INFLUENCE OF MICROHABITAT ON BRYOPHYTE DIVERSITY
IN ONTARIO MIXEDWOOD BOREAL FOREST

A Thesis

Presented to

The Faculty of Graduate Studies

of

The University of Guelph

by

HEATHER ASHLEY COLE

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ABSTRACT

INFLUENCE OF MICROHABITAT ON BRYOPHYTE DIVERSITY IN ONTARIO MIXEDWOOD BOREAL FOREST

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University of Guelph, 2006

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This thesis is an investigation of the little-known influence of bryophyte microhabitats on forest bryophyte diversity. Conservation of diversity in Ontario forests is a growing concern and a better understanding of forest bryophyte diversity will improve management efforts. The influence of microhabitats on bryophyte diversity was investigated by comparing eight different boreal mixedwood microhabitats (ground, early decay stage log, mid decay stage log, late decay stage log, rock, stump, snag and tree). Species accumulation, species richness, structural and compositional diversity and microhabitat specificity were quantified and compared among microhabitats. Ordinations and analyses of community structure indicate that microhabitats have considerable influence on bryophyte diversity and abundance. Frequency and indicator analyses show that some bryophytes are restricted to or prefer particular microhabitats. Decayed log microhabitats are shown to be the largest contributors to bryophyte diversity. Forest management should plan to preserve microhabitats within silvicultural treatments in order to conserve and restore bryophyte diversity.

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INTRODUCTION

As demand for forest resources continues to increase, efforts are being directed into developing methods to increase forest yield and productivity (FAO 1999), this in turn is prompting concern for the conservation of biodiversity. These increasingly intensive methods of forest management are often cited as major contributors to the loss of species and species diversity from forest ecosystems (May 1975; Miller et al. 1990; Burton et al. 1992; Mosquin et al. 1995). The potential elimination of native forest flora through these intensifying forestry operations is a growing concern in many developed countries (Conde et al. 1983; Kimball and Hunter 1990; Oswald 1990; Halpern and Spies 1995; Mosquin et al. 1995; May 1998; Ramovs and Roberts 2003; Wikström and Eriksson 2000; Fenton and Frego 2005). It is conceivable that forestry operations could, over time, cause species to become locally extinct and convert biologically diverse forests into monocultures of preferred tree species (Conde et al. 1983; Halpern and Spies 1995; Mosquin et al. 1995; May 1998; Niemelä 1999; Snäll et al. 2003). Research on the impacts of forest management on plant diversity has identified bryophytes as the most diverse group and the most vulnerable group to forest silvicultural treatments (Gustafsson and Hallingbäck 1988; FEMAT 1993; Frisvoll and Prestø 1997; Bell and Newmaster 1998; Ross-Davis and Frego 2002; Fenton et al. 2003).

Within forest ecosystems, bryophytes are a diverse group of plants with distinctive features of their biology that give rise to particular life strategies, ecology and functions in forests that differ from other forest plants. Bryophytes can be divided into three classes: Bryopsida (mosses), Hepaticopsida (liverworts) and Anthocerotopsida (hornworts) (Schofield 1985; Shuster 1984, Vitt 1984). All of these classes can be

characterized by a dominant haploid gametophyte, which is a leafy or thallose structure that gives rise to a sporophyte (Longton and Miles 1982). Bryophytes can be separated into several life-forms ranging from rare, short-lived *fugitives* in unpredictable habitats to long-lived *perennial stayers* in stable habitats (During 1992). Despite accounting for considerable species richness in many ecosystems, little consideration has been given to the ecology of this group of plants while herbs and woody plants have received much attention (During et al. 1987, Slack 1988, Wilson et al. 1995; Newmaster and Bell 2002). Studies have shown bryophytes to have many important roles in forests. These included nitrogen cycling (Brown and Bates 1990; Heras et al. 1996), seed bed formation (During 2001), early colonization of disturbed sites, creation of habitat in harsh environments (Heras-Ibáñez et al. 1991), and as food and habitat resources for animals and insects (Peck et al. 1995).

