

Distribution and diversity of terrestrial mosses, liverworts and lichens along
productivity gradients of a southern boreal forest

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Abstract

Terrestrial cryptogams (mosses, liverworts and lichens) provide a useful suite of species for monitoring forests, especially when species distributions and diversity attributes are well defined from benchmark sites. To facilitate this, we surveyed contrasting plant associations of an upland boreal forest (in British Columbia, Canada) to explore the association of soil productivity with cryptogam distribution and diversity. Total terrestrial cryptogam richness of the study sites (19 plots of 0.15 ha each) was 148 taxa, with 47 mosses, 23 liverworts, and 78 lichens. Soil productivity was strongly related to the distribution of cryptogams by guild (i.e. lichen species richness declined with productivity, while moss and liverwort richness increased) and substrate (i.e. species richness on forest floor and cobbles declined with productivity as species richness increased on coarse woody debris). Generalists comprised only 15% of the cryptogam community by species, and mesotrophic sites lacked some of the species adapted to the dry-poor or moist-rich ends of the productivity spectrum. Consequently, plot diversity was lowest on mesic-Huckleberry sites, while rich-Oak fern replicates had the highest cumulative diversity. Patterns in cryptogam species distribution reflect soil productivity through corresponding gradients in understory humidity, soil moisture, light and microhabitat availability (exposed cobbles, large coarse woody debris), which emphasizes the need to consider inherent site conditions in ecosystem monitoring.

Keywords: cryptogam, coarse woody debris, species richness, indicator species, biogeoclimatic ecosystem classification

Introduction

The forest cryptogam community (mosses, liverworts and lichens) provides a potentially useful benchmark suite of species to gauge anthropogenic effects on forest biodiversity and ecosystem integrity (Frego, 2007). For example, many cryptogam species are sensitive to the changes in environmental conditions and habitat loss from timber harvesting, and patterns in species distribution can provide insights into the maintenance or re-establishment of climax forest conditions (e.g. Fenton and Frego, 2005; Nelson and Halpern, 2005; Hylander et al., 2005). There are also clear differences in cryptogam communities across unaltered landscapes, presumably due to variations in site factors such as humidity, edaphic characteristics and substrate availability (Robinson et al., 1989; Carleton, 1990; Pharo and Beattie, 1997), which greatly contribute to beta-level species diversity. Given this complexity, Frego (2007) emphasized the need for better information from reference undisturbed forests to improve our knowledge of species-specific ecological tolerances and desired endpoints of forest integrity.

Cryptogam surveys are often directed over very large areas encompassing climatic zones or biomes to highlight the differences in primary community assemblages along forest landscapes (La Roi and Stringer, 1976; Schofield, 1988; Belland, 2005). At a much finer scale, a close relationship between cryptogam communities and site properties has been reported through correlations of diversity with variables such as soil texture or vascular plant cover (Pharo et al., 1999; Saetersdal et al., 2003; Vanderpoorten and Engels, 2003). Patterns in cryptogam guild distribution generally follow edaphic gradients as well, with moss and liverwort diversity increasing with soil moisture availability as lichen diversity decreases (Pharo and Beattie, 1997). Diversity indices and

the abundance of key species could therefore change abruptly in complex landscapes, and inherent site differences only metres apart could potentially obscure the interpretation of forest management effects via these indicators.

Accounting for the association of cryptogam indicator species with inherent site features within landscapes would therefore be an essential component of effective and accurate forest stand monitoring. In British Columbia, the provincial biogeoclimatic ecosystem classification describes a logical progression of benchmark sites based on plant associations that reflect gradients in soil moisture and nutrient regimes (Pojar et al., 1987). In most of the provincial forest classification, however, the majority of lichen, moss and liverwort species were infrequent and of low abundance, and were not comprehensively evaluated due to their relatively minor biomass and difficulties in identification. We undertook complete cryptogam surveys of well-recognized plant associations encompassing the widest range in productivity of a southern old-growth boreal landscape to explore the association of soil productivity with terrestrial moss, liverwort, and lichen distributions. Plot size was limited to 0.15 ha to ensure soil moisture/nutrient regimes and related site features were entirely homogenous and consistent among replicates, and sites were chosen within a localized landscape to minimize macroclimate effects on cryptogam distribution.

Our hypothesis in this study was that cryptogam species distribution would strongly reflect site, while diversity overall would not differ due to the replacement of lichens by bryophytes as sites progress from dry-poor to moist-rich (i.e. Robinson et al., 1989; Pharo and Beattie, 1997). We also noted how substrate types (forest floor, coarse woody debris [CWD], surface cobbles, and tip-up mounds) differed between plant

associations and explored whether this habitat distribution could be a factor in species composition and diversity. The results of this study will provide insight into the sensitivity of cryptogam communities to site features that may need to be recognized in forest stand monitoring, as well as provide detailed information on old-growth terrestrial cryptogam communities that will facilitate the definition of desired endpoints for ecosystem stewardship.

Materials and Methods

Site descriptions

The southern boreal forest of British Columbia is designated as the Sub-Boreal Spruce Zone (SBS), and is located in the montane landscape of the central interior of the province, within the closed forest portion of the Cordilleran boreal region (Pojar, 1996). The SBS has a continental climate characterized by severe, snowy winters and short, warm, moist summers. Upland coniferous forests are comprised of lodgepole pine (Pl) (*Pinus contorta* Dougl. ex Loud), hybrid white spruce (Sx) (*Picea glauca* x *Picea engelmannii* [Moench] Voss) and subalpine fir (Bl) (*Abies lasiocarpa* [Hook.] Nutt.). Soils are free of permafrost and are predominantly deep blankets of glacial tills with coarse fragments of mixed lithology.

