



## Relationships between the structural complexity and lichen community in coniferous forests of southwestern Nova Scotia

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### ARTICLE INFO

#### Article history:

Received 18 December 2009

Received in revised form 19 May 2010

Accepted 24 May 2010

#### Keywords:

Structural complexity

Lichen community

Old-growth

Continuity

Acadian forest

Nova Scotia

Sustainable forest management

### ABSTRACT

The relationships between the structural complexity of coniferous forests and the epiphytic lichen communities that inhabit them were examined in 51 conifer-dominated stands in southwestern Nova Scotia. One hundred and fifteen lichen species were studied in stands in the age range of 50–300 years. Environmental variables shaping the structural complexity of each forest stand were measured and their relationship with lichen species were assessed using a canonical correspondence analysis (CCA). The CCA revealed that the considerable variation in lichen community composition can be explained by several environmental variables associated with forest structure. The stand orientation on the first axis of the CCA found the most important variables for lichen richness to be stand age, tree stem density and snag stem density. The stand orientation on the second axis is strongly correlated with deciduous stem density and abundance including specific deciduous tree species such as *Acer rubrum* abundance. The analysis indicates that the greater the structural complexity in the forest, and thus the more microhabitats available, the greater the lichen species richness. These results should provide forest managers with a better understanding of the environmental variables that influence lichen diversity, and contribute to the development of more sustainable forest management strategies.

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### 1. Introduction

Lichen community composition in forest stands has been shown to change over time (Rose, 1974, 1976; Selva, 1994, 2003). As a forest develops, its structural complexity increases, which includes an increase in canopy irregularity, thus allowing for greater light variation (Stewart et al., 2003; Pesklevits, 2006). When trees age, increasingly fissured bark and lignum at different stages of growth and decay become available for colonization (Pipp et al., 2001; Stewart et al., 2003; Pesklevits, 2006). As variability in these conditions increase, so does microhabitat diversity, which in turn increases the number of organisms able to survive in the forest (Carey, 1989; Carey and Johnson, 1995). One of the most ubiquitous and diverse groups of organisms in forests is the lichen community, some species of which tend to be unique to old-growth forests; this is underscored by the application of lichens as surrogates or

“bioindicators” of forest structure (Goward, 1994; McMullin et al., 2008).

Rose (1974, 1976) was the first to use lichens as bioindicators of forest continuity, which is a measure of time since a forest was undisturbed by major natural or unnatural events. He used a particular suite of lichen species that appeared to prefer older forests to determine a continuity value for forests in Britain. The greater the number of lichen species from his suite meant a greater continuity value. In recent years, Selva (1994, 1999, 2002), and Coppins and Coppins (2002) have extended Rose's work by developing unique suites of lichen species that exhibit preference for mature forests in different ecological regions in Canada, the United States and Britain. If the number of lichen species in the forest increases with time and the structural complexity of the forest also increases with time, then the environmental variables that shape structural complexity may be predictors of the lichen communities in forest stands.

Individual environmental variables are often examined for their influence on lichen diversity (Adams and Risser, 1971; Kuusinen, 1996; Coxson and Stevenson, 2007). A comparison among those variables, however, appears to not have been done in the Acadian

