

Changes in bryophytes assemblages along a chronosequence in eastern boreal forest of Quebec

C. Boudreault, M. Paquette, N.J. Fenton, D. Pothier, and Y. Bergeron

Abstract: Old-growth forests are often considered as biodiversity hotspots for bryophytes because of their diversity in environmental niches or microhabitats and forest continuity. Following this hypothesis, old-growth forests would be expected to house species and functional traits associated with species dispersal different from mature forests. In this study, we compared bryophytes in old-growth and younger forests in terms of species composition, functional trait values, and microhabitat associations. We studied bryophytes in 22 sites distributed across three age classes (18 to >200 years) in boreal forests (eastern Quebec). Richness of liverworts, vegetative-reproducing species, and species with infrequent sexual reproduction were higher in the oldest age class. Species richness was best explained by the availability of coarse woody material (CWM) and other microhabitats, and community structure was best explained by balsam fir basal area. Microhabitats most often associated with indicator species were organic matter, CWM, and pits. Our results indicate that communities associated with older forests are potentially sensitive to forest management as they differ in composition and functional traits from other age classes, with many species characterized by reduced dispersal capabilities and tolerance to competition. An approach that combines critical source habitat protection for dispersal-limited species with protection of critical microhabitats in neighboring managed stands are necessary to allow successful recolonization and maintain bryophyte diversity in managed landscapes.

Key words: bryophytes, old-growth forests, boreal forests, species traits, chronosequence, coarse woody debris.

Résumé : Les vieilles forêts sont souvent considérées comme des centres de biodiversité pour les bryophytes en raison de leur grande diversité de niches environnementales, de microhabitats et de leur continuité forestière. Selon cette hypothèse, les vieilles forêts renfermeraient des espèces et traits associés à la dispersion différents des forêts plus jeunes. Dans cette étude, nous avons comparé les bryophytes de vieilles forêts et de forêts plus jeunes en fonction de la composition en espèces, des traits fonctionnels et des associations avec les microhabitats. Nous avons étudié les bryophytes dans 22 sites répartis en trois classes d'âge (18 à >200 ans) en forêt boréale de l'est du Québec. La richesse des hépatiques, des espèces se reproduisant de façon végétative et des espèces dont la reproduction sexuée est infrequente étaient supérieures dans la classe d'âge la plus vieille. Les variables les plus influentes pour expliquer la richesse en espèces étaient les matériaux ligneux grossiers (MLG) et les autres microhabitats, et la variable la plus influente pour expliquer la composition en espèces était la surface terrière du sapin baumier. Les microhabitats les plus souvent associés aux espèces indicatrices étaient la matière organique, les MLG et les dépressions. Nos résultats indiquent que les communautés associées aux vieilles forêts sont potentiellement sensibles à l'aménagement forestier puisqu'elles renferment plusieurs espèces caractérisées par une faible capacité de dispersion et une tolérance moindre à la compétition. Une approche combinant la protection d'habitats essentiels pour les espèces avec une faible capacité de dispersion avec la protection de microhabitats essentiels dans les peuplements avoisinants aménagés est nécessaire pour assurer le succès de recolonisation des espèces avec une faible capacité de dispersion et maintenir la diversité des bryophytes dans les paysages aménagés.

Mots-clés : bryophytes, vieilles forêts, forêts boréales, traits fonctionnels, chronoséquence, débris ligneux grossiers.

Introduction

Old-growth forests are generally considered as biodiversity hotspots because they typically contain a great diversity of environmental niches or microhabitats, which generate colonization opportunities for large numbers of plant species, including bryophytes (Söderström 1988; Vitt et al. 1995; Rambo 2001; Mills and Macdonald 2005; Browning et al. 2010; Turner et al. 2011). Old-growth forests are also thought to be habitats with high levels of forest continuity, here defined as the uninterrupted presence of

forest cover for periods of several decades or centuries at a given location, which favours the establishment of dispersal-limited species (Nordén and Appelqvist 2001). Forest continuity has been mentioned as an important factor determining the presence of many taxonomic groups in natural ecosystems, including some groups of bryophytes (e.g., liverworts; Gustafsson et al. 1992; Nilsson et al. 1995; Frego 2007).

Species with different values for functional traits associated with dispersal (e.g., reproductive strategy and frequency) are also expected to respond differently to forest continuity (Laaka-Lindberg

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2000; Nordén and Appelqvist 2001; Barbé et al. 2016). For example, species that primarily use asexual reproduction, particularly those that disperse through fragments, would be disadvantaged for long-distance dispersal (Söderström and Jonsson 1989; Rydgren et al. 1998; Kimmerer 2005; Söderström and During 2005) compared with species reproducing sexually with spores. Indeed, a large proportion of asexual fragments are thought to disperse at relatively short distances from the parent colony. Similarly, species that reproduce infrequently, either sexually or asexually, are more likely to be dispersal-limited (Laaka-Lindberg 2000). Hence, those species that reproduce primarily asexually or infrequently are more likely to be dependent on long forest continuity compared with species with frequent sexual reproduction that are believed to be better long-distance dispersers (Nordén and Appelqvist 2001; Barbé et al. 2016).

In boreal forests, large forest floor feathermoss species (*Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis*) generally form a continuous mat under mature conifer stands (Taylor et al. 1988; Hart and Chen 2008) and tend to outcompete other bryophyte species (Benscoter and Vitt 2008). However, forest gap dynamics that are generally observed in old-growth stands tend to favor the presence of microhabitats (e.g., deadwood, large tree bases, and boles) that could facilitate colonization by small-sized, less competitive bryophyte species. These species, also called small-pocket species (sensu R.H. Økland et al. 2003), benefit from the presence of small spatially and temporally distinct habitat. Among the microhabitats that become increasingly available in old-growth forests, coarse woody material (CWM) is generally recognized as particularly important for many bryophyte species, particularly for liverworts (Söderström 1988; Andersson and Hytteborn 1991; Rambo and Muir 1998; Pharo and Lindenmayer 2009).

In the central and eastern sections of the Canadian boreal forest, a significant portion of the pre-industrial landscape (between 40% and 70%; Cyr et al. 2009) was occupied by old stands (>100 years) of irregular structure. This high proportion of old stands was generated by long natural fire return intervals and has declined significantly in contemporary eastern Canadian boreal landscapes (Cyr et al. 2009; Bouchard and Pothier 2011), mostly because natural fires continue to occur concomitantly with clear-cut logging (Bergeron et al. 2017). In northeastern Quebec (Canada), the fire return interval is relatively long (>500 years) compared with other areas of the North American boreal forest (Cyr et al. 2007; Bouchard et al. 2008), and forests are dominated by a mixture of *Picea mariana* (Mill.) BSP (black spruce) and *Abies balsamea* (L.) Mill. (balsam fir). In contrast, the landscape structure favoured by forest management in the boreal forest of Quebec tends to limit stand age at 100 years because stands are commercially mature and can be harvested when they reach 75–100 years (i.e., the rotation age). Therefore, the biodiversity in managed landscapes is potentially lower than in natural landscapes because of the absence of old-growth stands.

The general objective of this study was to determine how old-growth forest bryophyte communities differ from those in younger forests and what drives this difference to design appropriate silvicultural and conservation approaches for bryophyte communities in managed forests. To do this, we compared bryophyte communities in forests of different age classes (regenerating (18–56 years old), commercially mature (68–113 years old), and old-growth (198–209 years old) forests) in terms of bryophyte richness, cover, overall taxonomic composition, and functional trait values associated with dispersal (mode of reproduction, frequency of reproduction, and shoot size).

Material and methods

Study area

The study area is located at the interface between two bioclimatic domains, the balsam fir – white birch to the south and the

black spruce – feathermoss to the north (Morneau and Landry 2007) (49°N–50°N, 68°W–70°W). Surficial deposits are mostly represented by glacial tills of various thicknesses and by fluvio-glacial deposits (Bouchard et al. 2008). Mean annual temperature was 1.5 °C during the 1971–2000 period in the southern part of the study area (Baie-Comeau weather station; Environment Canada 2009), and temperature was colder in the northern part of the study area, approaching 0 °C on average. Average annual rainfall and snowfall were 684 mm and 362 cm, respectively (Environment Canada 2009). Large forest fires are an important natural disturbance in this region, with fire return intervals that vary between 250 and 500 years (Cyr et al. 2007; Bouchard et al. 2008). The forests are dominated by *Picea mariana* (black spruce) and *Abies balsamea* (balsam fir), with a secondary occurrence of hardwoods such as *Betula papyrifera* Marsh. (white birch) and *Populus tremuloides* Michx. (trembling aspen), particularly in early successional forests (Bouchard et al. 2008).