The study sites were located in the moist cold (mc) subzone of the SBS near Smithers, British Columbia, Canada (54°49'N 127°10'W; elevation 522 m). Smithers has a mean annual air temperature of 3.9°C and mean annual precipitation of 513 mm (354 mm as rainfall) (1960-1990; Environment Canada). Four site series (represented by climax plant communities corresponding to soil moisture and nutrient regime; Pojar et al., 1987) were sampled to provide a wide range in upland edaphic conditions: (02) xeric and

poor P1 – Cladonia; (01) mesic and medium Sx – Huckleberry; (06) subhygric and rich Sx – Oak fern; and (09) subhygric and very rich Sx – Devil’s club (Banner et al., 1993). Site series are hereafter referred to by their nutrient regime and plant association name.

Five transects, each with one replicate of each site series, were located along a 25 km portion of the McDonnell Forest Service Road (54°40’ to 47’N and 127°16’ to 36’W) at approximately 900 m elevation. The study was limited to 19 plots because we were unable to find a suitable Sx – Devil’s club plot on the fourth transect. Each plot was 50 m x 30 m (0.15 ha) in size. Plots were separated by a minimum 50 m within each transect. All plots had climax coniferous forests, and were mostly multicohort due to gap-phase disturbances caused by bark beetles, root pathogens and wind throw, as well as a small amount of partial harvesting (ranging from 0-10% of the basal area) that occurred throughout the valley in the 1950s.

The old-growth forests (~ 180 years) on our sites had ceased height growth (i.e. reached an asymptote) decades earlier, and we used the asymptotic or ‘maximum obtainable’ stand height as a measure of site potential (Ryan and Yoder, 1997). Additional forest stand attributes and soil properties of the study plots were published previously (Kranabetter et al., 2007) as summarized in Table 1. Briefly, the in situ buried bag soil incubation was initiated June 5-9, 2006. Forest floor F and H horizons were sampled as intact cores, avoiding pure decayed wood, and mineral soils were sampled down to 20 cm with an auger. Mineral soils were sealed in a polyethylene bag within the sample hole, and forest floors were placed on top of this sample in a separate bag. This was repeated at 5 random microsites per plot. After 5 weeks, the bags were retrieved and gently run through a 5 mm sieve, followed by an analysis of dissolved organic N and

inorganic N. Gravimetric soil moisture content (w/w) of the forest floor and mineral soil (0-20 cm depth) was measured every 3 weeks from mid May to early September. Forest floors (F, H horizons and buried wood) were sampled with a 15 cm diameter template to the mineral soil interface, and mineral soils were sampled to a 20 cm depth using a stony soil auger (4 cm in diameter). Three random microsites were sampled and bulked together per plot, and different microsites were chosen on each sample day. Available light in the understory was assessed at 5 microsites within each plot using hemispherical canopy photographs (set at a 1 m height) using a Nikon Coolpix 5000 camera with a Nikon FC-E8 fisheye converter lens. Any nearby understory trees or shrubs were tipped back, away from the lens, to allow for a measure of light levels reaching the ground surface. The growing season light availability (direct + diffuse light sources from May 15 to September 15), was expressed as a percentage of full sun and was computed from each photograph using the Gap Light Analyser (GLA) 2.0 software, following Frazer et al. (2000).

Forest substrate measures

Coarse woody debris (CWD) was defined as dead woody material in various stages of decomposition, not incorporated into the soil, and larger than 7.5 cm in diameter. CWD did not include stumps, snags, or partially uprooted live trees. Coarse woody debris was sampled using the line intercept method (Van Wagner, 1982). Two 24 m transects were initiated near the plot centre; the first line followed a random compass bearing and the second at the same bearing plus 90 degrees (British Columbia Ministry of Forests, 1998). Diameter was measured perpendicular to the bole at the intersection of the transect and the CWD. Species and the decay class were also noted for each piece.

The latter were defined as follows: decay class 1 – intact wood, with bark, elevated on support points; 2 – intact wood, bark removed, sagging slightly; 3 – hard wood but decaying, sagging near ground, some invading roots in sapwood; 4 – decayed with blocky wood texture, resting on ground, roots in heartwood; and 5 – well decayed with friable wood texture, partly sunken into ground; roots in heartwood). Tip-up mounds are formed by fallen trees that leave a small pit and exposed root mat with subsoil (Beatty and Stone, 1986). The number of tip-up mounds was determined through a visual survey of each plot.

Cryptogam community assessment

Each plot was first examined for the most abundant ($> 1\%$ ground cover) terrestrial cryptogams, with an estimate of percent cover, as is routinely undertaken in ecosystem classification (British Columbia Ministry of Forests, 1998). Next, a timed one-hour search was undertaken to record the less abundant species, which included collecting specimens to provide voucher material and to identify unknown species at a later date. In addition to the forest floor habitat (humus layer and leaf/needle litter), we focused our search on coarse woody debris, tip-up mounds, and surface cobbles (rocks 7.5 to 25 cm in diameter). Epiphytic cryptogams on live trees, shrubs or standing snags were not included, nor were saxicolous (rock-dwelling) species on bedrock or large boulders (a large rock surface was present only a very small portion of one plot). To document the limitations in species distribution by substrate types, we counted occurrences on forest floor habitat first, coarse woody debris second, surface cobbles third and tip-up mounds last. No attempt was made to estimate percent cover for each species recorded in the timed search.

