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Bryophyte species composition and diversity at different scales in conifer-dominated boreal forest stands

by

Suzanne Elizabeth Mills 

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

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Only what is entirely lost – demands to be endlessly named: there is a mania to call the lost thing until it returns.

-Günther Grass

Abstract

I examined patterns in bryophyte species diversity and composition at different scales in the boreal forest. Bryophyte occurrence and abundance were sampled at three scales: stand (10 ha); mesosite (25 X 25 m plots); and microsite (substrate types for moss colonization: logs, stumps, tree bases, undisturbed patches of forest floor and disturbed patches of forest floor). I used log-linear regression to model species richness and multivariate analyses to examine bryophyte species composition.

Microsite type (and not stand or mesosite spatial scales) was the principle driver of bryophyte species richness. Microsite properties (hardwood vs. softwood and log and stump decay class) dictated species occurrence on woody microsite types; hardwood logs of decay class 5 were most speciose and hardwood and softwood substrates were compositionally different. Soil pH and moisture were positively related to species diversity of forest floor microsites and explained stand scale variation in species composition of mesosites and forest floor microsites.

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Chapter 1: Introduction

Bryophyte species in the boreal forest

The boreal forest is the largest forested eco-region in the world, covering 14.7 million km^2 (Carleton 1991). Bryophyte species are diverse, abundant and functionally important in the boreal forest. They insulate the forest floor and soil from solar heating (Ipatov & Tarkhova 1983), increase the retention of nutrients from precipitation and provide a source of food for invertebrates (Longton 1984). The cryptic nature of bryophytes, however, has precluded their inclusion in forest inventories and limited the number of scientific studies on their ecology; the result is an incomplete knowledge of the distribution and ecology of bryophyte species in the boreal forest. This is problematic because many bryophyte species are sensitive to forest management (Anderson & Hytteborn 1991, Ohlson et al. 1997) and bryophyte species diversity is not well represented by diversity hotspots of other taxa, specifically vascular plants (Slack 1977, Pharo & Beattie 1997, Dirkse & Martakis 1998). Knowing to what extent habitat parameters are driving bryophyte species diversity and composition would facilitate bryophyte conservation and monitoring efforts.

Upland conifer-dominated mixed-wood boreal forest stands are structurally diverse. They are often older than aspen-dominated boreal stands (La Roi 1992) and thus have greater structural heterogeneity. Økland (2000) found that small scale processes in the Finnish boreal forest (such as tree falls and fine-scaled paludification), were more important for bryophyte species composition than time since disturbance in stands over 100 years old. In Finland, the abundance of birch logs peaked at 100 years post disturbance, while the peak in spruce logs occurred after 300 years post disturbance (Kuuluvainen 1994). These structural attributes can affect the bryophyte community composition of spruce dominated boreal forest. For example, La Roi & Stringer (1976) found different bryophyte communities on tree bases, disturbed patches of forest floor, undisturbed forest floor and dead wood substrates. Species abundance and composition of stands also varied as a result of geography and moisture conditions (La Roi & Stringer 1976).

Factors controlling bryophyte species diversity and composition

There is a well-developed discourse on whether habitat availability (Watson 1980, Vitt et al. 1995) or dispersal limitations (Hedersson 1992, Herben 1994) have greater importance in determining bryophyte species occurrence and abundance. Species richness (the number of species) is the most simple measure of species diversity. Habitat heterogeneity was related to bryophyte species richness in peatlands (Vitt et al. 1995), and is thought to be the cause of differences in bryophyte species richness between managed and non-managed boreal forest stands (Söderström 1988a, Jonsson & Esseen 1990, Lesica et al. 1991, Ohlson et al. 1997). Conversely, dispersal appears to be important for species reliant on substrate types which are temporally unstable or rare (Herben 1994).

At small scales, habitat parameters thought to dictate the occurrence of bryophyte species are divisible into two broad categories: microclimatic variables and substrate characteristics. Substrates supporting bryophyte communities are often associated with structural elements of the forest floor (Vitt et al. 1995, Vitt & Belland 1997) while microclimatic variables important for bryophyte species are more likely to vary along a continuum (Bell et al. 1993).

a) Substrates for bryophyte colonization

The nature of substrates for bryophyte colonization (hereafter termed "microsites") affects bryophyte species occurrence. Microsite types such as logs, stumps, trees and disturbed and undisturbed patches of forest floor, have different physical properties which may affect bryophyte species occurrence. These include: substrate moisture availability; substrate chemistry; the spatial distribution of substrates; temporal variability of substrates; and the frequency of small scale disturbance on a given substrate disrupting the competitive dominance of faster growing species. Thus differences in species diversity and composition between microsite types are expected. Jonsson & Esseen (1990) documented higher bryophyte species richness in patches of disturbed

forest floor relative to undisturbed forest floor and Slack (1977) documented compositional differences (in terms of species importance) between substrate types in the Adirondacks.

Variability within each microsite type can also influence bryophyte species occurrence. The temporal variability of logs as they decay supports a change in bryophyte community composition (McCullough 1948, Muhle & LeBlanc 1975, Söderström 1988b, Söderström 1989, Crites and Dale 1995), and epiphytic bryophyte species often have preferences for certain tree species (Palmer 1986), or for trees with large diameters and/or rough bark (Lesica et al. 1991, Hazell et al. 1998).

b) Microclimate

Moisture is also an important determinate of bryophyte species occurrence. While most bryophyte species are drought tolerant, surface water is one of the most important factors controlling growth (Vitt & Pakarinen 1977, Vitt 1989, Vitt 1990). Mesic sites with fine soil texture in forest-tundra were found to have a greater number of moss species than dry sites with coarse soil (Robinson et al. 1989), and *Pleurozium shreberi*, one of the dominant pleurocarps of the boreal forest, was found to be especially sensitive to moisture conditions (Longton & Greene 1979). Though bryophyte species differ in their response to moisture gradients (Yenhung & Vitt 1995), the significance of moisture to bryophyte species diversity is evident as species richness varies more along moisture gradients than elevational ones (Lee & La Roi 1979).

Temperature and light are also related to bryophyte abundance. Temperature and relative humidity relate to bryophyte growth because they determine the vapour pressure deficit of bryophyte species (Skyre et al. 1983). Mosses were more abundant on cold soils under a coniferous canopy than a deciduous one (Jeffrey 1963, Viereck et al. 1983), and moss cover in Russian *Pinus* forests decreased upon increasing illumination (Ipatov & Tarkhova 1983).

c) Dispersal

Some authors argue that it is dispersal that ultimately controls bryophyte species occurrence. Although bryophyte spores are small and wind dispersed, which makes them capable of long distance dispersal (van Zanten 1978), many species reproduce predominantly through vegetative propagules and fragments, and differences in dispersal distances have been related to spore size (During & van Tooren 1986). Moreover, evidence of clumped species distribution in the absence of clumped substrates (Söderström & Jonsson 1989), and of higher asexual reproduction in rare bryophyte species than in their non-rare counterparts (Hedderson 1992), suggest that dispersal is a driver (at least in part) of bryophyte community composition. Whether or not some species are dispersal limited does not negate the importance of habitat to bryophytes species occurrence. Herben (1994) proposes that the persistence and size of habitat is a key factor determining whether a species is dispersal limited. Thus the temporal variability and spatial discontinuity of microsite types is likely important to bryophyte species occurrence (Herben & Söderström 1992). For example, species with short life spans on temporary habitat patches require more efficient dispersal for persistence and are more likely to be dispersal limited. Thus forest fragmentation, by increasing distances between habitat patches and reducing patch size will have more severe consequences for fugitive species reliant on frequent dispersal than on their long-lived counterparts (Herben & Söderström 1992). In this respect habitat is not only important in and of itself, but may also dictate the level of dispersal needed for species persistence.

In the broad picture, however, bryophytes are considered to be situated at the bottom of Grime's triangle. Here they exist by being stress tolerant, by exhibiting ruderal life strategies, or by some combination of the two; their ability to disperse widely and tolerate unfavorable conditions is more vital to their persistence than competitive ability (Grime 1977). Thus bryophyte species are often opportunistic (Slack 1977), or are habitat specialists (Söderström 1993). The broad distributions of many locally uncommon species (Vitt & Belland 1995) suggests that dispersal is relatively less important for bryophyte species occurrence than for the occurrence vascular plants (Vitt

& Belland 1997). Rather, the poor competitive ability of most bryophyte species limits their occurrence to unoccupied or specialized substrates that may themselves be rare.

Bryophytes in relation to scale

Few studies have had the principle focus of comparing bryophyte communities across spatial scales. Multi-scale studies by Økland (1994) and Zamfir et al. (1999) were restricted to small (<1 m^2) spatial scales and to bryophyte species growing on the ground. Results of other studies, however, suggest that patterns of bryophyte species occurrence are affected by variation at more than one spatial scale. Kimmerer & Allen (1982) found that riparian bryophyte community composition was influenced by both small scale variation in disturbance level and larger scaled variation in elevation. Moreover Økland (2000) found bryophyte species in Finish boreal forest to vary at two spatial scales. Bryophyte species composition responded to between stand variation in time since last disturbance as well as smaller scaled within-stand variation in stand structure (Økland 2000). Further, Muhle & LeBlanc (1975) describe differences in bryophyte communities of logs in relation to the log's spatial position (i.e. proximity to water bodies, stones).

Regardless of the existence of within-stand variability in microclimate of the boreal forest (Kuuluvainen 1994), spatial scales within the stand but larger than microsite spatial scales are generally overlooked. Newmaster (2000) found that variation in species composition of coastal and interior forests in British Columbia were related to mesohabitats; these are consistent physiognomic or physiographic features which represent areas of unique bryophyte habitat (Vitt & Belland 1997)). Mesohabitats may be either restricted (have defined boundaries, for example a stream or a cliff) or unrestricted (not have defined boundaries, for example a forest type) (Newmaster 2000). In most upland boreal mixed wood stands there are few to no "restricted mesohabitats" as defined by Newmaster (2000), hence in reality there is only one mesohabitat: conifer-dominated forest.

The scale at which bryophyte habitat heterogeneity affects species diversity is important to bryophyte management. Criteria for the maintenance of ecosystem diversity need to be relevant on a variety of organizational levels and take into account different

spatial scales (Noss 1990) since often species are responding to more than one spatial scale (Fahrig 1992). Structural heterogeneity viewed at the landscape level often increases with management while stand level heterogeneity decreases, having important implications for species diversity (Dettki & Esseen 1998). At the regional level bryophyte diversity may be determined by the presence of a variety of physiographic or physiognomic forms (Vitt & Belland 1997), or the moisture regime of the area (Lee & La Roi 1979). Variation at larger spatial scales may affect species diversity at small spatial scales and vice versa.

Implications for community processes

The stability of a community can be defined as the tendency for species assemblages to persist over time in a state of relative equilibrium (Krebs 1985). Thus stable communities are often characterized by fully occupied niches while unstable communities are changing over time, influenced by immigration and emigration. Cornell & Lawton (1992) and Srivastava (1999) have used the relationship between local and regional richness to infer niche saturation (when immigration=extinction in a community (Lincoln et al. 1982)). If species richness at fine-grained scales (local richness) is proportional to species richness at coarser-grained scales (regional richness) we can conclude that local habitats are unsaturated because their richness is being determined by the regional species pool (Cornell & Lawton 1992). If, however, local richness is independent of regional richness, then we can conclude that local habitats are saturated because the regional species pool is not dictating species composition. Moreno & Halffter (2000) relate the degree of saturation for a given community to the shape of its species area curve; an asymptotic species area curve suggests that a community is reaching a state of saturation while a non-asymptotic curve is indicative of unstable community structure (Moreno & Halffter 2000).

Unanswered questions

In synthesis, bryophyte species diversity appears to be dictated by a forest's structural diversity: small-scale disturbance, presence of fallen logs, and variation in tree size. Whether a species can take advantage of the substrate provided by the microsite, however, may depend on surrounding environmental factors; for bryophytes, this may be those affecting plant water content, a principal limitation to photosynthesis (Skyre et al. 1983). To determine if these relationships exist, the scale and degree of the relationship between habitat availability and species diversity must be examined. Neitlich & McCune (1997) have addressed how within stand microsite availability affects lichen species diversity in Swann Valley Montana, however this has not yet been attempted for bryophytes.

Few studies have looked at bryophytes in northern Alberta boreal forest (but see La Roi & Stringer 1976, and Crites & Dale 1995), consequently, the nature of bryophyte communities in this region are relatively unknown. In this study I attempted to discern how habitat is related to bryophyte species composition and diversity in the boreal forest at substrate specific (microsite) and within-stand (mesosite) spatial scales. I used the relations between species composition, diversity, and habitat at different spatial scales to infer ecological properties of bryophyte communities.

Chapter 2 addresses the influence of habitat and spatial scale on bryophyte species diversity. I examined whether bryophyte species richness, evenness, beta diversity, and species area curves varied between microsite types, whether species richness of each microsite type was influenced by substrate characteristics and/or variation at larger spatial scales, and whether species richness at the mesosite scale related to patterns observed at the microsite scale. The underlying cause of the patterns observed in Chapter 2 became evident in chapter 3 where I discussed bryophyte species associations at microsite and mesosite spatial scales and how they varied in response to microsite characteristics and variation at larger spatial scales.

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Chapter 2:

Predicting bryophyte species diversity at two scales in conifer dominated boreal forest.

Introduction

Heterogeneity exists at many temporal and spatial scales in an ecosystem (Fahrig 1992). Although bryophytes are responsive to habitat variation at fine grained scales (Økland 1994, Kimmerer 1996), they are still encompassed by larger ecosystems which are variable at many spatial scales. The breadth of environmental variation at fine-grained scales may be dictated by environmental heterogeneity of coarser-grained scales. Ultimately, species occurrence and abundance are likely a function of variability acting at many spatial scales (Kotliar & Wiens 1990). The extent to which processes operating at one scale are linked to patterns observed at other spatial scales defines the hierarchical complexity of the ecological system (Allen 1984 et al.) and provides clues about community stability (Cornell & Lawton 1992, Srivastava 1999).

Bryophyte species occurrence and abundance at fine-grained scales is contingent on the presence of specific substrates (Watson 1980, Kimmerer 1993, Herben 1994, Vitt et al.1995, Vitt and Belland 1997). At coarser-grained scales, however, regional species pools, microclimate (Lee and La Roi 1979, Molau & Alatalo 1998, Pitkänen, 2000), and anthropogenic or natural disturbance (Ohlson et al. 1997, Rambo & Muir 1998, Lesica et al. 1991) 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, Vitt & Belland 1997). To a lesser or greater degree, forest microsites, logs, stumps, tree bases, and disturbed patches of forest floor, are temporally unstable (Slack 1990) and spatially isolated. Consequently, bryophyte communities on these microsites may be in non-steady states; they are more likely to be governed by establishment and dispersal rather than by interspecific interactions (Slack 1990). Undisturbed forest floor diverges from other substrate types by not having clear boundaries and by being less variable over time.

Microclimatic variables pertinent to bryophyte occurrence and abundance (i.e. temperature, soil pH and moisture, light) are likely to be continuous (Bell et al. 1993) and

not readily divisible into discrete habitat patches. Microclimate may influence species distributions by controlling the quality or quantity of substrate types available or by directly affecting bryophyte growth and reproduction.

Though habitat may influence species diversity, stochastic factors controlling species dispersal, establishment and persistence may hold equal importance. Söderström & Jonsson (1989) and Kimmerer (1994), found clumped species distributions in the absence of clumped habitats, demonstrating the influence of dispersal on species occurrence. Spatial scales of importance for bryophyte species occurrence may not only be linked to the scales at which important environmental factors are heterogeneous, but also to scales at which autoecological mechanisms are taking place.

While there are many landscape scale (Robinson et al. 1989, Wolf 1993, Pharo & Beattie 1997, Dirkse & Martakis 1998, Newmaster 2000, Doubt 2001), and microsite scale (Økland 1990, Kuusinen 1994) studies of bryophyte species diversity, there are few studies at intermediate spatial scales, or at more than one spatial scale (Økland 1994). Despite the lack of studies, there is some indication that large scale variation may be affecting bryophyte species at smaller scales. Hazell et al. (1998) found that the abundance of four bryophyte species on aspen tree bases was related to their spatial aggregation at a larger spatial scale. A study by Palmer (1990), which included but did not differentiate bryophytes from other vegetation, demonstrated significant positive associations between vegetation patterns within 0.1 ha plots and patterns among-plots (thus large scale patterns were related to small scale patterns).

The objective of this study was to identify patterns in bryophyte species diversity at microsite and mesosite spatial scales in conifer dominated boreal forest. I hypothesized:

(H.1) that variation in microsite species diversity would be a function of microsite type, microsite properties and variation occurring at larger spatial scales; and

(H.2) that the driving factors of bryophyte species diversity at the mesosite scale would be related to factors operating at the microsite scale.

To test these hypotheses I:

(Q.1) determined whether environmental factors thought to be important for bryophyte species were heterogeneous at measured spatial scales; and

(Q.2) examined if bryophyte species diversity of microsites and mesosites varied at mesosite and stand spatial scales; and

(Q.3) constructed predictive models linking bryophyte species diversity of mesosites and microsite types to microclimate, substrate characteristics, and spatial scale.

The relevance of results to bryophyte ecology will be discussed in the context of hierarchical complexity and community stability.

Methods

Study area

I assessed patterns of bryophyte diversity in northwestern Alberta, north of Hines Creek, in the P2 forest management area, township 90, Range 03, W6M 56°N and 118°W. The study area is located in the Lower Boreal-Cordilleran Ecoregion, a region typified by co-dominance of *Populus tremuloides* Michx., *Populus balsamifera* L., *Pinus contorta* Loudon *Picea mariana* (Mill.) BSP. and *Picea glauca* (Moench) Voss, rolling topography and a more tempered climate than adjacent Boreal Forest subregions (Beckingham et al. 1996). Mean daily temperature May-August 1999 was 12.25 °C while cumulative precipitation during this period was 171.19mm (Rick Hurdle 2000 pers. comm.). In this area soils are either luvisolics and brunisolics (well drained areas) and gleyed luvisols and gleysolics (poorly drained areas) (Achuff 1992) and the dominant vegetation is mixed boreal forest characterized by a high proportion of *Populus tremuloides*, *Populus balsamifera* mixed with *Picea glauca* and *Picea mariana* in the canopy. Canopy composition in conifer dominated sites of this area is dominated by *Picea glauca* (~ 73%), with some *Picea mariana* (~ 14%), *Populus tremuloides* (~ 7%), *Populus balsamifera* (~ 3%), and *Abies balsamea* and *Pinus contorta* (both < 1%).

Study site

The study stands were located within the EMEND (Ecosystem Management Emulating Natural Disturbance) experimental area. This is a large-scale forest management project aiming to better understand dynamics of natural disturbance in the boreal forest and the capacity to which these can be replicated using alternative forest harvesting practices. Stand forest types were determined by canopy cover designations of Alberta Vegetation Inventory maps, followed by ground truthing the first summer of the project. (conifer dominated = 70-95% conifer composition).

I limited the scope of my study to the older boreal forest which often has a greater degree of stand complexity and higher bryophyte species diversity than the younger boreal forest (Laaka 1992).

To better understand which factors lead to high bryophyte species diversity within stands, I focused my study on three, 10 ha conifer dominated stands (basal area with 70-95% conifer composition), EMEND stand numbers 889, 918 and 930 (hereafter called stands 1, 2 and 3). Stands were of natural fire origin and had not been previously managed. Stands were classified as separate stands by AVI (Alberta Vegetation Inventory polygons which classify forest by age, canopy, understory composition), were no closer than 2.2 km from one another, and were physically separated by water bodies. Mean estimates of *Picea glauca* ages were similar between the three stands: 120 y (stand 1), 100.3 y (stand 2), and 113.4 y (stand 3) (EMEND core data 1998). These are underestimates because tree growth to DBH was not accounted for (Peters et al. 2001 pers. comm.). Each stand contained some *Populus tremuloides* trees over 100 years old (EMEND core data 1998), and had a large amount of structural diversity due to large fallen logs, uprooted trees and stumps. The forest floor was covered with an almost continuous carpet of *Hylocomium splendens*, *Pleurozium schreberi* and *Ptilium crista-castrensis*. *Sphagnum warnstorfii* dominated ground cover in the wetter areas of stands 1 and 3.

Sample design

I used a nested sample design (Figure 2.1) to look at scale dependent determinates of bryophyte species diversity. I determined bryophyte species richness at three scales: the stand (10 ha), the mesosite (25 x 25 m plots to capture within stand variation), and the microsite (structural elements of the boreal forest providing unique substrates for moss colonization). Each scale (sample grain) was nested within the scale of the next order of magnitude. Thus I sampled up to 25 microsites in each mesosite, and six mesosites in each of three stands.

I located mesosites within each stand by randomly choosing grid squares from a ruled map. I discarded locations that were less than 30 m from stand edges or within 100 m of the boundary of another mesosite.

Within mesosites, the random placement of five centre points served two functions: they facilitated microsite selection, and they became permanent points for the sampling of environmental variables for the mesosite. The five center points were located by dividing the mesosite into 5 - 5 X 25m blocks and randomly selecting 1 point within each (see Figure 2.1). At each centre point, the nearest microsite of each type (logs, tree bases, stumps, $1m^2$ patches of undisturbed forest floor and disturbed patches of forest floor) were sampled provided they were within a 7m radius of the centre point and they met suitability criteria (Table 2.1). Because logs of decay class 1 were prevalent and floristically similar to trees they were not sampled at the microsite level in order to increase the sample size of logs of latter decay stages. Though it was theoretically possible to have 25 microsites sampled per mesosite (5 microsites X 5 centre points), this was never the case due to the scarcity of some microsite types (stumps and disturbed soil patches). In total, 22 patches of disturbed soil, 72 stumps, 86 logs, 90 trees and 90 patches of undisturbed soil were sampled. Circular plots extending 2.52m from each centre point (to form circular plots of 20 m^2) were used to sample substrate availability at the mesosite scale (see below).

Data collection

Environmental and substrate availability measurements were taken at each circular plot within each mesosite. Point measurements were taken from the centre of each circular plot.

Substrate availability was evaluated by measuring the dimensions of all logs, tree bases (to 1.5 m high), stumps, and disturbed patches of forest floor located within the circular plot (Table 2.1). Criteria for the inclusion of logs, stumps, trees and disturbed soil patches were identical to those used for microsite selection, with the addition of including logs of decay class one. Portions of logs and disturbed patches lying outside of the 2.52m radius circular plot were not included. Trees and stumps were included if more than 50% of their base was within plot boundaries. I recorded species and decay class (Table 2.2) for logs and stumps, species for trees, and approximate age for disturbed patches within the circular plots. Live moss and litter depth were measured at three random points within the circular plot.

I measured below canopy Photosynthetic Photon Flux Density, PPFD on days with continuous overcast sky (July 27, 29 and 30, 1999). Gendron et al. (1998) found instantaneous measurements of light transmittance on sunny days to overestimate PPFD in high light and underestimate PPFD in low light. There is evidence that light transmittance measurements taken on overcast days are less variable, and that these measurements are a more accurate representation of mean daily PPFD values (Messier & Puttonen 1994, Messier & Parent 1996).

Below canopy PPFD of wavelengths from 400 to 700nm was measured in micromoles [μ]/cm/second using a hand held ceptometer (AccuPAR, Decagon Devices, Inc. Pullman, WA) composed of 80 sensors. Readings from a quantum point sensor (LICOR Inc.), in an adjacent clear cut simulated above canopy PPFD. At each circular plot I took 12 readings while sweeping the ceptometer around the centre point 1m above the ground and recorded the average reading. All readings were taken between 10:30 am and 2:00 pm. The point light sensor and ceptometer were calibrated in full light with one another before and after light measurement in each stand. Below canopy readings were

calibrated and then divided by the clear-cut readings (which were taken simultaneously) to obtain %PPFD expressed as percent full light for each point.

Soil samples were taken on August 15th, 1999, after six days of no precipitation, to determine soil moisture content and pH. A 10.3 cm diameter core of the LFH layer, to a maximum depth of 10 cm was taken from the centre point of each circle plot. LFH layers were individually double sealed in plastic bags. Samples were stored in cool conditions for 48 hours. On August 17th, we manually mixed and subsampled each sample. Subsamples (21g-45g) were placed in pre-weighed tins, weighed to the nearest hundredth gram, dried at 50°C until there was no change in weight, (10 days), and reweighed. Percent moisture loss was calculated based on wet weight because of the high organic content of the soils.

The non-subsampled portion of each soil sample was used to determine the pH of the LFH layers. Soil was air dried for 60 days and passed through a 2mm sieve. Large fragments, excluding sticks over 1cm in diameter, were ground mechanically to 2mm. Subsamples from each sample were used to create a soil solution with a 7:1 ratio of 0.01 M $CaCl_2$ to soil by weight. In acid forest soils pH measurements are less affected by air drying if $CaCl_2$ solution is used rather than water (Courchesne et al. 1995). Some light weight samples required ratios of 9:1, 13:1 and 15:1. Each solution was stirred 2 times and allowed to sit ½ hour. Readings of supernatant pH were made using an electrode pH meter. Running one standard every 10 samples ensured reading accuracy.

The difference in surface water evaporation between sites after rainfall was measured with pieces of cork tile of dimensions 5 X 15 X 0.8 cm. I placed marked cork pieces at the surface of the soil, above soil litter but below live vegetation, at each centre point. Cork pieces remained out for one week at the beginning of July, and were collected one day after a rainfall. Cork pieces were sealed in plastic bags for transport. I recorded wet weight of cork pieces on the day of collection and reweighed them after oven drying. Percent moisture absorption was calculated based on the dry weight of the cork peices.

I measured the microtopography of each mesosite by recording the height difference between the mesosite centre and each circle plot centre point using a cladometer and a surveying rod. The variance of the elevation measurements within each

mesosite was used as a proxy for the amount of microtopography present in each mesosite.

At each circular plot, an unbroken *Hylocomium splendens* stem was collected. The number of intact modules and the length of the module corresponding to summer 1998 growth were recorded to determine if *Hylocomium* decomposition or growth could act as indicators of bryophyte diversity, or approximate measured environmental variables.

The inversion method of sucrose to glucose and fructose was used to measure the relative difference between exponential mean temperatures at each microsite. Since the rate of sucrose inversion varies as a function of temperature and pH, the conversion becomes a function of only temperature when pH is kept constant with the use of a buffer (Jones & Court 1980). This method has been used successfully in a plant distribution study in Newfoundland (Damman 1976). Because this method is sensitive to both mean temperature as well as temperature extremes it is thought to reflect the sensitivity of physiological processes to temperature change. This technique was suitable for temperature measurement at the microsite level because sucrose vials are cost effective and small in size.

