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Factors Influencing Bryophyte Assemblage at Different Scales in the Western Canadian Boreal Forest

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Abstract. *This study examined bryophyte community composition in relation to microsite and microenvironmental variation at different scales in three conifer-dominated stands in the boreal forest of Alberta, Canada. We documented bryophyte assemblage on specific microsite types (physiognomic forms providing substrates for moss colonization: logs, stumps, tree bases, undisturbed patches of forest floor, disturbed patches of forest floor), and at coarser scales: mesosites (625 m^2 plots within stands), and stands (10 ha). Patterns of variation in bryophyte composition arising from the microsite sampling were clearly related to microsite type and, for woody substrates, to microsite quality (decay class; hardwood vs. softwood). Microenvironment (moisture, pH, temperature, light) also had some influence on bryophyte composition of woody microsite types. Forest floor moisture, pH, and light were related to bryophyte composition of undisturbed patches of forest floor while forest floor moisture and temperature were significant correlates for disturbed forest floor. At the coarser-scale, surface moisture and forest floor moisture were related to bryophyte assemblage of mesosites; this was partially reflective of differences among stands. We conclude that bryophyte species composition in these forests is related to a hierarchy of factors including fine scale variation in the type and quality of available microsites along with microenvironmental variation at different scales. Management efforts to preserve bryophyte biodiversity will need to incorporate this complexity.*

Keywords. Alberta, boreal forest, bryophytes, dead wood, decay class, liverwort, microenvironment, microsite, moss, species assemblage.

Bryophytes are both abundant and ecologically important in the boreal forests of western Canada yet our understanding of bryophyte communities in these forests is limited. Habitat has generally been thought to be an important determinant of bryophyte species occurrence (Vitt et al. 1995; Watson 1980) and studies of bryophytes in the boreal forest have made distinctions between communities on the basis of habitat at both coarse and fine-grained spatial scales (Berglund & Jonsson 2001; Jonsson & Esseen 1990; Söderström 1988, 1993; Vitt & Belland 1995). ''Habitat'' for bryophytes typically has included consideration of substrate and/or environment, but these have been envisioned in varying ways and at varying scales.

Studies examining the relationship between bryophyte species occurrence and habitat in the boreal forest have varied from those which focus on the occurrence of select species on one microsite type (Söderström 1993) to larger scaled studies examining variation in bryophyte community composition along environmental gradients (Lee & La Roi 1979; Vitt et al. 1995). These studies have provided conflicting information on the relationship between different habitat parameters and bryophyte species occurrence. While some studies have suggested that many species are substrate specific (Söderström 1988, 1993) others have found little evidence for substrate specificity (Frego & Carleton 1995, 1998; La Roi & Stringer 1976). It is thus difficult to discern the relative importance of microsite or substrate and microenvironment to bryophyte occurrence in the boreal forest. This variation among studies likely arises because sampling approaches have varied in both scale and scope. The sampling scale and approach used often determine the strength of observed relationships between bryophyte species composition and habitat (Økland 1994).

Due to the small size and presumed habitat specificity of bryophytes, the use of the microsite as a sampling unit has become commonplace in bryophyte ecology. Microsite types studied in the boreal forest include patches of soil on the forest floor exposed by treefalls (Jonsson & Esseen 1990), decaying logs (Söderström 1988), and trees (Gustafs-

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son & Eriksson 1995). Since undisturbed forest floor is continuous rather than discrete, it has typically been examined in studies of bryophyte species composition that were not examining relationships with microsite *per se* (Økland 1994; Økland & Eilertsen 1996). Studies that have focused on only one microsite type have related compositional variation to microsite quality or microenvironment. For example, log decay class has been related to the occurrence of certain epixylics (Muhle & LeBlanc 1975; Söderström 1988) and tree species and stratum have been related to the occurrence of some epiphytes (Culberson 1955; Sillett 1995). In addition, forest floor bryophytes have been shown to respond to variation in pH (Zamfir et al. 1999), microtopography (Økland 1994), and soil moisture (Robinson et al. 1989). Although these studies have been integral to our understanding of habitat preferences and requirements of many bryophyte species (Kimmerer 1993; Koponen 1990; Söderström 1988, 1993) their focus on either specific microsite types or certain bryophyte taxa have limited our ability to untangle the relative importance of various factors in determining bryophyte species assemblages.

Studies examining the relation between bryophyte species occurrence and variation at coarser grained spatial scales have similarly demonstrated that compositional variation may be linked to habitat variables including microsite availability (Frisvoll & Prestø 1997; Rambo & Muir 1998); stand structure (Berglund & Jonsson 2001; Håkan & Jonsson 2001); stand integrity (time since last disturbance; Økland 2000); stand fertility (Pitkänen 2000); and elevation (van Reenen & Gradstein 1983). The relationship between microsite availability and composition and diversity of bryophytes within forest stands implies that variation in bryophyte species occurrence at coarser grained spatial scales is linked to variation at finer scales. Økland (2000) found that factors operating at a fine scale become more important in older stands, such that fine-grained within-stand heterogeneity may be more important than landscape scale patterns of time since disturbance in explaining bryophyte composition and diversity of a region. Thus, species assemblages of individual microsites may be influenced by environmental variation at coarser grained spatial scales, and the species assemblage of microsites might also be an important determinant of species composition at coarser scales.

In this study we examined patterns of variation in bryophyte (mosses and liverworts) species composition at different scales in the boreal forest of western Canada as related to microsite type (substrates for bryophyte colonization), microsite quality for woody substrates (decay class, hardwood vs. softwood), and microenvironmental variation. Our objective was to provide an understanding of the relationship of these factors to patterns of variation in bryophyte species assemblage.

Methods

Study site.—We assessed patterns of bryophyte composition in three 10 ha conifer-dominated stands [70–95% conifer by basal area (ba)] in the Lower Boreal-Cordilleran Ecoregion of northwestern Alberta, 56°47′ N, 118°21′ W (Strong & Leggat 1992). This region has an average annual precipitation of 464 mm, two-thirds of which falls in the summer (median of 295 mm). Temperatures average 12.8°C in summer and −7.8°C in winter.

Mesic sites in this region host boreal mixedwood forest with varying dominance by *Populus tremuloides* and *Picea glauca*. We focused on conifer-dominated stands because they were thought to have a greater degree of stand complexity and higher bryophyte species diversity than stands dominated by *Populus tremuloides*. We chose stands that were of natural fire origin and had not been previously managed, based on accessibility and % conifer basal area. Stands were composed of *Picea glauca* (~73% ba), *Picea mariana* (~14% ba), *Populus tremuloides* (~7% ba), *Populus balsamifera* (~3% ba), and *Abies balsamea* and *Pinus contorta* (both <1% ba). Some distinguishing structural features of these stands included *Populus tremuloides* trees over 100 years old, large fallen logs, uprooted trees, and stumps, and an almost continuous carpet of the feathermosses *Hylocomium splendens*, *Pleurozium schreberi* and *Ptilium crista-castrensis*. *Sphagnum warnstorfii* dominated ground cover in the wetter areas of stands 1 and 3. Soils of two stands (1, 3) were imperfectly drained Luvisols (Dark Grey Luvisol, Orthic Grey Luvisol) and the soil of stand 2 was a well drained Orthic Luvic Gleysol. The parent material of all three stands was glaciolacustrine and the pH of the soil F layers ranged from 4.41 (stand 2) to 4.74 (stand 1) (B. Kishchuk, pers. comm.).

Sampling design.—We used nested sampling designed to explore variation in species assemblage at different scales in relation to substrate and microenvironment. Bryophyte species composition was documented at three spatial scales: the microsite (structural elements providing substrates for bryophyte colonization); the mesosite (625 m^2 plots within stands); and the stand (10 ha).

