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Predictors of moss and liverwort species diversity of microsites in conifer-dominated boreal forest

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Abstract. Patterns of moss and liverwort species diversity – species richness and species turnover (β-diversity) – in three conifer-dominated boreal forest stands of northern Alberta, Canada are described. We examined the relationship between bryophyte species diversity and micro-environment at two sample grains, the microsite – substrate types for moss colonization: logs, stumps, tree bases, undisturbed patches of forest floor (dominated by feather moss species), and disturbed patches of forest floor – and the mesosite (25 m × 25 m plots). Microsite type and properties (e.g. decay class, hardwood vs softwood, pH) were the principal predictors of bryophyte species diversity and not micro-environment variation among mesosites. Microsite type was the strongest predictor of microsite species richness and β-diversity was higher among microsites and types and within microsites than among mesosites or stands. Microsite properties were significant predictors of species richness for all microsite types. Log and stump decay classes, influenced also by hardwood vs softwood predicted species richness of woody microsite types and soil pH and moisture predicted species richness of forest floor microsites. β-diversity was highest for tree bases and disturbed patches of forest floor and lowest for logs. Mesosite β-diversity was lower than that among microsites, and mesosite species richness was not well explained by measured environmental parameters. Results suggest that in conifer-dominated boreal stands, species richness of microsites is only negligibly influenced by within-stand variation at the mesosite grain and that substrate characteristics are the most important predictors of bryophyte species diversity in this ecosystem.

Keywords: Aspen; Bryophyte; Canada; Cryptogam; Micro-environment; Microsite; Mixed wood; *Populus tremula*, *Populus tremuloides*; Richness; Substrate.

Nomenclature: Anderson et al. (1990) for bryophytes except for *Sphagnaceae* (Anderson1990) and *Hepaticae* (Stotler & Crandall-Stotler 1977); *Orthotrichum elegans* is recognized as a distinct species from *Orthotrichum speciosum* (Vitt & Darigo 1997).

Introduction

A fundamental goal in plant ecology has been to explain observed patterns in species diversity over space. Many studies have explored the relationship of species diversity to ecosystem attributes and processes (Grace 1999; McCann 2000). Habitat attributes perceived to be predictors of plant species diversity, however, are often contingent on the sample frame of the inquiry and on characteristics of the studied taxon (Fahrig 1992; Pharo & Beattie 1997; Dirkse & Martakis 1998).

Bryophytes (mosses and liverworts) have received relatively little attention in studies of biodiversity because of their cryptic nature and small size. This is a concern since many bryophyte species are sensitive to anthropogenic disturbances, such as forest management (Anderson & Hytteborn 1991; Ohlson et al. 1997), and since bryophyte species diversity is not well represented by diversity hot spots of other taxa, specifically vascular plants (Slack 1977; Pharo & Beattie 1997; Dirkse & Martakis 1998).

The occurrence and abundance of some bryophyte species is contingent on the presence of specific substrates (Watson 1980; Kimmerer 1993; Vitt et al. 1995). In landscape level studies, however, species pools, micro-environment (Lee & La Roi 1979), and anthropogenic or natural disturbance (Lesica et al. 1991; Ohlson et al. 1997; Rambo & Muir 1998) are likely to play dominant roles.

Substrates for moss colonization are typically associated with structural elements (microsites) of the forest floor (Vitt et al. 1995). Forest microsites include logs, stumps, tree bases, disturbed and undisturbed patches of forest floor. Micro-environment variables pertinent to bryophyte occurrence and abundance, for example temperature (Skre et al. 1983), soil moisture (Vitt & Pikarinen 1977), and light (Ipatov & Tarkhova 1983), may influence species distributions by controlling the quality or quantity of substrate types available or by directly affecting bryophyte growth and reproduction.

Though bryophytes are responsive to fine-grained

variation in substrate properties (Kimmerer 1996), they are situated within a broader context of coarse-grained environmental heterogeneity (Fahrig 1992). Thus, species occurrence and abundance are likely to be a function of habitat heterogeneity at several sample grains (Kotliar & Wiens 1990).

While there are many studies of bryophyte species diversity at landscape (Robinson et al. 1989; Pharo & Beattie 1997; Dirkse & Martakis 1998; Newmaster 2000; Doubt 2001), and microsite sample grains (Økland 1990; Kuusinen 1994), there are few studies that have examined bryophyte species richness at intermediate sample grains, or that have examined whether species richness of finer sample grains are affected by larger sample grains (Økland 1994).

