

Predicting canopy macrolichen diversity and abundance within old-growth inland temperate rainforests

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ABSTRACT

Windward slopes of the inland mountain ranges in British Columbia support a unique inland temperate rainforest (ITR) ecosystem. Increasing fragmentation and the loss of old ITR stands have highlighted the need for determining conservation biology priorities among remaining old forest stands. We have addressed this issue by surveying foliose macrolichens within 53 old ITR stands in British Columbia's 135,000 ha very wet-cool interior-cedar hemlock (ICHvk2) biogeoclimatic subzone in the upper Fraser River watershed. Study plots were stratified by leading tree species and by "wet" versus "dry" relative soil moisture conditions. Other plot variables included: temperature, precipitation, incident solar loading, and canopy openness. Ordination plots showed a distinct assemblage of foliose cyanolichens, including *Lobaria pulmonaria*, *Lobaria retigera*, *Sticta fuliginosa*, *Nephroma isidiosum*, *Nephroma occultum*, and *Pseudocyphellaria anomala*, whose abundance was correlated with increasing relative soil moisture, temperature, canopy openness, precipitation, and basal area of spruce. Logistic regression models similarly identified relative soil moisture and temperature in all parsimonious models. Leading tree species, in combination with "wet" relative soil moisture and/or temperature, were important factors explaining the presence or absence of five (*Cavernularia hultenii*, *L. retigera*, *N. occultum*, *Platismatia norvegica*, and *Sticta oroborealis*) of the eight modeled old-growth associate lichen species. This combination of conditions favouring the development of canopy lichen communities in old forests was best expressed in low elevation water receiving sites. We hypothesize that groundwater availability in these sites promotes species richness and abundance of canopy lichens by creating more favourable conditions for growth, and by reducing fire return intervals which allows for the accumulation of rare species over time. Historically, forests in these wet "toe-slope" positions were disproportionately targeted for logging. Their conservation should now be a high priority, given their disproportionate significance to maintaining canopy lichen diversity in the present-day landscapes.

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1. Introduction

Temperate rainforest ecosystems have been widely recognized as a major repository for biodiversity, particularly for organisms that live within forest canopies. In western North America, coastal temperate rainforest ecosystems have been the focus of increased attention in recent years, with important steps being taken towards the implementation of landscape level conservation biology measures (Anon., 1995). However, in British Columbia (B.C.) a second major temperate rainforest ecosystem is found on the windward slopes of interior mountain ranges. This inland temperate rainforest (ITR) has many unique characteristics, including globally significant assemblages of canopy lichens and

mosses (Arsenault and Goward, 2000; Botting and Fredeen, 2006; Goward, 1994). Some 40% of oceanic epiphytic macrolichens found in Pacific coastal rain forests also occur in these inland rainforests (Goward and Spribille, 2005). Among oceanic epiphytic species found in the inland rainforest are the hanging moss (*Antitrichia curtipendula*) and lichen genera such as *Chaenotheca*, *Chaenothecopsis*, *Collema*, *Fuscopannaria*, *Lichinodium*, *Lobaria*, *Nephroma*, *Parmeliella*, *Polychidium*, *Sphaerophorus*, and *Sticta* (Arsenault and Goward, 2000). Goward and Arsenault (2000) conclude that "conifer forests of intermontane British Columbia support at least 31 cyanolichen species—one of the richest epiphytic cyanolichen assemblages in the world". They suggest that maximum cyanolichen diversity is associated with the co-occurrence of nutrient-rich sites in lowland old-growth inland rainforest sites. Campbell and Fredeen (2004) further note that many of the oceanic lichen taxa in the ITR are associated largely with very old forest stands, and are largely absent from younger stands.

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Although plant communities of the ITR show significant oceanic influences, they may be more constrained in their landscape level distribution patterns than are their counterparts in coastal temperate rainforests. A major difference between coastal and inland temperate rainforest ecosystems in B.C. is that ITR ecosystems receive approximately half the annual precipitation of that received in coastal temperate rainforests. As a result, the development of ITR is more dependent on local patterns of snowmelt and ground moisture conditions than are their coastal counterparts. These local differences in moisture availability are apparent when examining fire frequency in the ITR. Eng (2000) noted that stands located on cool north-facing slopes showed a near tenfold reduction in stand destroying fire frequency compared to stands associated with warm south-facing aspects. Beaty and Taylor (2001) also examined the influence of slope and aspect on fire frequency, noting that fire frequency was reduced on lower slope, water receiving topographic positions. DeLong (1998) reported that fire return intervals in wet montane forests of the upper Fraser River watershed ranged from 244 to over 1600 years while Sanborn et al. (2006) found a median time since fire in wet inland temperate rainforests between 800 and 1200 years. These results suggest that disturbance processes in the wettest portions of ITR may be similar to those in coastal temperate rainforests, where single-tree gap dynamics dominate due to tree age (Lertzman et al., 2002).

In the mountainous topography of the upper Fraser River watershed, resistance to fire in these wet “toe-slope” or water receiving locations has favoured the development of western redcedar (*Thuja plicata*) stands that often contain trees of exceptional age and stature (Benson and Coxson, 2002). Goward and Arsenault (2000) describe these stands as “antique” forest stands; sites where the last major disturbance event, such as fire, happened well before the current generation of trees established. Preliminary studies of Goward (2003) in the Upper Fraser River watershed suggested that antique forest stands in “toe-slope” positions represented areas of exceptional diversity for arboreal lichen species. However, the future of old forests in these wet landscape positions is far from assured. Current landscape level management policies in the upper Fraser River watershed specify that 53% of the landscape must be retained as old forest cover, based on a 140-year age threshold (DeLong, 2007). However, this does not necessarily ensure that high-value old forest stands will be retained in future landscapes. Indeed, the opposite may be true, in that the placement of transportation corridors through “toe-slope” stands in the upper Fraser River watershed has led to disproportionate logging of the very oldest stands. A major challenge for forest managers has therefore been to develop criteria that could be used to support the spatial designation of high-value reserves in the remaining areas of old forest.

In the U.S. Pacific Northwest and elsewhere lichens have been used as an indicator group to assess old forest status (Bollinger et al., 2007; McCune et al., 2000; Rolstad et al., 2000; Rosso et al., 2000). Given that the presence and abundance of arboreal lichen communities can integrate both site continuity and old-growth habitat values, we would suggest that a landscape level assessment of old-growth associate canopy lichen communities in BC's ITR could assist in providing a ranking of the conservation biology potential of remaining old-growth forest stands and an assessment of environmental variables that promote canopy lichen diversity. When we look to previous studies in coastal wet-temperate rainforests, they suggest that wet microsites play an important role in supporting canopy lichen diversity (McCune et al., 2002; Lidén and Hilmo, 2005) and that groundwater receiving sites, in particular, are strongly associated with the development of rich wet-temperate rainforest habitats (Spies and Franklin, 1991). Substrate characteristics have further been found to be an

important determinant of lichen diversity in old-growth forests (Hauck and Spribille, 2002). Goward and Arsenault (2000) suggest that elevation is also primary determinant of canopy macrolichen diversity, with lower elevation sites having the richest canopy lichen communities.

We would therefore hypothesize that the primary factors influencing canopy macrolichen diversity in old-growth ITR forests will be elevation, moisture availability, and stand composition. We would hypothesize that warmer low elevation sites will have greater canopy macrolichen diversity and abundance. We would further hypothesize that canopy macrolichen diversity will be strongly influenced by moisture availability; both from precipitation, and from groundwater transport, in topographic positions that are water receiving sites. Finally, we would hypothesize that individual lichen species may show substrate preference for different host tree species, reflecting their individual autecology and life history traits. Our primary objective is that of providing land-use planners with criteria that can be used to assess the conservation biology potential of remaining old-growth ITR stands for canopy macrolichen communities. This is a critical need, given the progressive conversion of old-growth ITR stands to plantation forestry. Secondary objectives include the evaluation of how old-growth associated lichens differ one-from-another in their response to major environmental variables.

We have now conducted a landscape level assessment of factors influencing lichen diversity and abundance in the upper Fraser River watershed. We have based our ranking of stands on an evaluation of the abundance of canopy macrolichens in 53 old forest stands located within the “very wet-cool” interior-cedar hemlock (ICHvk2) biogeoclimatic zone of the upper Fraser River watershed. Selection of study sites was stratified to ensure representation from sites with both “wet” and “dry” relative soil moisture conditions, and from stands with western redcedar (*T. plicata*), western hemlock (*Tsuga heterophylla*), and hybrid white spruce (*Picea engelmanni* × *glauca*) as leading tree species.

2. Materials and methods

2.1. Study sites

The study area is located in east-central British Columbia, Canada in the upper Fraser River watershed, focusing on forests in the ICHvk2 biogeoclimatic zone of Meidinger and Pojar (1991), and to a limited extent, in adjacent valley bottom forests within the “very wet-cool” sub-boreal spruce (SBSvk) biogeoclimatic zone, at elevations between 640 and 1076 m a.s.l. SBSvk forests are dominated by hybrid white spruce (*P. engelmanni* × *glauca*), hereafter referred to as spruce (Sx) and subalpine fir (*Abies lasiocarpa*) (Bl). ICHvk2 forests are dominated by western redcedar (*T. plicata*) (Cw), western hemlock (*T. heterophylla*) (Hw); with some Douglas-fir (*Pseudotsuga menziesii*), subalpine fir, and spruce present, depending on site conditions.