We randomly placed six mesosites in each of the three stands and each of these had five randomly located center points. Microenvironment data were collected at these points (see below) and we selected the closest example of each microsite type (logs, tree bases, stumps, one m^2 patches of undisturbed forest floor, and disturbed patches of forest floor) for microsite sampling of bryophytes. Logs, stumps, and trees were sampled if their diameter (measured at the widest point for logs and stumps and at breast height for trees) exceeded 10 cm. In addition, logs were sampled only if they were in contact with the ground and if they were in a decay class beyond decay class one (logs of decay class one were floristically similar to trees; see below for decay class descriptions). Disturbed patches of forest floor were limited to areas where mineral soil was exposed by tree falls. The scarcity of some microsite types (stumps and disturbed soil patches) resulted in an unbalanced sample design.

Bryophyte sampling.—At each sampled microsite (one of each microsite type at each of the five center points within each of the six mesosites per stand) bryophyte spe-

cies composition was estimated by searching the entire microsite surface. Abundance was estimated for each species using a plastic grid of 5.4 × 5.4 cm squares to measure the microsite surface area colonized. Cryptic species that were not observed in the field, but were later identified in the lab, were ascribed a value of one square. To characterize species assemblage at the mesosite level we used a Floristic Habitat Sampling (FHS) (Newmaster 2000) approach wherein the species list arising from the sampling of microsites within a given mesosite was supplemented by additional species found during a search of the mesosite (625 m^2). Similarly, to develop species lists for each stand (10 ha) the species lists for each mesosite within a given stand were combined and supplemented with additional species found during a thorough search of the stand until no new species were found (3.5 to five hours). All bryophyte specimens were collected for identification. Bryophyte nomenclature follows: Anderson et al. (1990) except for the following taxa: Sphagnaceae follow Anderson (1990), Hepaticae follow Stotler and Crandall-Stotler (1977), and *Orthotrichum elegans* is recognized as distinct from *Orthotrichum speciosum* following Vitt and Darigo (1997). Species vouchers are deposited in the University of Alberta herbarium (ALTA). Data for *Lophozia excisa, L. guttulata,* and *L. ventricosa* were pooled prior to analysis.

Microsite quality for woody substrates.—For each sample of the woody microsite types we recorded microsite quality that included species and decay class (stumps and logs), and species and dbh (trees). Log decay classes were as follows: 1 = log whole and undecayed, bark branches and twigs intact; 2 = log hard, some bark loss, >50% bark remaining; 3 = log soft in patches, < 50% bark remaining; 4 = little to no bark remaining, no branches, wood soft with small crevices, and small pieces lost; 5 = large wood fragments lost, outline of trunk deformed; 6 = wood mostly well decayed, some wood visible; and 7 = humification nearly 100%, hard to define as a log [based on Crites & Dale's (1995) modification of McCullough (1948)]. Stump decay classes were as follows: 1 = inner wood hard, bark intact, neither decayed nor weathered to any appreciable extent; 2 = inner wood soft, somewhat decayed, bark 100% intact; 3 = inner wood very soft, wood pieces breaking off, some bark missing; and 4 = all bark missing, large wood pieces missing, stump becoming overgrown with feather moss.

Microenvironment.—Most microenvironment measurements were made at the five center points within each mesosite. We measured below canopy Photosynthetic Photon Flux Density, as percent full light, at a height of 1.2 m, on days with continuous overcast sky using a hand held ceptometer (AccuPAR, Decagon Devices, Inc. Pullman, WA) calibrated with above canopy PPFD in an adjacent opening using a quantum point sensor (LICOR Inc.). Forest floor samples (a 10.3 cm diameter core of the LFH layer, to a maximum depth of 10 cm) were taken following a period of six days without precipitation for measurement of forest floor moisture (percent moisture loss after oven drying at 105°C for 6 hours). The samples were then air dried, ground, and mixed for determination of pH following the methods for organic soils outlined by Kalra (1995), using an 0.01M $CaCl_2$ solution at a soil $CaCl_2$ ratio of 1:7. Moss and litter depths were also measured at three random points within each circular plot. Litter depth included all non-living forest floor material that was not decomposed, while moss depth measured the living moss layer.

Though evaporation rates are important to moss species occurrence (Deltoro et al. 1998), comparing surface moisture conditions relevant for bryophyte growth across habitats is challenging due to the variability in species present from site to site (barring the use of moss water content as a comparable measure), and to the difficulty of emulating moss water uptake and evaporation. To provide a coarse estimate of surface moisture conditions for mosses we applied a method similar to that used by Cleavitt (2002) who used the total water content of sponges as a proxy for moss water content. We placed 60 cm^3 pieces of cork within the forest floor moss layer near each center point and collected them one day after a heavy rainfall. Percent moisture content was expressed as percent of air-dry weight.

At each sampled microsite (associated with each center point) we measured mean temperature using the inversion of sucrose to glucose and fructose following the method of Jones and Court (1980). We attached sucrose vials covered with foil to each sampled microsite on May 14th and collected them on August 25th, 1999.

Vascular plant species richness was documented at the scale of the mesosites using FHS.

Substrate availability.—Availability of the different microsite types was estimated in circular plots (20 m^2) located at each of the five center points in each mesosite by calculating the surface area of logs, tree bases (to 1.5 m high), stumps, and disturbed patches of forest floor and expressing it as a percent of the plot ground area. Substrates were included if they met the criteria mentioned above. We further characterized the woody substrates by recording species for trees and species and decay class for logs and stumps (decay classes as above).

Analyzing patterns of variation from microsite sampling.—To explore patterns of variation in bryophyte species composition at the microsite scale, in the absence of pre-defined notions of the important factors, we used two-way indicator species analysis to define idealized groups using species relative abundance data from the microsite sampling. The idealized groups were created by maximizing within-group similarity along one principal gradient using TWINSPAN (Hill 1979) with PC-ORD software (McCune & Mefford 1997). Pseudospecies cut levels of 0.0, 0.01, 0.05, 0.5, 5.0, 20.0, and 50.0 corresponded to abundance categories with relatively equal numbers of species in the data set. Cluster groups resulting from the second level of divisions were the most informative and were used as ''idealized'' groups (hereafter referred to as TWINSPAN groups).

To examine the relevance of our pre-defined microsite types, as compared to the patterns arising from the TWINSPAN clustering, we used Nonmetric Multidimensional Scaling (NMDS) ordination. NMDS was chosen because it can be performed on non-normal data and preserves the rank order of dissimilarities among samples thus facilitating interpretation of ordination diagrams (McCune & Mefford 1997). Ordinations were performed on untransformed species relative abundance data from the microsite sampling after removing rare species (occurrence <3 microsites) using PC-ORD version 4 (McCune & Mefford 1997). Ordinations were performed using random starting configurations, stability criterion of 0.0005, 10 initial runs with real data, and Sørenson's similarity index as the distance measure. Monte Carlo tests (20 randomized runs), and stress were used to assess dimensionality of ordinations. In all cases, adding a third dimension resulted in considerable reductions in stress, thus 3D solutions were chosen for all NMDS ordinations. Monte Carlo tests in all cases showed the first three axes to be significantly different from random at $p < 0.05$. The number of iterations for the final solution was 69. The stability of solutions

was assessed by examining plots of stress vs. iteration; final instability of all ordinations was <0.0005. The resulting ordination diagram was examined in relation to both our predefined microsite types and to the TWINSPAN groups.

We used Indicator Species Analysis (ISA) to identify species indicators for the idealized TWINSPAN groups and our predefined microsite types (Dufrêne & Legendre 1997) using PC-ORD (McCune & Mefford 1997). We identified dominant species assemblages for TWINSPAN groups and microsite types using species with indicator values greater than 20% (hereafter termed indicator species). All included species were significant at $p < 0.05$ when tested using 1,000 randomized Monte Carlo runs (McCune & Mefford 1997).

Microsite quality for woody substrates.—To explore patterns of variation in the bryophyte composition of the different woody microsite types as related to substrate quality (decay class, species) we performed three separate NMDS ordinations (as described above) on the data of species relative abundance for each sample of a log, stump, or tree. The iterations for the final solution for the ordinations of logs, stumps, and trees were 108, 68, and 164, respectively. In order to increase interpretability of representations of 3D ordinations in two dimensions the 3D solutions were rotated until the variation in microsite properties along two axes was maximized. We examined ordination diagrams in relation to microsite properties: hardwood or softwood (for trees, stumps, and logs), diameter class (trees), and decay class (stumps and logs). There were no clear patterns of variation related to tree diameter class or stump decay class so these are not presented or discussed further. We used ISA (as described above) to identify species indicators for log decay classes.