There is some evidence, however, that bryophyte species richness of microsites might be affected by coarser-grained patterns. Hazell et al. (1998) found that bryophyte species abundance on the trunks of *Populus tremula* was related to the spatial aggregation of trees and Palmer (1990) demonstrated that fine-grained (within 0.1 ha plots) patterns of vascular and non-vascular species were related to coarser patterns (among plots).

The objectives of this study were: (1) to determine whether bryophyte species richness of microsites was related to variation occurring at an intermediate sample grain (mesosites, 25 m × 25 m plots within stands), and (2) to determine which environmental factors had the greatest effect on bryophyte species richness of microsites and mesosites. Variation in bryophyte species composition of microsites and mesosites was examined simultaneously and will be presented in a separate publication (Mills 2001 and in prep.).

Methods

Study site

The study was situated in the Lower Boreal-Cordilleran Ecoregion of northwestern Alberta, 56°47' N, 118°21' W (Strong & Leggat 1992). Mesic sites in this region host boreal mixedwood forest with varying dominance by *Populus tremuloides* and *Picea glauca*. We studied three 10-ha conifer-dominated stands with 70 - 95% conifer by basal area (*BA*) since conifer-dominated stands were thought to have a greater degree of stand complexity and higher bryophyte species diversity than *Populus tremuloides* dominated stands. Stands were composed of *Picea glauca* (*BA* ~ 73%), *Picea mariana* (*BA* ~ 14%), *Populus tremuloides* (*BA* ~ 7%), *Populus balsamifera* (*BA* ~ 3%), and *Abies balsamea* and *Pinus contorta* (both *BA* < 1%), were of natural fire origin and had not been previously managed. Mean estimates of *Picea glauca* ages were similar among the stands: 120-yr stand 1, (S1), 100-yr stand 2, (S2), and 113-yr stand 3, (S3). Some distinguishing structural features of these stands included *Populus tremuloides* trees over 100 yr old, large fallen logs, uprooted trees and stumps and an almost continuous carpet of *Hylocomium splendens, Pleurozium schreberi* and *Ptilium crista-castrensis*. *Sphagnum warnstorfii* dominated ground cover in the wetter areas of S1 and S3**.** Soils of S1 and S3 were imperfectly drained Luvisols (Dark Grey Luvisol, Orthic Grey Luvisol) and the soil of S2 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 (S2) to 4.74 (S1) (B. Kishchuk pers. comm.). Mean daily temperature May-August 1999 was 12.2 °C while cumulative precipitation during this period was 171 mm (R. Hurdle pers. comm.).

Sample design

We used a nested sample design to examine the effect of environmental variation occurring within forest stands on the species richness of microsites (structural elements providing substrates for moss colonization located). Bryophyte species richness was determined for each microsite, mesosite (within stands), and stand. Environmental variables were measured for mesosites and microsites.

We randomly located six mesosites (25 m × 25 m plots) in each of three replicate stands. Within each mesosite five centre points were randomly placed. Circular plots of 2.52 m radius were extended around each centre point. Centre points were also used to facilitate the selection of microsites for bryophyte sampling and as locations to take point measurements of microenvironment data. Circular plots were used to estimate substrate availability within each mesosite.

From each centre point, we selected the nearest microsite of each type (logs, tree bases, stumps, 1-m^2 patches of undisturbed forest floor and disturbed patches of forest floor) to record microsite species diversity. Logs, stumps and tree bases were selected only if their diameter (measured at the widest point for logs and stumps, and breast height for tree bases) exceeded 10 cm. In addition, logs were selected only if they were in contact with the ground and if they were in a decay class beyond decay class 1 (see below), since logs of decay class 1 were floristically similar to tree bases. Disturbed patches of forest floor were limited to areas with a minimum of 25 cm^2 of mineral soil exposed by tree falls, with at least one bryophyte species present. No other disturbance events had exposed mineral soil in areas greater than 25 cm^2 for a long enough period to be colonized by bryophytes. Total surface area of microsites available for colonization

was determined by measuring microsite dimensions. Since microsites differed in size, the surface area sampled varied within and among microsite types (with the exception of undisturbed forest floor which remained constant at 1 m^2). Disturbed patches of forest floor ranged from 0.64 to 4.12 m^2 and the mean area sampled was 0.78 ± 0.33 m^2; sampled tree bases ranged from 0.62 to 3.02 m^2 with a mean of 1.64 ± 0.06 m^2; stumps ranged from 0.07 to 6.89 m^2 with a mean of 0.66 ± 0.11 m^2; and logs ranged from 0.29 to 12.68 m^2 with a mean of 3.43 ± 0.28 m^2. The scarcity of some microsite types (stumps and disturbed patches of forest floor) resulted in an unbalanced sample design with 23 patches of undisturbed forest floor, 72 stumps, 86 logs, 90 tree bases and 90 patches of undisturbed forest floor. Selected microsites that were further than 7 m from centre points (one log and seven stumps) were deemed unrelated to circular plot environmental measurements and were not included for the development of predictive models.