Sucrose vials were placed at each marked microsite. The preparation of sucrose vials was adapted from Jones and Court (1980): A 386.2g-sucrose/L solution buffered at a pH of 3 with sodium citrate-HCl (approximately 100mM). Sucrose vials were kept frozen for storage and transportation before placement at each microsite. Relative temperature was measured from May 14 until August 25, 1999. Vials were attached to the outer surface of logs, stumps, and trees with wire, approximately 10-20cm above the forest floor. Foil coverings shielded vials from direct sunlight at all microsite types except undisturbed forest floor. The feather moss provided shield from the sun at undisturbed sites. Sucrose vials were collected and kept frozen until analysis (January 2000). Vials were removed from the freezer 13-19 hours before being analyzed. The amount of sucrose inversion was determined by measuring the rotation angle of the solution from each vial using a Perkin Elmer 241 polarimeter.

Bryophyte diversity

Bryophyte species richness was assessed at each of the spatial scales of interest: the stand, the mesosite and the microsite. The maximum extent for all grains was the delineation of the three sampled stands.

Total bryophyte and vascular plant species richness for each stand were determined by creating a species list that included: 1. all species found in either microsite sampling (see below) and 2. additional species found using FSH sampling at the mesosite and stand scales. Bryophyte species lists at the stand level were supplemented using an adjusted form of Floristic Habitat Sampling (FHS) (Newmaster 2000) . This method maximizes the number of species found in an area by focusing the researcher's sampling effort on structural features with unique bryophyte species composition (Newmaster 2000). Though FHS is typically done without pre-determined search boundaries we limited our search to the 10 ha of each stand. Unique structural features in the sampled stands included seeps, wet depressions, areas with a higher proportion of *Populus tremuloides*, and one stream (stand 1). Within each structural feature, all microsite types (Table 2.1) that had not been adequately sampled in mesosites were sampled until no new species were found. Two people sampled each stand within a 3.5 to five hour time window, sampling time varying in accordance with the habitat diversity of the stand. Vascular plant species lists for each stand were also tabulated during this process.

Mesosite scale

Bryophyte species diversity at the mesosite scale was also assessed using a combination of FHS and plot sampling. Because mesosites were only 625 m^2, they rarely extended across more than one unique structural feature of the landscape. Thus FHS sampling sought to ensure that all variants of each microsite type within the mesosite were sampled extensively. Bryophyte species richness at the mesosite scale was determined by creating a species list that included all species found in microsite sampling

within the mesosite (see below), in addition to the species found using FHS. To estimate the abundance of bryophyte and vascular plant species the abundance scale developed by Vitt et al. (1990) was adjusted by adding a fourth category as follows; 1 = one to few occurrences; 2 = frequent occurrences in one area of the mesosite or several occurrences in more than one area of the mesosite; 3 = frequent occurrences throughout the mesosite; 4 = greater than 70 % total ground cover, dominant understory species. Vascular plant species richness was determined by scanning the mesosite for all vascular plants.

Microsite scale (within mesosite)

Each microsite was measured and described according to Table 2.1
Moss species diversity was evaluated on each microsite by searching the entire surface of each log, stump, disturbed and undisturbed patch, and the tree trunk/base below breast height. I estimated the total abundance of each species by measuring the total area of cover to the nearest 7.9 cm^2 using a 5.4 X 5.4cm flexible plastic grid. I collected all unknown species. Species abundance measurements were converted to % of surface area to account for differences in microsite size. Because 1 m^2, undisturbed forest floor plots maintained constant dimensions, species were estimated visually to the nearest % cover.

Species identification

I identified to species all bryophytes found in 1,621 samples (3,570 bryophyte specimens). Bryophyte nomenclature follows: Anderson et al. (1990) except for the following taxa: Sphagnaceae follows Anderson (1990), Hepaticae follows Stotler, & Crandall-Stotler (1977), and *Orthotrichum elegans* is recognized as a distinct species from *Orthotrichum speciosum* by Vitt & Darigo (1997). Species vouchers are deposited in the University of Alberta herbarium (ALTA).

Analysis

Environmental variables

To determine the percent of total variation in microclimate and substrate availability, parameters that was explained by the stand and mesosite scales Nested ANOVAS [1] were performed using SAS V. 8.01, (1999-2000) to determine the percent using PROC GLM and PROC VARCOMP functions in SAS V. 8.01, (1999-2000) where a_i= stand, $B_{j(i)}$= mesosite within stand, and ε_{ijkl}= residual error (circle plot within mesosite within stand), Y_{ijkl}= environmental variable.

$$Y_{ijk} = \mu + a_i + B_{j(i)} + \varepsilon_{ijk} \quad [1]$$

Percent available substrate was calculated as the substrate surface area/area of forest floor within each circle plot for each substrate type (Table 2.1) . In addition I created subgroups of some substrate types: logs of decay classes 3 - 5, and deciduous tree bases, because I predicted that species richness may be higher for these subtypes than for other logs and trees respectively. In order for the residuals of substrate availability and bryophyte data to meet conditions of normality, percent bryophyte cover was arcsine transformed, and percent area for logs, wood (stumps +logs), logs of decay classes 3 through 5, and tree bases were log transformed Y'=log(Y+.01). Temperature, and percent area of deciduous tree bases and stumps did not normalize upon transformation and were left untransformed. All other variables met the assumption of normality using Shapiro-Wilk's test. All transformed and non-transformed variables except for pH, light, litter, available logs and deciduous tree bases met the condition of homoscedasticity using Bartlett's test (Sokal & Rohlf 1981). Interpretations of conclusions involving these latter variables should therefore be made with caution.

Species richness and evenness

I used mixed Analysis of Deviance (ANODEV) and Analysis of Variance (ANOVA) models for two purposes: 1) to test whether bryophyte species richness and evenness varied significantly at the stand and mesosite scales, and 2) to describe the relationship of mesosite and microsite species richness and evenness to microclimate, substrate availability, and microsite characteristics.

Because species richness is a count variable, it tends to a have skewed distribution with a variance that increases with the mean. Though species numbers at the mesosite scale were large enough to be approximated by a normal distribution, species richness data at the microsite scale were highly skewed. For consistency, I chose to use generalized linear models with Poisson error distribution to analyze all richness data. The fit of richness 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 outside of the range –2 to 2, I tested the influence of removing outlying observations. Overdispersion often occurs when the variance is greater than the mean in Poisson data resulting in inflated test statistics (Littell et al. 1996). Species richness models were constructed using the glimmix macro (SAS V. 8.01 TS Level 01M0, 1999-2000) which scales the variance in terms of an overdispersion parameter (Littell et al. 1996) removing the risk of inflated test statistics.

Evenness (E) was calculated using Pielou's method (1977) [2] , where H'= Shannon Wiener index, and S= total species richness.

$$E = H' / \ln S \quad [2]$$

Evenness met the conditions of normality and homoscedasticity using Shapiro-Wilk's and Bartlett's tests, respectively (Sokal & Rohlf 1981) at the microsite scale. Models for species evenness at the mesosite and microsite scales were constructed using PROC MIXED (SAS V. 8.01 TS Level 01M0, 1999-2000), with the ddfm=satterth option.

Complete ANODEV and ANOVA models of microsite species richness and evenness were used to determine if random effects (stand and mesosite scales) explained a significant amount of variation in species richness [3] and evenness [4], respectively, at each scale where η_{ijkl}= linear predictive function for richness, λ_{ijkl}= conditional mean count (dependent variable) given the random effects, m= intercept, a_i= stand, $B_{j(i)}$= mesosite within stand, $c_{k(ij)}$= circle plot within mesosite within stand, τ_l= microsite type, $(a\tau)_{il}$= interaction between microsite type and stand, $(B\tau)_{jl}$= interaction between microsite type and mesosite and ε_{ijkl}= residual error, Y_{ijkl}= predicted evenness.

$$\eta_{ijkl} = \log(\lambda_{ijkl}) = m + a_i + B_{j(i)} + c_{k(ij)} + \tau_l + (a\tau)_{il} + (B\tau)_{jl} \quad [3]$$

$$Y_{ijkl} = \mu + a_i + B_{j(i)} + c_{k(ij)} + \tau_l + (a\tau)_{il} + (B\tau)_{jl} + \varepsilon_{ijkl} \quad [4]$$

Models of mesosite and microsite species richness and evenness were constructed according to the following procedure. For each response variable, biologically meaningful effects were fit singularly to the model (Table 2.3). Parameters that explained a significant amount of additional model deviance in ANODEV models (tested against a Chi-square distribution), or variance in ANOVA models (tested using an F test) were retained and added to the model in a stepwise fashion in descending order of deviance or variance explained. In order to guard against spatial autocorrelation, all random effects and interactions with random effects were retained in models unless they accounted for no variation (were without a coefficient). Biologically meaningful interactions between fixed factors were tested and retained if they were significant. The fit of polynomial terms was examined when residuals suggested that polynomial relationships may exist. Model fit was assessed by calculating the coefficient of determination, R^2 (Sokal & Rohlf 1981) for all models (replacing residual and total sum of squares with residual and total deviance for ANODEV models), and by comparing residual deviance against the Chi-Square distribution with n-p degrees of freedom, where n=total number of observations, and p=number of independent fixed factor levels for ANODEV models. The importance of random effects in terms of variation or deviance explained was assessed using Wald's test (Littell et al. 1996). The significance of

treatment differences were assessed using a Tukey test to control for comparisonwise error. Tests were conducted on means that were adjusted for all parameters included in the model in order to ensure that differences were due to the treatment in isolation of other factors affecting bryophyte species richness. Percent random deviance and variance explained for each random factor was calculated using model estimates.

Beta diversity

The heterogeneity of bryophyte species composition across stands, mesosites and microsite types were compared by calculating Beta diversity using the gradient length of the first DCA axis and Whittaker's method (1972) adjusted to remove sample size biases.

DCA (Detrended Correspondance Analysis) ordination scales species composition gradients in units of the average standard deviation of species amplitudes (Hill & Gauch 1980), and thus Økland (1986) proposed that the gradient length of the axes can be seen as a measure of beta diversity. DCA ordinations were performed with presence absence data and without the down weighting of rare species in order to protect against biases caused by differences in abundance range or numbers of species deletions (Eilertsen et al. 1990, Pitkänen 2000). I used DCA as a measure of beta diversity, despite the sensitivity of this method to differences in sample size, to facilitate broad based comparisons with other studies.

Whittaker's method, using $\beta = S_t/S_m$ to approximate $\beta = \gamma/\alpha$, where S_t = the total number of species found among all samples and S_m =the mean number of species found in each sample, is also sensitive to differences in sample size (Whitaker 1972). I was able to remove these biases using the following procedure: 1) I generated values of (S_t) at n min (minimum sample size amongst comparison groups) using species area curves generated using PC-ORD for Windows, V3.20 (McCune & Mefford 1997) - The species area curve function in PC-ORD subsamples populations 500 times (or with all possible combinations if less than 500) to obtain the average number of species for each number of samples. 2) I calculated β diversity values for each comparison group using values of S_t at n min. I compared Adjusted Whittaker's β diversity across microsite types and spatial scales.

Species area-curves

To illustrate variation in species richness along a continuum of increasing area, I created species area curves (Gleason 1922). Because sampled microsites were not equal in size, the number of microsites (patches) was substituted for area in species-area curves. Species-area curves and first order jacknife estimates of species richness (Palmer 1995) were generated using PC-ORD, V3.20 (McCune & Mefford 1997). I used SPSS for Windows (Release 10.05) to determine the values of constants of species-area curves fit to the power function and logarithmic functions.

Results

Environmental variation

There was significant variation in environmental parameters at both the stand and mesosite scales (Table 2.4). Substrate availability varied only at the mesosite scale (Table 2.5). Percent variation explained by the stand and mesosite scales and by error (circle plot scale) differed amongst microclimate and substrate variables (Tables 2.4, 2.5). Stand differences explained a significant amount of the variation in soil moisture, pH, surface moisture, number of *Hylocomium splendens* modules and growth of *Hylocomium splendens*. Availability of log, wood and deciduous tree base substrate, light, temperature, litter and feather moss depth varied between mesosites but not between stands. Measured microclimatic variables were more variable than substrate availability variables.

Species richness

Unlike variation in environmental and substrate availability response variables, bryophyte species richness did not vary at stand or mesosite scales. There was a significant amount of variation in bryophyte species richness among microsite types and

the richness of a microsite type varied significantly among mesosites (significant microsite type X mesosite within stand interaction (Table 2.6). Circle plots also explained a significant amount of variation in bryophyte species richness. Adjusted mean species richness values of different microsite types were significantly different (Figure 2.2). Logs had the highest mean species richness, while undisturbed patches of forest floor had the lowest.

Stand species richness was highest in stand 1 followed by stands 3 and 2 (77, 66 and 59 species respectively).

Area of tree base (as percent of circle plot area) was a significant predictor in the ANODEV model for mesosite species richness, having a strong negative relationship with species richness. This model had an adequate fit with G^2=5.27 relative to $\chi^2_{(17)}$ (Table 2.7). The removal of one outlying residual improved model fit (to R^2= 0.74 from 0.64) but did not change the significance of terms.

The most important predictors of log species richness, in order of addition to the model were: log decay class, log surface area, total bryophyte cover, and whether logs were hardwood or softwood (Table 2.8). After the removal of three outlying logs (one that was off the ground for most of its length, two that were likely to have data recording errors), G^2=72.35 and R^2=0.81, indicating no lack of fit relative to $\chi^2_{(67)}$ (Table 2.8). Hardwood logs had higher species richness than softwood logs and logs of decay class 5 had higher species richness than decay classes 4 and 2 (Figure 2.3 & 2.4) when using Tukey-Kramer adjusted p values to compare adjusted means. Both bryophyte cover and log surface area were positively related to bryophyte species richness (Table 2.8).

Measured parameters were only able to explain half of the total deviance in stump species richness, G^2=58.74 at $\chi^2_{(56)}$, R^2=0.49 (Table 2.8). Thirty-five percent of the total variation in species richness was explained by stump decay class, surface area and their interaction. There was a trend of increasing species richness from early to late stages of decay for stumps; however adjusted mean richness did not differ between decay classes (using Tukey-Kramer adjusted p values). Since stand and mesosite scales only accounted for a minor portion of model deviance, I constructed generalized linear models (Poisson errors, log link) of species richness against stump area separately for each decay class. Of these, only decay classes 2 and 3 showed a significant positive relationship between

surface area and bryophyte species richness (Figure 2.5).

The best fitting model of bryophyte species richness on tree bases (R^2=0.53 G^2=85.11 indicating no lack of fit at $\chi^2_{(87)}$), included bryophyte cover (as a polynomial) and tree base surface area (positive relationship) as predictors of bryophyte species richness (Table 2.9). The removal of two outliers improved model fit but did not change the significance of terms; these outliers were left in the final model because there was no biological justification for their removal. Because bryophyte species richness has been related to the softwood/hardwood nature of tree bases (Culberson 1955, Palmer 1986), I constructed a second, less well fitting model (G^2=113 at $\chi^2_{(88)}$) with both deciduous/coniferous and tree base area as significant explanatory variables (not shown). Adjusted mean species richness of softwood and hardwood tree bases in the model differed at $p<0.05$ when tested with Tukey-Kramer adjusted p values. Bryophyte cover on tree bases was significantly higher on hardwood tree bases than on softwood tree bases (using a nested ANOVA), explaining why hardwood/softwood and bryophyte cover were not significant in the same model (not shown).

Variation in undisturbed patch species richness was not related to any measured environmental parameters, G^2=56.2364 at $\chi^2_{(89)}$ (Table 2.9). The residuals of three undisturbed patches were not within acceptable range of variation and their removal did not change the result of the overall analysis. Because exploratory analysis suggested that patterns may differ between stands I constructed separate predictive models for each stand. Models constructed for stands 2 and 3 did not reveal any relationships between species richness of undisturbed patches and environmental parameters. Species richness of undisturbed patches in stand 1 however was positively related to soil moisture and pH (Figures 2.6 & 2.7). After removing two outlying undisturbed patches (above), a model of stand 1 species richness (Y= mesosite (random N.S.)+ soil moisture(**)+soil pH (N.S.)+ soil ph*soil moisture (*) +mesosite*moisture*ph (random N.S.)) had a good fit (G^2=7.56 at $\chi^2_{(25)}$).

Two univariate models of species richness of disturbed patches of forest floor were significant: richness = pH and richness = area. Both pH and area were positively related to species richness. When both terms were included in the model, area of disturbed patch was no longer significant, so pH was left as the sole explanatory variable

in the final model (Figure 2.8, Table 2.10). One outlying observation was removed because it was a disturbed patch created from a newly fallen tree with a species richness of one. Model fit was satisfactory (R^2=0.36, G^2=22.64) indicating no lack of fit relative to $\chi^2_{(21)}$.

Species evenness

Species evenness is not related to species richness at any of the sampled scales. Species evenness of microsite types is not significantly different, however there is a significant interaction between microsite type and mesosite.

Species evenness of logs was poorly explained by any of the measured parameters (Table 2.12). Both total bryophyte cover and the hardwood versus softwood nature of logs explained significant amounts of variation in bryophyte species evenness when tested singularly; when tested together only cover remained significant because of a stand by hardwood/softwood interaction. Cover had a weak, negative relationship with species evenness (R^2 = 0.23). The species evenness of hardwood logs was significantly higher than for softwood logs when tested with the alternative model including hardwood/softwood as a fixed factor, R^2=0.31 . The significance of cover and deciduous/conifer log characteristics differed between stands, with neither factor being significant in stand 1 (not shown).

Species evenness of stumps was adequately explained (R^2=0.35) by total bryophyte cover (negative relationship) and by whether the stump was of a hardwood or softwood tree species (Table 2.12). Species evenness of hardwood stumps was significantly higher for softwood stumps (Adjusted least squares means). Two stumps in decay class 1, being very species poor, decreased model fit (were outliers). When forcing the inclusion of decay class (n.s.) into model, this lack of fit disappeared. Because decay class 1 stumps affected the observed pattern between stump species evenness and other variables, a final model was constructed without decay class 1 to predict the species richness of stumps of decay classes 2-4. This model had a much improved fit (R^2=0.64).

Tree species evenness was not related to any of the measured environmental parameters (Table 2.13). A random model resulted in an R^2 of only 0.17. Neither stand

nor mesosite were significant, however both explained some variation in the model.

Species evenness of undisturbed patches was poorly predicted by a mixed model with temperature as an effect (R^2=0.27) (Table 2.13). Interactions between temperature and stand and mesosite scales explained some observed variation but were not significant. The relationship between temperature and bryophyte species evenness varied among mesosites and thus can not be generalized. Since the fit of residuals was satisfactory it was not necessary to test the removal of any observations.

Area of disturbed patch was negatively related to bryophyte species evenness in disturbed patches (R^2=0.53) (Table 2.14). Model fit improved after the removal of one young, species poor, disturbed patch (R^2=0.63).

Beta diversity

Microsite beta diversity was higher than either stand or mesosite beta diversity using both DCA and Whittaker's method (Figure 2.9, Table 2.15). Stand 1 had the highest between mesosite beta diversity, (Whittaker β = 1.73 at n=6) while stands 2 and 3 were less heterogeneous (β = 1.55 and 1.57 respectively) (not shown). Beta diversity within microsite type using Whittaker's method was highest for trees followed by disturbed patches, stumps, undisturbed patches and logs (Table 2.15). Beta diversity using DCA was highest for disturbed patches of forest floor followed by logs, tree bases, undisturbed forest floor and stumps.

Species area-curves

All species area curves fit the power function adequately (R^2 values ranged from 0.86 to 0.99) (Table 2.16). The slope of the species area curve constructed with all 18 mesosites did not approach zero, but did decline dramatically after the addition of 9 mesosites (72-80 species). The second-order jackknife estimate of total species richness was 93.6 (observed species = 82). Stands differed in total species richness, however they were similar in terms of the shape of species area curves (Figure 2.10).

While the species area curve for undisturbed patches was best fit by the power

function, all other microsite curves were better represented by logarithmic functions, indicative of the relatively abrupt decline in the species accumulation (slope) of these microsite types (Figure 2.11). Stumps had the highest estimated species richness (76.8), followed by logs, disturbed patches, trees and undisturbed patches. The slope of the species area curve at the mesosite grain declined dramatically after the addition of four mesosites (Figure 2.12).

Discussion

Bryophyte species diversity was most variable between and within microsite types. Although we did find within-stand variation in microclimate and substrate availability, the effect of this heterogeneity on bryophyte species diversity was slight. Results suggest that if bryophyte species diversity is governed by hierarchical patch structure, this hierarchy is not acting at intermediate (meso) scale patch sizes, rather patch sizes are likely smaller (within the microsite), or larger (at a landscape level) than those examined in this study. Patterns in species richness, beta diversity and species area curves support this conclusion. Species evenness was homogenous at all scales of analysis. The strong connection between microsite type and species diversity reaffirms the importance of substrate for bryophyte species occurrence and abundance (Watson 1980, Vitt et al.1995).

Habitat heterogeneity at stand and mesosite scales

In general, substrate availability was homogenous within and among sampled stands. Although there was significant variation in substrate availability at the mesosite scale, not more than 30% of the variation in availability of any substrate type was explained, suggesting that patterns in substrate availability in older conifer-dominated stands are either non-existent, or are occurring at a different spatial scale. These results are analogous to those of Lee et al. (1997) who found no spatial patterns in the distribution of downed wood in old aspen dominated stands. Measured microclimate parameters did not span large gradients because of the limited extent of the study site.

Soil pH and moisture, growth of *Hylocomium splendens* and surface moisture however, did vary significantly at the stand scale and may be linked to site hydrology. Light varied significantly between mesosites while substrate temperature varied at the microsite scale.

Does bryophyte species diversity differ between microsite types?

There were substantial differences in species diversity between microsite types. Differences in species richness, beta diversity and species area curves signal that microsite types have different ecological functions for bryophyte communities related to their physical characteristics.

Microsite type was the principal factor explaining bryophyte species richness in the boreal forest. Since species evenness did not differ significantly between microsite types we can conclude that some communities within all microsite types had similar dominance structure. The lack of trends in community evenness validates the use of richness as a primary measure of bryophyte species diversity.

Logs had the highest species richness followed by disturbed patches, stumps, trees and undisturbed patches of forest floor. These patterns are in agreement with previous comparisons made between substrate types; Kimmerer (1993) found logs to have higher species richness than stumps and Jonsson & Esseen (1990) found disturbed patches of forest to have higher species richness than undisturbed forest floor. Our observed patterns of microsite species richness are also compatible with patterns illustrated by species area curves. The asymptotic species area curves of logs and stumps illustrate the rapid species accumulation for these communities, while the non-asymptotic species area curves of undisturbed patches of forest floor and trees demonstrate that these substrate types require increased sampling effort to reach maximum species capture (likely because they are species poor)(Moreno & Halffter 2000). The small sample size of disturbed patches of forest floor hinder drawing conclusions based on the derived species area curve.

Logs are likely to be species rich for four reasons: 1. they provide a micro-climate favourable for many bryophyte species; 2. they provide substrate above the feather moss carpet allowing the persistence of less competitive species; 3. they are

internally heterogeneous (in terms of decay class) and 4. their large size.

The shape of the species area curve for trees does not conform to species area curves constructed for epiphytes in tropical environments; Wolf (1993) and Gradstein et al. (1990) found species area curves for bryophytes in the tropics to plateau quickly after the addition of 5 trees. Whereas bryophyte growth in the tropics is often abundant high in tree branches, the most favourable bryophyte habitat in the boreal zone is at the rooting zone of tree bases where species are protected from winter temperatures by snow cover, and from summer drought by higher moisture availability (Smith 1982). The flora of tree bases at the rooting zone may consist of a handful of epixilics or forest floor bryophytes that are abundant in the immediate vicinity (see Chapter 3). The stochastic nature of these facultative epiphytes renders tree base communities more variable than communities of other microsite types (higher beta diversity).

This reasoning does not explain the slow continuous accumulation of species and low mean species richness in undisturbed patches of forest floor. Both the species composition and the continuous nature of undisturbed forest floor provide explanations for the lack of community saturation and low diversity on this microsite type. In having no discrete boundaries, species growing in undisturbed patches of forest floor are not limited by dispersal. A species area curve constructed using 30 forest floor bryophyte plots of sizes 0.5 m^2, 1 m^2 and 2 m^2 in southern Finland, also failed to reach a plateau, indicating that either more plots or larger plot sizes are needed in the boreal forest (Jalonen 1998). However, species that are prevalent on the undisturbed forest floor are strong competitors (typically long lived perennials; During 1979). The competitive dominance of a few feather moss species likely impedes establishment and persistence of most bryophyte species thus the small size of the sampling frame (1 X 1m) relative to the total area of undisturbed forest floor did not provide adequate species capture (Figure 2.11). New species are able to colonize when there is a dramatic change in forest floor nutrient or moisture dynamics (Økland 2000), or small scale disturbance (Jonsson & Esseen 1990). For these reasons, species richness on undisturbed forest floor is typically low with a climax of dominant species attained early, but with a slow accumulation of additional species associated with small scale disturbance, small pieces of dead woody debris and fluctuations in moisture and pH.

Do microsite properties affect bryophyte species diversity?

In general, factors explaining microsite species richness did not explain variation in species evenness of each microsite type. Species evenness did not vary in consort with species richness suggesting that the evenness of species distribution was not affecting the richness of bryophyte communities. Taken together, these results imply that species occurrence on woody substrates is not being limited by competitive interactions despite the fact that increasing bryophyte cover was linked to increasing dominance (typically one or more of the three dominant feather mosses: *Hylocomium splendens*, *Ptilium crista-castrensis*, and *Pleurozium schreberi*.).

Microsite surface area and the hardwood or softwood nature of microsites were important for all woody substrate types. Factors explaining log and stump species richness and evenness were almost identical suggesting ecological similarity. Undisturbed and disturbed patches of forest floor were related to soil moisture and pH respectively.

Many authors have found higher bryophyte species richness on logs of later decay stages, (Muhle & LeBlanc 1975), with species often peaking at decay stage 6 (Kruys et al. 1999, Crites and Dale 1995). Large coarse woody debris (Kruys et al. 1999) is also related to higher bryophyte species richness. My results reaffirm the importance of logs in later stages of decay as well as log size for the maintenance of bryophyte species richness. We found log species richness to peak at decay stage five, rather than at decay stage 6. This may be due to the large proportion of liverworts in our species pool (24% of microsite species richness). Kruys et al (1999), and Crites & Dale (1995), found liverwort species richness to peak on logs of mid-late stages of decay 4-5.