Mean annual precipitation of the ICHvk2 is 839.8 mm (374.3 mm in summer and 465.5 mm in winter) with a mean summer temperature of 14.7 °C and a mean winter temperature of −12.1 °C. Recorded mean annual snowfall is 306.8 cm persisting on the ground 9 months of the year (Reynolds, 1997). Slow-melting snow pack tends to keep soil moisture levels high during the summer (Ketcheson et al., 1991). Minimum and maximum climate data for the 53 study sites selected (see below for methodology) were as follows: mean annual precipitation, 736–917 mm; average minimum temperature, −3.1 °C to −1.6 °C; average maximum temperature, 7.9–9.9 °C; mean annual average temperature: 2.4–4.0 °C; and average March to October minimum temperature range: 0.5–2.4 °C.

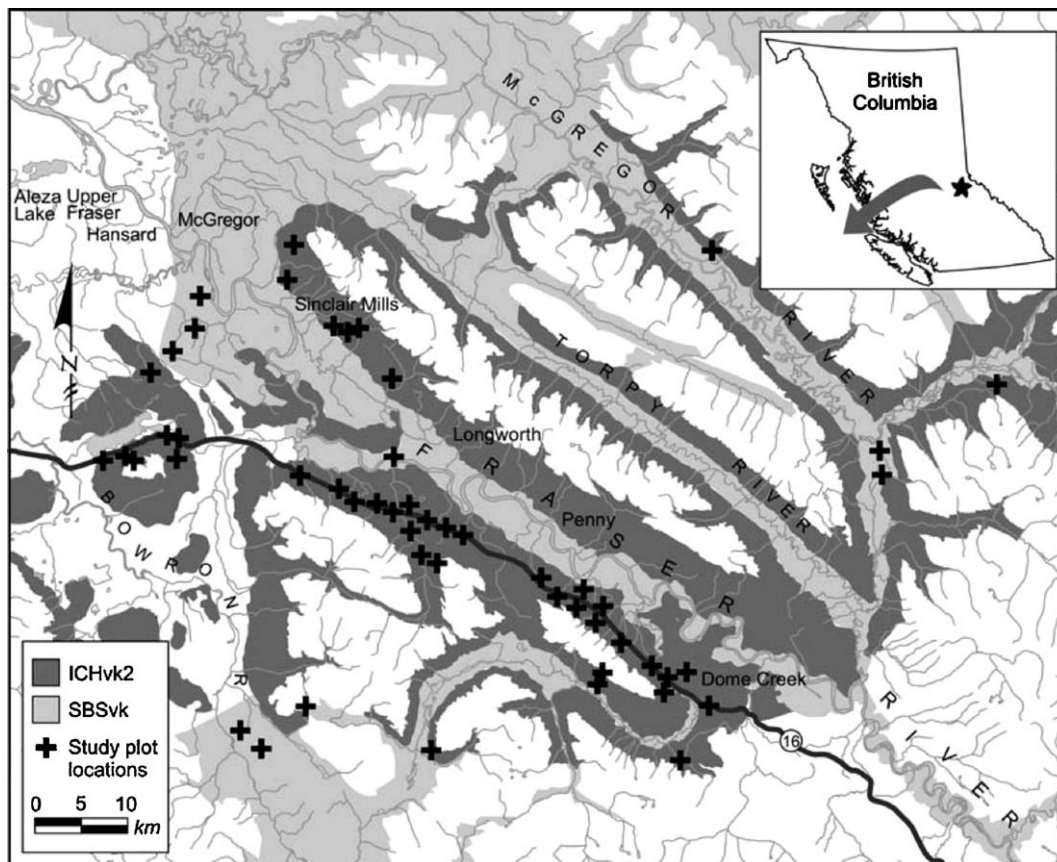


Fig. 1. Location of “wet”-cool interior-cedar hemlock (ICHvk2) and adjacent very-“wet” sub-boreal spruce (SBSvk) biogeoclimatic zones in central interior British Columbia.

2.2. Study design

Field data were collected in summer 2004 and 2005. We selected 53 GIS polygons to sample from a total of 120 randomly selected candidate polygons (Fig. 1). Selection criteria for eligible polygons (hereafter called stands) included: (a) location in the ICHvk2 or in the adjacent SBSvk (within 5 km of the ICHvk2) biogeoclimatic subzones; (b) forest greater than 140 years in age; (c) cedar-, hemlock-, or spruce-leading; (d) 500 m or less from road access (for logistical purposes) and; (e) at least 50 m from cutblock edges, riparian areas, and deciduous forest types. We used the B.C. Ministry of the Environment Predictive Ecosystem Mapping (PEM) database, an ecosystem mapping conducted at a 1:50,000 scale (see Anon., 1999) and the B.C. Ministry of Forests Vegetation Resources Inventory database, a forest inventory mapping (see Anon., 1998), to identify candidate polygons that met our selection criteria. When identifying the leading species, a stand was determined leading in cedar (Cw), hemlock (Hw), or spruce (Sx), based on the tree species that had the highest Basal Area in the stand. It should be noted that the leading tree species, i.e. the species that is most abundant in a given stand, may not be the same as the dominant tree species as the term is commonly used in forestry, referring to trees that emerge above the main canopy.

Sampling within old-growth forests was stratified to ensure representation from each of cedar-, hemlock-, and spruce-leading stands (using Vegetation Resources Inventory data), and from stands representing “wet” or “dry” relative soil moisture conditions (hereinafter called soil moisture) was obtained using PEM. At each stand, we laid out 2 plots that shared a common centre. The lichen assessment plot was a rectangular survey area 40 m × 100 m, with the long axis parallel with the slope to avoid marked topographic changes (see Fig. 2). Each plot was assessed

for 37 possible arboreal foliose lichens (checklist adapted from Goward et al., 1994) using a time-limited visual search method from the USDA Forest Health monitoring lichen protocols (available at <http://www.fia.fs.fed.us/library/field-guides-methods-proc/>), described also by McCune et al. (2002). Each macrolichen species observed was given an abundance rating between 0 and 4 (with the exception of *Lobaria pulmonaria*): 0 = absent, 1 = rare [1–3 individuals/plot], 2 = uncommon [4–10 individuals/plot], 3 = common [>10 individuals], 4 = very abundant [covering more than half of available substrates]. The population being sampled with this procedure consists of all visible macrolichens occurring on live or standing dead woody plants, excluding the 0.5 m basal portion of trees, snags, saplings and shrubs. For *L. pulmonaria*, similar categorical assignments were made, yet because of its ubiquity and abundance of *L. pulmonaria* in this ecosystem we used an area based measurement of the number of

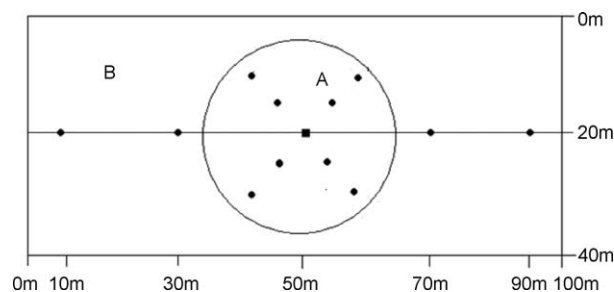


Fig. 2. Sample plots used for data collection: (A) Circular stand structure plot ($r = 17.84$ m); (B) lichen plot = area inside the 40 m × 100 m (0.4 ha) rectangle. Locations of densiometer measurements are identified by point locations (square point indicating plot centre).

“hand-sized” clumps (these ca. 10 cm × 20 cm) in each lichen plot. These values were converted back to our 0–4 abundance rating scale based on the mean number of individuals in a subset of destructively sampled “hand-sized” clumps.

The stand structure plot was a circular plot with a radius of 17.8 m. The purpose of the stand structure plot was to provide more detailed information on the structural components of the forest stand structure and soil moisture conditions. Diameter at breast height (DBH) (1.3 m) was measured for all stems greater than 16.5 cm DBH, categorized by live and dead stems and identified by tree species. Soil moisture status of each stand identified from PEM was further classified on a seven point scale using the moisture regime key in DeLong (2003), which incorporates measurements of slope, mesoslope, aspect and soil texture. Soils were categorized as having a “wet” soil moisture status when classifications were above four on the seven point scale of DeLong (2003), and “dry” soil moisture when classifications were less than four (corresponding to mesic and submesic sites in DeLong’s (2003) moisture regime key). When stands were classified as a four (mesic) on DeLong’s soil moisture (2003) scale, additional vegetation and soil characteristics were used to assign plots to either a “wet” or “dry” soil moisture category following DeLong (2003). Soil samples for texture analysis were obtained from within a soil pit dug to approximately 1 m at plot centre. Stand elevation was taken from PEM mapping for each polygon.

At each of thirteen locations in each lichen assessment plot (equally spaced on six lines radiating from plot centre) 360° measurements of canopy openness were taken were taken at 90° intervals using a spherical densitometer (Fig. 2), with each set of 4 values averaged for that point. We subsequently pooled all thirteen averages to obtain an estimate of the overall canopy openness of the stand.