Sampling

A chronosequence was established in 2006 based on the work of Bouchard et al. (2008). This chronosequence was composed of 22 fire-origin stands that covered a 200-year period based on a fire map. There were seven stands in the youngest age class (range 18–56 years after fire), nine stands in the intermediate age class (range 68–113 years), and six stands in the oldest age class (range 198–209 years). During summers 2009 and 2010, within each mapped fire, one 400 m² circular plot was randomly established that met the following criteria: minimum distance of 100 m from the nearest road access or nearest harvested area and presence of relatively thick tills (>50 cm), with well or moderately well drained soils.

Within each 400 m² circular plot (radius of 11.28 m), we measured the diameter at breast height (DBH) of all trees (DBH ≥ 9.1 cm). We also measured length and diameter at the base and the upper end of all coarse woody material (CWM) longer than 1 m and with at least one extremity with a diameter ≥ 9.1 cm. A decay class was assigned to each piece of woody material (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 CWM volume (Fraver et al. 2007). At four locations within the plot (4 m from the centre in each cardinal direction and 50 cm from any rock or stump), we measured the organic matter depth.

For each 400 m² plot, we sampled bryophytes inside five 1 m² microquadrats located at 4 m intervals along transects (the first microquadrat being located 2 m from the centre) in each cardinal direction (20 microquadrats in total). Eight microquadrats were thus located immediately outside the circular plot. Some of those microquadrats were slightly re-positioned when they were located directly on large trees. Each group of five microquadrats located on transect sections pointing to different cardinal directions from the centre were considered as subplots in some statistical analyses. Thus, there were five microquadrats per subplot and four subplots per plot, for a total of 88 subplots in the study.

Within each microquadrat, we evaluated the cover of each bryophyte species (an arbitrary cover value of 0.5% was attributed to those with cover < 1%) on the ground, on coarse woody material, on tree bases (up to 30 cm), and on snag bases (up to 1 m). We also estimated the cover of needles, leaves, lichens, vascular plants, rock, stumps, shrubs, pits, and mounds. We also counted the number of microhabitats suitable for bryophyte establishment: large-sized CWM (diameter > 9 cm), medium or small-sized CWM (<9 cm), mineral soil, rock, organic matter, *Sphagnum* spp., living branches on the ground or tree bases, tree trunks, stumps, pits or water windows. Nomenclature for mosses follows Faubert (2013, 2014) except for *Sphagnum subtile* (Flora of North America Editorial Committee 2007), and nomenclature for liverworts follows Faubert (2012).

Species traits

Bryophytes were first divided in two taxonomic groups: liverworts and mosses (including *Sphagnum*). These two groups were separated because liverworts are known to be more sensitive to desiccation and environmental modifications due to a range of physiological traits, including drought tolerance (Söderström and Jonsson 1989; Fenton and Frego 2005). Bryophytes were also divided according to life-history traits that are susceptible to influence their dispersal capacities: (1) main mode of reproduction (sexual, vegetative, or sexual and vegetative) and (2) frequency of reproduction of both (i) sexual reproduction (frequent [frequent and abundant] or infrequent [rare and occasional]), and (ii) vegetative reproduction (frequent [frequent and abundant] or infrequent [rare and occasional]). (3) Bryophytes were also divided according to size of shoots (small-sized (<40 mm), medium-sized (40–79 mm), and large-sized (≥80 mm) species). Size classes have a biological influence as they indicate the type of role that species can play in the community. Large species tend to dominate the forest floor and be high competitors; medium-sized species are good competitors on specialized substrates; and small species are the “pocket species” (physically small species colonizing small pockets of specialized habitat; R.H. Økland et al. 2003) and are restricted to substrates free from these larger species. Each trait was evaluated individually; consequently, a species could, for example, be “sexual”, with “frequent” sexual reproduction and “infrequent” asexual reproduction. Species with no documented specialized asexual propagules were classified as “none” for the frequency of asexual reproduction and were not analyzed for that trait. The information on bryophyte species traits was found in regional floras (e.g., Ireland 1982; Ley and Crowe 1999; Paton 1999; BFNA 2004; Faubert 2012, 2013, 2014), in BRYOATT (Hill et al. 2007), and based on personal experience (laboratory of N.J. Fenton).

Statistical analyses

Bryophyte communities were compared among age classes in terms of richness, cover, and overall taxonomic composition. First, differences in bryophyte richness among age classes were evaluated using mixed models. Total richness per subplot of liverworts, mosses, small-, medium-, and large-sized species, vegetative species, sexual species, vegetative or sexual species, and species with frequent and infrequent vegetative or sexual reproduction were evaluated. Richness data were analyzed with the GLIMMIX procedure of SAS (SAS Institute 2002) and denominator degrees of freedom were calculated using the method of Kenward–Roger. Second, cover data of species were $\log(x)$ -transformed and analyzed with the MIXED procedure of SAS, and denominator degrees of freedom were calculated using Satterthwaite’s approximation. Response variables were the mean cover per subplot (average of the five microquadrats) of the liverworts, mosses, small-, medium-, and large-sized species, vegetative species, sexual species, vegetative or sexual species, and species with frequent and infrequent vegetative or sexual reproduction. In all models, age class was a fixed factor, and subplot nested within plot, nested within age class, were random factors. Significant differences ($p \leq 0.05$) between classes of models were detected with least squares means (LSmeans) Tukey’s honestly significant difference (HSD) tests. Third, overall species composition was compared among age classes with permutational MANOVA (McArdle and Anderson 2001) with the function *adonis* of the *vegan* package (Oksanen et al. 2008) in R (version 2.15.3; R Core Team 2013). We performed the analysis on species frequency data at the plot level ($n = 22$), with all species included in the analyses, and with the Bray–Curtis distance measure.

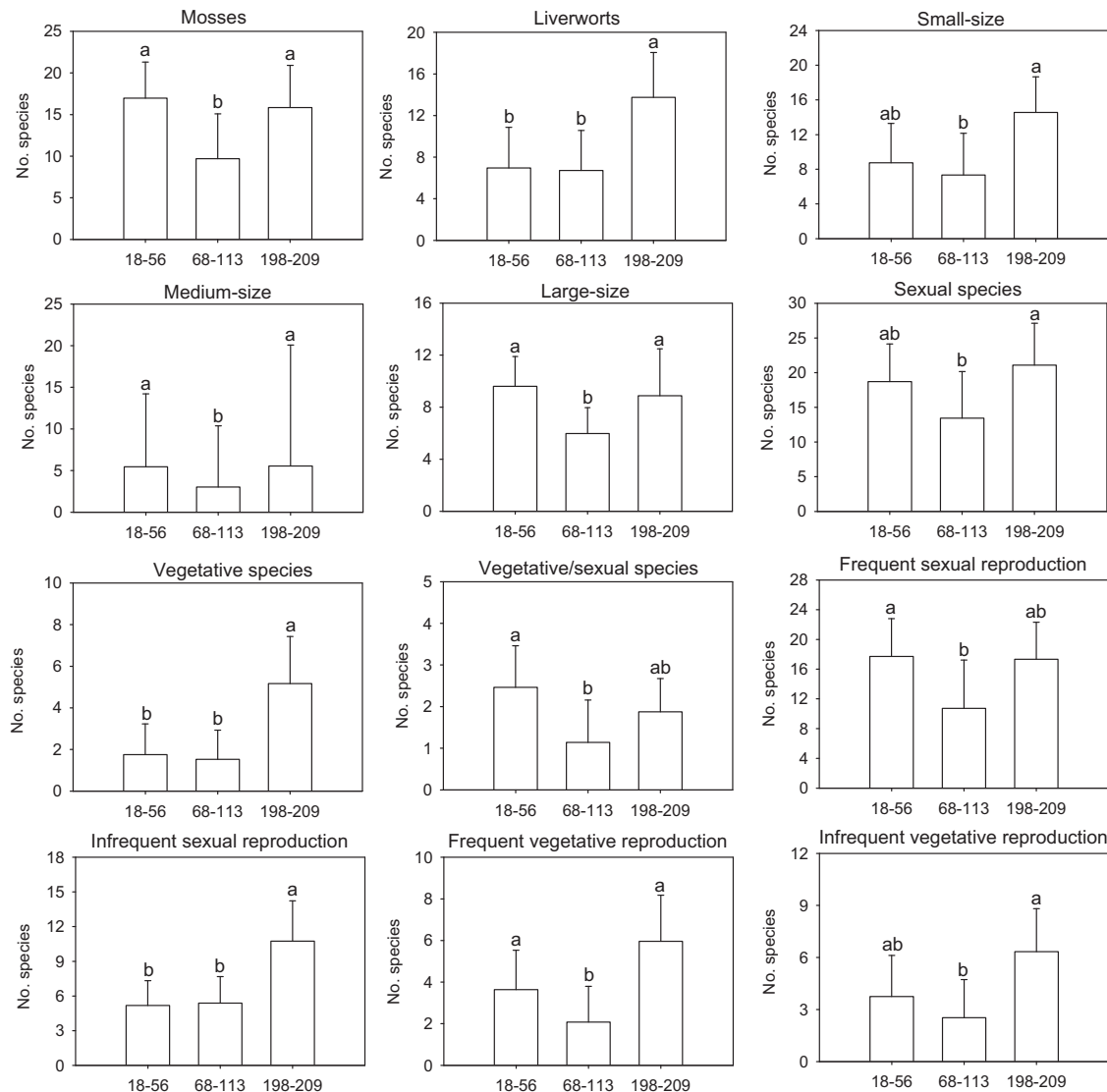
The association of the bryophyte community to microhabitats was addressed at the richness, species, and composition levels. First, models were developed to assess the relative importance of different habitat variables in explaining species richness. Species richness (same response variables as for mixed models) was mod-

