.95. Model averaging was based on the entire set of models. The 95% confidence intervals of coefficients in bold excluded 0. Perennials are species with a low reproductive effort and a long potential life span and colonists are species with a high reproductive effort and a short potential life span.

	Estim.	SE	95% CI	Estim.	SE	95% CI	Estim.	SE	95% CI	Estim.	SE	95% CI
	Moss richness			Liverwort richness			Perennial species richness			Colonist species richness		
Age (years)	−1.06	0.30	**(−1.64, −0.48)**	0.03	0.18	(−0.33, 0.39)	−1.02	0.29	**(−1.59, −0.45)**	−0.03	0.20	(−0.54, 0.48)
Balsam fir basal area (m^2/ha)	0.62	0.29	**(0.05, 1.19)**	0.50	0.16	**(0.19, 0.82)**	0.46	0.27	(−0.07, 0.99)	0.65	0.21	**(0.24, 1.07)**
Black spruce basal area (m^2/ha)	−0.97	0.26	**(−1.47, −0.47)**	−0.09	0.17	(−0.43, 0.25)	−0.91	0.21	**(−1.37, −0.44)**	−0.21	0.22	(−0.65, 0.23)
Hardwood basal area (m^2/ha)	0.33	0.33	(−0.31, 0.96)	0.06	0.16	(−0.25, 0.38)	0.15	0.31	(−0.46, 0.76)	0.33	0.19	(−0.04, 0.71)
Cover of vascular plants (%)	−0.51	0.23	**(−0.96, −0.06)**	−0.58	0.17	**(−0.91, −0.25)**	−0.49	0.21	**(−0.90, −0.08)**	−0.56	0.19	**(−0.94, −0.19)**
CWD volume (m^3/ha)	0.78	0.20	**(0.38, 1.18)**	0.33	0.16	**(0.02, 0.64)**	0.51	0.18	**(0.15, 0.87)**	0.60	0.18	**(0.25, 0.95)**
Cover of needles (%)	0.21	0.24	(−0.26, 0.69)	0.04	0.19	(−0.33, 0.42)	0.28	0.22	(−0.15, 0.72)	−0.03	0.21	(−0.45, 0.39)
Cover of leaves (%)	0.69	0.26	**(0.19, 1.20)**	−0.20	0.21	(−0.61, 0.20)	0.56	0.24	**(0.10, 1.03)**	−0.08	0.23	(−0.53, 0.37)
Cover of pits (%)	0.09	0.21	(−0.31, 0.50)	0.01	0.16	(−0.30, 0.33)	0.06	0.19	(−0.31, 0.43)	0.04	0.18	(−0.31, 0.39)

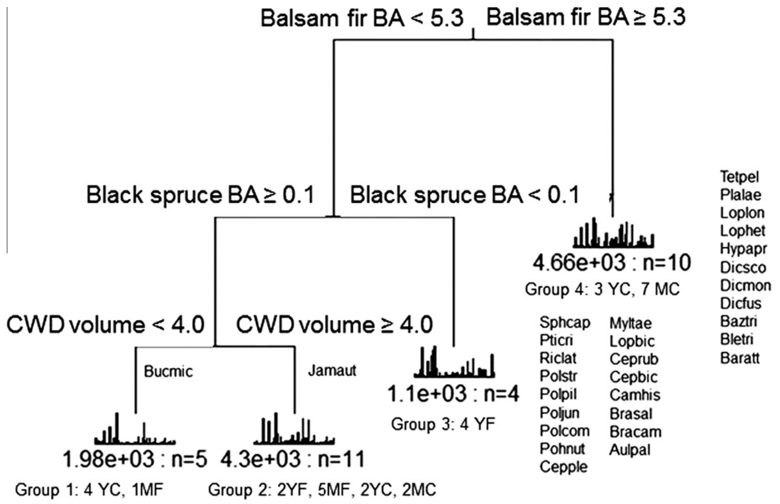

Fig. 3. Multivariate regression tree of all stands (fire and cut) based on bryophyte composition (species frequency) against habitat variables. Indicator species are written for terminal nodes (see Table S2 for species abbreviations). YC = Young-Cut, YF = Young-Fire, MC = Mature-Cut, MF = Mature-Fire, CWD volume = coarse woody volume, black spruce BA = black spruce basal area, balsam fir BA = balsam fir basal area.