Predicted mean annual precipitation and temperature for each stand was obtained from the Canadian Forest Service regional climate database (Hutchinson, 1995). We used mean monthly minimum temperature for the months March–October in our analysis; this reflected the seasonal time period during which most lichen growth occurs (Coxson and Stevenson, 2007). Potential mean annual solar insolation was calculated using SAGA-GIS Version 2.0 (Scilands GmbH, Göttingen, Germany) solar radiation model.

2.3. Data analysis

Nonmetric multidimensional scaling ordination was used to examine trends in lichen community composition across stands (PC-ORDV. 5.0, McCune and Mefford, 1999). Stress measurements in relation to dimensionality recommended a two-dimensional ordination. A two-dimensional NSM ordination was therefore run using the “slow and thorough” mode in PC-ORD on a matrix of 53 stands by 34 species, using untransformed cover class data. Final stress on a two-dimensional solution was 19.68 and an instability of 0.0436. We used multiple linear regression (SYSTAT Ver 8.0, SYSTAT Software Inc., Chicago, IL) to evaluate the following variables (log transformed data) against ordination scores for axis 1 and axis 2: temperature, mean annual precipitation, solar insolation, canopy openness, soil moisture, and basal area of cedar (BACw), hemlock (BAHw), spruce (BASx), and subalpine fir (BABI). The variables solar insolation, canopy openness, soil moisture, BACw, BAHw, BASx, and BABI were nonsignificant against axis 1 scores ($P < 0.05$). The variables solar insolation, BACw, BAHw, and BABI were nonsignificant against axis 2 scores. The model was subsequently rerun with significant environmental variables. Variables were tested for multicollinearity (Stata Corporation 2002, College Station, TX). For all variables, we used a tolerance

score of <0.2 to indicate significant multicollinearity (Menard, 2002).

Logistic regression was used to identify important environmental factors that influenced the distribution of lichens observed in our sample plots. Logistic regression models were fit to the presence–absence (untransformed) data for *Cavernularia hultenii*, *Lobaria retigera*, *Nephroma isidiosum*, *Nephroma occultum*, *Platismatia norvegica*, *Peltigera collina*, *Sticta fuliginosa* and *Sticta oroborealis*, species previously identified as old-growth associated by Goward (1994). Independent variables we assessed for each lichen species included: soil moisture status (categorized as “wet” or “dry”), canopy openness, average minimum temperature, mean annual precipitation, solar insolation, and categorized leading tree species (leading species, categorized as Cw, Hw, or Sx). We tested thirteen combinations of independent variables that served as plausible explanatory hypotheses for the distribution of each lichen species: (1) soil moisture + canopy openness + average minimum temperature + mean annual precipitation; (2) soil moisture + canopy openness + average minimum temperature + solar insolation; (3) soil moisture + mean annual precipitation; (4) soil moisture + average minimum temperature; (5) leading species + soil moisture; (6) leading species + canopy openness + average minimum temperature; (7) leading species + canopy openness + mean annual precipitation; (8) leading species + canopy openness + solar insolation; (9) leading species + mean annual precipitation; (10) leading species + average minimum temperature; (11) canopy openness + mean annual precipitation + solar insolation + average minimum temperature; (12) canopy openness + mean annual precipitation; (13) canopy openness + average minimum temperature. We used Akaike’s Information Criterion with a correction for small sample size (AIC_c) (Johnson and Omland, 2004) to identify the most parsimonious logistic regression model. All AIC_c values were subtracted from the lowest AIC_c value in each model set to derive the AIC difference (AIC_c dif). We then calculated the AIC_c weights ($AIC_c w$) and interpreted this value as the approximate probability that the model with the largest value was the most parsimonious of the set (Johnson and Omland, 2004). We calculated the area under the receiver operating characteristic (ROC) curve for the top-ranked models (Munoz and Felicísimo, 2004). ROC scores allowed us to evaluate the ability of the most parsimonious model to predict the distribution of lichens on the landscape.

We used Multi-Model Inference to determine the relative importance of the predictor variables for each species (Johnson and Omland, 2004). Multi-Model Inference uses the $AIC_c w$ to average the beta likelihood coefficients from all variables within the set of models for each lichen species and thus accounts for variation attributed to model selection uncertainty. We used 95% confidence intervals, corrected for model selection uncertainty, to assess the strength of effect of each predictor covariate on the dependent variable.

3. Results

Of the 53 stands used in the data analysis, 22 were cedar leading (11 classified as having “wet” and “dry” soil moisture site conditions respectively), 16 hemlock-leading (6 “wet”, 10 “dry”), and 17 spruce-leading (11 “wet”, 6 “dry”). Currently, 59.1% (67769 ha) of the total forested area of the ICHvk2 biogeoclimatic zone is composed of cedar-, hemlock-, and spruce-leading stands >140 years old (Table 1), with slightly greater than half of these stands categorized as having “dry” soil moisture conditions (31.8%). Approximately one-fifth of mapped old-growth stands fell in designated protected areas (provincial parks or old-growth management areas), this area representing slight less than 12% of the total area of the ICHvk2 climate subzone.

Table 1
Ecosystem representation of old forests (as a % of the total area in the ICHvk2 biogeoclimatic zone in the upper Fraser River watershed) by stand age, leading tree species, protected area status, and relative soil moisture (RSM) status.

Leading tree species	Stand age	% old forests by stand type			
		"Dry" RSM		"Wet" RSM	
		% total	% protection	% total	% protection
Cedar	140–250	8.5	0.81	5.9	0.65
	250+	5.8	1.19	7.1	1.44
Hemlock	140+	4.25	1.1	1.6	0.9
Spruce	140+	13.2	2.0	12.7	2.62
Other species	140+	3.5	0.65	1.7	0.32
Total		35.3	5.8	29	5.9

Other species consisted mainly of *Abies lasiocarpa*. Total forested area of ICHvk2 is 130,571 ha. Base year = 2001.

The distribution of remaining areas of old forest in our study area varies greatly across the upper Fraser River watershed (Fig. 3). Many of the tributary valleys have been heavily logged and have little remaining old forest cover. Furthermore, based on the location of most logging clear-cuts, it is evident that logging has disproportionately targeted low elevation wet soil moisture sites, most notably spruce and secondly cedar-leading stands. In general, wet soil moisture sites are primarily found on north-facing slopes in mid- to lower valley positions, although they do occur in a narrower "toe-slope" elevational band on south-facing slopes (i.e., compare inserts 2 and 3 for Driscoll Ridge in Fig. 3). Wet hemlock-leading sites are more spatially confined, often occurring in lower valley positions with standing surface water. Spruce-leading forests, both wet and dry, have a much wider distribution, extending upslope into adjacent subalpine forests, and downslope into adjacent sub-boreal spruce forests.

Mean annual precipitation was negatively correlated with mean annual temperature in stands, reflecting the trend of increasing precipitation in cooler high elevation sites. However, estimated mean annual temperature, when categorized by soil moisture status, was highest (3.5 °C) in our "wet" stands (Table 2). These stands were typically located in "toe-slope" positions at the edge of valley bottoms, where soil moisture availability was supplemented by groundwater flow. In contrast, "dry" stands, typically in mid-slope positions, showed lower estimated (3.1 °C) mean annual temperatures (Table 2). Mean basal area of cedar (43.1 m²/ha) was highest in "wet" stands, as was canopy openness. Live tree density was greatest in "dry" stands (381 stems/ha). Stands with "wet" soil moisture were generally warmer, had a more open canopy structure, and contained more basal area of subalpine fir, cedar, and spruce (Table 2). Although these differences between "wet" and "dry" soil moisture sites provide a snapshot of trends, they were not significant when tested at a $P < 0.05$ threshold (Bonferonni *t*-test). Of the differences tested canopy openness was the closest to being significant, with a P value of 0.084.

Of the 40 taxa of arboreal lichens surveyed within study plots, we found that 16 of the 19 cyanolichens were more frequent and occurred with greater abundance in stands that had "wet" soil moisture (Table 3). Exceptions to this pattern included cyanolichens such as *N. resupinatum*, which occurred infrequently (2 sites), but abundantly (greater than 10 thalli/site) in both "wet" and "dry" stands, and the cyanolichen *L. pulmonaria*, which was widely distributed in both wet and dry stands. Chlorolichens showed no clear patterns of differing frequency and abundance, the noticeable exception being *C. hultenii*, which had a much higher frequency of occurrence in stands with "wet" soils. Only 3 species had abundance ratings as high as category 4 (covering more than half of available

substrates), these being *L. pulmonaria* (in 6 plots), *P. glauca* (in 32 plots), and *Parmelia* sp. (in 1 plot).

Stand ordinations showed a cyanolichen cluster in the upper left quadrant of the plot (Fig. 4). This cluster included both regionally rare species, such as *L. retigera* and *N. occultum*, as well as the more abundant cyanolichens, such as *N. isidiosum*, *Pseudocyphellaria anomala*, and *S. fuliginosa*. In contrast, *L. pulmonaria*, though found in many stands, was most abundant in stands that placed in the upper left quadrant of the ordination plot (Fig. 4). Most chlorolichens were widely distributed across stands, showing no strong placement preference in stand placement along the ordination axes.