Bryophytes were identified using Lawton (1971), Schofield (2002), Paton (1999), Damsholt (2002), and the Flora of North America (2007). Lichen specimens were identified using Goward et al. (1994), Goward (1999), and Brodo et al. (2001). Nomenclature follows Anderson et al. (1990) for the mosses, Stotler and Crandall-Stotler (1977) for the liverworts, and Esslinger and Egan (1995) for the lichens. Vouchers of each species were deposited in the British Columbia Forest Service Herbarium in Smithers, B.C.

Statistical analyses

Analysis of cryptogam communities was based on species presence, rather than by relative abundance, as it was not possible to accurately measure percent cover for each species across the entire plot area. We described species richness in two ways, following Newmaster et al. (2003): species richness within plot (alpha diversity, α) and total species within plant association (gamma diversity, γ). Jackknife 1 estimates of total species richness by plant association and by all sites combined were calculated with EstimateS (Version 7.5) software (Colwell, 2005).

The study was organized in a randomized incomplete block design, with transects treated as blocks. Alpha diversity for all cryptogam species and by the three guilds (moss, liverwort and lichen) were tested among plant associations using Proc Mixed in SAS (SAS Inc. 2004) with block and block interactions set as random factors. Residuals from the analyses were examined and found to meet the assumptions of equal variance. Significant differences between least square means of each plant association were tested using pairwise *t* tests at a significance level of 0.05. The general linear model (GLM)

procedure in SAS using Type 1 Sums of Squares was used to test linear and curvilinear regressions between plot means of dependent and independent variables ($n = 19$).

A comparison of cryptogam communities among plots was undertaken by Bray - Curtis ordination with PC-ORD 5.0 software using the Sorenson (Bray-Curtis) distance measure (McCune and Grace, 2002). Separation of cryptogam communities by plant association was tested in pairwise comparisons using the multi-response permutation procedure with the Sorenson (Bray-Curtis) distance measure (McCune and Grace, 2002). Indicator species analysis was undertaken with the Monte Carlo technique of Dufrêne and Legendre, using 5000 randomizations and a significance p value of < 0.10 (McCune and Grace, 2002).

Results

Stand and soil characteristics

Increasing soil moisture and nitrogen availability across plant associations were associated with both taller trees and greater stand volumes (basal area) (Table 1). These forest stand attributes led to corresponding reductions in light availability, from 29% to 17% of full sun in the forest understory, on average (Table 1). Both the amount and size of CWD increased with stand productivity as well (Table 1), ranging from a low of 12 m³ ha⁻¹ and 8 cm diameter on a poor-Cladonia site to a maximum of approximately 400 m³ ha⁻¹ and 50 cm diameter on a very rich – Devil’s club site. Decay class 5 comprised 40% of the CWD volume across all sites, followed by approximately 19% each for classes 2, 3 and 4, while fresh CWD (decay class 1) contributed 3% of the total. The number of tip-up mounds ranged from 2 to 16 per plot, and were slightly more common on medium - Huckleberry sites (Table 1).

Terrestrial cryptogam community

Total terrestrial cryptogam richness of the study sites (2.85 ha in sum) was 148 taxa (47 mosses, 23 liverworts, and 78 lichens), of which 30% were uncommon (found on only 1 plot) (Appendix 1). Cryptogam community composition (all species presence/absence) aligned consistently with plant associations, with significant separation among poor – *Cladonia*, medium – Huckleberry and rich – Oak fern sites (Fig. 1). A small number of species dominated in abundance, with only 11 species contributing 2% or greater ground surface cover on at least one site (Table 2). Forest floor substrate hosted slightly less than half (43%) of the cryptogam species, with the remainder of the community limited in distribution to either coarse woody debris (35%), surface cobbles (14%) or tip-up mounds (8%).

Trends in species richness between cryptogam guilds corresponded with site productivity, as characterized in these plots by asymptotic stand height. Lichen richness declined with greater stand height, while moss and liverwort richness increased (Fig. 2a). We noted that liverwort richness tended to plateau in correlations with stand height, but the trend was not strong enough to warrant a nonlinear curve (Fig. 2a). The distribution of cryptogam species also varied by substrate across productivity gradients: cryptogam species richness on the undisturbed ground surface (forest floor and cobbles) declined with stand height, while species richness increased with productivity on the more isolated habitat provided by coarse woody debris (Fig. 2b). Tip-up mounds provided an additional 5 species per plot, on average, which did not change significantly among plant associations ($p = 0.745$).

With contrasting responses between lichens and bryophytes (mosses and liverworts), as well as by substrates, the α diversity for all terrestrial cryptogams was quite consistent at 39 taxa per plot (0.15 ha) among poor, rich and very rich sites, with a significant reduction in α diversity detected only for medium-richness sites (Table 3). Overall, however, we did not detect a linear or curvilinear relationship between cryptogam α diversity and asymptotic stand height (Fig. 3a). In contrast, vascular plant α diversity (unpublished plot data; W. MacKenzie) was positively correlated to stand height, which paralleled the pattern in bryophyte richness ($r^2 = 0.74$), but not cryptogam richness overall ($p = 0.620$).

Total species richness by plant association (γ diversity) was approximately twice that of α diversity due to the high number of uncommon species (Table 3), demonstrated by the cumulative species curves (Fig. 4). Unlike α diversity, we found a peak in γ diversity on rich - Oak fern sites (Table 3). Jackknife 1 estimates of total species richness also indicated the greatest diversity would be found on rich - Oak fern sites, followed by poor-Cladonia and very rich-Devil's club sites, with the lowest diversity on medium-Huckleberry sites (Table 3). The species richness of this landscape, based on all 19 plots, was estimated by jackknife 1 analysis to be 191 species.

