Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada

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Abstract: We sampled 22 black spruce (*Picea mariana*) – feathermoss (*Pleurozium schreberi*) sites (80 to >200 years) to describe and assess the diversity of bryophyte and lichen communities as a function of time since fire and site characteristics. Old growth had no more species than younger forests. We think that this result might be explained by the phenomenon of paludification, which is a major process in this region. Axis 1 of a nonmetric multidimensional scaling ordination (NMS) of terricolous species was interpreted as a paludification gradient. Mature forests were characterized by *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Polytrichum commune*, and *Dicranum polysetum*, and older sites by a greater abundance of *Sphagnum*. Axis 1 of epiphytic species ordination (NMS) was interpreted as a gradient of time since the last fire. Abundance of *Tuckermannopsis americana*, *Hypogymnia physodes*, and *Bryoria furcellata* was greater in mature forests. In contrast, *Mycoblastus sanguinarius*, *Bryoria trichodes*, and *Usnea* spp. were more abundant in older forests. The abundance of epiphytic lichens increased with tree age, whereas their richness was higher in sites where trembling aspen (*Populus tremuloides*) and jack pine (*Pinus banksiana*) were present. Since species composition varied with time since the last fire, it is important to preserve the diversity of successional stages at the landscape level and the structural diversity at the stand level to maintain the bryophyte and lichen communities.

Résumé : Nous avons échantillonné 22 pessières à mousses (80 à >200 ans) afin de décrire et d'évaluer la diversité des communautés de bryophytes et de lichens selon le temps écoulé depuis le dernier feu et selon certaines caractéristiques des sites. Les vieilles forêts ne renfermaient pas plus d'espèces que celles plus jeunes. Nous pensons que la paludification, processus important dans cette région, pourrait expliquer ce résultat. L'axe 1 d'une ordination (cadrage multidimensionnel non-métrique ou CMN) des espèces terricoles a été interprété comme un gradient de paludification. *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Polytrichum commune* et *Dicranum polysetum* étaient plus abondants dans les forêts matures alors qu'une forte abondance de sphaignes caractérisaient les vieilles forêts. L'axe 1 d'une CMN des espèces épiphytes a été interprété comme un gradient du temps écoulé depuis le dernier feu. L'abondance des espèces épiphytes *Tuckermannopsis americana*, *Hypogymnia physodes* et *Bryoria furcellata* était plus importante dans les forêts matures. À l'opposé, *Mycoblastus sanguinarius*, *Bryoria trichodes* et *Usnea* spp. étaient plus abondants dans les vieilles forêts. L'abondance des lichens épiphytes augmentait en fonction de l'âge des arbres alors que la richesse des lichens épiphytes était plus élevée dans les sites où le peuplier faux-tremble (*Populus tremuloides*) et le pin gris (*Pinus banksiana*) étaient présents. Puisque la composition des communautés variait en fonction du temps écoulé depuis le dernier feu, il est important de préserver la diversité des stades successionnels à l'échelle du paysage et la diversité structurale à l'échelle du site pour maintenir les communautés de bryophytes et de lichens.

Introduction

Throughout the northern hemisphere, forest landscapes are changing under the pressures of industrial forestry. Current practices have multiple consequences for forest ecosystems, including the potential elimination or at least a substantial reduction of the old-growth components of forested landscapes. For instance, in the boreal forest of eastern Canada (Ontario and Quebec), the goal of forest management has been equal age-class proportions to provide a constant and regular access to the fiber resource. Consequently, stands tend to be harvested when they reach 75–100 years (i.e., the rotation age (Ordre des ingénieurs forestiers du Québec 1996)), and the proportion of mature to old-growth stands tends to decrease considerably in the landscapes (Bergeron et al. 1999).

This loss of the mature to old-growth portion of the successional gradient may threaten some species. Many studies have shown that bryophyte and lichen communities change along a successional gradient, and some species are confined to the oldest forest stands (Rose 1976; Esseen et al. 1981; Gustafsson and Hallingbäck 1988; Soderström 1988;

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Lesica et al. 1991; Tibell 1992; Neitlich 1993; Goward 1994; Esseen et al. 1996). Old-growth communities might be at risk under the current forest practices. Indeed some bryophyte and lichen species may (*i*) need a very long period of time to attain maximum size, to reproduce, or to disperse; (*ii*) depend on processes and (or) habitat structures present only in old-growth stands, such as old trees or large-sized tree falls; and (*iii*) depend on specific microclimatic conditions that can only be found in old-growth stands (Esseen et al. 1992).

In contrast with the Pacific Northwest coastal forest biome, the status of old-growth forests and their contribution to landscape-scale biodiversity in boreal regions remain poorly documented probably because in many areas the short fire cycles do not allow forest stands to evolve long enough to develop old-growth stand characteristics (Johnson et al. 1995). However, recent studies conducted in eastern Canada (the Clay Belt of Ontario and Quebec) revealed that a large percentage of the territory (25%) consists of forests that have not burned for more than 200 years (Lefort 1998). Moreover, present knowledge of the ecological relationships between old-growth forests and nonvascular flora is derived mainly from research in Scandinavian forests and, in North America, from studies in Pacific Northwest Coast forests and eastern deciduous forests. Although some researchers have studied the successional patterns of bryophyte and lichen communities in the boreal forest (Yarranton 1972; La Roi and Stringer 1976; Maikawa and Kershaw 1976; Johnson 1981; Foster 1985; Morneau and Payette 1989), few have focused on the changes that occur in the mature to old-growth forest part of the successional gradient. Therefore, we do not know the contribution of each successional stage to the maintenance of the diversity of bryophyte and lichen communities and how site characteristics might affect these communities. Recommendations and management guidelines for sustainable forestry developed in other regions (Pacific Northwest, eastern United States, or Scandinavia) may not necessarily be applicable in the eastern boreal forest.

This study was part of a broader scale project undertaken in the eastern Canadian boreal forest to examine the contribution of old-growth forests to biodiversity using vascular plants, nonvascular plants, insects, and birds as indicator groups. In this study, we have three objectives: (*i*) to describe bryophyte and lichen (terricolous and epiphytic) communities as a function of time since fire (along a mature to old-growth gradient; we are not including early succession, i.e., 1 to 80 years after fire) and to define their relationship with site characteristics; (*ii*) to assess the changes in richness and abundance of bryophytes and lichens (terricolous and epiphytic) along this gradient and site characteristics; and (*iii*) to relate individual species abundance with time since fire and site characteristics. We also discuss the maintenance of the integrity of bryophyte and lichen communities in eastern black spruce (*Picea mariana*) forest ecosystems with respect to silvicultural practices.

Study area

The study was undertaken in a black spruce – feathermoss forest in the northwestern part of the Abitibi region of Quebec (49°13′17″–49°51′05″N, 78°38′35″–79°23′13″W) and in the Lake Abitibi Model Forest in Ontario (49°03′33″–49°42′20″N, 80°09′03″–80°38′35″W) (Fig. 1). These regions are part of the northern Clay Belt, a broad physiographic unit characterized by lacustrine deposits from the proglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). Clay soils are predominant in the region, the topography is relatively flat, and the forest mosaic is dominated by black spruce stands. Jack pine (*Pinus banksiana*) is dominant on drier sites such as outwash deposits, old beaches, and eskers (Rowe 1972).

The nearest weather station to the sampled sites in Quebec is located at La Sarre. At this station, the mean annual temperature is 0.8°C, annual precipitation is 856.8 mm, and there are, on average, 64 frost-free days during the year (Environment Canada 1993). Iroquois Falls in Ontario, which is the nearest weather station to the Lake Abitibi Model Forest, has a mean annual temperature of 0.9°C, annual precipitation of 792.4 mm, and a mean frost-free period of 90 days (Environment Canada 1993).