Logs of decay stage 4 were especially species poor in our sample. This is likely an artifact of classifying an entire log into one decay class. Because of their large size, logs can often encompass many decay classes. With our classification system (Table 2.2) however, logs of decay class 4 had "little or no bark remaining, no branches, wood soft with small crevices and small pieces lost" and were therefore typically devoid of epiphytes and not sufficiently decayed to have a complete set of epixilics. In contrast,

logs of decay class 3 (logs with less than 50% of their bark remaining), were often quite heterogeneous, providing habitat for epiphytes as well as epixilics on portions of the log in later stages of decay (see Chapter 3).

The deciduous or coniferous nature of the log was also a significant predictor of bryophyte species richness on logs after adjustments for log decay class, log area and bryophyte cover. This level of substrate specificity may be explained by differing establishment success (McAlister 1995) or persistence of bryophyte species; establishment on logs of deciduous trees was likely enhanced by the more diverse tree base flora of *Populus* sp. (the extent of compositional similarity between logs and tree bases is found in Chapter 3).

Stump species richness was lower, and less variable than log species richness (lower s.e.). The relatively low variation in stump species richness may indicate high within stump variation; if stumps have more heterogeneous texture and decay processes than logs we can expect them to be both more homogenous and more species rich. Kimmerer (1993) found stumps to have significantly more disturbance produced gaps (areas where the bryophyte community has been disrupted exposing bare wood surface). Also, the vertical orientation of stumps makes them amenable to having different stages of decay on their sides versus their top surface. Lee & Sturgess (1999), found the flora of the top surface of *Populus tremuloides* stumps to be more similar to vascular plant species found on the forest floor. The relationship between bryophyte species richness and stump decay parallels that found for vascular plants; Lee & Sturgess (1999) found soft stumps to have higher species richness than hard stumps.

Area of tree base available for colonization, total bryophyte cover, and whether trees were deciduous or coniferous were all significant predictors of bryophyte species richness on tree bases. Hardwood tree bases (*Populus tremuloides* and *Populus balsamifera,*), had higher bryophyte cover and species richness than conifers (*Picea glauca, Picea mariana* and *Abies balsamea*), supporting results of Culberson (1955) and Palmer (1986), who found that bryophyte communities differed between conifer and hardwood tree species, hypothesizing that this was due to the drier, more acidic nature of conifer bark.

Tree bases with larger colonizable area (essentially larger diameter), supported

greater numbers of bryophyte species, reaffirming the results of Hazell et al. (1998) who showed large aspen to be more favorable for bryophyte species abundance than smaller trees. Proposed explanations for the size/richness relationship are that larger trees have rougher bark resulting in more microsites for colonization (Hazell et al. 1998), that larger trees are older increasing the accumulation of species over time (Boudrealt et al. 2000), or simply that the larger the area, the more species will be able to colonize (species area relationship). In this study, the first and second hypotheses are not likely: the first because the majority of sampled trees were *Picea* species so bark texture was relatively uniform, the second because both Kuusinen (1994), and Boudreault et al. (2000) found no significant relationship between aspen DBH and tree age. Species composition also helps explain higher mean evenness on deciduous versus coniferous trees. The most prevalent tree base flora of both *Populus tremuloides* and *Populus balsamifera*, in our study area was a mixture of *Amblystegium serpens*, *Pylasiella polyantha*, *Orthotrichum elegans*, and *Orthotrichum obtusifolium*, each which can be considered a co-dominant species. In contrast, only one species was commonly abundant on conifer trees in our study site, *Ptilidium pulcherrimum*.

Species richness of undisturbed patches of forest floor was related to soil pH and moisture in only one of the three stands. Though the ranges of soil pH and moisture were quantitatively similar in each stand, the absolute values of soil pH and moisture were highest in stand 1. This allowed for the occurrence of some peatland species in the wettest areas of stand 1 that were not present in other stands. It appears that species richness of undisturbed forest floor is not responsive to soil pH and moisture gradients unless the values of these parameters are high. It is probable that if the study site encompassed a wider range of soil moisture and pH values, undisturbed forest floor would show greater variability at larger scales. Bryophyte communities often respond to moisture gradients. Moisture was the most important factor explaining bryophyte species richness in forest floor plots in Norway (Frisvoll & Prestø 1997), and in the forest-tundra of northwestern Canada (Robinson et al. 1989). In the Rocky Mountains beta diversity was greater along moisture gradients than elevational gradients (Lee & La Roi 1979).

Small scale disturbances in the forest floor are often hotspots of bryophyte species diversity, with higher species richness and diversity than undisturbed forest floor

(Linholm & Nummelin 1983, Jonsson & Esseen 1990, Henry et al. 1995). By eliminating the feather moss carpet, disturbance exposes mineral soil and or duff, allowing colonization by a larger number of ruderal species. Disturbed patches of forest floor had high species richness (ranking second of all microsite types), having double the mean species richness of undisturbed patches of forest floor. Jonsson & Esseen (1990) found the same ratio between bryophyte species richness of disturbed and undisturbed patches of forest floor in Norway. As area and pH increased, so did the species richness of disturbed patches. In addition to providing more spatial area (niche space) for colonization, larger disturbed patches have greater temporal stability; small disturbed patches will be overgrown by feather moss species more quickly. Our results are different from those of Jonsson & Esseen (1990) who did not find any relationship between bryophyte species richness and area or soil properties of disturbed patches. Higher pH, however, has been linked to bryophyte species richness in alvar grassland (Zamfir et al. 1999) and to the occurrence of unique species occurrence in subarctic forest-tundra (Robinson et al. 1989).

Is microsite species diversity related to variation at larger spatial scales?

Species richness differed, (ranging from 59 to 74 species), across the three sampled stands despite similar classification by Alberta Vegetation Inventory maps. While having the highest species richness stand 1 also had soil moisture and pH values in excess of those found in stands 2 and 3. Since most of the additional species found in stand 1 were peatland species, we can infer that these two environmental parameters explain some of stand 1's greater diversity.

These differences in species richness at the stand scale did not have any significant effect on species richness of sampled microsites or mesosites. Similarly, variation occurring at the mesosite scale did not affect microsite species richness (barring two significant interactions of fixed factors with mesosites). What this implies is that communities on specific microsites in the boreal forest are not being determined by closer proximity to a larger species pool in more diverse stands, or by environmental variation occurring at larger spatial scales. The lack of larger scale influence on

bryophyte microsite species composition may not be uncommon, Kuusinen (1994) found only a very slight affect of stand age on bryophyte species richness of *Populus tremula* in Finland.

Contrary to our findings, Palmer (1994) found species richness of vascular plants in adjacent scales to be correlated. According to Srivastava (1999), a direct relationship between species diversity at local and regional scales is indicative of unsaturated communities, while the absence of a relationship suggests community saturation. Cornell & Lawton (1992) propose that when local richness is independent of regional species richness communities are saturated; local species richness is limited by niche space and biological interactions rather than by regional species pools. Attributing the lack of relationship between local and regional diversity to inter specific interactions is problematic. Though niche segregation has been found to exist (Kimmerer & Young 1996, Slack 1997), interspecific interactions are not often reported for bryophytes (During & van Tooren 1987) and logs and stumps communities are considered to be unstable, subject to continuous small scale disturbance (Kimmerer 1993). We cannot ignore another possible explanation for this phenomenon: that bryophyte species growing on log and stump habitats have very effective rapid dispersal.

Are factors driving mesosite species diversity similar to those driving microsite species diversity?

While variation in bryophyte species richness at the microsite scale was closely tied to substrate type, quality and quantity, the subtle variation in bryophyte species richness at the mesosite and stand scale was not related to the availability of decayed logs, the most speciose microsite type (Figure 2.12).

Bryophyte species diversity at the mesosite scale (coarsest-grain), was relatively invariant regardless of significant variation in substrate availability at this scale. Bryophyte species richness was only related to one measured parameter: percent tree base area. The strong negative relationship between mesosite species richness and tree base area may be the result of a suite of environmental variables associated with canopy gaps such as increased soil moisture, light, and dead woody debris. Measured

environmental parameters do not support this conclusion, however neither light nor soil moisture were related to percent tree base area, and dead wood was positively rather than negatively correlated with tree base area (R=0.528, p=0.0237). Notwithstanding this, increasing bryophyte species richness with a decline in tree density is supported by the literature; Økland (1994) found strong patterns in species richness along a canopy closure gradient (with higher richness in more open areas), Lukasz & Sadowska (1997) found species richness to peak 1 m into the forest from the edge, and Økland et al. (1999), found bryophyte species abundances to increase with distance away from tree stems in spruce-forests. Økland et al. (1999) attributed this relationship to lower throughfall precipitation, soil moisture and litter beneath tree crowns.

What spatial scale is most important?

Variation in species richness was greater at the microsite scale than at the mesosite or stand scales. Palmer (1994) found the opposite to be true for vascular plants; that the probability of finding diversity hot spots increased with coarser grains. He also found species area curves to have steeper initial slopes at coarser grains (larger scales)) than at fine grains. In this study, the initial slope of species area curves was greater for fine grains, indicating faster species accumulation through the addition of microsites than mesosites. The contradiction between my results and those of Palmer (1994) may simply be due to the fact that bryophytes often respond to environmental variation differently from vascular plants (Dirkse & Martakis 1998, Pharo & Beattie 1997, Slack 1977).

Beta diversity was also greater at smaller sample scales (from stand through microsite scales), using both DCA and Whittaker's methods. Microsite beta diversity calculated using Økland's DCA method, ranged from 3.63 (stumps n=67) to 6.45 (all microsite types n=355). These values are high in comparison to beta diversity values found for lichens and mosses across regional environmental gradients in eastern Finland (ranging 2.031 to 3.374 S.D., n=289), and for bryophytes communities between $1m^2$ forest floor plots in the Norwegian boreal spruce forest (1.5-2.0 S.D. n=85) (Økland 1994). Beta diversity values between and within microsite types were approximately equivalent to bryophyte beta diversity found between sites spanning large moisture,

vegetation and geological gradients in southeastern Australia (4.78 S.D. n=36) (Pharo & Beattie 1997).

Other authors have found beta diversity to be inversely related to plot size (Økland et al. 1990, Smith & Urban 1988). Because fine-grained sample scales encompass less heterogeneity, reducing the average standard deviation of each species, they are less likely to underestimate habitat complexity, or overestimate a species' occupied niche (Palmer & Philip 1990).

The ability of the microsite scale to explain variation in species richness and beta diversity does not diminish the importance of sampling at larger sample scales. The slope of the species area curve of sampled mesosites decreased more quickly than the slope of the species area curve constructed using the average accumulation of species over 18 microsites (all types), (Figure 2.12). Thus, despite targeted sampling at the microsite level, larger plots are still necessary to ensure species capture (McCune & Lesica 1992).

Conclusions

The results of this study suggest that bryophyte species diversity is homogenous at intermediate spatial scales in the boreal forest. Microsite characteristics were the most important determinants of bryophyte species richness, and best explained differences in species composition (beta diversity) and species area curves. Species evenness was not clearly related to any measured environmental variables or spatial scales.

Some variation in species diversity at both intermediate and small scales in the boreal forest, however, remained unexplained. Species evenness was not well explained by spatial scale or environmental characteristics.

Patterns in microsite species diversity were not affected by the stand and mesosite spatial scales. Although bryophyte communities of microsites may individually be in various states of disequilibrium (Kimmerer 1994), their diversity does not appear to be limited by differences in the available species pool between stands or mesosites (no microsite types were affected by increased species diversity at larger spatial scales). Bryophyte communities on undisturbed patches of forest floor were the least stable

relative to other microsite types. Bryophyte communities on disturbed patches of forest floor were not present in great enough abundance to determine their stability. However, considering the low occurrence of tree fall disturbance on the landscape, bryophyte communities adapted to disturbance may be unsaturated because of limited habitats.

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Table 2.1. Summary of selection criteria, qualitative descriptive variables, and surface area measurements used for each microsite type. A= area, h=height, l=length, r_1=1/2 diameter at breast height, r_2 =1/2 basal diameter, d_1 and d_2 = diameter at opposing ends of a given log.

Microsite type	Suitability criteria	Qualitative measurements/ Assessment	Microsite measurements	Calculation of surface area
Undisturbed forest floor	1 m^2 of forest floor with no evidence of disturbance	Depth of: live moss and dead moss layer, litter depth	None	A=100*100 A=10,000 (cm^2)
Tree base (below 1.5m)	Over 10 cm DBH, live	Tree species	DBH, and basal diameter	$A=(h*2\pi r_1)+(h*2\pi r_2)$ h= 150cm
Log	More than 10 cm diameter at widest point, in contact with the ground, Decay class 2-7, some bark visible	Decay class*, log species	Maximum and minimum diameter, length.	$A=[(\pi(d_1/2)^2)+(\pi(d_1/2)^2)+[((\pi ld_1)+(\pi ld_2))/2]/3$* *note area of logs of decay classes 5-7 were divided by 2 rather than 3.
Stump	Less than 1.5 m high, some bark visible	Decay class*, species	Diameter (top and bottom), height	$A=(h*2\pi r)+\pi r^2$
Disturbed soil	Exposed soil from tree fall - greater than 0.625m^2		Dimensions (length and width) – formula depends on shape of patch	A=l*w A=1/2w*l

* See Table 2.2

Table 2.2 Decay classes for logs and stumps adjusted from Crites and Dale's (1995) modification of McCullough's (1948) seven decay classes.

Decay class	Description
logs	
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 slightly deformed, vascular plants beginning to colonize
6	wood mostly well decayed, log colonized by various herbs, and feather moss species, some wood visible
7	Humification nearly 100%, hard to define as a log outline indeterminable, covered by moss and vascular plants
Stumps	
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
4	All bark missing, large wood pieces missing, stump becoming overgrown with feather moss

Table 2.3 Variables tested as effects in ANODEV and ANOVA models of bryophyte species richness and evenness at the mesosite scale and for each microsite type. *Hylo. splend.=Hylocomium splendens.*

Substrate Characteristics	Mesosite	Disturbed patches of forest floor	Logs	Tree bases	Stumps	Undisturbed patches of forest floor
Surface area		X	X	X	X	
Bryophyte cover		X	X	X	X	X
Decay class			X		X	
Species			X	X	X	
Hardwood/softwood			X	X	X	
Temperature		X	X	X	X	X
Microclimate						
Soil pH	X	X				X
Soil moisture	X	X				X
Litter depth	X	X	X	X	X	X
Feather moss depth	X	X				X
Vascular plant sp. richness	X					
Micro-topography	X					X
No. *Hylo splend.* Platforms	X					X
Surface moisture	X	X	X		X	X
Substrate availability						
Logs	X					
Logs decay classes 4-6	X					
Stumps	X					
Tree bases	X					
Deciduous tree bases	X					

Table 2.4 Results of nested ANOVA models for environmental variables. Percent of total variation (% Var) of each variable explained by stand, mesosite and experimental error (circle plots) are presented. *d.f.*= degrees of freedom. See text for model design [1] and sampling methodology. var.=variables, moist.=moisture, platf.=platform.

	All env. var.s	Soil moist.	Soil pH	Light %PPFD[1]	Surface moist. dry wt	Temp.[1]	No. *Hylo. spl* platf.	*Hylo. spl* 1999 growth	Litter depth	Feather moss depth
Source	*d. f.*	% Var.	% Var.	% Var.	% Var.	% Var.	% Var.	% Var.	% Var.	% Var.
Stand	2	72**	30**	0	20**	2	20*	26**	9	2
Meso(stand)	15	4*	6	57**	2	19*	12*	0	12*	42**
Error	72	22	63	42	76	79	67	73	78	55

[1]Variable could not be normalized.
* $p<0.05$, ** $p<0.01$.

Table 2.5 Results of nested ANOVA models for substrate availability variables. Percent of total variation (% Var) of each variable explained by stand, mesosite and experimental error (circle plots) are presented. *d.f.*= degrees of freedom. See text for model design [1] and sampling methodology.

Percent of colonizable area/cm²		Log area [1]	Log area [1] Dec 3,4,5	Wood area [1]	Stump area[2]	Tree base area [1]	Deciduous tree base area[2]
Source	*d.f.* (all)	% Var.	% Var.	% Var.	% Var.	% Var.	% Var.
Stand	2	0	6	0	0	0	0
Meso(stand)	25	28**	5	30**	0	12 (p=.07)	18*
Error	72	72	89	70	95	88	82

[1]Variable was log transformed using Log(Y+0.01).
[2]Variable could not be normalized.
* $p<0.05$, ** $p<0.01$

Table 2.6 Results of nested ANODEV model of bryophyte species richness of all microsite types (R^2 =0.59), distribution=poisson, link=log. Type = sampled substrates: log, stump, tree, disturbed, and undisturbed forest floor. *d.f.*= degrees of freedom, random effects tested using Wald's test. See text for model construction and sampling methodology.

	Species Richness		
Random	*% variance explained*	*Z – Value*	*Pr Z*
Stand	0	.	.
Meso(Stand)	0	.	.
Circle(Meso(Stand))	2.5	2.04	0.0204
Type*Stand	0.8	0.82	0.2069
Type*Meso(Stand)	1.7	1.82	0.0340
Residual Error	95.0	9.63	<0.0001
Fixed	*d.f*	*Chi-Square*	*P > Chi-Square*
Type	3	83.49	0.0006

Table 2.7 Results of nested ANODEV model for bryophyte species richness of mesosites (species richness determined using FHS + microsite sampling), (R^2=0.64, and G^2=5.27, indicating no lack of fit relative to $\chi^2_{(17)}$ (when outlying observation is removed R^2=0.74, G^2=3.47, relative to $\chi^2_{(16)}$)), distribution=poisson, link=log. *d.f.*= degrees of freedom, random effects tested using Wald's test. See text for model construction and sampling methodology.

	Mesosite Species Richness		
Random factors	*% variance explained*	*Z – Value*	*Pr Z*
Stand	1.3	0.76	0.2227
Residual Error	98.7	2.64	0.0041
Fixed factors	*d.f*	*Chi-Square*	*P > Chi-Square*
Tree area	1	20.44	0.0001

Table 2.8 Results of nested ANODEV models of bryophyte species richness of logs, (R^2=0.81, G^2=72.35, indicating no lack of fit relative to $\chi^2_{(67)}$), and stumps (R^2=0.49, G^2=58.86, indicating no lack of fit relative to $\chi^2_{(56)}$), distribution=poisson, link=log. H/S = hardwood vs. softwood, Area = surface area of microsite, Cover = % bryophyte cover on substrate, Decay class = see table 2.2. *d.f.*= degrees of freedom, random effects tested using Wald's test. See text for model construction and sampling methodology.

Log Species Richness				Stump Species Richness			
Random factors	*% variance explained*	*Z – Value*	*Pr Z*	*Random factors*	*% variance explained*	*Z – Value*	*Pr Z*
Stand	0	.	.	Stand	0	.	.
Meso(Stand)	0	.	.	Meso(Stand)	0	.	.
Meso*H/S	4.3	1.82	0.0340	Decay class*Stand	0	0.02	0.4934
Residual Error	95.7	4.65	<0.0001	Residual Error	100.0	4.97	<0.0001
Fixed factors	*d.f*	*Chi-Square*	*P > Chi-Square*	*Fixed factors*	*d.f*	*Chi-Square*	*P > Chi-Square*
Decay class	5	76.15	<0.0001	Decay class	3	4.83	0.0613
Area	1	54.79	<0.0001	Area	1	9.26	0.0045
Cover	1	10.74	0.0010	Area* Decay class	3	6.49	0.0014
H/S	1	6.08	0.0137				

Table 2.9 Results of nested ANODEV model of bryophyte species richness of trees, (R^2=0.53, G^2=85.11 indicating no lack of fit relative to $\chi^2_{(87)}$), and undisturbed patches of forest floor, (R^2=0.42, G^2=56.24 indicating no lack of fit relative to $\chi^2_{(89)}$), distribution=poisson, link=log. Area = surface area of microsite, Cover = % bryophyte cover on substrate. No fixed factors were significant in model of species richness on undisturbed patches of forest floor. *d.f.*= degrees of freedom, random effects tested using Wald's test. See text for model construction and sampling methodology.

Tree Species Richness				Undisturbed Patch Species Richness			
Random factors	*% variance explained*	*Z – Value*	*Pr Z*	*Random factors*	*% variance explained*	*Z – Value*	*Pr Z*
Stand	0.4	0.26	0.3968	Stand	47.3	0.90	0.1851
Meso(Stand)	1.9	0.81	0.2095	Meso(Stand)	13.0	1.25	0.1065
Residual Error	97.7	5.28	<0.0001	Residual Error	39.7	6.02	<0.0001
Fixed factors	*d.f*	*Chi-Square*	*P > Chi-Square*	*Fixed factors*	*d.f*	*Chi-Square*	*P > Chi-Square*
Cover	1	40.66	<0.0001				
Cover^2	1	27.76	<0.0001				
Area	1	11.50	0.0007				

Table 2.10 Results of nested ANODEV model of bryophyte species richness of disturbed patches of forest floor, (R^2=0.53, G^2=22.64 indicating no lack of fit relative to $\chi^2_{(21)}$), distribution=poisson, link=log. pH = soil pH. *d.f.*= degrees of freedom, random effects tested using Wald's test. The lack of significance at the stand scale was confirmed using the likelihood ratio statistic because Wald's test is unreliable when sample sizes are small (Littell et al. 1996). See text for model construction and sampling methodology.

Disturbed Patch Species Richness			
Random factors	*% variance explained*	*Z – Value*	*Pr Z*
Stand	2.5	.50	0.3101
Residual Error	97.5	2.97	0.0015
Fixed factors	*d.f*	*Chi-Square*	*P > Chi-Square*
pH	1	10.20	0.0014

Table 2.11 Results of nested ANOVA of bryophyte species evenness of all microsite types (Pielou 1977) (R^2 =0.59). Type = sampled substrates: log, stump, tree, disturbed, and undisturbed forest floor. *d.f.*= degrees of freedom, random effects tested using Wald's test. See text for model construction and sampling methodology.

	Species Evenness		
Random	*% variance explained*	*Z – Value*	*Pr Z*
Stand	0	.	.
Meso(Stand)	0	.	.
Circle(Meso(Stand))	1.1	0.23	0.4073
Type*Stand	0.5	0.14	0.4447
Type*Meso(Stand)	14.7	2.25	0.0123
Residual Error	83.7	9.21	<0.0001
Fixed	*d.f.*	*F – Value*	*P > F*
Type	3	1.66	0.2730

Table 2.12 Results of nested ANOVA for bryophyte species evenness of logs (R^2=0.23) and stumps (R^2=0.35). H/S = hardwood softwood, Cover = % bryophyte cover on substrate. *d.f.*= degrees of freedom, random effects tested using Wald's test. See text for model construction and sampling methodology.

Log Species Evenness				Stump Species Evenness			
Random Factors	*% variance explained*	*Z – Value*	*Pr Z*	*Random* factors	*% variance explained*	*Z – Value*	*Pr Z*
Stand	5.8	0.38	0.3519	Stand	13.5	0.69	0.2452
Meso(Stand)	0	.	.	Meso(Stand)	7.5	0.54	0.2959
Residual Error	94.2	6.08	<0.0001	Residual Error	78.9	4.38	<0.0001
Fixed factors	*d.f*	*F – Value*	*P > F*	Fixed factors	*d.f*	*F – Value*	*P > F*
Cover	1	15.66	<0.0002	H/S	1	4.08	0.0488
				Cover	1	3.97	0.0515

Table 2.13 Results of ANOVA model of bryophyte species evenness of tree bases (R^2=0.17) and undisturbed patches of forest floor (R^2=0.27). Temp = mean relative temperature of microsite over growing season. *d.f.*= degrees of freedom, random effects tested using Wald's test. See text for model construction and sampling methodology.

	Tree Base Species Evenness				Undisturbed Patch Species Evenness		
Random Factors	*% variance explainede*	*Z – Value*	*Pr Z*	*Random* factors	*% variance explained*	*Z – Value*	*Pr Z*
Stand	0	.	.	Stand	0	.	.
Meso(Stand)	10.9	0.99	0.1618	Meso(Stand)	0	.	.
				Temp*Stand	0.02	0.18	0.4301
				Temp*Meso (Stand)	0.05	0.64	0.2595
Residual Error	89.1	5.71	<0.0001	Residual Error	99.93	4.92	<0.0001
Fixed factors	*d.f*	*F – Value*	*P > F*	Fixed factors	*d.f*	*F – Value*	*P > F*
				Temp	1	3.86	.0542

Table 2.14 Results of nested ANOVA model of bryophyte species evenness of disturbed patches (R^2=0.53). *d.f.*= degrees of freedom. The likelihood ratio statistic was used to confirm the lack of significance at the stand scale because Wald's test is unreliable when sample sizes are small (Littell et al. 1996). See text for model construction and sampling methodology.

Disturbed Patch Species Evenness			
Random factors	*% variance explained*	*Z – Value*	*Pr Z*
Stand	30.9	0.75	0.2276
Residual	69.9	3.00	0.0040
Fixed factors	*d.f*	*F – Value*	*P > F*
Area	1	15.51	0.0009

Table 2.15 Beta diversity calculated between all microsite types: logs, stumps, tree bases, disturbed and undisturbed patches of forest floor using two methods: 1. the gradient length of the first axis of Detrended Correspondence Analysis ordination (DCA) using all observations, and 2. Whittaker's method (1972), using $\beta = S_t/S_m$, where S_t = the total number of species found among all samples and S_m =the mean number of species found in each sample; 2a. S_t = total species richness using all observations (Whittaker all), 2b. S_t = average total species richness at n=23, (Whittaker n=23).

Technique	All microsite types	Logs	Stumps	Tree Bases	Undisturbed patches of forest floor	Disturbed patches of forest floor
1. DCA		4.89	3.63	4.23	4.14	5.36
2a. Whitaker		5.68	7.5	9.8	9.7	5
2c. Whitaker n=23		4.8	5.68	6.62	5.47	5.8

Table 2.16 Fit of species area curves for mesosite spatial scale and microsite types to the power function: $S=CA^z$, where S = number of species, A = number of sampled sites, C = the intercept and z = the slope of the line log S vs. log A. (Lomolino, 1989).