A total of 23 cryptogam species were found at least once in each of the four plant associations (7 mosses, 5 liverworts, 11 lichens) (Appendix 1). Some of the more abundant generalist species of these southern boreal stands include *Dicranum fuscescens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Ptilidium pulcherrimum*, *Cladonia coniocraea*, *Cladonia ochrochlora*, *Parmeliopsis ambigua*, *Parmeliopsis hyperopta*, and *Peltigera aphthosa*. A total of 30 species (9 mosses, 2 liverworts, 19 lichens) were

consistent and frequent enough in distribution to significantly characterize plant associations (Appendix 1). Species more abundant on dry, poor forests include *Dicranum polysetum*, *Cladina mitis*, *Cladina rangiferina*, *Cladonia uncialis*, *Nephroma arctica* and *Stereocaulon tomentosum*, while rich to very rich sites were characterized by the abundance of *Mnium spinulosum*, *Plagiomnium insigne*, *Rhizomnium magnifolium* and *Rhizomnium nudum*. Two liverwort species (*Barbilophozia hatcheri*, *Eremontus myriocarpus*) were indicative but not exclusive to mesic sites.

Discussion

The detailed survey of cryptogam species from these plots in northwest British Columbia revealed communities comparable to similar surveys of other northern coniferous forests. Species richness of terrestrial cryptogams averaged approximately 38 species per plot and 70-80 species for a study area in central British Columbia (Botting and Fredeen, 2006), while in montane forests Pharo and Vitt (2000) reported 36 species on average for stands and 90 species overall for bryophytes and lichens. Our total of 148 taxa was somewhat higher than other studies, possibly reflecting the wide gradient in sites and our inclusion of the saxicolous crust lichens that are often overlooked. The relatively high number of infrequent cryptogam species within a stand dominated in cover by a few common species (especially feathermosses) is also quite typical for many coniferous ecosystems (La Roi and Stringer, 1976).

This small-scale, detailed study of cryptogam communities presents a general model of guild (moss, liverwort and lichen) distribution and species richness that we expect to be consistent with many boreal and montane landscapes. Terrestrial cryptogam community composition was well aligned with plant associations, and this relationship

emphasized the linkage between species distribution and ecosystem attributes related to soil productivity. Key environmental variables for cryptogam distribution, such as light availability and air humidity (Robinson et al., 1989; Mills and MacDonald, 2005) were strongly interrelated with soil productivity and corresponding stand attributes, and within these old-growth boreal landscapes we found asymptotic stand height to be the simplest integrator of these covarying influences. For the purposes of a monitoring program, it is important to recognize that a wide range in site productivity can be found within short distances in these complex landscapes, and that a mosaic of plant associations such as the ones surveyed here can be found within a typical forest cutblock.

In addition to environmental variables, there were important substrate characteristics, especially the volume and diameter of CWD (Rambo and Muir, 1998; Mills and MacDonald, 2004), linked to soil and stand productivity. Without the additional surface area provided by CWD, for example, the cryptogam diversity of rich and very rich sites would have been largely reduced to only those leafy mosses occupying the forest floor. Some of the reduction in cryptogam species on mesic sites could perhaps be attributed to microsite limitations via smaller diameter CWD inherent to moderately productive forests (Kruys et al., 1999). Surface cobbles were also an important substrate and could be found on all site types, but the reduced plant vigour on poor sites provided an opportunity for saxicolous crustose lichens to establish, in contrast to richer sites where cobbles were overgrown by feathermosses.

The positive correlation between vascular plant and bryophyte (moss and liverwort) richness with site productivity was consistent with previous studies in boreal forests (Jonsson and Jonsell, 1999; Saetersdal et al., 2003), and lichens supplemented

total cryptogam richness to a large extent on poor, dry sites as we had hypothesized. Nevertheless, some reduction in combined species richness on mesic sites (30% compared to rich sites, both in α and γ diversity) was evident for the three guilds. Carleton (1990) concluded that cryptogam species were best adapted to contrasting conditions at either ends of fertility gradients, and we also noted only 15% of the cryptogam community in this landscape could be considered generalists (i.e. widely tolerant to site type). Mesotrophic sites were generally characterized by the lack of cryptogam species adapted to the dry-poor and moist-rich ends of the fertility spectrum (saxicolous/terricolous lichens and epixylic bryophytes, respectively), and it was these specialist species that had the most utility as indicators of undisturbed forest site conditions (Appendix 1).

The results of this study also emphasize the value of contrasting ecosystems encompassing wide edaphic gradients for the conservation of cryptogam diversity. Protected areas that included poor and rich plant associations with mesic sites in this boreal landscape would more than double terrestrial cryptogam richness (from 64 species on mesic sites vs. 139 species combined). In addition, intensive harvesting and short rotations would produce forest stands with low volumes of CWD and few tip-up mounds, which would be expected to result in reduced cryptogam diversity (Jonsson and Esseen, 1990; Crites and Dale, 1998; Rambo, 2001), especially in lush, productive sites. Every site type contained some uncommon species, as has often been reported (e.g. Vitt et al., 2003), and we suspect their distribution reflects the rich mosaic of microsites in old-growth forests (Cleavitt, 2005; Gignac and Dale, 2005), along with some influence of stochastic processes involving dispersal and establishment.

More detailed study of mechanisms responsible for species distribution, such as drought tolerance or competitive interactions (Frego and Carleton; 1998; Sulyma and Coxson; 2001), would strengthen these findings, along with further surveys by substrate type to test hypotheses related to habitat specificity. For example, most of the CWD in these old-growth stands was well decomposed (decay class 4 and 5) and hosted the majority of cryptogam species; less decayed wood may host fewer species, but exploring this substrate limitation further would require a separate inventory of cryptogams from each piece of CWD. Another observation worth further investigation is whether cryptogam species shift substrates with environmental conditions, and could be, for example, exclusively terrestrial or epixylic depending upon site. We noted a number of species occupying more than one substrate type, but as yet have not definitively established where habitat changes in response to site conditions.