and MC (R^2 = 35.3), followed in decreasing order of R^2, by YF and MF (R^2 = 28.1%), MF and MC (R^2 = 21.4%), YC and YF (R^2 = 20.6%), and YC and MC (R^2 = 14.1%).

We found 32 indicator species of age and disturbance type classes: 3, 16, 8 and 5 were indicator species of YC, MC, YF, and MF, respectively (see Table S2). All species indicators of YC were perennial. Seven out of the 16 species indicators of MC class were colonist liverworts. Many *Dicranum* species (*D. montanum*, *D. scoparium*, *D. majus*, *D. fuscescens*) were associated with MC. In fire origin stands, one liverwort colonist was indicator of YF (*Cephaloziella rubella*) and two liverwort colonists were indicators of MF (*Jamesoniella autumnalis* and *Anastrophyllum hellerianum*). Large perennial feathermosses species (*Ptilium crista-castrensis*, *Pleurozium schreberi* and *Hylocomium splendens*) were indicators of MF.

The best model of MRT explained 40% of the variation within the dataset. Plots were initially split based on their balsam fir BA with a critical value of 5.3 m^2/ha (Fig. 3, R^2 = 18.9%). Eleven species were associated with plots with a relatively high balsam fir BA, such as *Tetraphis pellucida*, *Plagiothecium laetum*, *D. scoparium* and *Blepharostoma trichophyllum* (group 4). Group 4 was composed of logged sites (3 from YC and 7 from MC). Plots with balsam fir BA <5.3 m^2/ha were then split depending on their black spruce BA (R^2 = 13.9%). Group 3 was composed of sites belonging to YF class with almost no trees, and 17 species were associated to this group (e.g., *Pohlia nutans*, *Polytrichum commune*, *Polytrichum juniperinum*, *Aulacomnium paslustre*). Sites where black spruces were present were split according to their volume of CWD (R^2 = 7.1%). Sites with low volume of CWD mostly from YC class had one indicator species: *Bucklandiella microcarpa* (Group 1). Group 2 was mostly composed of sites from MF class but also of some sites from the other classes; *J. autumnalis* was indicator of this group.

5. Discussion

Overall, our results indicate, as hypothesized, that species richness of colonist species was higher in young fire origin stands than in young clear-cut origin stands, and that perennial species and moss cover increase with time. However, our hypotheses of higher perennial species richness in young clear-cut origin stands and convergence in species composition in mature forests of clear-cut origin and fire origin after 50–90 years were not supported by the data. The abundance of balsam fir in the dominant canopy seemed to be a major driver to explain bryophyte community assembly, something that was not initially expected. In order to disentangle the effects of stand age and of environmental factors on bryophyte communities, we discuss the effect of environmental factors and type of disturbances separately for young and mature stands.

5.1. Short-term effects of disturbance type on bryophyte community assembly

As expected, our results show that bryophyte richness is higher in young fire origin stands than in clear-cut origin stands, suggesting that by killing the existing mosses and baring the mineral soil, fire tends to decrease the cover of perennial species (such as *Pleurozium scherberii*) and increase the presence of colonist species (such as *P. nutans*) compared with clear-cut. Indeed, few colonists were observed in young clear-cut origin stands compared with young fire origin stands, likely because the type of clear-cut used in this region does not disturb soils in a major way (Nguyen-Xuan et al., 2000; Lachance et al., 2013). The presence of exposed soil and the lower bryophyte layer depth in young fire origin stands are other signs that disturbance by fire has a stronger impact on organic layer than clearcutting.