Bryophytes are often thought to be influenced by habitat at both local and regional scales. In forest ecosystems bryophyte richness and abundance can be affected by changes in their immediate environment. Small scale natural disturbances such as falling trees, erosion and herbivory increase the heterogeneity of the forest and provide different types of microhabitats for bryophytes (Jonsson 1990, Kimmerer 1993). Large scale natural disturbances such as fires have detrimental *local* effects on bryophyte populations, destroying habitat and reducing richness, but have overall positive effects on the communities at a regional *landscape* scale by creating new environments for colonization and increasing bryophyte richness (Heras-Ibáñez et al. 1991, Belland 1995). Conversely, anthropogenic disturbances such as clear-cutting and intensive forest management have been shown to have negative impacts on bryophyte communities at a

landscape scale, because these types of disturbances disrupt the age of the stand and natural succession in addition to reducing habitat heterogeneity (Newmaster and Bell 2002, Roberts and Zhu 2002, Rose 1992). Unlike fire disturbances, intensive forest management typically results in the removal of most if not all microhabitat types.

Microhabitat type has been claimed to be stronger than mesohabitat (Vitt and Belland 1997) or stand type at predicting bryophyte species richness at the ecosystem scale (Mills and Macdonald 2004). Forest management alters the forest floor causing considerable microhabitat disturbance, which negatively impacts bryophyte diversity (Thomas et al. 2001; Newmaster and Bell 2002). Some work has shown that distribution and availability of microhabitats influence bryophyte community structure (Heinlen and Vitt 2003). If there are bryophyte species that only occur on one particular type of microhabitat then the microhabitat must be managed according to the spatial barriers (e.g., reproductive, dispersal) that may prevent establishment of the species (Økland et al. 2003). An understanding of how bryophyte diversity relates to microhabitat specificity is needed to develop and implement silvicultural techniques that conserve forest diversity.

Several studies have examined the relationship between bryophytes and their respective microhabitats and/or environmental variables. However, there is little consistency in the manner or scale at which those variables have been considered making it difficult to compare among studies or apply the knowledge at another scale. Most information is based on qualitative studies with narrow focus. Some studies have focused on a particular bryophyte species (Hedenäs et al. 1989, Herben et al. 1991) or small group of species (Cleavitt 2001, Söderström 1993). Others have examined select bryophyte microhabitats such as woody microhabitats (Crites and Dale 1998, McAlister 1995,

Rambo 2001, Rambo and Muir 1998), trees (Sillet et al. 2000), or boulders (Weibull and Rydin 2005).

The subject of microhabitat specificity in bryophyte species has been given much attention however; existing research provides inconsistent information on the relationships between bryophytes and their microhabitats. Most studies have focused on particular microhabitats; trees (Studlar 1982; Schmitt and Slack 1990), coarse woody debris (Rambo and Muir 1998; Söderström 1988, 1993; Berg et al. 2002; Ódor and van Hees 2004), rocks (Hedderson 1990; Vitt and Belland 1997), ground (Frego and Carleton 1995b), while some (Pharo and Beattie 2002; Wiklund 2002; Mills and Macdonald 2004) have compared multiple types of microhabitats. Results of these studies is varied with some (Frego and Carleton 1995a,b) showing no microhabitat preferences of the observed species, with others (Studlar 1982; Schmitt and Slack 1990; Mills and Macdonald 2004) reporting species to have distinctive microhabitat preferences. These varied responses are not unexpected as bryophyte communities have already been shown to be variable and there is little consistency in scope and scale of the studies performed. Sampling approaches vary from long transects through forests to small quadrats on individual microhabitats. Results of these studies are therefore dependent on scale and sampling effort, making it difficult to compare results between studies, or make generalizations. Similarly, results from studies that report on one microhabitat type or a small group of species are of little use when considering other microhabitat types, or the ecosystem as a whole because bryophyte species may be common on one microhabitat and rare or even absent on others. While these previous studies have provided useful information applicable to the particular species or microhabitat investigated, they fail to appropriately

address patterns of total bryophyte diversity and community composition across all the different microhabitats within a particular ecosystem. Approaches that quantitatively analyze all aspects of bryophyte diversity on and among microhabitats are necessary. In addition to quantifying bryophyte specificity, determining the reasons for these preferences would result in a better understanding of bryophyte microhabitat requirements and bryophyte diversity in forest environments. Measures diversity are useful to help describe species differences between microhabitats and the influence of microhabitat on bryophyte communities, but these measures do not identify why these differences are occurring. In seed plants, differences in these levels of diversity can often be attributed to differences in functional diversity. For example, plants that rely on wind for seed dispersal are distinguishable from those who need animal-facilitated dispersal and plants with underground rhizomes for vegetative growth separate from those without. These functional differences in diversity are useful in identifying biological characteristics that may be contributing to species diversity.