Materials and methods

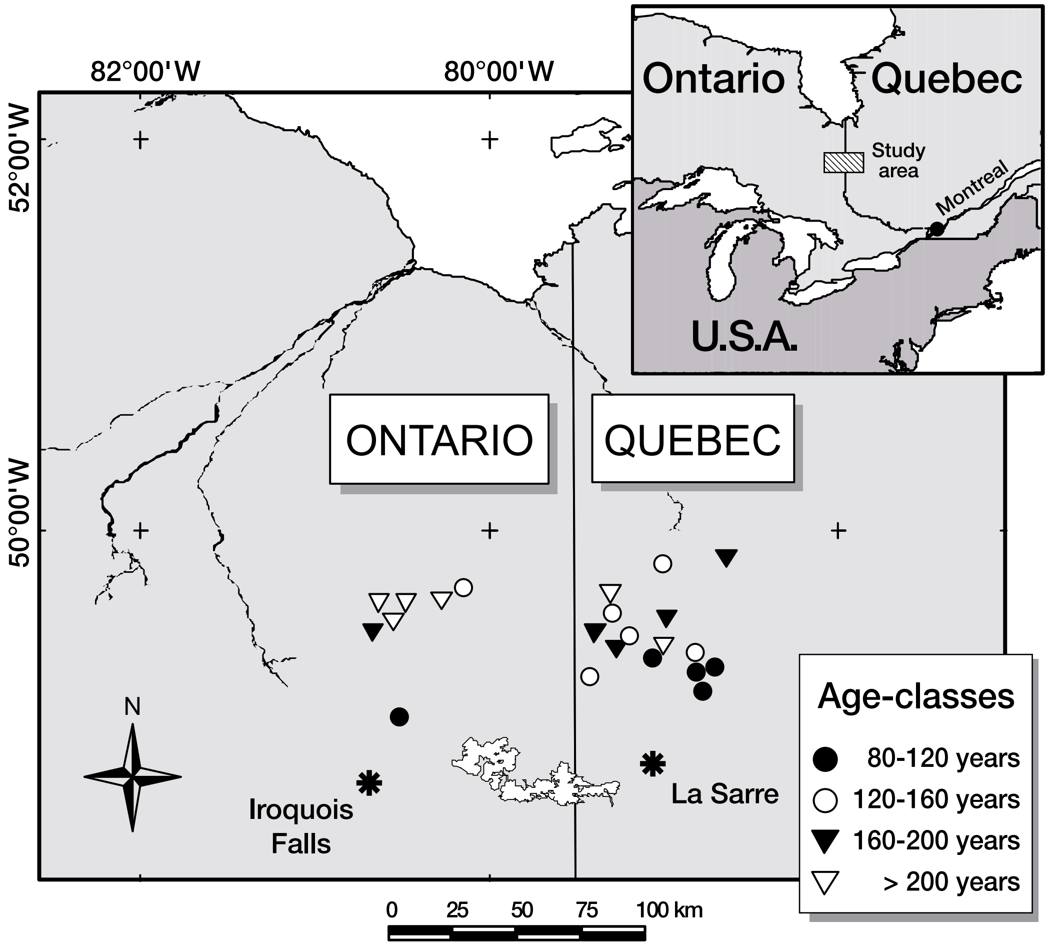
Sampling

Based on previous fire history reconstruction (Lefort 1998; Bergeron et al. 2001), we selected 22 sites belonging to mature to old-growth forests (80 to >200 years) within forests not subject to timber harvest and accessible by road: 15 of these sites were located in Quebec, and 7 were in the Lake Abitibi Model Forest in Ontario. To minimize external sources of variation, the selected sites were restricted to stands dominated by black spruce, with a minimal size of 2 ha; on clay or loamy soils, with an organic matter depth of less than 60 cm; and located on sites with slope of less than 5%. We determined the age of the stands, i.e., the time since fire, with the analyses of core samples collected from trees at each site. We assigned each site to an age-class: 80–120 years (five sites), 120–160 years (six sites), 160–200 years (five sites), and forests over 200 years old (six sites).

We sampled sites quantitatively in 1997. At each site along a subjectively located transect of 200 m in length, we measured site characteristics important to explain bryophyte and lichen distribution. We inventoried and assigned to a height class (1–5, >5–10 m, etc.) and a diameter at breast height class (1–5, >5–10, >10–15 cm, etc.) all trees present along the transect, encompassing an area of 2 m on either side. We measured the diameter of all coarse woody debris (CWD) intercepting the transect; this measure was taken where the transect crossed the CWD. CWD was separated into two decay classes according to their decay stage: CWD1, recently fallen, showing little decomposition; CWD2, fairly well decayed. We also recorded canopy openings by measuring the distance between the first living branches on either side of the gap. At 50-m intervals along the transect, we did a soil profile to measure the thickness of the organic matter.

We sampled bryophytes and lichens along the same transects. We estimated percent cover of terricolous species in twenty-one 0.25-m^2 (50 × 50 cm) microquadrats located at 5-m intervals along the transect over a distance of 100 m

Fig. 1. Map of study area and location of sampled sites. Locations of weather stations are indicated by stars.



(quantitative sampling). In this phase of sampling, we sampled only species present on the ground; thus, we excluded species present on woody debris. Within these microquadrats, we also gathered specimens for subsequent laboratory identification. Epiphytic lichens were sampled in the lower canopy stratum. Every 5 m, we collected two branches from the black spruce tree closest to the transect with a pole pruner — one branch pointing northward and the other southward for a total of 42 branches collected from 21 different trees at each site. We selected the first branch (living or dead) longer than 1 m located between 1.5 and 4 m. Cover of epiphytic species was estimated on the main section of each branch (50-cm segment). Epiphytic lichens on tree trunks were not studied. We estimated the area occupied by each species by measuring the length occupied by the species on these branch sections with a ruler (1 cm = 2%). For tree age determination purposes, we took a core sample from all selected trees using a Pressler increment borer.

We limited our sampling to mosses, *Sphagnum*, liverworts, foliose lichens, fruticose lichens, and fertile crustose lichens. Sterile crustose lichens (with no apothecia) were therefore ignored. Aside from certain easy-to-identify specimens, we grouped liverworts by genus. Since it was difficult to make separate percent cover estimates for *Cladina rangiferina* and *Cladina stygia*, we considered these two species as a single taxon during the analyses.

To find infrequent species or species specific to a particular microhabitat, we revisited all the sites except three that had been logged (in the >200-year age-class) and one site that could not be relocated (in the 160- to 200-year age-class) during the summer of 1998. Within a 400-m^2 area (2 m on either side of the transect over a distance of 100 m), we conducted a thorough reconnaissance of bryophyte and lichen species (species survey), with an emphasis on microhabitats such as the base of different tree species, tree trunks, stumps, CWD, and water-filled depressions.

Data analyses

We calculated basal area of tree species (m^2/ha), gaps (%), and CWD (m^3/ha) for each transect. For thickness of organic matter (cm) and tree age (years), the mean values along the transect were used in subsequent analyses. The Van Wagner (1968) formula was used in computing the volume of CWD per hectare per decay class:

$$\text{Volume of CWD/ha} = [(\text{sum of diameters} \times \pi)^2/8L] \times 10\,000$$

where L is the length of transect.

We computed for each site three estimates of diversity for each different group of organisms (liverworts, mosses (excluding *Sphagnum*), *Sphagnum*, terricolous lichens, and epiphytic lichens). Total number of species (TNS) corresponded to the number of species found at a given site during the species survey while richness corresponded to the number of species ob-

Table 1. Mean (±SD) of site characteristics for each age-class.

	Age-classes					
	80–120 years (n = 5)	120–160 years (n = 6)	160–200 years (n = 5)	>200 years (n = 6)	F	p
Time since fire (years)	93.6 (12.6)	141.6 (12.5)	181.2 (10.7)	220.0 (6.0)		
Mean tree age (years)	73.4 (9.6)*b*	99.8 (11.2)*ab*	123.9 (35.5)*a*	119.4 (31.2)*a*	4.14	0.022
Thickness of organic matter (cm)	16.1 (7.8)*b*	30.2 (10.2)*ab*	48.1 (17.1)*a*	42.6 (10.2)*a*	6.82	0.003
Coarse woody debris 1 (m^3/ha)	39.3 (22.3)*a*	58.6 (37.1)*a*	39.8 (39.4)*a*	58.7 (9.4)*a*	0.54	0.659
Coarse woody debris 2 (m^3/ha)	1.9 (4.2)*a*	0.9 (1.8)*a*	3.3 (5.5)*a*	0.6 (1.2)*a*	0.43	0.736
Gaps (%)	23.2 (12.4)*a*	46.0 (22.3)*a*	39.0 (29.6)*a*	77.0 (10.9)*a*	2.55	0.088
Basal area of *Abies balsamea* (m^2/ha)	0.5 (1.0)*a*	2.6 (1.9)*a*	1.0 (1.9)*a*	0.7 (1.2)*a*	1.02	0.405
Basal area of *Betula papyrifera* (m^2/ha)	0.0 (0.0)*a*	0.5 (0.9)*a*	0.0 (0.0)*a*	0.0 (0.0)*a*	0.76	0.532
Basal area of *Larix laricina* (m^2/ha)	0.0 (0.0)*a*	0.0 (0.0)*a*	0.3 (0.5)*a*	0.0 (0.0)*a*	1.72	0.198
Basal area of *Pinus banksiana* (m^2/ha)	5.5 (6.6)*a*	0.2 (0.3)*ab*	0.0 (0.0)*b*	0.0 (0.0)*b*	4.01	0.024
Basal area of *Picea mariana* (m^2/ha)	34.6 (9.2)*a*	31.7 (10.7)*ab*	26.0 (13.2)*ab*	17.2 (2.8)*b*	4.32	0.019
Basal area of *Populus tremuloides* (m^2/ha)	3.8 (6.5)*a*	0.4 (0.8)*b*	0.0 (0.0)*b*	0.0 (0.0)*b*	7.80	0.002
Basal area of conifers (m^2/ha)	40.6 (4.6)*a*	34.4 (10.0)*ab*	27.3 (13.8)*ab*	17.9 (1.9)*b*	5.51	0.007
Basal area of deciduous trees (m^2/ha)	3.8 (6.5)*a*	0.9 (1.0)*a*	0.0 (0.0)*a*	0.0 (0.0)*a*	2.76	0.072
Basal area of shrubs (m^2/ha)	0.4 (0.5)*a*	0.8 (1.4)*a*	0.2 (0.2)*a*	0.2 (0.2)*a*	0.80	0.509
Total basal area (m^2/ha)	44.8 (6.0)*a*	36.1 (8.6)*ab*	27.5 (14.0)*b*	18.1 (1.8)*b*	6.61	0.003

