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ARTICLE

Contrasting responses of epiphytic and terricolous lichens to variations in forest characteristics in northern boreal ecosystems[1]

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Abstract: The main environmental factors that drive lichen communities are still poorly known in northern boreal ecosystems. This study compares the effects of forest stand characteristics (height, canopy cover, and age) on fruticose epiphytic and terricolous lichen communities across a large region located at the interface between closed-crown boreal forests and northern open woodlands in the province of Quebec (Canada). The dataset consists of 875 plots spread across a 242 000 km^2 territory that ranges from the eastern to the western extremities of the province. The biomass of fruticose epiphytic lichens (*Alectoria*, *Bryoria*, *Evernia*, and *Usnea*) was evaluated at the branch, tree, and plot levels, and terricolous lichen cover (*Cladonia* spp.) was evaluated at the plot level. The results indicate that epiphytic and terricolous lichens respond significantly but differently to variations in forest characteristics. At the plot level, epiphytic lichen biomass was highest in the oldest stands (>100 years) and lowest in stand with low canopy cover (<25%) or in stands dominated by relatively short trees (<7 m). By contrast, terricolous lichen cover was highest in stands dominated by short (<7 m) or mid-sized (7–12 m) trees and lowest in stands with a relatively high canopy cover (>40%) or stands of intermediate age (60 to 100 years old). Species composition of epiphytic communities was also examined, and some species or genera exhibit a strong association with older stands (*Alectoria sarmentosa* (Ach.) Ach., *Bryoria* spp.) or with specific regions along the ca. 1500 km east–west gradient (*Evernia mesomorpha* Nyl. in the western part, *Bryoria* spp. in the central part, and *A. sarmentosa* in the eastern part). In terms of conservation, these results indicate that epiphytic lichens communities are potentially sensitive to the preferential logging of older stands. Both epiphytic and terricolous lichen communities are also potentially sensitive to expected climate change effects such as increased fire frequencies or increased forest growth.

Key words: lichen, boreal forest, epiphytes, *Bryoria*, *Cladonia*.

Résumé : Les principaux facteurs qui déterminent la composition des communautés de lichens sont encore mal connus dans les écosystèmes boréaux nordiques. Cette étude compare les effets des caractéristiques (hauteur, couvert forestier et âge) des peuplements forestiers sur les communautés de lichens épiphytes fruticuleux et terricoles à travers une vaste région située à la limite ente les forêts boréales à couvert fermé et les forêts nordiques ouvertes dans la province de Québec (Canada). Le jeu de données est composé de 875 placettes réparties sur un territoire de 242 000 km^2 qui s'étend entre les extrémités est et ouest de la province. La biomasse des lichens épiphytes fruticuleux (*Alectoria*, *Bryoria*, *Evernia* et *Usnea*) a été évaluée à l'échelle de la branche, de l'arbre et de la placette; le recouvrement de lichens terricoles (*Cladonia* spp.) a été évalué à l'échelle de la placette. Les résultats montrent que les lichens épiphytes et terricoles réagissent de façon significative mais différente aux variations des caractéristiques de la forêt. À l'échelle de la placette, la biomasse des lichens épiphytes était la plus élevée dans les plus vieux peuplements (>100 ans), et la plus faible dans les peuplements avec un faible couvert forestier (<25%) ou dans les peuplements dominés par des arbres de petite taille (<7 m). Par contre, le recouvrement de lichens terricoles était le plus élevé dans les peuplements dominés par des arbres de petite taille (<7 m) ou de taille intermédiaire (7–12 m) et le plus faible dans les peuplements avec un couvert forestier relativement important (>40 %) ou dans les peuplements d'âge intermédiaire (60–100 ans). La composition en espèces des communautés épiphytes a également été étudiée et certaines espèces ou genres étaient étroitement associés aux peuplements plus vieux (*Alectoria sarmentosa* (Ach.) Ach., *Bryoria* spp.), ou à des régions particulières le long du gradient est-ouest d'environ 1500 km (*Evernia mesomorpha* Nyl. à l'ouest, *Bryoria* spp. au centre et *A. sarmentosa* à l'est). En termes de conservation, ces résultats indiquent que les communautés de lichens épiphytes sont potentiellement sensibles à l'exploitation préférentielle des vieux peuplements. Les communautés de lichens épiphytes et terricoles sont aussi potentiellement sensibles aux effets appréhendés des changements climatiques tels que l'augmentation de la fréquence des feux ou l'augmentation de la croissance de la forêt. [Traduit par la Rédaction]

Mots-clés : lichen, forêt boréale, épiphytes, *Bryoria*, *Cladonia*.

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Introduction

The northern boreal zone is at the transition between the closed-crown boreal forest (to the south) and the open taiga (to the north). In North America, this ecosystem is mostly a mosaic of forests dominated by black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), interspersed with areas where trees are scarce or absent. Difficult conditions for tree populations in this zone are due to adverse climatic conditions, severe disturbance regimes, lack of suitable soil conditions, or a combination of these factors (Payette 1992). Because of their remoteness, these northern boreal forests used to be of little concern for land managers and conservation biologists. However, increased access to this zone for economic activities and potential effects of climate change might represent a significant conservation challenge in the years to come. These new processes could alter biological diversity and ecological processes in this zone, and an effort must be made to assess the vulnerability of representative biological communities. Epiphytic and terricolous lichens are important components of boreal forest ecosystems. They play a crucial role in many boreal food webs (e.g., invertebrates and their predators (Pettersson et al. 1995), woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788); Rominger et al. 1996)) and are used by many animals as shelters or for nest building (Sharnoff and Rosentreter 1998). Terricolous lichens (*Cladonia* spp.), which tend to form extensive mats in open northern woodlands (Crittenden 2000), have also been found to contribute significantly to major ecosystem processes by increasing albedo due to their pale colour (Bernier et al. 2011) and by contributing to the nutrient cycle. Lichens are also known to be particularly sensitive to environmental modifications brought by human activities. For example, microenvironmental modifications created by edge effects and forest fragmentation (Boudreault et al. 2008), reduction of old-forest attributes (e.g., large and old trees, snags (Esseen et al. 1996)), pollution (Conti and Cecchetti 2001), or climate change (Ellis et al. 2007) have been found to affect lichens.

A high abundance of epiphytic fruticose pendulous lichens is a striking characteristic of old boreal forests (Esseen et al. 1996). In eastern Canadian boreal forests, fruticose pendulous lichens are mainly represented by four genera (*Alectoria*, *Bryoria*, *Evernia*, and *Usnea*). Species of these genera can grow on tree trunks, but they reach their maximal abundance on branches of intermediate height (Arseneau et al. 1997; Boudreault et al. 2009). The accumulation of epiphytic lichen biomass in forests is a slow process: it is therefore generally believed that a long temporal continuity increases the probability that species with low potential of dispersal can reach a site and establish. Accordingly, richness and abundance of epiphytic lichens are generally higher in old forests than in young forests (McCune 1993; Esseen et al. 1996). Moreover, the great variety of microhabitats and particular environmental conditions (McCune 1993; Dettki and Esseen 1998) that are found within old forests are also generally favorable for epiphytic lichen establishment and growth.

Terricolous lichens are mainly represented by a high abundance of *Cladonia* spp., interspersed with *Cetraria* spp. (sensu lato), *Peltigera* spp., and *Stereocaulon* spp. In contrast to epiphytic lichens, terricolous lichens have been studied relatively often in the northern part of the boreal forest, mostly because they cover extensive areas, but also because they are an important food source for woodland caribou populations, an ecotype classified as threatened by the federal government (Environnement Canada 2003). Terricolous lichen communities have been found to be influenced by changes in forest structure and composition that are observed following severe disturbances (Foster 1985; Morneau and Payette 1989). In sparsely regenerated spruce–lichen woodlands, most lichen species can re-establish within 15 years after a fire, and after 130 to 250 years, the ground cover is usually dominated by *Cladonia stellaris* (Opiz) Pouzar & Vězda (Morneau and Payette 1989). However, terricolous lichens of the genus *Cladonia* are abundant in well-regenerated spruce forests before the forest canopy closure, but they are subsequently progressively replaced by feathermosses (Foster 1985), probably because shaded environments provide more favorable conditions for mosses than for lichens (Coxson and Marsh 2001).