elled with linear mixed-effects models (lme), which allowed for nested random effects. Analyses were performed with the *lme* function in R (version 2.15.3; R Core Team 2013), and Akaike’s information criterion corrected for small sample size (AICc). Fifteen models were tested in the model selection analyses for species richness (Appendix Table A1). Environmental variables were divided in three groups that could influence bryophyte communities: age, ground variables, and canopy variables. Ground variables describe colonization substrates and were represented by CWM-45 volume (CWM-4 + CWM-5), cover of litter (needles + leaves), cover of pits, and number of microhabitats. Canopy structure variables influence bryophytes mainly through their effect on factors such as light and microclimate and were represented by black spruce basal area (BA), balsam fir BA, hardwood BA, and vascular plant cover. Age² was added in four models because preliminary analyses showed that richness of mosses, medium-sized species, and species with frequent vegetative reproduction varied in a nonlinear way according to age (see Fig. 1). 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 (version 2.15.3; R Core Team 2013). Multicollinearity between the environmental variables was assessed using variance inflation factors (VIF). Balsam fir BA was excluded from models that already contained age (VIF > 5 indicating collinear variables). All variables were standardized before the analyses to facilitate assessment of their relative contribution in the models (Gelman 2008). For each variable, the R² of the best models was calculated with the function *r.squaredGLMM* of the *MuMIn* Package in R (version 3.3.2; R Core Team 2016).

We identified indicator species for each age class with the *multipatt* function of the *indicspecies* package (De Caceres and Legendre 2009) in R (version 3.3.2; R Core Team 2016). 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). Only species present in more than nine subplots (>10% frequency) were analyzed. Then, we tested if indicator species were significantly more frequent when microhabitats (rock, organic matter, *Sphagnum*, stumps, pits, CWM, and branches or tree bases) were present within the 1 m² microquadrat using logistic regressions (LOGISTIC procedure; SAS Institute 2002). Mineral soil was not considered in the analysis as this microhabitat is rarely encountered in our study (see Appendix Table A2). Analyses were conducted within each age class at the microquadrat scale and with subplot nested within plot as a random factor.

Finally, the influence of microhabitats and habitats on community composition was analyzed with a multivariate regression tree (MRT; De’ath 2002). 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 in which the data are recursively partitioned to minimize the dissimilarity within the resulting groups using different levels of the explanatory variables. The size of the tree was assessed by its predictive error, which is estimated from the cross-validated relative error (CVRE). The analyses were conducted with the function *mypart* of the *vegan* package in R (version 2.15.3; Oksanen et al. 2008). The following explanatory variables were considered: cover of vascular plants, cover of shrubs, cover of lichens, cover of pits, cover of mounds, cover of litter (needles + leaves), black spruce BA, balsam fir BA, hardwood BA, organic layer depth, and CWM-45 volume. The analysis was performed on species frequency data at the plot level ($n = 22$ plots) and all species were included; because stand age was correlated with balsam fir BA, stand age was not considered in the models. We identified indicator species for each node of the MRT with the *labdsv* function of the *vegan* package (Oksanen et al.

Fig. 1. Richness of mosses, liverworts, small-, medium-, and large-sized species, sexual species, vegetative species, vegetative and sexual species, species with frequent sexual reproduction, species with infrequent sexual reproduction, species with frequent vegetative reproduction, and species with infrequent vegetative reproduction. Mixed models were used to compare means. Differences that were significant ($p \leq 0.05$) according to LSmeans Tukey's HSD tests are indicated by different letters ($n = 88$).



2008) in R (version 2.15.3; R Core Team 2013). To be considered as an indicator species, a species should be present in more than 10% of the subplots (nine subplots).

Results

Bryophyte community differences among age classes

In this study, 102 taxa of bryophytes were recorded (Appendix Table A3): 36 liverworts, 55 mosses, and 11 *Sphagnum*. The most abundant species were *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Hylocomium splendens*, *Sphagnum capillifolium*, *S. girgensohnii*, and *S. fallax*.

Richness of liverworts, vegetative species, and species with infrequent sexual reproduction were significantly higher in the old-growth age class (198–209 years old) than in the regenerating forest (18–56 years old) and commercially mature (68–113 years old) age classes (Fig. 1; Table 1). Richness of mosses, medium- and large-sized species, and species with frequent vegetative reproduction were significantly lower in the intermediate age class than in the youngest and the oldest age classes, with the last two being statistically similar (Fig. 1; Table 1). Richness of small-sized

species, sexual species, and species with infrequent vegetative reproduction was higher in the old-growth age class but differed significantly only from the commercially mature age class. Richness of vegetative and sexual species and species with frequent sexual reproduction was higher in the regenerating forest (18–56 years old) age class but differed significantly only from the commercially mature (68–113 years old) age class.

Significantly higher cover of liverworts, small-sized species, vegetative species, and species with infrequent vegetative reproduction was found in the old-growth age class (Fig. 2; Table 1), and significantly lower cover of mosses, large-sized species, sexual species, and species with infrequent sexual reproduction was found in the regenerating forest (18–56 years old) age class (Fig. 2). Cover of species with frequent sexual reproduction and frequent vegetative reproduction was lower in the intermediate age class (68–113 years).

Species composition varied significantly among age classes ($F = 5.54$, $p = 0.001$, $R^2 = 36.8$). Significant differences were found between classes (18–56 years vs. 68–113 years: $F = 5.79$, $p = 0.001$,

Table 1. Mixed model summaries for the effects of age on species richness and species cover.

	dfn, dfd	F	P
Species richness			
Taxonomical group			
Moss	2,17.6	6.52	0.008
Liverwort	2,15.3	5.24	0.019
Size of shoot			
Small	2,15.6	3.83	0.044
Medium	2,16.0	5.48	0.015
Large	2,18.5	6.45	0.008
Main mode of reproduction			
Sexual	2,17.6	3.91	0.039
Vegetative	2,11.5	10.4	0.003
Vegetative and sexual	2,14.9	6.67	0.009
Frequency of reproduction			
Frequent sexual reproduction	2,16.8	4.55	0.026
Infrequent sexual reproduction	2,16.1	12.96	<0.001
Frequent vegetative reproduction	2,13.0	9.69	0.003
Infrequent vegetative reproduction	2,12.1	4.45	0.036
Species cover			
Taxonomical group			
Moss	2,19	9.00	0.002
Liverwort	2,19	7.36	0.004
Size of shoots			
Small	2,18.9	6.11	0.009
Medium	2,18.6	4.33	0.029
Large	2,19	9.06	0.002
Main mode of reproduction			
Sexual	2,19	11.18	<0.001
Vegetative	2,19	10.66	<0.001
Vegetative and sexual	2,19	11.14	<0.001
Frequency of reproduction			
Frequent sexual reproduction	2,19	7.06	0.005
Infrequent sexual reproduction	2,19	11.77	<0.001
Frequent vegetative reproduction	2,19	12.50	<0.001
Infrequent vegetative reproduction	2,19	10.74	<0.001

Note: Significant *p* values ($p \leq 0.05$) are given in bold type. dfn, degrees of freedom numerator; dfd, degrees of freedom denominator.

$R^2 = 29.6$; 18–56 years vs. 198–209 years: $F = 5.38$, $p = 0.002$, $R^2 = 32.9$; 68–113 years vs. 198–209 years: $F = 5.37$, $p = 0.007$, $R^2 = 29.2$).

Bryophyte community and microhabitats

Richness of liverworts ($R^2 = 72.2\%$), small-sized species ($R^2 = 74.0\%$), vegetative species ($R^2 = 62.1\%$), species with infrequent sexual reproduction ($R^2 = 71.9\%$), and species with infrequent vegetative reproduction ($R^2 = 60.3\%$) were best explained by the “age + ground” model (Table 2). Moss richness ($R^2 = 75.7\%$), medium-sized species richness ($R^2 = 67.0\%$), sexual species richness ($R^2 = 73.7\%$), and richness of species with frequent sexual reproduction ($R^2 = 76.0\%$) were best explained by the “canopy + ground” model (Table 2 and Appendix Table A1). The top-ranking models explaining large-sized species richness ($R^2 = 35.5\%$), richness of species with frequent vegetative reproduction ($R^2 = 68.3\%$), and vegetative and sexual species richness ($R^2 = 54.8\%$) were “habitats”, “age + ground”, and “age + canopy + ground”, respectively (Table 2).