Temperature and mean annual precipitation were significantly correlated with both axis 1 and axis 2 ordination scores (Table 4). When fit to a linear regression, data for axis 2 demonstrated the best fit ($R^2 = 0.604$), with the variables soil moisture ($P < 0.001$), temperature ($P < 0.001$), canopy openness ($P = 0.033$), mean annual precipitation ($P = 0.013$), and basal area of spruce ($P = 0.002$) accounting for a significant proportion of the variation. Only temperature ($P < 0.001$) and mean annual precipitation ($P = 0.011$) were correlated with axis 1 ordination scores ($R^2 = 0.308$).

The variables associated with the most parsimonious logistic regression models for the eight old-growth associate were: temperature (6 species), leading tree species (5 species), soil moisture condition (4 species), canopy openness (4 species), and mean annual precipitation (1 species) (Table 5). ROC scores ranged from 0.7175 (*P. norvegica*) to 0.9183 (*N. isidiosum*), indicating a good to excellent fit for each of the lichen species (Table 5). Averaged beta likelihood coefficients suggested that all variables, other than mean annual precipitation and insolation, had some influence (positive or negative) on the distribution of one or more old-growth associated lichen species (Fig. 4). "Dry" soil moisture status had a 0 to negative effect on the presence of the eight lichen species, and "wet" soil moisture status showed positive effects. Canopy openness showed 0 or slightly positive effects. The temperature variable had the largest effect on the distribution of *N. isidiosum* and *S. oroborealis*, though confidence intervals were quite large. In combination with temperature and/or soil moisture status, *L. retigera*, *P. norvegica*, and *S. oroborealis* showed greatest affinities to stands leading in hemlock and to a lesser degree cedar. *C. hultenii*, a chlorolichen, was related almost exclusively to hemlock and negatively to both cedar- and spruce-leading stands whereas *N. occultum*, a cyanolichen, showed preference to cedar dominated forests and a negative association with both hemlock and spruce dominated forests. Spruce had either no effect or a negative influence on the presence of the 8 lichen species we tested. As with temperature, confidence intervals were often quite large for leading tree species (Fig. 5).

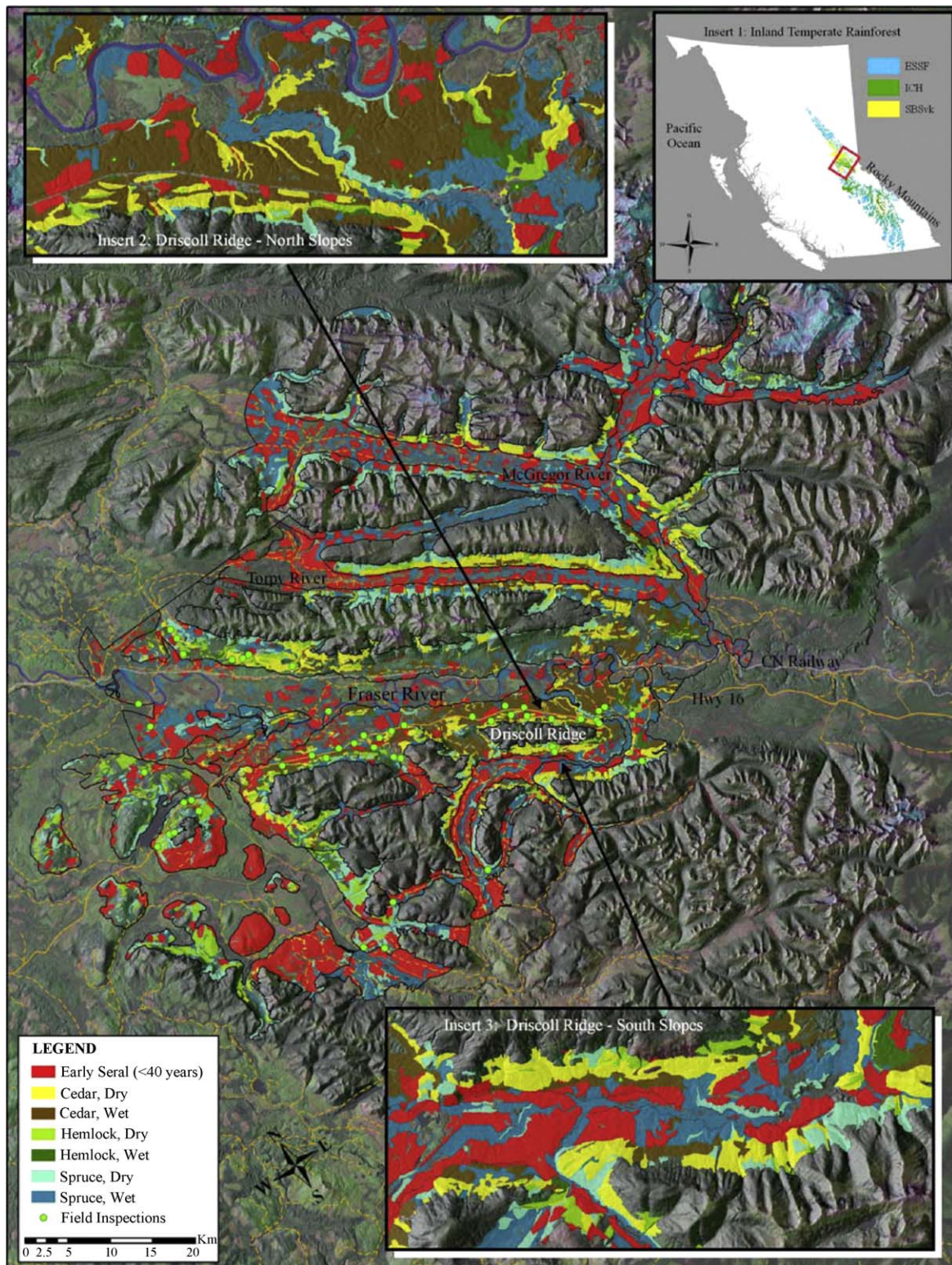


Fig. 3. Landscape distribution of old-growth cedar-, hemlock-, and spruce-leading forests with “wet” and “dry” relative soil moisture conditions in the very “wet” cool interior-cedar hemlock (ICHvk2) and adjacent very-“wet” cool sub-boreal spruce (SBSvk) biogeoclimatic zones (outlined in black lines) of the upper Fraser River watershed. Shaded relief shows adjacent mountain ranges outside the ICHvk2. Insert 1 indicates study location in British Columbia, Canada. Inserts 2 and 3 identify old-growth forest types on north- and south-facing aspects of sample mountain valley (Driscoll ridge) respectively. Reference points (green dots) indicate plot-sampling locations. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of the article.)

4. Discussion

Lichen communities in old forest ITR stands showed a significant association with environmental gradients within a

regional inland temperate rainforest landscape (approximately 60 km in radius). Of the old forest associate species designated by Campbell and Fredeen (2004) *C. hultenii*, *L. hallii*, *N. isidiosum*, and *N. occultum* were more common in stands with “wet” soil moisture

Table 2
Mean and standard deviation of stand variables.

Stand type	Stand variables									
	Mean annual temperature (°C) ^a		Minimum March–October temperature (°C) ^a		Mean annual precipitation (mm) ^a		Solar loading (kWh/m ²) ^a		% canopy openness ^b	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
“Dry”	3.1	0.4	1.4	0.4	831.3	41.2	1208.7	238.0	8.6	2.8
“Wet”	3.5	0.4	1.8	0.3	811.5	32.9	1218.0	108.2	14.1	6.3

Stand type	Stand variables									
	Stand basal area (m ² /ha) ^b		Basal area–Bl (m ² /ha) ^b		Basal area–Cw (m ² /ha) ^b		Basal area–Hw (m ² /ha) ^b		Basal area–Sx (m ² /ha) ^b	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
“Dry”	76.6	27.7	2.9	2.8	34.8	41.0	16.1	14.9	8.4	9.8
“Wet”	80.2	48.8	4.0	4.9	43.1	64.9	13.7	21.3	11.0	11.5

N=27 and 26 respectively for stands with “dry” and “wet” relative soil moisture conditions. Basal area measurements were determined for subalpine fir (Bl), western redcedar (Cw), western hemlock (Hw), and spruce (Sx).

^a From Canadian Forest Service regional climate database (Hutchinson, 1995).

^b From stand level measurements with spherical densitometer.

conditions in our study. Others of their old-growth associates, such as *Lobaria scrobiculata*, *Nephroma helveticum*, *Nephroma parile*, *P. anomala* and *S. fuliginosa*, were more widely distributed in our ITR stands, but were still far more abundant on “wet” sites. A third set of old-growth associates, including lichen species such as *Hypogymnia rugosa*, *Hypogymnia vittata*, *L. pulmonaria* and *P. norvegica*, were widely distributed in both “wet” and “dry” stands. *L. pulmonaria* was not highly sensitive to site-specific conditions within our study area. This result concurs with the findings of Kalwij et al. (2005), who suggested that *L. pulmonaria* was not a sensitive indicator of disturbance within their regional landscapes.