In conclusion, terrestrial cryptogam communities of old-growth coniferous forests were linked to soil fertility, as characterized by vascular plant associations or asymptotic stand height, presumably due to the combined resource availability of light, moisture, nutrients and substrate types. The relationship to soil fertility was most notable in the distribution of species within guilds (lichens versus bryophytes) and by substrate types (forest floor and cobble habitat versus CWD). Soil fertility effects associated with α and γ diversity indices were more subtle, and were primarily indicated by reductions in species richness on mesic sites. Only a small number of generalist cryptogam species were found across these site types, and the majority of species were more limited in distribution, although often infrequent and of low abundance as well. As an indicator group for ecosystem assessment, terrestrial cryptogam communities should be referenced

to plant associations (or a similar characterization of site) with benchmarks of diversity indices and species distributions established from climax forests.

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Table 1. Forest stand and soil characteristics among four plant associations across a productivity gradient (mean, with SE in brackets).

Plant association*	Asymptotic stand height (m)	Forest basal area (m ² ha ⁻¹)	Soil N availability (kg ha ⁻¹)	Soil moisture (kg m ⁻²)	Available sunlight (%)	CWD volume (m ³ ha ⁻¹)	CWD diameter (cm)	Tip-ups mounds (# per ha)
P – Cladonia	21a (1.4)†	36a (2)	17.6a (2.7)	13.4a (1.2)	29a (0.8)	22a (4)	13.2a (1.3)	4.2a (0.8)
M – Huckleberry	28b (0.5)	58b (5)	30.2b (1.9)	18.7a (1.5)	20b (0.6)	165b (51)	15.4a (1.0)	10.2b (1.9)
R – Oak fern	32c (0.4)	70b (6)	40.8c (2.0)	29.3b (2.1)	18bc (0.6)	232b (41)	20.7b (1.7)	7.4ab (0.7)
VR – Devil’s club	36d (0.7)	104c (4)	46.7c (4.3)	27.6b (2.0)	17c (0.6)	274b (82)	23.3b (1.7)	6.0a (0.7)

* soil nutrient regimes ‘P’ poor, ‘M’ medium, ‘R’ rich, ‘VR’ very rich

†Means within columns separated by letters are significantly different ($p < 0.05$)

Table 2. Abundance of dominant terricolous cryptogam species across plant associations.

Values are % groundcover with % frequency in brackets.

Cryptogam species	Poor – Cladonia (n = 5)	Medium – Huckleberry (n = 5)	Rich – Oak fern (n = 5)	Very Rich – Devil’s club (n = 4)
Mosses				
<i>Pleurozium schreberi</i>	79% (100)	43% (100)	35% (100)	20% (100)
<i>Ptilium crista-castrensis</i>	0.2% (20)	32% (100)	30% (100)	12% (100)
<i>Hylocomium splendens</i>	0	7% (80)	12% (100)	0.5% (25)
<i>Dicranum fuscescens</i>	1% (100)	5% (80)	1% (20)	3% (25)
<i>Plagiomnium insigne</i>	0	0	3% (40)	7% (100)
<i>Rhizomnium nudum</i>	0	0	0	3% (50)
<i>Rhytidiadelphus triquetrus</i>	0	0.1% (20)	1% (40)	2% (50)
<i>Timmia austriaca</i>	0	0	0.5% (40)	3% (25)
Liverworts				
<i>Barbilophozia lycopodioides</i>	0.1% (20)	0.5% (60)	0.1% (40)	0.5% (25)
Lichens				
<i>Cladina mitis</i>	5% (100)	0	0	0
<i>Cladina rangiferina</i>	5% (100)	0	0	0
<i>Cladonia ecmocyna</i>	2% (80)	0	0	0
<i>Peltigera aphthosa</i>	0.5% (80)	0.1% (40)	0.1% (20)	0
<i>Nephroma arctica</i>	0.5% (60)	0	0	0

Table 3. Species richness of moss, liverwort and lichen guilds by plant association (mean number of species per 0.15 ha plot, with SE in brackets)

Plant association*	Moss species	Liverwort species	Lichen species	α diversity	γ diversity	Jackknife estimate
P – Cladonia	9a (0.7)†	3a (0.4)	28a (0.6)	40a (0.9)	78	94 (3.2)
M – Huckleberry	10a (0.9)	7b (0.7)	12b (1.9)	29b (2.1)	64	86 (5.7)
R – Oak fern	15b (0.6)	10b (0.6)	15b (2.1)	40a (2.7)	89	122 (5.9)
VR – Devil’s club	16b (0.8)	8b (1.1)	12b (1.1)	37a (1.2)	72	99 (3.9)

Note: γ diversity for very rich sites was determined from 4 plots rather than 5.

* soil nutrient regimes ‘P’ poor, ‘M’ medium, ‘R’ rich, ‘VR’ very rich

†Means within columns separated by letters are significantly different ($p < 0.05$)

Fig. 1. Bray-Curtis ordination of cryptogam communities (all species presence/absence). Axis 1 = 34% and axis 2 = 13% of the total variance. Selected pairwise p values: poor vs. medium = 0.002; medium vs. rich = 0.002; rich vs. very rich = 0.666.

Fig. 2. Terrestrial cryptogam species richness per plot (0.15 ha) as a function of asymptotic stand height for a) moss, liverwort and lichen guilds, and b) substrate ('ground' = forest floor and surface cobbles).