The most influential variable for species richness was the number of microhabitats (Table 3). Among canopy variables, balsam fir BA was the most influential variable for richness of liverworts, vegetative species, small-sized species, species with infrequent sexual reproduction, species with frequent vegetative reproduction, and species with infrequent vegetative reproduction. Black spruce BA had a negative influence on richness of large-sized species, vegetative and sexual species, and species with frequent sexual reproduction. Vascular plant cover favoured richness of medium-sized species and species with infrequent vegetative reproduction. Among ground variables, CWM-45 was the most

influential variable after the number of habitats. CWM-45 influenced positively liverworts, sexual species, small-sized species, and species with frequent vegetative reproduction. The cover of pits increased richness of small-sized species, species with frequent vegetative reproduction, and species with infrequent vegetative reproduction. Stand age had a positive influence on richness of liverworts, vegetative species, small-sized species, species with infrequent sexual reproduction, and species with infrequent vegetative reproduction.

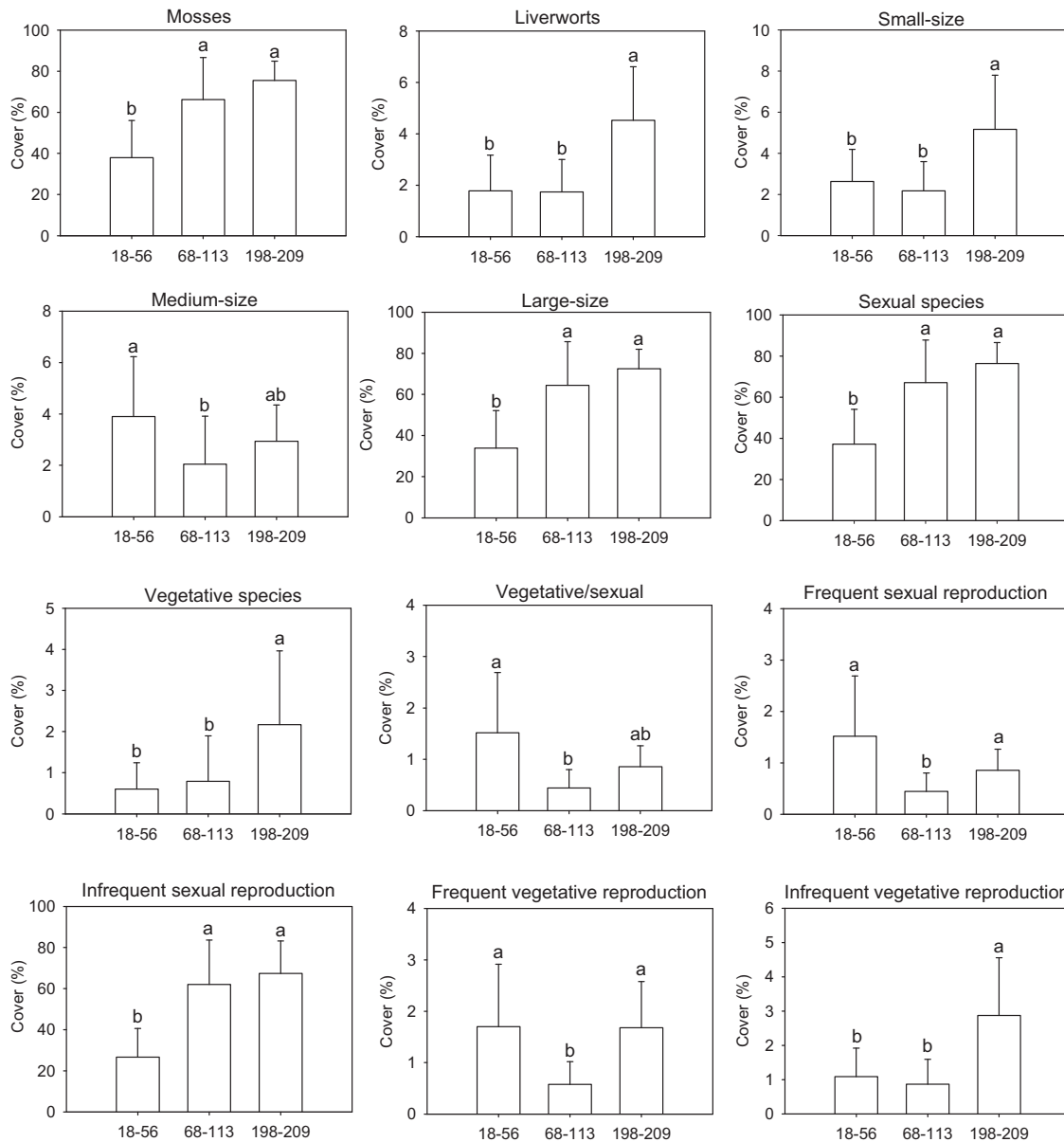
Five species had an importance value that was significantly higher (indicator species) in forests of the regenerating forest (18–56 years old) age class (one liverwort and four mosses; Table 4). None of these species was influenced by CWM or stumps. One species was positively influenced by pits (*Sphagnum capillifolium*) and one by branches or tree bases (*Cephalozia pleniceps*). *Polytrichum commune* was positively influenced by organic matter (OM), *Aulacomnium palustre* by OM and *Sphagnum* spp., and *P. juniperinum* by rock and OM (Table 4). No indicators of the commercially mature (68–113 years old) age class were found. In contrast, eight species were indicators of the oldest age class (two mosses and six liverworts). Those species were positively associated with CWM (*Anastrophyllum minutum*, *Nowellia curvifolia*), with OM (*Calypogeia neesiana*), branches or tree bases (*Barbilophozia barbata*), with stumps (*Geocalyx graveolens* and *Plagiothecium cavifolium*), or with pits (*P. cavifolium*) (Table 4). *Sphagnum girgensohnii* was associated with older sites without being associated with any microhabitat variables (Table 4). Five species were indicators of both the younger (18–56 years) and older (198–209 years) age classes. Among those species, *Herzogiella turfacea* was positively influenced by CWM, *Brachythecium reflexum* by *Sphagnum* spp. and OM, and *Pohlia nutans* was ubiquitous. Two liverworts (*Anastrophyllum hellerianum* and *Blepharostoma trichophyllum*) and one moss (*Hylocomium splendens*) were indicators of the 68–113 year and 198–209 year age classes. *Anastrophyllum hellerianum* was favoured by pits, OM, and CWM, *H. splendens* by CWM, and *B. trichophyllum* was ubiquitous.

The best model of MRT explained 50% of the overall dataset variation (Fig. 3). Plots were initially split based on their balsam fir BA, with a critical value of $1.60 \text{ m}^2 \cdot \text{ha}^{-1}$ (Fig. 2, $r^2 = 22.8\%$). Ten species were associated with plots with balsam fir (group 4), including *Lepidozia reptans*, *G. graveolens*, *H. splendens*, and *P. cavifolium*. Group 4 was composed of six sites from the old-growth age class (198–209 years old) and two sites from the commercially mature (68–113 years old) age class. Plots without balsam fir or with very low balsam fir BA were then split depending on their black spruce BA (critical value = $0.182 \text{ m}^2 \cdot \text{ha}^{-1}$, $r^2 = 17.9\%$). Group 3 (black spruce BA < $0.182 \text{ m}^2 \cdot \text{ha}^{-1}$) was composed of sites from the younger age class (four sites 18–56 years old) and four species were associated with this group (*B. reflexum*, *P. nutans*, *P. commune*, and *P. juniperinum*). Sites where black spruce BA was $\geq 0.182 \text{ m}^2 \cdot \text{ha}^{-1}$ were split based on litter cover ($r^2 = 9.3\%$). Sites with high black spruce BA and low cover of litter belonged mostly to the intermediate age class (group 1), and *Dicranum polysetum* was an indicator of this group. Group 2 with higher cover of litter was composed of sites from the younger age class, and *Ptilidium pulcherrimum* was an indicator of this group.

Discussion

Bryophyte communities in old-growth forests differed significantly from the younger forest age classes, with more liverworts, small-sized species, vegetative species, and species with infrequent sexual reproduction. The presence of at least three processes may explain the higher richness and different communities found in old-growth forests. First, in natural boreal forests of eastern Quebec, changes in canopy structure increase with mortality of the initial postfire cohort of trees approximately 100–150 years after fire (Bouchard et al. 2008). These canopy gaps are generally associated with the development of irregular, multi-aged canopy

Fig. 2. Cover (%) of mosses, liverworts, small-, medium-, and large-sized species, sexual species, vegetative species, vegetative and sexual species, species with frequent sexual reproduction, species with infrequent sexual reproduction, species with frequent vegetative reproduction, and species with infrequent vegetative reproduction. Mixed models were used to compare means. Differences that were significant ($p \leq 0.05$) according to LSmeans Tukey's HSD tests are indicated by different letters ($n = 88$).



structures, often with a progressive increase in the abundance of late-successional tree species such as balsam fir (see [Appendix Table A2](#)). This process increases spatial heterogeneity in the availability of resources such as light, nutrients, and water. The abundance of balsam fir in the dominant canopy seemed to be a major driver explaining bryophyte species composition and species richness of many groups of species, which is coherent with results found in [Paquette et al. \(2016\)](#).

