Contrasting terrestrial lichen, liverwort, and moss diversity between old-growth and young second-growth forest on two soil textures in central British Columbia

Rachel S. Botting and Arthur L. Fredeen

Abstract: The diversity and abundance of terrestrial lichens, mosses, and liverworts were examined and compared between two ages of forest (old-growth and young second-growth) on two dominant soil types (fine- and coarse-textured soils) in subboreal spruce forests in central British Columbia. Major differences in species composition were found between forest ages, with 30% of species found only in old-growth forest and 21% found only in young second-growth forest. Liverworts were much more common in old-growth sites with half the liverwort species found exclusively in old-growth, and 90% of the recorded liverwort observations occurring there. Different moss species assemblages dominated old-growth and second-growth sites, with much of the terrestrial cover of second-growth sites composed of *Polytrichum juniperinum* Hedw. Young second-growth forest had higher cover of lichen species than old-growth forest. Lichens and bryophytes used different terrestrial substrates in each forest age, with higher cover of mosses and lichens occurring on woody substrates in old-growth, irrespective of substrate availability. Nonmetric multidimensional scaling ordination clearly separated plots by forest age and also showed soil texture to be a defining variable. Though not statistically significant, there was increased bryophyte diversity on coarse-textured soils and increased lichen cover on fine-textured soils.

Key words: bryophyte, liverwort, lichen, subboreal spruce forest, forest management, biodiversity.

Résumé : Les auteurs ont comparé la diversité et l’abondance des lichens terrestres, des mousses et des hépatiques dans des forêts de deux âges (surannée, et jeune de seconde venue) sur deux types de sol dominants (sols à texture fine ou grossière), dans des forêts d’épinettes sub-boréales du centre de la Colombie-Britannique. On observe de grandes différences dans la composition en espèces selon l’âge des forêts, 30 % des espèces ne se trouvant que dans la forêt surannée et 21 % seulement dans la jeune forêt de seconde venue. Les hépatiques sont beaucoup plus communes sur le site de la vieille forêt, la moitié des espèces d’hépatiques n’habitant exclusivement que la forêt surannée, 90 % des observations d’hépatiques provenant de ce site. Ce sont des assemblages différents d’espèces de mousses qui dominent les sites de forêt surannée et de la jeune forêt, une bonne partie de la couverture terrestre des sites de seconde venue étant constituée de *Polytrichum juniperinum* Hedw. La jeune forêt de seconde venue présente un couvert plus important en espèces de lichens que la vieille forêt. Les lichens et les bryophytes utilisent différents substrats terrestres dans les forêts de chaque âge, les mousses et les lichens occupant une plus grande surface sur les substrats ligneux de la vieille forêt, indépendamment de la disponibilité du substrat. Une ordination par strate multidimensionnelle non-métrique, sépare clairement les parcelles selon l’âge de la forêt et démontre également que la texture du sol est une variable déterminante. Bien que non statistiquement significative, on note une augmentation de la diversité des bryophytes sur les sols à texture grossière, et une augmentation de la couverture en lichens sur les sols à texture fine.

Mots clés : bryophytes, hépatique, lichen, forêt d’épinette sub-boréale, aménagement forestier, biodiversité.

[Traduit par la Rédaction]

Introduction

Forest harvesting is a major industry in British Columbia and has been identified as a threat to bryophyte and lichen diversity (Goward 1994; Ryan 1996). Forest harvesting in the form of clearcut logging affects terrestrial bryophyte and lichen communities through disturbance, changes in substrate and microclimate, and through habitat fragmentation (Lesica et al. 1991; Fenton et al. 2003). In managed stands, the canopy is more structurally homogeneous and even-aged, while features such as old trees and snags are rare (Wells et al. 1998). The quality and quantity of terrestrial substrates can be altered, particularly the amount and type of coarse woody debris and the amount of exposed mineral soil (Lesica et al. 1991; Frisvoll and Presto 1997). Microclimate changes including reduced humidity, increased light and temperature, and altered nutrient regimes may create unsuitable conditions for many bryophyte and lichen

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Table 1. Number of moss, lichen, and liverwort species observed only in old-growth, only in young second-growth, and in both forest ages in subboreal spruce forests of central British Columbia.

	Moss species	Lichen species	Liverwort species	Total no. of species	% of total
Old-growth specific species	8	16	11	35	30
Second-growth specific species	4	17	3	24	21
Species found in both forest ages	19	30	8	57	49
Total species from all sites	31	63	22	116	100
Total species found in old-growth	27	46	19	92	
Total species found in second-growth	23	47	11	81	

species (Saunders et al. 1991; Frisvoll and Presto 1997; Renhorn 1997). Habitat fragmentation can reduce the probability of a species dispersing into a disturbed area, and the dispersal of propagules is potentially a limiting factor in the reestablishment of nonvascular species in second-growth forests (Dettki et al. 2000; Sillett et al. 2000; Fenton and Frego 2005).

Logging is widespread in the Sub-Boreal Spruce biogeoclimatic zone (SBS) in central British Columbia. A recent study suggested that some biogeoclimatic subzones have 47% old-growth forest remaining, while others have as little as 2.5% remaining (Burton et al. 1999). Neither the effects of extensive forest management on lichen and bryophyte species in subboreal spruce forests, nor whether these effects are uniform across all types of forest stand are well documented. Studies in other areas of North America and Europe have shown bryophyte diversity to be greatest in old-growth forests (Söderström 1988; Lesica et al. 1991; Crites and Dale 1998; Rambo and Muir 1998; Newmaster et al. 2003). Liverwort species appear to be particularly restricted to old-growth conditions and may be dependent upon certain substrates, including coarse woody debris of particular decay classes found in these sites (Söderström 1988; Lesica et al. 1991; Crites and Dale 1998; Newmaster et al. 2003). Epixylic liverwort species diversity may be greatest on intermediate and more decayed logs (Crites and Dale 1998; Rambo and Muir 1998; Rambo 2001). Epiphytic lichen species have shown specificity to old-growth conditions in other areas of Canada, and epiphytic lichen communities may become richer over time (Goward 1994; Selva 1994; Campbell and Fredeen 2004). In a mixedwood boreal forest study, terrestrial lichen species showed different species assemblages in old-growth forests than in second-growth forests (Crites and Dale 1998). To date similar studies have not been performed in subboreal spruce forests. As well, this study compares old-growth forest with younger second-growth forest (15 years old) rather than mature forest (>50 years old) as in most of the studies cited above to examine the influence of forest harvesting on cryptogam species diversity earlier in forest succession.