Group	*d.f.*	*C*	*z*	R^2	*F – Value*	*P > F*
Logs	84	20.19	0.2884	0.8769	598.79	<0.0001
Stumps	70	3.89	0.3917	0.9450	1205.09	<0.0001
Trees	88	8.28	0.4305	0.9567	1943.21	<0.0001
Disturbed patches	21	10.88	0.5223	0.9701	714.83	<0.0001
Undisturbed patches	88	4.02	0.4664	0.9935	13417.39	<0.0001
All microsites	359	20.29	0.2475	0.8611	2226.19	<0.0001
Mesosites	16	45.72	0.2153	0.9545	336.15	<0.0001

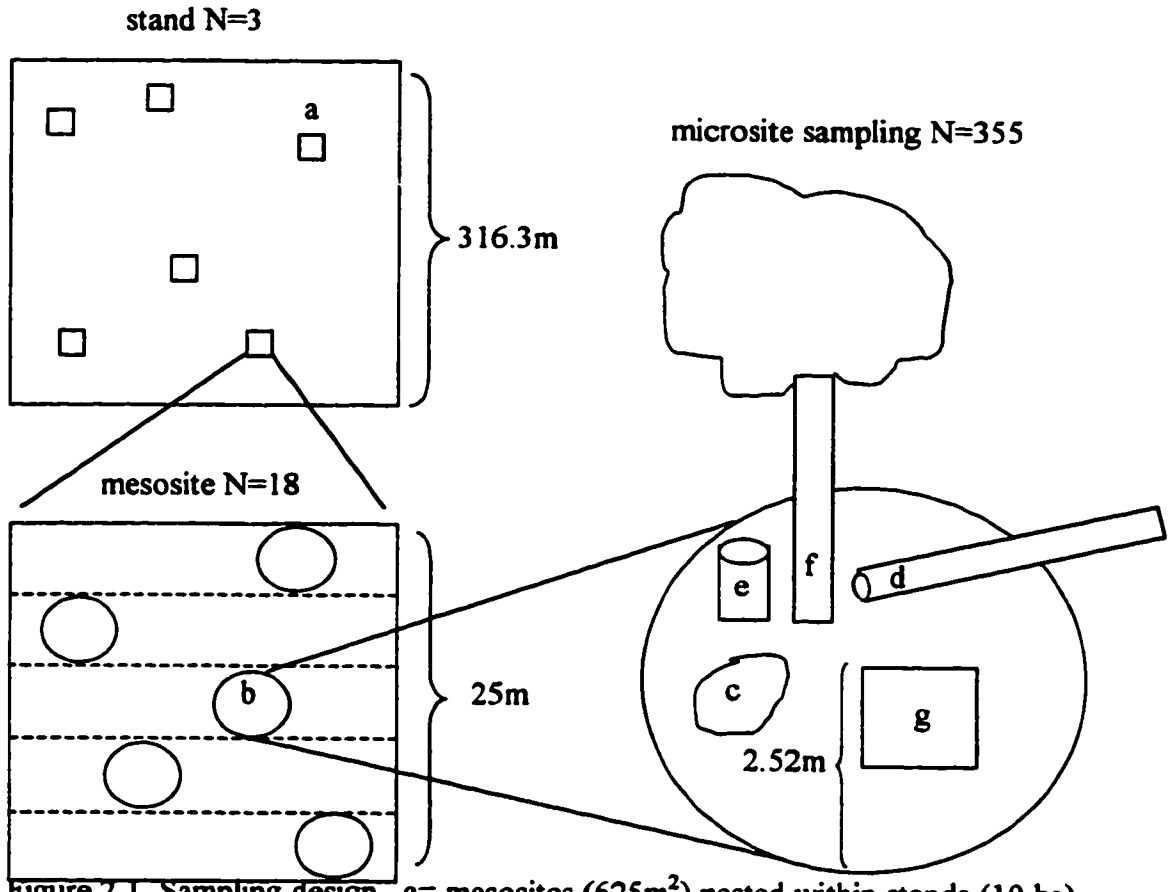

Figure 2.1 Sampling design. a= mesosites ($625m^2$) nested within stands (10 ha), b=circular plots ($10\ m^2$), c=disturbed patches of forest floor, d=logs, e=stumps, f=tree bases, g=1 m^2 patches of undisturbed forest floor.

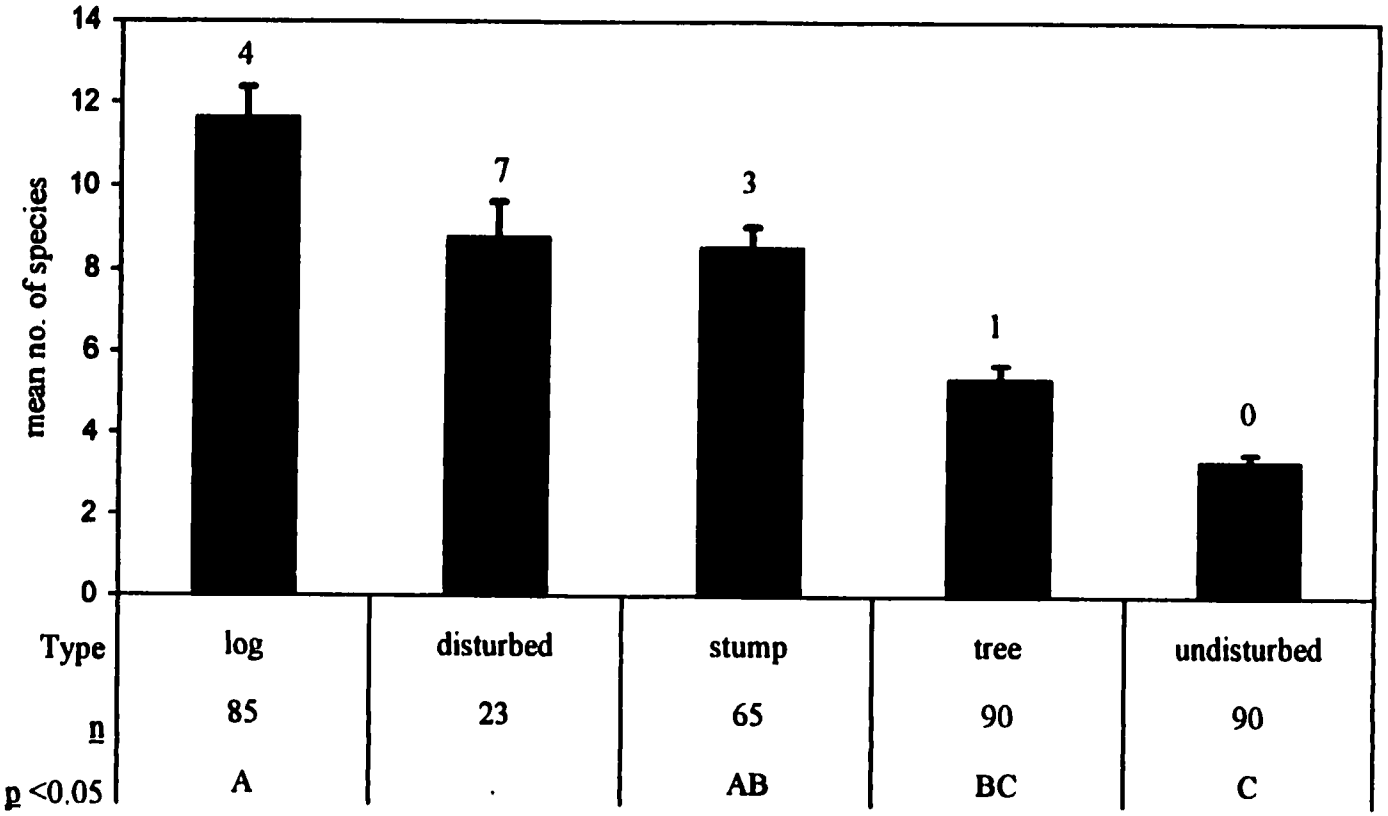

Figure 2.2 Unadjusted mean microsite species richness of microsite types (standard error). Significant differences (Tukey-Kramer adjusted p values) between mean species richness (adjusted for stand, mesosite and circle plot scales) indicated by different letters. Disturbed patches of forest floor were not be included in multiple comparisons because of their small sample size. Numbers above bars indicate the number of species unique to each microsite type.

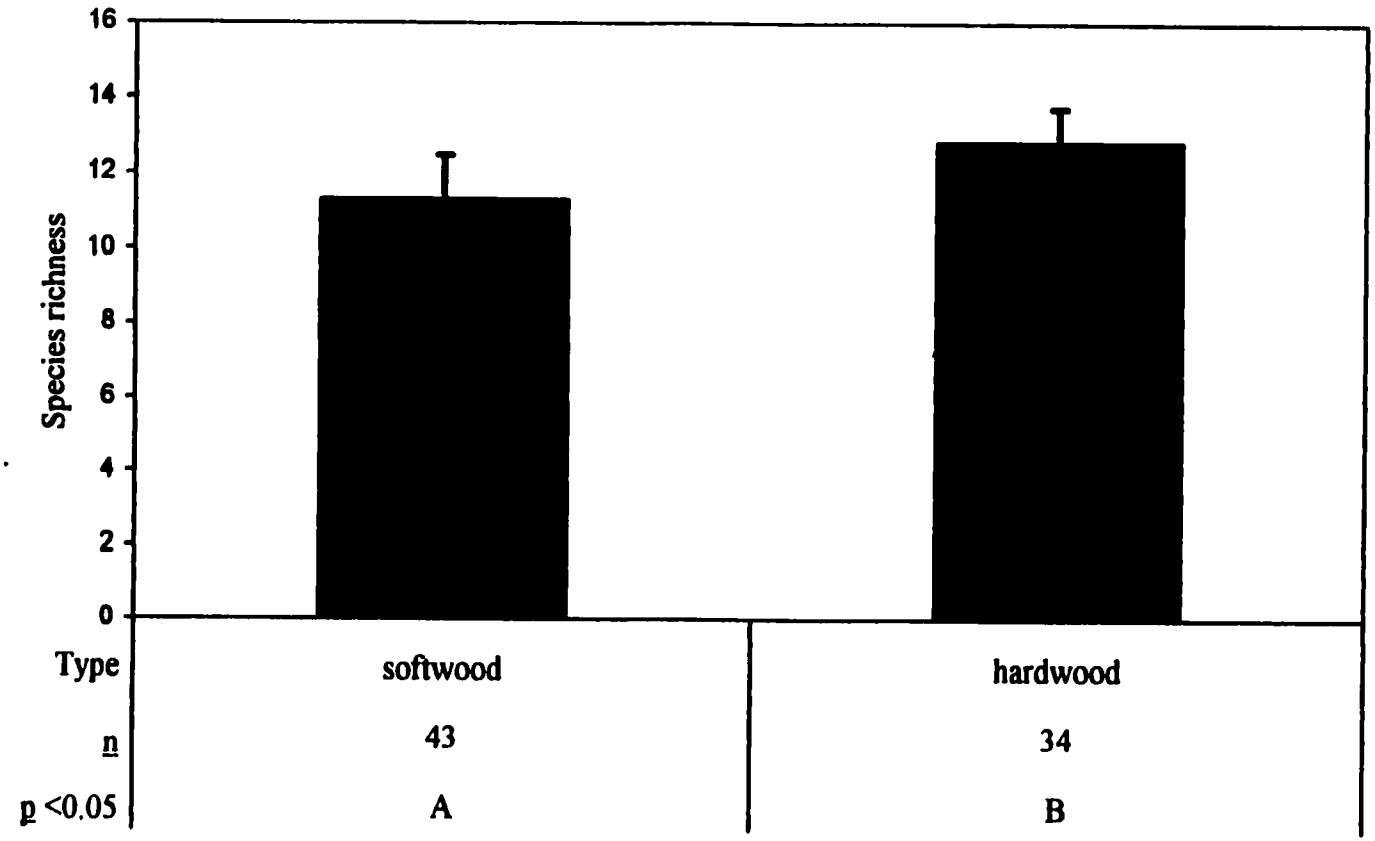

Figure 2.3 Unadjusted mean species richness for hardwood and softwood logs. Significant differences between mean species richness (adjusted for log area, bryophyte cover and decay class) indicated by different letters.

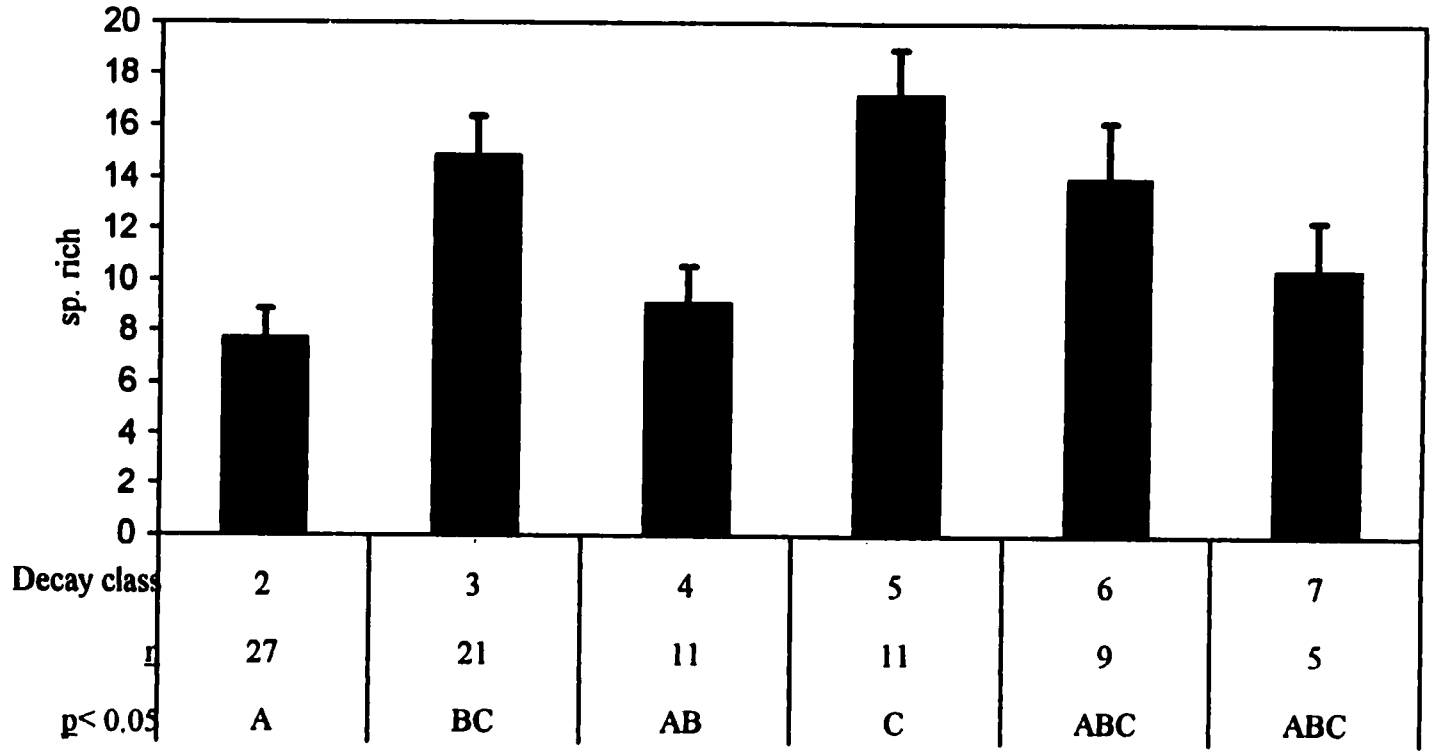

Figure 2.4 Unadjusted mean species richness (standard error) for log decay classes 2-7. Significant differences (Tukey-Kramer adjusted p values) between adjusted mean species richness (adjusted for area, bryophyte cover and deciduous/coniferous logs) indicated by different letters.

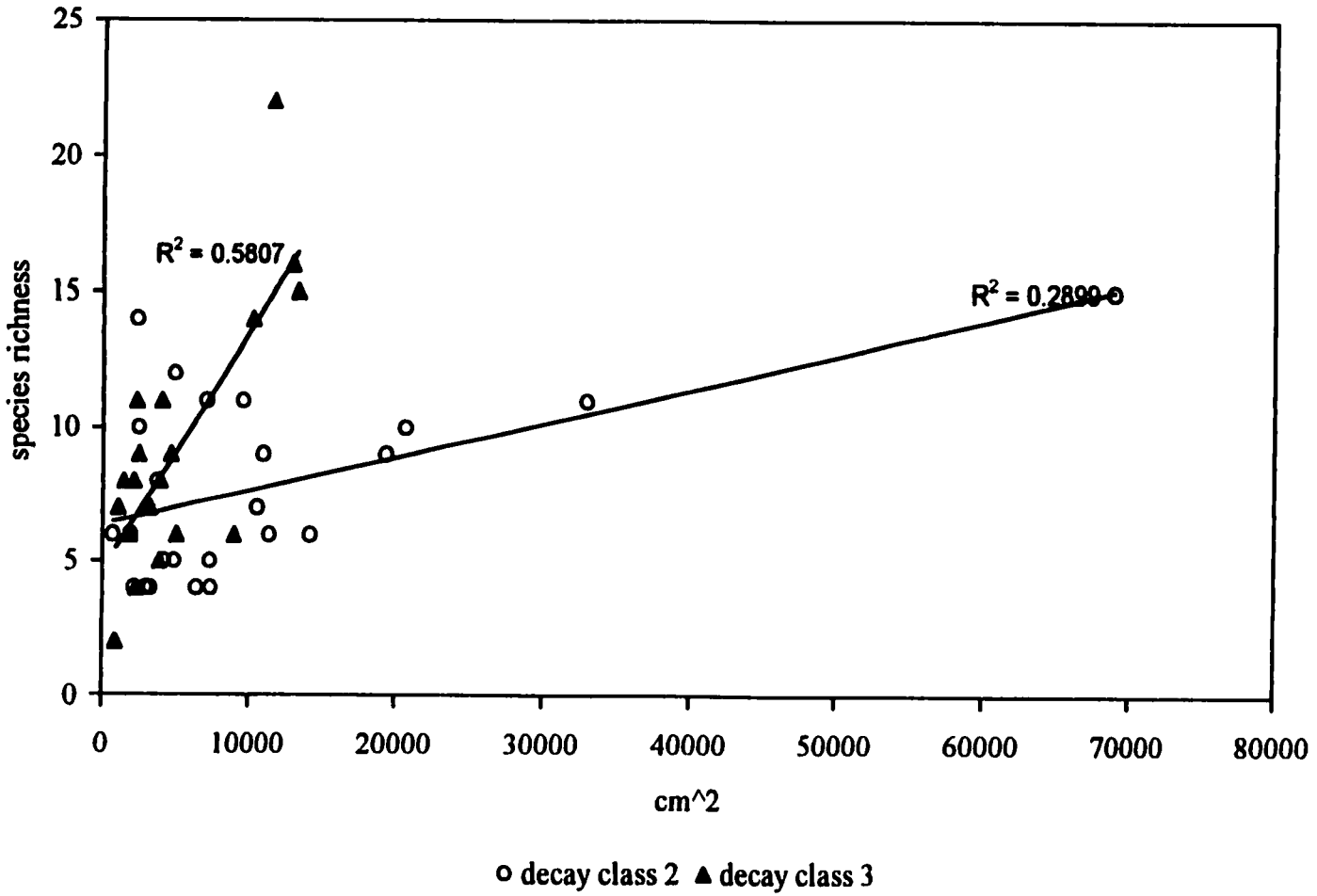

Figure 2.5 The relationship between bryophyte species richness of stump decay classes 2 and 3 and stump surface area. The slope of each line was significantly different from 0.

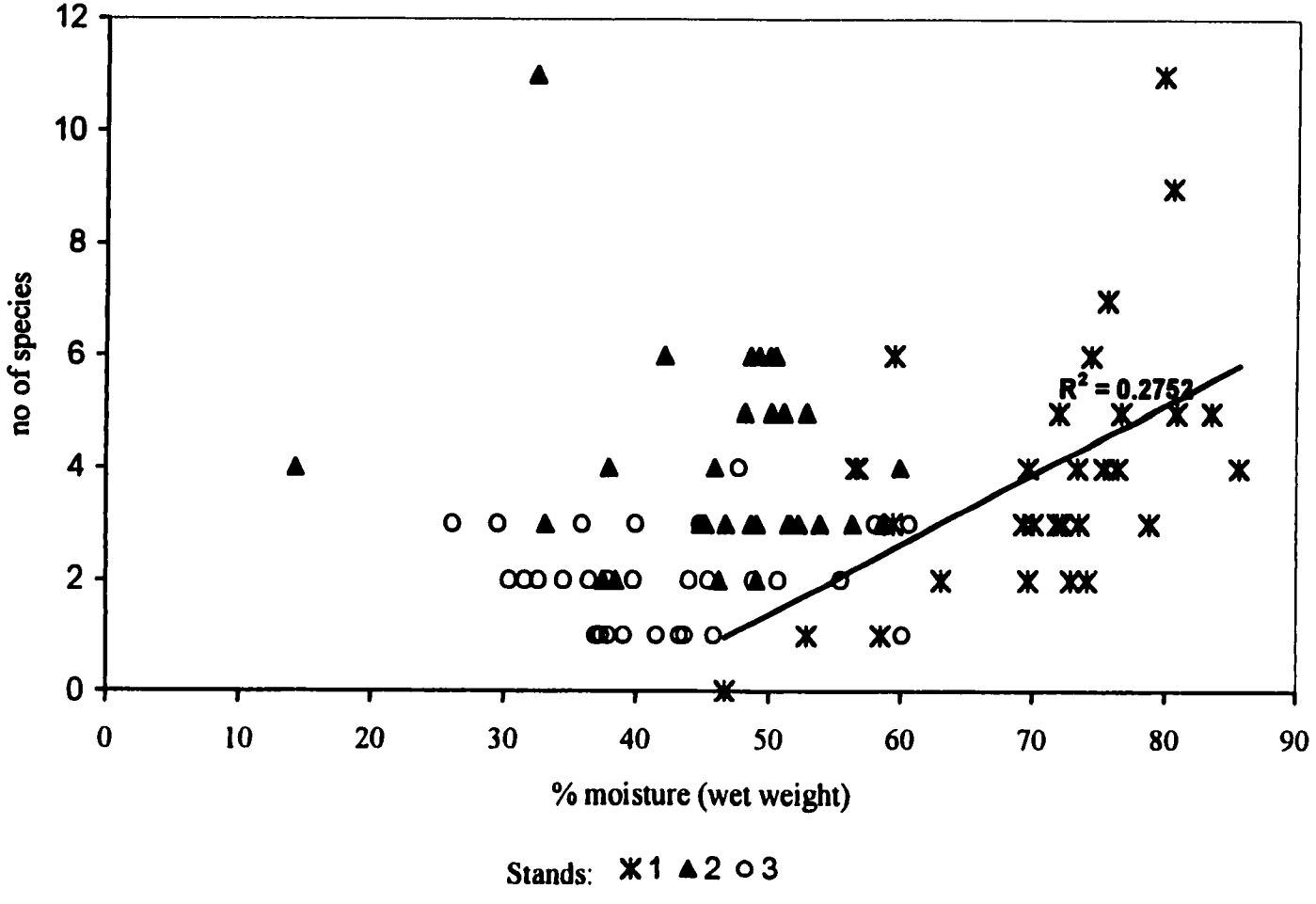

Figure 2.6 The relationship between species richness of undisturbed forest floor and percent soil moisture for stands 1, 2 and 3. Soil moisture was significant in an ANODEV model of species richness constructed for stand 1.

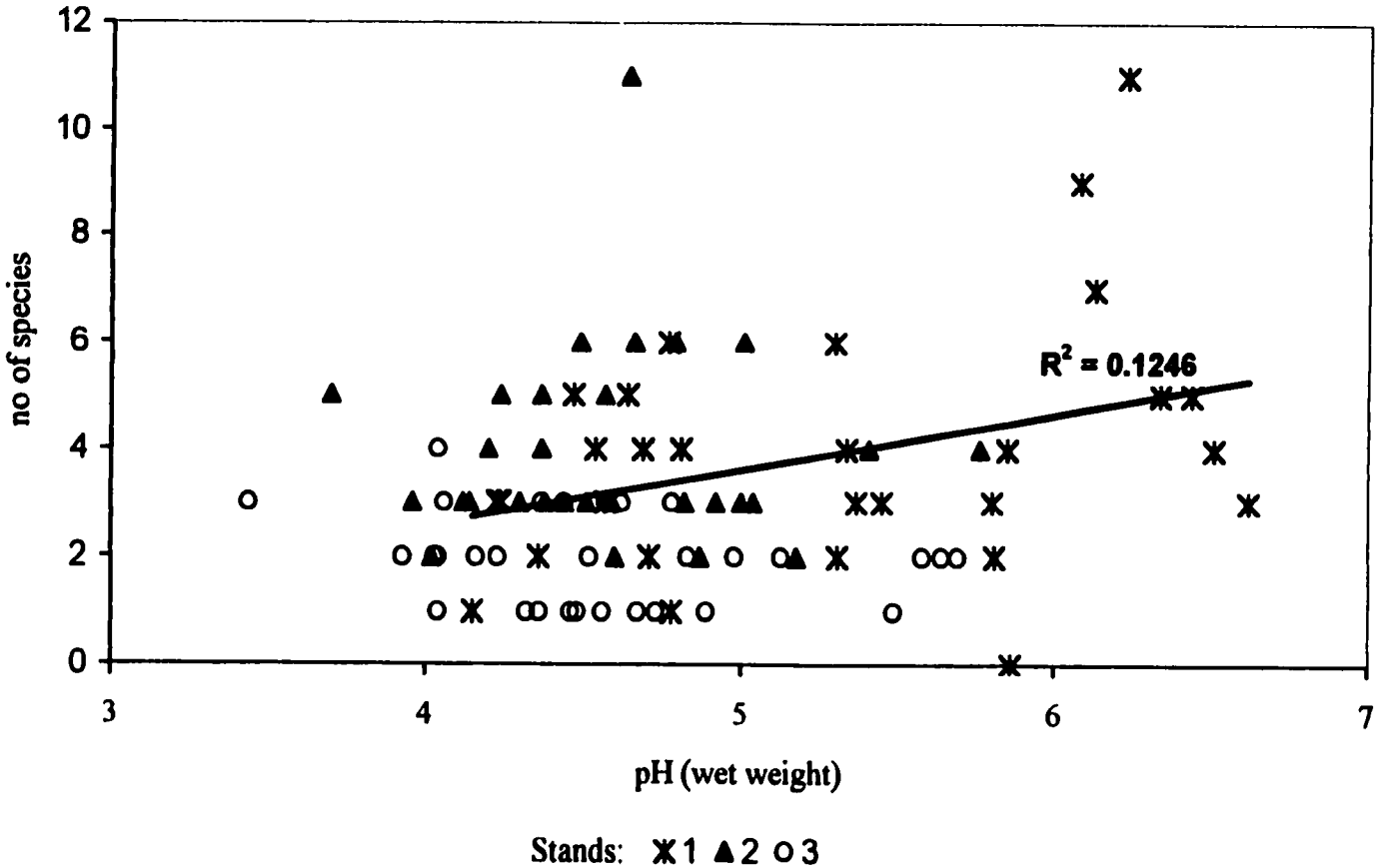

Figure 2.7 The relationship between species richness of undisturbed patches of forest floor and soil pH for stands 1, 2 and 3. Soil pH was significant in an ANODEV model of species richness constructed for stand 1.