Collection of environmental variables

Substrate availability was estimated by calculating the percent surface area of logs, tree bases (to 1.5 m high), stumps, and disturbed patches of forest floor in relation to the surface area (20 m^2) for each of the five circular plots per mesosite. Substrates were included if they met the criteria used for microsite selection. We recorded species and decay class for logs and stumps, and species for tree bases. Log and stump decay classes were adjusted from Crites & Dale's (1995) modification of McCullough's (1948) seven decay classes as follows: log decay classes: 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, wood soft with small crevices and small pieces lost; 5 = large wood fragments lost, outline of trunk slightly deformed; 6 = wood mostly well decayed, log colonized by herbs and feather moss species, some wood visible; 7 = humification nearly 100%, hard to define as a log, covered by moss and vascular plants; stump decay classes: 1 = inner wood hard, bark intact, neither decayed nor weathered; 2 = inner wood soft, somewhat decayed, bark 100% intact; 3 = inner wood very soft, wood pieces breaking off, some bark missing; 4 = all bark missing, large wood pieces missing, stump becoming overgrown with feather moss. Live moss and litter depth were measured at three random points within each circular plot.

Micro-environment measurements were made at the five centre points within each mesosite. We measured below-canopy Photosynthetic Photon Flux Density, as percent full light, on days with continuous overcast sky using readings from a hand held ceptometer (AccuPAR, Decagon Devices, Inc. Pullman, WA) calibrated with above canopy PPFD taken in an adjacent opening using a quantum point sensor (LICOR Inc.). Soil cores (10.3 cm diameter of the LFH layer, to a maximum depth of 10 cm) were taken after six days of no precipitation. Gravimetric soil moisture was measured as the percent moisture loss after oven drying soils at 105 °C for 6 hr. The pH of air dried mixed soils were determined following the methods of pH determination for organic soils outlined by Kalra (1995), using an 0.01M $CaCl_2$ solution at a soil $CaCl_2$ ratio of 1:7.

Though evaporation rates are important to moss species occurrence (Deltoro et al. 1998), comparing moisture availability across habitats is challenging due to the variability in moss abundance and occurrence among sites. To provide a coarse estimate of relative differences in evapotranspiration after rainfall among mesosites we applied a method similar to that used by Cleavitt (2002) who used the total water gained by 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 over a three week period. Pieces were collected one day after a heavy rainfall. Percent moisture absorption was expressed as percentage of air-dry weight.

At each microsite we measured: total surface area and surface area colonized by bryophytes (all microsite types); species and decay class (woody substrates); and feather moss depth (patches of undisturbed forest floor). Area colonized by bryophytes was measured using a plastic grid. Relative difference among exponential mean temperatures of microsites was measured using the inversion of sucrose to glucose and fructose following the method of Jones & Court (1980). We attached sucrose vials covered with foil to each selected microsite on 14 May 1999 and collected them on 25 August 1999.

Sampling bryophyte species richness

We assessed bryophyte species richness for each selected stand, mesosite and microsite as follows. Within each stand (10 ha) we determined total bryophyte species richness by creating a species list that included: (1) all species found in either microsite or mesosite sampling (see below), and (2) additional species found using Floristic Habitat Sampling (FHS) (Newmaster 2000). FHS involves sampling all unique structural features (which included seeps, wet depressions, areas with a higher proportion of *Populus tremuloides*, or *Picea mariana*). Within each structural feature all microsite types that had not been adequately sampled in mesosites were sampled until no new species were found. Similarly, mesosite species richness included all species found in microsite sampling within the mesosite (see below), as well as those found using FHS within the

mesosite. We sampled each microsite in its entirety in order to capture the complete flora of each microsite type. All bryophyte specimens were collected and identified in the laboratory.

Analysis

Environmental variables

Nested Analyses of Variance (ANOVAs) were performed on micro-environment and substrate availability variables to determine the percent variation explained by the random effects stand and mesosite within stand using PROC GLM and PROC VARCOMP functions in SAS V. 8.01, (1999-2000). All variables were tested for normality using Shapiro-Wilk's test and for homoscedasticity using Bartlett's test (Sokal & Rohlf 1981). Variable significance was tested at an α-level of 0.01 to minimize experiment wise error.