Two major soil texture types underlie the Aleza Lake Research Forest (ALRF). While fine-textured soils (silty clay loam to silty clay) are the predominant soil types, an overlying veneer of coarse-textured soils (silt loam to sandy loam) occurs in parts of the ALRF (Arocena and Sanborn 1999). Soil type affects the composition of vascular plant communities, resulting in varying species assemblages and different site productivity. Generally, sites on coarse-textured soils have better drainage, more productive forests, and different herb and shrub species than sites on fine-textured soils (Meidinger and Pojar 1991; DeLong 2003). Differences in soil drainage, productivity, and vascular plant composition may affect the poikilohydric, terrestrial bryophyte, and lichen species. However, the relationships between soil texture type and bryophyte and lichen species diversity and abundance have not been well examined. Given that forests on coarse-textured soils are more productive and have been disproportionately logged, knowledge of lichen and bryophyte diversity on the different soil types would be of interest to forest managers concerned with diversity conservation.

In the subboreal spruce forests of British Columbia, little information is currently available on the diversity and distribution of terrestrial lichen and bryophyte species and the threats facing them. Biogeoclimatic references (e.g., Schofield 1988; Meidinger and Pojar 1991) and bryophyte and lichen identification references (e.g., Goward et al. 1994; Schofield 2002) provide some information, but a comprehensive survey has not been performed (T. Goward, personal communication 2002). This study documents the diversity and abundance of terrestrial moss, liverwort, and lichen species (cryptogams) in the Aleza Lake Research Forest in central British Columbia and examines the relationships between bryophyte and lichen species diversity and abundance, and both forest age (old-growth versus young second-growth forest) and underlying soil texture type (coarse-versus fine-textured soils).

Methods

Study area

The study area was located in the Aleza Lake Research Forest (ALRF) in central British Columbia, 60 km northeast of Prince George, British Columbia (122′40″W, 54′11″N). The ALRF is located in the wet cool variant of the Sub-Boreal Spruce (SBSwk1) biogeoclimatic zone (Meidinger and Pojar 1991). Hybrid spruce (*Picea glauca* (Moench) Voss ×*engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) are the dominant tree species with lesser components of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), trembling aspen (*Populus tremuloides* Michx.), and paper birch (*Betula papyrifera* Marsh.) (DeLong 2003). At an elevation of 600–700 m, the climate of the SBSwk1 region is characterized by cool snowy winters and moist cool summers (DeLong 2003). The ALRF receives 900 mm of precipitation a year with 65% of that falling as rain and 35% as snow. Average monthly temperatures

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Table 2. Frequency of observation, mean percent cover, and indicator species analysis status of all terrestrial moss, lichen, and liverwort species encountered in old-growth forest and young second-growth forest in subboreal spruce forests of central British Columbia.

	Old-growth		Second-growth		
	f	% cover	*f*	% cover	Indicator species[a]
Lichen species					
Alectoria spp.	10	0.010	1	0.001	O
Bryoria spp.	1	0.001	2	0.002	
Cladina arbuscula subsp. *beringiana*	—	—	10	0.010	Y
Cladina rangiferina	3	0.003	7	0.008	
Cladina spp.	1	0.001	—	—	
Cladonia acuminata	—	—	1	0.001	
Cladonia bacilliformis	—	—	1	0.001	
Cladonia botrytes	4	0.004	22	0.023	Y
Cladonia cariosa	—	—	66	0.524	Y
Cladonia carneola	5	0.005	25	0.026	Y
Cladonia cenotea	3	0.003	2	0.002	
Cladonia cervicornis	—	—	1	0.001	
Cladonia chlorophaea	8	0.008	24	0.025	Y
Cladonia coniocraea	1	0.001	2	0.002	
Cladonia cornuta subsp. *cornuta*	—	—	30	0.109	Y
Cladonia crispata var. *crispata*	1	0.001	7	0.007	
Cladonia cfr cyanipes	—	—	1	0.001	
Cladonia deformis	—	—	4	0.004	
Cladonia digitata	1	0.001	1	0.001	
Cladonia ecmocyna	1	0.001	1	0.001	
Cladonia fimbriata	14	0.015	65	0.086	Y
Cladonia gracilis subsp. *turbinata*	3	0.003	69	0.275	Y
Cladonia norvegica	1	0.001	—	—	
Cladonia ochrochlora	36	0.264	61	0.153	
Cladonia phyllophora	—	—	4	0.004	
Cladonia spp.	16	0.046	48	0.190	Y
Cladonia sulphurina	6	0.006	34	0.065	Y
Cladonia umbricola	—	—	1	0.001	
Hypogymnia occidentalis	8	0.028	—	—	O
Hypogymnia physodes	8	0.008	2	0.002	
Hypogymnia spp.	1	0.001	1	0.001	
Hypogymnia tubulosa	3	0.003	—	—	
Lobaria pulmonaria	7	0.077	—	—	O
Mycoblastus sanguinarius	1	0.001	—	—	
Nephroma bellum	22	0.256	—	—	O
Nephroma helveticum	1	0.010	—	—	
Nephroma parile	13	0.111	2	0.002	O
Parmelia hygrophila	1	0.010	—	—	
Parmelia sulcata	20	0.071	2	0.002	O
Parmeliopsis ambigua	7	0.017	3	0.003	
Parmeliopsis hyperopta	4	0.004	—	—	
Peltigera aphthosa	4	0.024	1	0.001	
Peltigera canina	2	0.042	25	0.425	Y
Peltigera degenii	1	0.010	—	—	
Peltigera extenuata	1	0.001	44	1.189	Y
Peltigera horizontalis	13	0.082	—	—	O
Peltigera leucophlebia	2	0.011	37	0.315	Y
Peltigera membranacea	24	0.323	16	0.153	
Peltigera neckeri	1	0.010	5	0.272	
Peltigera neopolydactyla	11	0.325	6	0.034	
Peltigera polydactylon	—	—	1	0.001	
Peltigera praetextata	—	—	1	0.010	

Table 2 (*continued*).