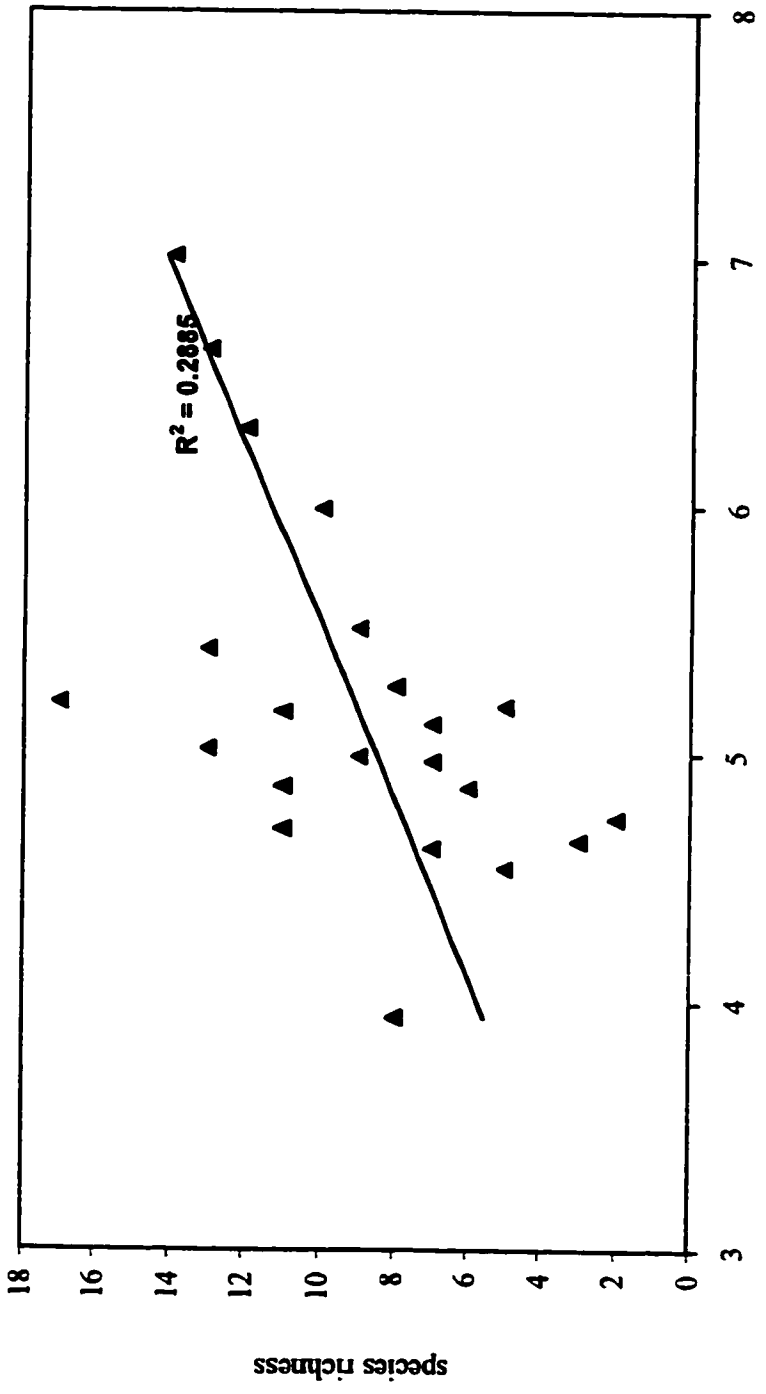

Figure 2.8 The relationship between bryophyte species richness of disturbed patches (from all stands) and soil pH.

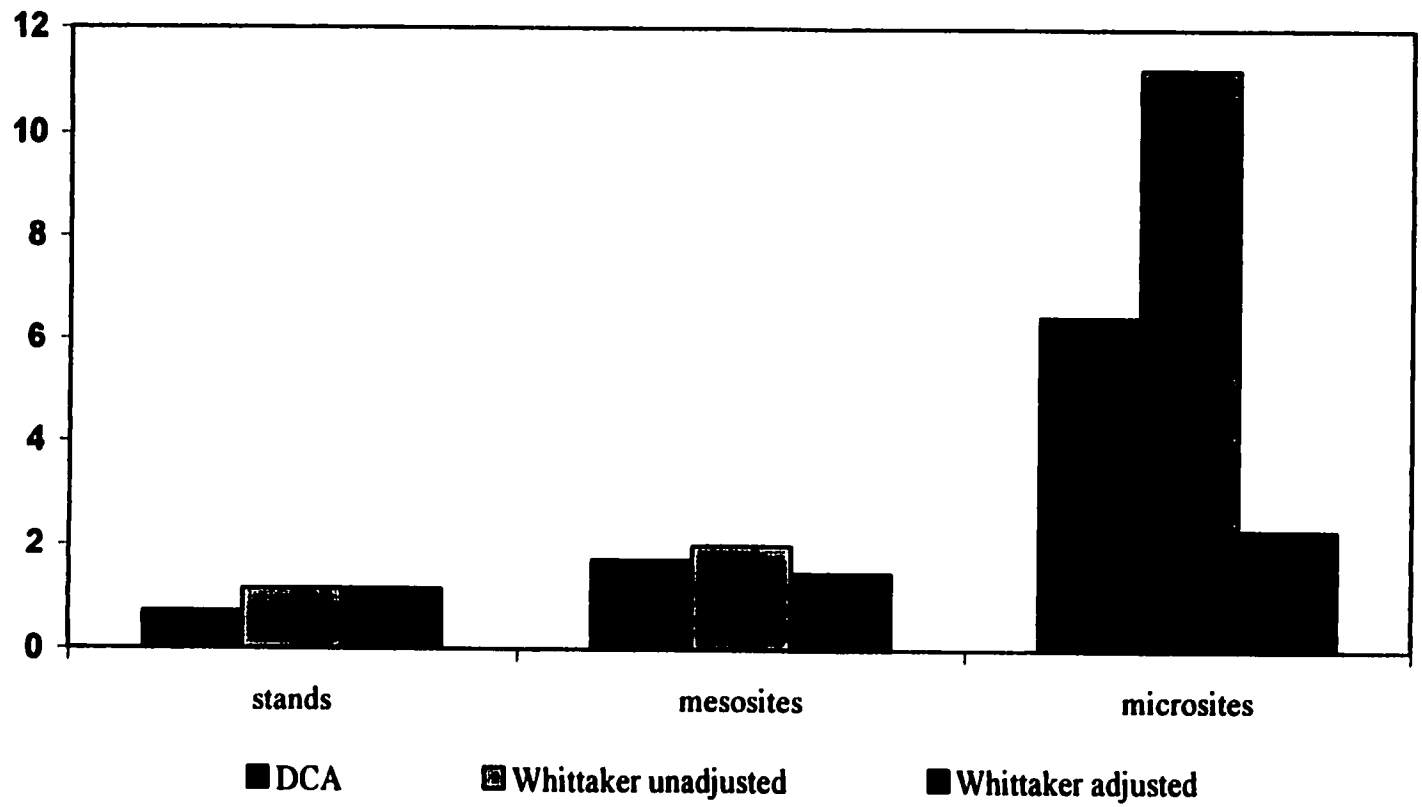

Figure 2.9 Beta diversity between stands, mesosites and all microsites calculated using the gradient length of the first axis of Detrended Correspondence Analysis ordination (DCA) and Whittaker's method (1972): $\beta = S_t/S_m$, where S_t = the total number of species found among all samples and S_m =the mean number of species found in each sample. Whittaker unadjusted S_t = total species richness using all observations, Whittaker adjusted S_t = average total species richness at n=23.

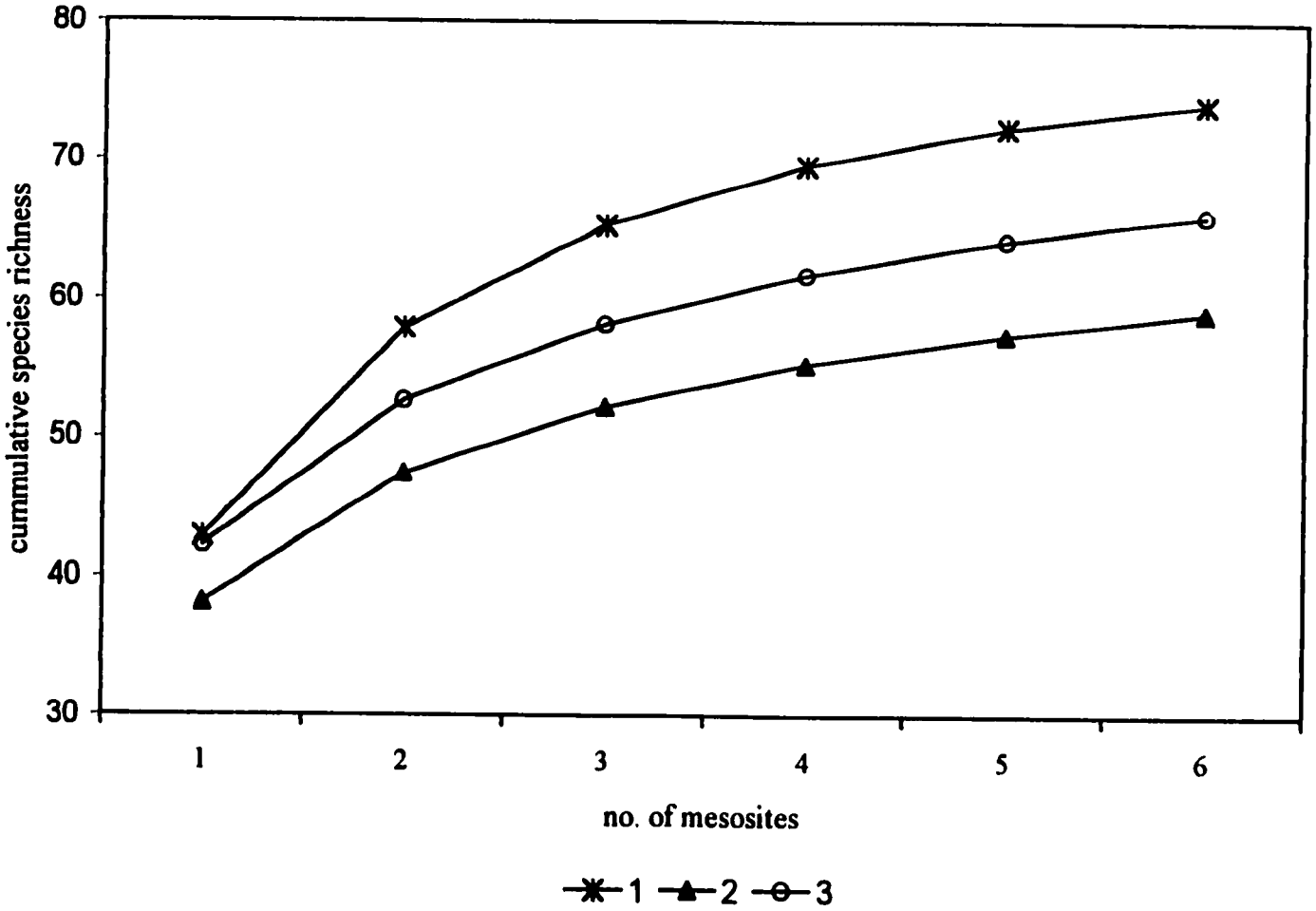

Figure 2.10 Species area curves of stands, using species richness at the mesosite scale, generated using PC-ORD, V3.20 (McCune and Mefford 1997)), second order jacknife estimates for stands 1, 2, and 3 (total observed species), 80.5 (74), 70.3 (59) and 77.2 (66) respectively.

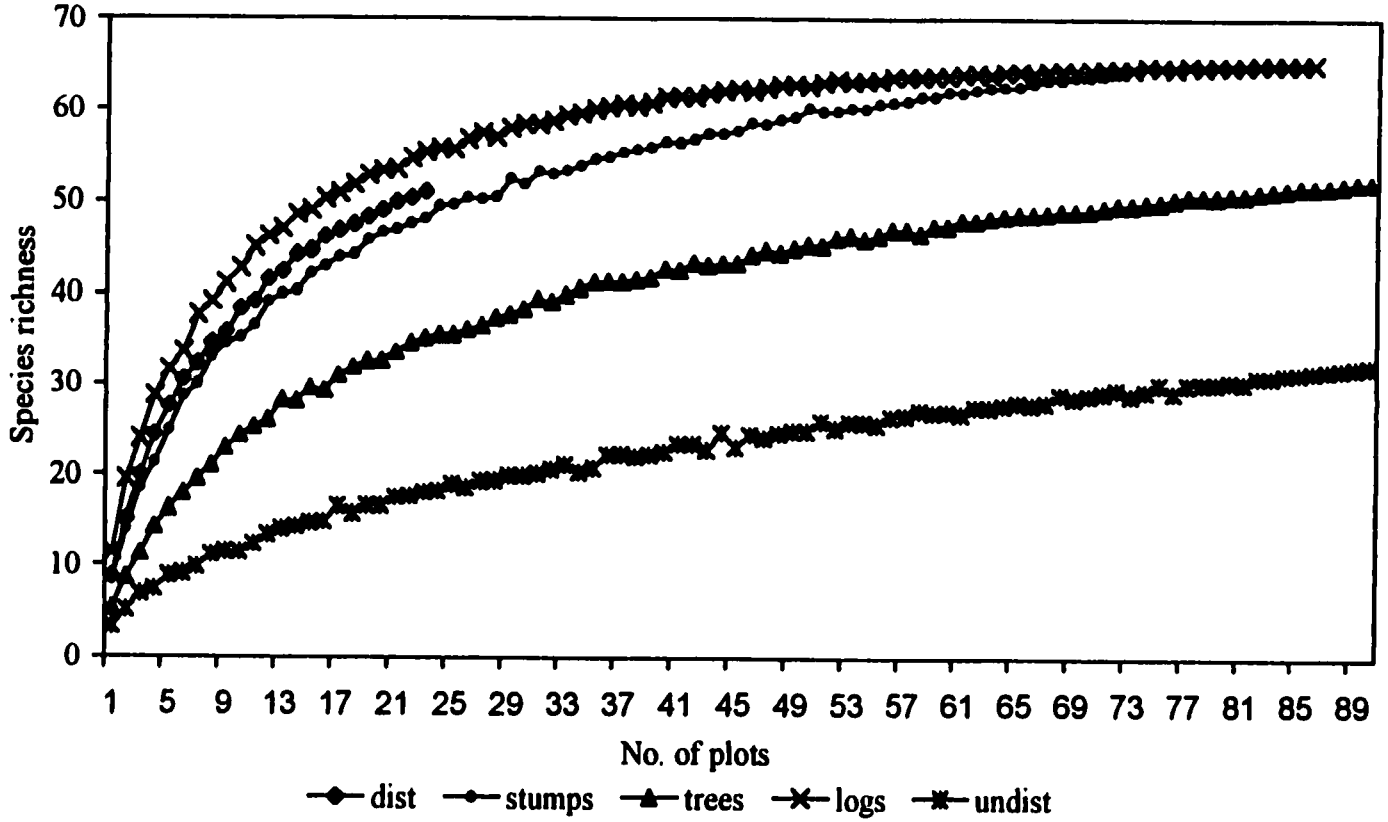

Figure 2.11 Species area curves for logs, stumps, trees disturbed and undisturbed patches of forest floor using number of plots as a surrogate for area. First order jackknife estimates of species richness (total observed species richness): disturbed patches: 64.4 (32), stumps 76.8 (64), trees 52.0 (62.9), logs 68.0 (65.0), undisturbed patches 45.8 (32.0), all microsite types 87 (80).

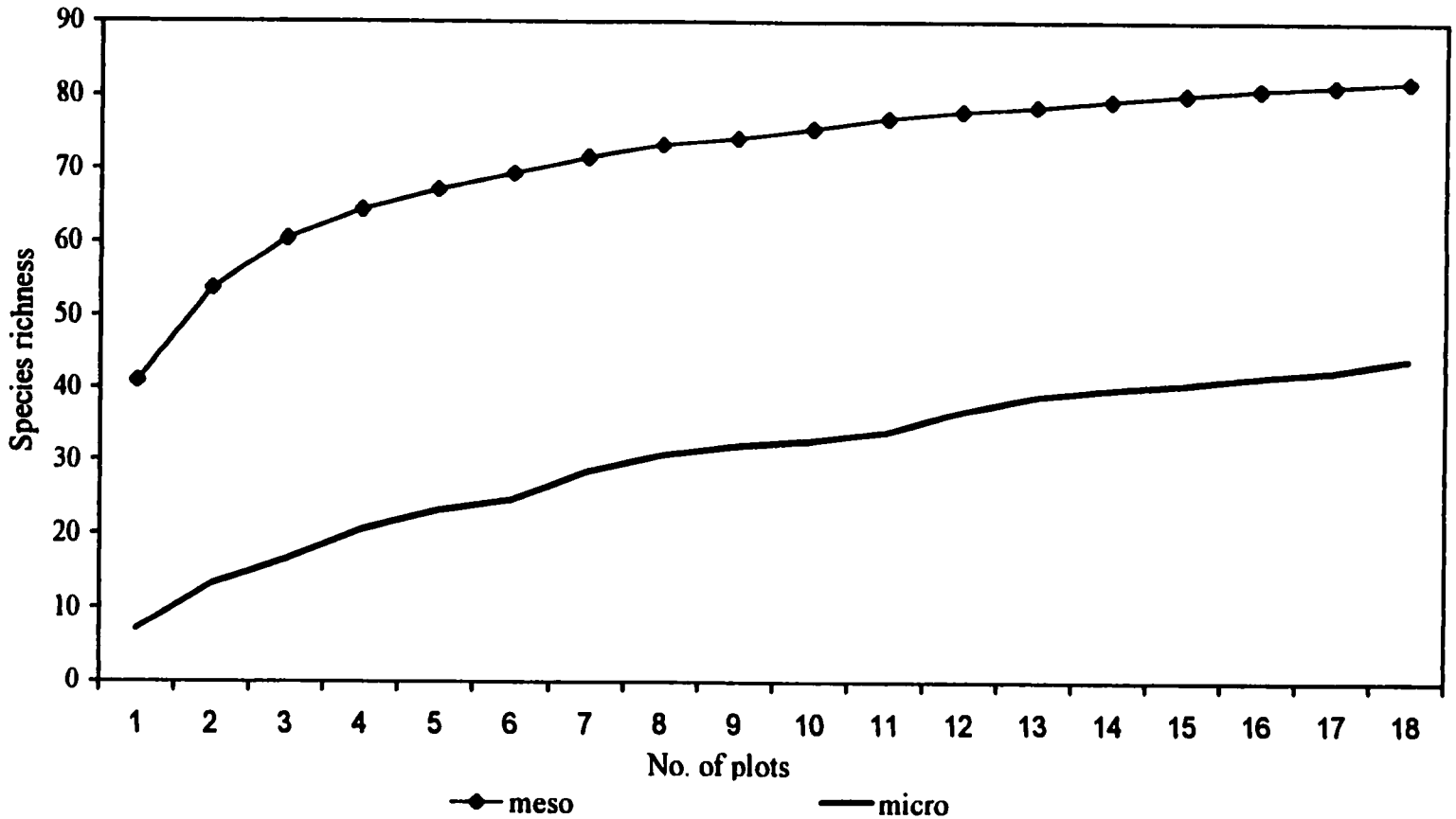

Figure 2.12 Species area curves of mesosites (no plots 1-6 stand 1, 7-12 stand 2, 13-18 stand 3), and 18 microsites (all microsite types) generated using average number of species for each no. of sample plots. First order jackknife estimates of species richness (observed species richness): mesosites 91.4 (82.0), microsites (n=355), 87 (80).

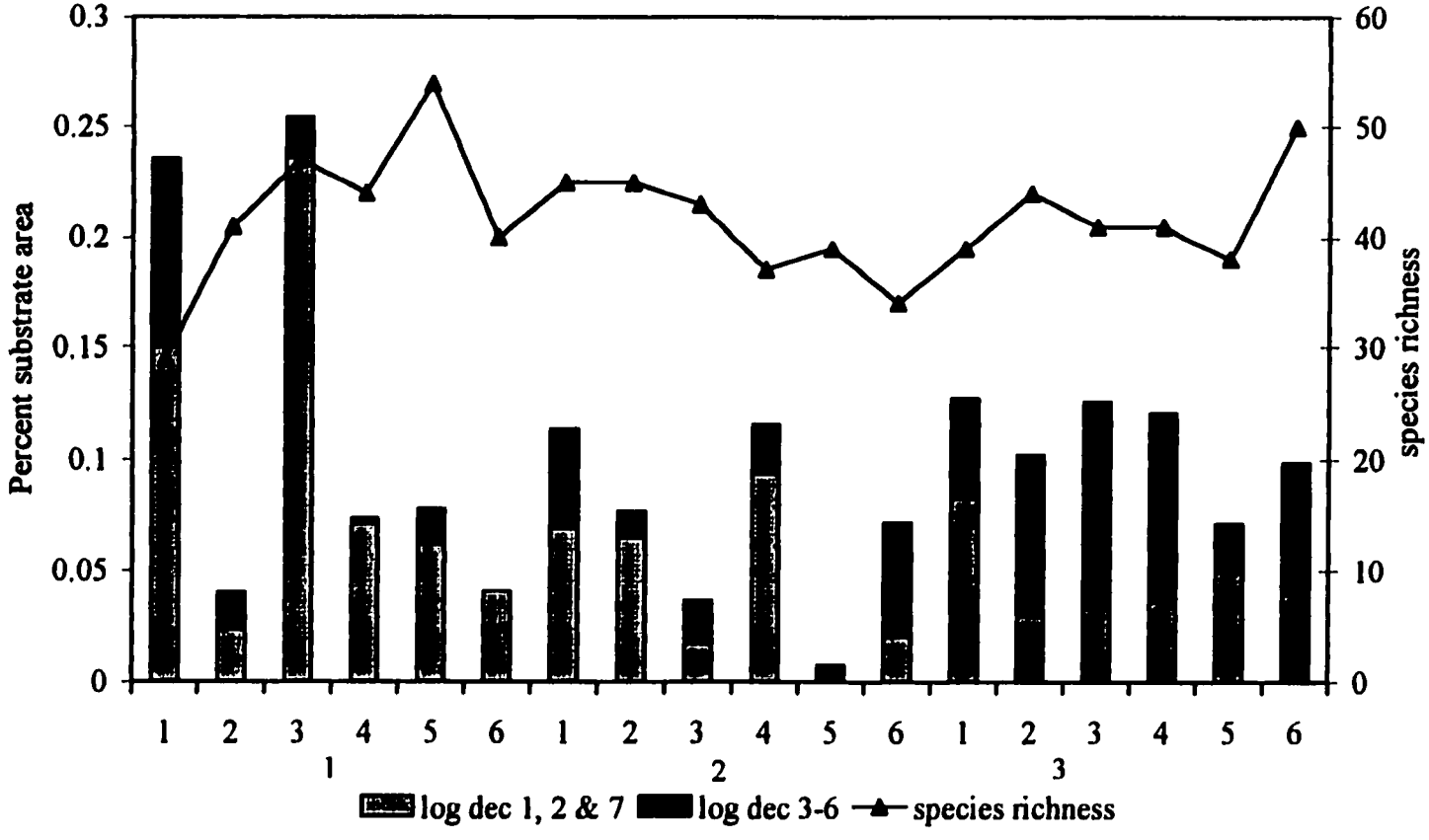

Figure 2.13 Bryophyte species richness and percent log area (subdivided into decay classes with high species richness (3-6) and low species richness (1, 2 & 7)) for mesosites 1-6 of stands 1, 2 and 3.

Chapter 3:
The relationship of bryophyte species composition to microsite in a boreal forest of Alberta, Canada.

Introduction

Habitat availability is a significant determinant of bryophyte species occurrence (Watson 1980, Vitt & Belland 1995, Gagnon & Bradfield 1987). The degree that we observe habitat parameters to control bryophyte community composition however, is contingent on the sampling frame used (Økland 1994). Examining the validity of pre-conceived ideas about what governs bryophyte community composition necessitates a multi-scaled sampling scheme.

At small local scales in the boreal forest, many authors have looked at bryophyte species composition on specific substrates (microsite types) including disturbed patches of forest floor created by treefalls (Jonsson & Esseen 1990), decaying logs (Söderström 1988), and trees (Gustafsson & Eriksson 1995, Hazell et al. 1998). Some boreal bryophyte species only establish and persist on specific substrate types (Koponen 1990, Söderström 1988) while other species occur on many substrates but show preference for some substrate types over others (Kimmerer 1993, Söderström 1993). If most bryophyte species show either preference (facultative specialists) or specificity (obligate specialists) for a particular microsite type, then microsite types should host different bryophyte communities. Several authors have compared differences in the bryophyte species composition of microsite types. Jonsson and Esseen (1990) observed differences in species composition between patches of undisturbed forest floor and forest floor disturbed by tree falls (perennial stayers versus colonizers and fugitive species), while Söderström (1993) found that the abundance of some epixylic species differed between logs and stumps.

Microsite type properties are also important for bryophyte species composition. Some epixylics occur only on logs of specific decay classes (Muhle & LeBlanc 1975, Söderström 1988), while some epiphytes prefer certain tree species (Culberson 1955), or a specific stratum within the same tree (Sillett 1995). Forest floor bryophytes are

responsive to differences in pH (Zamfir et al. 1999), micro-topography (Økland 1994), and soil moisture (Robinson et al. 1989).