Moss species richness = $-1.3 + 0.48(\text{Ht})$; $r^2 = 0.61$

Liverwort species richness = $-3.6 + 0.37(\text{Ht})$; $r^2 = 0.50$

Lichen species richness = $45.0 - 0.97(\text{Ht})$; $r^2 = 0.52$

Forest floor and cobble species richness = $50.6 - 1.21(\text{Ht})$; $r^2 = 0.51$

Coarse woody debris species richness = $-14.0 + 1.02(\text{Ht})$; $r^2 = 0.67$

Fig. 3. Alpha (α) diversity (0.15 ha) for terrestrial cryptogams by plant association across stand height.

Fig. 4. Cumulative species richness (γ diversity) across replicates (0.75 ha, except very rich sites at 0.60 ha) for the four plant associations.

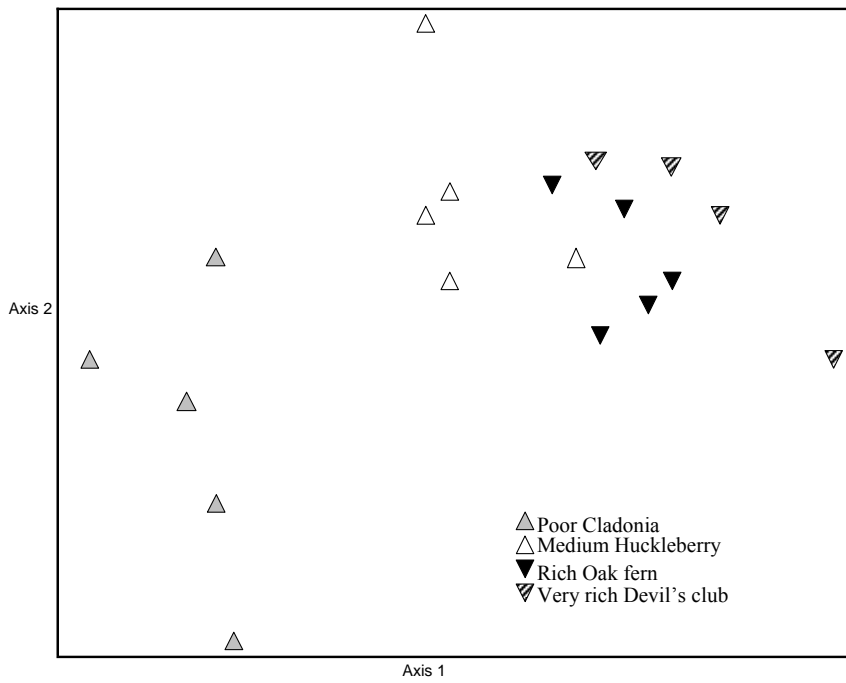


Fig. 1

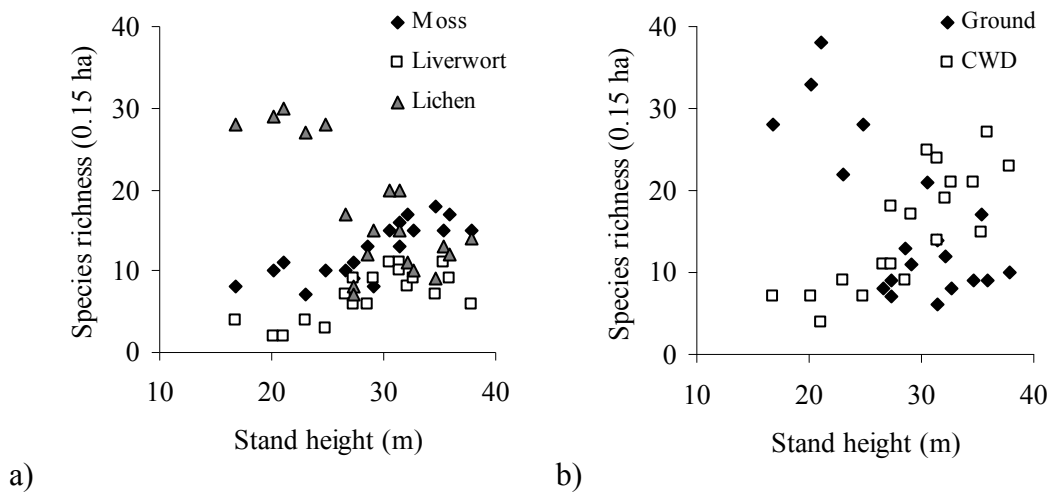


Fig. 2

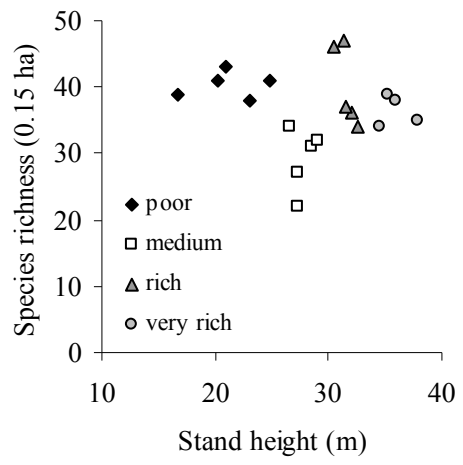


Fig. 3

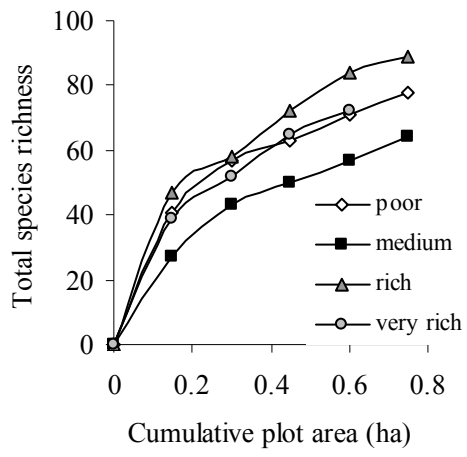


Fig. 4

Appendix 1. Terrestrial cryptogam species distribution (% frequency) across the four plant associations. Species in bold have significant indicator value for characterizing plant associations ($p < 0.10$ with Monte Carlo analysis). Habitat distribution summarized for all plots; F = forest floor; R = rock; W = coarse woody debris; T = tip up mound.