Acquiring additional information on how forest characteristics are associated with epiphytic and terricolous lichens is particularly important in the context in which human access to northern ecosystems is increasing, and pressure to develop economic activities such as forest management and mining is likely to increase in the near future in many jurisdictions (Berteaux 2013). Thus, the overall objective of this study is to determine the effects of stand structure on fruticose epiphytic and terricolous lichens across a very large region, located at the interface between closed-crown boreal forests and taiga. This region has not been affected significantly by management activities thus far. To our knowledge, no study has examined these questions across large geographic gradients until now. Therefore, the specific objectives of our study were (*i*) to determine the effects of stand structure (height, canopy cover, and age) and geographic position along large latitudinal and longitudinal gradients on the structure and composition of epiphytic and terricolous lichen communities and (*ii*) to identify the main challenges for the conservation of these two groups in northern ecosystems.

Methods

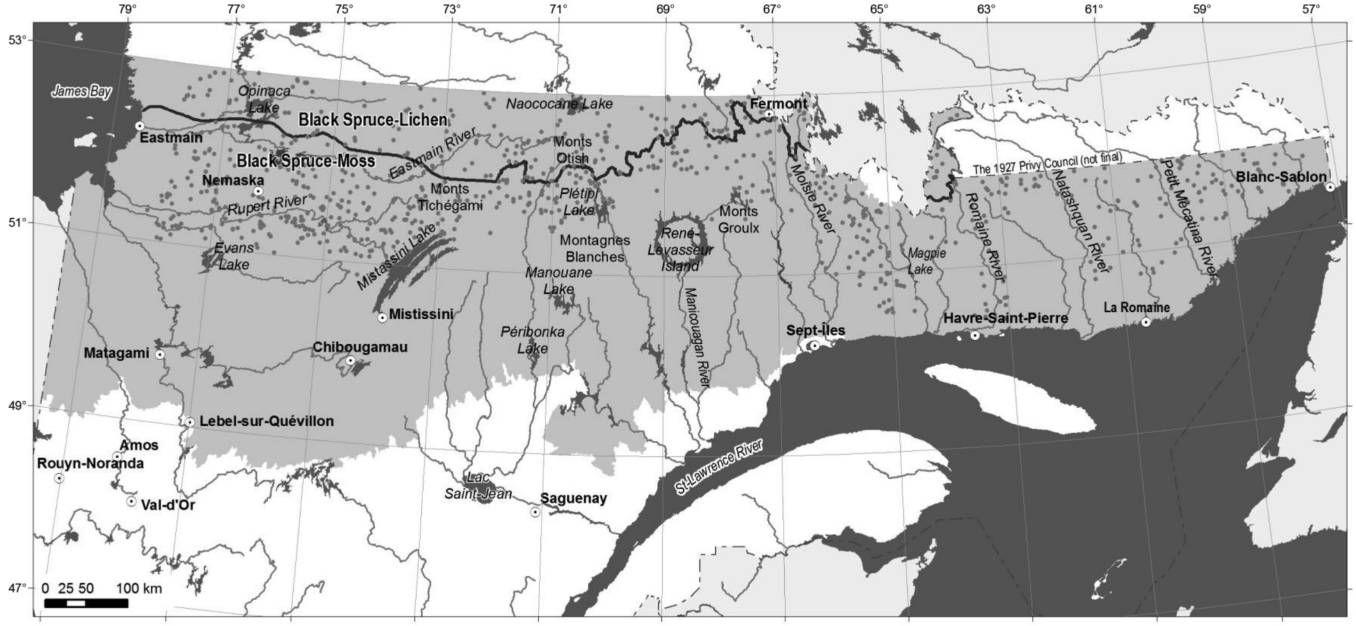
Study area

The study area extends from James Bay to Labrador (79°30′W to 57°W) and is comprised within latitudes 50°N to 53°N, encompassing an area of 242 000 km^2 (Fig. 1). It covers the northern portion of the spruce–moss bioclimatic domain and the southern portion of the spruce–lichen domain (Lord and Robitaille 2013). Black spruce is by far the dominant species in the study area. Balsam fir (*Abies balsamea* (L.) Mill.) is only abundant in the eastern part of the study area, where most stands consist of a mixture of black spruce and balsam fir. Paper birch (*Betula papyrifera* Marsh.) is more abundant in the southern part and is often mixed with conifers. Jack pine (*Pinus banksiana* Lamb.) occurs mainly within the western part of the study area and can sometimes form pure stands. Industrial forest harvesting activities have been almost completely absent from this zone in the past, essentially because of poor access (absence of a developed road network) and low standing volumes at the stand and landscape levels that translate into low margins of profitability for the forest industry.

Glacial deposits (mostly tills of various thicknesses), sometimes overlaid with relatively thick organic deposits, are the most abundant types of surficial deposits in this region. Relatively thick till deposits (e.g., >50 cm) are more frequent in areas of gentle relief, particularly in the centre and in the north, whereas relatively thin tills are more frequent in hilly areas. Organic soils dominated by peat (>40 cm in thickness) cover vast areas near James Bay and at the mouths of the major rivers of the Côte-Nord region. The topography is variable across the study area, with the highest plateau at 900 to 1100 m above sea level (Lord and Robitaille 2013).

Precipitation is at a minimum in the immediate vicinity of James Bay (from 650 to 700 mm) and at a maximum at the eastern end of the Côte-Nord region and in some rugged areas of the Laurentian shield (around 1150 mm). Mean annual temperatures range from −4.9 to 1.6 °C, decreasing gradually from south to north and also with elevation. Total growing degree-days (annual cumulative total of daily average temperatures above 5 °C) range from 618 to 1376, on average. Climatic information was calculated with BioSIM 9 (Régnière and Saint-Amant 2008), which interpolates climatic information from the nearest meteorological stations (c.f. Lord and Robitaille 2013).

Fig. 1. Localization of the study area. Dots indicate the location of sample plots across the study area. (Reproduced with permission of the Ministère des Forêts, de la Faune et des Parcs du Québec.)



Sampling

The data used in this study were gathered during forest inventories undertaken during summers of 2006 to 2009 across the 242 000 km² territory (Berger et al. 2008). Before sampling, forest stands were first categorized according to important descriptors such as canopy cover, stand height, and stand composition. The 875 sample plots were assigned to each forest type according to its relative importance across the territory, using a stratified sampling design (Berger et al. 2008). One 400 m² circular plot was located randomly inside each selected stands. Due to the absence of a road network, the plots were accessed by helicopter.

Inside each plot, stand composition and structure were characterized with forest inventories. The diameter of each tree was measured at 1.3 m above ground level. The canopy cover of the tree stratum (>9 cm at 1.3 m height) was evaluated visually by 20% classes (0%–20%, 21%–40%, 41%–60%, 61%–80%, and 81%–100%). Stand age was evaluated by counting growth rings on sample cores taken from dominant trees or from information derived from fire maps (when available). Stand height was evaluated by measuring the height of five dominant trees present in the plot. Further information about the sampling of compositional and structural characteristics is detailed in Berger et al. (2008).