Species richness

We used mixed Analysis of Deviance (ANODEV) with Poisson error distribution to analyze all richness data (McCullagh & Nelder 1983). Since species richness is a count variable it is assumed to follow a Poisson distribution (McIntyre & Lavorel 1993; Mourelle & Ezcurra 1996). Models were built with Poisson error distribution since microsite species richness values were highly skewed towards 0. The fit of microsite and mesosite data to Poisson distribution was assessed by examining the standardized residuals of models for evenness of spread and deviations from 0. When model standardized residuals were not between – 2 and +2 we tested the influence of removing outlying observations. All predictive models for species richness were constructed using the glimmix procedure (SAS V. 8.01 TS Level 01M0, 1999-2000) (Littell et al. 1996) since this model allows the modeling of fixed and random effects for distributions other than normal.

The first model constructed tested whether species richness differed among microsite types. We constructed a complete ANODEV model which included the random factors: stand, mesosite within stand, circular plot within mesosite; the random interactions: mesosite X type and stand X type; and the fixed factor: microsite type. We included all random factors in the model in order to account for variation associated with the spatial structure of our sample design when examining microsite type.

To determine predictors of species richness we constructed separate ANODEV models for each microsite type as well as a predictive model for mesosites as follows: 1. Micro-environment and substrate variables microsite were fit singularly to the model. Variables fit to models included: surface area, bryophyte cover, litter depth, feather moss depth, surface moisture and temperature (all models); hardwood/softwood (all woody microsite models); decay class (stump and log models); soil moisture and pH (mesosite model and models of disturbed and undisturbed patches of forest floor); and substrate availability (mesosite model). 2. Variables that explained a significant amount of additional model deviance in univariate ANODEV models (tested against a χ^2 distribution) were retained and added to the model in a stepwise fashion in descending order of deviance or variance explained. 3. To minimize the influence of spatial variation all random effects and interactions with random effects were retained in models unless they accounted for no variation (were without a coefficient); 4. Interactions between fixed factors were tested and retained if they were significant; 5. Model fit was assessed by calculating the coefficient of determination, R^2 (Sokal & Rohlf 1981) calculated using residual and total deviance, and by using the deviance goodness-of-fit test (Ramsey & Schafer 1997), which uses residual deviance (G^2) as a χ^2 statistic with ($n - l$) degrees of freedom, where n = total number of observations, and l = number of independent fixed factor levels. If the model fit is good, it will not differ significantly from the χ^2 distribution. The importance of random effects in terms of variance or deviance explained was assessed using Wald's test (Littell et al. 1996) which tests the distribution of estimated coefficients using a normal distribution. Since this test is unreliable when sample sizes are small, the lack of significance of the stand spatial scale for disturbed patches of forest floor was confirmed using the likelihood ratio statistic (Littell et al. 1996). Differences among classes for categorical fixed factors were tested using Tukey-Kramer adjusted l-values.

β-*diversity*

To quantify turnover of bryophyte species composition among stands, mesosites, and among and within microsite types we calculated an Adjusted Whittaker's β-diversity (Whittaker 1972). To adjust for sensitivity to sample size we calculated $b = S_t/S_m$ where S_t = the total number of species found among samples at N_{min} (minimum sample size amongst comparison groups) and S_m = the mean number of species found in each sample. Number of species at (S_t) at N_{min} was determined using the species area curve function in PC-ORD for Windows, V3.20 (McCune & Mefford 1997), which subsamples populations 500 × (or with all possible combinations if less than 500) to obtain the average number of species for a given number of samples

Species area-curves

To illustrate variation in species richness with area we generated species area curves using PC-ORD, V3.20 (as described above, McCune & Mefford 1997). The mean area of each microsite type was used. First order Jackknife estimates of species richness were generated using SPSS for Windows (Release 10.05) to fit curves to power and logarithmic functions.

Results

Environmental variation

Micro-environment variables varied significantly among stands and mesosites. Soil moisture, pH and surface moisture varied significantly among stands while light and feather moss depth varied significantly among mesosites within stands (Table 1a). Substrate availability showed no significant variation at the stand level, but the availability of logs and all woody substrates varied significantly among mesosites (Table 1b).