	Old-growth		Second-growth		
	f	% cover	*f*	% cover	Indicator species[a]
Peltigera rufescens	—	—	5	0.044	Y
Peltigera spp.nov. No. 1	—	—	1	0.010	
Peltigera spp.nov. No. 2	—	—	9	0.502	
Peltigera spp.	2	0.002	4	0.004	
Platismatia glauca	19	0.118	—	—	O
Pseudocyphellaria anomala	1	0.001	—	—	
Stereocaulon tomentosum	—	—	1	0.001	
Tuckermannopsis chlorophylla	3	0.003	—	—	
Tuckermannopsis orbata	1	0.001	—	—	
Usnea spp.	5	0.005	1	0.001	
Vulpicida pinastri	—	—	4	0.004	
Total[b]	301[c]	1.9[d]	661[c]	4.5[d]	
Moss species					
Aulacomnium androgynum	—	—	38	0.164	Y
Aulacomnium palustre	—	—	1	0.001	
Brachythecium spp.	82	1.371	63	2.333	C
Campylium calcareum	—	—	1	0.010	
Ceratodon purpureus	1	0.001	76	5.117	Y
Dicranum fuscescens	20	0.191	8	0.008	O
Dicranum polysetum	3	0.003	19	0.049	Y
Dicranum scoparium	10	0.020	9	0.029	
Dicranum spp.	8	0.038	4	0.004	
Dicranum tauricum	35	0.125	6	0.006	O
Eurhynchium praelongum	5	0.024	1	0.001	
Eurhynchium pulchellum	5	0.126	—	—	
Herzogiella seligeri	1	0.001	—	—	
Hylocomium splendens	56	8.100	7	0.058	O, F
Lescuraea stenophylla	1	0.001	—	—	
Mnium lycopodioides	15	0.092	1	0.001	O
Mnium spinulosum	5	0.065	1	0.001	
Orthotrichum speciosum	1	0.001	—	—	
Plagiomnium insigne	66	2.733	11	0.317	O
Plagiomnium spp.	29	0.205	10	0.141	
Plagiothecium cavifolium	1	0.001	—	—	
Plagiothecium denticulatum	1	0.001	—	—	
Plagiothecium laetum	4	0.043	—	—	
Pleurozium schreberi	87	7.344	59	0.456	O
Pohlia nutans	3	0.023	46	0.800	Y
Polytrichum juniperinum	—	—	87	26.017	Y
Ptilium crista-castrensis	83	7.235	39	0.493	O
Rhizomnium nudum	25	1.204	2	0.002	O
Rhytidiadelphus triquetrus	88	8.595	20	0.050	O
Sanionia uncinata	42	0.689	15	0.124	O
Tetraphis pellucida	3	0.003	—	—	
Total	680[c]	38.2[d]	524[c]	36.2[d]	
Liverwort species					
Anastrophyllum hellerianum	1	0.010	—	—	
Barbilophozia barbata	35	0.155	5	0.005	O
Barbilophozia spp.	4	0.024	2	0.011	
Blepharostoma trichophyllum	17	0.046	—	—	O
Cephalozia spp.	7	0.026	—	—	O
Cephaloziella rubella	—	—	1	0.010	
Cephaloziella spp.	5	0.107	1	0.001	C
Geocalyx graveolens	2	0.002	—	—	
Harpanthus flotovianus	20	0.021	2	0.002	O, F

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Table 2 (*concluded*).

	Old-growth		Second-growth		
	f	% cover	*f*	% cover	Indicator species[a]
Jamesoniella autumnalis	3	0.032	—	—	
Jamesoniella spp.	2	0.031	—	—	
Jungermannia spp.	16	0.066	—	—	O
Lophocolea heterophylla	1	0.001	—	—	
Lophocolea minor	13	0.144	1	0.001	O
Lophocolea spp.	—	—	1	0.001	
Lophozia longiflora	4	0.004	—	—	
Lophozia spp.	14	0.209	—	—	O
Marchantia polymorpha	—	—	1	0.010	
Plagiochila porelloides	3	0.003	1	0.010	
Ptilidium californicum	22	0.251	1	0.001	O, F
Ptilidium pulcherrimum	2	0.022	—	—	
Ptilidium spp.	20	0.347	4	0.004	O, C
Total[b,e]	191[c]	1.5[d]	20[c]	0.06[d]	
Other					
Unknown species	23	0.173	18	0.058	
Total mean percent cover		41.8		40.8	

Note: Frequency (*f*) indicates the number of quadrats in which a species was observed of a total of 96 quadrats sampled in old-growth and second-growth forests, respectively. The % cover is the mean % cover per quadrat for mosses, lichens, and liverworts from the 96 quadrats sampled in old-growth and second-growth forests, respectively.

[a] Indicator species analysis results for each lichen, moss, and liverwort species indicating significant indicators of old-growth forest (O), young second-growth forest (Y), coarse-textured soils (C), and fine-textured soils (F).

[b] Significant effect of forest age on frequency of observation (ANOVA, α = 0.05).

[c] Sum of the frequency of all species in that group (moss, lichen, or liverwort) over all quadrats.

[d] Sum of the mean percent cover per quadrat of all species in that group (moss, lichen, or liverwort). Indicates the mean percent cover of that group in an average quadrat.

[e] Significant effect of forest age on % cover (ANOVA, α = 0.05).

range from 20 °C in July to –20 °C in January (Murphy 1996).

Soils in the ALRF have a parent material of glaciolacustrine sediments of which the top 50 cm of most areas consists of fine-textured soil ranging from silty clay loam to silty clay. Scattered throughout the research forest are areas with an overlying layer of coarse-textured soil 1–2 m thick, which ranges in texture from silt loam to sandy loam (Arocena and Sanborn 1999).

The planted second-growth stands sampled in this study (subsequently referred to as young second-growth) were clearcut logged, and all canopy trees were removed in 1989 or 1990. This was the first time these sites had been logged, and all sites were then broadcast burned and planted with hybrid spruce seedlings.

Definitions of old-growth for subboreal spruce forest range from >140 years of age (MacKinnon and Vold 1998) to more detailed structural assessments including an age >185 years (Kneeshaw and Burton 1998). Old-growth stands in this study had no history of partial cutting, were >200 years of age, and had an uneven-aged stand structure.

Moss, lichen, and liverwort species diversity

Eight study sites were selected for sampling based on stand age and soil texture characteristics. Four sites each were located in old-growth forest (>200 years of age) and young second-growth forest (14–15 years of age). Within each forest age, two sites were located on coarse-textured soils (B.C. Ministry of Forests site series 07/08) and two on fine-textured soils (site series 01) (DeLong 2003).

At each site, a site centre was located and three plot centres were placed along randomly assigned compass bearings from the site centre, ensuring that no plot was within 50 m of a forest edge. At each plot centre, two parallel 20 m transects were established, 10 m apart, bounding half of a 20 m × 20 m plot.

Terrestrial lichen, moss, and liverwort species diversity and abundance were analyzed in a series of 1 m^2 quadrats. Four quadrats were placed at equal distances along each 20 m transect line. Eight quadrats were sampled per plot for a total of 8 m^2 of forest floor sampled per plot, 24 m^2 per site, and a total of 192 m^2 sampled over all 24 plots (eight sites). At each quadrat, all terrestrial lichen, moss, and liverwort species were recorded along with the percent cover of each species. Species were included if they were growing on the ground or on coarse woody debris that was less than 1 m above the ground. Species growing on the base of living trees were not recorded, nor were species that had obviously fallen from trees. For each quadrat, the substrate upon which a species was most frequently growing was recorded. The substrate was classified into four major types, which included soil (growing on bare mineral soil or humus), litter

Table 3. Species diversity, frequency of observation, and mean percent cover of lichens, liverworts, and mosses on coarse-textured and fine-textured soils in old-growth, in young second-growth, and in both forest ages of subboreal spruce forest in central British Columbia.