To sample epiphytic lichens, three stems (>3 m in height, dead or alive) that were located closest to the centre of each plot were selected. On each selected stem, the biomass of fruticose epiphytic lichens (all species combined) was estimated visually at a height of between 1 and 3 m. The estimation was undertaken using the clump method, which consists of visually comparing lichen accumulations on a given tree with standard units of known mass for each species or species group (Campbell et al. 1999). Thus, lichen mass is estimated according to how many standard units are present on that tree. In this study, we used standard units of 2.5 g. Then, the proportion of epiphytic lichens that belonged to the *Bryoria* genus (which is generally the most abundant genus) was estimated in 10% classes. To estimate epiphytic lichen biomass at the plot level, the biomass estimated at the tree level was averaged for the three sampled trees and multiplied by the total number of trees with a diameter at breast height (1.3 m) of more than 9 cm in the plot.

On each stem, we selected one branch > 50 cm that was located closest to a height of 2.5 m from the tree base. When no branch > 50 cm was present, the longest branch located between 1 and 2.5 m was selected. Length and diameter of each branch were measured. Back in the laboratory, lichens found on each collected branch were sorted by taxa (*Alectoria sarmentosa* (Ach.) Ach., *Bryoria* spp., *Evernia mesomorpha* Nyl., and *Usnea* spp.), dried at 60 °C for 24 h, and weighed (to the nearest 0.0001 g). On one of the two collected branches (total = 527 branches), species of *Bryoria* were identified. As *Bryoria* spp. can be very abundant on a branch, the branches were subsampled by randomly positioning seven points along the main axis of the branch. Each point was considered the centre of a 5 cm long microplot along the main axis. In each of these microplots, all *Bryoria* species were recorded. For shorter branches (<50 cm), a fewer microplots were usually sampled. We then calculated the species' abundance, i.e., relative frequency, with this formula:

$$\begin{aligned}&\text{Relative frequency of species } x\\&\quad = (\text{number of micoplots where the species } x \text{ was present/}\\&\qquad\qquad \text{number of microplots sampled on the branch}) \times 100\end{aligned}$$

The abundance of *Cladonia* subgroup *Cladina* was studied as this group constitutes important winter forage for woodland caribou (Webb 1998). Abundances were evaluated at the plot scale (400 m²) with cover classes (<1%, 1% to 5%, 6% to 10%, 11% to 25%, 26% to 40%, 41% to 60%, 61% to 80%, 81% to 100%). Median values of class cover for each species of the *Cladonia* subgroup *Cladina* (*Cladonia mitis* Sandst., *Cladonia rangiferina* (L.) F.H. Wigg., and *C. stellaris*) present in a site were then added up. Species such as *Cladonia arbuscula* (Wallr.) Rabenh. and *Cladonia stygia* (Fr.) Ruoss were present in the study area but not quantified directly in this study: when present, these species were respectively lumped with *Cladonia arbuscula* subsp. *mitis* (Sandst.) Ruoss and *C. rangiferina*, from which they are difficult to differentiate in the field.

Data analyses

Mixed models were used to compare the effect of stand height, canopy cover, and stand age on (1) biomass of *Bryoria* spp., *Usnea*

Table 1. Climatic variables selected across the study area (means and standard deviations (SD)).

	West		Centre-west		Centre-east		East	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Growing degree-days* (°C)	906	131	722	106	717	104	723	100
Mean annual temperature (°C)	–2.3	0.7	–4.0	0.8	–2.9	1.25	–1.4	1.0
Growing season radiation ($\mathrm{MJ\cdot m^{-2}}$)	1732	387	1692	345	1765	380	1932	362
Total precipitation (mm)	846	71	921	34	900	80	1082	38

Note: Study area was divided in four regions: west, 78.2°W to 73.0 °W; centre-west, 73.0°W to 67.9°W; centre-east, 67.9°W to 62.7°W; east, 62.7°W to 57.5°W.

*Annual cumulative total of daily average temperatures above the 5 °C threshold.

spp., *A. sarmentosa*, and *E. mesomorpha* at the branch level, (2) fruticose lichen biomass (all fruticose epiphytic lichens combined) and *Bryoria* spp. biomass at the tree level, (3) fruticose lichen biomass and *Bryoria* spp. biomass at the plot level, and (4) cover of terricolous lichens at the plot level. For the branch-level analyses, branches from 2006 were excluded from the analyses because they were not, as the ones from 2007–2009, selected according to the systematic procedure presented above (in 2006 representative branches were selected subjectively). At the tree and plot levels, data from summer 2006 were kept in the analyses because the lichen biomass on the selected trees were not systematically higher than the lichen biomass on selected trees from the other years ($p > 0.05$). Only stands that were dominated by conifers such as black spruce, balsam fir, white spruce (*Picea glauca* (Moench) Voss), jack pine, or tamarack (*Larix laricina* (Du Roi) K. Koch) were included in the analyses. Stands dominated by hardwoods were not analysed because they are relatively uncommon in this ecosystem and were not well represented in the dataset. In each model, stand height, canopy cover, and stand age were fixed factors, and latitude, longitude, and longitude^2 were added as covariates in the analyses. A quadratic term (longitude^2) was added for longitude because preliminary analyses showed that lichen biomass varied in a nonlinear way according to longitude. At the branch and tree levels, sampling site was considered a random factor. The interactions between fixed factors was tested in all models and then removed when they were not significant ($p > 0.05$). Stand height, canopy cover, and age classes were defined from forest maps available for the territory (1 : 20 000) as follows: stand height, <7 m, 7–12 m, and >12 m; canopy cover, <25%, 26%–40%, and >40%; stand age, <60 years old, 61–100 years old, and >100 years old.

To facilitate the interpretations, we also used mixed models to compare the abundance of epiphytic and terricolous lichens across regions. The territory was divided into four regions, each of which covered approximately 5° of longitude (west, 78.2°W to 73.0°W; centre-west, 73.0°W to 67.9°W; centre-east, 67.9°W to 62.7°W; and east, 62.7°W to 57.5°W); climatic information regarding these four regions is indicated in Table 1, and basic stand information is indicated in Table 2. The interaction between region (a fixed factor) and latitude (a covariate) was tested and removed from models when it was not significant ($p > 0.05$), and site was considered as a random factor. All analyses were performed with the MIXED procedure of SAS (SAS Institute Inc. 2002). Denominator degrees-of-freedom were calculated using Satterthwaite's approximation (Littell et al. 1996). Significant differences ($p \leq 0.05$) between classes were detected with least squares means Tukey HSD tests. Logarithmic transformations of lichen data were applied to meet the assumptions of ANOVA.

For epiphytic lichens, we identified indicator species for each class of height, age, and density and for each region using the method described by Dufrêne and Legendre (1997). The indicator values were calculated using the relative abundance and percent cover of species for each plot. Indicator values ranged from 0 to 100, where 100 was given to a species found exclusively in all plots of a single class. Significance of these indicator values was tested by 9999 permutations. No indicator species analysis was performed for some *Bryoria* species that were recorded but were less abundant in our study. These species were *Bryoria bicolor* (Ehrh.) Brodo & D. Hawksw., *Bryoria capillaris* (Ach.) Brodo & D. Hawksw., *Bryoria fuscescens* (Gyelnik) Brodo & D. Hawksw., *Bryoria tenuis* (E. Dahl) Brodo & D. Hawksw., and *Bryoria trichodes* subsp. *americana* (Mot.) Brodo & D. Hawksw. Only species with greater than 10% frequency were included in the analyses.

Table 2. General forest characteristics in the four regions of the study area.

	Proportion of sample plot (%)			
	West	Center-west	Center-east	East
Stands > 100 years	38	77	81	87
Stands > 40% cover	29	11	30	23
Stands > 7 m height	27	18	33	27

Note: The percentages indicate the proportion of the sample plots that are dominated by relatively old stands (>100 years), relatively dense stands (>40% canopy cover), and relatively high stands (dominant height > 7 m).