At larger scales differences in bryophyte species composition have been related to a number of factors including: the number and type of microsites present in a defined area (Frisvoll & Prestø 1997, Rambo & Muir 1998); stand integrity (time since last disturbance) (Økland 2000); stand fertility (Pitkänen 2000); and elevation (Reenen & Gradstein 1983). Bryophyte species composition at intermediate spatial scales (within the stand) however, has often been overlooked. Økland (2000) found that in mature boreal forest stands the importance of fine scaled processes increased as stands aged and suggested that within-stand heterogeneity may be more important to bryophyte species composition than time since last disturbance.

It is therefore important to examine bryophyte species composition of a microsite not only in relation to its type (i.e. tree, log, stump) and properties (i.e. decay class, size) but also in relation to environmental variation occurring at intermediate and large spatial scales (i.e. fluctuations in soil pH and moisture, light and temperature).

The objective of this study is to identify the drivers of bryophyte species composition at small scales in the boreal forest. I will examine whether variation in bryophyte species composition of microsites is related to microsite type, microsite properties and/or environmental variation acting at larger spatial scales (mesosite (within stand) and stand scales). Since microsite type and properties, and not larger scaled environmental variation, were the most important predictors of bryophyte species diversity at small spatial scales in the boreal forest (see chapter 2), we can assume that similar patterns may exist for bryophyte species composition.

Methods

Site description, study area and sampling protocol were identical to those presented in Chapter 2.

Analysis

Species identification

Bryophyte nomenclature follows: Anderson et al. (1990) except for the following taxa: Sphagnaceae follow Anderson (1990), Hepaticae follow Stotler, & Crandall-Stotler (1977), and *Orthotrichum elegans* is recognized as distinct from *Orthotrichum speciosum* following Vitt & Darigo (1997). Species vouchers are deposited in the University of Alberta herbarium (ALTA). Prior to analysis *Lophozia excisa, Lophozia guttulata* and *Lophozia ventricosa* were grouped because of identification difficulties due to small amounts of material. In subsequent analyses these species were grouped.

Microsite species composition

To understand the extent of influence that pre-defined microsite types had on bryophyte species composition, I compared the compositional similarity within each of the microsite types with the compositional similarity of microsites placed in "idealized" groups (groups maximizing within group similarity and minimizing between group similarity). Cluster analysis was used to define idealized microsite groupings based on compositional similarity and Nonmetric multidimensional scaling (MDS) ordination and Indicator Species Analysis (ISA) were used to assess the ecological importance of both groupings. Further, within each microsite type I examined microsite species composition in relation to relevant habitat parameters and spatial structure at mesosite and stand scales. Only habitat parameters that best explained the compositional variation between microsites of each microsite type are presented in ordination diagrams.

Species clustering

I classified microsites according to species composition using two-way indicator species analysis (TWINSPAN). TWINSPAN is a hierarchical divisive clustering method that uses pseudospecies (user-defined abundance categories for species) to classify sites

and species (Hill 1979). I used cut levels that best represented variation in the data set (0.0, 0.01, 0.05, 0.5, 5.0, 20.0 and 50.0), to create pseudospecies. The minimum group size for division was 5, the maximum number of species in the final tabulation was 100 and the maximum level of divisions was 7. Cluster groups resulting from the second level of divisions had the greatest ecological meaning (further levels of divisions did not correspond to any measured environmental variables or microsite descriptors) and so were used as "idealized" microsite groups (hereafter referred to as TWINSPAN groups).

Ordination

The fidelity of species assemblages to pre-defined microsite types and TWINSPAN groups was assessed with Nonmetric multidimensional scaling, using the statistical package PC-ORD (McCune & Mefford 1997). Rather than maximizing the variability along axes, MDS best represents the similarity and dissimilarity among objects in few dimensions (Legendre & Legendre 1998). To facilitate interpretability, MDS ordinations were conducted and presented in two dimensions. I used the Sorenson distance measure with 100 iterations to perform MDS analyses. Stress is a measure of the degree to which the placement of objects on the ordination correspond to the actual dissimilarities between objects (ter Braak 1987). Percent variation in species data explained by each ordination was determined by calculating the coefficient of determination for the correlation between ordination distances and distances in original n space (McCune & Mefford 1997). Centroids (2 dimensional average position of points) and standard deviations were plotted for each microsite type to compare within microsite type variances.

The influence of habitat parameters on species composition of microsite types were assessed using MDS (following the above methods) for categorical descriptors of woody substrates and Canonical Correspondence Analysis (CCA) for continuous environmental variables for all microsite types. CCA ordinations of woody microsite types were not informative and were discarded.

I examined the importance of microsite properties to bryophyte species composition of tree base, stump and log microsite types using MDS ordinations of each

microsite type. Microsite points in MDS ordinations were coded according to properties thought to be important for a given microsite type. Microsite properties examined for trees included whether trees were hardwood or softwood (the hardwood group consisted of *Populus tremuloides* and *Populus balsamifera* while the softwood group was predominantly *Picea glauca* and *Picea mariana*, with rare occurrences of *Abies balsamea*), and tree diameter class. Properties examined for stumps and logs included whether they were from hardwood or softwood trees and their decay class (see Table 2.2). Microsite properties showing no relationship to microsite species data were not presented.

The influence of environmental variation on bryophyte species composition of both disturbed and undisturbed patches of forest floor, were assessed with separate CCA ordinations (CANOCO for Windows V 4.02, (ter Braak & Smilauer 1997)). CCA allows the interpretation of variation in species composition between sites based on species' niche breadth for selected environmental variables (ter Braak & Verdonschot 1995). I used forward stepwise selection to reduce the number of environmental variables in final ordinations. The significance of adding each variable was tested using Monte Carlo permutation tests (199 permutations); these tests are free from the assumption of normality (ter Braak & Smilauer 1997). Tested environmental variables for both ordinations included: soil moisture, soil pH, surface moisture, light, temperature, litter depth and *Hylocomium splendens* growth (see Chapter 2 for explanation of how environmental variables were sampled). Subsequently, CCA ordinations were re-run with smaller sets of environmental variables; those that explained a significant amount of variation in the species data at $p>0.05$ or the best 3 variables when <3 were significant. Eigenvalues, species/environment correlations and percent variation of species data explained are presented in Table 3.4. Correlation coefficients between environmental variables and sample scores (derived from species data), were calculated for each environmental variable of final ordinations (inter set correlations of environmental variables with axes (Table 3.5)) (ter Braak & Smilauer 1997). Biplots of environmental variables were overlain on ordinations of disturbed and undisturbed patches of forest floor to illustrate each environmental variable's maximum rate and direction of change

(ter Braak & Verdonschot 1995). I coded sites on ordination diagrams by stand. Coding undisturbed patches of forest floor by mesosite did not illustrate any patterns.

To determine if any variation in bryophyte species composition was occurring at the mesosite scale, CCA analysis was performed on mesosites following the procedures outlined for undisturbed and disturbed patches of forest floor. Environmental variables tested in stepwise CCA of mesosites included: light, surface moisture, soil moisture, soil pH, litter depth, feather moss cover, feather moss depth, availability of logs and proportion of aspen tree bases.

Indicator Species Analysis

To identify species indicators and evaluate the distinctiveness of species assemblages belonging to microsite types, sub-types (identified in TWINSPAN clustering) and log decay classes I performed Indicator Species Analysis (ISA) (Dufrêne & Legendre 1997) using PC-ORD (McCune & Mefford 1997). ISA calculates the indicator value (i.v.) (% of perfect indication) for each species in each pre-defined group by multiplying the species' proportional abundance by its' proportional frequency for that group (Dufrêne & Legendre 1997). Dufrêne & Legendre (1997) proposed that ISA be used to determine the optimum number of cluster divisions in cluster analysis (when i.v. values of species in groups begin declining further division of groups no longer adds information). Thus comparing i.v. values of species can be seen as a measure of how well groups are differentiated by bryophyte species composition. I identified dominant species assemblages for TWINSPAN groups, microsite types and log decay class groupings using species which had an i.v. greater than 20%. Thus to be included, a species with an equal presence and relative abundance for a group would need to be present in at least 45% of all sample plots with a relative abundance of at least 45%. All included species were significant at $\alpha = .05$ when tested using 1000 randomized Monte Carlo runs (McCune & Mefford 1997). I compared TWINSPAN groups to microsite types using both the number of species included in species assemblages and the magnitude of i.v.s.

Species identification

The sampled conifer-dominated boreal mixed-wood stands contained 90 bryophyte species (19 hepatic and 71 moss species) in 30 hectars (Table 3.1). Floristic Habitat Sampling (FHS) at the mesosite scale added 7 additional species that were not found in microsite sampling. Stand scale FHS added another 9 species. All but 3 of the species added using FHS were forest floor species.

The moss flora in the study site contained a higher proportion of pleurocarpous species (45%), of species from the Hypnales lineage (lineages follow those of Vitt (1984)) (45%), and of species with boreal and cosmopolitan distributions (74% and 16% respectively) than the overall Alberta moss flora (data from Vitt and Belland (1997)) (Table 3.2). This allocation of species attributes is opposite that found by Vitt and Belland (1997) for rare species. Rare species in Alberta were found to have a higher relative proportion of acrocarpous species, of species in the Bryales and Dicranales lineages and of species with temperate and montane distributions (Vitt and Belland 1997). Thus the distribution of moss species attributes in the flora of this study (a flora with a lower than average proportion of provincially rare species) follows the conclusions of Vitt and Belland (1997) that common species are more likely to be pleurocarpous, in the Hypnales lineage, with boreal or cosmopolitan distributions.

Species clustering

TWINSPAN clustering did not follow pre-defined microsite types (Table 3.3). The first division separated undisturbed patches of forest floor (U) (group B) from logs (L), stumps (S) and tree bases (T) (group A). Feather moss species *Hylocomium splendens* and *Pleurozium schreberi* were species indicators for group B which was composed of 81 U and 20 L + S + T microsites. Species indicators for group A were *Ptilidium pulcherrimum*, *Eurhynchium pulchellum* and *Pylasiella polyantha*. Group A was composed of 8 U and 248 L + T + S + D. All logs found in group B were from

decay classes 2, 6 and 7. Within group B, the second level of classification discerned undisturbed patches containing the peatland species *Aulacomnium palustre*, *Tomenthypnum nitens*, as well as *Brachythecium starkei* (group B2) from typical patches of undisturbed upland forest floor that contains a high abundance of *Hylocomium splendens* (group B1). The second division in group A divided logs, stumps and trees primarily on the basis of whether they were hardwood (group A2) or softwood (group A1). *Pylasiella polyantha*, *Eurhynchium pulchellum*, and *Amblystegium serpens* were indicative of group A2 which was composed of predominantly hardwood trees, logs and stumps (69 hardwood T, L & S, 8 D, 7 U and 22 softwood T, L & S). The majority of the softwood microsites included in this group were trees (13 T vs 6 S and 3 L). In group A1, *Ptilidium pulcherrimum* and *Dicranum fuscescens* identified logs, trees and stumps that were almost exclusively softwood (only 9 hardwood L , T & S, 9 D and 1 U were included). Four of the hardwood logs and stumps that were included in group A1 were from one mesosite with a canopy composed of only *Picea* species. Because divisions beyond this point were less informative, I used TWINSPAN groups A1, A2, B1 and B2 in further analysis. One third level division is worth mentioning. The hardwood group (group A2) separated stumps and logs from trees based on the presence of *Hylocomium splendens*, *Ptilium crista-castrensis*, *Pleurozium schreberi* and *Pohlia nutans* on stumps and logs.

Ordination

Though all two dimensional MDS ordinations performed on the data set had fairly high stress values (between 20 and 26), adding a third dimension impeded interpretation. Results are therefore presented in two dimensions.

MDS ordination of all microsite types (Figure 3.1 a, b), showed reasonable separation between trees and undisturbed patches of forest floor but not between stumps, logs and disturbed patches of forest floor. This suggests that despite the discrete nature of most bryophyte substrates, bryophyte species composition between microsite types exists on a continuum due to high compositional turnover within each microsite type (see Chapter 2). Variation in bryophyte species composition between microsites of one

microsite type was greatest for disturbed patches of forest floor and smallest for undisturbed patches of forest floor (Figure 3.1 a). Aggregation was more pronounced when TWINSPAN groups rather than microsite types were coded on the ordination diagram (Figure 3.2). Thus for woody substrates, hardwood and softwood groups appear to have greater compositional similarity than microsite types.

When analysed separately, MDS ordinations of logs (Figures 3.5), stumps (Figure 3.7) and trees (Figure 3.8) show separation between hardwood and softwood microsites. Species composition of logs also varied with decay class; within log variation in bryophyte species composition decreasing as decay class increased (Figure 3.6). No other environmental variables or substrate attributes for logs, stumps, and trees were interpretable from CCA ordinations (environmental variables) or overlays on MDS ordinations (categorical microsite attributes).

In the CCA ordination of undisturbed patches of forest floor the environmental variables soil moisture, light and soil pH explained significant amounts of the total variation in species data using forward stepwise selection with Monte Carlo permutation tests (Figure 3.7). CCA ordination constrained with these three environmental variables, explained only 9.1 % of the variation in species data on the first axis (Table 3.4), with an additional 3.8 % on the second axis (eigenvalue=0.17). All three variables were very weakly positively correlated with the first ordination axis (Table 3.5). TWINSPAN groups B1 and B2 (dry and wet undisturbed patches of forest floor) did not show any clustering on the ordination diagram suggesting that TWINSPAN groups were not related to measured environmental variables. Stand 1 separated from stands 2 and 3 along the first axis, likely because of the higher soil moisture and pH in this stand (Figure 3.8).

In the CCA ordination of disturbed patches of forest floor species composition was explained almost exclusively by soil moisture along the first axis (r^2=0.87); this was the only environmental variable that explained a significant amount of variation in the species data set. Constraining the ordination with soil moisture, litter depth and pH (order following stepwise selection), resulted in separation between stands 1, 2 and 3.

Soil moisture and surface moisture both explained significant amounts of variation in mesosite species composition (Figure 3.9); in total explaining 40.8% of the variation in the species data. Light, although strongly correlated with the second axis

(Table 3.5), explained very little of the variation in species data. Mesosites from stand 1 had a wider spread than those in stands 2 or 3.

Mesosites and undisturbed and disturbed patches of forest floor in stand 1 had more variable species composition (sites were further apart from one another in CCA ordinations) than mesosites and undisturbed and disturbed patches of forest floor in stands 2 and 3 respectively.

Indicator Species Analysis

Because of the marked difference in species composition of hardwood and softwood microsites for trees, stumps and logs, species indicator values for these microsite types were low (Table 3.3). Of all microsite types, disturbed patches of forest floor had the most distinctive flora with the greatest number of species with indicator values above 20% and undisturbed patches of forest floor had more distinct species than logs and stumps. There were no indicator species for trees when hardwood and softwood trees were included in one group. This illustrates that hardwood and softwood trees host very different bryophyte floras. High indicator values for species in TWINSPAN groups and log decay classes demonstrate the importance of microsite properties in delineating species composition. Hardwood and softwood logs, stumps and trees had many species with high indicator values. Indicator values of species categorized by log decay class were very low for logs in early decay classes and peaked at decay class 5 (Table 3.6).

Discussion

General comments on the flora

The northern boreal forest has a lower concentration of rare bryophyte species than other areas in Alberta. This may be due to a lack of unique physiographic forms; lower habitat heterogeneity has been linked to low bryophyte species diversity (Vitt et al. 1995). If extrapolated over the landscape, the sampled forest type was species poor (λ diversity = 93.6 (second order jacknife estimate of total species richness based on

mesosite sampling – (Chapter 2)) in relation to some other forest types in western North America (λ diversity (excluding cliffs, streams and seeps) = 151 and 128 for Oceanic rainforest and Mainland coastal rainforest respectively in the Coastal Western Hemlock biogeoclimatic zone of British Columbia (Newmaster 2000)). The number of species found at smaller scales in the conifer-dominated stands of this study was comparable to that of other bryophyte studies done in forested areas of Alberta. Mean species richness of study stands (67.3) was greater than mean richness of mixed-wood stands in the Rocky Mountains (36 ± 2) (Doubt 2001), total bryophyte species richness in *Pinus contorta* stands in the upper foothills of the Rocky Mountains in Alberta (37) (Pharo & Vitt 2000), and *Populus tremuloides* dominated stands in the boreal forest (Crites & Dale 1995). Mesosite species density (mean 41.7 species/625 m^2), was roughly equivalent to the species density in Dutch coniferous forest (maximum of 23 species/300m^2), the most bryologically diverse habitat type in Holland (Dirske & Martakis 1998). Though eight species that had rare species distinction S1 or S2 in Alberta (S1: ≤ 5 occurrences, S2: 6 – 20 occurrences (Gould 2001)), I suspect that four (which were prolific in my collections) are under represented in herbaria because of under collection and problematic taxonomy. The low percentage of rare moss species (a maximum of 11%) and the pattern of species attributes (higher percentage of cosmopolitan and boreal distributed moss species) within the study flora suggest that the flora is predominantly made up of common moss species. Furthermore, only 15 species were restricted to one microsite type. Many epixylics were found in small abundance at the bases of trees, or on undisturbed patches of forest floor. Although as a groups bryophyte species are thought to be habitat specialists, this study suggests that a higher proportion of the bryophyte species in the boreal forest of northern Alberta are habitat generalists.

Do microsites differ in terms of species composition?

Microsite type as defined in this study was not always the most suitable criterion for categorizing bryophyte species associations. All analyses (TWINSPAN, MDS ordination and I.S.A.) show some separation in bryophyte species composition on the basis of microsite type. Bryophyte species associations on undisturbed patches of forest

floor separated from other microsite type communities using all three techniques, while stumps and logs did not host distinct bryophyte species associations in any analysis; TWINSPAN groups and MDS separated all woody microsite types on the basis of the hardwood/softwood distinction and not on the basis of microsite type.

Other authors have found only small differences in the bryophyte species composition of logs versus stumps. Andersson & Hytteborn (1991) found only one epixylic species (*Lophocolea heterophylla*) with a preference for logs over stumps (significantly higher abundance using t-test) and Kimmerer (1993) found *Tetraphis pellucida* to be more abundant on stumps than on logs. In both of these cases, species amplitudes were examined separately. The high variability in bryophyte species composition of both logs and stumps likely overshadows any small compositional differences that may exist between these two microsite types.

Disturbed patches of forest floor were the most variable microsite type and did not form a distinct group in MDS or TWINSPAN yet several species characteristic of disturbed patches were identified with high i.v. values in I.S.A.. This indicates that, although the abundances of many species may be homogenous among disturbed patches and woody substrates, there exists a distinct set of species associated with disturbed patches of forest floor (Table 3.2). All of the species indicative of disturbed patches are acrocarpous and most (barring *Mnium spinulosum*) exhibit a colonists life strategy: short life spans, high asexual and sexual reproductive effort and small spores (During 1979).

Although trees separated from other microsite types in the MDS ordination (having small variance in bryophyte species composition relative to other microsite types), they did not cluster cohesively in TWINSPAN, or have any species with i.v. values over 20% in I.S.A. These inconsistencies reflect both the sensitivities of each analysis and the floristic characteristics of hardwood and softwood trees. Because TWINSPAN clusters sites hierarchically and dichotomously based on the first axis of CA or DCA ordinations, strong gradients may hide other patterns that exist in the data (Dufrêne and Legendre 1997). In the case of trees, the strong compositional differences of softwood versus hardwood trees, stumps and logs may have overshadowed differences between trees and other wood substrates. Softwood trees (which were the majority) did split from softwood logs and stumps at a lower level of division. Similarly, in order for

species to have high i.v.s in I.S.A., they require both a high relative abundance for the group and a high occurrence within the group. Softwood trees have very few true epiphytes (species occurring above a height of 50 cm), and since *Picea* species made up 90% of the total tree population the softwood flora dominated. Softwood trees in this area of the boreal forest are more easily characterized by a lack of species than by any species in particular. The one exception being *Ptilidium pulcherrimum*. Although this species occurred on 93% of softwood trees and 85% of all trees it is also very abundant on softwood logs and stumps. At 85% occurrence I.S.A. would require a relative abundance over 23% in order to have an i.v. of 20%. The high abundance of *Ptilidium pulcherrimum* on all substrate types made this unattainable.

Are microsite characteristics important?

TWINSPAN groups were based on properties of microsite types rather than the microsite types themselves indicating that the variation in bryophyte composition within any given type may be greater than the variation between microsite types.

Softwood logs, stumps and trees were compositionally similar, as were hardwood logs, stumps and trees. MDS analyses, TWINSPAN groups and I.S.A. supported these groups. Although the specificity of bryophyte communities to different tree species has been recognized (Culberson 1955, Smith 1982, Palmer 1989, Newmaster 2000), strong positive associations between the bryophyte communities of tree species and their log counterparts have not. Studlar (1982) recognized succession on tree bases as species accumulated from saplings to mature trees and Muhle & LeBlanc (1975) described the change in bryophyte species composition with log decay. The similarity between species composition of trees and logs of the same species, as found in this study, suggests that bryophyte community succession continues over the course of tree senescence; with many bryophyte species of live trees persisting on the log after the tree falls. Compositional differences between hardwood and softwood logs begin to disappear in later decay classes as log communities become more decay class specific (Figures 3.3 and 3.4) suggesting that epixylics of later decay classes are not sensitive to log species but rather to log decay.

Hardwood vs. softwood

Woody microsites in the hardwood group (almost exclusively *Populus* sp.) in TWINSPAN were characterised by a more diverse flora and more hydrophilic species than those in the softwood group (almost exclusively *Picea* sp.). The three species with the highest i.v.s for the hardwood group in I.S.A. conform to TWINSPAN indicator species: *Eurhynchium pulchellum, Pylasiella polyantha* and *Amblystegium serpens*. Tree substrates expose bryophyte species to more severe microclimatic conditions (lower relative humidity, higher wind) than logs or stumps and thus have a more limited flora (Smith 1982). Thus the dominant bryophyte species on *Picea* species (see below) and *Populus* species (see above) substrates also grow abundantly in the more favourable microclimate of logs and stumps. These species are the best indicators of the hardwood/softwood division. The majority of species indicators for the hardwood group are pleurocarpous and in the Hypnales lineage with smooth-rough mat life forms (following La Roi & Stringer's (1976) application of Gimingham & Birse's (1957) life forms to the boreal bryophyte flora). Smooth mats have a single plane of interwoven shoots and branches, and are often closely appressed to a substrate growing horizontally, rough mats also grow horizontally but differ in the erect growth of lateral branches giving the mat an irregular texture (Gimingham & Birse 1957).

No pleurocarpous mosses were indicative of the softwood group. Only the liverwort *Ptilidium pulcherrimum* (smooth mat) and *Dicranum* sp. (short turf life forms: erect shoots and branches vertical growth), were indicative of the softwood group. These species act as facultative epiphytes at trees bases (Smith 1982). *Ptilidium pulcherrimum* is unlike other liverworts in that it is tolerant of drought. This allows it to be common on softwood tree bases, stumps and logs in Spruce forests in Scandinavia (Söderström 1993). The higher frequency of pleurocarps on *Populus* sp. may be due to the higher moisture levels (Smith 1982) or higher pH (Culberson 1955) of *Populus* sp. bark relative to *Picea* sp. bark. 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. Smith (1982) and

Bates (1998) hypothesized that the smooth mat life form allows drought sensitive species to persist in harsh environments by extracting moisture from tree bark. A study in a cove forest in Virginia confirmed these results; Studlar (1982) found an increase in the short turf life form and a decrease in the rough mat life form moving from tree species with mesic bark towards those with xeric bark.

Of the woody substrate communities, only log species composition varied in response to microsite properties other than the hardwood/softwood designation. Two interesting trends in log species composition occurred with increasing decay class: 1. Log species composition became more homogenous between log species, and 2. Log communities became more decay class specific; log communities within latter decay classes had higher indicator values and less variable site scores (MDS ordination) than log communities of earlier decay classes (Figure 3.4, Table 3.6)). These trends are interdependent in the following way: If bryophyte species composition is a function of log species in early decay classes, the presence of many log species will make log species composition in early decay classes more variable. The extent of the compositional specificity of logs in early decay classes is evident in logs of decay class 2 and 3. *Pylasiella polyantha* was the best indicator of decay class 2 logs despite its limited occurrence on softwood logs (one out of 15 softwood logs sampled in decay class 2) while decay class 3 had no indicator species. The floras of softwood and hardwood logs began to homogenize by decay class 4 with *Ptilidium pulcherrimum* and *Eurhynchium pulchellum* occurring on both softwood and hardwood logs. Logs of decay class 5 had the greatest number of species with high indicator values (11), of which seven were liverworts. Of these species, 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 suitable conditions for the establishment and growth of epixylics having no bark, uneven wood texture and a humid microclimate (wood at this decay stage has greater porosity thus having higher moisture availability). High species indicator values on logs of decay class 5 suggest that the epixylics requiring decayed logs have a narrower niche breadth than the facultative epiphytes or forest floor species occurring on logs of other decay classes. Newmaster (2000) found the same trend in the Interior Cedar-Hemlock forests of British Columbia.

Species with high indicator values in decay classes 6 and 7 were predominantly ground flora species. One late epixylic species (sensu Söderström 1988), *Plagiothecium denticulatum*, was indicative of logs of decay stage 7. Another species thought to be indicative of old growth forests *Plagiomnium ellipticum* (Boudreault et al. 2000), was also an indicator species for logs of decay stage 7. Some species had high i.v.s for more than one log decay class: *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis* and *Eurhynchium pulchellum*, and *Ptilidium pulcherrimum*. Each of these species has a broad niche while being highly abundant in each microsite, thus the strong correlation between abundance and niche breadth in bryophytes in boreal mires of Scandinavia (Økland 1989) likely holds forest bryophytes here.

Variation in stump species composition with decay class was not illustrated by MDS. This may be because stumps contain more internal heterogeneity; stump tops are often in latter stages of decay than stump sides, which are protected by bark, or because the four decay classes used for stump classification were insufficient to separate distinct bryophyte communities.

The effect of larger spatial scales on microsites

Unlike tree, stump and log communities, bryophyte composition on disturbed and undisturbed patches of forest floor were affected by environmental variation at the stand scale. Variation due to stand, although present, was minimal for both disturbed and undisturbed patches of forest floor (9.1 and 8.1 % variation explained by the first ordination axis respectively). Using stand differences to explain compositional variation in patches of undisturbed and disturbed forest floor is therefore somewhat limited.