Note: ANOVAs (computed on ranks) were used to compare means between different age-classes. Values with the same letter are not significantly different ($p > 0.05$) between age-classes.

served during the quantitative sampling, and abundance is the mean percent cover of species by microquadrat.

To evaluate differences between site characteristics and estimates of diversity among the different age-classes, ANOVAs were performed on ranks of diversity indices. Comparison of means were made by using the Student–Newman–Keuls multiple comparison test.

We used nonmetric multidimensional scaling ordination (NMS) performed with the PC-ORD software (McCune and Mefford 1997) (*i*) to describe the species composition of bryophyte and lichen communities along the mature to old-growth gradient and (*ii*) to relate the community structure to environmental gradients and diversity estimates. We conducted two NMS analyses, one on the terricolous species data set and the other one on the epiphytic species data set, to provide a representation of the position of the sites on two axes of a dispersion diagram. For both data sets, analyses were based on the abundance data collected during quantitative sampling. Only species present in at least four sites were incorporated into the ordinations. The quantitative version of Sorensen's similarity index was used as a distance measure. Analyses were run with three axes as the reduction in stress was small beyond the third axis when plotting final stress versus the number of dimensions. However, only results for the two axes with the higher coefficients of determination (estimates of amount of variation in the original data matrix represented on an axis) are given since they expressed more than 85% of the variation for the terricolous species community and 91% of the variation for the epiphytic species community. We performed Spearman correlations between site scores on the ordination axes, and species, site characteristics, and diversity estimates. Each age-class was represented by a different symbol on the dispersion diagram to facilitate the interpretation of successional trends. As we have conducted many statistical tests (mean comparisons and correlations), tests where $0.01 < p < 0.05$ should be interpreted with caution.

To determine if individual species showed preferences for specific successional stages, we used the indicator species analysis approach of Dufrêne and Legendre (1997) with PC-ORD software (McCune and Mefford 1997). Indicator values corresponding to the combined relative frequency and relative abundance of each species were obtained by this method for each group. The maximum indicator value was then tested by using a Monte Carlo permutation test to determine whether it was significantly different from the other values.

Results

Site characteristics

Mean tree age and organic matter depth were lower in the 80- to 120-year age-class than in older age-classes (Table 1). Inversely, basal area values of jack pine, black spruce, trembling aspen (*Populus tremuloides*), all conifers combined and total basal area were highest in the 80- to 120-year age-class (Table 1). The volume of woody debris, gaps, basal area of balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), deciduous combined, and shrubs did not vary with time since fire.

Species

A total of 139 taxa were observed during this study: 40 species of mosses, 10 species of *Sphagnum*, 13 taxa of liverworts, 38 species of epiphytic lichens, and 38 species of terricolous lichens. The species list is presented in Appendix A. *Pleurozium schreberi* was the most abundant terricolous species. *Bryoria trichodes*, *Bryoria furcellata*, *Mycoblastus sanguinarius*, and *Hypogymnia physodes* were the most abundant epiphytic lichens (Appendix A). More than a quarter of the species encountered in the study were exclusive species, i.e., they were observed in only one age-class (37 species: 17 mosses, 2 liverworts, 2 *Sphagnum* species, 4 terricolous lichens, and 12 epiphytic lichens (Appendix A)). Exclusive species were also rare species. None of the species commonly encountered (present in at least four

Table 2. Effects of time since fire on species cover and richness indices as shown by ANOVAs (computed on ranks; $n = 22$ sites, except for TNS in the different groups that were sampled in 18 sites).

	Age-classes					
	80–120 years ($n = 5$)	120–160 years ($n = 6$)	160–200 years ($n = 5$)	>200 years ($n = 6$)	F	p
Liverwort cover	0.45 (0.97)*b*	0.21 (0.30)*b*	1.76 (1.52)*a*	3.13 (1.96)*a*	7.78	0.002
Liverwort richness	0.40 (0.55)*b*	1.33 (0.52)*a*	1.40 (0.55)*a*	1.33 (0.52)*a*	3.64	0.033
TNS of liverworts	3.20 (1.30)*a*	5.17 (3.60)*a*	5.25 (1.71)*a*	4.33 (3.06)*a*	0.58	0.639
Moss cover	65.07 (22.28)*a*	40.81 (29.31)*a*	42.50 (22.38)*a*	54.74 (38.00)*a*	1.00	0.418
Moss richness	5.00 (1.00)*a*	6.83 (2.79)*a*	6.40 (1.82)*a*	5.00 (0.89)*a*	1.38	0.282
TNS of mosses	12.80 (3.03)*a*	13.33 (5.50)*a*	13.50 (2.38)*a*	9.67 (2.08)*a*	1.06	0.396
Sphagnum cover	15.10 (14.07)*b*	44.18 (21.36)*a*	41.68 (20.98)*a*	43.18 (14.49)*a*	3.11	0.050
Sphagnum richness	2.20 (1.92)*a*	3.67 (1.86)*a*	3.20 (1.30)*a*	4.00 (1.55)*a*	1.07	0.385
TNS of *Sphagnum*	4.20 (1.79)*a*	5.33 (1.63)*a*	5.75 (0.50)*a*	6.33 (2.08)*a*	0.49	0.697
Epiphytic lichen cover	54.22 (13.88)*a*	65.20 (16.57)*a*	77.13 (14.88)*a*	70.20 (6.18)*a*	2.18	0.126
Epiphytic lichen richness	14.20 (0.84)*a*	15.33 (1.51)*a*	15.60 (1.34)*a*	14.17 (1.47)*a*	1.33	0.295
TNS of epiphytic lichens	21.40 (3.21)*a*	19.67 (2.80)*a*	19.50 (2.08)*a*	17.67 (2.31)*a*	1.12	0.374
Terricolous lichen cover	1.63 (1.95)*a*	1.58 (1.61)*a*	7.32 (10.05)*a*	6.20 (7.02)*a*	1.59	0.227
Terricolous lichen richness	2.00 (2.55)*a*	3.83 (3.66)*a*	2.80 (3.49)*a*	5.67 (2.34)*a*	2.07	0.141
TNS of terricolous lichens	14.60 (2.07)*a*	13.83 (3.31)*a*	14.50 (3.87)*a*	14.33 (0.58)*a*	1.20	0.347

Note: Richness is the number of species observed during the quantitative sampling and total number of species (TNS) is the number of species found at a given site during the species survey. Values with the same letter are not significantly different ($p > 0.05$) between age-classes.

sites) in our study were found exclusively in one age-class. A larger number of species were found in sites between 120 and 160 years of age than in the other age-classes (Appendix A). In general, we observed nearly twice as many species in the species survey as we did during quantitative sampling (Appendix A). We found significantly more species in each age-class during the survey sampling for all taxonomic groups except for *Sphagnum* (Table 2). Liverwort cover was significantly higher in the 160- to 200-year and >200-year age-classes than in the other two classes. Liverwort richness as well as *Sphagnum* cover were lowest in the 80- to 120-year age-class (Table 2).