Second, older forests contain CWM adequate for the colonization and persistence of specialized bryophyte species, notably liverworts and small-sized species ([Jonsson and Esseen 1990](#); [Frivoll and Prestø 1997](#)). Indeed, CWM provides the moisture conditions necessary for the germination and growth of these bryophytes ([Söderström and During 2005](#)) and tends to exclude feather-mosses, which are unable to immediately establish on the surface ([Økland 1994](#)). As expected and in accordance with results found in other studies ([Vitt et al. 1995](#); [Cole et al. 2008](#); [Fenton and](#)

[Bergeron 2008](#)), the number of microhabitats and CWM were influential variables in explaining species richness, and many indicator species were positively associated with CWM (e.g., *Anastrophyllum minutum* and *Nowellia curvifolia*). Accordingly, the overall higher species richness in the oldest age class compared with the intermediate age class (68–113 years) can be partly explained by differences in volume of CWM ([Brassard and Chen 2006](#)).

Third, the uprooting of large trees that frequently occurs in forests > 150 years old creates a pit and mound microtopography and exposes patches of organic matter and woody material associated with roots, which increases the number of substrates for species colonization, especially small-sized species and species with frequent sexual reproduction ([Jonsson and Esseen 1990](#); [Økland 2000](#)). Consequently, many indicator species of old-growth forests were positively related to pits (e.g., *Plagiothecium cavifolium*, *Geocalyx graveolans*, and *Calypogeia neesiana*) or to organic matter

Table 2. Model selection results for richness of mosses, liverworts, small-, medium-, and large-sized species, sexual species, vegetative species, vegetative and sexual species, species with frequent sexual reproduction, species with infrequent sexual reproduction, species with frequent vegetative reproduction, and species with infrequent vegetative reproduction.

	K	AICc	ΔAICc	AICc weight
Mosses				
canopy + ground	11	455.39	0	0.49
age + canopy + ground	12	457.02	1.63	0.22
age ² + canopy + ground	13	457.25	1.85	0.19
age ² + ground	10	459.17	3.77	0.07
Liverworts				
age + ground	9	437.09	0	0.97
Small-sized species				
age + ground	9	431.61	0	0.95
age + canopy + ground	12	438.43	6.81	0.03
Medium-sized species				
canopy + ground	11	377.05	0	0.6
age ² + canopy + ground	13	379.58	2.53	0.17
age + canopy + ground	12	379.6	2.56	0.17
age ² + ground	10	382.28	5.23	0.04
Large-sized species				
habitats	5	381.15	0	0.34
age + canopy + ground	12	381.26	0.11	0.32
canopy + ground	11	382.12	0.97	0.21
ground	8	384.4	3.25	0.07
age + ground	9	384.98	3.83	0.05
Sexual species				
canopy + ground	11	489.89	0	0.4
ground	8	490.74	0.85	0.27
age + ground	9	492.31	2.42	0.12
age + canopy + ground	12	492.39	2.5	0.12
habitats	5	492.84	2.95	0.09
Vegetative species				
age + ground	9	324.59	0	0.89
age + canopy + ground	12	329.74	5.15	0.07
Vegetative and sexual species				
age + canopy + ground	12	224.89	0	0.31
age + ground	9	225.08	0.19	0.28
ground	8	225.65	0.75	0.21
canopy + ground	11	226.08	1.19	0.17
Species with frequent sexual reproduction				
canopy + ground	11	473.6	0	0.43
ground	8	474.28	0.68	0.31
age + canopy + ground	12	475.5	1.9	0.17
age ² + ground	9	476.64	3.04	0.09
Species with infrequent sexual reproduction				
age + ground	9	381.55	0	0.95
Species with frequent vegetative reproduction				
age ² + ground	10	328.89	0	0.61
age + canopy + ground	12	331.93	3.04	0.13
age + ground	9	332.18	3.29	0.12
ground	8	334.33	5.44	0.04
habitats	5	334.56	5.67	0.04
age ² + canopy + ground	13	334.69	5.79	0.03
Species with infrequent vegetative reproduction				
age + ground	9	362.68	0	0.65
age + canopy + ground	12	364.91	2.23	0.21
ground	8	367.71	5.03	0.05
habitats	5	368.05	5.38	0.04

Note: Models are classified using Akaike's information criterion corrected for small sample size (AICc), including difference in AICc (ΔAICc) and AICc weight.

Table 3. Average estimates (Est.) and unconditional standard errors (SE) for each variable predicting richness of mosses, liverworts, small-, medium-, and large-sized species, sexual species, vegetative species, vegetative and sexual species, species with frequent sexual reproduction (FR sex), species with infrequent sexual reproduction (INFR sex), species with frequent vegetative reproduction (FR veg), and species with infrequent vegetative reproduction (INFR veg) in the models for which the sum of AICc weights reached ≥0.95.

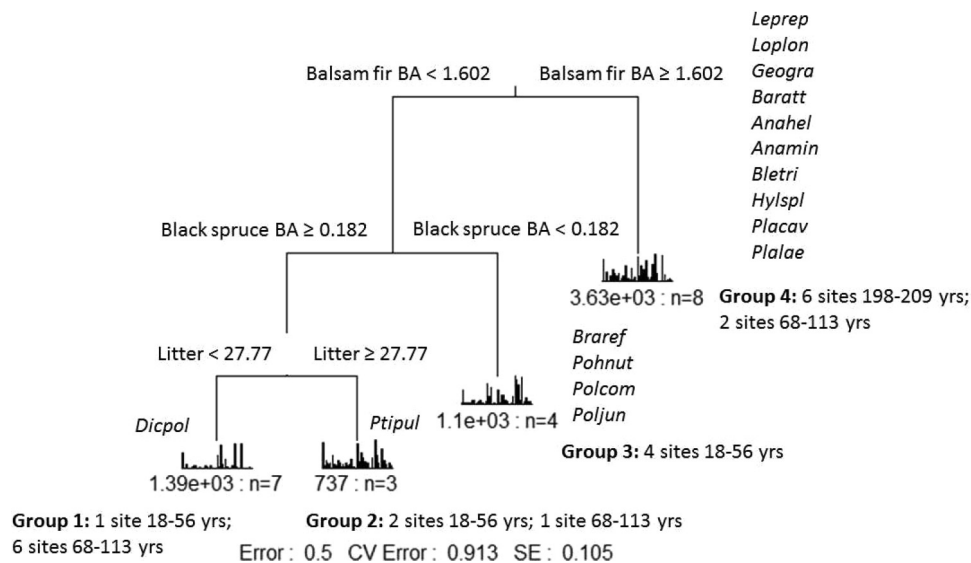
	Age		Age ²		Balsam fir		Black spruce		Hardwood		Cover of vascular (%)		CWM-45 volume		Cover of litter (%)		Cover of pits (%)		No. of microhabitats	
	Est.	SE	Est.	SE	BA	SE	BA	SE	BA	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE
Moss	-0.94	0.71	1.59	0.86	0.08	0.74	0.67	0.52	0.52	0.52	0.68	0.43	0.1	0.5	0.61	0.58	0.47	0.32	3.4	0.46
Liverwort	1.78	0.46			3.1	0.62	0.07	0.48	0.01	0.37	0.14	0.39	1.37	0.43	-0.04	0.46	0.5	0.29	2.56	0.4
Small-sized species	1.72	0.5			2.84	0.66	-0.39	0.51	0.33	0.4	-0.12	0.4	1.91	0.47	0.46	0.47	0.63	0.28	2.34	0.4
Medium-sized species	-0.1	0.38	0.81	0.47	0.4	0.37	-0.14	0.34	0.1	0.25	0.79	0.24	0.33	0.26	0.31	0.29	0.22	0.21	1.91	0.28
Large-sized species	-0.66	0.35			-0.12	0.44	-1.05	0.35	0.03	0.28	0.2	0.28	-0.47	0.34	-0.22	0.43	0.22	0.21	1.73	0.31
Sexual species	0.48	0.7			1.44	0.98	-1.04	0.64	0.81	0.5	0.86	0.51	1.28	0.62	0.59	0.73	0.69	0.39	4.21	0.61
Vegetative species	0.91	0.27			1.67	0.2	-0.09	0.27	-0.3	0.21	0.09	0.21	0.14	0.26	-0.33	0.27	0.23	0.15	1.32	0.22
Vegetative and sexual species	-0.23	0.12			-0.15	0.12	-0.32	0.12	-0.05	0.09	-0.11	0.1	0.21	0.12	0.23	0.15	0.15	0.09	0.41	0.13
FR sex	-0.41	0.61			0.4	0.86	-1.48	0.58	0.46	0.45	0.43	0.47	1.09	0.56	1.18	0.65	0.7	0.36	3.67	0.52
INFR sex	1.53	0.29			2.48	0.36	0	0.3	-0.03	0.22	0.32	0.26	0.35	0.27	-0.37	0.3	0.36	0.21	2.04	0.27
FR veg	0.4	0.3	0.57	0.28	1.24	0.25	-0.5	0.26	-0.27	0.2	0.08	0.2	0.45	0.23	-0.13	0.26	0.19	0.16	1.35	0.24
INFR veg	0.81	0.3			1.37	0.4	0.06	0.28	-0.12	0.22	0.56	0.24	0.3	0.35	0.46	0.29	0.45	0.19	1.51	0.27

Note: Model averaging was based on the entire set of models. The 95% confidence intervals of coefficients in bold excluded 0. BA, basal area.