Patterns in both disturbed and undisturbed patches of forest floor separated microsites in stand 1 (the oldest stand) from those in stands 2 and 3 along moisture and pH gradients (variation in soil moisture and pH were significant at the stand scale – see Chapter 2). Bryophyte compositional changes have been related to pH (Zamfir et al.1999) and moisture (Lee and La Roi 1979, Wolf 1993, Robinson et al. 1989) gradients in different ecosystems.

Species composition at the mesosite scale.

Patterns in mesosite species composition were similar to patterns in species composition of undisturbed and disturbed patches of forest floor. This suggests that, although only a small amount of variation in mesosite species composition was explained by the CCA (14 % by the first axis), variation explained was likely a result of variation occurring in the bryophyte species composition of undisturbed and disturbed forest floor. Neither substrate availability or light were important descriptors of bryophyte species composition at the mesosite scale. Pharo & Vitt (2000) also found a very weak relationship between species composition and measured environmental variables in montane forests of western Canada. Both of these studies illustrate that in natural systems where many species are habitat generalists, patterns in bryophyte species composition may not be related to present environmental variation but rather they may be the result of stochastic factors governing occurrence, dispersal and establishment or a reflection of past disturbance or environmental patterns. Alternatively, the relative invariance in bryophyte species composition of these habitat types at the studied spatial scales renders the small variation that does exist difficult to interpret. A study in Sweden showed very few compositional differences between managed and non-managed stands. Differences that did exist were due to differences in substrate availability (missing large logs in the managed stand) (Gustafsson & Hallingbäck 1988). Compositional differences in bryophyte communities at scales larger than those examined in this study are often related to landscape heterogeneity (ie. differences between forest types, cliffs, grasslands) (Newmaster 2000). Although some variation does occur at the mesosite scale in the boreal forest (Chapter 2), this variation was not great enough to create large differences in bryophyte species composition. A meso-scale vegetation study in Finland showed similar results; very few patterns were explained by either spatial scale or environmental variables. When examining different spatial scales Økland (1994), found most bryophyte species associations to exist at a scale of 1 by 1 m in the boreal forest of Scandinavia.

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Table 3.1 Species occurrence (for all species in the study site) expressed as the proportion of sampled microsites within each microsite type. 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 not shown. n= number sampled for each microsite type.

	relative frequency of microsites (by type) were each species is present					Species names
	d	l	s	t	u	
n	23	87	65	90	90	
	0.22	0.27	0.32	0.1	0.01	*Amblystegium serpens* (Hedw.) Schimp.
**				0.01		*Amblystegium varium* (Hedw.) Lindb.
		0.19	0.06			*Anastrophyllum hellerianum* (Nees) Schust.
	0.44	0.13	0.03	0.01	0.02	*Aulacomnium palustre* (Hedw.) Schwaegr.
*		0.1				*Blepharostoma trichophyllum* (L.) Dum.
	0.09	0.05	0.13	0.04		*Brachythecium albicans* (Hedw.) Schimp.
	0.3	0.4	0.26	0.18	0.03	*Brachythecium campestre* (C. Müll.) Jaeg.
		0.08	0.04	0.01	0.02	*Brachythecium erythrorrhizon* Schimp.
**						*Brachythecium reflexum* (Stark) Schimp.
	0.13	0.16	0.19	0.06	0.01	*Brachythecium salebrosum* (Web & Mohr) Schimp.
	0.3	0.31	0.19	0.09	0.11	*Brachythecium starkei* (Brid.) Schimp.
	0.09	0.1	0.08	0.01		*Brachythecium velutinum* (Hedw.) Schimp.
*	0.04					*Bryohaplocladium microphyllum* (Hedw.) Wat. & Iwats.
	0.26	0.09	0.01	0.03		*Bryum lisae De Not. var. cuspidatum* (Bruch & Schimp.) Marg.
*	0.09					*Bryum pseudotriquetrum* (Hedw.) Gaertn. et al.
	0.13	0.03	0.07			*Bryum sp.*
***						*Calliergon cordifolium* (Hedw.) Kindb.
**						*Calliergon richardsonii* (Mitt.) Kindb.
	0.13	0.3	0.21	0.06	0.01	*Campylium hispidulum* (Brid.) Mitt.
	0.09	0.08	0.03			*Cephalozia lunulifolia* (Dum.) Dum.
	0.35	0.06	0.06	0.03		*Ceratodon purpureus* (Hedw.) Brid.
***						*Climacium dendroides* (Hedw.) Web & Mohr.
			0.04	0.02		*Dicranum acutifolium* (Lindb. & Arnell) Weinm.
	0.04	0.19	0.11	0.1		*Dicranum flagellare* (Hedw.)
	0.13	0.23	0.17	0.2	0.01	*Dicranum fragilifolium* Lindb.
	0.04	0.28	0.19	0.26	0.01	*Dicranum fuscescens* Turn.
*			0.01			*Dicranum groenlandicum* Brid.
	0.09	0.1	0.06	0.07	0.01	*Dicranum polysetum* Sw.
		0.05	0.01	0.01		*Dicranum scoparium* Hedw.
		0.05	0.01	0.04		*Dicrcanum tauricum* Sapeh.
	0.04	0.05	0.1	0.04	0.01	*Dicranum undulatum* Brid.
**						*Drepanocladus aduncus* (Hedw.) Warnst.
	0.57	0.56	0.79	0.56	0.2	*Eurhynchium pulchellum* (Hedw.) Jenn.
*	0.04					*Funaria hygrometrica* Hedw.
**						*Helodium blandowii* (Web. & Mohr) Warnst.
	0.17	0.15	0.13	0.06	0.01	*Herzogiella turfacea* (Lindb.) Iwats.
	0.61	0.7	0.57	0.3	0.89	*Hylocomium splendens* (Hedw.) Schimp.
			0.02	0.01		*Hypnum pratense* (Rabenh.) Spurce
*			0.01			*Isopterygiopsis pulchella* (Hedw.) Schimp. Iwats.
	0.04	0.36	0.13	0.04		*Jamesoniella autumnalis* (DC.) Steph.
	0.04	0.07	0.07	0.02		*Lepidozia reptans* (L.) Dum.
	0.3	0.05	0.01			*Leptobryum pyriforme* (Hedw.) Wilw.
	0.04	0.07	0.03	0.01		*Leptodictyum riparium* (Hedw.) Warnst.
	0.04	0.22	0.1	0.02		*Lophocolea heterophylla* (Schrad.) Dum.
	0.04	0.06	0.01	0.01	0.01	*Lophocolea minor* Nees
		0.01	0.01			*Lophozia ascendens* (Warnst.) Schust.
		0.03	0.04			*'Lophozia excisa* (Dicks.) Dum.

		0.01	0.01			*Lophozia incisa* (Schrad.) Dum.
		0.11	0.06	0.04		*Lophozia longidens* (Lindb.)
*		0.07				[1]*Lophozia guttulata* (Lindb. Et H.Arnell) Evans
	0.04	0.1	0.03	0.01		[1]*Lophozia ventricosa* (Dicks.) Dum.
*	0.13					*Marchantia polymorpha* L.
	0.35	0.34	0.44	0.24	0.03	*Mnium spinulosum* Bruch & Schimp.
	0.17	0.03	0.22	0.06	0.01	*Oncophorus wahlenbergii* Brid.
		0.18	0.14	0.09		*Orthotrichum obtusifolium* Brid.
		0.14	0.14	0.07		*Orthotrichum elegans* Hook. & Grev.
			0.02		0.01	*Plagiochila porelloides* (Nees) Lindenb.
	0.22	0.08	0.19	0.07	0.01	*Plagiomnium cuspidatum* (Hedw.) T. Kop.
	0.09	0.13	0.08	0.03	0.07	*Plagiomnium drummondii* (Bruch & Schimp.) T. Kop.
	0.13	0.07	0.03	0.02	0.09	*Plagiomnium ellipticum* (Brid.) T. Kop.
	0.13	0.18	0.06	0.03	0.07	*Plagiomnium medium (Bruch & Schimp.) T. Kop.*
	0.17	0.07	0.06	0.01		*Plagiothecium denticulatum* (Hedw.) Schimp.
***						*Plagiothecium laetum* Schimp.
	0.09	0.06	0.13	0.07		*Platydictya jungermannioides* (Brid.) Crum
	0.3	0.74	0.42	0.27	0.63	*Pleurozium schreberi* (Brid.) Mitt.
*			0.04			*Pohlia cruda* (Hedw.) Lindb.
	0.57	0.23	0.36	0.1	0.01	*Pohlia nutans* (Hedw.) Lindb.
*	0.09					*Polytrichum commune* Hedw.
*	0.26					*Polytrichum juniperinum* Hedw.
***						*Polytrichum longisetum* Brid.
***						*Polytrichum piliferum* Hedw.
*				0.01		*Pseudotaxiphyllum elegans* (Brid.) Iwats.
	0.09	0.58	0.39	0.86	0.02	*Ptilidium pulcherrimum* (G. Web.) Hampe.
	0.3	0.75	0.29	0.17	0.5	*Ptilium crista-castrensis* (Hedw.) De Not.
	0.17	0.43	0.44	0.27	0.01	*Pylasiella polyantha* (Hedw.) Grout
***						*Rhizomnium gracile* T. Kop.
*		0.02				*Rhizomnium pseudopunctatum* (Bruch & Schimp.) T. Kop.
**						*Rhytidiadelphus triquetrus* (Hedw.) Warnst.
*		0.03				*Riccardia latifrons* Lindb.
	0.26	0.45	0.31	0.36	0.03	*Sanionia uncinata* (Hedw.) Loeske
		0.2	0.01			*Scapania glaucocephala* (Tayl.) Aust.
**						*Sphagnum russowii* Warnst.
		0.05	0.01		0.06	*Sphagnum warnstorfii* Russ.
***						*Splachnum luteum* Hedw.
***						*Splachnum rubrum* Hedw.
***						*Splachnum vasculosum* Hedw.
	0.04	0.05	0.1			*Tetraphis pellucida* Hedw.
		0.05	0.04	0.03	0.08	*Thuidium recognitum* (Hedw.) Lindb.
	0.04	0.06	0.01		0.12	*Tomenthypnum nitens* (Hedw.) Loeske.
		0.03	0.06			*Tritomaria exsectiformis* (Breidl.) Loeske

** = only found at the stand scale
** = only found at the mesosite scale
* = only found on one microsite type

[1]taxa were grouped in subsequent analyses

Table 3.2 Attributes of moss species found in the study area as compared with moss attributes in all of Alberta, and in a subset of provincially rare species[2] expressed as percentage of total moss species[1].

Attribute		Study area	Alberta wide*	Rare component*
	(% of flora)			
carpy	*acrocarpous*	55	69	78
	pleurocarpous	45	31	22
lineage[3]	*Bryales*	20	20	27
	Dicranales	16	20	24
	Hypnales	45	26	14
	Pottiales	7	12	11
	Others	12	22	24
phytogeography[4]	*boreal*	74	54	42
	cosmopolitan	16	6	3
	temperate	6	17	27
	arctic-alpine	4	12	12
	montane	0	11	15

[1] data published in Vitt & Belland (1997)
[2] with an occurrence of 1-5 locations in the province
[3] following Vitt (1984)
[4] developed by Belland (1987)

Table 3.3 Results of Indicator Species Analysis (Dufrêne & Legendre 1997) for each microsite type and TWINSPAN groups; species with indicator values (i.v.) greater than 20 are presented. p = probability of type 1 error for species i.v.s tested using a Monte Carlo test with 1000 runs.

TWINSPAN groups			Microsite types		
Species	i.v.	p	Species	i.v.	p
Softwood group A1			Disturbed patches of forest floor		
Ptilidium pulcherrimum	70	0.001	*Pohlia nutans*	53	0.001
Dicranum fuscescens	42	0.001	*Leptobryum pyriforme*	35	0.001
Dicranum fragilifolium	22	0.008	*Ceratodon purpureus*	29	0.001
Dicranum flagellare.	20	0.006	*Polytrichum juniperinum*	26	0.001
			Bryum lisae	25	0.001
Hardwood group A2			*Mnium spinulosum*	23	0.003
Eurhynchium pulchellum	70	0.001			
Pylasiella polyantha	66	0.001	Logs		
Amblystegium serpens	42	0.001	*Ptilidium pulcherrimum*	29	0.003
Brachythecium campestre	33	0.003	*Jamesoniella autumnalis*	24	0.002
Sanionia uncinata	24	0.037	*Ptilium crista-castrensis*	23	.
Orthotrichum elegans	24	0.006			
Orthotrichum obtusifolium	24	0.002	Stumps		
Mnium spinulosum	22	0.019	*Eurhynchium pulchellum*	54	0.001
Plagiomnium cuspidatum	20	0.002	*Pylasiella polyantha*	26	0.002
Brachythecium salebrosum	20	0.001			
			Trees		
Undisturbed (dry) group B1			none	.	.
Hylocomium splendens	68	0.001			
Pleurozium schreberi	41	0.003	Undisturbed forest floor		
Ptilium crista-castrensis	33	0.005	*Hylocomium splendens*	54	0.001
			Pleurozium schreberi	34	0.001
Undisturbed (wet) group B2			*Ptilium crista-castrensis*	29	0.006
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			

Table 3.4 Results of Canonical Correspondence Analysis (CCA) for undisturbed and disturbed patches of forest floor and mesosites.

Sites	Axis	1	2	3	4
Undisturbed forest floor	Eigenvalue	0.41	0.17	0.04	0.63
	Species/environment correlation	0.68	0.60	.329	0
	Cumulative % variance of species data explained	9.1	12.9	13.8	27.8
Disturbed forest floor	Eigenvalue	0.58	0.43	0.26	0.97
	Species/environment correlation	0.93	0.93	0.74	0
	Cumulative % variance of species data explained	8.1	14.1	17.1	31.2
Mesosites	Eigenvalue	0.13	0.07	0.04	0.12
	Species/environment correlation	0.88	0.96	0.82	0
	Cumulative % variance of species data explained	14.6	22.6	26.8	40.8

Table 3.5 Inter set correlations (Pearson) of environmental variables with axes for CCA of undisturbed and disturbed patches of forest floor, and mesosites. Axis 4 is not included because species environment correlations were 0.

Sites	env. variable	Axis 1	Axis 2	Axis 3
Undisturbed patches of forest floor	soil moisture*	0.489	0.166	-0.210
	pH*	0.557	-0.340	-0.031
	light*	0.435	0.291	0.197
Disturbed patches of forest floor	moist*	0.886	-0.030	0.225
	pH	0.505	0.106	-0.612
	litter	-0.279	0.869	-0.131
Mesosite	light	0.040	-0.209	0.803
	surface moisture*	0.161	0.928	0.163
	soil moisture*	0.871	-0.153	0.018

*explain a significant amount of additional variance in species data when added in order of forward stepwise selection and tested with a Monte Carlo test $p<0.05$ (McCune & Mefford 1997).

Table 3.6 Results of Indicator Species Analysis (Dufrêne & Legendre 1997) for log decay classes; species with indicator values (i.v.) greater than 20 are presented. p = probability of type 1 error for species i.v.s (only calculated for the maximum i.v. of each species, (.) indicate that species is a better indicator for a different group) tested using a Monte Carlo test with 1000 runs.

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

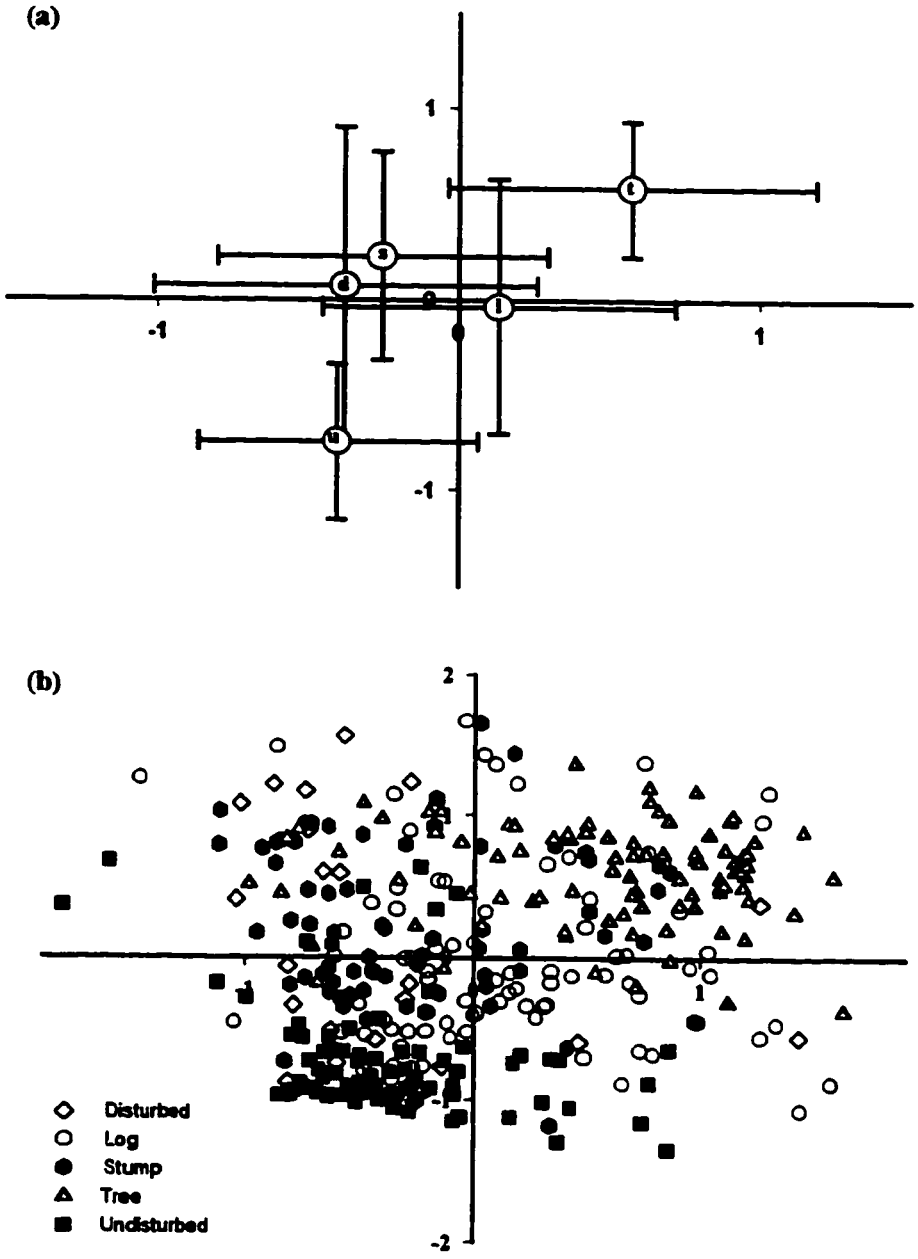

Figure 3.1 NMDS ordination in 2 dimensions of microsite types. Stress=22.95, % variation explained = 47. (a) centroids (mean sample scores +/- s.d) d=disturbed patches of forest floor, l=log, s=stump, t=tree, u=undisturbed patch of forest floor. (b) all sample scores.

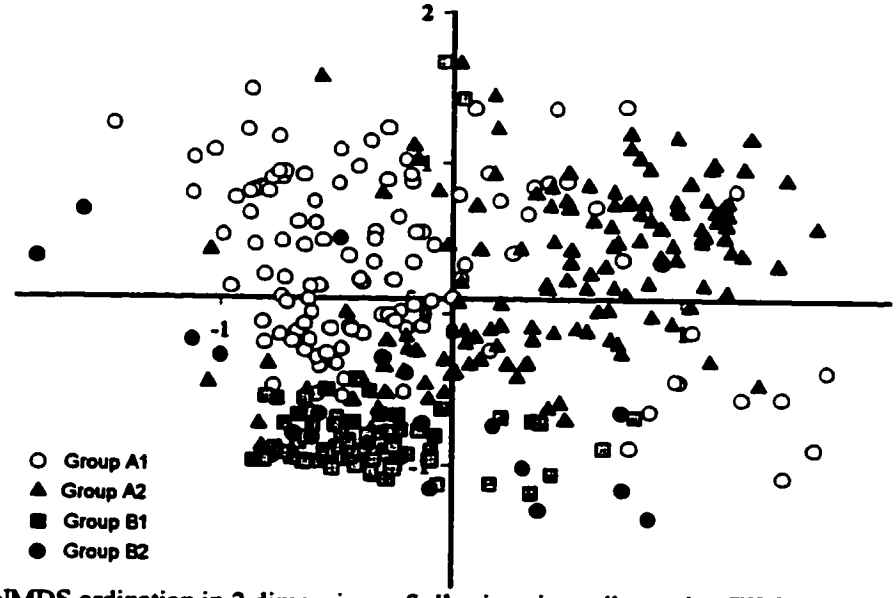

Figure 3.2 NMDS ordination in 2 dimensions of all microsites, allocated to TWINSPAN groups related to microsite characteristics. Group A1= hardwood group, A2 = softwood group, B1= undisturbed patches of forest floor (dry), B2 = undisturbed patches of forest floor (wet). Stress=22.95, 47% variation explained.

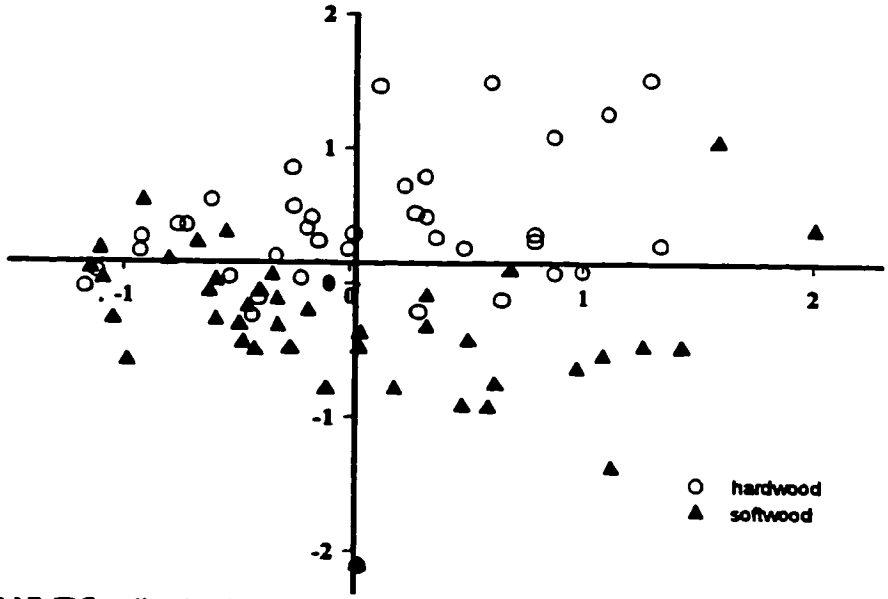

Figure 3.3 NMDS ordination in 2 dimensions of logs; hardwood and softwood logs. Stress = 22.27, 70% variation explained.

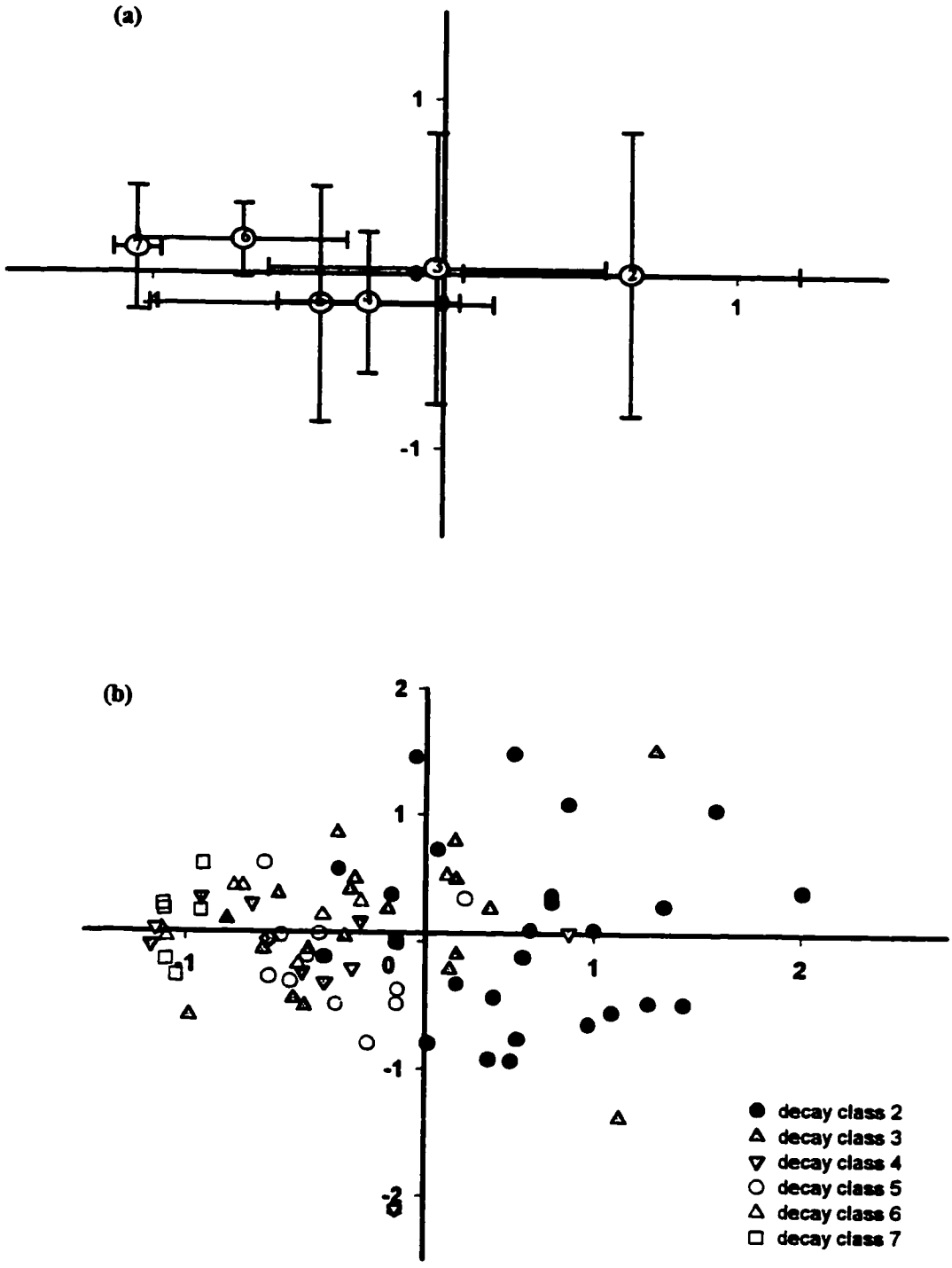

Figure 3.4 NMDS in 2 dimensions of logs; decay classes 2-7. Stress = 22.27, 70% variation explained. (a) centroids (mean sample scores +/- s.d.), numbers=log decay classes, (b) all sample scores.