	Coarse-textured soil			Fine-textured soil		
	No. of species	*f*	% cover	No. of species	*f*	% cover
Old-growth						
Lichens	36	162	1.8	37	139	2.1
Liverworts[a]	19	71	1.6	13	120	1.4
Mosses	25	327	26.7	18	353	49.8
Total	80	560	30.1	68	612	53.2
Second-growth						
Lichens[b]	33	302	2.9	42	359	6.1
Liverworts[c]	10	14	0.1	4	6	0.0
Moss	23	275	36.6	16	249	35.8
Total	66	604	39.6	62	619	42.0
Both forest ages						
Lichens[b]	52	464	2.3	56	498	4.1
Liverworts[a]	22	85	0.8	13	126	0.7
Moss	30	602	31.6	21	602	42.8
Total	104	1151	34.8	90	1226	47.6

Note: Frequency (*f*) indicates the number of times lichen, moss, or liverwort species were observed in the sampled quadrats. The % cover indicates the mean % cover of moss, lichen, and liverwort species in quadrats in that forest age and soil texture type. The number of quadrats sampled included: old-growth coarse-textured soils, 48; fine-textured soils, 48; second-growth coarse-textured soils, 48; fine-textured soils, 48; both forest ages coarse-textured soils, 96; fine-textured soils, 96.

[a] Significant effect of soil texture type on frequency of occurrence (ANOVA, $\alpha = 0.05$).

[b] Significant effect of soil texture type on % cover (ANOVA, $\alpha = 0.05$).

[c] Significant effect of site on frequency (ANOVA, $\alpha = 0.05$).

(growing on the forest floor litter layer), wood (growing directly on decaying wood), and moss (growing on top of a living moss mat).

Sampling method affects species capture and accuracy of cover measurements. Sampling using many microplots may result in the most accurate cover estimates and may be most suitable for areas with dense understory vegetation, while belt transects or visual estimation of larger plots may result in higher species capture and may be best for areas with sparse vegetation (McCune and Lesica 1992). This study used many relatively large microplots (1 m^2), which were intended to provide accurate cover estimates but may have missed some rare species.

All terrestrial lichen and bryophyte species were identified to the species level where possible with the exception of two genera. Because of the high degree of gametophyte variability displayed by members of the *Brachythecium* Schimp. genus and a lack of available sporophyte material, members of this genus were not determined to the species level. With the exception of *Plagiomnium insigne* (Mitt.) T. Kop., all young specimens and other *Plagiomnium* T. Kop. species were identified only to genus. Nomenclature follows Anderson et al. (1990) for mosses, Stotler (1977) for liverworts, and Hitchcock and Cronquist (1996) for vascular plants. Nomenclature for lichens follows Esslinger (1997) with the exception of *Peltigera* spp. 1 and 2 *fide* Goward. Voucher specimens for lichens and bryophytes reside at the University of Northern British Columbia herbarium.

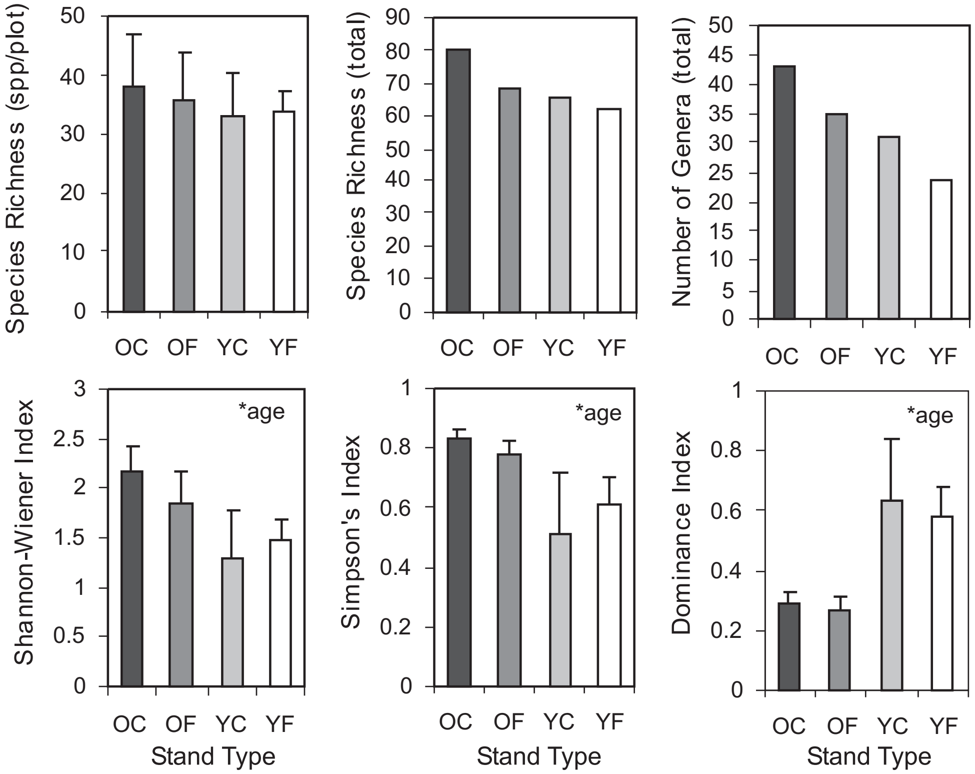
Ecological and stand characteristics

Forest canopy characteristics were collected for each 20 m × 20 m plot. Canopy cover was derived from the average of four spherical densiometer measurements. The diameter at breast height (dbh) of all trees with dbh >10 cm was measured. The largest one or two individuals of each tree species were cored to determine maximum stand age, and the height of each was measured. Shrub and herbaceous plant species and percent cover were assessed in a randomly selected 10 m × 10 m subplot of the 20 m × 20 m plot. Shrubs were considered to be any woody vascular plant species >0.15 m and <2 m tall. Herbs were considered to be any nonwoody vascular plant species and any shrubs or trees <0.15 cm tall. Coarse woody debris (CWD) intercepted by two perpendicular 20 m transects was assessed by length, diameter, and decay class. Only logs of diameter >10 cm lying or suspended <1.3 m off the ground were included. The CWD decay classes ranged from 1 (least decayed) to 5 (most decayed) using definitions taken from the BC Ministry of Forests (British Columbia Ministry of Forests and Ministry of Environment, Lands and Parks 1998). The CWD volume per hectare was calculated according to Marshall et al. (2000).