Results

Overall epiphytic and terricolous lichen abundance

Throughout the study area, biomass of *Bryoria* spp. at the branch level was 13, 92, and 347 times higher than biomass of *A. sarmentosa*, *E. mesomorpha*, and *Usnea* spp., respectively. Indeed, close to 92% of the total biomass of epiphytic lichens was composed of *Bryoria* species. The biomass of epiphytic lichens per branch varied between 0 and 32.9 g, with a mean biomass of 1.5 ± 2.9 g (mean ± 1 SD; $n = 1158$). Biomass at the branch level was strongly correlated with branch length ($r = 0.348$, $p < 0.001$, $n = 1151$) and branch diameter ($r = 0.321$, $p < 0.001$, $n = 1109$). Mean biomass of epiphytic lichens at the tree level, estimated between 1 and 3 m from the ground, was 6.1 ± 7.6 $\mathrm{g\cdot tree^{-1}}$, whereas biomass at the plot level was 6.7 ± 7.6 $\mathrm{kg\cdot ha^{-1}}$. Mean cover of terricolous lichens was 31.5% ± 32.5%.

Lichen abundance along geographic gradients

Epiphytic lichen taxa varied significantly across regions (Table 3). At the branch level, the biomass of *A. sarmentosa* was significantly higher in the east region than in the other regions and was particularly low in the west region (Figs. 2 and 3). Conversely, the abundances of *E. mesomorpha* and *Usnea* spp. were significantly higher in the west region (Figs. 2 and 3), and the abundance of *Usnea* spp. decreased with latitude (Fig. 3). At the branch level, the biomasses of *Bryoria* spp. and the fruticose lichens were significantly higher in the centre-west region compared with other regions, and both biomass estimates increased significantly with latitude (Table 3; Figs. 2 and 3).

The indicator species analysis carried out at the branch level also shows that *Usnea* spp. and *E. mesomorpha* were significantly associated with the west region, *Bryoria lanestris* (Ach.) Brodo & D. Hawksw. and *Bryoria* spp. were associated with the centre-west region, *Bryoria trichodes* (Michx.) Brodo & D.Hawksw. and *Bryoria simplicior* (Vainio) Brodo & D. Hawksw. were associated with the

Table 3. ANOVA summaries for the effects of region and latitude on biomass of (*a*) fruticose lichens, *Bryoria* spp., *Alectoria sarmentosa*, *Evernia mesomorpha*, and *Usnea* spp. at the branch level, (*b*) fruticose lichens and *Bryoria* spp. at the tree level, and (*c*) fruticose epiphytic lichens and terricolous lichens at the plot level.

	(*a*) Branch level				(*b*) Tree level				(*c*) Plot level			
	dfn	dfd	*F*	*p*	dfn	dfd	*F*	*p*	dfn	dfd	*F*	*p*
Fruticose												
Region	3	624	10.06	**<0.001**	3	699	25.05	**<0.001**	3	744	23.45	**<0.001**
Latitude	1	624	1.38	0.240	1	699	10.54	**0.001**	1	744	0.019	0.891
Region × latitude				ns	3	699	5.89	**0.001**				ns
***Bryoria* spp.**												
Region	3	624	13.86	**<0.001**	3	699	32.25	**<0.001**	3	741	24.21	**<0.001**
Latitude	1	624	2.17	0.141	1	699	24.45	**<0.001**	1	741	3.65	0.057
Region × latitude				ns	3	699	8.78	**<0.001**	3	741	4.81	**0.003**
Alectoria sarmentosa												
Region	3	621	24.09	**<0.001**								
Latitude	1	621	0.03	0.866								
Region × latitude	3	621	3.57	**0.014**								
Evernia mesomorpha												
Region	3	624	5.60	**<0.001**								
Latitude	1	624	2.18	0.140								
Region × latitude				ns								
***Usnea* spp.**												
Region	3	621	4.48	**0.004**								
Latitude	1	621	8.17	**0.004**								
Region × latitude	3	621	3.00	**0.030**								
Terricolous lichens												
Region									3	760	33.30	**<0.001**
Latitude									1	760	20.04	**<0.001**
Region × latitude									3	760	2.99	**0.030**

Note: Region was a fixed factor, latitude was a covariate, and sampling site was a random factor. Significant values ($p \le 0.05$) are given in boldface type. dfn, numerator degrees of freedom; dfd, denominator degrees of freedom; ns, not significant.

centre-east region, and *A. sarmentosa* was associated with the east region (Table 4).

At the tree level, the biomass of fruticose lichens was lowest in the west region and the biomass of *Bryoria* spp. was lowest in the west and east regions (Fig. 4). At the plot level, the lowest biomass of fruticose lichens was found in the west region, and for *Bryoria* spp., the highest value was found in the centre-east region and the lowest value in the west region (Fig. 5). The significant interaction between region and latitude for the biomasses of *Bryoria* spp. and fruticose lichens at the tree level indicates that latitude had a positive influence on lichen biomass except in the west region where their biomass decreased with latitude (Table 3); at the plot level, the same pattern was found for the biomass of *Bryoria* spp. (Table 3).

The highest terricolous lichen cover was found in the centre-west region but did not differ significantly from the west region, and the lowest cover was found in the east region (Table 3; Fig. 6). Latitude had a significant positive influence on the terricolous lichen cover (Table 3).

Relationships between lichen abundance and stand characteristics

Branch level

Significant differences in lichen abundance among stand height classes were detected only for *Bryoria* spp. and for the fruticose lichens (Table 5). Stands of the height class 7–12 m had a significantly higher biomass of *Bryoria* spp. compared with stands of height class <7 m (Fig. 2). The biomass of *Bryoria* spp. was much lower on branches located in stands with relatively high canopy cover (>40%) compared with stands with a lower canopy cover (Table 5; Fig. 2). The biomass of *A. sarmentosa* was significantly higher in stands with a 25%–40% canopy cover than in stands with <25% canopy cover.

Biomasses of *A. sarmentosa*, *Bryoria* spp., and fruticose lichens were significantly higher in stands more than 100 years old compared with younger stands (Table 5; Fig. 2). The biomass of *E. mesomorpha* was highest in the intermediate age class (60–100 years; Table 5; Fig. 2). The indicator species analyses shows that *A. sarmentosa*, *Bryoria* spp., and *B. lanestris* were indicators of stands of height class 7–12 m, *Bryoria nadvornikiana* (Gyelnik) Brodo & D. Hawksw. was an indicator of stands of height class >12 m, and *B. simplicior* was an indicator of stands of height class <7 m (Table 4). *Bryoria furcellata* (Fr.) Brodo & D. Hawksw., *B. simplicior*, *Bryoria* spp., and *E. mesomorpha* were indicator species of relatively open stands (<25%) (Table 4). *Bryoria lanestris*, *B. trichodes*, *Bryoria* spp., and *A. sarmentosa* were indicator species of the oldest stands (>100 years), *E. mesomorpha*, *B. furcellata*, and *B. nadvornikiana* were indicators of stands of intermediate age (60–100 years), and *B. simplicior* was an indicator of younger stands (<60 years) (Table 4).