Species composition of the terricolous community

The ordination derived from the matrix of terricolous species (abundance data) is shown in Fig. 2, and the Spearman correlation coefficients between site characteristics, species, diversity estimates, site locations, and ordinations axes are presented in Table 3. The first two axes explained 85% of the variation in the terricolous species community. Axis 1 ($R^2 = 0.500$) was mainly linked to a paludification gradient as reflected by the positive correlations of this axis with thickness of the organic matter, time since fire, mean tree age, basal area value of larch, *Sphagnum* TNS, *Sphagnum* richness, *Sphagnum* cover, and lichen cover. The total basal area value and basal area values for conifers, deciduous trees, balsam fir, and black spruce as well as moss cover were negatively correlated with the first axis. Sites at which *Sphagnum* were more abundant can be observed toward the right of the graph. Species with a preference for sites with a high organic matter depth such as *Sphagnum angustifolium*, *Sphagnum capillifolium*, *Sphagnum fuscum*, *Dicranum undulatum*, *Aulacomnium palustre*, and *Cladina rangiferina – Cladina stygia* typified these sites. A clustering of sites where species composition was dominated by forest species such as *Pleurozium schreberi*, *Dicranum polysetum*, *Polytrichum commune*, and *Ptilium crista-castrensis* can be observed in the left part of the ordination, which roughly corresponded to the younger “half” of age gradient. The second axis ($R^2 = 0.353$) was positively correlated with basal area of deciduous trees and *Sphagnum* cover. *Sphagnum girgensohnii* and *Sphagnum magellanicum* were more abundant in sites located in the upper part of the graph. The cover of lichen and the abundances of *Pleurozium schreberi* and *Cladina rangiferina – Cladina stygia* were inversely correlated to the second axis. Therefore, the second axis could be interpreted as a gradient in microtopographic variation, which was probably higher in sites located in the lower part of the ordination, providing *Sphagnum*-free drier sites for *Cladina* spp. and other lichen species.

Species composition of the epiphyte community

The first two axes explained 91% of the variation in the epiphytic lichen matrix. The first axis, representing 80% of the variation, was negatively correlated to epiphytic cover, time since fire, and mean tree age (Table 4). The first axis may be interpreted as a gradient of time since fire. Pioneer tree species jack pine and trembling aspen, and TNS of epiphytic lichens were positively correlated with the first axis (Table 4). Most of the sites in the 80- to 120-year and 120- to 160-year age-classes were located in the right-hand part of the ordination (Fig. 3). These forests were characterized by a greater abundance of *Tuckermannopsis americana*, *Parmeliopsis ambigua*, *Hypogymnia physodes*, and *Bryoria furcellata*. Sites belonging to the 160- to 200-year and over 200-year age-classes were found in the left-hand part of the ordination and *Mycoblastus sanguinarius*, *Bryoria trichodes*, and *Usnea* spp. were more abundant there. The second axis explained only 12% of the variation and, thus, provided much less information than axis 1. Epiphytic lichen cover, mean tree age, and the abundance of *Bryoria furcellata* and *Imshaugia aleurites* were negatively correlated with the second axis, whereas the abundance of *Parmeliopsis hyperopta* was positively correlated to the second axis.

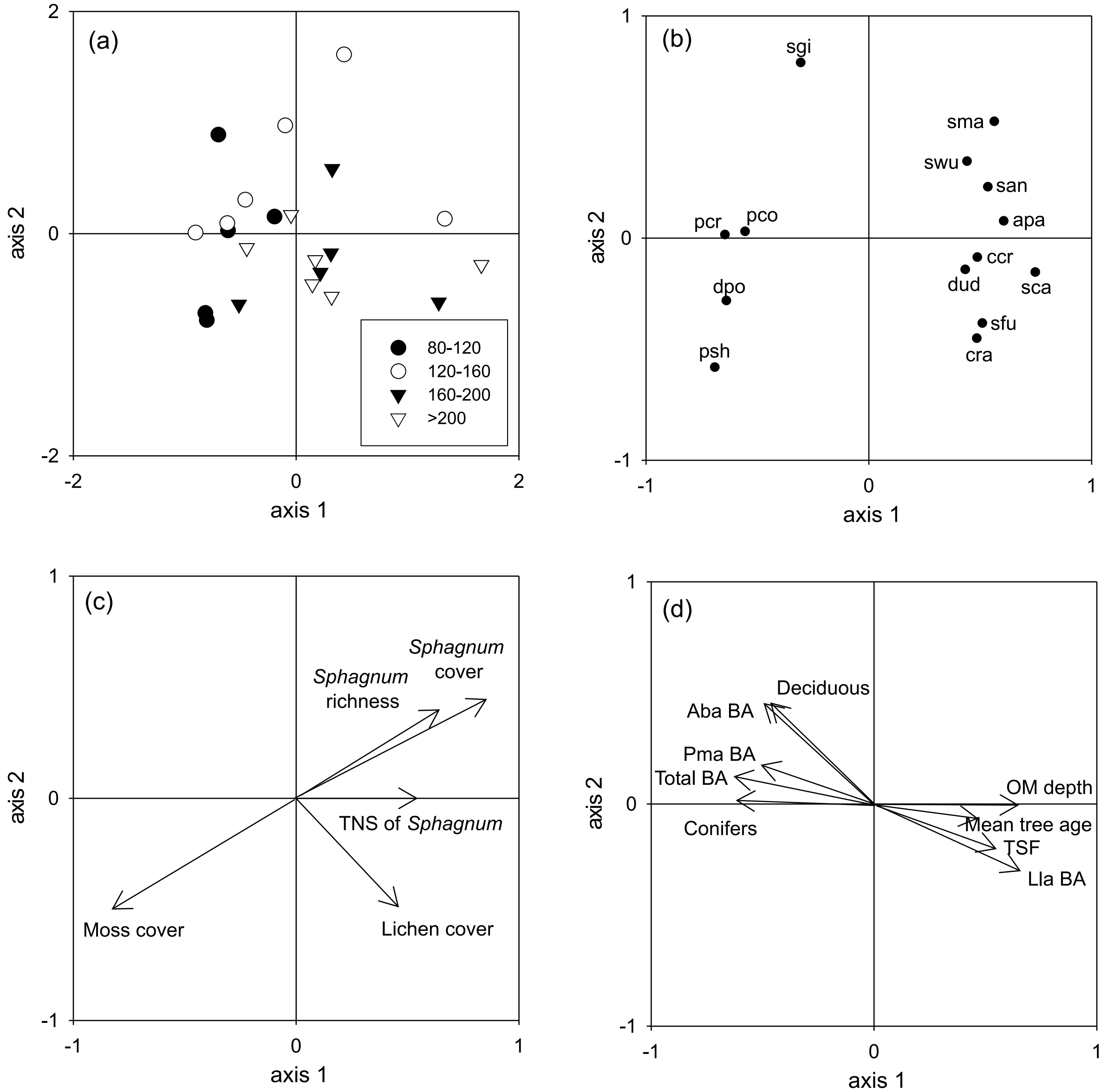


Fig. 2. Nonmetric multidimensional scaling ordination showing (*a*) the position of sites according to their terricolous species composition, (*b*) the position of terricolous species, (*c*) vector plot showing relationships of diversity variables with the ordination axes, and (*d*) vector plot showing relationships of environmental variables with the ordination axes. Species, site variables, and diversity estimates that are significantly correlated ($p < 0.05$) with one of the two axes are shown in this figure. Only species present in at least four sites were incorporated into the ordination ($n = 22$ sites; 23 species). Species codes are as follows: apa, *Aulacomnium palustre*; cra, *Cladina rangiferina – Cladina stygia*; ccr, *Cladonia crispata*; dpo, *Dicranum polysetum*; dud, *Dicranum undulatum*; pco, *Polytrichum commune*; pcr, *Ptilium crista-castrensis*; psh, *Pleurozium schreberi*; san, *Sphagnum angustifolium*; sca, *Sphagnum capillifolium*; sfu, *Sphagnum fuscum*; sgi, *Sphagnum girgensohnii*; sma, *Sphagnum magellanicum*; swu, *Sphagnum wulfianum*. Environmental variable codes are as follows: total BA, total basal area; conifers, basal area of conifers; deciduous, basal area of deciduous trees; Aba BA, basal area of *Abies balsamea*; Pma BA, basal area of *Picea mariana*; Lla BA, basal area of *Larix laricina*; OM depth, thickness of organic matter; TSF, time since fire.

Indicator species

Polytrichum commune, *Dicranum polysetum*, *Ptilium crista-castrensis*, and *Japewia tornoënsis* each had an importance value that was significantly higher in forests between 80 and 120 years old than in the older age-classes (Appendix A). By contrast, the importance values of *Ptilidium ciliare* and *Sphagnum fuscum* increased with time since fire and were maximal in forests over 200 years old. *Sphagnum capillifolium* was more frequent and (or) abundant in forests between 160 and 200 years old but was nonetheless common in forests over 200 years of age.