Our correlation of environmental attributes with ordination scores suggests that gradients of temperature and moisture play an important role in shaping cyanolichen communities within the upper Fraser ITR landscape. Temperature has previously been inferred as an important environmental variable in structuring ITR cyanolichen communities (Werth et al., 2005). As one moves upslope from cedar–hemlock to spruce–fir dominated forests, canopy cyanolichens diminish greatly in abundance (Goward, 1994). Studies on cyanolichen physiology further suggest that processes of carbon assimilation and nitrogen fixation may be severely rate-limited at low temperatures (Sundberg et al., 1996). Finally, mean annual precipitation is highly correlated with the duration of cyanolichen hydration in ITR stands (Coxson and Stevenson, 2007). Coxson and Stevenson found that most growth events in ITR *L. pulmonaria* populations coincided with precipitation events in the spring and summer. Although thalli are often hydrated in the late fall and winter, they are commonly frozen and experience very low light availability during these periods.

The contrasting trends in temperature and precipitation within ITR mountain valleys would, initially, seem to pose major constraints on the distribution and abundance of canopy cyanolichens. As one moves upslope in ITR valleys precipitation increases; at the same time, however, mean annual temperature decreases. Thus, there would seem to be no optimal environment for growth of canopy cyanolichens in the ITR. An environment that is “wet” enough is too cool; one that is warm enough is too “dry”. These constraints on optimal growth rates, however, may not apply in low elevation topographic sites that have high soil moisture status. Relative soil moisture status was significantly correlated with axis 2 of the ordination and was a significant variable in a majority of best model sets predicted by logistic regression for individual species. Our mapping of sites with high soil moisture status in old forest stands of the upper Fraser River valley shows that most high soil moisture sites occur in areas

extending outwards from the base or “toe-slope” of mountain faces, where groundwater flow emerges to create small seepage areas and springs. These water receiving sites represent a unique combination of “wet” soil moisture status in low elevation sites that have relatively higher temperatures, with up to a 1.5 °C difference in mean annual temperatures predicted between high and low elevation study sites. The greater relative humidity found within the lower canopy of these stands may extend the duration of periods of metabolic activity experienced by canopy lichens after precipitation events. This factor may be particularly important for cyanolichens, which need direct contact with water to resume physiological activity (Budel and Lange, 1991). Adjacent stands that do not have high soil moisture status show lower canopy lichen diversity, with indicator cyanolichens such as *L. retigera* largely absent, notwithstanding their very similar exposure to temperature and precipitation. Our study suggests an important linkage between canopy biodiversity and slope hydrology, in that sites with high soil moisture status are dependent upon snowmelt from adjacent higher elevations, which provides continued groundwater flow during the summer period. Snowpack in adjacent subalpine forests can reach 3+ m in depth by mid-April each year, with final snow melt commonly occurring in the mid- to late-June period (Campbell and Coxson, 2001).

Old forest stands that develop in water receiving positions tend to share many common attributes. Basal areas of cedar, fir, and spruce are higher than those in dry soil moisture sites, presumably reflecting the influence of subsurface water on tree growth, and indirectly, the greater exclusion of fire as a major natural disturbance agent (DeLong, 1998; Sanborn et al., 2006). Although we have not directly measured stand continuity in these sites, tree ring counts (extending back 800+ years, unpublished data), dating of charcoal layers and calculations of fire return intervals (DeLong, 1998; Sanborn et al., 2006) all suggest a very long site continuity in these water receiving stand positions. Importantly, these “wet” stands tend to have a more open canopy structure, reflecting the greater role of gap dynamics within very old forest stands on wet “toe-slope” positions (Benson and Coxson, 2002). In addition, the many small seepage areas found within these wet “toe-slope” stands create natural canopy openings where trees do not establish, an attribute DeLong et al. (2004) associated with old forests of the upper Fraser River valley. For canopy cyanolichens, this combination of abundant light in a humid lower canopy environment creates ideal conditions for biomass accumulation (Coxson and Stevenson, 2007). McCune et al. (2002) documented the importance of small streams as an important factor influencing

Table 3

Macrolichen taxa frequency (number of stands in which indicated taxa were present) by stand type (“dry” versus “wet” relative soil moisture conditions).

Lichen taxa	Stand type							
	Dry				Wet			
	Frequency by category ^a							
	Very low	Low	Common	Dry total	Very low	Low	Common	Wet total
Chlorolichens								
<i>Cavernularia hultenii</i>	7	5	2	7	14	7	3	14
<i>Cetraria cetroides</i>	0	0	0	0	1	1	0	1
<i>Hypogymnia austeriodes</i>	2	2	0	2	1	1	0	1
<i>H. bitterii</i>	18	3	7	18	17	2	6	17
<i>H. imshaugii</i>	0	0	0	0	1	1	0	1
<i>H. metaphysodes</i>	19	4	4	19	14	7	3	14
<i>H. occidentalis</i>	26	0	1	26	26	0	0	26
<i>H. oroborealis</i>	3	3	0	3	2	2	0	2
<i>H. physodes</i>	27	0	0	27	26	0	0	26
<i>H. rugosa</i>	19	4	11	19	20	4	10	20
<i>H. tubulosa</i>	27	0	4	27	26	0	2	26
<i>H. vittata</i>	23	4	9	23	25	0	4	25
<i>Melanalia</i> sp.	15	11	3	15	15	7	7	15
<i>Parmelia</i> sp.	27	0	0	27	26	0	0	26
<i>Parmielopsis ambigua</i>	26	3	11	26	26	1	9	26
<i>P. hyperopta</i>	27	2	6	27	26	1	4	26
<i>Platismatia glauca</i>	27	0	0	27	26	0	0	26
<i>P. norvegica</i>	18	5	8	18	17	5	7	17
<i>Tuckermannopsis chlorophylla</i>	27	1	9	27	26	2	1	26
<i>T. orbata</i>	7	3	3	7	2	2	0	2
<i>Vulpicida pinastri</i>	12	6	4	12	14	7	4	14
Cyanolichens								
<i>Leptogium burnatiae</i>	0	0	0	0	1	1	0	1
<i>L. saturninum</i>	2	1	0	2	4	2	0	4
<i>Lobaria hallii</i>	0	0	0	0	3	3	0	3
<i>Lobaria pulmonaria</i>	27	1	1	27	26	0	0	26
<i>Lobaria retigera</i>	2		2	2	12	6	2	12
<i>Lobaria scrobiculata</i>	19	9	7	19	22	1	10	22
<i>Nephroma bellum</i>	11	4	5	11	18	7	7	18
<i>Nephroma helveticum</i>	23	4	6	23	26	0	3	26
<i>Nephroma isidiosum</i>	11	4	6	11	23	6	5	23
<i>Nephroma occultum</i>	3	3	0	3	11	10	1	11
<i>Nephroma parile</i>	24	4	7	24	26	0	3	26
<i>Nephroma resupinatum</i>	1	0	1	1	1	0	0	1
<i>Peltigera collina</i>	1	0	1	1	5	3	1	5
<i>Polychidium dendriscum</i>	0	0	0	0	7	2	3	7
<i>Pseudocypellaria anomala</i>	19	8	8	19	26	3	6	26
<i>Sticta fuliginosa</i>	17	10	4	17	23	2	4	23
<i>Sticta limbata</i>	0	0	0	0	2	2	0	2
<i>Sticta oroborealis</i>	6	1	2	6	12	5	4	12
<i>Sticta wrightii</i>	2	2	0	2	1	1	0	1

N=27 and 26 respectively and by assessment categories: very low (1–3 individuals), low (3–10 individuals), or common (>10 individuals).

^a Data for the few species with very abundant rankings (covering more than half of available substrates) is provided in Section 3.

canopy lichen diversity in mountainous watersheds of western Oregon. Similarly, Lidén and Hilmo (2005) found that proximity to watercourses was essential for the occurrence of *P. norvegica* in suboceanic fringe habitats.

Spies and Franklin (1991) postulated that groundwater receiving sites and the attendant transfer of nutrients was a major determinant of the overall growth and development of coastal “wet” temperate rainforests. Spies et al. (2006) further pointed out the importance of recognizing these site-specific factors when developing plans for the conservation of old-growth forests. Conversely, high fire return intervals in “dry” hemlock forests of the upper Fraser River valley (Eng, 2000) will limit the accumulation of rare lichen species and may reflect more limiting growth conditions for canopy lichens that do establish in these forests.

Among common predictive variables found in our examination of the presence/absence patterns in old-growth associate lichens were the parameters temperature and site soil moisture status. All 8 of the so-called ‘oceanic’ or old-growth associate species had either temperature or soil moisture as major predictive variables in their best model sets (>0.1 Akaike’s

weight), with 6 of the indicator species having both predictor variables present. Temperature clearly plays an important role in predicting the presence or absence of old forest associate cyanolichens at a regional scale within ITR watersheds of the upper Fraser River. Glavich et al. (2005) similarly pointed to temperature as a major predictor of cyanolichen presence or absence in coastal “wet” temperate rainforests, though across much larger regional scales.