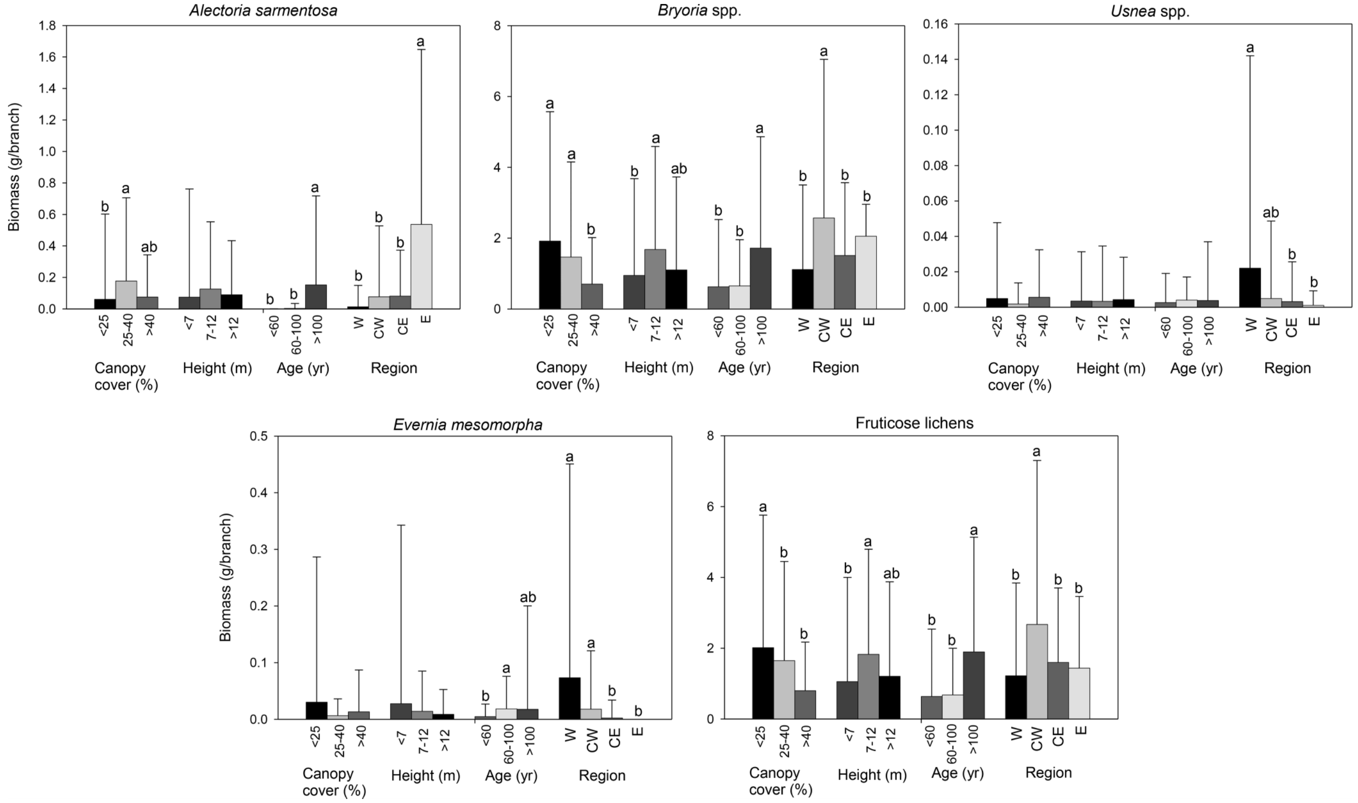
Tree level

The biomass of fruticose lichens and the biomass of *Bryoria* spp. at the tree level varied across stand height classes, canopy cover classes, and stand age classes, with the lowest values observed in stands of height class <7 m, in stands with a relatively high canopy cover (>40%), and in young stands (<60 years) (Table 6; Fig. 4). The biomass of fruticose lichens increased significantly with stand age (Table 6; Fig. 4). Stand composition had a significant influence on epiphytic lichen biomass ($F = 62.49$, $p < 0.001$), with a significantly higher biomass observed in black spruce stands compared with balsam fir and jack pine stands.

Plot level

Canopy cover, stand height, and stand age had a significant influence on lichen biomass at the plot level (Table 6). The biomasses of fruticose lichens and *Bryoria* spp. were significantly

Fig. 2. Biomass of *Alectoria sarmentosa*, *Bryoria* spp., *Usnea* spp., *Evernia mesomorpha*, and the fruticose lichen group at the branch level by canopy cover classes (<25%, 25%–40%, and >40%), height classes (<7 m, 7–12 m, and >12 m), age classes (0–60 years, 60–100 years, and >100 years), and region (W, west; CW, centre-west; CE, centre-east; E, east). Error bars are standard deviations. Means with different letters are significantly different ($p \leq 0.05$) according to least squares means Tukey HSD tests.



higher in plots of canopy cover classes >40% and 25%–40% than in plots of canopy cover class <25% (Fig. 5). These biomasses were also higher in plots with relatively tall trees (stand height classes >12 m and 7–12 m) compared with plots dominated by shorter trees (<7 m) (Fig. 5). The biomass of fruticose lichens and *Bryoria* spp. also increased with stand age at the plot level (Table 6; Fig. 5).

The cover of terricolous lichens varied significantly among stand height classes, canopy cover classes, and stand age classes (Table 6). The cover was about three times lower in stands of height class >12 m compared with stands of height classes 7–12 m and <7 m (Fig. 6). Terricolous lichen cover was also higher in stands with a relatively low canopy cover (i.e., <25% and 25%–40%; Fig. 6). Stands between 60 and 100 years old had significantly more terricolous lichens than stands <60 years and >100 years (Fig. 6). Terricolous lichen cover differed significantly among stand composition types ($F = 57.45$, $p < 0.001$), with significantly higher values in jack pine stands, intermediate values in black spruce stands, and lower values in balsam fir stands.

Discussion

Effects of stand age on epiphytic and terricolous lichen accumulation

The effects of stand age on terricolous and on epiphytic lichen communities were not the same. Stand age was the most important factor in explaining variations in epiphytic lichen biomass in the study area: branches and trees from stands <100 years old had few epiphytic lichens compared with older ones. Stands <60 years old were sparsely colonised by epiphytic lichens, possibly because they were still too young following a major disturbance to provide enough time for propagules dispersal and establishment. Many studies found a higher biomass of epiphytic lichens in old-growth forests (Esseen et al. 1996; Boudreault et al. 2009), and some dispersal-limited lichen species have been considered as indicators of forest continuity (Nordén and Appelqvist 2001). Typical dispersal-limited species are mainly those that are dispersed by thallus fragments (Esseen 1985; Dettki et al. 2000) such as long filamentous species found in our study (e.g., *B. trichodes* and *A. sarmentosa*). In our study, these long filamentous species were indicators of stands >100 years old, whereas bushy species with abundant soredia were more abundant in young forests (e.g., *B. furcellata* and *B. simplicior*). Tree branches that have been exposed to colonization events for long periods are an important feature of old forests that has been found to promote epiphytic lichen richness and biomass (Esseen et al. 1996; Arseneau et al. 1997). In this study, we also found significant relationships between branch characteristics associated with older forests such as branch length and branch diameter and lichen biomass, corroborating previous studies (e.g., Esseen et al. 1996; Boudreault et al. 2009).

In sparsely regenerated woodlands, a period of 100 years is generally needed for re-establishment of an important terricolous lichen cover after a fire; subsequently, this cover can maintain itself if no perturbation occurs (Morneau and Payette 1989; Arseneault et al. 1997). In forests that are densely regenerated by black spruce, however, a shift from lichen dominance towards a dominance of feathermosses is generally observed after canopy closure (Foster 1985). In the present study, the decline in terricolous lichen abundance observed in older forests (>100 years old) was likely related to this factor.

Fig. 3. Distribution of the different fruticose lichen genera in Quebec (west, 78.2°W to 73.0°W; centre-west, 73.0°W to 67.9°W; centre-east, 67.9°W to 62.7°W; east, 62.7°W to 57.5°W).