Discussion

Effects of time since fire and site characteristics on species diversity

Surprisingly our results showed that a long forest continuity did not result in old-growth forests building up a larger

Table 3. Spearman rank correlations between environmental variables, diversity estimates, species, and site locations along the two axes with the higher coefficients of determination of the nonmetric multidimensional scaling ordination performed on abundance data of terricolous species (n = 22 sites; 23 species).

	Axis 1 (R^2 = 0.500)	Axis 2 (R^2 = 0.353)
Environmental variables		
Time since fire	0.557**	–0.200
Mean tree age	0.448*	–0.060
Organic matter depth	0.640***	–0.002
Abies balsamea basal area	–0.487*	0.446
Larix laricina basal area	0.657***	–0.298
Picea mariana basal area	–0.511*	0.181
Deciduous basal area	–0.458*	0.446*
Coniferous basal area	–0.602**	0.034
Total basal area	–0.627**	0.123
Diversity estimates		
Sphagnum cover	0.864***	0.443*
Sphagnum richness	0.624**	0.387
TNS of *Sphagnum*	0.703***	0.064
Lichen cover	0.452*	–0.491*
Moss cover	–0.823***	–0.403
Species		
Aulacomnium palustre	0.605**	0.077
Dicranum polysetum	–0.640***	–0.281
Dicranum undulatum	0.432*	–0.141
Polytichum commune	–0.556**	0.030
Ptilium crista-castrensis	–0.646***	0.016
Pleurozium schreberi	–0.692***	–0.581**
Cladonia crispata	0.487*	–0.086
Cladina rangiferina – C. stygia	0.484*	–0.451*
Sphagnum angustifolium	0.534**	0.231
Sphagnum capillifolium	0.747***	–0.153
Sphagnum fuscum	0.509*	–0.383
Sphagnum girgensohnii	–0.306	0.790***
Sphagnum magellanicum	0.563**	0.525**
Sphagnum wulfianum	0.440*	0.346

Note: Only those variables with significant correlations ($p < 0.05$) with one or both ordination axes are shown. ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

Table 4. Spearman rank correlations between environmental variables, diversity estimates, species, and site locations along the two axes with the higher coefficients of determination of the nonmetric multidimensional scaling ordination performed on abundance data of epiphytic species (n = 22 sites; 16 species).

	Axis 1 (R^2 = 0.797)	Axis 2 (R^2 = 0.117)
Environmental variables		
Time since fire	–0.626**	0.078
Mean tree age	–0.542**	–0.496*
Pinus banksiana basal area	0.647***	–0.319
Populus tremuloides basal area	0.573**	–0.024
Diversity estimates		
Epiphytic cover	–0.535**	–0.473*
TNS of epiphytic lichens	0.453*	–0.219
Species		
Bryoria furcellata	0.587**	–0.723***
Bryoria trichodes	–0.845***	–0.137
Hypogymnia physodes	0.641***	–0.386
Imshaugia aleurites	–0.378	–0.572**
Mycoblastus sanguinarius	–0.833***	–0.039
Ochrolechia pseudopallescens	–0.489*	–0.177
Parmeliopsis ambigua	0.615**	–0.278
Parmeliopsis hyperopta	–0.379	0.609**
Tuckermannopsis americana	0.836***	0.332
Usnea spp.	–0.517*	0.207

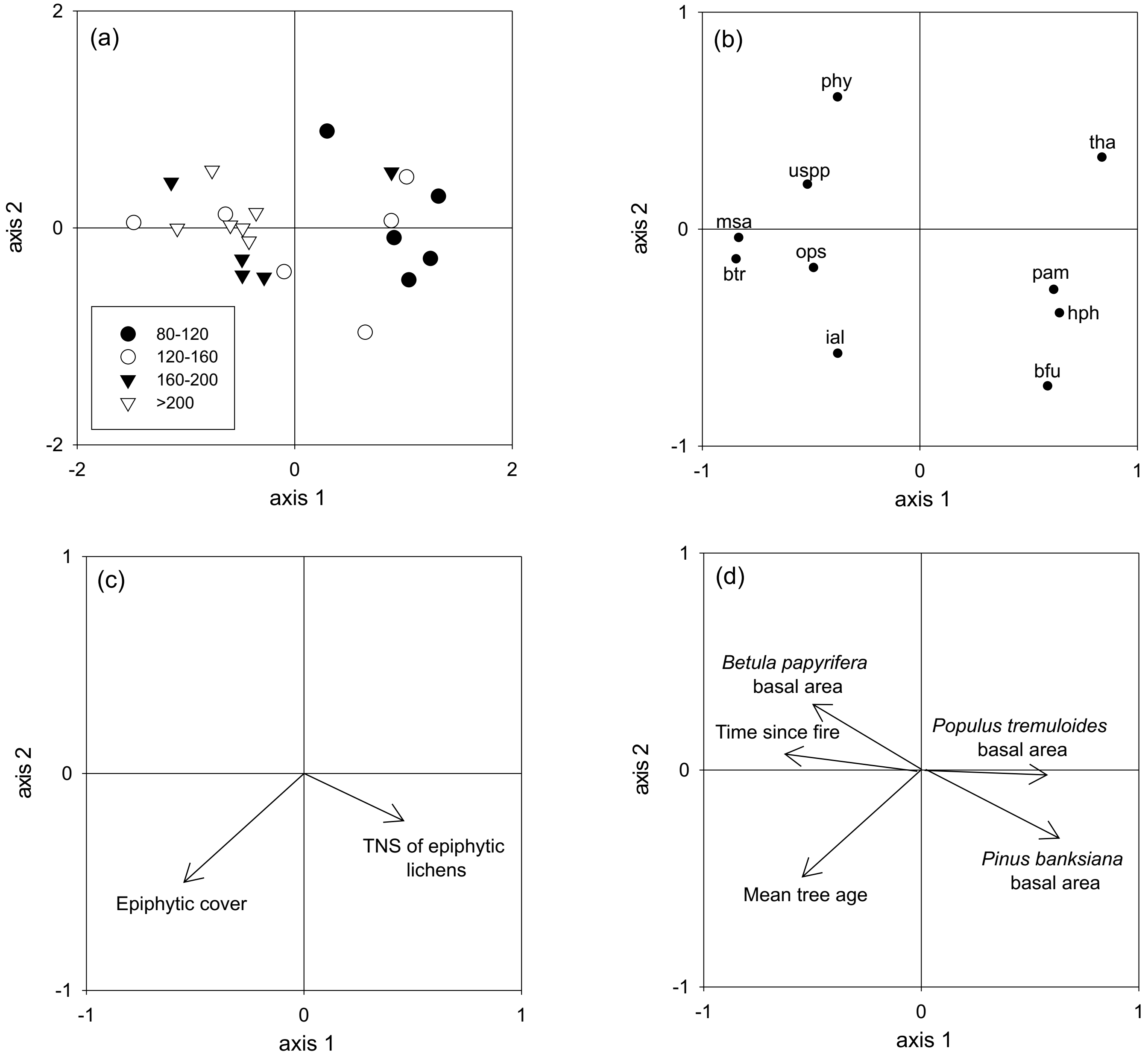
Note: Only those variables with significant correlations ($p < 0.05$) with one or both ordination axes are shown. ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

number of species compared with our youngest stands. None of the species commonly encountered in our study were found exclusively in old growth. However, a structuring of bryophyte and lichen communities in terms of abundance was observed in relation to the time since fire gradient (80 to >200 years). The particularity of our results might be explained by the presence of paludification in our region. According to Heinselman (1981), on gently sloping mesic to wet terrain, long fire-free periods may allow so much organic matter to accumulate that mineral soil sites become permanent peatland. This phenomenon, called paludification, occurs in various regions of Canada, such as the Hudson Bay Lowlands, the Clay Belt of Ontario and Quebec, and many areas of Newfoundland (Heinselman 1981; Taylor et al. 1987). This accumulation causes a lowering of soil temperature and reduces decomposition rates (Van Cleve et al. 1983) and nutrient availability to plants, since elements are immobilized in the organic soil layers (Paré et al. 1993). With time since fire, we observed a degradation in site quality in terms of the diversity and availability of microhabitats suitable for colonization by terricolous and epiphytic bryophytes and lichens.