Microenvironment.—We explored relationships between microenvironment and species composition for each microsite type using constrained ordinations. As described above, NMDS was the preferred method for unconstrained ordination, but there is no corresponding constrained ordination method for continuous environmental variables. Therefore, we chose Canonical Correspondence Analysis (CCA) for this analysis. First we ran unconstrained ordinations [CA (Correspondence Analysis) using CANOCO for Windows V 4.02 (ter Braak & Šmilauer 1997)] to check the gradient length of the first axis and look for any obvious outliers. Outlying species and samples were removed for subsequent analyses. The gradient lengths were 3.4, 3.7, 4.1, 4.1, and 3.6 for undisturbed forest floor, disturbed forest floor, logs, stumps, and trees, respectively; verifying CCA (assumes a unimodal response) was the appropriate method for constrained ordination. The CCAs utilized the species abundance data for each of the different microsite types and the following environmental variables: temperature (measured at each sampled microsite), forest floor moisture, pH, surface moisture, light, forest floor moss depth, and litter depth (each with one measure per circle plot). Environmental variables were added using forward stepwise selection. The significance of each variable was tested using Monte Carlo permutation tests (199 permutations); only the significant (or the three best) environmental variables were included in the final CCAs (ter Braak & Šmilauer 1997). All CCAs were run with and without ''stand'' as a (categorical) covariable. Since the NMDS analyses had indicated the extent to which species composition varies with microsite quality for woody substrates all CCAs for woody microsite types included microsite quality parameters as (categorical) covariables (logs: species and decay class; stumps: species; trees: species).

Constrained ordination was similarly used to examine relationships between environmental variation and the species assemblage (presence/absence) of the mesosites. The CA gradient length of the first axis in the CA was 1.6 so Redundancy Analysis (RDA, assumes a linear response) was chosen for this constrained ordination. For each mesosite we used mean values (across circle plots within each mesosite) for the environmental variables: light, surface moisture, forest floor moisture, pH, litter depth, forest floor moss depth, and substrate availability [area as a percent of total ground surface area for: logs (by decay class), stumps (by species), and tree bases (by species)]. As described above, environmental variables were added using forward stepwise selection; significance testing was by Monte Carlo permutation and only the significant (or the three most highly correlated) environmental variables were included in the final CCAs (ter Braak & Šmilauer 1997). RDAs were run with and without ''stand'' as a (categorical) covariable.

Results

The 30 ha of sampled conifer-dominated boreal mixed-wood stands contained 89 bryophyte species (19 hepatic and 70 moss species) (Table 1). Floristic Habitat Sampling (FHS) at the mesosite scale added six additional species that were not found in microsite sampling while the Stand-level FHS added another nine species. Thirteen out of the 15 species added using FHS were found only on the forest floor.

Patterns of variation arising from microsite sampling.—The idealized groups arising from TWINSPAN clustering did not follow closely our predefined microsite types (Table 2). The first division separated the woody microsite types (a group comprised of 8 undisturbed forest floor and 248 log, stump, tree, and disturbed forest floor samples) from undisturbed forest floor (a group including 81 undisturbed forest floor and 20 log, stump, and tree samples). Within the undisturbed forest floor group, the second level of classification distinguished wetter [Undisturbed (wet) Group] from drier [Undisturbed (dry) Group] sites. The second division in the woody substrate group separated hardwood from softwood substrates (Hardwood Group: 69 hardwood trees, logs, and stumps, 8 disturbed forest floor, 7 undisturbed forest floor and 22 softwood samples; Softwood Group: 131 softwood, 9 hardwood, 9 disturbed forest floor, and one undisturbed forest floor samples). Further divisions were not informative.

The 3D solution for the NMDS ordination of all microsite samples explained 57% of total variation. The ordination diagram showed little separation between the different microsite types (Fig. 1A), whereas distinction between the TWINSPAN groups was more pronounced (Fig. 1B). For woody substrates there was greater compositional similarity within the TWINSPAN hardwood and softwood groups than within the log, stump, or tree groupings.

TABLE 1. Species occurrence (for all species in the study site) expressed as the proportion of sampled microsites, within each microsite type, in which that species was present. D = disturbed patches of forest floor, L = logs, S = stumps, T = trees and U = undisturbed patches of forest floor. '*Pre ex*' end and '*post in*' authority names are not shown. *** = only found at the stand scale; ** = only found at the mesosite scale; * = only found on one microsite type; [1]data from these taxa were grouped in subsequent analyses. *n* = number of samples of that microsite type.

Species name		Frequency of occurrence within each microsite type				
		D	L	S	T	U
	n	23	86	72	90	90
Amblystegium serpens (Hedw.) Schimp.		0.22	0.27	0.32	0.10	0.01
Amblystegium varium (Hedw.) Lindb.	*				0.01	
Anastrophyllum hellerianum (Nees) Schust.			0.19	0.06		
Aulacomnium palustre (Hedw.) Schwaegr.		0.44	0.13	0.03	0.01	0.02
Blepharostoma trichophyllum (L.) Dum.	*		0.10			
Brachythecium albicans (Hedw.) Schimp.		0.09	0.05	0.13	0.04	
Brachythecium campestre (C. Müll.) Jaeg.		0.30	0.40	0.26	0.18	0.03
Brachythecium erythrorrhizon Schimp.			0.08	0.04	0.01	0.02
Brachythecium reflexum (Stark) Schimp.	**					
Brachythecium salebrosum (Web. & Mohr) Schimp.		0.13	0.16	0.19	0.06	0.01
Brachythecium starkei (Brid.) Schimp.		0.30	0.31	0.19	0.09	0.11
Brachythecium velutinum (Hedw.) Schimp.		0.09	0.10	0.08	0.01	
Bryohaplocladium microphyllum (Hedw.) Wat. & Iwats.	*	0.04				
Bryum lisae De Not. var. *cuspidatum* (Bruch & Schimp.) Marg.		0.26	0.09	0.01	0.03	
Bryum pseudotriquetrum (Hedw.) Gaertn. et al.	*	0.09				
Calliergon cordifolium (Hedw.) Kindb.	***					
Calliergon richardsonii (Mitt.) Kindb.	**					
Campylium hispidulum (Brid.) Mitt.		0.13	0.3	0.21	0.06	0.01
Cephalozia lunulifolia (Dum.) Dum.		0.09	0.08	0.03		
Ceratodon purpureus (Hedw.) Brid.		0.35	0.06	0.06	0.03	
Climacium dendroides (Hedw.) Web. & Mohr.	***					
Dicranum acutifolium (Lindb. & Arnell) Weinm.				0.04	0.02	
Dicranum flagellare Hedw.		0.04	0.19	0.11	0.10	
Dicranum fragilifolium Lindb.		0.13	0.23	0.17	0.20	0.01
Dicranum fuscescens Turn.		0.04	0.28	0.19	0.26	0.01
Dicranum groenlandicum Brid.	*			0.01		
Dicranum polysetum Sw.		0.09	0.10	0.06	0.07	0.01
Dicranum scoparium Hedw.			0.05	0.01	0.01	
Dicranum tauricum Sapeh.			0.05	0.01	0.04	
Dicranum undulatum Brid.		0.04	0.05	0.10	0.04	0.01
Drepanocladus aduncus (Hedw.) Warnst.	**					
Eurhynchium pulchellum (Hedw.) Jenn.		0.57	0.56	0.79	0.56	0.20
Funaria hygrometrica Hedw.	*	0.04				
Helodium blandowii (Web. & Mohr) Warnst.	**					
Herzogiella turfacea (Lindb.) Iwats.		0.17	0.15	0.13	0.06	0.01
Hylocomium splendens (Hedw.) Schimp.		0.61	0.7	0.57	0.30	0.89
Hypnum pratense (Rabenh.) Spruce				0.02	0.01	
Isopterygiopsis pulchella (Hedw.) Iwats.	*			0.01		
Jamesoniella autumnalis (DC.) Steph.		0.04	0.36	0.13	0.04	
Lepidozia reptans (L.) Dum.		0.04	0.07	0.07	0.02	
Leptobryum pyriforme (Hedw.) Wils.		0.30	0.05	0.01		
Leptodictyum riparium (Hedw.) Warnst.		0.04	0.07	0.03	0.01	
Lophocolea heterophylla (Schrad.) Dum.		0.04	0.22	0.10	0.02	
Lophocolea minor Nees		0.04	0.06	0.01	0.01	0.01
Lophozia ascendens (Warnst.) Schust.			0.01	0.01		
[1]*Lophozia excisa* (Dicks.) Dum.			0.03	0.04		
Lophozia incisa (Schrad.) Dum.			0.01	0.01		
Lophozia longidens (Lindb.) Macoun			0.11	0.06	0.04	
[1]*Lophozia guttulata* (Lindb. & H. Arnell) Evans	*		0.07			
[1]*Lophozia ventricosa* (Dicks.) Dum.		0.04	0.10	0.03	0.01	
Marchantia polymorpha L.	*	0.13				
Mnium spinulosum Bruch & Schimp.		0.35	0.34	0.44	0.24	0.03
Oncophorus wahlenbergii Brid.		0.17	0.03	0.22	0.06	0.01
Orthotrichum obtusifolium Brid.			0.18	0.14	0.09	
Orthotrichum elegans Hook. & Grev.			0.14	0.14	0.07	
Plagiochila porelloides (Nees) Lindenb.				0.02		0.01
Plagiomnium cuspidatum (Hedw.) T. Kop.		0.22	0.08	0.19	0.07	0.01