Cryptogam species	Poor – Cladonia (n = 5)	Medium – Huck.berry (n = 5)	Rich – Oak fern (n = 5)	V. Rich – Devil’s cl. (n = 4)	Habitat (FRWT)
Mosses					
<i>Amblystegium serpens</i>	-	-	20	25	W,T
<i>Andreaea rupestris</i>	80	-	-	-	R
<i>Brachythecium albicans</i>	-	20	80	75	F,W,T
<i>Brachythecium asperrimum</i>	-	20	20	25	F,T
<i>Bryum capillare</i>	-	-	20	-	T
<i>Buxbaumia aphylla</i>	-	20	-	-	T
<i>Buxbaumia piperi</i>	-	-	20	-	W
<i>Buxbaumia viridis</i>	-	-	20	-	T
<i>Campylium chrysophyllum</i>	-	-	20	-	T
<i>Ceratodon purpureus</i>	60	20	-	25	F,T
<i>Dicranella hetermalla</i>	20	20	-	-	T
<i>Dicranoweisia crispula</i>	40	-	-	-	R
<i>Dicranum fuscescens</i>	100	100	100	100	F,W
<i>Dicranum polysetum</i>	80	60	20	-	F
<i>Dicranum scoparium</i>	40	40	60	50	F,R,W,T
<i>Dicranum tauricum</i>	-	20	-	50	W
<i>Distichium inclinatum</i>	-	-	20	-	T
<i>Eurhynchium pulchellum</i>	-	-	40	25	W,T
<i>Hygrohypnum dilitata</i>	-	-	-	25	F
<i>Hylocomium splendens</i>	40	80	100	25	F
<i>Hypnum circinale</i>	-	-	40	50	W
<i>Isopterygium pulchellum</i>	-	-	20	25	W
<i>Mnium spinulosum</i>	-	20	80	100	F,W,T
<i>Orthotrichum striatum</i>	-	-	-	25	T

<i>Plagiomnium cuspidatum</i>	-	-	-	25	F
<i>Plagiomnium insigne</i>	-	20	60	100	F,W,T
<i>Plagiothecium denticulatum</i>	-	60	60	100	F,W,T
<i>Pleurozium schreberi</i>	100	100	100	100	F
<i>Pohlia nutans</i>	80	100	100	75	F,W,T,R
<i>Polytrichum alpinum</i>	-	-	20	50	F
<i>Polytrichum commune</i>	-	20	-	-	F
<i>Polytrichum juniperinum</i>	100	40	40	25	F,T
<i>Polytrichum piliferum</i>	20	-	-	-	F
<i>Pseudoleskeella nervosa</i>	-	-	20	-	R
<i>Ptilium crista-castrensis</i>	40	100	100	100	F
<i>Racomitrium heterostichum</i>	60	-	-	-	R
<i>Rhizomnium magnifolium</i>	-	-	80	25	F,T
<i>Rhizomnium nudum</i>	-	-	20	100	F,W
<i>Rhytidiadelphus loreus</i>	-	-	20	-	F
<i>Rhytidiadelphus triquetrus</i>	-	20	80	75	F,W
<i>Rhytidiopsis robusta</i>	20	40	40	-	F
<i>Sanionia uncinata</i>	-	20	40	75	W
<i>Scouleria aquatica</i>	20	20	-	25	F
<i>Tayloria serrata</i>	20	20	-	25	F
<i>Tetraphis pellucida</i>	-	-	20	50	W
<i>Tetraplodon mnioides</i>	20	-	-	-	F
<i>Timmia austriaca</i>	-	20	20	50	F,T
Liverworts					
<i>Anastrophyllum hellerianum</i>	-	-	60	50	W
<i>Barbilophozia hatcheri</i>	80	100	60	25	F,R,W,T
<i>Barbilophozia lycopodioides</i>	20	80	80	50	F
<i>Blepharostoma trichophyllum</i>	-	20	100	100	W
<i>Calepogeia mulleriana</i>	-	-	20	-	T
<i>Calepogeia suecica</i>	-	-	20	-	W
<i>Cephalozia lunulifolia</i>	-	80	60	50	W
<i>Eremontus myriocarpus</i>	-	60	20	-	W
<i>Jamesoniella autumnalis</i>	-	-	40	50	W
<i>Leicolea alpestris</i>	-	-	-	25	W

<i>Lepidozia reptans</i>	-	-	60	25	F,W
<i>Lophozia capitata</i>	-	-	20	25	T
<i>Lophozia guttulata</i>	-	100	100	100	W,T
<i>Lophozia incisa</i>	-	40	60	75	W
<i>Lophozia longidens</i>	20	80	80	75	W,T
<i>Lophozia obtusa</i>	-	-	20	-	W
<i>Marchantia polymorpha</i>	-	-	20	-	T
<i>Plagiochila porelloides</i>	-	-	20	25	F,W
<i>Pleuroclada albescens</i>	20	-	-	-	T
<i>Ptilidium californicum</i>	60	40	20	25	R,W,T
<i>Ptilidium pulcherrimum</i>	80	100	100	100	F,W,T
<i>Scapania bolanderi</i>	-	40	-	25	W
<i>Unknown liverwort</i>	-	-	20	-	W