Although logistic regression only accommodates one dependent variable (i.e., one species per model), the beta likelihood coefficients can be compared to determine if different species are responding similarly or differently to response variables. These comparisons show that the presence of individual old-growth associate lichen species was predicted by unique combinations of environmental variables. Four of the eight indicator species, *C. hultenii*, *L. retigera*, *P. norvegica*, and *S. oroborealis* showed leading hemlock as a predictor variable in logistic regression models. These species tended to be present in sites that were classified as “wet” hemlock-leading, often in valley bottom positions where subsurface drainage slowed, leading to standing surface water that

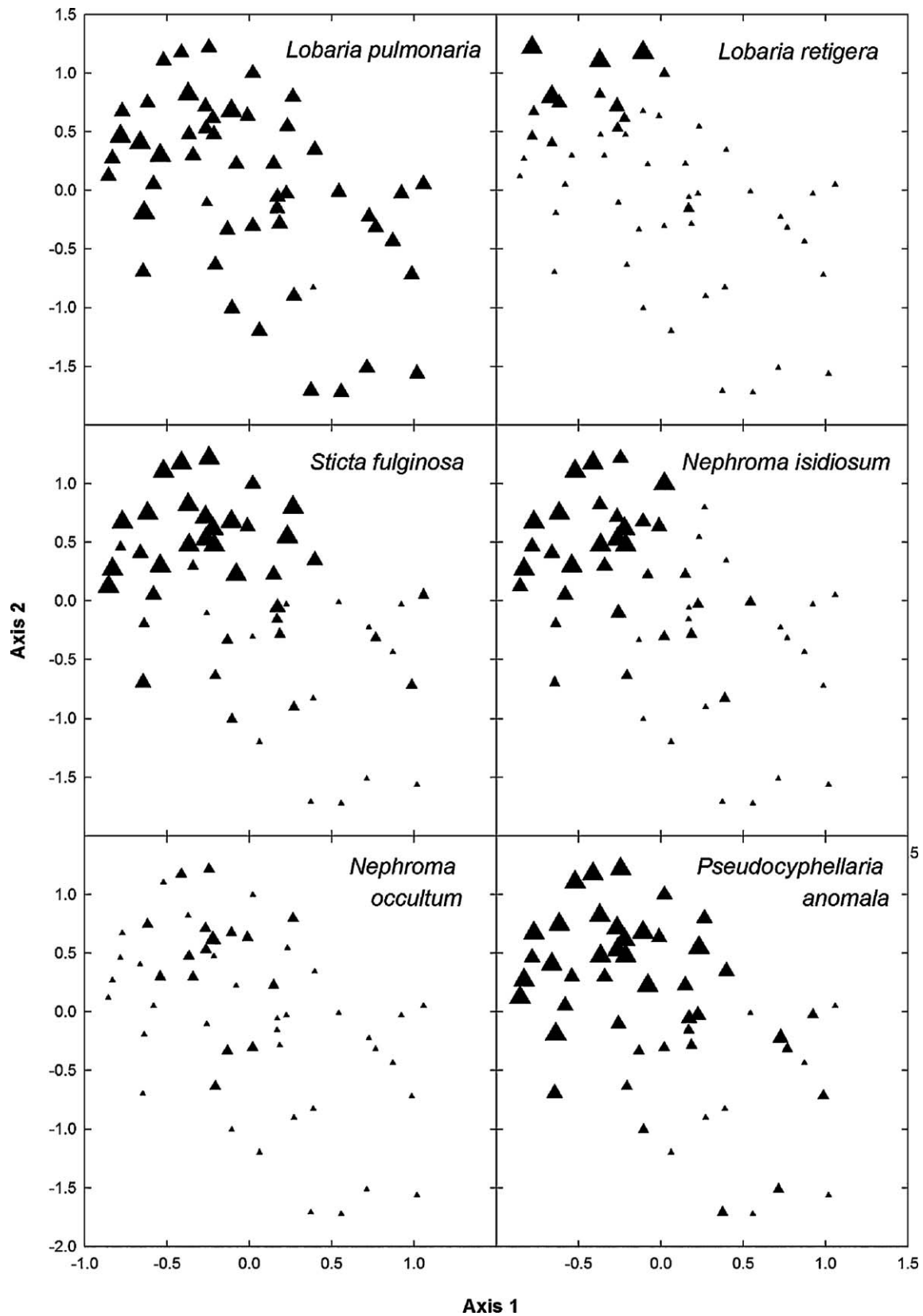


Fig. 4. Overlay of species abundance in the upper Fraser River watershed in 2005 on stand ordinations for the tripartate macrolichen *Lobaria pulmonaria*, and the bipartate cyanolichens: *L. retigera*, *Sticta fuliginosa*, *Nephroma isidiosum*, *Nephroma occultum*, and *Pseudocyphellaria anomala*.

precluded cedar establishment. These sites, in common with cedar-leading stands in wet “toe-slope” positions, share the attributes of longevity and relatively open (and likely humid) lower canopy environments.

The rough surface texture of bark on hemlocks in these sites may also play a role in facilitating lichen establishment and survival. Armstrong (1990) found that rough bark texture was a significant factor promoting establishment of *H. physodes*. Sillett

Table 4

Multiple linear regression estimates for log transformed environmental variables: temperature (average March–October mean minimum temperature), precipitation (mean annual), solar loading (mean annual), canopy openness, relative soil moisture, and basal area of spruce (S_x), calculated against axis 1 and axis 2 ordination scores ($N=53$).

Variable	Coefficient	SE	<i>t</i>	<i>P</i>
Axis 1				
Constant	5.862	1.922	3.051	0.004
Temperature	−1.470	0.318	−4.617	0.001
Precipitation	−0.011	0.003	−3.796	0.001
Axis 2				
Constant	−7.516	2.764	−2.719	0.009
Relative soil moisture	0.404	0.119	3.403	0.001
Basal area (S_x)	−0.025	0.008	−3.328	0.002
Temperature	1.277	0.419	3.046	0.004
Precipitation	0.011	0.004	2.595	0.013
Canopy openness	0.036	0.017	2.195	0.033

et al. (2000), however, suggests that site continuity is far more important for cynolichens, noting that “particular substrates and microenvironments found only in old growth are not essential for *Lobaria* establishment and growth”. Öckinger et al. (2005) similarly suggests that dispersal capacity is likely the most important factor limiting the local distribution of *L. pulmonaria*, a constraint which emphasizes the importance of site continuity for source populations. This is consistent with research emphasizing the importance of ecological continuity to canopy lichen biodiversity (Selva, 1994; Holien, 1996).

Nordén and Appelqvist (2001) note that bioindicators of long-term habitat persistence should generally be organisms with limited dispersal characteristics and should be “perennial stayers”, organisms which live for many years on stable substrates. Certainly some members of our cyanolichen assemblage, for instance *L. retigera*, would fulfill these criteria; having a presumed low dispersal capability typical of that in many foliose cyanolichens (Sillett et al., 2000; Scheidegger, 1995), and generally colonizing stable substrates, such as the leaning mossy surfaces of large fallen cedars, which have a very long persistence in wet ITR stands. Other members of our ITR cyanolichen assemblage, for instance *L. pulmonaria*, though possibly dispersal limited, tended to grow on small diameter dead branches, a relatively ephemeral habitat. They should therefore not be regarded as indicators of site continuity, *per se*; although as Campbell and Fredeen (2004) note, stands with high *L. pulmonaria* biomass typically show much greater diversity of rarer canopy cyanolichen.

The presence of the threatened lichen species *N. occultum*, was best predicted by the site variables “wet” soil moisture conditions and cedar-leading stands, conditions encountered most often in “wet” toe-slope positions. Although most trees in our “toe-slope” stands could not be dated due to hollow or rotten cores, the general

absence of soil charcoal, and cedar trees in which the outer intact shell of much larger diameter trees reaches in excess of 500 years in age, suggests that many of these stands have persisted without disturbance for periods approaching or even exceeding 1000 years. Interestingly, Gavin et al.’s (2009) recent paleoecology work in the upper Fraser ITR suggests that the oldest cedar stands in this region may represent the first generation of post-glacial ITR colonizers, some 2000 years ago when regional climate became cooler and wetter, allowing for the development of the vegetation communities that characterize today’s ITR forests. In these sites, thalli of species such as *N. occultum* may simply be able to accumulate over long time periods, influenced as much by habitat stability as by site conditions.

From the perspective of setting priorities for the conservation of canopy lichen communities the retention of representative old forest stands in areas of water receiving valley bottom positions, often in wet toe-slope positions, should be a priority for land-use planners. Protecting these sites, which apparently are already buffering to a large degree from natural disturbance events such as fire, may be particularly important if the conservation value (for canopy lichens) of surrounding more fire-prone forests (Eng, 2000) diminishes even further in the face of predicted ITR climate change (Hamann and Wang, 2006). Drever et al. (2006) suggests that maintaining ecological resilience in managed forests is dependent upon sustaining natural disturbance regimes. We would argue that in the inland rainforest wet soil moisture sites play a disproportionate role in maintaining ecological resilience, providing a major refugia as disturbance events sweep across surrounding landscapes.

We would echo previous recommendations that where logging does occur in wet-temperate old forest dominated ecosystems, that harvest practices need to be more complex, including variable retention, single tree and small patch cuts; harvest practices that better reflect the natural range of variability in disturbance events (Lertzman et al., 2002; Radies and Coxson, 2004; Rolstad et al., 2000). On the other hand, in our dry soil moisture sites, particularly in those areas that are more prone to fire and insect outbreaks, clearcut logging may be an appropriate logging type.