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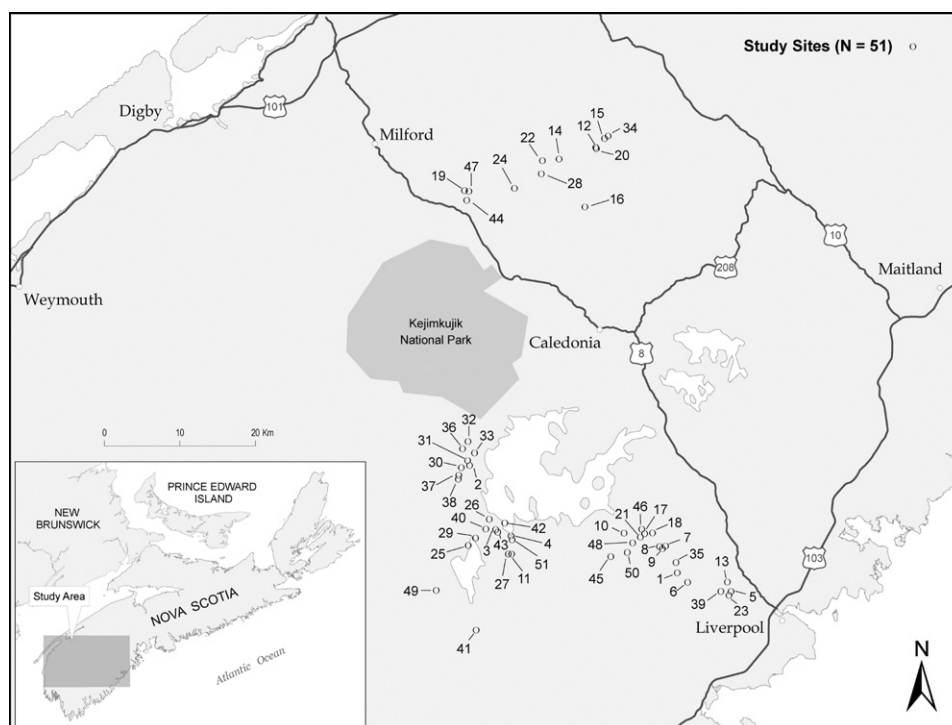


Fig. 1. Location of study sites in southwestern Nova Scotia, Canada.

forest region of northeastern North America. Therefore, the aim of the present study was to explore patterns of lichen community composition at a stand scale using relationships between stands, species, and environmental variables in forests from southwestern Nova Scotia. The lichen richness data used in this study were first presented by McMullin et al. (2008). In that study, 135 lichen species were identified, but that number was reduced to 115 for this study. All genera that were not broken down into species, and species with a high uncertainty of being located in each stand, particularly those in the genus *Usnea*, were not included to maintain accurate community compositions. The data obtained by examining the environmental variables in each forest stand are newly presented information.

The results of this study should provide forest managers with a better understanding of the environmental variables that influence lichen diversity, and contribute to the development of more sustainable forest management strategies. Additionally, this research contributes information to a larger project supported by the Sustainable Forest Management Network that is focused on gaining a greater understanding of old-growth forests and ultimately on developing conservation strategies for these forests (Brassard et al., 2008; McMullin et al., 2008; Moyer et al., 2008; Owen et al., 2008).

## 2. Methods

### 2.1. Study sites

During the summers of 2005 and 2006, 115 epiphytic lichen species were identified in 51 conifer-dominated forest stands in southwestern Nova Scotia that ranged between 52 and 292 years of age (estimated using dendrochronology) and had no visible evidence of timber harvesting (Fig. 1). The UTM coordinates of each stand are listed in McMullin (2007), coordinates range between 4875697 and 4934239N and 316510 and 355584E (Zone 20T). This area is covered by the Rossignol and South Mountain eco-districts which are characterized by undulating low-elevation post-glacial

topography and forests with well-drained medium-textured till (Neily et al., 2003). The criteria for the composition of the trees in each stand was > 70% conifer. The minimum stand size was large enough to establish a 30 m × 300 m sampling plot within a 50 m marginal buffer. The stands were initially identified using Bowater Mersey Paper Company's (now AbitibiBowater) forest resource inventory maps and aerial photos. A visual ground survey was then conducted to ensure that the site criteria were met. The stands were assessed by recording the stem density of live trees and snags ( $\geq 1.3$  m in height and  $\geq 8$  cm dbh), the composition of tree species, stand coordinates (in the universal-transverse-mercator projection), the proximity of wetlands (lakes and rivers) and swamps (marsh and treed bogs), the amount of light reaching the forest floor throughout the stand (canopy closure), and the calculated stand ages using tree cores. Additional details about the methods are provided in Pesklevits (2006), McMullin (2007), and McMullin et al. (2008).