TABLE 1. Continued.

Species name		Frequency of occurrence within each microsite type				
		D	L	S	T	U
Plagiomnium drummondii (Bruch & Schimp.) T. Kop.		0.09	0.13	0.08	0.03	0.07
Plagiomnium ellipticum (Brid.) T. Kop.		0.13	0.07	0.03	0.02	0.09
Plagiomnium medium (Bruch & Schimp.) T. Kop.		0.13	0.18	0.06	0.03	0.07
Plagiothecium denticulatum (Hedw.) Schimp.		0.17	0.07	0.06	0.01	
Plagiothecium laetum Schimp.	***					
Platydictya jungermannioides (Brid.) Crum		0.09	0.06	0.13	0.07	
Pleurozium schreberi (Brid.) Mitt.		0.30	0.74	0.42	0.27	0.63
Pohlia cruda (Hedw.) Lindb.	*			0.04		
Pohlia nutans (Hedw.) Lindb.		0.57	0.23	0.36	0.10	0.01
Polytrichum commune Hedw.	*	0.09				
Polytrichum juniperinum Hedw.	*	0.26				
Polytrichum longisetum Brid.	***					
Polytrichum piliferum Hedw.	***					
Pseudotaxiphyllum elegans (Brid.) Iwats.	*				0.01	
Ptilidium pulcherrimum (G. Web.) Hampe		0.09	0.58	0.39	0.86	0.02
Ptilium crista-castrensis (Hedw.) De Not.		0.30	0.75	0.29	0.17	0.50
Pylaisiella polyantha (Hedw.) Grout		0.17	0.43	0.44	0.27	0.01
Rhizomnium gracile T. Kop.	***					
Rhizomnium pseudopunctatum (Bruch & Schimp.) T. Kop.	*		0.02			
Rhytidiadelphus triquetrus (Hedw.) Warnst.	**					
Riccardia latifrons Lindb.	*		0.03			
Sanionia uncinata (Hedw.) Loeske		0.26	0.45	0.31	0.36	0.03
Scapania glaucocephala (Tayl.) Aust.			0.20	0.01		
Sphagnum russowii Warnst.	**					
Sphagnum warnstorfii Russ.			0.05	0.01		0.06
Splachnum luteum Hedw.	***					
Splachnum rubrum Hedw.	***					
Splachnum vasculosum Hedw.	***					
Tetraphis pellucida Hedw.		0.04	0.05	0.10		
Thuidium recognitum (Hedw.) Lindb.			0.05	0.04	0.03	0.08
Tomenthypnum nitens (Hedw.) Loeske		0.04	0.06	0.01		0.12
Tritomaria exsectiformis (Breidl.) Loeske			0.03	0.06		

The Indicator Species Analysis (ISA) showed that our predefined microsite types had fewer indicator species and lower indicator values than did the TWINSPAN groups (Table 2). The Undisturbed (wet) Group was characterized by species often found growing on organic soil and peat in moist conditions (*Aulacomnium palustre*, *Tomenthypnum nitens*, *Plagiomnium ellipticum*) while the feather moss species *Hylocomium splendens* and *Pleurozium schreberi* had the highest indicator values for the Undisturbed (dry) Group. *Eurhynchium pulchellum*, *Pylaisiella polyantha*, and *Amblystegium serpens* were the best indicators of the Hardwood Group while *Ptilidium pulcherrimum* and *Dicranum fuscescens* identified the Softwood Group. In the ISA of our pre-defined microsite types, disturbed patches of forest floor had the greatest number of indicator species with *Pohlia nutans*, *Leptobryum pyriforme*, and *Ceratodon purpureus* having the highest indicator values. Undisturbed patches of forest floor were characterized by the feather mosses (as in the TWINSPAN Undisturbed (dry) Group). For logs *Ptilidium pulcherrimum* and *Jamesoniella autumnalis* had the highest indicator values while stumps were characterized by *Eurhynchium pulchellum* and *Pylaisiella polyantha*. Trees had no significant indicator species.

Microsite quality for woody substrates.—When analyzed separately, NMDS ordinations of logs, stumps, and trees all showed separation between hardwood and softwood types (Figs. 2A, C, D). Species composition of logs also varied with decay class; as decay class increased the variation in bryophyte species composition among log samples decreased (Fig. 2B). Indicator values were very low for logs in early decay classes and peaked at decay class 5 (Table 3). *Pylaisiella polyantha* was the only indicator of decay class 2 logs, while there were no suitable indicators for logs of decay class 3. The floras of softwood and hardwood logs began to converge by decay class 4, with *Ptilidium pulcherrimum* and *Eurhynchium pulchellum* occurring on logs of both types. Logs of decay class 5 had the greatest number of species with high indicator values (11), of which seven were liverworts. Some species had high indicator values for more than one log decay class: *Hylocomium splendens*, *Pleuro-*

TABLE 2. Results of Indicator Species Analysis (Dufrêne & Legendre 1997).—A. The TWINSPAN groups.—B. The pre-defined microsite types. Species with indicator values (iv) greater than 20 are presented. p = probability of type 1 error for indicator values tested using a Monte Carlo test with 1,000 runs.

Species	iv	p
A) TWINSPAN groups		
Softwood group		
Ptilidium pulcherrimum	70	0.001
Dicranum fuscescens	42	0.001
Dicranum fragilifolium	22	0.008
Dicranum flagellare	20	0.006
Hardwood group		
Eurhynchium pulchellum	70	0.001
Pylaisiella polyantha	66	0.001
Amblystegium serpens	42	0.001
Brachythecium campestre	33	0.003
Sanionia uncinata	24	0.037
Orthotrichum elegans	24	0.006
Orthotrichum obtusifolium	24	0.002
Mnium spinulosum	22	0.019
Plagiomnium cuspidatum	20	0.002
Brachythecium salebrosum	20	0.001
Undisturbed (dry) group		
Hylocomium splendens	68	0.001
Pleurozium schreberi	41	0.003
Ptilium crista-castrensis	33	0.005
Undisturbed (wet) group		
Aulacomnium palustre	78	0.001
Tomenthypnum nitens	58	0.001
Plagiomnium ellipticum	51	0.001
Sphagnum warnstorfii	44	0.001
Brachythecium starkei	32	0.001
Thuidium recognitum	32	0.008
B) Microsite types		
Disturbed patches of forest floor		
Pohlia nutans	53	0.001
Leptobryum pyriforme	35	0.001
Ceratodon purpureus	29	0.001
Polytrichum juniperinum	26	0.001
Bryum lisae	25	0.001
Undisturbed forest floor		
Hylocomium splendens	54	0.001
Pleurozium schreberi	34	0.001
Ptilium crista-castrensis	29	0.006
Logs		
Ptilidium pulcherrimum	29	0.003
Jamesoniella autumnalis	24	0.002
Ptilium crista-castrensis	23	0.002
Stumps		
Eurhynchium pulchellum	54	0.001
Pylaisiella polyantha	26	0.002
Trees		
none		

zium schreberi, *Ptilium crista-castrensis*, *Eurhynchium pulchellum*, and *Ptilidium pulcherrimum*.