Species richness

The results of the model of species richness including all microsite types indicated that microsite species richness did not vary at the stand or mesosite scale (0% variance explained; not shown). Though a significant amount of variation in bryophyte species richness was explained by microsite type (3% variation explained, $P < 0.001$), circular plots within mesosites (2.5% var. explained, $P = 0.020$), and an interaction between microsite type and mesosite (1.7% var. explained, $P = 0.034$), more than 90% of variation in microsite species richness was left unexplained. The significant interaction between microsite type and mesosite indicates that a small amount of variation among microsite types were contingent on mesosite. Logs had the highest mean species richness of all microsite types, and undisturbed patches of forest floor had the lowest (Fig. 1); this must be interpreted bearing in mind that logs were, on average 3.4 × bigger than undisturbed patches of forest floor.

The ANODEV model constructed to predict mesosite species richness included stand (1.3% var. explained, $P = 0.223$) and availability of tree bases ($P < 0.001$), model fit: $G^2 = 5.27$ ($P > 0.5$), $R^2 = 0.64$; (not shown).

Overall, ANODEV models constructed to predict species richness of each microsite type demonstrated that substrate properties were more influential than factors operating at the stand or mesosite spatial scales. The most important predictors of log species richness, in order of addition to the model were: decay class, surface area, total bryophyte cover, and whether logs were hardwood or softwood, model fit: $R^2 = 0.81$ and $G^2 = 72.35$ ($P = 0.31$) (Table 2). Hardwood logs had higher species richness than softwood logs (not shown) and logs of decay class 5 had higher species richness than decay classes 4 and 2 (Fig. 2).

Measured variables were able to explain only half of the total deviance in stump species richness, model fit: $R^2 = 0.49$, $G^2 = 58.86$ ($P = 0.37$); decay class, surface area and their interaction comprised 35% of variation explained (Table 2). A trend of increasing species richness from early to late stages of decay was not significant when tested with the Tukey-Kramer test.

The best fitting model of bryophyte species richness on tree bases, model fit: $R^2 = 0.34$, $G^2 = 85.11$ ($P > 0.5$), included bryophyte cover (as a polynomial) and tree base surface area (positive relationship) (Table 2). Because bryophyte species richness has been related to the soft-

Table 1. Results of nested ANOVA models for micro-environment variables (**a**) and substrate availability (**b**) presented as percent of total variation (% Var) explained by stand, mesosite and experimental error (circular plots). *df* = degrees of freedom; DC = decay class; HW = hardwood; PPFD = Photosynthetic Photon Flux Density.

a.

Source	Micro-environment variables *df*	Soil moisture % Var.	Soil pH[3] % Var.	Light %PPFD[1,3] % Var.	Surface moisture % Var.	Temperature[1] % Var.	Litter depth[3] % Var.	Feather moss depth % Var.
Stand	2	72**	30**	0	21**	2	10	3
Meso(stand)	15	5*	6	57**	2	19*	12*	42**
Error	72	23	64	43	77	79	78	55

b.

Source	Substrate availability (%) *df* (all)	Logs [2,3] % Var.	Logs[2] DC 3,4,5 % Var.	All woody substrates [2] % Var.	Stumps[1] % Var.	Tree bases [2] % Var.	HW tree base [1,3] % Var.
Stand	2	0	6	0	1	0	0
Meso(stand)	15	28**	5	30**	0	12 ($P = 0.07$)	18*
Error	72	72	89	70	99	88	82

[1]Variable could not be normalized. [2]Variable was log transformed using Log(Y + 0.01). [3]Variable did not meet the condition of homoscedasticity.
Note: interpretations of conclusions involving variables [1] and [3] should be made with caution. *$P < 0.05$, **$P < 0.01$.

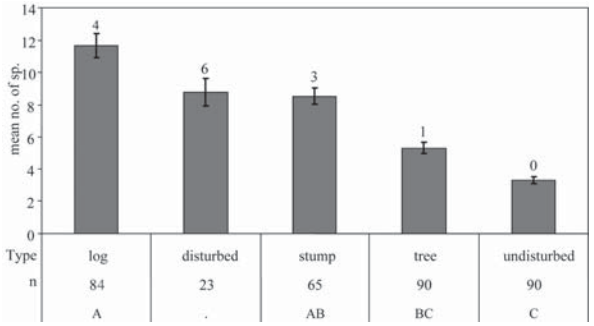

Fig. 1. Mean microsite species richness (± SE) of microsite types. Significant differences between means (adjusted for stand, mesosite and circular plot scales) indicated by different letters. Disturbed patches of forest floor were not included in multiple comparison tests because of their small sample size. Mean surface area of microsite types: disturbed patches of forest floor = 0.78 ± 0.33 m^2; sampled tree bases = 1.64 ± 0.06 m^2; stumps = 0.66 ±0.11 m^2; logs = 3.43 ± 0.28 m^2; undisturbed patches of forest floor = 1.0 ± 0.0 m^2. Number above bars indicate number of species unique to each microsite type.