### 2.2. Lichen diversity (richness) plots

Within each forest stand, a plot was established at least 50 m from the stand edge (as depicted on forest-inventory maps) to limit edge effects (Esseen and Renhorn, 1998; Rheault et al., 2003), which results in increased light exposure, reduced moisture and greater wind exposure (Chen et al., 1993; Renhorn et al., 1997). A total of 51 plots for assessing lichen richness were established. Lichens were surveyed within a rectangular plot (30 m × 300 m; 9000 m<sup>2</sup>), which included five plots that were used to examine structural complexity (see below). The sampling effort in each lichen plot was 2.5 h by one person (the lead author). Sampling was restricted to 0.5–2.0 m above the ground on the boles of all trees, snags, and shrubs including accessible branches within this zone. The lower trunk was not examined to avoid terricolous lichens that often grow on the base of boles. The 'floristic habitat sampling' method described by Newmaster et al. (2005) was used and each epiphytic lichen species encountered in a plot was collected, including both microlichen and macrolichen species. Selva (1994, 1999, 2003) described this

method as an ‘intelligent meander’ that reduces the chances of missing species by providing the freedom to explore lichen-rich microhabitats in greater detail and spend less time in areas where the trees are colonized by fewer species.

### 2.3. Structural complexity plots

Within the 30 m × 300 m lichen plot in each stand, five equally spaced circular plots, with a 13.8 m radius (600 m<sup>2</sup>) covering a total area of 0.3 ha per stand, were established to examine the structural complexity. The design consisted of a transect running the length of the lichen plot, on which the structural complexity plots were centred with a one-plot-width (27.6 m) distance between plot boundaries.

In each of the five plots, all trees and snags were identified to species and the diameter at breast height (dbh) was measured. In each of the stands, eight coniferous trees of average stand size that were dominant or co-dominant in the primary canopy were selected for coring (Peskelevits, 2006). Based on the cores, the ages of the eight oldest trees were averaged to provide a working age for each forest stand. The density of the stems per hectare was calculated using stems and snags with a dbh ≥ 8 cm. Canopy closure was measured with a densiometer. In each forest stand, four readings were taken in each of the five circular plots; each reading was done 7 m from the centre of each plot in a north, south, east and west direction. The amount of wetland (ha) and swamp (ha) within 500 m of each stand was determined using Bowater Mersey's digital forest resource inventory. Using ArcGIS, a 500 m zone was drawn around each stand and the amount of wetland and swamp within this area was calculated.

### 2.4. Lichen identification

Approximately 6000 lichen specimens were collected and identified from the 51 forest stands examined. Most species were identified using a stereoscope or compound microscope with the help of chemical spot tests (alcohol and stable para-phenylenediamine, sodium hypochlorite, 10% potassium hydroxide, and Lugol's iodine) (Brodo et al., 2001; Smith et al., 2009). Specimens that could not be reliably identified by structural features and spot tests were studied further using thin-layer chromatography at the Canadian Museum of Nature in Ottawa, Ontario. Voucher specimens are stored at the Canadian Museum of Nature (CANL), the Nova Scotia Museum of Nature (NSPM) and the Biodiversity Institute of Ontario Herbarium (OAC) at the University of Guelph, Ontario.

### 2.5. Multivariate ordination analysis of community composition

Multivariate analysis was used to explore patterns in community organization. Principal component analysis (PCA, ter Braak, 1998) was used to identify the length of the ordination axis and the need for either a linear or unimodal ordination technique. Unimodal, direct ordination (canonical correspondence analysis—CCA) of 51 stands and 115 species was used to explore variation in species and site scores using 25 environmental variables (Tables 1 and 2) to constrain the ordination. The ordination generated axis scores for each subplot value, with the axes correlated to the most important environmental variables in the analysis.

## 3. Results

### 3.1. Tree species composition

Thirteen tree species occurred throughout the 51 forest stands assessed. Individual tree species had the following stand composi-

**Table 1**

The mean and standard deviation of the environmental variables measured across 51 forest stands.