Lichens

<i>Amandinea punctata</i>	20	-	-	-	F
<i>Baeomyces placophyllus</i>	20	-	-	-	T
<i>Baeomyces rufus</i>	40	40	20	-	F,T
<i>Bellemerea alpina</i>	20	-	-	-	R
<i>Bellemerea cinereorufescens</i>	80	-	-	-	R
<i>Bellemerea subsorediza</i>	60	-	-	-	R
<i>Biatorella sp.</i>	-	20	-	-	R
<i>Catinaria atropurpurea</i>	-	-	20	-	W
<i>Cetraria ericetorum</i>	60	-	20	-	F,W
<i>Chaenotheca furfuracea</i>	20	40	80	50	W,T
<i>Cladina mitis</i>	100	-	-	-	F
<i>Cladina rangiferina</i>	100	-	-	-	F
<i>Cladina stellaris</i>	20	-	-	-	F
<i>Cladonia bellidiflora</i>	60	-	-	-	F,T
<i>Cladonia carneola</i>	40	40	20	25	W
<i>Cladonia cenotea</i>	80	-	60	25	F,W,T
<i>Cladonia chlorophaea</i>	40	-	40	25	F,W,R
<i>Cladonia coniocraea</i>	40	60	60	100	W
<i>Cladonia cornuta</i>	80	-	-	-	F
<i>Cladonia deformis</i>	80	60	-	-	F,W

<i>Cladonia ecmocyna</i>	80	-	-	-	F
<i>Cladonia fimbriata</i>	-	-	20	25	W
<i>Cladonia gracilis</i>	60	-	-	-	F
<i>Cladonia multiformis</i>	100	-	40	-	F,W,R
<i>Cladonia norvegica</i>	20	20	40	-	W
<i>Cladonia ochrochlora</i>	40	80	80	75	W,T
<i>Cladonia parasitica</i>	-	-	20	-	W
<i>Cladonia prolifica</i>	20	60	20	-	W,T
<i>Cladonia pyxidata</i>	40	-	-	-	F,T
<i>Cladonia umbricola</i>	-	20	-	-	W
<i>Cladonia uncialis</i>	100	-	-	-	F
<i>Cyphelium inquinans</i>	-	-	40	-	W
<i>Lecanora intricata</i>	40	-	-	-	R
<i>Fuscopannaria praetermissa</i>	-	-	-	25	W
<i>Lecanora polytropia</i>	80	-	-	-	R
<i>Lepraria incana</i>	-	20	40	50	W, T
<i>Lobaria halleri</i>	-	-	-	25	W
<i>Lobaria pulmonaria</i>	-	-	-	25	W
<i>Mycoblastus sanguinarius</i>	-	-	40	25	W
<i>Nephroma arctica</i>	80	20	-	-	F
<i>Nephroma bellum</i>	-	40	20	75	W
<i>Nephroma parile</i>	-	-	40	25	W
<i>Nephroma resupinatum</i>	-	-	20	25	W
<i>Ochrolechia arborea</i>	-	20	-	-	W
<i>Ochrolechia gowardii</i>	20	-	-	-	W
<i>Parmeliopsis ambigua</i>	100	100	100	100	W
<i>Parmeliopsis hyperopta</i>	100	100	100	100	W
<i>Peltigera aphthosa</i>	100	80	100	50	F,W,T
<i>Peltigera bacilliformis</i>	20	-	-	-	W
<i>Peltigera canina</i>	40	20	40	25	F,W,T
<i>Peltigera chionophila</i>	40	20	20	-	F,R
<i>Peltigera didactyla</i>	40	-	-	-	F,T
<i>Peltigera horizontalis</i>	20	20	40	25	F,W,T
<i>Peltigera leucophlebia</i>	40	40	40	25	F,T

<i>Peltigera malacea</i>	60	20	20	-	F,W,T
<i>Peltigera membranacea</i>	-	-	80	75	F,W,T
<i>Peltigera neopolydactyla</i>	20	20	80	100	F,W,T
<i>Peltigera polydactylon</i>	-	20	-	50	W,T
<i>Peltigera praetextata</i>	-	40	40	25	F,W,T
<i>Peltigera venosa</i>	-	-	20	25	F,T
<i>Pertusaria pupillaris</i>	-	40	20	-	W
<i>Placynthiella dasaea</i>	-	-	20	-	F
<i>Placynthiella sp.</i>	-	20	-	-	F
<i>Platismatia glauca</i>	-	-	20	-	W
<i>Porpidia cinereoatra</i>	80	-	-	-	R
<i>Porpidia contraponenda</i>	60	-	-	-	R
<i>Porpidia speirea</i>	40	60	20	-	R
<i>Protothelenella corrosa</i>	20	-	-	-	R
<i>Psoroma hypnorum</i>	-	-	20	-	W
<i>Rhizocarpon geographicum</i>	80	-	-	-	R
<i>Rhizocarpon hochstetteri</i>	80	-	-	-	R
<i>Stereocaulon tomentosum</i>	80	20	-	-	F,R,T
<i>Trapeliopsis granulosa</i>	20	-	-	-	F
<i>Umbilicaria deusta</i>	20	-	-	-	R
<i>Umbilicaria hyperborea</i>	60	-	-	-	R
<i>Vulpicida pinastri</i>	20	-	-	-	W
<i>Xylographa vitiligo</i>	20	20	-	-	W