Data analysis

The study was laid out as 24 plots in eight sites with 6 plots located in each combination of forest age and soil texture type. Data analyses were performed using a series of

Fig. 1. Diversity statistics, including species richness per plot, species richness per stand type, number of genera per stand type, Shannon–Wiener index, dominance index, and Simpson's index, for sites in old-growth (O) and young second-growth (Y) subboreal spruce forest growing on coarse-textured (C) and fine-textured (F) soils. Note: Species richness per plot, Shannon–Wiener index, dominance index, and Simpson's index are all calculated at the plot level (n = 6 plots). Total species richness and total number of genera are calculated as totals for that stand type (OC, OF, YC, YF). Standard deviation is given where applicable (n = 6). Significant effects (forest age (age), soil texture, site) are noted with an asterisk on each graph (ANOVA; α = 0.05).



ANOVAs (α = 0.05) with main effects of forest age class and soil texture type and with site as a nested effect. To attempt to account for site differences, site was examined as a random variable nested in forest age and soil texture type. ANOVAs were used to examine site, forest age, and soil texture effects on cryptogam diversity, cover, and frequency of occurrence. Differences in CWD and forest stand characteristics were also analyzed using ANOVAs.

Four diversity statistics were calculated. Species richness was considered to be the number of species present. The Shannon-Wiener and Simpson's indices were used to give an indication of the species richness and evenness. The dominance index was used to show the proportion of the plot that was dominated by the most common species (Gotelli and Entsminger 2001). An ANOVA was used to examine each of these diversity statistics and the total number of genera of lichens and bryophytes.

Overall bryophyte and lichen community composition patterns were analysed using nonmetric multidimentional scaling (NMS) (Kruskal 1964; Mather 1976) with PC-ORD software (McCune and Mefford 1999). Rare species were retained because the communities contained many rare species and these species were considered important in examining species diversity patterns. Data were log-transformed before ordination to give more weight to rare species and to reduce the effect of several dominant species. The Sörenson distance measure was used with a random starting configuration, 40 runs of real data, and a stability criterion of 0.0001. NMS was first applied to the full data set to elucidate species patterns between the plots and the associated environmental variables. There were 116 species and 24 plots in the main matrix and 9 environmental variables and 24 plots in the secondary matrix. Old-growth and second-growth sites were then separated, and NMS analysis was conducted on each forest age individually. The old-growth main matrix contained 92 species and 12 plots, and the second-growth main matrix contained 81 species and 12 plots.

Indicator species analysis (Dufrêne and Legendre 1997) was used in PC-ORD (McCune and Mefford 1999) to determine whether certain species could be indicators of forest age or soil texture type. Indicator analysis assigns each species an indicator value based on its abundance in a certain group and its faithfulness to that group (McCune and Grace 2002). A Monte Carlo test with 1000 randomizations was used to test for significance.

Results

Species diversity

Overall, 116 terrestrial bryophyte and lichen species were recorded across all sites including 31 mosses, 63 lichens, and 22 liverworts. In total, 92 species were found in old-growth forests, and 81 were found in second-growth forests. Thirty-five species (30%) were found only in old-growth

Fig. 2. Nonmetric multidimensional scaling ordination results for old-growth forest showing the distribution of study plots in two dimensions. Axis 1 accounted for 30% of the variation and was most strongly correlated with CWD length ($R^2 = 0.62$). Axis 2 accounted for 49% of the variation and was most strongly correlated with soil texture ($R^2 = 0.53$) and herbaceous plant cover ($R^2 = 0.52$). Plots on coarse-textured (OC) and fine-textured (OF) soil are encompassed by a circle with the exception of an outlier plot (OC2).

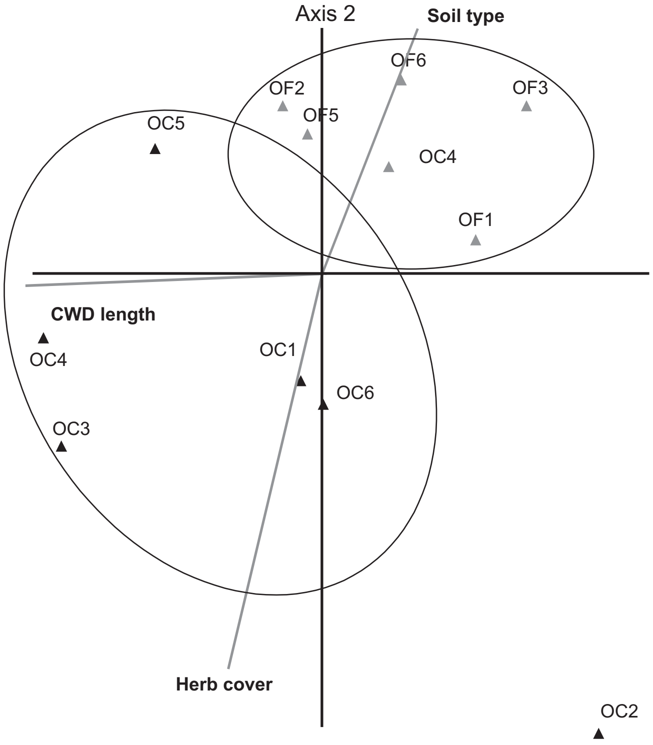
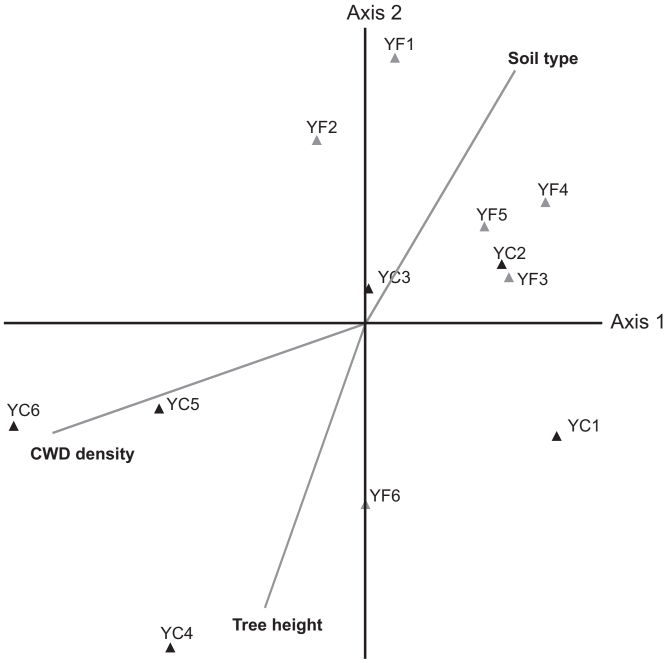


Fig. 3. Nonmetric multidimensional scaling ordination results for young second-growth forest showing the distribution of study plots in two dimensions. Axis 1 accounted for 50% of the variation and was most strongly correlated with CWD density ($R^2 = 0.77$). Axis 2 accounted for 32% of the variation and was most strongly correlated with soil texture ($R^2 = 0.33$) and average tree height ($R^2 = 0.39$). Young second-growth plots are indicated by YC on coarse-textured soils and YF on fine-textured soils.



forest, 24 (21%) were found only in second-growth forest, and 57 (49%) were found in common between forest ages (Table 1).