Environmental variable	Mean	St. dev.
Lichen alpha diversity ( $\alpha$ )	25.5	5.4
Stand age (Ag)	162.8	69.6
% Conifer abundance (C)	87.7	9.2
Conifer stem density/ha (Dc)	725.6	258.0
% Deciduous abundance (D)	12.4	9.2
Deciduous stem density/ha (Dd)	131.6	92.4
Live tree stem density/ha (Dt)	857.2	280.8
Light (canopy closure) – mean (Lm)	2.9	1.8
Light (canopy closure) variance – st. deviation (Lv)	3.9	–
Lake proximity – ha within 500 m (Lk)	4.4	5.4
Swamp proximity – ha within 500 m (Swmp)	2.2	4.1
Site continuity (SC)	21	7.4
Calicioid species (CF)	1.6	1.4
% <i>Tsuga canadensis</i> cover (eH)	40.6	30.3
% <i>Picea</i> spp. cover (S)	26.3	17.0
% <i>Pinus strobus</i> cover (wP)	18.6	20.1
% <i>Acer rubrum</i> cover (rM)	8.3	7.7
% <i>Betula papyrifera</i> cover (wB)	1.1	2.2
% <i>Betula alleghaniensis</i> cover (yB)	0.6	2.8
% <i>Quercus rubrum</i> cover (rO)	0.4	1.3
% <i>Populus</i> spp. cover (P)	0.7	3.6
% <i>Acer pensylvanicum</i> cover (sM)	0.1	0.4
Snag stem density/ha (DS)	263.4	173.5

tion percentages across all of the stands: *Tsuga canadensis* (0–90%), *Pinus strobus* (0–80%), *Picea* spp. (*Picea rubens*, *Picea glauca* and *Picea mariana*) (1–59%), and *Abies balsamea* (0–15%). The rest of the stand composition primarily consisted of *Acer rubrum* (0–33%), with small amounts of *Populus* spp. (*Populus grandidentata* and *Populus tremuloides*) (0–25%), *Betula alleghaniensis* (0–19%), *Betula papyrifera* (0–9%), *Quercus rubra* (0–4%), and *Acer pensylvanicum* (0–3%). The mean and standard deviation of the percent of stand composition of each tree species in all stands is shown in Table 1. The specific tree composition of each stand, and stem densities, are presented in McMullin et al. (2008).

### 3.2. Lichen species diversity

One hundred and fifteen epiphytic lichen species were located within the 51 forest stands examined. The lichen species selected for inclusion in the analyses were those that could be reliably identified when mature and were typically conspicuous enough to be found, when present, in any of the forest stands visited. Twenty-six species (23%) occurred in only 1 stand, 51 species (51%) were found in 5 or fewer stands, and only 3 species occurred in all 51 stands, *Hypogymnia physodes*, *Parmelia squarrosa* and *Platismatia glauca*. Sixteen species (14%) of the total number of lichens found were calicioid (stubble), and 21 species (18%) contained blue-green algae (cyanolichens) (Table 3 and Supplement 1).

### 3.3. Multivariate analysis of community composition

Relationships between species, stands, and environmental variables were interpretable in the canonical correspondence analysis (CCA; Fig. 2; Table 2). The overall inertia (i.e. variance) was 3.357 indicating considerable dispersion among the species data. The 25 environmental variables explained 57% of the variance (as inertia) in the lichen species composition. High species/environment correlations indicate a close correspondence between the species and environmentally constrained ordination (Table 4). Although there are no distinct groups on the ordination, there is considerable variation among the stand and species scores of which the bi-plot indicates the direction and relative influence of several environmental variables along two gradients (Fig. 2). A Monte Carlo

**Table 2**

Sampling statistics for variables used in canonical correspondence analysis (CCA) of 51 stands, 115 lichen species and 25 environmental variables. Asterisks indicate significance at  $p < 0.05$ . Absolute  $t$ -values  $> 2.1$  are used to indicate important canonical coefficients (ter Braak, 1998). Bold values indicate variables with significant correlation and canonical coefficients.