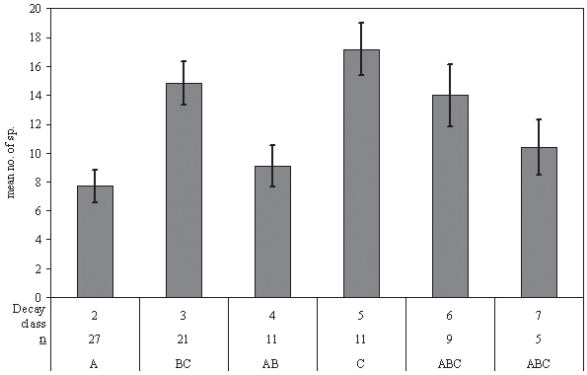

Fig. 2. Mean species richness (±SE) for log decay classes 2-7. Significant differences among means (adjusted for area, bryophyte cover and hardwood/softwood) indicated by different letters.

wood/hardwood nature of tree bases (Culberson 1955; Palmer 1986), we constructed a second model with hardwood/softwood and tree base area as significant explanatory variables. Adjusted mean species richness of softwood and hardwood tree bases differed at $P < 0.05$ though this model had a poorer fit: $G^2 = 113$ ($P = 0.038$).

Variation in species richness of undisturbed patches was not related to any measured environmental parameter model fit: $R^2 = 0.42$, $G^2 = 56.24$ ($P > 0.5$) (Table 2). Because exploratory analysis suggested that patterns of species richness of undisturbed patches differed among stands we constructed separate predictive models for each stand, with mesosite included as a random factor. In S1, where mean pH and soil moisture were highest, the constructed model included soil moisture and pH as significant positive predictors of species richness of undisturbed patches, model fit: $G^2 = 7.56$ ($P > 0.5$). This relationship did not hold in models constructed for the other stands.

Soil pH was the best predictor of species richness of disturbed patches of forest floor, model fit: $R^2 = 0.52$, $G^2 = 22.64$ ($P = 0.36$) (Table 4). A second univariate model, built using area as a predictor of species richness was also significant but had a poorer fit than the model built using pH. Area was not significant when included in a bivariate model with pH.

Table 2. Results of nested ANODEV models of bryophyte species richness for different microsite types: logs, stumps, trees bases, undisturbed patches of forest floor, and disturbed patches of forest floor. Random effects for all substrate types were tested using Wald's test (*Pr Z*). Since this test is unreliable when sample sizes are small, the lack of significance of the stand spatial scale for disturbed patches of forest floor was confirmed using the likelihood ratio statistic (Littell et al. 1996). The random effect mesosite could not be tested for disturbed patches because of a low sample size. No fixed factors were significant in the model of species richness on undisturbed patches of forest floor. Interactions of random factors with fixed factors were only included in models if they had a coefficient > 0. See text for model construction and sampling methodology. %V = percent of total variation explained. r.f .= random factors; f.f. = fixed factors; S = stand; M(S) = mesosite within stand; h/s = hardwood vs. softwood; M = mesosite; E = residual error; A = surface area of microsite; C = % bryophyte cover on substrate; *dc* = decay class; PPFD = Photosynthetic Photon Flux Density.*df* = degrees of freedom.

Logs ($R^2 = 0.81$)			Stumps ($R^2 = 0.49$)			Tree Bases ($R^2 = 0.34$)			Undisturbed patches ($R^2 = 0.42$)			Disturbed patches ($R^2 = 0.52$)		
r.f.	% V	Pr Z	r.f.	% V	Pr Z	r.f.	% V	Pr Z	r.f.	% V	Pr Z	r.f.	% V	Pr Z
S	0	.	S	0	.	S	0.4	0.397	S	47.3	0.185	S	2.5	0.310
M(S)	0	.	M(S)	0	.	M(S)	1.9	0.210	M(S)	13.0	0.107			
M*h/s	4.3	0.034	dc*S	0	0.493									
E	95.7	< 0.001	E	1.0	< 0.001	E	97.7	< 0.001	E	39.7	< 0.001	E	97.5	0.002
f.f.	*df*	Pr > χ^2	f.f.	*df*	Pr > χ^2	f.f.	*df*	Pr > χ^2				f.f.	*df*	Pr > χ^2
dc	5	< 0.001	dc	3	0.061	C	1	< 0.001				pH	1	0.001
A	1	< 0.001	A	1	0.005	C^2	1	< 0.001						
C	1	0.001	A*dc	3	0.001	A	1	0.001						
h/s	1	0.014												