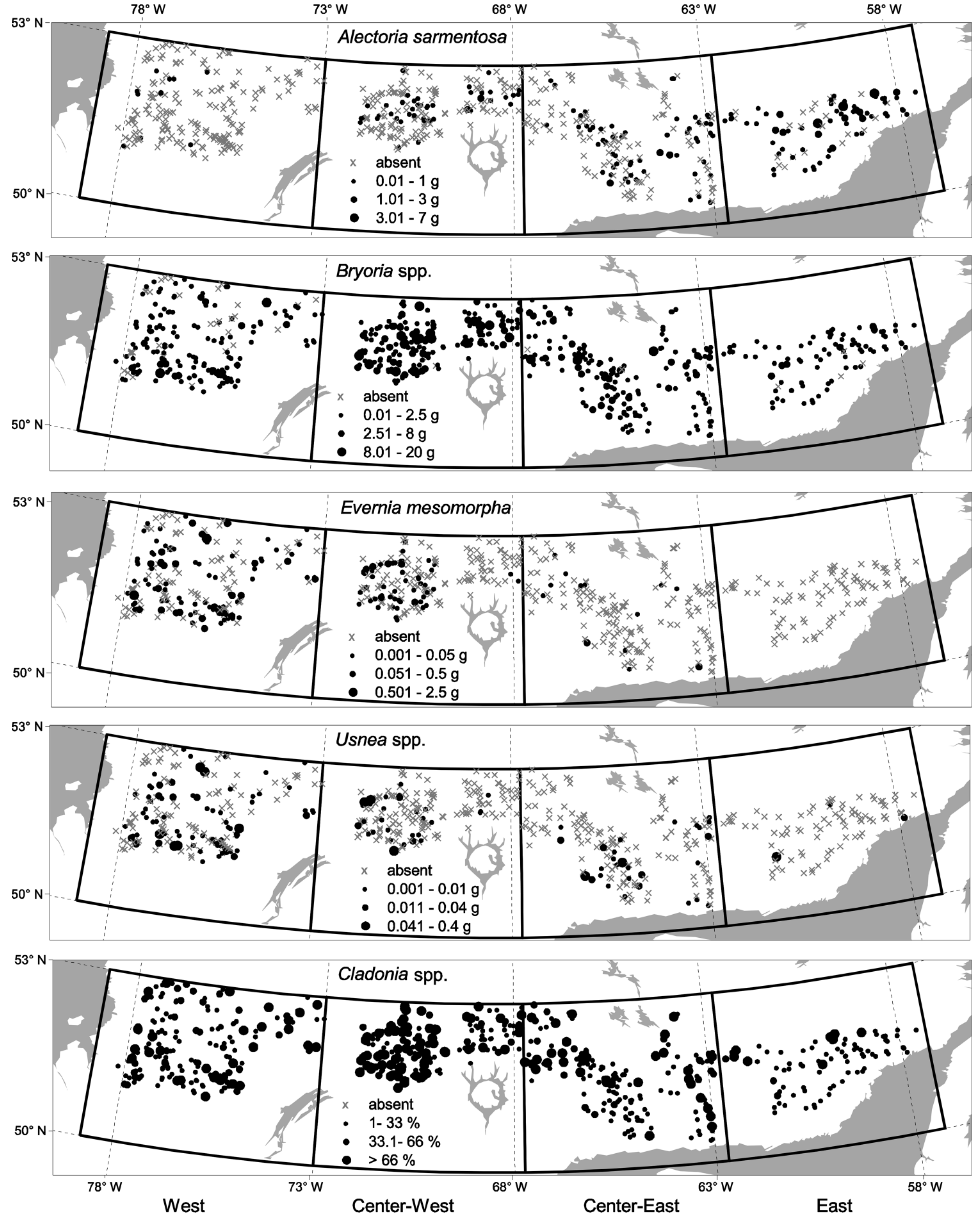


Table 4. Indicator species based on indicator species analyses of stand age, stand height, stand cover classes, and region. Only species with greater than 10% frequency were included in the analyses.

Species	Stand age (years)	Stand height (m)	Canopy cover (%)	Region
Biomass per branch				
Alectoria sarmentossa	>100	7–12	25–40	East
Bryoria spp.	>100	7–12	<25	Centre-west
Evernia mesomorpha	60–100	—	<25	West
Usnea spp.	—	—	—	West
Relative mean frequency				
Bryoria furcellata	60–100	—	<25	—
B. lanestris	>100	7–12	—	Centre-west
B. nadvornikiana	60–100	>12	—	—
B. simplicior	0–60	<7	<25	Centre-east
B. trichodes	>100	—	—	Centre-east

Fig. 4. Biomass of the fruticose lichen group and *Bryoria* spp. at the tree level by stand cover classes (<25%, 25%–40%, and >40%), height classes (<7 m, 7–12 m, >12 m), age classes (0–60 years, 60–100 years, and >100 years), and region (W, west; CW, centre-west; CE, centre-east; E, east). Error bars are standard deviations. Means with different letters are significantly different ($p \leq 0.05$) according to least squares means Tukey HSD tests.

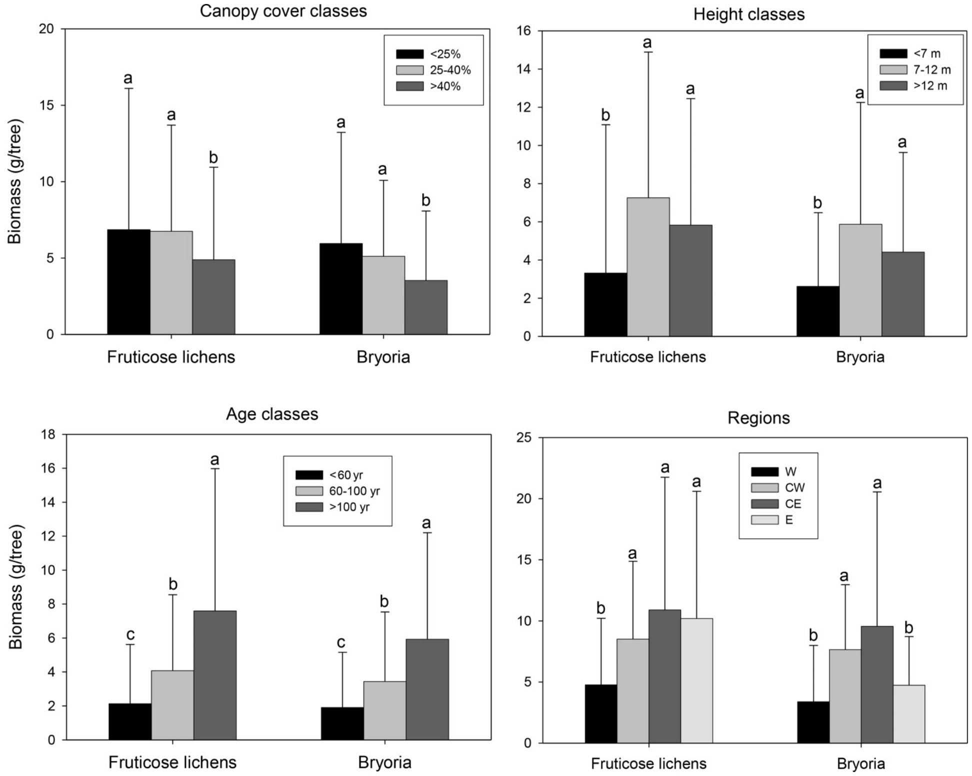


Fig. 5. Biomass of the fruticose lichen group and *Bryoria* spp. at the plot level by stand cover classes (<25%, 25%–40%, and >40%), height classes (<7 m, 7–12 m, and >12 m), age classes (0–60 years, 60–100 years, and >100 years), and region (W, west; CW, centre-west; CE, centre-east; E, east). Error bars are standard deviations. Means with different letters are significantly different ($p \leq 0.05$) according to least squares means Tukey HSD tests.