Ideally, we would like to predict the effects of forest management practices on species diversity and identify those treatments that might lead to localized plant extinctions. This would require an understanding of the relationship(s) between disturbance effects on local environmental conditions, habitat patterns and the life histories of plant species being affected (Halpern 1989; Haeussler *et al.* 1999; Buse and Bell 1992; Sutherland and Foreman 1995; Bell *et al.* 1998; Newmaster *et al.* 2003). An understanding of the mechanisms controlling plant diversity in forests is essential to propose ecologically sustainable forest management based on both the number of species in a forests and an understanding of how those species coexist (Lindenmayer *et al.* 2000).

An important issue in forest management is to construct diversity models along silvicultural treatment, successional and site quality gradients in order to predict to what extent management practices influence diversity patterns (Gilliam and Roberts 1995). Diversity indices commonly used in ecological investigations also describe structural diversity. Structural diversity describes species richness, abundance and evenness. Compositional diversity describes differences in community structure; measures of beta-diversity (differences in species diversity among microhabitats) and ordination techniques are used to describe this type of diversity. Functional diversity is described by biological characteristics of species such as regeneration, growth and dispersal (Lavorel et al. 1997). Models must consider the three dimensions of biodiversity (structure, composition and function) in order to be useful for management. Research employing this information is needed to address the claim of bryophyte microhabitat specificity (Noss 1990, Söderström et al. 1992, Vitt et al. 2003) and to adequately describe bryophyte diversity (Lavorel 1997, Noss 1990; Aubert et al. 2003). This study directly investigates the first two measures of diversity; structural and compositional.

STUDY OBJECTIVE AND APPROACH

The purpose of this research is to quantitatively compare bryophyte diversity among boreal forest microhabitats and to investigate the claim of microhabitat specificity.

To do this I examined three areas:

- 1) I compared structural diversity of bryophytes among microhabitats; examining species richness and abundance.
- 2) I compared bryophyte compositional diversity among microhabitats using beta-diversity and ordination methods to explore patterns of bryophyte community organization
- 3) I identified microhabitat preferences of bryophyte species.

The eight boreal forest microhabitats that were investigated are:

- i) Ground
- ii) Logs in early stages of decay (Early logs)
- iii) Logs in mid stages of decay (Mid logs)
- iv) Logs in late stages of decay (Late logs)
- v) Rocks
- vi) Stumps
- vii) Snags
- viii) Trees

RESEARCH QUESTIONS

Structural Diversity

1a. Is there a difference in the accumulation of total bryophyte species richness over surface area sampled among forest microhabitats?

The species-area relationships of bryophytes were compared among eight microhabitats in Ontario mixedwood boreal forest.

1b. Is there a difference in total species richness among forest microhabitats?

Total bryophyte species richness was compared among eight microhabitats in Ontario mixedwood boreal forest.

1c. What is the difference in species presence and abundance among bryophyte forest microhabitats?

Bryophyte diversity was compared using the Shannon-Weiner function, Simpson's index and Pielou's Evenness among eight microhabitats in Ontario mixedwood boreal forest.