Liverwort species richness was significantly different between forest ages (ANOVA; $p < 0.001$), in fact, almost twice as many liverwort species were found in old-growth (19) than in second-growth forest (11) (Table 1). Eleven of the liverwort species encountered were found only in old-growth, while three were found only in second-growth forest (Table 2). There was no significant difference in the number of moss or lichen species recorded between the two forest ages or the two soil types (Table 3).

A significantly greater number of cryptogam genera occurred in old-growth plots than in second-growth plots (ANOVA; $p = 0.01$) (Fig. 1). Forty-six genera were encountered in old-growth forests compared with 35 genera in second-growth forests. Soil type had no significant effect on diversity at the genus level.

There was a significant effect of forest age on the Shannon–Wiener diversity index (ANOVA; $p = 0.045$) with higher cryptogam diversity in old-growth forest than in second-growth forest (Fig. 1). The Simpson's diversity index also showed a significant effect of forest age (ANOVA; $p < 0.001$), indicating that cryptogams were more diverse and evenly distributed in old-growth forest than in second-growth forest. The uneven distribution of species in second-growth forest was highlighted by the significantly higher dominance indices in those sites (ANOVA; $p = 0.020$). Between 46% and 80% of second-growth sites were dominated by one species compared with 27% to 36% of the old-growth sites. The dominant species in second-growth forest was *Polytrichum juniperinum* Hedw., and it represented an average of 63% percent of the terrestrial cover of the sites. There was no significant effect of soil texture type on any of the diversity indices.

Terrestrial cover of mosses, lichens, and liverworts

Total cryptogam percent cover was similar (about 40%) for old-growth and second-growth sites (Table 2). The frequency of occurrence and cover of mosses was also similar, and mosses made up the greatest proportion of terrestrial cover in both forest ages. In contrast, liverworts were significantly more frequent (ANOVA; $p < 0.001$) and had higher cover (ANOVA; $p < 0.001$) in old-growth forest compared with young second-growth forest. Old-growth forest had a 25-fold higher percent cover of liverworts and a 10-fold higher frequency of occurrence of liverworts than second-growth forest. Lichen cover was significantly influenced by forest age (ANOVA; $p = 0.014$) as was lichen frequency (ANOVA; $p = 0.015$) with second-growth forest having twice the average percent cover and frequency of occurrence of lichens than old-growth forest.

Only lichen cover was significantly affected by soil texture (ANOVA; $p = 0.043$) and was greater on fine-textured soils than on coarse-textured soils. Soil type had a signifi-

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Table 4. Subboreal spruce forest stand and coarse woody debris (CWD) characteristics recorded in old-growth and young second-growth forest on coarse-textured (coarse) and fine-textured (fine) soils, respectively.

	Old-growth		Second-growth	
	Coarse	Fine	Coarse	Fine
Stand characteristics				
Stand age class	8	8	1	1
Age of oldest canopy tree (years)	255	203	15	15
Mean canopy height (m)	33±7	33±3	5	3
Mean DBH > 10 cm (cm)	31±17	24±12	na	na
Mean shrub cover (%)[a]	71±10	44±7	21±8	30±15
Mean herb cover (%)	55±11	32±9	41±12	56±18
CWD characteristics				
Mean no. of pieces CWD (per 40 m transect)[a]	11±4	15±3	9±2	6±2
Mean length of CWD (m)[a,b]	14±9	11±7	5±4	5±4
Mean diameter of CWD (cm)[b,c]	26±12	20±9	24±12	18±8
Mean CWD volume ($m^3 \cdot ha^{-1}$)[a]	279±160	221±56	126±199	46±76
Mean decay class of CWD[c]	3.1±1.2	2.5±1.4	2.7±1.0	3.2±1.0

Note: Means ± standard deviation are given (n = 6 plots).

[a] Significant effect of forest age on the characteristic (ANOVA; α = 0.05).

[b] Significant effect of site on the characteristic (ANOVA; α = 0.05).

[c] Significant effect of soil texture type on the characteristic (ANOVA; α = 0.05).

cant effect on liverwort frequency (ANOVA; p = 0.023) with a greater frequency observed for fine-textured soils (Table 3).

Twenty N_2-fixing lichens belonging to 5 genera (*Lobaria* (Schreber) Hoffm., *Nephroma* Ach., *Peltigera* Willd., *Pseudocyphellaria* Vainio, and *Stereocaulon* Hoffm.) were encountered (Table 2). Fourteen species from 4 genera of N_2-fixing lichen occurred in old-growth sites compared with 14 species from 3 genera in second-growth sites.

Indicator species

Indicator species analysis determined 27 species were significant indicators of old-growth forest: 10 mosses, 9 liverworts, and 8 lichens (Table 2). Four species were N_2-fixing lichens, *Lobaria pulmonaria* (L.) Hoffm., *Nephroma bellum* (Sprengel) Tuck., *N. parile* (Ach.) Ach., and *Peltigera horizontalis* (Hudson) Baumg. Nineteen species were significant indicators of second-growth forest including 5 mosses and 14 lichens, of which 9 were *Cladonia* species. Four species were N_2-fixing lichens, *Peltigera canina* L. Willd., *P. leucophlebia* (Nyl.) Gylenik, *P. extenuata* (Vainio) Lojka, and *P. rufescens* (Weiss) Humb. Indicator species analysis for soil texture type resulted in 6 indicator species, 3 indicative of fine-textured soils and 3 indicative of coarse-textured soils (Table 2).

Nonmetric multidimensional scaling ordination

Nonmetric multidimensional scaling (NMS) ordination of all sites resulted in a one-dimensional final solution. This solution had a final stress of 5.028, an instability of 0.000 01 after 76 iterations, and a significant Monte Carlo test (p = 0.02). The single axis described 95% of the variation and showed a very strong separation of plots based on forest age, with old-growth and second-growth plots located at opposite ends of the axis. This strong relationship suggests that forest age greatly affected species assemblages.

To elucidate the effect of other environmental variables within the two forest ages, NMS ordinations were conducted on old-growth and second-growth plots separately. The NMS ordination of old-growth plots suggested a three-dimensional solution. The ordination had a final stress value of 5.71, an instability value of 0.000 01 after 84 iterations, and a Monte Carlo test gave significant p values ($p < 0.05$). The first axis explained 30% of the variation, the second axis explained 49%, and the third axis explained 14%. The two most explanatory axes are displayed in Fig. 2. Ordination of the old-growth plots showed plots grouped by soil texture with the exception of one outlier (OC2). Coarse woody debris length (r^2 = 0.62) corresponded most strongly with the first axis, while soil texture (r^2 = 0.53) and herb cover (r^2 = 0.52) corresponded most strongly with the second axis.