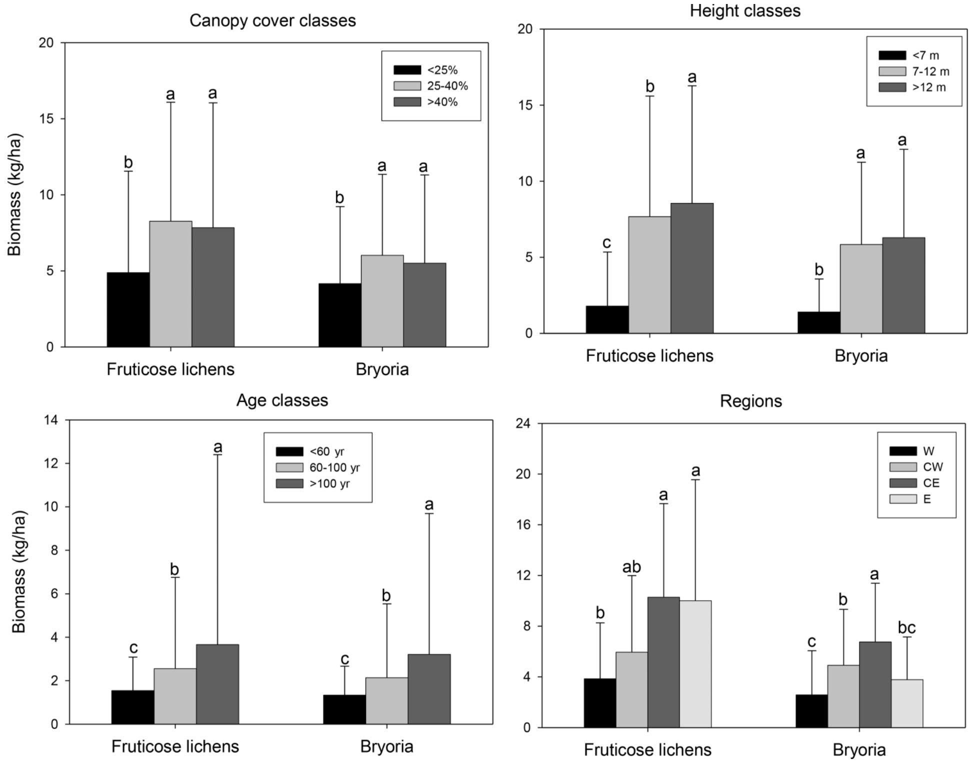


Fig. 6. Cover of terricolous lichens at the plot level by stand cover classes (<25%, 25%–40%, and >40%), height classes (<7 m, 7–12 m, and >12 m), age classes (0–60 years, 60–100 years, and >100 years), and region (W, west; CW, centre-west; CE, centre-east; E, east). Error bars are standard deviations. Means with different letters are significantly different ($p \leq 0.05$) according to least squares means Tukey HSD tests.

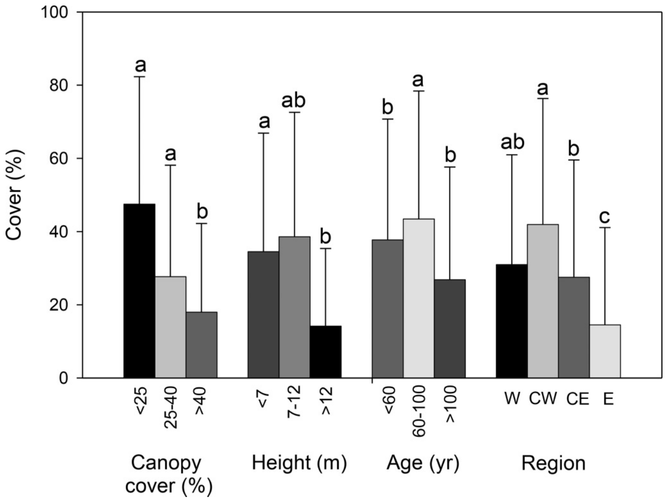


Table 5. ANOVA summaries for the effects of stand cover, stand height, stand age, and geographical location on biomass of *Alectoria sarmentosa*, *Bryoria* spp., *Evernia mesomorpha*, *Usnea* spp., and fruticose lichens at the branch level.

	dfn	dfd	*F*	*p*
Alectoria sarmentosa				
Cover	2	552	5.56	**0.004**
Height	2	547	0.73	0.482
Age	2	537	3.42	**0.034**
Latitude	1	558	1.62	0.203
Longitude	1	546	54.84	**<0.001**
Longitude^2	1	546	49.66	**<0.001**
***Bryoria* spp.**				
Cover	2	574	5.26	**0.006**
Height	2	568	3.14	**0.044**
Age	2	555	10.47	**<0.001**
Latitude	1	583	11.57	**<0.001**
Longitude	1	567	37.78	**<0.001**
Longitude^2	1	567	39.36	**<0.001**
Evernia mesomorpha				
Cover	2	582	2.61	0.074
Height	2	575	1.68	0.187
Age	2	561	6.17	**0.002**
Latitude	1	592	0.24	0.627
Longitude	1	574	5.89	**0.016**
Longitude^2	1	574	7.13	**0.008**
***Usnea* spp.**				
Cover	2	605	1.52	0.219
Height	2	599	0.11	0.897
Age	2	585	0.45	0.638
Latitude	1	614	0.57	0.452
Longitude	1	597	0.05	0.825
Longitude^2	1	597	0.02	0.888
Fruticose lichens				
Cover	2	572	4.25	**0.015**
Height	2	566	3.10	**0.046**
Age	2	553	12.72	**<0.001**
Latitude	1	580	11.89	**<0.001**
Longitude	1	564	16.25	**<0.001**
Longitude^2	1	564	17.76	**<0.001**

Note: Stand cover, height, and age were fixed factors; latitude, longitude, and longitude^2 were covariates; and sampling site was a random factor. Significant values ($p \leq 0.05$) are given in boldface type. dfn, numerator degrees of freedom; dfd, denominator degrees of freedom.

Effects of horizontal and vertical canopy structures

The structure of the forest canopy strongly influences microclimatic and light conditions in the stand, which in turn influence lichen biomass accumulation. Epiphytic lichen biomass responses to stand structure varied across the three levels studied (branch, tree, and plot) because different factors influence lichen accumulation across these levels. At the branch level, our results showed that lichen abundance in the lower tree strata is particularly low in more closed canopies. Lichen photosynthesis has often been considered to be limited in closed-canopy forests because of the low light level reaching lichens (Gauslaa et al. 2006; Jansson et al. 2009). The opening of the canopy will allow the penetration of light and humidity (McCune 1993) and will promote epiphytic lichen growth (Muir et al. 2006). It is likely that many epiphytic species found in our study benefited from canopy openings, for instance, some *Bryoria* species that are well adapted to high light environments (Coxson and Coyle 2003; Färber et al. 2014). Some species such as *B. simplicior* and *B. furcellata* were indicator species of the more open stands, which supports this explanation.

However, too much light can also have a detrimental effect for some lichens, particularly those that do not possess pigments that can act as sunscreen (Gauslaa and Solhaug, 2001; Färber et al. 2014). Stands with a relatively low canopy cover (<25%) did not provide adequate conditions for *A. sarmentosa*, which is known to be better adapted to relative humid environments that are protected from very high light levels and strong winds (Campbell and Coxson 2001). *Bryoria nadvornikiana* is also particularly well adapted to low light levels (Brodo and Hawksworth 1977; Boudreault et al. 2013*a*). In our study, this species was also more frequent and abundant in stands dominated by midsized (7–12 m) or tall (>12 m) trees, presumably because branches harvested at heights between 1 and 3 m were more shaded than branches located at the same height in stands composed of shorter trees.