Effects of time since fire and site characteristics on terricolous species

In mature forests (80–120 years), the high basal areas of trees and the relatively low organic matter depth created conditions favourable for the development of a carpet of mosses heavily dominated by *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Polytrichum commune*, and *Dicranum polysetum*. These mosses are typical of closed boreal forests located on fairly well-drained sites (La Roi and Stringer 1976; Heinselman 1981; Johnson 1981; Foster 1985; Esseen et al. 1997). With time and provided that no fires occur, a thick moss layer is built up. Our oldest sites were paludified sites: they were poorly drained with a high organic matter depth and were less productive than mature sites. This situation is reflected by a decline in the basal area of trees. In such sites, the richness and cover of *Sphagnum* are generally higher than in mature sites. *Pleurozium schreberi* was still dominating the ground cover in the older sites, but the abundance of *Sphagnum*, in particular *Sphagnum fuscum*, *Sphagnum angustifolium*, and *Sphagnum capillifolium*, is higher than in younger sites. *Cladina rangiferina – Cladina stygia*, *Aulacomnium palustre*, and *Dicranum undulatum* were companion species to *Pleurozium schreberi* and *Sphagnum*. The high abundance of liverworts, a group normally sensitive to desiccation and thus found in closed canopy forests, is due

Fig. 3. Nonmetric multidimensional scaling ordination showing (*a*) the position of sites according to their epiphytic species composition, (*b*) the position of epiphytic species, (*c*) vector plot showing relationships of diversity variables with the ordination axes, and (*d*) vector plot showing relationships of environmental variables with the ordination axes. Species, site variables, and diversity estimates that are significantly correlated ($p < 0.05$) with one of the two axes are shown in this figure. Only species present in at least four sites were incorporated into the ordination ($n = 22$ sites; 16 species). Species codes are as follows: bfu, *Bryoria furcellata*; btr, *Bryoria trichodes* ssp. *trichodes*; hph, *Hypogymnia physodes*; ial, *Imshaugia aleurites*; msa, *Mycoblastus sanguinarius*; ops, *Ochrolechia pseudopallescens*; pam, *Parmeliopsis ambigua*; phy, *Parmeliopsis hyperopta*; tha, *Tuckermannopsis halei*; uspp, *Usnea* spp.



to the abundance of the robust species *Ptilidium ciliare*. Other liverwort species were often observed in small water holes at the base of trees.

Although we observed differences in the terricolous bryophyte and lichen communities along the successional gradient, these differences are based mainly on changes in species abundance rather than the number of species. The change in species dominance as seen above is mainly due to changes in site characteristics, such as organic matter depth and change in tree basal area with time since fire. However, site history could also explain some differences in the species composition of terricolous bryophytes and lichens observed among age-classes and among sites belonging to the same age-class. For example, a site disturbed by a fire of extreme severity that burned the organic matter right down to the mineral soil might progress more slowly to the stage where *Sphagnum* dominate the moss cover than a site disturbed by a low-severity fire that still possesses remnant mounds of old-growth typical species that existed prior to the last fire. In our study, small mounds of *Sphagnum* interspersed with mosses and liverworts, which comprised species that were associated with older forests, such as *Sphagnum fuscum*, *Sphagnum capillifolium*, and *Sphagnum angustifolium* were frequently observed in the mature sites. However, the abundance of these mounds and species was highly variable from one site to another.

The *Pleurozium schreberi* and *Ptilium crista-castrensis* moss carpet found in the mature stands and the *Pleurozium schreberi* and *Sphagnum* moss carpet of older stands tend to reduce the diversity of bryophyte and terricolous lichen species by acting as a barrier to the establishment of other smaller and less competitive species and by overgrowing species already established. Thus, as reported by Jonsson and Esseen (1990), species richness was highest on sites where disturbances such as uprooting had broken the continuity of the moss cover and increased the number of potential substrates for colonization (personal observation).

The presence of woody debris on the ground is known to be important for the establishment of many bryophytes and lignicolous lichens, as the debris provides a variety of habitats and has been reported to be more abundant in old-growth forests (Esseen et al. 1997; Gustafsson and Hallingbäck 1988; Soderström 1988; Rambo and Muir 1998; Kruys and Jonsson 1999). In this study, the volume of coarse woody debris on the ground did not increase with time since fire, implying that there are no more substrates for species colonization in old sites (see Table 1). As basal area of black spruce declines with time since fire, coarse woody debris observed in old sites was relatively small and was quickly covered by various *Sphagnum* species and feathermosses and integrated into the moss or *Sphagnum* carpet. Coarse woody debris was not as important as expected in increasing the overall terricolous species diversity and the individual species abundance; woody debris was not associated with bryophyte and lichen species or with any diversity estimates. Again, the presence of paludification in our region may explain why our results differ from other reports from Scandinavia or the Pacific Northwest coast.

Effects of time since fire and site characteristics on epiphytic species

The differences observed in epiphytic communities along the mature to old-growth sequence are mainly related to changes in individual species abundance rather than changes in species richness. Dettki and Esseen (1998) in Sweden and Hyvärinen et al. (1992) in Finland found similar results. As also observed by Dettki and Esseen (1998), exclusive species (those found in only one age-class) were neither common nor abundant. However, mature forest stands encompassed a greater abundance of *Tuckermannopsis americana*, *Bryoria furcellata*, *Hypogymnia physodes*, and *Parmeliopsis ambigua* than older forests. By contrast, *Mycoblastus sanguinarius*, *Bryoria trichodes*, and *Usnea* spp. were more abundant in old-growth stands. Although quantitative sampling was conducted only on spruce branches, other tree species appear to influence species abundance on spruce branches. For instance, increased importance of jack pine favours colonization of spruce by some species particularly abundant on jack pine, such as *Bryoria furcellata*.

The number of epiphytic lichen species found in the survey sampling was greater in forests where trembling aspen and jack pine were present. The within-site tree heterogeneity increased epiphytic species richness by offering a greater variety of substrates to species colonization. Furthermore, the presence of hardwoods in coniferous stands has been reported to increase the epiphytic species richness of mature stands, since they are colonized by a unique set of species (Kuusinen 1994; Neitlich and McCune 1997; Dettki and Esseen 1998; Boudreault et al. 2000). According to Dettki and Esseen (1998), the smaller proportion of deciduous trees in old-growth stands could explain the slight decrease in epiphytic lichen richness in old-growth stands.

Several authors have shown that the abundance of epiphytic lichens increases with stand age (McCune 1993; Neitlich 1993; Esseen et al. 1996). Based on our results and previous studies carried out on trembling aspen in mixed boreal forest (Boudreault et al. 2000), epiphytic lichen abundance is closely and positively related to mean tree age. As explained by Hazell et al. (1998), old trees have been present for a longer time for colonization than younger trees. Similarly, there is a greater period for vegetative and sexual expansion once the species have colonized. Old trees supporting an abundant epiphytic lichen flora could be of a great importance for this region’s woodland caribou (*Rangifer tarandus caribou*) during winter. Indeed, the primary winter forage species of woodland caribou are arboreal lichens (Rominger et al. 1994).

Species assemblage within communities appears to differ from one region to another. For example, *Evernia mesomorpha* is a very abundant lichen which is ubiquitous in the study area but rare in Sweden (Tibell 1992). By contrast, *Alectoria sarmentosa* is abundant there, especially in old-growth forests, but it was not observed in our samples, even though it is a common species in North America. *Bryoria furcellata* and *Bryoria nadvornikiana* were much more abundant in our study, whereas *Platismatia glauca* and a number of other species were inventoried much more frequently in Sweden. In addition, *Usnea longissima*, a species symbolic of old-growth forests in Scandinavia (Esseen et al. 1981, 1992), did not occur in our paludified old-growth forests, even though it occurs in Quebec and can be relatively abundant in some areas (personal observation).

Implications for forest management

Bergeron et al. (1999) have indicated that a forest management approach that emulates “natural” stand composition and structure at the scale of the entire forest management unit (FMU; approximately 100 000 ha) while modifying allowable cuts only slightly, might guarantee the maintenance of biodiversity in the area. This goal could be achieved by diversifying silvicultural treatments at the FMU scale through an approach that takes into account the natural disturbance regime and maximum rotation age (Bergeron et al. 1999). For the black spruce forest zone, these authors propose that a portion of stands be managed as follows: (*i*) return stands to the first cohort of seeded black spruce through a clear-cut followed by replanting or seeding, (*ii*) carry out partial cuts that emulate natural succession in mature stands (cohort 2), and (*iii*) mimic the gaps that are typical of old growth through selection harvesting in old-growth forests (cohort 3). It should be noted that rejuvenation of forests toward first-cohort stands can be done within any of the three cohorts.

This management model would make it possible to maintain the different successional stages in the landscape (at the FMU scale). On one hand this model, by diversifying treatments, is clearly better for bryophyte and lichen diversity than using only clear-cut treatment on the entire management unit. However, this management model alone seems insufficient to maintain structural differences within stands to preserve bryophyte and lichen diversity across the different successional stages. Therefore, we should also integrate into this model recommendations made at a smaller scale, such as stand level, to ensure integrity of these communities.