The NMS ordination for the second-growth plots also suggested a three-dimensional solution. The final stress value was 7.34 with an instability of 0.000 01 after 94 iterations, and a Monte Carlo test gave p values of <0.05 for all three axes. The first axis explained 50% of the variation, the second axis explained 32%, and the third axis explained 8%. Figure 3 gives a two-dimensional display of the most explanatory ordination axes. Coarse woody debris density (r^2 = 0.77) corresponded most strongly with the first axis, while soil texture (r^2 = 0.31) and average tree height (r^2 = 0.39) corresponded most strongly with the second axis. Plots did not group as strongly with soil texture in this forest age.

Stand and coarse woody debris characteristics

Dominant canopy trees in the old-growth forest ranged from 200 to 255 years of age with an average canopy height of 33 m (Table 4). Young second-growth forest had a canopy height ranging from 3 m on fine-textured soils to 5 m on coarse-textured soils. When compared with the young second-growth forest, the old-growth forest had a more het-

Table 5. Percent cover of mosses, lichens, and liverworts, on available terrestrial substrates (litter layer, wood, bare soil, and living moss mat), normalized by stand age or across all sites.

		% cover normalized by stand age			% cover normalized across sites		
Forest age	Substrate	Moss	Lichen	Liverwort	Moss	Lichen	Liverwort
Old-growth	Litter	73.2	0.5	8.7	37.6	0.1	8.3
	Wood	26.8	99.5	91.2	13.8	29.9	87.6
	Soil	—	—	—	—	—	—
	Moss	0.0	0.0	0.1	0.0	0.0	0.1
Old-growth total		100	100	100	51.4	30.0	96.1
Second-growth	Litter	2.9	0.1	0.0	1.4	0.0	0.0
	Wood	4.3	18.8	46.4	2.1	13.2	1.7
	Soil	92.7	75.2	53.6	45.1	52.6	2.0
	Moss	0.0	5.9	0.0	0.0	4.2	0.0
Second-growth total		100	100	100	48.6	69.9	3.8
Total					100	100	100

Note: Bare soil substrates did not occur in old-growth sites.

erogeneous stand structure with greater tree canopy cover and a multilayer canopy. Shrub cover was affected by forest age (ANOVA; $p = 0.023$) and was significantly higher in old-growth forest. Within old-growth forest, shrub cover was higher in sites on coarse-textured soils than on fine-textured soils, though this was only marginally significant (ANOVA; $p = 0.058$). Herbaceous species cover was not significantly different across all sites.

Analysis of CWD data showed significant variation in decay class, diameter, and piece length between sites (Table 4). Forest age had a significant effect on CWD volume (ANOVA; $p = 0.020$), CWD length (ANOVA; $p = 0.02$), and the number of pieces of CWD present at the plots (ANOVA; $p = 0.003$). Old-growth forests contained 50% more pieces of CWD, and pieces of CWD were twice as long. Soil texture type had a significant effect on CWD diameter (ANOVA; $p = 0.044$) with higher CWD diameters on coarse soils in both forest ages.

Substrate

Substrate use by moss, lichen, and liverwort species varied with forest age (Table 5). In old-growth and second-growth forest, mosses had the highest cover on litter (73%) and soil (93%) substrates, respectively. Mosses had more cover on wood in old-growth (26.8%) than in second-growth forest (4.3%). While there was a greater abundance of wood substrate in old-growth forest relative to second-growth (Table 4), there was still more moss cover on wood in old-growth than second-growth forest, when relative wood abundance was accounted for. The majority of lichen cover was recorded growing on wood in old-growth sites (99.5%) compared with 75% on soil in second-growth sites. However, the absolute cover of lichen on wood was not higher in old-growth than second-growth sites, when relative wood abundance was considered. Liverworts predominantly used wood substrates in old-growth sites (91%), and used soil (54%) and wood (46%) equally in second-growth sites. Given the low cover of liverworts in second-growth forest, liverwort cover on wood was much higher in old-growth forest, even when relative wood abundance was considered.

Discussion

Influence of forest age

Liverwort species diversity and abundance

Liverwort diversity and abundance were strongly affected by forest age, and both were much greater in old-growth forests. Eleven of 22 liverwort species were found only in old-growth sites compared with only 3 species found exclusively in second-growth sites. As well, 96% of the overall recorded liverwort cover occurred in old-growth sites. All of the liverwort species observed in second-growth sites had fewer than five recorded occurrences and most had only a single observed occurrence. Only the genus *Marchantia* L., which is often found in moist, burned sites (Schofield 2002), had observations restricted to a second-growth site. No liverworts were identified as indicators of second-growth forest, while 9 species were identified as potential indicators of old-growth forest. These results are consistent with other studies that found liverworts to be most diverse and abundant in old-growth forests (e.g., Söderström 1988; Lesica et al. 1991; Crites and Dale 1998; Newmaster et al. 2003).

Greater liverwort diversity and abundance in old-growth forest may occur for several reasons. First, leafy liverworts are commonly drought sensitive and have life forms that make them particularly susceptible to desiccation (During 1992). In fact, liverworts have been observed to reach greatest diversity on moist substrates (Pharo and Beattie 1997). Second, many liverwort species are exclusively epixylic (Söderström 1988), and the vast majority of liverworts observed in this study were growing on woody substrates. As previously noted, less volume and fewer pieces of coarse woody debris were available in the young second-growth sites. Managed forest landscapes, with stands harvested at short return intervals, may result in a decline in amount and decay classes of CWD because of reduced inputs and the lower maximum ages of such stands (Clark et al. 1998; Ross-Davis and Frego 2002). The wood that was available in second-growth forest was more desiccated, and this more exposed wood may not be of suitable habitat quality for these moisture-dependent species. Microclimate conditions at the forest floor in second-growth forest include higher light levels, altered moisture availability and humidity, and increased soil surface temperatures (Lewis 1998) that, when combined with reduced substrates, are likely to create unsuitable conditions for the growth of most liverwort species.

Moss species diversity and abundance

Moss species composed the greatest proportion of the terrestrial cryptogam cover in all sites. This study found that moss diversity and cover were not significantly different between the two forest ages or the two soil texture types; however, different species were common in old-growth and second-growth sites. Moreover, moss species were found primarily growing on soil in second-growth sites and on litter and wood in old-growth sites. Old-growth sites were dominated by *Plagiomnium* species and feather mosses including *Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not., and *Hylocomium splendens* (Hedw.) Schimp. In contrast, second-growth sites were dominated by *Polytrichum juniperinum* (65% of moss cover) and *Ceratodon purpureus* Brid. (14% of moss cover). Indicator species analysis identified these and several other moss species as indicators of second-growth forest. Moss species such as *P. juniperinum* and *C. purpureus* are colonist species and have characteristics that make them drought tolerant (During 1992; Newmaster and Bell 2002) and therefore well suited to second-growth environments. However, some of the old-growth indicator species, such as *Pleurozium schreberi*, are more common but not restricted to old-growth forest and may not be effective indicators of that forest age.