Microenvironment.—CCA ordinations for each woody microsite type showed some evidence of microenvironmental influence on species composition, but overall the constrained ordinations explained a relatively low percentage of variation in species data (Table 4). The percent variance explained by the ordinations changed very little when stand was added as a categorical covariable. In the constrained ordination of tree bryophyte composition, moss and litter depths, temperature, pH, and surface moisture were significant; when stand was included as a covariate the significant variables were moss and litter depths and forest floor moisture. For logs, temperature and light were significant variables, but when stand was included as a covariable temperature and forest floor moisture were significant. For stumps, the first axis was not significant in the CCA with or without the covariable stand and the only significant environmental variable was litter depth in the ordination without ''stand'' (Table 4). The diagrams of the ordinations of woody microsite types (not including stand) did not show any separation of samples among stands and did not provide further insight other than the distribution of sample points in relation to the main axes, therefore we do not present them.

In the CCA of undisturbed patches of forest floor the environmental variables forest floor moisture, pH, and light explained significant amounts of the total variation in species data (Table 4); moisture was not significant when stand was included as a covariable. For bryophyte composition of disturbed forest floor the significant environmental variables were forest floor moisture and temperature (Table 4); no environmental variables were significant when stand was included as a covariable. The ordination diagrams for both forest floor microsite types showed considerable variation among samples and also some separation among stands (Stand 1 separated from 2 and 3) along a moisture gradient (Fig. 3). Stand 1 had higher forest floor moisture and pH than Stands 2 and 3, but all stands showed extensive variation among mesosites for all the sampled environmental variables (Table 5).

Examination of correlations between microenvironment and species assemblage at the mesosite scale showed that surface moisture and forest floor moisture were significant environmental variables in the RDA but only forest floor moisture was significant when stand was included as a covariable (Table 6). The diagram of the ordination without the covariable showed some separation among stands along a moisture gradient associated with the first axis. In stand one there was more variability in species composition among patches of undisturbed forest floor, disturbed forest floor, and among mesosites (points were farther apart from one another in the ordination diagrams) than in stands 2 and 3 (Fig. 3).

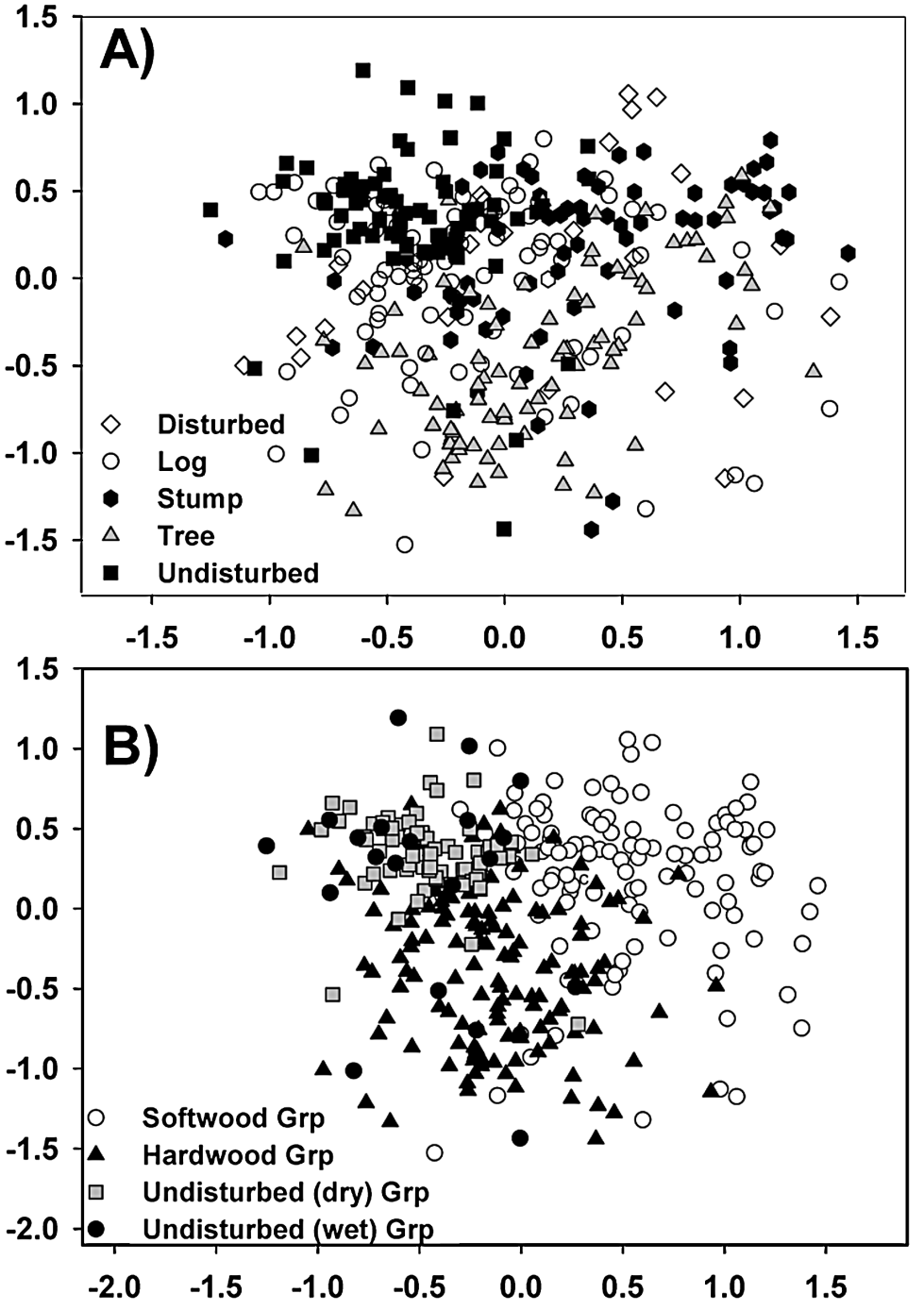

FIGURE 1. Scatterplot of sample scores on the first two axes of the NMDS ordination in three dimensions.—A. Species assemblage data from the microsite sampling coded by microsite type.—B. Coded by idealized TWINSPAN groups. R^2 for Axes 1, 2, & 3 = 0.24, 0.20, & 0.13, respectively. Cumulative % variation explained = 57; stress = 18.1.

DISCUSSION

Patterns of variation among microsite types.—Our pre-defined microsite types were not closely related to patterns of variation in bryophyte species composition. Instead, for woody microsite types bryophyte species composition varied by species (hardwood vs. softwood) and decay class while variation among samples of disturbed and undisturbed forest floor appeared to be related to microenvironmental variation in moisture.