Current representation of old forests in protected areas in our 135,000 ha study area is approximately 6%. Given that many of the rare lichens that we documented were only found in one or two of the wet soil moisture stands (and not the same ones), we do not expect that the current protected areas will be sufficient to maintain canopy lichen diversity once surrounding landscapes are logged. Agee (2003) notes that the longer old forest patches remain as small refugia within the landscape, the greater the extinction risk local biota face from stochastic events. Indeed, past harvesting of old forest stands in wet soil moisture sites may already have incurred an “extinction debt” (Berglund and Jonsson, 2005) in upper Fraser ITR stands.

Table 5

Predicted best model sets (>0.1 AIC_w) for presence of the old forest associated macrolichens and receiver operating characteristic (ROC) results for best models in the upper Fraser River watershed.

Species	Best model sets (>0.1 AIC _w)	AIC _w	ROC
<i>Cavernularia hultenii</i>	LEAD (Hw) + SMR (“wet”)	0.972	0.856
<i>Lobaria retigera</i>	LEAD (Hw) + canopy openness + TEMP	0.607	0.914
<i>Nephroma isidiosum</i>	SMR (“wet”) + canopy openness + TEMP + PRECIP	0.419	0.918
<i>Nephroma occultum</i>	LEAD (Cw) + SMR (“wet”)	0.881	0.815
<i>Platismatia norvegica</i>	LEAD (Hw) + TEMP	0.525	0.718
<i>Peltigera collina</i>	SMR (“wet”) + TEMP	0.333	0.737
<i>Sticta fuliginosa</i>	Canopy openness + TEMP	0.458	0.850
<i>Sticta oroborealis</i>	LEAD (Hw) + canopy openness + TEMP	0.956	0.956

Abbreviations for model variables are as follows: relative soil moisture (RSM); leading tree species (LEAD); canopy openness, mean annual precipitation (PRECIP) and mean minimum temperature, March–October (TEMP). Abbreviations in brackets – cedar (Cw), hemlock (Hw) and wet BRSM (wet) – represent categorical variables with greatest influence.

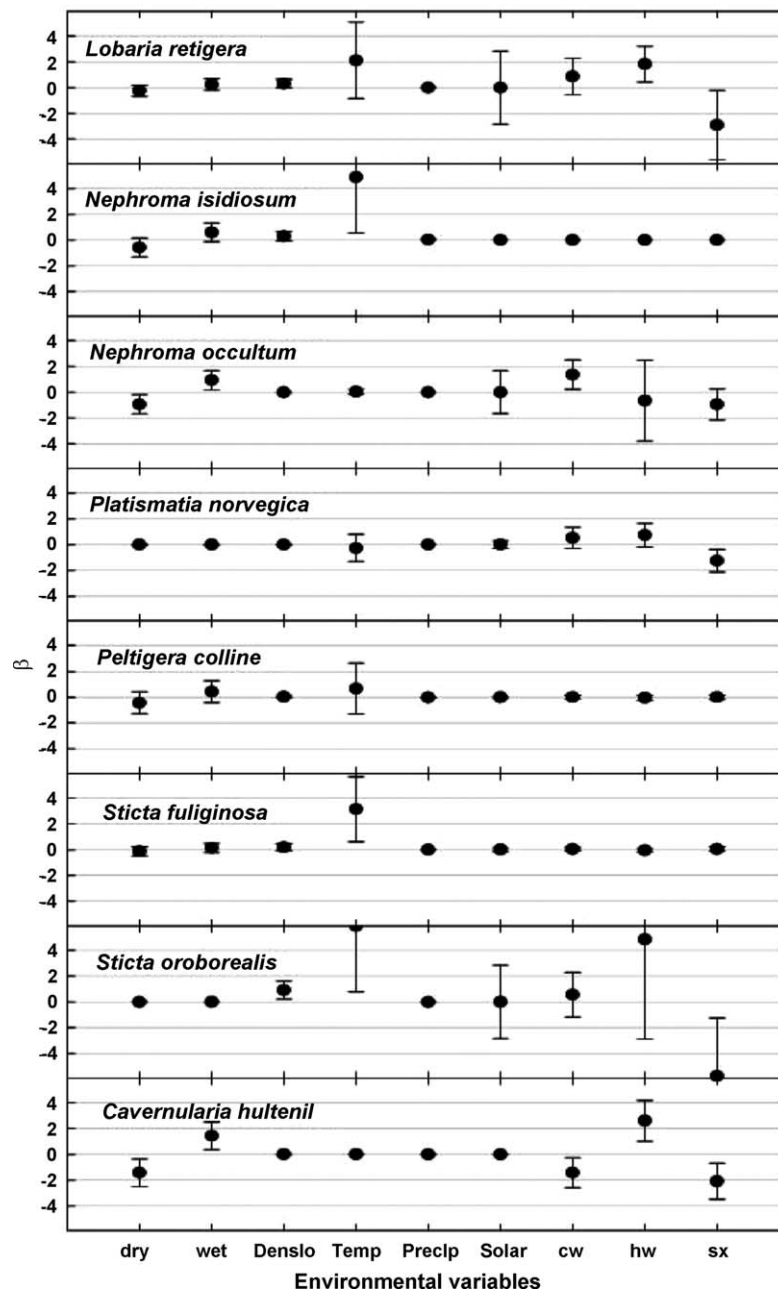


Fig. 5. Average beta likelihood coefficients (β) and 95% confidence intervals of the independent variables relative soil moisture status (categorized as “wet” or “dry”), canopy openness (Densio), average minimum temperature (Temp), average annual precipitation (Precip), solar insolation (Solar), and the leading tree species western redcedar (*Thuja plicata*) (Cw), western hemlock (*Tsuga heterophylla*) (Hw), or subalpine-white spruce hybrids (*Picea engelmanni* \times *glauca*) (Sx) for each the eight ‘old growth dependent’ lichen species *L. retigera*, *N. isidiosum*, *N. occultum*, *P. norvegica*, *Peltigera collina*, *S. fuliginosa*, *S. Oroborealis*, and *C. hultenii*.

5. Conclusions

Topographic position is a major determinant of canopy lichen communities in old-growth inland temperate rainforest stands. Old forest stands located in wet “toe-slope” and adjacent water receiving valley bottom topographic positions supported much higher canopy lichen diversity and abundance than old forest stands with drier relative soil moisture status, these often located on hill-slope positions. We recommend that old forest stands in the upper Fraser River watershed that have “wet” relative soil moisture status be given special management consideration, either for designation as protected areas, or where logging occurs, for adoption of partial-cutting forest harvesting techniques that approximate more closely the natural disturbance regime of these

stands (i.e., single-tree gap dynamics). Furthermore, cedar-leading stand types of exceptional age and stature should be immediately designated for protection, given their rarity in the landscape, and their lack of representation in protected areas. Based on our research these sites represent significant biodiversity hotspots for canopy lichens, and are key to the maintenance of biodiversity within regional landscapes.