Lichen species diversity and abundance

Similar numbers of lichen species were identified in young second-growth and old-growth forests. However, species composition and abundance varied between old-growth and second-growth with significantly greater lichen cover in second-growth forest. This study concurs with other studies that have found terrestrial lichens to be more abundant in open stands than closed stands (e.g., Pharo and Vitt 2000). Second-growth had higher diversity of *Cladonia* species, agreeing with other research that has shown *Cladonia* species to be more numerous and to have greater diversity in younger forests as compared with older forests (Söderström 1988; Lesica et al. 1991). *Cladonia* species thrive in the drier environment of the open, young stands and can grow on exposed mineral soil (Söderström 1988). In contrast with old-growth, bare soil was common in young second-growth sites that had been burned after logging and lost much of the litter layer. Furthermore, N_2-fixing *Peltigera* species were 3.5-fold more abundant in second-growth than old-growth forest, likely making them an important contributor of nitrogen to these disturbed second-growth ecosystems. *Peltigera* species contribute nitrogen to forest ecosystems through leaching and thallus decomposition (Knowles 2004).

Old-growth sites had a greater number of epixylic lichen species and a greater proportion of lichen occurrences recorded on wood (99%) compared with second-growth (19%) sites. Old-growth indicator species were primarily epixylic or epiphytic species, including *Nephroma bellum* (Sprengel) Tuck., *Platismatia glauca* Taylor, and *Hypogymnia occidentalis* L. Pike species. This may have been partly due to the relatively higher abundance of woody substrates in old-growth sites; however, it may also have been due to wood quality differences between forest ages. The greater availability of CWD combined with the microclimate of old-growth stands likely makes for more suitable terrestrial habitat for these epixylic species.

Influence of soil texture

Although differences in species abundance and diversity were anticipated between sites on different soil types, this study could not determine a clear relationship with soil texture in either forest age class. Also, indicator species analysis did not reveal many strong indicators of soil type, and some of those that were identified may not be ecologically relevant.

In old-growth forest, bryophytes and lichens may not be as strongly affected by differences in underlying soil composition because of the fact that they are commonly found growing on woody substrates or on the litter layer and so are somewhat buffered from the effects of the underlying soil properties. However, though statistical comparison of the totals was not possible, there was a trend towards greater bryophyte diversity on coarse-textured soils than on fine-textured soils in old-growth forest. Also, NMS ordination of old-growth plots showed soil texture to influence the distribution of bryophyte and lichen species. Vanderpoorten and Engels (2003) found that bryophyte species diversity increased with increasingly sandy forest soils.

In old-growth wet, cool subboreal forest, stands on coarse-textured soil are more productive (M. Jull, personal communication 2003) and so may have a higher input of woody debris, though in this study only CWD diameter was significantly greater on coarse-textured soils. Sites on coarse-textured soils had higher shrub cover, which may result in more varied microhabitats, may hold more moisture on CWD, or may provide more shade in the summer months. These factors may contribute to slightly higher species diversity on coarse-textured soils.

In second-growth, fine-textured soils had a significantly higher percent cover of lichens than coarse-textured soils, possibly because of the fact that fine-textured second-growth sites had a shorter canopy than coarse-textured sites. The NMS analysis of second-growth plots revealed differences in the lichen and bryophyte community between coarse- and fine-textured soils, though the pattern was not strong. The effects of soil type in the second-growth stands may not be obvious because of the overriding effects of logging on these sites. Clearcut logging would almost certainly cause a greater modification to the overall forest floor environment than differences in underlying soil texture. Further study is needed to resolve the relationship between soil texture and cryptogam species composition and abundance.

Succession of bryophytes and lichens after disturbance

Natural succession of lichen and bryophyte communities has been studied in several other systems. Chronosequence studies in boreal forests have noted a transition in terrestrial species composition from colonist moss species, to lichen species, to feather moss mats as the forest reaches canopy closure (Maikawa and Kershaw 1976; Sulyma and Coxson 2001). A study on a postfire chronosequence in a lodgepole pine forest showed a transition from dominant moss cover of *Polytrichum* spp., to lichen species cover, and then finally to feathermoss mats such as *Pleurozium* spp. (Coxson and Marsh 2001). A similar trend may occur in this ecosystem as shrub and tree cover increases. Over time, *Polytrichum juniperinum* and *Cladonia* species in the second-growth forest may give way to the more shade-tolerant and old-growth forest dependent moss, lichen, and liverwort species. For this transition to occur, microclimate conditions and substrate availability in the second-growth forest must move towards those found in old-growth forests. Given the young age of the second-growth forest in this study, it is not clear if and when these conditions will arise. Recent studies in interior cedar hemlock forests of central British Columbia suggest that arboreal lichen assemblages do not recover, even after stands are more mature (Campbell and Fredeen 2004) and appear to require old-growth microclimatic and canopy structure conditions (Radies and Coxson 2004). As well, propagules must be available for a species to move into a disturbed area. Increasingly, concerns have been raised in the literature as to the inability of many moss, lichen, and liverwort species to disperse over long distances, as is the case for some old-growth associated lichen species (Dettki et al. 2000; Sillett et al. 2000). With logging continuing across the landscape, the proximity of remaining old-growth forests, and indeed the uncertain future of all old-growth forests, could create dispersal limitations into logged areas. Conservation of small areas of old-growth forest may aid in protecting propagule sources for recolonization of adjacent areas (Dettki et al. 2000; Newmaster and Bell 2002; Fenton and Frego 2005); however, bryophyte diversity may not be conserved in overly small patches (<1 ha) because of edge effects on bryophytes extending into the patch (Baldwin and Bradfield 2005).

Even with a propagule source, the length of time required to accomplish the transition from second-growth to old-growth nonvascular floristics is unknown. Will shorter return intervals for harvesting be long enough to allow for the regeneration of the lichen and bryophyte community before the subsequent harvest events? Climate change in northern regions may even preclude regeneration of many species when combined with the multiple effects of forest harvesting disturbance. Retaining a mosaic of forest ages across the landscape may be the only way to ensure that all species have suitable habitat. Schofield (1988) has noted the importance of maintaining old-growth forest as a bench mark against which to compare the diversity and abundance of bryophytes in successional forests. Additional study of the relationships between soil substrate and forest age and the diversity of the terrestrial lichen and bryophyte community is needed. Until the community dynamics and habitat requirements are better understood, forest managers should retain as much old-growth subboreal spruce forest on the landscape as possible.

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