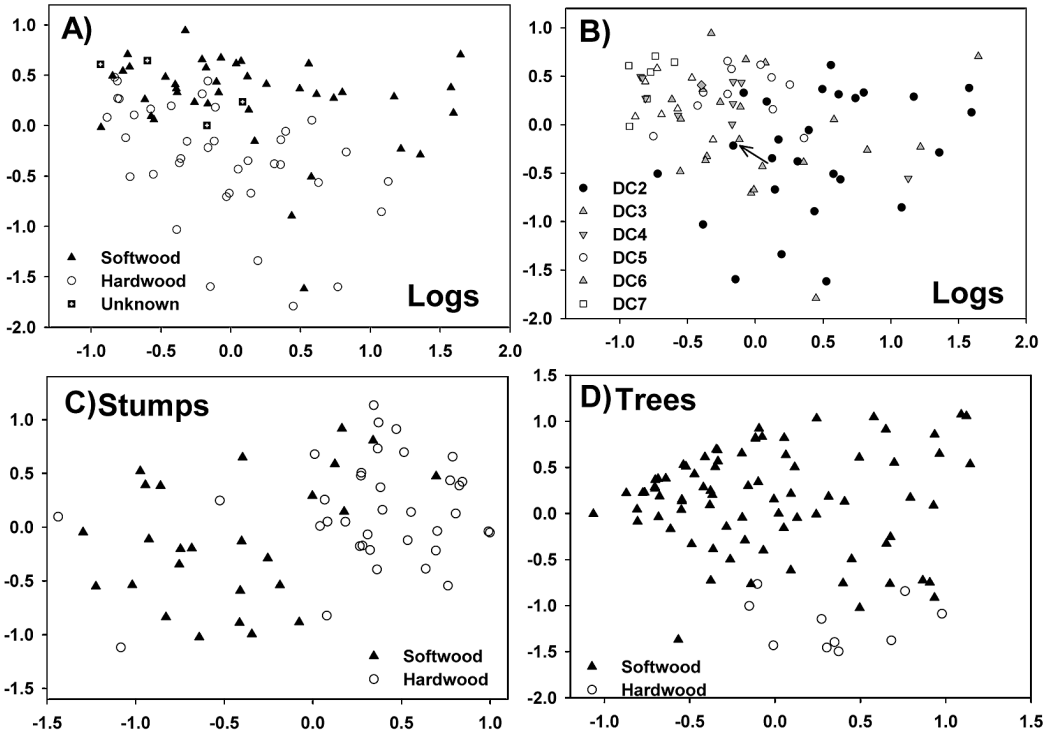

FIGURE 2. Scatterplot of sample scores for the NMDS ordinations in three dimensions of species assemblage data for each of the pre-defined woody microsite types.—A. Logs coded by hardwood and softwood (R^2 for Axes 1, 2, & 3 = 0.32, 0.12, & 0.19; cumulative % variation explained = 63; stress = 14.9).—B. Logs coded by decay class (arrow indicates increasing decay class).—C. Stumps coded by hardwood and softwood (R^2 for Axes 1, 2, & 3 = 0.14, 0.38, & 0.23; cumulative % variation = 75; Stress = 15.7).—D. Trees coded by hardwood and softwood (R^2 for Axes 1, 2, & 3 = 0.32, 0.20, & 0.21; cumulative % variation explained = 73; stress = 16.2). In each case the axes displayed are the two most important (highest R^2).

Other authors have also found little difference in the bryophyte species composition of logs vs. stumps. Andersson and Hytteborn (1991) found only one epixylic species (*Lophocolea heterophylla*) with a preference for logs over stumps while Kimmerer (1993) found *Tetraphis pellucida* to be more abundant on stumps than on logs. Trees did not separate clearly from stumps or logs and they did not have any strong indicator species but they did show somewhat less variation in species composition. Softwood trees have few true epiphytes (species occurring above a height of 50 cm) and in our study area appeared to be characterized by a small set of species that also grow on other substrates; for example while *Ptilidium pulcherrimum* occurred on 93% of softwood trees, it was also common on logs and stumps. Disturbed patches of forest floor did not form a distinct cluster nor did they separate clearly in the NMDS; however, they were characterized by several species with high indicator values. This suggests the existence of a distinct set of species associated with disturbed patches of forest floor. All of the species indicative of disturbed patches were acrocarpous and most (barring *Mnium spinulosum*) exhibit a colonist life strategy: short life spans, high asexual and sexual reproductive effort, and small spores (During 1979).

Woody microsite types and quality.—There was more variation in bryophyte assemblage among samples of a given woody microsite type (e.g., among different logs) than between microsite types (e.g., logs vs. trees). This is a reflection of the predictive value of microsite quality (e.g., hardwood vs. softwood, decay class) for bryophyte species composition of woody substrates. Softwood logs, stumps, and trees were compositionally similar, as were hardwood logs, stumps, and trees. Although the specificity of bryophyte communities to different tree species has been recognized (Culberson 1955; Newmaster 2000; Palmer 1989; Smith 1982), the importance of log species to bryophyte communities and the similarities among bryophyte communities on trees, stumps, and logs of the same species has not been thoroughly explored.

Species indicators of the hardwood vs. softwood woody microsite groups were species characteristic of hardwood and softwood trees in the boreal forest. Trees in our study had a more limited flora than

TABLE 3. Results of Indicator Species Analysis (Dufrêne & Legendre 1997) for log decay classes; species with indicator values (iv) greater than 20 are presented. p = probability of type 1 error for indicator values tested using a Monte Carlo test with 1,000 runs (only calculated for the maximum iv of each species). (.) indicates that species is a better indicator for a different decay class.

Species	iv	p
Decay class 2		
Pylaisiella polyantha	20	0.567
Decay class 3		
None		
Decay class 4		
Ptilidium pulcherrimum	20	.
Eurhynchium pulchellum	20	.
Hylocomium splendens	20	.
Decay class 5		
Anastrophyllum hellerianum	42	0.009
Ptilidium pulcherrimum	34	0.021
Lophozia ascendens	31	0.026
Dicranum fragilifolium	28	0.064
Oncophorus wahlenbergii	27	0.044
Dicranum flagellare	27	0.032
Riccardia latifrons	27	0.011
Lophozia spp. (pooled)	26	0.036
Lophozia longidens	23	0.063
Jamsoniella autumnalis	22	0.171
Pohlia nutans	20	0.138
Decay class 6		
Pleurozium schreberi	37	0.069
Lophocolea heterophylla	32	0.013
Brachythecium campestre	28	0.095
Hylocomium splendens	27	.
Ptilium crista-castrensis	25	.
Eurhynchium pulchellum	23	0.255
Decay class 7		
Aulacomnium palustre	48	0.003
Sphagnum warnstorfii	40	0.001
Hylocomium splendens	37	0.036
Ptilium crista-castrensis	36	0.095
Brachythecium starkei	32	0.021
Plagiomnium ellipticum	32	0.014
Plagiothecium denticulatum	31	0.006
Tomenthypnum nitens	26	0.033
Pleurozium schreberi	23	.

the other woody microsite types, however their flora was not specific to tree substrates; all species commonly found on trees were also found on other substrates. Thus while all of the species growing on trees were also found on other woody substrates, many of the species on other woody substrates were not present on trees. Our finding that hardwood or softwood species found on trees were also common on logs and stumps of the same species suggests that many bryophyte species found on live trees persist after tree fall. Studlar (1982) recognized succession on tree bases as species accumulated over the time span from saplings to mature trees and Muhle and LeBlanc (1975) described the change in bryophyte species composition with log decay. The similarity among bryophyte communities on logs, trees, and stumps of the same species thus may be an indication of bryophyte community succession over the course of tree senescence.

Woody microsites in the hardwood TWINSPAN group were characterized by a more diverse flora and more hydrophilic species (*Eurhynchium pulchellum*, *Pylaisiella polyantha*, and *Amblystegium serpens*) than those in the softwood group. The majority of species indicators for the hardwood group were pleurocarpous and in the Hypnales lineage. The higher frequency of pleurocarps on hardwoods may be due to the higher moisture levels (Smith 1982) or higher bark pH (Culberson 1955) of *Populus* spp. relative to *Picea* spp. Robinson et al. (1989) found that the proportion of pleurocarpous species increased along a gradient of increasing moisture indicating that pleurocarpous species may be more susceptible to moisture stress than acrocarpous species.