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References

- Agee, J.K., 2003. Historical range of variability in eastern Cascades forests, Washington, USA. *Landscape Ecology* 18, 725–740.
- Anon., 1995. Sustainable Ecosystem Management in Clayoquot Sound: Planning and Practices. CSS Panel—Gov. of British Columbia, Victoria, B.C., 63 pp.
- Anon., 1998. Vegetation Resources Inventory: Implementation Strategy to Integrate Management, Provincial and National Inventories. Resources Inventory Branch, B.C. Ministry of Forests, Victoria, B.C. 28 pp., available at: <http://www.forest.gov.bc.ca/hts/vri/> (September 15, 2009).
- Anon., 1999. Standards for Predictive Ecosystem Mapping, Version 1.0. The Resources Inventory Committee, Province of B.C., Victoria, B.C. available at: <http://www.env.gov.bc.ca/ecology/tem/index.html> (September 15, 2009).
- Armstrong, R.A., 1990. Dispersal, establishment and survival of soredia and fragments of the lichen, *Hypogymnia physodes* (L.) Nyl. *New Phytologist* 114, 239–245.
- Arsenault, A., Goward, T., 2000. Ecological characteristics of inland rainforests. *Ecoforestry* 15, 20–23.
- Beatty, R.M., Taylor, A.H., 2001. Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, Southern Cascades, California, USA. *Journal of Biogeography* 28, 955–966.
- Benson, S., Coxson, D.S., 2002. Lichen colonization and gap structure in wet-temperate rainforests of northern interior British Columbia. *The Bryologist* 105, 673–692.
- Berglund, H., Jonsson, B.G., 2005. Verifying an extinction debt among lichens and fungi in northern Swedish boreal forests. *Conservation Biology* 19, 338–348.
- Bollinger, J., Bergamini, A., Stofer, S., Kienast, F., Scheidegger, C., 2007. Predicting the potential spatial distributions of epiphytic lichen species at the landscape scale. *The Lichenologist* 39, 279–291.
- Botting, R., Fredeen, A.L., 2006. Contrasting terrestrial moss, lichen and liverwort diversity and abundance between old-growth and young second-growth sub-boreal spruce forest in central British Columbia. *Canadian Journal of Botany* 84, 120–132.
- Budel, B., Lange, O.L., 1991. Water status of green and blue green phycobionts in lichen thalli after hydration by water vapour uptake? Do they become turgid?. *Botanica Acta* 104, 361–366.
- Campbell, J., Coxson, D.S., 2001. Canopy microclimate and arboreal lichen loading in subalpine spruce–fir forest. *Canadian Journal of Botany* 79, 537–555.
- Campbell, J., Fredeen, A.L., 2004. *Lobaria pulmonaria* abundance as an indicator of macrolichen diversity in interior cedar hemlock forests of east-central British Columbia. *Canadian Journal of Botany* 82, 970–982.
- Coxson, D.S., Stevenson, S.K., 2007. Growth rate responses of *Lobaria pulmonaria* to canopy structure in even-aged and old-growth cedar–hemlock forests of central-interior British Columbia, Canada. *Forest Ecology and Management* 242, 5–16.
- DeLong, S.C., 1998. Natural disturbance rate and patch size distribution of forests in northern British Columbia: implications for forest management. *Northwest Science* 72, 35–48.
- DeLong, S.C., 2003. A Field Guide for Site Identification and Interpretation for the Southeast Portion of the Prince George Forest Region. Research Branch, B.C. Ministry of Forests, Victoria, B.C., Land Management Handbook No. 51.
- DeLong, C., 2007. Implementation of natural disturbance-based management in Northern British Columbia. *Forestry Chronicle* 83, 338–346.
- DeLong, S.C., Burton, P.J., Harrison, M., 2004. Assessing the relative quality of old-growth-forest: an example from the Robson Valley, British Columbia. *B.C. Journal of Ecosystems and Management* 4, 1–16.
- Drever, C.R., Peterson, G., Messier, C., Bergeron, Y., Flannigan, M., 2006. Can forest management based on natural disturbances maintain ecological resilience? *Canadian Journal of Forest Research* 36, 2285–2299.
- Eng, M., 2000. Fire Analysis for the Robson Valley Forest District. Unpublished Report. Research Branch, Ministry of Forests, Victoria, B.C..
- Gavin, D.G., Hu, F.S., Walker, I.R., Westover, K.S., 2009. The northern inland temperate rainforest of British Columbia: old forests with a young history? *Northwest Science* 83, 70–78.
- Glavich, D.A., Geiser, L.H., Mikulin, A.G., 2005. Rare epiphytic coastal lichen habitats, modeling, and management in the Pacific Northwest. *The Bryologist* 108, 377–390.
- Goward, T., 2003. Lichens of the Robson Valley Provincial Parks: Grizzly–Sugarbowl, West Twin Creek, Sliim Creek. Unpublished Report. B.C. Parks, Prince George, 35 pp.
- Goward, T., 1994. Notes on old growth dependent epiphytic macrolichens in inland British Columbia, Canada. *Acta Botanica Fennica* 150, 31–38.
- Goward, T., McCune, B., Meidinger, D.V., 1994. The Lichens of British Columbia Illustrated Keys. Part 1. Foliose and Squamulose Species. Special Report Series, B.C. Ministry of Forests, Research Branch, 181 pp.
- Goward, T., Arsenault, A., 2000. Inland old-growth rain forests: safe havens for rare lichens? In: Darling, L.M. (Ed.), *Proceedings, Biology and Management of Species and Habitats at Risk*. Kamloops, B.C., 15–19 February 1999. B.C. Min. Environ., Lands and Parks, Victoria, B.C. and University College of the Cariboo, Kamloops, B.C. pp. 759–766.
- Goward, T., Spribille, T., 2005. Lichenological evidence for the recognition of inland rainforests in western North America. *Journal of Biogeography* 32, 1209–1219.
- Hamann, A., Wang, T., 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* 87, 2773–2786.
- Hauck, M., Spribille, T., 2002. The Mn/Ca and Mn/Mg ratios in bark as possible causes for the occurrence of *Lobaria* lichens on conifers in the dripzone of *Populus* in western North America. *Lichenologist* 34, 527–532.
- Holien, H., 1996. Influence of site and stand factors on the distribution of crustose lichens of the Caliciales in a suboceanic spruce forest area in central Norway. *Lichenologist* 28, 315–330.
- Hutchinson, M.F., 1995. Interpolating mean rainfall using thin plate smoothing splines. *International Journal of Geographical Information Systems* 9, 385–403.
- Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19, 101–108.
- Kalwij, J.M., Wagner, H.H., Scheidegger, C., 2005. Effects of stand-level disturbances on the spatial distribution of a lichen. *Ecological Applications* 15, 2015–2024.
- Ketcheson, M.V., Braumandl, T.F., Meidinger, D., Utzig, G., Demarchi, D.A., Wikeem, B.M., 1991. Interior cedar–hemlock zone. In: Meidinger, D., Pojar, J. (Eds.), *Ecosystems of British Columbia*. Special Report Series No. 6, BC Ministry of Forests (Chapter 11).
- Lertzman, K., Gavin, D., Hallett, D., Brubaker, L., Lepofsky, D., Mathewes, R., 2002. Long-term fire regime estimated from soil charcoal in coastal temperate rainforests. *Conservation Ecology* 6, 1–13.
- Lidén, M., Hilmo, O., 2005. Population characteristics of the suboceanic lichen *Platismatia norvegica* in core and fringe habitats: relations to macroclimate, substrate, and proximity to streams. *The Bryologist* 108, 506–517.
- McCune, B., Mefford, M.J., 1999. PC-ORD. Multivariate Analysis of Ecological Data. Version 4.0. M/JM Software, Glenden Beach, OR, U.S.A..
- McCune, B., Rosentreter, R., Ponzetti, J.M., Shaw, D.C., 2000. Epiphyte habitats in an old conifer forest in western Washington, U.S.A. *The Bryologist* 103, 417–427.
- McCune, B., Hutchinson, J., Berryman, S., 2002. Concentration of rare epiphytic lichens along large streams in a mountainous watershed in Oregon, U.S.A. *The Bryologist* 105, 439–450.
- Meidinger, D., Pojar, J., 1991. *Ecosystems of British Columbia*. Special Report Series 6, Research Branch, Ministry of Forests, Victoria, B.C.
- Menard, S., 2002. *Applied logistic Regression Analysis*, 2nd ed. Sage Publications Inc., California, 128 pp.
- Munoz, J., Felicísimo, A., 2004. Comparison of statistical methods commonly used in predictive modelling. *Journal of Vegetation Science* 15, 285–292.
- Nordén, B., Appelqvist, T., 2001. Conceptual problems if ecological continuity and its bioindicators. *Biodiversity and Conservation* 10, 779–791.
- Öckinger, E., Niklasson, M., Nilsson, S., 2005. Is local distribution of the epiphytic lichen *Lobaria pulmonaria* limited by dispersal capability or habitat quality? *Biodiversity and Conservation* 14, 759–773.
- Radies, D.N., Coxson, D.S., 2004. Macrolichen colonization on 120–140 year old *Tsuga heterophylla* in “wet” temperate rainforests of central-interior British Columbia: a comparison of lichen response to even aged versus old-growth stand structures. *Lichenologist* 36, 235–248.
- Reynolds, R.R., 1997. Climatic Data Summary for the Biogeoclimatic Zones of British Columbia. British Columbia Ministry of Forests, Research Branch, Victoria, B.C., Unpublished Report.
- Rolstad, J., Gjerde, I., Storaunet, K.E., Rolstad, E., 2000. Epiphytic lichens in Norwegian coastal spruce forest: historic logging and present forest structure. *Ecological Applications* 11, 421–436.
- Rosso, A.L., McCune, B., Rambo, T.R., 2000. Ecology and conservation of a rare, old-growth-associated canopy lichen in a silvicultural landscape. *The Bryologist* 103, 117–127.
- Sanborn, P.M., Geertsema, M., Jull, A.J.T., Hawkes, B., 2006. Soil and sedimentary charcoal evidence for Holocene forest in an inland temperate rainforest, east-central British Columbia, Canada. *Holocene* 16, 415–427.
- Scheidegger, C., 1995. Early development of transplanted isidioid soredia of *Lobaria pulmonaria* in an endangered population. *Lichenologist* 27, 361–374.
- Selva, S.B., 1994. Lichen diversity and stand continuity in the northern hardwoods and spruce–fir forests of northern New England and western New Brunswick. *The Bryologist* 97, 424–429.
- Sillett, S.C., McCune, B., Peck, J.E., Rambo, T.R., Ruchty, A., 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecological Applications* 10, 789–799.
- Spies, T.A., Franklin, J.F., 1991. *The Structure of Natural Young, Mature, and Old-Growth Douglas-Fir Forests in Oregon and Washington*. Published by: U.S. Department of Agriculture, Forest Service Pacific Northwest Research Station Portland, Oregon General Technical Report PNW-GTR-285. 21 pp.
- Spies, T.A., Hemstrom, M.A., Youngblood, A., Hummel, S., 2006. Conserving old-growth forest diversity in disturbance-prone landscapes. *Conservation Biology* 20, 351–362.
- Sundberg, B., Palmqvist, K., Esseen, P.A., Renhorn, K.E., 1996. Growth and vitality of epiphytic lichens. II. Modelling of carbon gain using field and laboratory data. *Oecologia* 109, 10–18.
- Werth, S., Tømmervik, H., Elvebakk, A., 2005. Epiphytic macrolichen communities along regional gradients in Northern Norway. *Journal of Vegetation Science* 16, 199–208.