Research conducted in the study area has already shown that young forests originating from clearcuts and those originating from recent fires differed in terms of their bryophyte and terricolous lichen communities (Nguyen-Xuan et al. 2000). Bryophyte communities that were present prior to a clearcut were able to maintain themselves after the disturbance, whereas sites disturbed by fire were colonized by pioneer species of bryophytes and lichens. The terricolous flora of stands that have resulted from logging can be expected to differ from that found in fire-origin stands once these stands reach maturity. We can hypothesize that logged stands will be paludified more rapidly than fire-origin stands. Consequently, in a managed territory if we want to mimic natural succession and preserve the different terricolous species community by using clear-cutting, we should modify the groundcover to reduce the organic matter layer. For example, scarification and controlled burning of sites after cutting might mitigate the differences between fire-origin stands and logged stands. On the other hand, partial cutting and selective harvesting should be implemented in a way to limit damage to the groundcover, since we observed that numerous terricolous species were restricted to various microhabitats in the species survey.

Green-tree retention approach in the clear-cut treatments might help epiphytic species recolonization of successive generations of trees. However, the species must be able to survive on remnant trees in the new habitat created by logging. Consequently, groups of remnant trees may provide a more suitable habitat for these species than isolated trees (Neitlich and McCune 1997). Old trees play an important role in promoting epiphytic lichen abundance. In a management approach that includes a proportion of partial or selective cuttings, old trees should be preserved within managed forests to favour the overall abundance of epiphytic lichen communities. Stand rejuvenation and diversification of substrates suitable for epiphyte colonization might help to increase epiphytic species richness. Neitlich and McCune (1997) in Oregon showed that managed forests can be as diverse or even more diverse than old-growth forests, particularly if gaps conducive to the regeneration of deciduous species are created. Retention of large old deciduous trees should be adopted, since these trees possess a particular flora (Kuusinen 1994; Neitlich and McCune 1997; Dettki and Esseen 1998; Boudreault et al. 2000) and are a potential source of propagules for the inoculation of conifers (Sillett and Goslin 1999). Extending rotation age may also lead to an increase in epiphytic lichen biomass, since lichens have more time for colonization and growth (Esseen et al. 1996).

Conclusion

Our results suggest that a combination of landscape- and stand-level recommendations is essential to maintain bryophyte and lichen diversity. A landscape-level objective of maintenance of the different successional stages in a FMU can partly preserve the diversity of habitats, which is responsible for bryophyte and lichen diversity. However, this has to be complemented by recommendations made at a smaller scale. For example, as many species are restricted to microhabitats, we should minimize disturbances to the groundcover and preserve diversity of epiphytic substrates. Moreover, retention of old trees should be adopted to increase epiphytic biomass. Furthermore, as a complement to the proposed approach, integral protection of some areas in each stage of the mature to old-growth sequence would ensure that all species will be preserved. As mentioned above, species communities varied from one region to another, and the presence of a paludification gradient can completely change the expected pattern of species diversity over time since last disturbance (80 to >200 years after fire). Such observations show that the boreal forest is, to a certain extent, heterogeneous and that managers should consult studies conducted at the local and (or) regional scale when establishing forest management plans for given regions.

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Appendix A

Table A1. Mean cover of species (%), number of sites where species were present during quantitative sampling (QS) and species survey (SS), and total number of species within each taxonomic group for the two types of sampling in the different age-classes.

	80–120 years			120–160 years			160–200 years			>200 years		
	%	QS (*n* = 5)	SS (*n* = 5)	%	QS (*n* = 6)	SS (*n* = 6)	%	QS (*n* = 5)	SS (*n* = 4)	%	QS (*n* = 6)	SS (*n* = 3)
Liverworts												
Barbilophozia sp.	0	0	0	0	0	2	0	0	1	0	0	0
Bazzania trilobata	0	0	1	+[†]	1	2	0	0	0	+	1	0
Blepharostoma trichophyllum	0	0	2	0	0	2	+	1	2	0	0	0
Cephalozia sp.	0	0	0	0	0	2	0	0	0	0	0	0
Cephalozia lunulifolia	0	0	2	0	0	4	0	0	3	0	0	2
Chiloscyphus sp.	0	0	0	0	0	2	0	0	1	0	0	0
Lepidozia reptans	0	0	3	0	0	3	0	0	2	0	0	2
Lophozia sp.	0	0	0	0	0	2	0	0	2	0	0	1
Lophozia incisa	0	0	0	0	0	1	0	0	0	0	0	0
Mylia anomala	0	0	0	0	0	0	+	1	1	+	1	2
*Ptilidium ciliare**	0.5	2	3	0.2	5	6	1.7	5	4	3.1*	6	3
Ptilidium pulcherrimum	0	0	5	+	1	5	0	0	4	0	0	2
Scapania sp.	0	0	0	+	1	1	0	0	0	0	0	1
No. of liverwort species		1	6		4	12		3	9		3	7
Mosses												
Aulacomnium palustre	+	1	2	0.5	3	4	0.2	3	4	+	2	1
Brachythecium campestre	0	0	1	0	0	0	0	0	0	0	0	0
Brachythecium reflexum	0	0	1	0	0	0	0	0	0	0	0	0
Brachythecium rutabulum	0.1	1	2	0.1	1	3	+	1	3	0	0	0
Callicladium haldanianum	0	0	0	0	0	1	0	0	0	0	0	1
Calliergon richardsonii	0	0	0	0	0	0	0	0	1	0	0	0
Campylium chrysophyllum	0	0	0	0	0	1	0	0	0	0	0	0
Campylium hispidulum	0	0	1	0	0	0	0	0	0	0	0	0
Campylium stellatum	0	0	0	0	0	0	0	0	1	0	0	0
Dicranella heteromalla	0	0	1	0	0	1	0	0	0	0	0	0
Dicranum flagellare	0	0	0	+	1	2	0	0	0	0	0	0
Dicranum fuscescens	0	0	5	0.1	3	6	+	2	4	0	0	3
Dicranum montanum	0	0	0	0	0	1	0	0	0	0	0	0
Dicranum ontariense	0	0	0	0.1	1	4	0	0	3	0	0	2
*Dicranum polysetum**	2.7*	5	5	0.5	6	6	1.0	5	4	0.3	5	3
Dicranum undulatum	0	0	2	+	1	2	0.3	2	3	0.1	1	1
Drepanocladus fluitans	0	0	0	0	0	1	0	0	1	0	0	0
Drepanocladus uncinatus	0	0	4	0.2	2	3	+	1	2	0	0	0
Drepanocladus vernicosus	0	0	0	0	0	0	0	0	1	0	0	0
Hylocomium splendens	2.0	3	5	5.5	3	5	1.2	5	4	2.5	5	2
Hypnum pratense	0	0	0	0	0	1	0	0	0	0	0	0
Isopterygium distichaceum	0	0	0	0	0	1	0	0	0	0	0	0
Mnium spinulosum	0	0	3	0	0	0	0	0	0	0	0	0
Orthotrichum speciosum	0	0	2	0	0	0	0	0	0	0	0	0
Plagiomnium ciliare	0	0	0	0	0	1	0	0	0	0	0	0
Plagiothecium denticulatum	0	0	0	+	1	1	0	0	0	0	0	0
Plagiothecium laetum	0	0	1	0	0	4	0	0	1	0	0	2
Platydictya jungermannioides	0	0	0	0	0	0	0	0	1	0	0	0
Pleurozium schreberi	48.5	5	5	29.8	6	6	35.5	5	4	38.6	6	3
Pohlia nutans	0	0	5	+	1	4	0	0	3	8.9	2	1
*Polytrichum commune**	2.5*	4	4	0.2	2	5	+	1	0	+	2	2
Polytrichum strictum	+	1	2	0.1	2	3	+	1	3	0	0	1
*Ptilium crista-castrensis**	8.9*	5	5	3.4	6	6	2.2	5	4	1.2	5	2
Pylaisiella polyantha	0	0	3	0	0	0	0	0	0	0	0	0
Rhizomnium punctatum	0	0	1	0	0	1	0	0	1	0	0	1
Rhytidiadelphus triquetrus	0	0	1	0	0	0	0	0	1	0	0	0
Tetraphis pellucida	0	0	3	0	0	5	0	0	2	0	0	2
Tomenthypnum nitens	0	0	0	0	0	0	0.2	1	1	0	0	0
Tomenthypnum falcifolium	0	0	0	0.1	2	2	0	0	2	+	2	2
No. of moss species		8	23		16	27		12	23		9	16
Sphagnum												
Sphagnum angustifolium	+	1	3	11.7	4	5	2.3	1	4	3.3	3	2
*Sphagnum capillifolium**	4.0	3	4	3.8	5	6	22.3*	5	4	18.4	6	3
Sphagnum cuspidatum	0	0	0	0	0	0	0	0	2	0.6	1	1
Sphagnum fallax	0	0	0	+	1	1	0	0	0	0	0	0

Table A1 (*continued*).