Indicator species for the softwood group were the liverwort *Ptilidium pulcherrimum*, *Dicranum* spp., and no pleurocarpous mosses. These bryophytes act as facultative epiphytes at tree bases (Smith 1982). *Ptilidium pulcherrimum*, unlike most liverworts, is tolerant of drought and this allows it to be common on softwood tree bases, stumps, and logs in spruce forests in Scandinavia (Söderström 1993).

In addition to the hardwood-softwood distinction for woody substrates there was substantial variation in bryophyte species composition with log decay class. As logs decayed over time the hardwood vs. softwood differences diminished and communities became more specific to a given decay class. Of the species indicators for decay class 5 logs, Söderström (1988), classified *Lophozia longidens*, *Lophozia ascendens*, and *Anastrophyllum hellerianum* as early epixylics, and *Pohlia nutans* as a late epixylic in Swedish forests. Logs of decay class 5 have no bark, uneven wood texture, and a humid microclimate making them suitable for the establishment and growth of epixylics. High indicator species values on logs of decay class 5 suggest that epixylics requiring decayed logs have a narrower niche breadth than the facultative epiphytes or forest floor species occurring on logs of other decay classes. Species with high indicator values for decay classes 6 and 7 were predominantly ground flora species. *Plagiothecium denticulatum*, a late epixylic species (*sensu* Söderström 1988), was also indicative of logs of decay stage 7. Another species thought to be indicative of old growth forests, *Plagiomnium ellipticum* (Boudreault et al. 2000), was an indicator species for logs of decay stage 7. Several species with high abundance had high indicator values for

TABLE 4. Results of constrained ordination examining the impact of microenvironmental variation on bryophyte species composition for each of the different pre-defined microsite types (Undisturbed Forest Floor, Disturbed Forest Floor, Trees, Logs, Stumps). Results are given for Canonical Correspondence Analysis (CCA) including inter set correlations (Pearson) of environmental variables (in order of forward stepwise selection) with the first three CCA axes. Only significant, or the three best, environmental variables were included. Results are shown for ordinations without and with covariables. For woody substrates microsite quality was included as a covariable in all analyses (trees: species; logs: species and decay class; stumps: species). Results for all microsites are shown for ordinations without and with stand as a covariable. Total inertia for Undisturbed forest floor = 2.651, Disturbed forest floor = 4.415, Trees = 4.023, Logs = 4.417, Stumps = 5.337.

					Inter set correlations			
	Axis 1	Axis 2	Axis 3	Axis 4	EnvVariable[2]	Axis 1	Axis 2	Axis 3
Undist. FF								
Eigenvalue[1]	0.19*	0.06	0.02	0.45	FF moisture*	0.37	0.34	−0.06
Sp./env. Correl.	0.63	0.43	0.25	0.00	Light*	0.45	−0.11	0.16
Cum % var. explained	7.2	9.4	10.2	27.3	pH*	−0.15	0.35	0.13
Undist. FF with ''stand''								
Eigenvalue[1]	0.12*	0.03	0.02	0.44	Light*	0.40	−0.03	0.16
Sp./env. Correl.	0.57	0.37	0.23	0.00	pH*	−0.32	−0.21	0.14
Cum % var. explained	4.9	6.3	7.1	24.6	FF moisture[ns]	0.27	−0.30	−0.07
Dist. FF								
Eigenvalue[1]	0.49*	0.43	0.18	0.63	Temperature*	−0.77	0.22	−0.37
Sp./env. Correl.	0.93	0.87	0.75	0	FF moisture*	−0.047	0.81	0.25
Cum % var. explained	11.0	20.6	24.7	39.1	Moss depth[ns]	−0.38	−0.39	0.60
Dist. FF with ''stand''								
Eigenvalue[1]	0.47*	0.31	0.17	0.67	Temperature[ns]	−0.76	−0.21	0.38
Sp./env. Correl.	0.94	0.87	0.70	0.00	Litter depth[ns]	−0.39	0.79	−0.01
Cum % var. explained	12.4	20.6	25.0	42.4	Moss depth[ns]	−0.47	0.06	−0.60
Trees with ''softwood vs. hardwood''								
Eigenvalue[1]	0.22*	0.19	0.07	0.03	Moss depth*	−0.56	−0.07	0.20
Sp./env. Correl.	0.72	0.61	0.48	0.37	Litter*	0.06	−0.45	0.29
Cum % var. explained	6.1	9.9	11.9	12.7	Temperature*	0.28	0.24	0.37
					pH*	0.21	0.49	0.02
					Surf. Moist.*	−0.35	0.32	0.23
Trees with ''stand'' and ''softwood vs. hardwood''								
Eigenvalue[1]	0.23*	0.12	0.02	0.47	Moss depth*	−0.59	0.16	−0.14
Sp./env. Correl.	0.75	0.59	0.26	0.00	Litter*	0.10	0.58	0.04
Cum % var. explained	6.7	10.2	10.7	24.3	FF moisture*	0.46	0.20	−0.18
Logs with ''decay class'' and ''softwood vs. hardwood''								
Eigenvalue[1]	0.27*	0.08	0.07	0.38	Temperature*	−0.91	−0.05	−0.08
Sp./env. Correl.	0.93	0.59	0.58	0.00	Light*	−0.18	0.54	0.21
Cum % var. explained	7.4	9.6	11.5	22.0	FF moisture[ns]	0.05	0.13	−0.56
Logs ''stand'' and ''decay class'' and ''softwood vs. hardwood''								
Eigenvalue[1]	0.26*	0.08	0.04	0.36	Temperature*	−0.91	−0.04	−0.01
Sp./env. Correl.	0.92	0.62	0.44	0.00	FF moisture*	−0.12	−0.46	−0.29
Cum % var. explained	7.5	10.0	11.1	21.5	pH[ns]	0.02	−0.48	0.30
Stumps with ''decay class''								
Eigenvalue[1]	0.19[ns]	0.14	0.07	0.56	Litter depth*	0.65	−0.08	0.16
Sp./env. Correl.	0.70	0.67	0.46	0.00	pH[ns]	0.42	0.38	−0.26
Cum % var. explained	3.7	6.4	7.6	18.5	Temperature[ns]	0.15	−0.48	−0.30
Stumps with ''stand'' and ''decay class''								
Eigenvalue[1]	0.16[ns]	0.12	0.06	0.54	Litter depth[ns]	−0.51	0.32	0.24
Sp./env. Correl.	0.71	0.63	0.49	0.00	Temperature[ns]	−0.48	−0.24	−0.31
Cum % var. explained	3.2	5.6	6.8	17.9	pH[ns]	0.08	0.50	−0.29

[1] First axis was significant (*) or not (ns).

[2] Environmental variable explained a significant (*) amount of variance in species composition data (forward stepwise selection) based on a Monte Carlo test $p < 0.05$ or was not significant (ns).