In this study, we combined two subgroups of colonist species that shared similar life-history strategies but differed according to their ecology: colonist species *sensu stricto* which tend to be associated with ephemeral microhabitats such as CWD, and pioneer–colonist species that are well adapted to colonize harsh environments. The first subgroup of species (colonist species *sensu stricto*) were less abundant in young fire stands that the second subgroup of colonist species (pioneer–colonist species, see Table S1), indicating that some microhabitats that were present in pristine forests, such as large woody debris, disappeared after fire, or that source populations inside the stands were eliminated and that suitable microhabitats could not be recolonized due to dispersal limitations.

We expected higher perennial and moss richness in young clear-cut origin stands, but we found few differences in terms of perennial and moss species richness between young clear-cut origin stands and young fire origin stands. One possible explanation is the presence of fire-refugia in young-fire origin stands that preserved patches of perennial bryophytes that were present prior to disturbance. Hylander and Johnson (2010) suggested that boulders and vertical rocks can act as fire-refugia for bryophytes, thus accelerating recolonization by poor dispersers in burnt areas. In our study area, rocks were scarce and unlikely to serve as fire-refugia. However, other habitats such as humid microsites could play an important role in this respect. For example, Forsman (2008) found that creeks maintained substantial patches of unburned bryophyte habitat.

Perennial species such as *P. schreberi* and *H. splendens* are relatively large, considered as good competitors, and they were probably able to tolerate the increased exposure to light and lower moisture level associated with removal of the dominant canopy (their species cover were higher in YC than in YF, see Table S2). The potential effects of canopy removal on microclimatic conditions at the ground level might also have been buffered by the fact that an important part of the advance regeneration is left on site during forest operations (Harvey and Brais, 2002). Similarly, logging residues (Dynesius et al., 2008) and boulders and stumps (Schmalholz and Hylander, 2011) constituted shelters in clear-cut areas for bryophytes in Sweden.

5.2. Long-term effect of disturbance type on bryophyte community assembly

Our results indicate that 50–90 years after the stand-origin disturbance, bryophyte communities in clear-cut stands and fire origin stands have not converged which is contrary to what was initially expected. These differences can be explained by at least two factors: the presence of balsam fir in the dominant canopy of clear-cut stands, and structural characteristics such as the degree of canopy openness and the presence of CWD.

In eastern Canadian boreal forests, it is well known that balsam fir tends to be more abundant after clearcutting than after fire (Bouchard and Pothier, 2011; Fourrier et al., 2013). In our study, the presence of balsam fir has a strong influence on the overall bryophyte community composition (see Fig. 3) and on species richness (see Table 4), many bryophyte species being significantly associated with a dominant balsam fir canopy. The effect of the presence of a dominant balsam fir canopy on understory communities has already been observed in eastern boreal forests (De Grandpré et al., 2000), but the causal pathway that could explain this effect remains unclear. It has been hypothesized that balsam fir is more abundant in nutrient-rich or relatively humid sites, and that bryophyte richness could be influenced by these site factors (La Roi and Stringer, 1976). However, because site quality can be considered to be relatively equivalent in post-fire and post-clearcutting stands in this study (all sites were localized on tills with mesic drainages), this effect is unlikely in our study. Differences in nutrient inputs from throughfall, differences in the capacity to produce shade between balsam fir and black spruce (balsam fir produces more shade than black spruce, Messier et al., 1998), or differences in terms of litter characteristics in stands dominated by different coniferous tree species (Barbier et al., 2008) could also influence understory communities, but the impact of such factors on bryophyte growth or community composition has not been tested directly thus far to our knowledge.