Variable	Inter-set correlation		Canonical coefficient		$t$ -value	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Lichen alpha diversity ( $\alpha$ )	0.120	−0.275	−0.105	*−0.407	−1.145	−4.406
Stand age (Ag)	−0.723	0.239	*−0.514	*0.578	−3.752	4.191
% Conifer abundance (C)	0.441	0.229	0.097	*1.630	0.254	4.321
Conifer stem density/ha (Dc)	0.214	0.512	1.250	*−1.928	2.012	−4.203
% Deciduous abundance (D)	−0.028	−0.459	0.373	*−1.334	0.662	−2.348
Deciduous stem density/ha (Dd)	−0.158	−0.595	0.416	*−1.827	0.845	−2.523
Live tree stem density/ha (Dt)	0.707	0.283	*7.771	*−11.502	2.468	−3.626
Light (canopy closure) – mean (Lm)	−0.223	−0.199	*−0.541	−0.080	−4.488	−0.656
Light (canopy closure) variance – st. dev. (Lv)	−0.040	−0.182	*0.323	−0.151	2.652	−1.226
Lake proximity – ha within 500 m (Lk)	−0.146	0.005	0.154	*0.249	1.295	2.084
Swamp proximity – ha within 500 m (Swmp)	−0.183	0.014	−0.172	*−0.254	−1.579	−2.315
Stand continuity (SC)	−0.045	0.288	0.210	*0.891	1.903	7.996
Calicioid species (CF)	−0.455	−0.053	*−0.443	*−0.588	−4.894	−6.436
% <i>Tsuga canadensis</i> cover (eH)	−0.644	0.225	*−1.734	0.944	−2.247	1.214
% <i>Picea</i> spp. cover (S)	0.379	0.038	*−1.223	0.878	−2.646	1.885
% <i>Pinus strobus</i> cover (wP)	0.596	−0.140	*−1.304	0.520	−2.547	1.009
% <i>Acer rubrum</i> cover (rM)	0.087	−0.404	0.324	*0.221	1.026	2.695
% <i>Betula papyrifera</i> cover (wB)	0.018	0.052	0.096	0.039	0.855	0.345
% <i>Betula alleghaniensis</i> cover (yB)	−0.163	0.100	−0.010	*0.466	−0.053	2.340
% <i>Quercus rubrum</i> cover (rO)	−0.088	−0.097	*0.320	*0.321	2.275	2.265
% <i>Populus</i> spp. cover (P)	0.007	0.038	0.192	*0.302	1.452	2.269
% <i>Acer pensylvanicum</i> cover (sM)	−0.145	0.040	0.343	−0.363	1.834	−1.930
Snag stem density/ha (DS)	0.697	0.192	*−2.661	*5.088	−2.057	3.903
Aspect – Easting (E)	−0.385	−0.152	*−0.345	*0.556	−3.177	5.087
Aspect – Northing (N)	−0.244	0.132	−0.072	−0.124	−0.758	−1.293

**Table 3**

Lichen richness across all forest stands and ordination quadrants.

Lichen groups	Total	Stand		Ordination quadrant			
		Mean	St. dev.	A	B	C	D
Total lichen richness	115	–	–	70	72	64	81
Green-algal lichens	94	20.7	4	52	59	53	66
Cyanolichens	21	4.8	2.5	18	13	11	15
Macrolichens	50	14.4	3.1	36	34	33	39
Foliose	42	11.9	2.8	30	28	26	33
Fruticose	8	2.5	1.1	6	6	7	6
Microlichens (crustose)	65	11.1	2.2	34	38	31	42
Calicioid lichens (stubble)	16	1.6	1.4	5	6	10	14

permutation test confirmed that the first two axes are statistically significant ( $0.001 < P < 0.01$ ) in explaining some of the variation in the species data set (Table 2). Significant ( $0.001 < P < 0.01$ ;  $n = 51$ ) inter-set correlations and  $t$ -values were used to identify important environmental variables for axis one (Table 2). The stand ordination identifies stand age (Ag; inter-set correlation  $IC = -0.7233$ ), live tree stem density (Dt;  $IC = 0.7071$ ) and snag stem density (DS;  $IC = 0.6969$ ) as the most important variables that explain variation in the species along the first CCA axis. Other considerable variables include the abundance of specific species of coniferous trees such as *T. canadensis* (eH;  $IC = -0.6442$ ) and *Pinus strobus* (wP;  $IC = 0.5956$ ). The second CCA axis in stand ordination is strongly correlated with deciduous stem density (Dd;  $IC = -0.5952$ ) and abundance (D;

$IC = -0.4592$ ) including specific deciduous tree species such as *A. rubrum* abundance (rM;  $IC = -0.4042$ ).