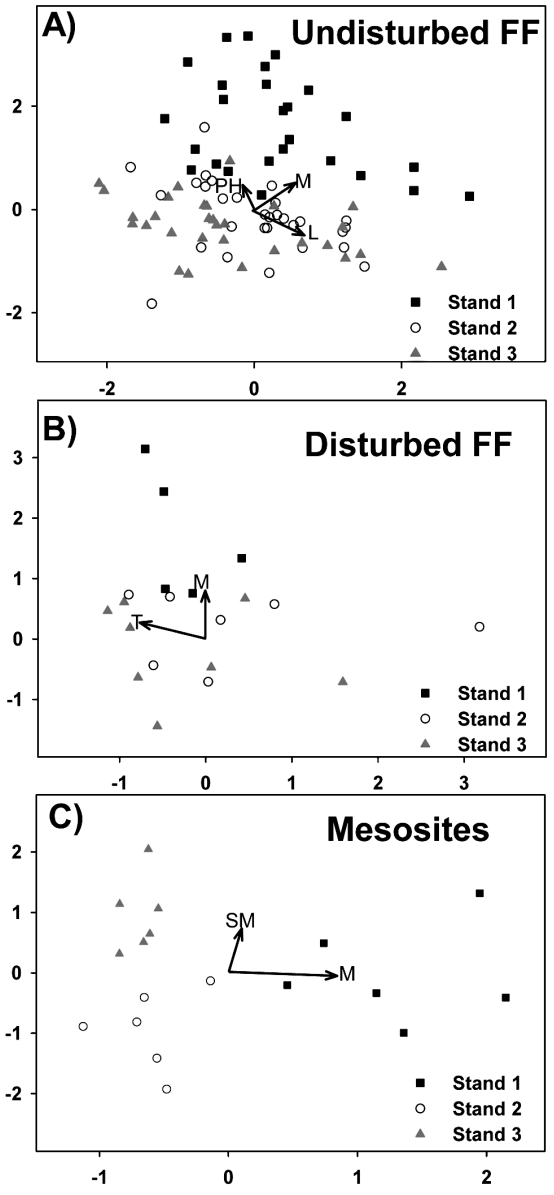

FIGURE 3. Scatterplot of sample scores on the first two axes for constrained ordination (without ''stand'' as a covariable).—A. Species composition of undisturbed forest floor [CCA constrained by: forest floor moisture (M), pH (PH), light (L)].—B. Species composition of disturbed forest floor [CCA constrained by: forest floor moisture (M), temperature (T), moss depth].—C. Species assemblage of mesosites [RDA constrained by: surface moisture (SM), forest floor moisture (M), and vascular plant diversity]. Arrows to a letter indicate direction of increasing value for significant environmental variables. Results were plotted using Hill's scaling. See Tables 4 and 6 for further details.

several decay classes suggesting that the correlation between abundance and niche breadth in bryophytes in boreal mires of Scandinavia (Økland 1989) may also hold true for boreal forest bryophytes in Canada.

We found no evidence of variation in stump species composition with decay class. This may be because the four decay classes used for stump classification were insufficient to separate distinct bryophyte communities or because stumps contained more internal heterogeneity.

Microenvironmental variation.—Results of the constrained ordinations suggested that bryophyte composition of both woody substrates and forest floor substrates was to some extent related to microenvironmental variation at various scales, from microsite to mesosite and stand. The ordination diagrams showed variation in bryophyte composition along environmental gradients among samples of a given microsite type as well as among mesosites and stands.

For the woody microsite types, relationships to the measured microenvironmental parameters within stands appeared to be relatively weak; when microsite quality and stand were included as covariables the first axis of the ordination was never significant for stumps and few environmental variables were significant for trees, logs, or stumps. There was little difference in the percent variation explained in the ordinations with vs. without the covariable ''stand'' suggesting that the detected microenvironmental influence was not largely due to differences among stands. For trees, the significance of litter depth and moss depth may reflect influence on the bryophyte community at the tree base. While our results suggest that microenvironment might affect bryophyte composition of woody substrates this needs to be explored further via intensive sampling of a given microsite type while controlling for variation due to ''quality'' (species, decay class), and perhaps over a greater range of microenvironmental variation than found in our stands.

For the forest floor microsites, again, the percent variation explained was not much different when stand was included as a covariable, suggesting that microenvironmental influence was not only a result of differences among stands. Overall, the constrained ordinations explained relatively low percent of variation in species data. When stand was included as a covariable, bryophyte composition of undisturbed patches of forest floor varied with pH and light. These results support those in other ecosystems, in which bryophyte composition has been related to gradients in pH (Zamfir et al. 1999) and moisture (Lee & La Roi 1979; Robinson et al. 1989; Wolf 1993). In the ordination of disturbed forest floor in which stand was included as a cov-

TABLE 5. Mean values and range (among mesosite mean values) for microenvironmental variables.

	Forest floor moisture (% moisture loss)	Surface moisture (% moisture loss)	Relative temp. (°rotation)	pH	Light (% PPFD)	Litter depth (cm)	Moss depth (cm)
Stand 1							
mean	70.9	12.3	18.0	5.3	28.7	3.6	2.9
range	62.8–79.6	8.9–15.7	17.3–18.3	4.7–5.9	21.0–40.7	2.1–5.4	2.4–3.3
Stand 2							
mean	46.6	8.8	17.7	4.6	31.0	3.2	2.2
range	39.1–51.8	7.3–11.5	17.3–18.1	4.2–4.7	27.3–33.8	2.2–4.5	0.7–3.8
Stand 3							
mean	41.8	13.2	17.8	4.6	29.4	4.6	3.0
range	38.2–43.8	11.7–16.7	17.5–18.0	4.2–4.9	20.5–40.9	3.1–5.4	2.0–4.4

ariable there were no significant environmental variables. This further supports the idea that bryophytes occupying these disturbed sites are a reflection of stochastic processes relating to dispersal and colonization, rather than environmental influence.

For both forest floor microsite types samples from stand one separated from those of stands 2 and 3 when stand was not included as a covariable; this pattern of variation was also seen at the mesosite scale. This suggests that there was also some important environmental variation at the scale of stands, likely due to the fact that stand one had higher forest floor moisture and pH and was older (the mean age of *Picea glauca* trees in stand one was 120 years while in stands 2 and 3 it was 100.3 and 113.4 years respectively; Mills 2001). Despite the documented predictive value of microsite type and quality, substrate availability was not a significant predictor of species assemblage at the mesosite scale; this suggests that there was not important variation in substrate availability at this scale. Further, we did not see separation among stands in the CCA of woody microsite types (without stand). Thus the observed variation in bryophyte assemblage among stands may have been due largely to responses of the forest floor bryophyte community to the environmental differences between stands.

Pharo and Vitt (2000) found a similarly weak relationship between species composition and measured environmental variables in montane forests of western Canada. Compositional differences in bryophyte communities at scales larger than those examined in this study are often related to landscape heterogeneity (i.e., differences between forest types, cliffs, grasslands–Newmaster 2000). The relatively weak patterning of bryophyte communities in relation to microenvironment at the mesosite spatial scale may reflect the fact that there was insufficient environmental variation among mesosites in the study area (Mills 2001), or an absence of processes related to microenvironment that govern bryophyte species occurrence at this scale.

The results of this study suggest that while the majority of boreal bryophytes occur on more than

TABLE 6. Results of constrained ordination examining the impact of microenvironmental variation on bryophyte species assemblage at the scale of the mesosites. Results are given for Redundancy Analysis (RDA) including inter set correlations (Pearson) with the RDA axes for the environmental variables (in order of forward stepwise selection). Only the three best environmental variables were included in the analysis. Results are given for ordinations without and with ''stand'' as a covariable. Total inertia for the corresponding unconstrained analysis (PCA) = 0.563.

					Inter set correlations			
	Axis 1	Axis 2	Axis 3	Axis 4	EnvVariable[2]	Axis 1	Axis 2	Axis 3
Mesosites								
Eigenvalue[1]	0.14*	0.10	0.06	0.11	Surface moist*	0.15	0.87	−0.32
Sp./env. Correl.	0.92	0.94	0.92	0.0	FF moisture*	0.90	−0.14	−0.07
Cum % var. explained	13.8	24.1	30.4	41.6	Vasc. Diver.^{ns}	0.30	−0.47	−0.74
Mesosites with ''stand''								
Eigenvalue[1]	0.08^{ns}	0.07	0.05	0.11	FF moisture*	−0.91	−0.04	0.21
Sp./env. Correl.	0.94	0.93	0.85	0.0	Surface moist^{ns}	0.02	−0.63	0.58
Cum % var. explained	9.9	18.1	24.9	38.4	Vasc. Diver.^{ns}	−0.16	−0.78	−0.45

[1] First axis was significant (*) or not (ns).

[2] Environmental variable explained a significant (*) amount of variance in species composition data (forward stepwise selection) based on a Monte Carlo test $p < 0.05$ (McCune & Mefford 1997) or was not significant (ns).

one microsite type, bryophyte composition clearly varies with microsite type and quality of woody microsites. Further, bryophyte composition is also related to microenvironmental variation at the scale of microsites, mesosites, and stands. Management efforts aimed at preserving bryophyte composition and diversity will need to incorporate this complexity rather than focusing only on substrate availability without consideration of substrate quality or the microenvironmental context.

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