Table 4. Indicator species of age classes and significant relationships (+ or –) between microhabitats (rock, organic matter (OM), *Sphagnum* spp., stumps, pits, coarse woody material (CWM), and branches or tree bases) and species according to logistic regressions conducted at the micro-quadrat scale within each age class.

		Age (years)	Rock	OM	<i>Sphagnum</i>	Stumps	Pits	CWM	Branches or tree bases
<i>Atacomnium palustre</i>	Moss	18–56		+	+				
<i>Cephalozia pleniceps</i>	Liverwort	18–56							+
<i>Polytrichum commune</i>	Moss	18–56		+					
<i>Polytrichum juniperinum</i>	Moss	18–56	+	+	–				
<i>Sphagnum capillifolium</i>	Moss	18–56					+		
<i>Anastrophyllum minutum</i>	Liverwort	198–209						+	
<i>Barbilophozia barbata</i>	Liverwort	198–209					–	–	+
<i>Calypogeia neesiana</i>	Liverwort	198–209		+					
<i>Geocalyx graveolens</i>	Liverwort	198–209				+			
<i>Lophozia longidens</i>	Liverwort	198–209			–				
<i>Nowellia curvifolia</i>	Liverwort	198–209						+	
<i>Plagiothecium cavifolium</i>	Moss	198–209				+	+	–	
<i>Sphagnum girgensohnii</i>	Moss	198–209							
<i>Brachythecium reflexum</i>	Moss	18–56 and 198–209		+	+				
<i>Herzogiella turfacea</i>	Moss	18–56 and 198–209						+	
<i>Myliia taylorii</i>	Liverwort	18–56 and 198–209							
<i>Pohlia nutans</i>	Moss	18–56 and 198–209	+	+	+	+	+		
<i>Riccardia latifrons</i>	Liverwort	18–56 and 198–209							
<i>Anastrophyllum hellerianum</i>	Liverwort	68–113 and 198–209		+			+	+	
<i>Blepharostoma trichophyllum</i>	Liverwort	68–113 and 198–209		+	+	+	+	+	+
<i>Hylocomium splendens</i>	Moss	68–113 and 198–209						+	

Fig. 3. Multivariate regression tree of stands based on bryophyte composition (species frequency) against habitat variables. Indicator species are written for terminal nodes (for species abbreviations, see Appendix Table A3). BA, basal area.



(*C. neesiana*). Also, the abundance of *P. nutans*, a species typically associated with mineral soil and exposed organic matter, followed a U-shaped pattern over time, with peaks in early successional and older forests.

The oldest forest age class examined in this study also contained bryophyte communities that are different from those present in the young and intermediate age classes in terms of life-history traits, which is coherent with observations made in previous studies conducted in similar ecosystems (Gustafsson and Hallingbäck 1988; Rambo and Muir 1998; Fenton and Bergeron 2008). Specifically, some species with traits suggesting limited dispersal ability (i.e., primarily vegetative reproduction and species with infrequent sexual reproduction) are more numerous in old-growth forests, suggesting that the abundance of these species is influenced by forest continuity. The importance of forest continuity for these dispersal-limited species has also been demonstrated by other

studies (Nordén and Appelqvist 2001; Fenton and Bergeron 2008; Caners et al. 2013; Barbé et al. 2017).

Many factors that were not measured in this study could also influence bryophyte assemblages. For example, the distance from source populations that have been spared by fire (fire skips) (Barbé et al. 2016), the size and configuration of the studied forest stands (Rydgren et al. 1998), the proportion of the landscape that is occupied by old forests, and harvesting history in a given region (Lindborg and Eriksson 2004; Paltto et al. 2006) can influence bryophyte populations. Barbé et al. (2016) found that long-distance dispersal was more common than expected in community assembly, and consequently, environmental factors during establishment and species' ability to produce copious amounts of spores might be more important than dispersal distance alone. Stochastic processes can also influence species occurrence at a given location. Indeed, many studies suggest that community

composition for a given site can be explained by an accumulation of random establishment events at a given site, thus causing differences between sites that do not result from factors such as stand age or other environmental factors (McCune and Allen 1985; Kimmerer and Driscoll 2000; T. Økland et al. 2003).

Our results show that richness of mosses and sexual species was relatively high in young sites that were recently disturbed. The great diversity of microhabitats present in early successional stages probably facilitates the presence of species that have good dispersal and colonization capabilities. Moreover, many medium- and large-sized species were present in these young stands. These species are considered as good competitors and can perform relatively well in open habitats and in the presence of some environmental characteristics that are generally detrimental for small bryophytes such as broadleaved litter (During 1992). The lower liverwort richness in the younger age class might be explained by the fact that CWM is mostly prefire stems that were killed by the fire and may consequently present different characteristics (e.g., charred portions) compared with the woody material found in older forests.

The lower canopy openness in stands that belong to the intermediate age class (68–113 years) is probably mostly responsible for the decrease in bryophyte richness observed in these stands. In addition to generating decreases in available resources for understory plants, canopy closure is associated with a decrease in habitat heterogeneity at the ground level as it acts as a bottleneck for understory communities (R.H. Økland et al. 2003), slowing the creation of new colonization microsites and eliminating the species that are not well adapted for persistence when resources are limited, particularly shade-intolerant species. The understory in these stands was dominated by feathermosses, mainly *P. schreberi* and *P. crista-castrensis*. Feathermosses dominated likely because they reach their 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 high growth rates (Longton and Greene 1969). Under dense forest canopies, feathermoss cover represents a barrier for the colonization of other moss species, as shown by lower species richness in the intermediate (68–113 years) age class. On the other hand, moss cover of medium- to large-sized species is relatively high in the intermediate age class (see Fig. 2).

Conclusion

Our study clearly shows that bryophyte communities in old-growth stands differ from those of mature stands in terms of composition and functional traits. Furthermore, our results suggest that both temporal continuity and microhabitat availability promote the establishment of late-successional bryophyte communities, but disentangling the influence of these two factors seems difficult. Still, both factors should be considered when devising conservation approaches in managed landscapes. On one hand, the preservation of older stands seems necessary to improve the likelihood of maintaining source populations of sensitive species in managed landscapes. Among those species, those that are dispersal-limited or that have important delays before being able to produce spores seem particularly vulnerable. On the other hand, the promotion and maintenance of a variety of suitable microhabitats in managed stands, for example CWM, would enhance the probability that sensitive species can successfully establish and build up viable populations on the long term.

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Appendix A

Appendix Tables A1–A3 appear on the following pages.

Table A1. Candidate models used to relate bryophyte richness to age, ground, and canopy variables.

Age + Canopy + Ground	Age + BAHARD + BAEPN + Vascular_plants + CWM-45 + no. of microhabitats + litter + pits Age + Age ² + BAHARD + BAEPN + Vascular_plants + CWM-45 + no. of microhabitats + litter + pits
Age + Ground	Age + CWM-45 + no. of microhabitats + litter + pits Age + Age ² + CWM-45 + no. of microhabitats + litter + pits
Age + Canopy	Age + BAHARD + BAEPN + Vascular_plants Age + Age ² + BAHARD + BAEPN + Vascular_plants
Canopy + Ground	BAEPN + BASAB + BAEPN + Vascular_plants + CWM-45 + no. of microhabitats + litter + pits
Age	Age Age + Age ²
Canopy	BAEPN + BASAB + BAHARD + Vascular_plants
BAEPN	BAEPN
BASAB	BASAB
BAHARD	BAHARD
Vascular_plants	Vascular_plants
Ground	CWM45 + no. of microhabitats + litter + pits
CWD-45	CWM45
No. of habitats	No. of microhabitats
Litter	Litter
Pits	Pits
Intercept only	

Table A2. Mean (\pm standard deviation (SD)) of environmental variables for each age class. Mixed models were used to compare means between different age classes.