Community composition is highly varied among stands with considerable beta diversity. The species ordination identifies less frequently occurring species falling progressively further from the centre of the ordination (Fig. 2). A considerable number of unique species are found in all quadrants of the ordination (Table 3; Fig. 2). Forty-two species are unique to a single quadrant of the ordination, 40 are in all quadrants, 19 species are found in three quadrants, and 14 species are found in two quadrants (Fig. 2). Proportionally, there are more species unique to a particular stand along an environmental gradient than those common to all stands. The total number of lichens is greatest in quadrant D, within the oldest stands. The calicioid lichens (stubbles) are also grouped in the upper top left corner, within the older stands. Perhaps the most striking pattern, however, is that no one or group of environmental gradients can be used to explain community composition; unique species are found across all stands and thus all environmental variables are important to lichen diversity.

**Table 4**

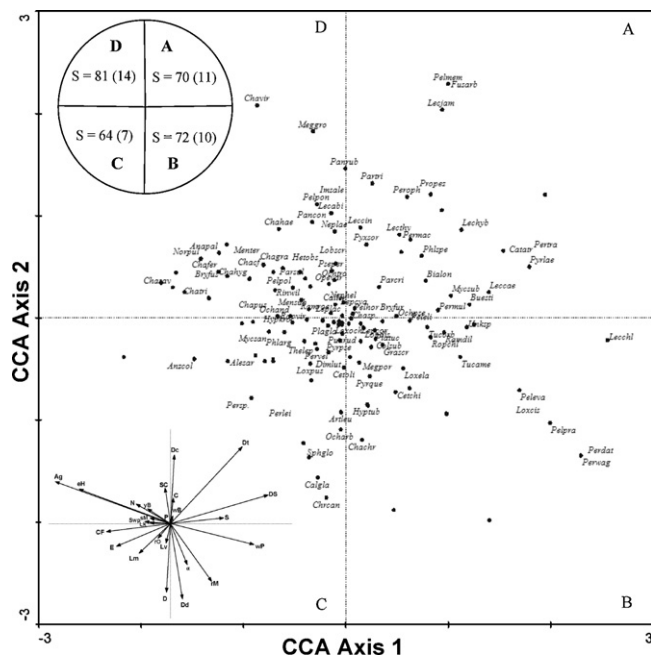
Summary of canonical correspondence analysis (CCA) of 51 stands, 115 lichen species and 25 environmental variables.

Axis	1	2	3	4
Eigenvalue	0.212	0.149	0.137	0.121
Species/environment correlation	0.964	0.955	0.935	0.917
Cumulative % variance of species data explained	13.9	23.5	31.1	38.1

#### 4. Discussion

The CCA revealed that considerable variation in lichen community composition can be explained, in varying degrees, by all





**Fig. 2.** CCA ordination of 115 lichen species and 51 stands constrained by 25 environmental variables in the inserted bi-plot diagram. Ordination is divided into quadrants with an insert diagram listing total richness and per quadrant (S) with the number of unique species in that quadrant in parenthesis. Abbreviations for environmental variables and lichen species are listed in Table 2 and in Supplement 1, respectively.

environmental variables associated with forest structure. This suggests that the microhabitat requirements of the various lichen species examined were generally different. Otherwise, species would have clustered more around particular environmental variables; instead of forming a single large cluster centred in the middle of the two axes (Fig. 2). Dividing the ordination into quadrants also indicated that stands are grouped along respective environmental gradients and they do not contain the same species. In fact, there are many unique groups of species occurring in the quadrants and along the gradients. The total number of species (115), however, is greater than any group of stands within any particular quadrant. The division of biologically related species is also spread out over the quadrants and along gradients; this includes: macrolichens, green-algal lichens, calicioid (stubble) lichens, cyanolichens and different form types (foliose, crustose and fruticose). It appears that all the environmental variables that shape structural complexity are important to lichen richness. As the variation of the structural components in a forest stand increases, an increase in the number of unique microhabitats occurs, with each environmental variable contributing exponentially to the number of microhabitats. The greater the number of unique microhabitats, the larger the number of lichen species that can colonize a stand because more ecological requirements of more lichen species will be met.