Stand height also influenced overall epiphytic lichen biomass, with stands <7 m having fewer lichens compared with stands >7 m. Because there were as many young stands as older ones in stands dominated by short trees (results not shown), causes for differences in lichen biomass probably arose mainly from differences in branch characteristics. Branches collected from shorter stands (<7 m) were significantly shorter than branches collected in taller stands (>7 m) ($p < 0.05$). A positive relationship between branch length and lichen biomass was found in many studies (Esseen et al. 1996; Campbell and Coxson 2001), including this one. Shorter branches, independent from branch age, limit overall lichen accumulation because the number of microsites for species establishment (Esseen et al. 1996) and the probability of intercepting propagules, nutrients, and moisture (Lyons et al. 2000) are lower on shorter branches than on longer ones. We suggest that branch length may be a limiting factor for the lower lichen biomass accumulation observed in stands <7 m in this study.

Our study also indicates that even if lichen biomass per branch is generally much higher in stands with a low canopy cover (<25%), this translates into lower epiphytic lichen biomasses at the plot level. Therefore, the higher number of branches at the plot level in dense stands compensates for lower lichen biomass per branch associated with more shaded conditions. In addition to their overall stand-level abundance, the spatial distribution of lichens within stands could have important implications for ecosystem processes and animal populations. For example, even if biomass of lichens at the plot level is lower in opened-canopy stands, the fact that lichens are more concentrated on a limited

Table 6. Summary of mixed models results for the effects of stand cover, stand height, stand age, and geographical location on (*a*) biomass of *Bryoria* spp. and fruticose lichens at the tree level and (*b*) biomass of Bryoria spp., fruticose lichens, and terricolous lichens at the plot level.

	(*a*) Tree level				(*b*) Plot level			
	dfn	dfd	*F*	*P*	dfn	dfd	*F*	*p*
***Bryoria* spp.**								
Cover	2	691	6.54	**0.002**	2	697	6.10	**0.002**
Height	2	692	9.96	**<0.001**	2	697	10.52	**<0.001**
Age	2	699	42.10	**<0.001**	2	697	16.78	**<0.001**
Latitude	1	690	14.59	**<0.001**	1	697	13.58	**<0.001**
Longitude	1	678	52.86	**<0.001**	1	697	35.36	**<0.001**
Longitude^2	1	678	53.42	**<0.001**	1	697	36.52	**<0.001**
Fruticose lichens								
Cover	2	692	3.89	**0.020**	2	697	9.02	**<0.001**
Height	2	692	9.09	**<0.001**	2	697	6.25	**0.002**
Age	2	699	47.98	**<0.001**	2	697	15.54	**<0.001**
Latitude	1	690	7.25	**0.007**	1	697	4.69	**0.031**
Longitude	1	679	19.14	**<0.001**	1	697	4.45	**0.035**
Longitude^2	1	670	20.15	**<0.001**	1	697	5.36	**0.021**
Terricolous lichens								
Cover					2	687	8.35	**<0.001**
Height					2	687	9.50	**<0.001**
Age					2	687	12.93	**<0.001**
Latitude					1	687	2.23	0.136
Longitude					1	687	50.46	**<0.001**
Longitude^2					1	697	47.42	**<0.001**
Cover × age × height					20	697	2.20	**0.002**

Note: Density, height, and age were fixed factors; latitude, longitude, and longitude^2 were covariates; and sampling site was a random factor. Significant values ($p \leq 0.05$) are given in boldface type. dfn, numerator degrees of freedom; dfd, denominator degrees of freedom.

number of branches could be more suitable for animal (e.g., caribou) foraging (Rominger et al. 1996).

The cover of terricolous lichens was also influenced by stand structure. Our results indicate that a low occurrence of terricolous lichens in tall and dense stands, which was also observed in several local-scale studies (Morneau and Payette 1989; Lesmerises et al. 2011), is generally observed throughout our extensive study area. In closed-canopy forests, the shaded and humid microenvironment and the presence of organic matter are favorable for the development of a feathermoss carpet on the ground, a situation in which terricolous lichens are less competitive (Foster 1985; Fenton et al. 2005).

Macroclimatic context

The generally dryer climate observed in the western part of the study area (Table 1) may explain the lower abundance of *A. sarmentosa*. This species, generally associated with humid habitats (Campbell and Coxson 2001), was clearly more abundant in the east region. Indirectly, climate is also expected to affect lichen abundance through its effect on the fire cycle and the relative proportion of the different types of habitats. Several studies on the fire regimes of the boreal forest in Quebec have found that the fire cycle is likely to be shorter in the northwestern portion of the territory than in eastern Quebec, for example <150 years vs. >500 years (Bergeron et al. 2006; Bouchard et al. 2008). As such, a higher portion of old forests are expected to be found in the eastern areas and epiphytic lichens are expected to be more abundant at the regional level. Climate may also partly explain the higher terricolous lichen cover that we observed in the western part of the boreal forest, which corroborates Crête et al. (1990) study for James Bay lowlands. The increase in terricolous lichen cover with increasing latitude could be explained by factors that compromise black spruce regeneration such as the more frequent fires and the generally shallow mineral soils (Payette et al. 2000).

Concluding remarks: conservation challenges

The present study presents a unique dataset that consists of an intensive survey of a vast, unmanaged northern environment located at the interface between the closed-crown boreal forests to the south and open taiga to the north. As such, it provides an excellent opportunity to examine which ecological factors influence lichen population structure and biomass across large latitudinal and longitudinal gradients. Knowing that factors such as canopy openness or stand age are most important for lichens is particularly important in a context where these regions might eventually be affected by management activities. By including both terricolous and epiphytic lichens, it was also possible to illustrate how these two groups face different conservation challenges.

Terricolous lichens are mostly found in open stands, for example, in sites where tree density is low as a consequence of tree regeneration failures. At the northern tree line, these regeneration failures following disturbance were relatively frequent due to the negative influence of cold climatic conditions on tree regeneration processes. Terricolous lichen communities might be less affected by direct management actions because areas of high terricolous lichen density are open stands of little interest for the forest industry. By contrast, some epiphytic communities are potentially sensitive to the harvesting of old stands, which seem to be optimal for the retention of lichen biomass in northern ecosystems at the tree and plot levels. Older stands with a relatively open canopy structure are unlikely to be targeted first in the eventuality that forest management activities are undertaken in this region. However, they are susceptible to being harvested when they are located close to denser stands (>40% cover) that could be targeted by forest operations. These older stands are generally dominated by *Bryoria* species, which is by far the preferred species group for woodland caribou, particularly during winter when the snowpack is deep and terricolous lichens become inaccessible

(Rominger et al. 1996). Old stands also contain specialized species such as *A. sarmentosa* and probably many other species that were not included in this study such as crustose lichens (Tibell 1992).

Warming climatic conditions should lead to better conditions for the regeneration and growth of tree species (Sirois 2000) and to a densification of forest canopies in northern boreal environments. At the stand level, such densifications could lead to lower biomasses of terricolous lichens, which are likely to be outcompeted by feathermosses or vascular plant species in shaded conditions (Coxson and Marsh 2001). For epiphytic lichens, stand densification could have contrasting effects depending on context. Epiphytic lichen abundance could increase in stands that were initially very open and that become moderately dense (Fig. 5), but the reverse could happen in stands that become very dense, where light availability becomes a limiting factor (Boudreault et al. 2009).

However, the higher future fire frequencies that are expected for the studied region (Bergeron et al. 2010) may induce more frequent shifts from closed-canopy black spruce forests to open lichen–spruce woodlands (Bernier et al. 2011). At the landscape and regional levels, these shifts could have a positive effect on terricolous lichen abundance in boreal forests by creating open habitats favoring lichen growth (Jonsson Čabrajić et al. 2010; Boudreault et al. 2013*b*) but worse conditions for epiphytic lichens due to scarcer habitats and, possibly, higher colonization distances. How these two processes (better forest growth, higher fire frequency) will interact and impact terricolous and epiphytic lichen communities will be an important topic for future researches. Likewise, changes in relative humidity or in precipitation patterns could also affect the relative performance of the different species (Boudreault et al. 2013*a*, 2013*b*).

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