	18–56 years (n = 7)		68–113 years (n = 9)		198–209 years (n = 6)		F	p
	Mean	SD	Mean	SD	Mean	SD		
Stand age (years)	29.9	15.7	95.4	18.8	203.8	5.7		
Black spruce BA (m ² .ha ⁻¹)	0.27b	0.38	28.91a	10.28	7.13b	4.91	32.19	<0.001
Balsam fir BA (m ² .ha ⁻¹)	0.08b	0.21	0.71b	0.97	17.27a	4.35	100.05	<0.001
Total basal area (m ² .ha ⁻¹)	0.46c	0.54	33.84a	4.56	24.98b	4.04	154.94	<0.001
Hardwood BA (m ² .ha ⁻¹)	0.11	0.14	2.74	3.24	0.59	0.77	3.15	0.066
CWM-123 volume (m ³ .ha ⁻¹)*	68.9	41.4	35.2	26.9	63.7	27.5	2.71	0.092
CWM-45 volume (m ³ .ha ⁻¹)†	59.5a	52.8	16.4b	14.4	60.8a	45.6	5.43	0.014
CWM volume (m ³ .ha ⁻¹)	128.4a	76.5	51.6b	31	124.5a	59.5	6.63	0.007
Mean DBH (cm)	7.85b	5.16	16.07a	2.22	16.86a	1.45	14.18	0.001
Cover of shrubs (%)	4.78a	6.21	0.93b	2.22	1.57a	2.67	4.78	0.021
Cover of lichens (%)	7.36	15.9	0.85	1.08	0.63	0.38	2.14	0.145
Cover of litter (needles + leaves) (%)	46.57a	21.11	17.88b	15.51	12.6b	6.38	10.96	0.001
Cover of vascular plants (%)	15.54	11.49	7.52	7.46	10.7	11.14	1.46	0.257
Cover of pits (%)	13.56	7.72	13.93	4.41	14.06	3.28	0.01	0.985
Cover of mounds (%)	11.61	6.19	14.46	7.23	16.48	6.92	1.99	0.164
Cover of rocks (%)	0.80a	1.52	0.02b	0.10	0.08b	0.33	6.29	0.008
Cover of stumps (%)	0.68	1.54	0.21	0.62	0.24	0.64	1.42	0.267
Cover of mineral soil (%)	0.24	0.68	0.31	1.83	0	0	0.45	0.642
Organic matter depth (cm)	156.58	50.89	198.1	36.14	213.04	30.83	3.21	0.067
Number of regenerating trees (no.)	3.43b	3.07	10b	9.37	29.5a	20.46	7.41	0.004
Number of saplings (no.)	73.43a	42.76	10b	12.75	20.33b	16.94	10.58	0.001
Number of microhabitats (no.)	2.44ab	0.85	1.57b	1.07	2.91a	1.09	4.4	0.027

Note: BA, basal area; CWM, coarse woody material; DBH, diameter at breast height. Age classes: 18–56 years old, regenerating forests; 68–113 years old, commercially mature forests; 198–209 years old, old-growth forests. Means with different letters differed significantly ($p \leq 0.05$) according to LSmeans Tukey’s HSD tests.

*From decay classes 1, 2, and 3.

†From decay classes 4 and 5.

Table A3. Mean species cover and frequency at the subplot level for each age class with their associated life strategy.

	Codes	Mode of reproduction	Frequency of sexual reproduction	Frequency of vegetative reproduction	Size	18–56 years (n = 28)		68–113 years (n = 36)		198–209 years (n = 24)	
						Cover (%)	Frequency (%)	Cover (%)	Frequency (%)	Cover (%)	Frequency (%)
Liverworts											
<i>Anastrophyllum hellerianum</i>	ANAHEL	v	r	a	sm	0.01	10.71	0.05	36.11	0.14	70.83
<i>Anastrophyllum michauxii</i>	ANAMIC	vs	f	f	sm	0	0	0	0	0	4.17
<i>Anastrophyllum minutum</i>	ANAMIN	v	r	a	m	0	3.57	0.01	8.33	0.06	41.67
<i>Barbilophozia attenuata</i>	BARATT	v	f	a	sm	0.06	53.57	0.09	50	0.31	79.17
<i>Barbilophozia barbata</i>	BARBAR	s	f	x	m	0	0	0.02	11.11	0.2	45.83
<i>Barbilophozia hatcheri</i>	BARHAT	v	f	r	m	0	3.57	0	2.78	0	4.17
<i>Barbilophozia kunzeana</i>	BARKUN	s	?	r	m	0.01	3.57	0	0	0.01	4.17
<i>Barbilophozia lycopodioides</i>	BARLYC	s	r	r	m	0	3.57	0	0	0.01	4.17
<i>Bazzania demudata</i>	BAZDEN	v	r	a	sm	0	0	0	0	0	4.17
<i>Bazzania trilobata</i>	BAZTRI	v	r	x	l	0	3.57	0.11	8.33	0.42	29.17
<i>Blepharostoma trichophyllum</i>	BLETRI	s	f	r	sm	0.05	32.14	0.17	55.56	0.58	95.83
<i>Calypogeia neesiana</i>	CALNEE	v	r	f	sm	0.02	17.86	0	2.78	0.15	58.33
<i>Cephalozia bicuspidata</i>	CEPBIC	s	f	r	sm	0.03	14.29	0	2.78	0.07	33.33
<i>Cephalozia lunulifolia</i>	CEPLUN	s	f	o	sm	0.08	46.43	0.04	27.78	0.31	83.33
<i>Cephalozia pleneiceps</i>	CEPPLE	s	f	o	sm	0.05	32.14	0	0	0.01	8.33
<i>Cephaloziella</i> spp.	CEPSPP					0.04	32.14	0.01	8.33	0.05	37.5
<i>Cephaloziella rubella</i>	CEPRUB	vs	f	a	sm	0.09	53.57	0.02	22.22	0.02	12.5
<i>Chiloscyphus coadunatus</i> var. <i>rivularis</i>	CHICOA	s	r	x	m	0.03	7.14	0.04	22.22	0.06	45.83
<i>Chiloscyphus profundus</i>	CHIPRO	s	a	r	sm	0.05	28.57	0.06	33.33	0.11	50
<i>Frullania oakesiana</i>	FRUOAK	s	a	x	sm	0	3.57	0.03	11.11	0.03	16.67
<i>Geocalyx graveolens</i>	GEOGRA	s	r	x	m	0.01	10.71	0.03	22.22	0.2	79.17
<i>Jamesoniella autumnalis</i>	JAMAUT	s	a	x	sm	0.06	35.71	0.19	69.44	0.19	54.17
<i>Lepidozia reptans</i>	LEPREP	s	a	x	sm	0.05	35.71	0.08	50	0.22	75
<i>Lophozia ascendens</i>	LOPASC	v	r	a	sm	0	0	0	0	0.03	20.83
<i>Lophozia bicrenata</i>	LOPBIC	vs	f	f	sm	0.02	17.86	0	0	0	0
<i>Lophozia longidens</i>	LOPLON	v	r	f	sm	0	3.57	0.04	16.67	0.09	58.33
<i>Lophozia ventricosa</i>	LOPVEN	vs	f	a	sm	0.19	64.29	0.1	55.56	0.33	87.5
<i>Mylia taylorii</i>	MYLTAY	v	o	f	m	0.01	14.29	0	0	0.03	20.83
<i>Nowellia curvifolia</i>	NOWCUR	s	f	r	sm	0.03	14.29	0.02	13.89	0.14	70.83
<i>Ptilidium ciliare</i>	PTICIL	s	r	x	m	0.07	28.57	0.08	30.56	0.02	12.5
<i>Ptilidium pulcherrimum</i>	PTIPUL	s	a	x	sm	0.75	89.29	0.53	97.22	0.66	100
<i>Radula complanata</i>	RADCOM	vs	a	f	sm	0	0	0	2.78	0	0
<i>Riccardia latifrons</i>	RICLAT	s	f	r	sm	0.03	17.86	0	2.78	0.02	16.67
<i>Scapania apiculata</i>	SCAAPI	v	r	a	l	0	0	0	2.78	0.02	16.67
<i>Schistochilopsis incisa</i>	SCHINC	v	r	a	sm	0	3.57	0	2.78	0.02	16.67
<i>Tritomaria exsectiformis</i>	TRIEXS	v	r	a	sm	0.01	10.71	0	2.78	0.03	16.67
Mosses											
<i>Aulacomnium palustre</i>	AULPALU	vs	f	f	sm	0.88	82.14	0	0	0	4.17
<i>Brachythecium campestre</i>	BRACAM	s	f	x	sm	0.08	46.43	0.18	22.22	0	0
<i>Brachythecium reflexum</i>	BRAREF	s	f	x	m	0.12	64.29	0.03	22.22	0.07	33.33
<i>Brachythecium rutabulum</i>	BRARUT	s	a	x	l	0.09	32.14	0.02	16.67	0.03	20.83
<i>Brachythecium starkei</i>	BRASTA	s	a	x	l	0.45	89.29	0.16	38.89	0.45	75
<i>Brachythecium</i> spp.	BRASPP					0.21	100	0.24	100	0.05	100
<i>Brotherella recurvans</i>	BROREC	s	o	x	m	0	0	0	0	0.08	20.83
<i>Brynhia graminicolor</i>	BRYGRA	s	r	x	sm	0	3.57	0	0	0	0

Table A3 (continued).