Studies on particular environmental variables help to build a picture of the relationships between epiphytic lichens and forest structure. For example, lichen species tend to colonize particular tree species that have the necessary bark properties (Adams and Risser, 1971; Brodo, 1973; Esseen, 1981; Schmitt and Slack, 1990; Kuusinen, 1996). Light levels and relative humidity have also been found to influence epiphytic lichen species diversity (Kenkel and Bradfield, 1986; Kuusinen, 1995; Coxson and Coyle, 2003; Coxson and Stevenson, 2007). Each environmental variable is important for lichen diversity, but it is the interrelationships between them that determine the number of microhabitats available for colonization by lichens.

Lichen diversity, however, is not shaped by structural complexity alone. Environmental variables beyond the structure of the forest can also influence lichen diversity, which includes ecoregions (Coppins and Coppins, 2002; McMullin et al., 2008), elevation (McCune, 2000), soil nutrient levels and rainfall pH (Goward and Arsenault, 2000; Richardson and Cameron, 2004). Such variables need to be considered in forest management strategies for a better understanding of the relationships between lichen communities and environmental variables within a stand.

Quantifying structural diversity for preservation and management is a multi-faceted challenge. This is exemplified by the lack of definition for old-growth forests. There is agreement that they must reach certain ecological, or political, thresholds, but there is no agreement on how such thresholds are determined (Frelich and Reich, 2003; Mosseler et al., 2003; Stewart et al., 2003; Pesklevits, 2006). Attempts have been made to use lichens to gauge continuity, which is related to structural complexity and age (Rose, 1974, 1976; Selva, 1994, 2002). Selva (2002) created an index of ecological continuity that uses calicioid (stubble) lichens exclusively to measure the continuity of a forest stand, which is supported by our CCA that confirmed calicioid lichens are associated with older stands. Determining continuity by using environmental variables, however, is more complex. The present study illustrates that high variation within and between many environmental variables in a stand is important as it leads to an increase in lichen diversity.

Despite the lack of accepted thresholds and definitions for old-growth, forest stands can be managed to maximize structural complexity which will maintain or enhance lichen diversity (i.e. uneven aged stands with a large range of tree species). The present study illustrated that unmanaged old-growth forests in southwestern Nova Scotia contain a rich lichen flora and are important for the preservation of epiphytic lichen diversity in the province. The largest number of lichen species unique to a single stand was found in quadrant D of the ordination (14), which is representative of the oldest stands. Quadrant B, which is representative of younger stands, had fewer species unique to a single stand (10) (Fig. 2). Preserving areas of unharvested forests is important because managed stands have been shown to have 23% less epiphytic lichen richness than natural stands (Dettki and Esseen, 1998). Additionally, the retention of individual old trees or small clumps does not preserve epiphytic lichen diversity (Edman et al., 2008; Cleavitt et al., 2009). To optimize lichen diversity at a stand scale, management strategies need to enhance as much variation within the environmental variables of the forest as possible. This will primarily include a variation in the amount of canopy closure and in tree species and ages. To maintain lichen diversity at the landscape level, however, the preservation of old-growth forests is necessary and should be incorporated into any management plan.

### Acknowledgements

We gratefully acknowledge identification assistance from Frances Anderson, Irwin Brodo, Stephen Clayden, and Steven Selva. Thanks to Caroline Urquhart and Scott Wile for their statistical assistance, and to Mari Decker and two anonymous reviewers for their helpful comments on the manuscript. Many thanks to all field staff, particularly Anthony Pesklevits, and to Heidi Faulkner for assisting with mapping and GIS work. This project was supported by the Sustainable Forest Management Network, the Bowater Mersey Paper Company (which also provided exceptional field assistance), and Dalhousie University.

### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.05.032.

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