The importance of balsam fir as a driver of bryophyte communities could also be explained by an indirect effect through stand structural characteristics. Clear-cut origin stands have a more diversified structure, including an increased abundance and diversity of CWDs compared to post-fire stands mainly due to natural mortality caused by the last spruce budworm outbreak (Fourrier et al., 2013). Similarly, Schmalholz et al. (2011) explained the higher species richness of epixylic species found in New Brunswick stands disturbed by spruce budworm outbreaks by a greater availability and quality (decay stage variation and proper microclimatic conditions) of CWDs. CWDs are a good substrate for the establishment and growth of colonists because they provide humid conditions that tend to persist during dry periods (Muhle and LeBlanc, 1975). Moreover, because parts of large CWDs tend to be suspended above ground level, the individuals that can establish on them are relatively protected from competition by perennial fast-growing feathermosses or dominant *Sphagnum* that are often present on the forest floor (Frego, 1996; Rydin et al., 1997; Arseneault et al., 2012). Many colonist species that depend on ephemeral substrates such as CWD to establish were thus favored in mature clear-cut stands such as *Lophozia longidens*, *Lepidozia reptans*, *T. pellucida*, and *B. trichophyllum* (see indicator species analyses, Table S2).

In fire origin mature stands, tolerant perennial species such as the feathermosses *P. schreberi*, *H. splendens* and *P. crista-castrensis* are abundant (they are also indicator species of this class). Dominance by these species also probably impede colonization by other moss species. Feathermosses dominate because they reach maximal photosynthetic capacity at low light levels (Williams and Flanagan, 1998), they are capable of tolerating desiccation and of reactivating their photosynthetic apparatus in a relatively short period (Silvola, 1991; Williams and Flanagan, 1998), and they have relatively high growth rates compared with other species (Longton and Greene, 1969). The relatively dense dominant canopy in mature fire origin stands probably acts as a bottleneck for understory communities (Økland et al., 2003), generating limited opportunities for colonization by new species, and leading to the gradual elimination of colonists that were present in young fire origin stands, but are poorly adapted to survive in deep shade conditions.

6. Conclusion

In this study, the main surprise came from the fact that bryophyte community assembly in mature forest is largely driven by dominant tree composition, and, in particular, that an increase in balsam fir content has a positive effect for many species. This finding suggests that the maintenance of some late-successional moss species in managed landscapes could be facilitated, since balsam fir is well known to be abundant in post-clear-cut stands. Still, two caveat should be noted. First, even if colonists and liverworts were relatively abundant in some clear-cut origin stands in this study, they can be even more abundant in old-growth eastern Canadian boreal stands (e.g. >100 years) (Paquette et al., submitted for publication). Hence, clear-cut origin stands are no perfect substitute for true old growth stands. Second, mature balsam fir stands in the region were probably in an ideal situation to be colonized relatively quickly by late-successional mosses, as they possessed heterogeneous canopy structures as a result of the last spruce budworm outbreak, and were largely imbedded in a mosaic where virgin forests were abundant (Bouchard and Pothier, 2011). This last factor is potentially important, because some species could be limited by the presence of source populations nearby (Lõhmus and Lõhmus, 2008; Kimmerer, 2005; Fenton and Bergeron, 2006; but see Hylander, 2009). It will be important in future studies to examine how the rate of accumulation of these sensitive species is modulated by stand and landscape characteristics. In the meantime, conservation strategies could focalize on the retention of a variety of stand types at the landscape scale, including stands of natural origin (fire or old-growth) which may harbor sensitive species and be used as sources of propagules for harvested stands.

Our results are also in agreement with studies conducted elsewhere in the boreal zone, which generally state that CWD is an important habitat for some forest-dwelling bryophytes. Promoting silvicultural approaches that maintain such attributes in managed forests will thus likely contribute to maintain some sensitive colonist species. However, in this study, the CWD that were left after wildfire were relatively poor habitats, perhaps due to unsuitable bark and wood characteristics, or because they were in exposed conditions unfavorable for colonization by drought-sensitive bryophytes. Similarly, the presence of balsam fir in the dominant canopy, as well as the above mentioned landscape factors, are also likely to be determinant for an effective colonization of available CWDs. Taken together, these elements confirm that leaving CWD after silvicultural interventions is important, but their characteristics and the context where they are left are also critical.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.09.031.

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