	Codes	Mode of reproduction	Frequency of sexual reproduction	Frequency of vegetative reproduction	Size	18–56 years (n = 28)		68–113 years (n = 36)		198–209 years (n = 24)	
						Cover (%)	Frequency (%)	Cover (%)	Frequency (%)	Cover (%)	Frequency (%)
<i>Callicladium haldanianum</i>	CALHAL	s	a	x	m	0.01	10.71	0.01	5.56	0	0
<i>Campyliadelphus chrysophyllum</i>	CAMCHR	s	r	x	m	0	3.57	0	0	0.01	4.17
<i>Campylophyllum hispidulum</i>	CAMHIS	s	f	x	sm	0.01	7.14	0	0	0	4.17
<i>Campylium stellatum</i>	CAMSTE	s	r	x	l	0	0	0	0	0	4.17
<i>Ceratodon purpureus</i>	CERPUR	s	a	r	m	0.06	28.57	0	0	0.01	8.33
<i>Dicranella heteromalla</i>	DICHET	s	a	r	sm	0	0	0	2.78	0	4.17
<i>Dicranum fuscescens</i>	DICFUS	s	f	x	m	0.93	92.86	1.08	91.67	1.54	100
<i>Dicranum majus</i>	DICMAJ	s	o	x	l	0	0	0.01	2.78	0.01	4.17
<i>Dicranum montanum</i>	DICMON	vs	f	f	sm	0.05	28.57	0.06	33.33	0.15	79.17
<i>Dicranum ontariense</i>	DICONT	s	f	x	m	0.02	21.43	0.02	13.89	0	0
<i>Dicranum polysetum</i>	DICPOL	s	f	x	l	0.47	92.86	1.62	100	0.64	83.33
<i>Dicranum scoparium</i>	DICSCO	s	o	x	l	0.06	50	0.18	50	0.35	75
<i>Dicranum undulatum</i>	DICUND	s	o	x	m	0	3.57	0.01	2.78	0.01	4.17
<i>Eurhynchiastrum pulchellum</i>	EURPUL	s	o	x	sm	0	0	0.06	8.33	0	0
<i>Herzogiella striatella</i>	HERSTR	s	a	x	m	0	3.57	0	0	0	0
<i>Herzogiella turfaca</i>	HERTUR	s	a	x	sm	0.09	35.71	0.03	19.44	0.18	70.83
<i>Hygroamblystegium varium</i>	AMBVAR	s	o	x	sm	0	0	0	2.78	0	0
<i>Hylocomiastrum umbratum</i>	HYLUMB	s	r	x	l	0	3.57	0	0	0	4.17
<i>Hylocomium splendens</i>	HYLSPL	s	r	x	l	0.13	35.71	7.15	75	29.05	87.5
<i>Hypnum pallescens</i>	HYPPAL	s	f	x	m	0.08	53.57	0.04	25	0.02	16.67
<i>Mnium spinulosum</i>	MNISPI	s	f	x	sm	0	3.57	0.02	13.89	0.04	20.83
<i>Oncophorus wahlenbergii</i>	ONCWAH	s	f	x	sm	0	3.57	0	0	0	0
<i>Paraleucobryum longifolium</i>	PARLON	s	f	x	m	0	3.57	0	0	0	0
<i>Plagiothecium cavifolium</i>	PLACAV	s	o	r	m	0.03	17.86	0.01	8.33	0.13	54.17
<i>Plagiothecium denticulatum</i>	PLADEN	s	f	r	m	0.02	7.14	0	2.78	0.03	20.83
<i>Plagiothecium laetum</i>	PLALAE	s	a	o	sm	0.2	71.43	0.14	47.22	0.58	91.67
<i>Plagiomnium medium</i>	PLAMED	s	o	x	sm	0.03	3.57	0	0	0	0
<i>Platidictya subtilis</i>	PLASUB	s	f	x	sm	0	3.57	0	0	0	0
<i>Platygyrium repens</i>	PLAREP	v	f	a	m	0	3.57	0	2.78	0	0
<i>Pleurozium schreberi</i>	PLESCH	s	o	x	l	21.36	100	34.89	97.22	24.25	100
<i>Pogonatum dentatum</i>	POGDEN	s	f	x	m	0	0	0	0	0	4.17
<i>Pohlia nutans</i>	POHNUT	s	a	x	m	1.21	92.86	0.06	25	0.24	75
<i>Polytrichastrum formosum</i> var. <i>densifolium</i>	POLFOR	s	f	x	l	0	0	0	0	0	4.17
<i>Polytrichastrum ohioense</i>	POLOHI	s	f	x	m	0	0	0	0	0.07	8.33
<i>Polytrichastrum longisetum</i>	POLLON	s	a	x	l	0	0	0	0	0.03	12.5
<i>Polytrichum commune</i>	POLCOM	s	a	x	l	0.81	53.57	0.04	8.33	0.09	16.67
<i>Polytrichum juniperinum</i>	POLJUN	s	a	x	m	0.92	71.43	0.06	5.56	0.01	8.33
<i>Polytrichum piliferum</i>	POLPIL	s	a	x	m	0.01	7.14	0	0	0	0
<i>Polytrichum strictum</i>	POLSTR	s	f	x	l	0.05	17.86	0	0	0	4.17
<i>Pseudotaxiphyllum elegans</i>	PSEELE	v	r	a	sm	0	0	0	2.78	0	0
<i>Ptilium crista-castrensis</i>	PTICRI	s	o	x	m	3.87	96.43	18.92	100	8.48	100
<i>Racomitrium microcarpum</i>	RACMIC	s	o	x	m	0.1	7.14	0	0	0	0
<i>Rhytidiadelphus triquetrus</i>	RHYTRI	s	r	x	l	0	0	0.39	13.89	0	0
<i>Rhizomnium punctatum</i>	RHIPUN	s	f	r	m	0	3.57	0	2.78	0.01	4.17
<i>Sanionia uncinata</i>	SANUNC	s	f	x	l	0.15	67.86	0.22	47.22	0.37	70.83
<i>Schistostega pennata</i>	SCHPEN	s	o	o	sm	0	0	0	0.02	0	0.02
<i>Tetraphis pellucida</i>	TETPEL	vs	o	a	sm	0.11	46.43	0.02	16.67	0.25	79.17

Table A3 (concluded).

Codes	Mode of reproduction	Frequency of sexual reproduction	Frequency of vegetative reproduction	Size	18–56 years (n = 28)		68–113 years (n = 36)		198–209 years (n = 24)		
					Cover (%)	Frequency (%)	Cover (%)	Frequency (%)	Cover (%)	Frequency (%)	
Sphagnum											
<i>Sphagnum angustifolium</i>	SPHANG	s	f	x	1	0.01	7.14	0	0	0.01	8.33
<i>Sphagnum capillifolium</i>	SPHCAP	s	a	x	1	1.99	57.14	0.23	5.56	0.59	12.5
<i>Sphagnum fallax</i>	SPHFAL	s	o	x	1	0.18	3.57	0	0	0	0
<i>Sphagnum fuscum</i>	SPHFUS	s	f	x	1	0.14	3.57	0	0	0	0
<i>Sphagnum girgensohnii</i>	SPHGIR	s	r	x	1	0.58	17.86	0	0	3.42	33.33
<i>Sphagnum magellanicum</i>	SPHMAG	s	r	x	1	0	3.57	0	0	0	0
<i>Sphagnum quinquefarium</i>	SPHQUI	s	o	x	1	0	3.57	0.06	2.78	0.05	4.17
<i>Sphagnum russowii</i>	SPHRUS	s	f	x	1	1.54	46.43	0.17	5.56	2.72	29.17
<i>Sphagnum</i> spp.	SPHSPP					0.81	32.14	0	0	1.34	33.33
<i>Sphagnum subtile</i>	SPHSUB	s	f	x	1	0.05	3.57	0	0	0	0
<i>Sphagnum wulfianum</i>	SPHWUL	s	f	x	1	0	0	0	0	0	4.17

Note: Mode of reproduction: v, vegetative; vs, vegetative and sexual; s, sexual. Frequency of sexual reproduction: a, abundant; f, frequent; o, occasional; r, rare. Frequency of vegetative reproduction: a, abundant; f, frequent; o, occasional; r, rare; x, inexistent. Size: sm, small; m, medium; l, large. Age classes: 18–56 years old, regenerating forests; 68–113 years old, commercially mature forests; 198–209 years old, old-growth forests.