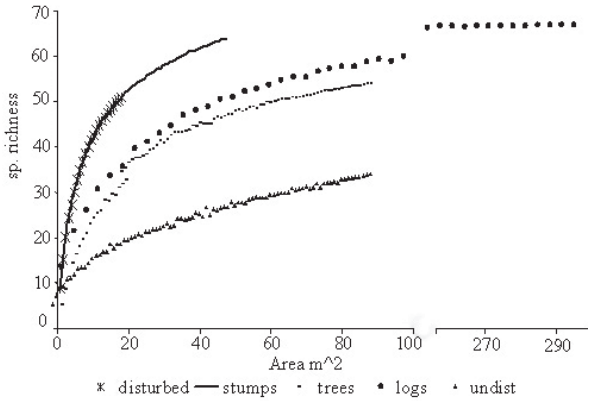

Fig. 3. Species area curves for logs, stumps, tree bases, disturbed and undisturbed patches of forest floor. First order jackknife estimates of species richness (total observed species richness): disturbed patches 64.4 (32), stumps 76.8 (64), tree bases 62.9 (52), logs 68.0 (65), undisturbed patches 45.8 (32), all microsite types 87 (80).

β-diversity

β-diversity was higher among all microsite types than among stands or mesosites (calculated using $N_{min} = 3$, Table 3). β-diversity within each microsite type was highest for tree bases followed by disturbed patches, stumps, undisturbed patches and logs (calculated using $N_{min} = 23$, Table 3).

Species-area curves

The slope of the species-area curve constructed with all 18 mesosites did not approach zero, but did decline dramatically after the addition of nine mesosites (72 - 80 species, not shown). The second-order jackknife estimate of total species richness was 93.6 while the total number of observed species was 80 using mesosite level sampling and 89 using stand level sampling.

All species-area curves fit the power function (R^2 values ranged from 0.86 to 0.99), all curves except for undisturbed patches of forest floor were better represented by logarithmic functions (Fig. 3). This indicates a more abrupt leveling off in species accumulation (slope) in these microsite types. Stumps had the highest estimated species richness (77), followed by logs, disturbed patches, tree bases and undisturbed patches.

Discussion

In this study, bryophyte species richness of microsites was not related to variation within the stand. Bryophyte species diversity (species richness and β-diversity) was most variable among and within microsite types. Microsite properties were more important predictors of microsite species richness than micro-environment, reaffirming the importance of substrate to the occurrence and abundance of many bryophyte species (Watson 1980; Vitt et al. 1995).

Substrate availability and micro-environment variables that varied significantly among mesosites were not significant predictors of species richness of mesosites or microsites. The lack of a clear relationship between mesosite micro-environment and species richness of microsites or mesosites suggests that variation at the mesosite grain in the study stands is unimportant to bryophyte species richness.

Microsite types

Patterns of species diversity (richness, β-diversity and species area curves) in this study differed among microsite types.

These differences are likely partly the result of differences in sizes of the various microsite types. They are in agreement, however, with previous comparisons among substrate types; logs species richness > stump species richness (Kimmerer 1993) and species richness of disturbed patches of forest floor > species richness of undisturbed forest floor (Jonsson & Esseen 1990). Species area curves add insight into these differences; generally microsite types with higher mean species richness (stumps and disturbed patches of forest floor) had a more rapid initial accumulation of species than microsite types with lower mean species richness (trees and undisturbed forest floor) (Fig. 3). Logs, the microsite type with the highest mean species richness however, had a more gradual accumulation of species with increasing area than either stumps or disturbed patches of forest floor because of their large size. Logs and stumps are likely to be species-rich for three reasons: 1. They provide a microclimate favourable for many bryophyte species. 2. They provide substrate above the feather moss carpet allowing the

Table 3. *β*-diversity calculated among stands (Sd), mesosites (Me), all microsite types (Mi), logs (L), stumps (S), tree bases (T), disturbed patches of forest floor (D) and undisturbed patches of forest floor (U) using Whittaker's method (1972), at two different minimum sample sizes (N_{min}).

N_{min}	Sd	Me	Mi	L	S	T	U	D
3	1.13	1.47	2.32	-	-	-	-	-
23	-	-	6.7	4.8	5.68	6.62	5.47	5.8

persistence of less competitive species. 3. They are internally heterogeneous (in terms of decay class).