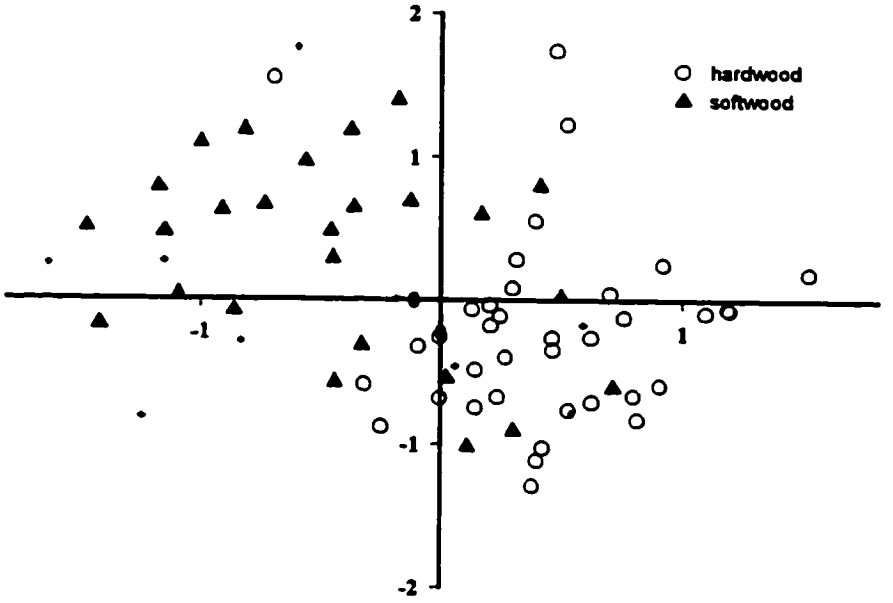

Figure 3.5 NMDS ordination in 2 dimensions of stumps; hardwood and softwood stumps. Stress=23.27, 63% variation explained.

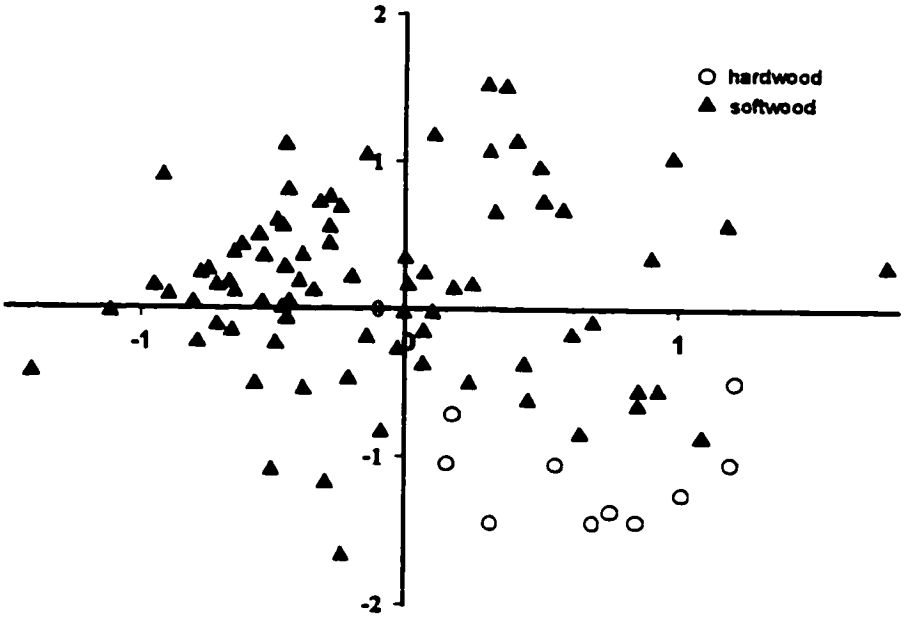

Figure 3.6 NMDS ordination in 2 dimensions of trees; hardwood and softwood trees. Stress=22.95, 59% variation explained.

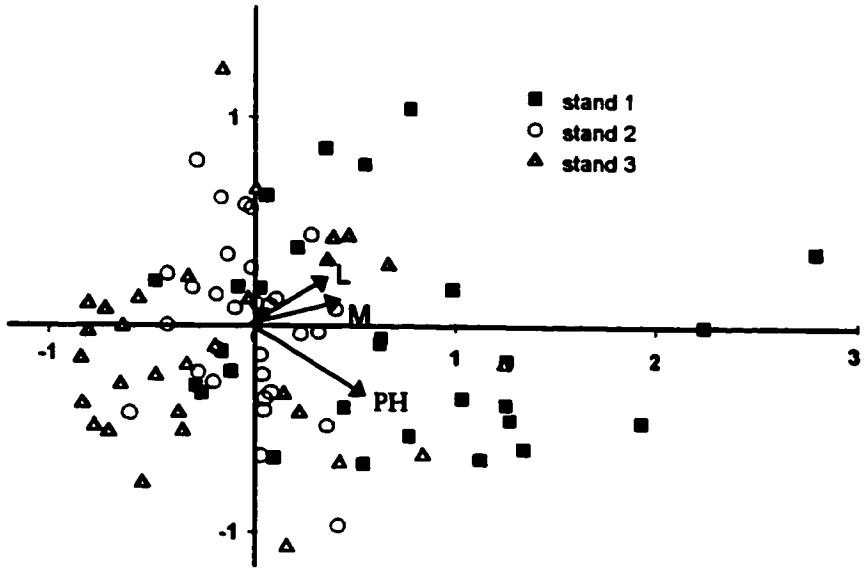

Figure 3.7 CCA ordination of undisturbed patches of forest floor showing stands constrained by the following environmental variables: soil moisture (M), soil pH (PH), and light (L). These three variables significant at p <.05 using Monte Carlo permutation (arrows=biplots).

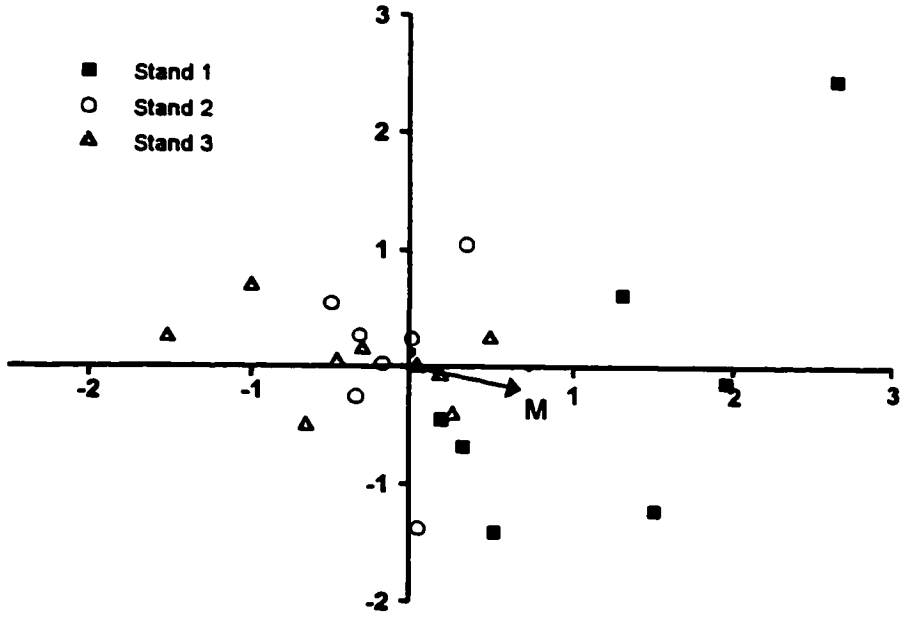

Figure 3.8 CCA ordination of disturbed patches of forest floor showing stands constrained by the following environmental variables: soil moisture, soil pH, and litter. Soil moisture (M) was significant at p <.05 using Monte Carlo permutation test (arrow=biplot of soil moisture).

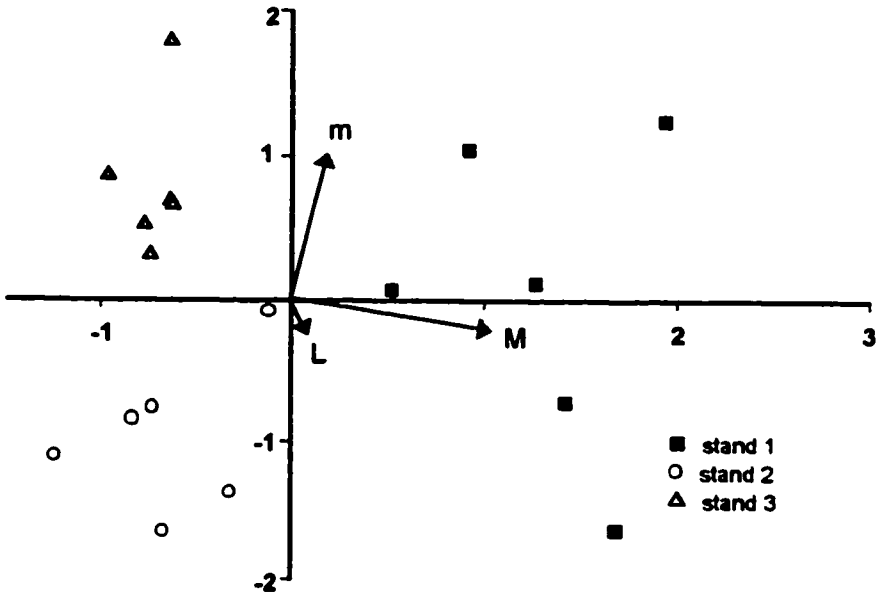

Figure 3.9 CCA ordination of mesosites showing stands constrained by the following environmental variables soil moisture (M), surface moisture (m), and light. Soil moisture and surface moisture were significant at $p < .05$ using Monte Carlo permutation tests (arrows=biplots of these variables).

Chapter 4: General Discussion

Results from this study support the argument that habitat is a key determinant of bryophyte species diversity and composition. Still, the existence of unexplained variation in the data sets indicates that measured habitat parameters are not the only factors driving bryophyte species occurrence. Other mechanisms, such as complex interactions, may be operating as well; these were not addressed in this study. The lack of influence of stand and mesosite spatial scales on bryophyte species composition and diversity implies that dispersal is not a strong force limiting bryophyte species occurrence. Thus the microsite spatial scale is likely the spatial scale best able to explain patterns in bryophyte communities.

The type and scale of habitat parameters governing bryophyte communities differ between microsite types. I will explain observed differences by inferring ecological processes related to physical properties of microsite types. I will discuss the relevance of these results to bryophyte sampling methodology and to forest management for bryophyte species diversity.

The importance of habitat

Interspecific interaction aside, three factors are apt to dictate bryophyte species occurrence. Successful persistence of a bryophyte species requires first, that a habitat suitable for bryophyte establishment and growth be available, second that the species is able to transport itself to the habitat (dispersal) and third, that the influence of random factors is either positive or neutral.

Although differences in species composition between microsite types did exist, there was a notable amount of compositional overlap between microsite types. Spatial proximity had no affect on these observed patterns. Microsite characteristics however, did to explain substantial variation in both bryophyte species richness and composition.

The majority of bryophyte species in this study did not exhibit strict habitat specificity; often a species showed a preference for one substrate type while occurring on many. La Roi & Stringer (1976) and Slack (1977) came to similar conclusions in their

study of eastern deciduous forest of the North American boreal forest and the Adirondacks respectively. Slack (1977) concluded that differences in species composition between substrate types were based on species abundance (importance) and not species occurrence and suggested that this was due to the opportunistic nature of most bryophyte species. If this is the case, it is probable that species occurrence on a given substrate type may be partially driven by either dispersal or by complex interactions (Wilson 1992). Alternatively, habitat parameters independent of microsite type may be driving bryophyte species composition; environmental heterogeneity acting at a larger spatial scale, or characteristics of a substrate may be more important to bryophyte species composition than substrate "type" *per se*.

The absence of stand or mesosite influence on microsite species richness undermines the hypothesis that dispersal (in isolation from habitat type) is driving bryophyte occurrence in the boreal forest. The lack of support for the dispersal hypothesis may be reflecting the minor importance of dispersal in observed patterns of bryophyte species occurrence. Alternatively, the spatial scales sampled may have been inappropriate for capturing patterns in species dispersal (see below).

Events that we perceive to be random (i.e. which diaspore is present when niche space becomes available) may also be responsible for unexplained variation in bryophyte species occurrence. Complex interactions allow communities on otherwise identical habitat patches to experience different ecological processes (with different community outcomes) as a result of differing initial conditions (Wilson 1992). Computer models have shown that one seemingly "stochastic" event can affect community outcome quite dramatically (Wilson 1992).

Nevertheless, habitat parameters were able to explain variation in species richness and composition within microsite types. Properties controlling bryophyte species richness paralleled those explaining bryophyte species composition. Substrate variables (decay class and hardwood/ softwood) were important to bryophyte occurrence on woody substrate types, and soil moisture and pH varying at larger spatial scales were important to bryophyte occurrence on forest floor substrate types. In general, microsite type and surface area were more important to bryophyte species diversity than to bryophyte species composition; hardwood/softwood was the most important determinate of

bryophyte species composition on woody substrate types.

What scale was the most important for bryophyte communities?

As evident from the above discussion, microsite type and properties had substantial influence on patterns of bryophyte species occurrence. Conversely, no patterns were apparent at the mesosite spatial scale, and patterns at the stand spatial scale were weak and only related to bryophyte species composition.

Sample scales should be relative to the patch dynamics of an organism (Addicott et al. 1987). Patchiness in the distribution of an organism may be related to habitat heterogeneity, or to source populations and dispersal distances. Dispersal did not seem to guide bryophyte species occurrence at mesosite or stand spatial scales. In terms of habitat, factors varying at the mesosite spatial scale included light, temperature, moss depth, litter depth and growth of *Hylocomium splendens*, none of which were important to bryophyte species occurrence. Because the mesosite scale was not related to microclimate variables important for bryophyte species occurrence, no strong patterns were observed at this scale. In contrast, soil moisture and pH, which were found to be important for bryophyte species on forest floor microsites, did vary at the stand scale. Thus bryophyte species composition of forest floor microsites did vary at the stand scale.

Similarly, analysis of vascular plant species richness in subalpine forests at a meso spatial scale of 1 X 1 km did not reveal any patterns in vegetation that were not linked to habitat differences (Heikkinen & Birks 1996). This study, like that of Heikkinen & Birks (1996) chose an arbitrary scale to study bryophyte species distribution, one that was not linked to biotic or abiotic variability.

The lack of variation in bryophyte habitat at within-stand spatial scales in the boreal forest is also likely linked to the absence of mesohabitats (areas of unique bryophyte habitat linked to physiographic structures as defined by Vitt & Belland (1997) and Newmaster (2000)). The only "mesohabitat" within the three stands was a stream running through the wettest stand. Bryophyte species distribution within the three similarly classified stands was thus more or less homogenous.

Bryophyte community stability on different microsite types

Each microsite type was affected differently by larger-scale variation. The sensitivity of bryophyte communities on different microsite types to variation at larger spatial scales may be a result of how bryophyte communities with different characteristics respond to environmental variation, and/or to interspecific processes. Microsite types have unique sets of physical properties: temporal variability; spatial continuity or discontinuity; internal heterogeneity; and favourability for bryophyte establishment and growth. These properties likely drive bryophyte community behaviour. Strangely, bryophyte communities on ephemeral substrate types (logs, stumps and disturbed patches of forest floor), appeared more saturated (all available niche space filled) than those on substrate types which were relatively more stable (tree bases and undisturbed forest floor).

Analysis of species diversity on logs inferred community saturation. The species area curve for logs was asymptotic relative to other substrate types, and larger spatial scales were unimportant for bryophyte species diversity and composition on logs. The fact that bryophyte communities on logs were saturated is not intuitive considering their properties. Söderström (1988a) found that often only a small percentage of a log surface area is colonized which indicates unsaturated niche space. Further, logs are patchily distributed (Söderström 1990) and temporally variable (subject to decay and continuous small disturbance) (Muhle & Leblanc 1975, Kimmerer 1994). This makes species inhabiting logs more reliant on effective dispersal for persistence (Herben 1994). Stumps have not been studied to the same extent, but are also heterogeneous due to small scale disturbance (Kimmerer 1993). Thus understanding bryophyte community dynamics on logs and stumps in relation to species dispersal (Söderström 1990) seems more reasonable than inferring interspecific interaction to explain the fact that they appear to be saturated.

Conversely, undisturbed forest floor has greater temporal stability (Jonsson & Esseen 1990), and is continuous resulting in habitat patches that are not well defined. However, bryophyte communities on these substrate types appeared less saturated. Larger spatial scales had some effect on species composition and richness, and the

species area curve failed to approach an asymptote.

The contrast between expectations and observations in terms of community saturation for bryophyte communities on logs and undisturbed patches of forest floor can be explained by examining: a) within- and between-habitat heterogeneity of microsite types; b) the scale of environmental variation important for each microsite type; c) characteristics of species occurring on microsite types; and d) the potential for interspecific interactions on different microsite types.

a) Within- and between- habitat heterogeneity

Species area curves reflect between and within patch variation. If species occurrence is dictated by habitat, asymptotic species area curves (i.e. logs and stumps) result when all environmental variants of a plot (microsite type in this case) are encountered (Scheiner et al. 2000). Thus when sampling a habitat type with high internal habitat heterogeneity and species turnover, all environmental factors controlling bryophyte occurrence will be encountered more rapidly. Consequently, fewer plots will be required to attain the maximum number of species in the study area for that habitat type. Thus required sample effort is less when within and between patch habitat heterogeneity are high (Moreno & Halffter 2000). Given the same total number of species, substrate types with low species turnover and within-patch heterogeneity (i.e. undisturbed patches of forest floor) will require more plots to reach an asymptote (the maximum number of species which will be encountered).

b) Spatial scale of environmental variation

Substrate properties, and not environmental variation at mesosite or stand spatial scales, affected species composition and richness of woody substrate types (logs, trees and stumps). Because all variants of each woody substrate types occurred in each stand we did not see a relationship between species richness or composition of woody microsite types and mesosite or stand species richness and composition. In contrast, species composition of disturbed and undisturbed patches of forest floor was affected by

variation in soil moisture and pH at the stand spatial scale. The spatial autocorrelation of environmental variables (Brown 1984) in this case likely explains the greater influence of larger spatial scales on these bryophyte communities; the stand spatial scale was only important because environmental variables important for bryophytes on forest floor microsites varied at the stand spatial scale.

c) Species characteristics

In this study, the specificity of bryophytes on logs to log decay class increased with increasing log decay class as the community changed from epiphytes and facultative epixylics to true epixylic species. Many bryophyte species occurring on logs and stumps may be regarded as substrate specific (Söderström 1988a) and most obligate and facultative epixylic species on dead wood produce perianths or capsules as well as gemmae (Söderström 1993). This indicates investment in both sexual and asexual reproduction. Herben (1994) examined the trade-offs between dispersal, patch size, distance between patches and patch duration for bryophyte persistence. He determined that the persistence of bryophyte species occurring on less stable substrate types is reliant on effective dispersal which is facilitated by smaller distances between habitat patches (Herben 1994). Thus the relative stability of bryophyte species composition and diversity on logs and stumps may be due to efficient dispersal mechanisms by epixylic species, the high abundance of decayed logs in each stand (reducing between-log dispersal distances), or to the long time for colonisation which begins before the tree falls.

Although the dominant species on undisturbed patches of forest floor were species with fast growth rates and "perennial stayer" life strategies (During 1979), species found in lower abundance on undisturbed forest floor included terricolous, humicolous and epixylic species which exhibited a diversity of life strategies. If we regard undisturbed forest floor as a stable habitat, with the potential for competitive exclusion (During & van Tooren 1987), then non-dominant species will only be found when environmental conditions shift the competitive balance in their favour. In this study, epixylics were found on undisturbed forest floor when small well decomposed wood fragments were present and peatland species were present when soil moisture and

pH increased. Similarly, Økland (1995) found that *Hylocomium splendens* (the most abundant species on undisturbed forest floor in the study site) was not limited by competition, but only by fine-scale disturbance. Thus peculiarly, the apparent unsaturated nature of undisturbed forest floor bryophyte communities is likely the result of competition and few small scale disturbances. For the most part, dominant feather moss species restrict the colonization of additional species; only with fine scale disturbance does the dominance hierarchy shift allowing the existence of a greater number of species.

d) Interspecific interactions

Interspecific interaction has not often been seen as an important force in bryophyte community ecology (Grime et al. 1990). Despite this, niche relationships have been found to exist in many bryophyte communities (Slack 1997). Though not entirely logical, it is possible that saturation of bryophyte communities on logs is due to niche partitioning between species; Kimmerer & Young (1996) inferred that partitioning of re-establishment niches may explain differences in species abundances of *Tetraphis pellucida* and *Dicranum flagellare* on logs. Undisturbed forest floor is often seen as a highly competitive environment for bryophytes (During & van Tooren 1987). Because of the continuous accumulation of species in patches of undisturbed forest floor, it seems probable that competitive exclusion by feather moss species limits the establishment and persistence of other bryophyte species. The conclusion reached by Frego & Carleton (1994), that niche partitioning was not occurring in the adult life stages of coexisting forest floor bryophyte species, would not apply to the species with more rare occurrence on this substrate type. These species may only occur for a limited time before they are out competed.

What are the implications for bryophyte sampling?

The stability of microsite species diversity across mesosites and stands suggests that sampling efforts for woody substrates should focus on the number and variety of microsites while sampling effort for undisturbed and disturbed patches of forest floor should maximize sample area (almost all species that were only found using FHS and not in microsite sampling were forest floor species). Special effort should be made to include physiographic variability (such as streams and wet depressions), which affected species composition of forest floor plots in this study. Jalonen et al. (1998), after examining ground and field layer vegetation in Finland, found that large plot sizes were necessary to maximize species capture on the forest floor because of its heterogeneity. Further, Newmaster (2000) found that FHS was necessary to capture rare species found on all microhabitats.

Sampling of woody substrates should maximize the diversity of microsite properties sampled. These include sampling tree bases, logs and stumps from all tree species as well as logs and stumps in all decay classes. Although differences between the species composition of logs and stumps were not apparent in multivariate analysis, some species may be specialized to one or more microsite type (2 species only occurred on stumps and 4 only on logs). Since species accumulation on stumps did not reach an asymptote, more stumps should be surveyed than logs.

The high compositional turnover (change in which species are present) between disturbed patches of forest floor relative to their low occurrence in boreal forest stands makes it difficult to capture all of the species associated with this microsite type. For this reason, monitoring initiatives should seek to maximize the number of disturbed patches sampled in conifer-dominated stands.

What are the implications for forest management?

Clear-cutting is presently the most common logging method used in the boreal forest (cutting of almost all trees in an area larger than four tree lengths in diameter)

(Keenan & Kimmins 1993). Changes associated with clear-cutting include both short-term affects on the microclimate (Jeffrey 1963, Kubin & Kemppainen 1991), and long term affects of: reducing within stand structural heterogeneity (Mladenoff et al. 1993, Dettki & Esseen 1998); reducing the amount of dead wood (Anderson & Hytteborn 1991); and lowering the ratio of late to young succession forests over the landscape (Linder & Ostlund 1992, Ohlson et al. 1997).

This study reaffirmed the importance of structural heterogeneity for bryophyte species diversity. The high species richness in the study site (90 species), in relation to other boreal forest stands is likely due to the presence of *Populus* species trees, logs and stumps in a coniferous canopy, large sized dead wood in different stages of decay, disturbed forest floor from tree falls, and the variability in pH and moisture of the forest floor. Although the asymptotic species area curves of bryophytes on logs and stumps suggest that these bryophyte communities may be able to withstand a large reduction in microsite frequency, this may not be the case. Laaka (1992) found that some epixilic species were especially sensitive to large scale disturbance, proposing that this was due to their small size, their requirements for a certain size and decay stage of log (increasing distances between suitable habitat patches), and their location on the forest floor where air currents are weak. These factors limit dispersal. The abundance of dead woody debris in all decay classes in this study decreased the dispersal distance between suitable habitat patches. Deciduous logs in this study supported higher numbers of species, and were compositionally different than coniferous logs. Similarly, deciduous trees had greater species richness and had different species composition than coniferous trees. Deciduous logs were also found to have the highest number of epixylics in natural forests of Sweden (Andersson & Hytteborn 1991). Thus, the diversity in structure and tree composition of the stands in this study were likely responsible for their relatively high bryophyte species diversity.

In Scandinavia, the removal of snags and decaying wood has been linked to reduced bryophyte species diversity in managed stands (Söderström 1988b, Anderson & Hytteborn 1991). Natural forests have a greater amount of logs of later decay classes and of logs of large diameters, increasing the area of substrate available for epixylic

bryophyte species (Anderson & Hytteborn 1991) and are often more humid (Söderström 1988b).

Even harvesting techniques which intend to increase heterogeneity may not maintain the many scales of patchiness that exist over the natural forest landscape. Mladenoff et al. (1993) found old growth forests to have many structural features that were not present in disturbed forests; these included more heterogeneous patch sizes, different spatial arrangement of patches relative to one another, and the presence of large hemlock patches. Although perceived heterogeneity over large spatial scales increased, the complexity of patches at smaller spatial scales was lower after management (Mladenoff et al. 1993).

In order to ensure that we maintain the natural bryophyte species diversity over the landscape we must ensure that conifer dominated mixed wood stands continue to exist on the landscape. Mixed-wood management of the boreal forest would help support the persistence of bryophyte species dependent on large live and dead aspen. These species require both a hardwood substrate and the favourable moisture regime of a conifer-dominated canopy. To this aim, maintaining structural heterogeneity in the boreal forest over the course of forest management is the single most important consideration for the preservation of bryophyte species diversity.

Further research questions

It is important to determine if the patterns found in this study extend across larger areas in the boreal forest. From a management perspective "Is bryophyte species occurrence limited by dispersal at larger spatial scales?" and "Does relative isolation of forest patches affect bryophyte species occurrence?" are two questions that need to be answered to fully understand the impact of large scale forest management practices on bryophyte species diversity. From a bryological standpoint more manipulative experiments are needed to understand the forces controlling bryophyte community dynamics on different substrate types.

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