	80–120 years			120–160 years			160–200 years			>200 years		
	%	QS (*n* = 5)	SS (*n* = 5)	%	QS (*n* = 6)	SS (*n* = 6)	%	QS (*n* = 5)	SS (*n* = 4)	%	QS (*n* = 6)	SS (*n* = 3)
*Sphagnum fuscum**	0.1	1	2	0	0	2	6.2	2	3	11.3*	6	3
Sphagnum girgensohnii	10.8	4	4	23.6	5	6	5.2	3	2	9.6	4	3
Sphagnum magellanicum	0.1	1	4	4.9	4	5	4.0	3	4	0.1	1	3
Sphagnum russowii	0	0	0	+	1	2	0	0	1	+	1	2
Sphagnum squarrosum	0	0	0	0	0	1	0	0	0	0	0	0
Sphagnum wulfianum	0.1	1	4	0.1	2	4	1.7	2	3	+	2	2
No. of *Sphagnum* species		6	6		7	9		6	8		8	8
Epiphytic lichens												
Bryoria capillaris	0	0	1	0	0	0	0	0	0	0	0	0
Bryoria furcellata	31.8	5	5	29.0	6	6	25.5	5	4	16.1	6	3
Bryoria fuscescens	0	0	1	0	0	0	0	0	0	0	0	0
Bryoria nadvornikiana	0.2	2	4	0.2	1	4	0.3	3	3	0	0	1
Bryoria trichodes ssp. *trichodes*	6.8	5	5	25.4	6	6	43.5	5	4	48.1	6	3
Evernia mesomorpha	8.8	5	5	5.2	6	6	8.1	5	4	9.1	6	3
Hypocenomyce friesii	0	0	1	0	0	1	0	0	2	0	0	1
Hypogymnia physodes	25.4	5	5	16.9	6	6	20.8	5	4	15.1	6	3
Hypogymnia sp.	0	0	0	0	0	0	0	0	0	0	0	2
Imshaugia aleurites	4.2	5	5	10.0	6	6	12.3	5	4	10.0	6	3
Imshaugia placorodia	0	0	2	0	0	2	0	0	0	0	0	1
*Japewia tornoënsis**	4.5*	5	5	0.3	3	5	1.0	5	4	0.8	5	2
Lecanora circumborealis	+	2	3	0.1	2	3	0.3	3	2	0.4	3	1
Lobaria pulmonaria	0	0	0	0	0	0	0	0	0	0	0	1
Melanelia olivacea	0	0	1	0	0	0	0	0	0	0	0	0
Melanelia septentrionalis	0	0	0	0	0	1	0	0	0	0	0	0
Melanelia sp.	0	0	1	0	0	0	0	0	0	0	0	0
Mycoblastus sanguinarius	2.8	5	5	20.7	6	6	22.1	5	4	20.9	6	3
Ochrolechia pseudopallescens	2.2	4	5	2.6	6	6	2.7	4	4	2.8	6	3
Parmelia sulcata	1.2	3	5	0.7	5	6	1.1	2	4	2.2	5	3
Parmelina galbina	0	0	0	0	0	1	+	1	3	0	0	1
Parmeliopsis ambigua	1.9	5	5	1.2	6	6	1.1	5	4	1.2	6	3
Parmeliopsis hyperopta	0.5	2	5	0.3	3	5	0.3	4	4	0.4	4	2
Physcia aipolia	0	0	3	0	0	2	0	0	0	0	0	0
Platismatia glauca	0	0	1	0	0	0	0	0	1	0	0	0
Platismatia tuckermanii	0.1	1	3	0	0	0	0	0	0	0	0	0
Ramalina dilacerata	0	0	1	0	0	0	0	0	0	0	0	0
Tuckermannopsis americana	15.4	5	5	8.8	6	6	7.1	5	4	5.3	6	3
Tuckermannopsis orbata	0.1	1	4	0	0	1	0	0	1	0	0	0
Usnea diplotypus	0	0	0	0.2	1	1	0	0	0	0	0	0
Usnea filipendula	0	0	4	0.1	1	6	0.4	1	4	0	0	2
Usnea hirta	0.5	2	3	1.0	6	6	0.5	2	3	0.1	2	2
Usnea longissima	0	0	0	0.1	1	1	0	0	0	0	0	0
Usnea subfloridana	0	0	2	0.1	1	5	0.1	1	3	0	0	2
Usnea sp.	1.3	5	5	4.3	6	6	3.5	5	4	7.6	6	3
Vulpicida pinastri	0.1	4	5	0.3	5	6	0.2	5	4	0.3	5	3
Xanthoria parietina	0	0	0	0	0	1	0	0	0	0	0	0
Xanthoria sp.	0	0	2	0	0	0	0	0	0	0	0	0
No. of epiphytic lichen species		19	31		21	28		20	23		16	24
Terricolous lichens												
Cetraria arenaria	0	0	5	0	0	1	0	0	0	0	0	0
Cladina mitis	+	2	2	0.1	1	4	0.7	1	3	0.3	5	3
Cladina rangiferina – Cladina stygia	1.0	3	5	1.1	6	6	6.4	5	4	5.6	6	3
Cladina stellaris	0.1	1	3	0.1	1	3	0	0	2	+	1	2
Cladonia bacillaris	0	0	3	0	0	4	0	0	3	0	0	2
Cladonia botrytes	0	0	3	+	1	5	0	0	4	0	0	3
Cladonia cenotea	+	1	5	+	2	6	+	1	4	0.1	4	3
Cladonia cervicornis ssp. *verticillata*	0	0	2	0	0	0	0	0	0	0	0	1
Cladonia chlorophaea	0	0	5	0.1	3	5	+	1	4	0.1	4	3
Cladonia coccifera	0	0	0	0	0	1	0	0	0	0	0	0
Cladonia coniocrea	0	0	3	0.1	2	6	0	0	4	0	0	1
Cladonia cornuta	0	0	4	+	1	4	+	1	2	0	0	3
Cladonia crispata	0	0	5	0.1	2	6	0.1	1	4	+	4	3
Cladonia cristatella	0	0	3	0	0	4	0	0	4	+	1	3
Cladonia deformis	0	0	3	0	0	4	+	1	3	+	2	3
Cladonia digitata	0	0	5	+	2	5	0	0	3	+	1	1
Cladonia gracilis	+	1	3	+	2	4	0.1	1	3	0.1	4	3
Cladonia maxima	0	0	0	0	0	2	0	0	0	0	0	0

Table A1 (*concluded*).

	80–120 years			120–160 years			160–200 years			>200 years		
	%	QS (n = 5)	SS (n = 5)	%	QS (n = 6)	SS (n = 6)	%	QS (n = 5)	SS (n = 4)	%	QS (n = 6)	SS (n = 3)
Cladonia pleurota	0	0	0	0	0	0	0	0	1	0	0	0
Cladonia pyxidata	0	0	0	0	0	0	0	0	1	0	0	0
Cladonia squamosa	+	1	3	0	0	0	0	0	0	0	0	0
Cladonia sulphurina	0	0	0	0	0	4	+	1	3	+	1	2
Cladonia uncialis	0	0	1	0	0	0	0	0	0	0	0	0
Cladonia sp. 1	0	0	0	0	0	0	0	0	0	0	0	1
Cladonia sp. 2	0	0	1	0	0	0	0	0	0	0	0	0
Cladonia sp. 3	0	0	0	0	0	0	0	0	1	0	0	0
Cladonia sp. 4	0	0	0	0	0	0	0	0	1	0	0	0
Cladonia sp. 5	0	0	0	0	0	1	0	0	0	0	0	0
Icmadophila ericetorum	0	0	0	0	0	1	0	0	1	0	0	1
Loxospora elatina	0	0	0	0	0	2	0	0	1	0	0	0
Peltigera aphtosa	0	0	3	0	0	3	0.1	1	2	+	1	1
Peltigera malacea	0	0	1	0	0	0	0	0	0	0	0	0
Peltigera neopolydactyla	0.4	1	2	0	0	0	0	0	0	0	0	0
Peltigera praetextata	0	0	1	0	0	0	0	0	0	0	0	0
Peltigera scabrosa	0	0	2	0	0	2	0	0	1	0	0	1
No. of terricolous lichen species		7	24		11	23		10	23		12	20
No. of bryophyte and lichen species		41	90		59	99		51	86		48	75

*Indicator species for an age-class.

†Mean cover <0.1%.