Though tree bases had relatively low mean species richness, they had the highest β-diversity of all microsite types. Since tree bases hosted a small flora of true epiphytes, occurrences of species for which tree bases were not their primary habitat, were frequent. Moreover, the flora of tree bases included epixylics and forest floor bryophytes found in the nearby vicinity (Mills 2001). This gradual accumulation of species with increased sampled area likely resulted in the high β-diversity (Fig. 3).

The low mean species richness and more gradual species accumulation of undisturbed patches of forest floor are likely related to the species composition and continuous nature of this substrate type. Since undisturbed forest floor is typically dominated by a small number of strong competitors (typically long lived perennials; During 1979), new species continue to be found with increasing sampled area as small pieces of dead woody debris, variation in moisture and pH (Økland 2000), and random colonization events are accumulated. These results mirror those of Jalonen et al. (1998) who found that species area curves constructed using forest floor bryophyte plots in boreal Finland failed to reach a plateau.

Though significant differences existed among microsite types, much of the variation among microsites was not explained by microsite type. This is likely a consequence of the large amount of variation within each microsite type related to specific substrate characteristics.

Microsite properties

Factors explaining log and stump species richness were almost identical suggesting ecological similarity. Log species richness in this study peaked at log decay stage 5, while bryophyte species richness on logs in other studies peaked at decay stage 6 (Crites & Dale 1995; Kruys et al. 1999). This slight discrepancy may be the result of a large proportion of liverworts in our microsite species pool (24%). Liverwort species richness often peaks on logs of decay stages 4 - 5 (Crites & Dale 1995; Kruys et al. 1999). The low species richness of logs of decay stage 4 is likely a result of bryophyte community turnover that accompanies the loss of bark from logs as they decay. Since logs of decay class 4 had 'little or no bark remaining', they were typically devoid of epiphytes, while they were not sufficiently decayed to have a large set of epixylics. In contrast, logs of decay class 3 (logs with less than 50% of their bark remaining), by having both intact bark and decayed wood, provided habitat for epiphytes as well as epixylics (for further discussion of species composition see Mills 2001).

Whether logs and stumps were hardwoods or softwoods was a significant predictor of their species richness. This may be explained by higher establishment success (McAlister 1995) or persistence of bryophyte species on hardwood logs. Bark characteristics governing differences in the number of bryophyte species growing on hardwood and softwood trees likely influence the number of species present on fallen logs and stumps (see below). We found that hardwood tree bases, stumps and logs were compositionally similar (Mills 2001), suggesting that log and stump communities are influenced by the initial floristic composition of the newly fallen tree.

Bryophyte species richness on tree bases was predicted by area of tree base available for colonization, total bryophyte cover, and whether tree bases were hardwood or softwood. Hardwood tree bases had higher bryophyte cover and species richness than softwoods. Culberson (1955) and Palmer (1986) found compositional differences between hardwood and softwood trees, hypothesizing that these were a result of the drier, more acidic nature of conifer bark.

Species richness of undisturbed patches of forest floor was positively related to soil pH and moisture in S1. S1 had higher mean soil pH and moisture than S2 or S3 (though the ranges of these variables were similar for all stands). Other studies have found moisture to be the most important factor explaining bryophyte species diversity (Robinson et al. 1989; Frisvoll & Prestø 1997). If the study extent had encompassed a wider range of soil moisture and pH values we may have found a stronger relationship between these microclimatic factors and the bryophyte species richness of undisturbed patches of forest floor as well as higher a β-diversity for undisturbed patches of forest floor.

Species richness of disturbed patches of forest floor was positively related to their size and the soil pH of the mesosite. Though Jonsson & Esseen (1990) did not find species richness of disturbed patches to be related to pH, higher pH has been linked to bryophyte species richness in other studies (Robinson et al. 1989; Zamfir et al. 1999).

Species composition was more variable among microsites than among mesosites (β-diversity was greater among microsites than among mesosites or stands). Other authors have also found an inverse relationship between b-diversity and plot size (Smith & Urban 1988; Økland 1990). Since fine sample grains encompass less heterogeneity, they are less likely to underestimate habitat complexity, or overestimate a species' occupied niche (Palmer & Dixon 1990). Thus at coarser sample grains, species occurrence is likely to become more homogeneous. In this study, microsite type and properties were

the most important determinants of bryophyte species richness and best explained differences in species composition (β-diversity). These results endorse the use of microsite and within microsite sample grains to better understand patterns of bryophyte species diversity.

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