Predictions- There is no existing literature to serve as a foundation for predicting species-area patterns among bryophyte microhabitats. It is predicted that decaying wood microhabitat types will have higher species richness, greater change in species per area sampled and higher diversity than microhabitats such as trees, rocks and ground. It is also predicted that among all microhabitat types, logs in mid stages of decay will have the highest species richness, the steepest species-area curve and highest bryophyte diversity while the ground microhabitat will have the lowest richness, shallowest curve and lowest species diversity. Decaying wood microhabitats appear to be more heterogeneous than the other microhabitat types. A decaying log for example, may be at slightly different

stages of decay along its length, as well as being intermittently in contact with the ground. A rock by comparison seems to be more consistent over its surface area and therefore provides a less diverse habitat for potential colonizing species. Decaying wood microhabitats such as snags, stumps, and logs are often hold more moisture than rock and tree and ground microhabitats. As bryophytes are non-vascular, a more moist microhabitat may be more habitable than dryer microhabitats such as ground.

Justification- Little work has been published comparing the manner in which bryophyte species accumulate on different microhabitats. This is important for both understanding bryophyte diversity in boreal forests and for forest management protocols. If there is a microhabitat type upon which total species richness can be reached in half the sampling area it takes to reach total species richness on a different microhabitat type, it indicates that the microhabitat types function differently in the forest environment and must be given different management considerations. If they supported distinct communities, microhabitat types which require larger areas to reach total species richness would have to be more available in the forest than the microhabitats which reach total species richness at smaller areas. Research on bryophyte *mesohabitats* in British Columbia has shown that richness accumulation with increasing area is not the same for all mesohabitats (Newmaster et al. 2005). Unfortunately, this research does not provide a replicated design with appropriate confidence parameters. Mills and Macdonald (2004) examined both mesohabitats and the microhabitats within them, using estimates of species richness; they also showed species-area curves that differed among microhabitats. The work of Mills and Macdonald (2004), though insightful, is not sufficient, as microhabitats were sampled disproportionately and species richness was only estimated.

Vitt et al. (2003) have shown that microhabitat diversity is critical for understanding patterns of diversity at larger scales (mesohabitat, ecosystem). Conservation measures have made broad recommendations concerning all types of microhabitats within a mesohabitat or even an ecosystem. However, these recommendations would be inappropriate if bryophyte richness accumulates in a distinctive manner for different types of microhabitats. The role that microhabitats have on the accumulation of species must be quantified in order to better understand what factors are contributing to the variations among microhabitats, mesohabitats and ultimately to diversity in the forest ecosystems. My research will provide the first quantitative evidence with which to compare the accumulation of species on different microhabitat types.

Most studies of bryophyte richness or abundance have focused on particular species, species groups, or particular microhabitats. Research reporting species specificity among trees, has ignored the possibility that the same species may be occurring on rocks a few metres away. Similarly, research examining single species, or small groups of species provide informative data on the species investigated, but contribute little to understanding diversity in their environments. My work will quantitatively compare diversity using richness and abundance for all the species found on all the major microhabitats of Ontario mixedwood boreal forests.

Compositional Diversity

2a. Are comparisons of bryophyte beta-diversity different among forest microhabitats?

Beta-diversity was calculated among eight microhabitats in Ontario mixedwood boreal forest using Whittaker's measure of beta-diversity (β_w) and the Morisita-Horn index of similarity.

2b. Is there a difference in community structure among bryophyte forest microhabitats?

Multivariate analysis was used to explore patterns in community composition among eight microhabitats in Ontario mixedwood boreal forest.

Predictions- It is predicted that beta-diversity and community structure will be most similar among woody microhabitat types. It is predicted that early logs will be most like trees, that stumps and snags will be very similar to each other and more similar to trees than to all logs, rocks, or ground. Microhabitat types have specific attributes with respect to surface texture, moisture content and overall heterogeneity. If bryophyte diversity is influenced by these attributes, communities would be more similar on microhabitats with similar attributes. It seems that these attributes are more similar among woody microhabitats than non-woody microhabitats. As logs in early stages of decay are newly fallen trees, it would follow that they share many of these attributes.

Justification- The structural component of diversity (richness and abundance) is often reported without considering the importance of compositional diversity (beta-diversity) (Noss 1990). The distribution of species across different microhabitats, and the differences in richness and abundances that may occur among microhabitats are important components of bryophyte diversity in forests. Previous work on community

structure is related to chronosequence studies (Gignac et al. 1991; Li et al. 1994; Vitt 1990; Newmaster et al. 2003) designed to compare communities among forests along gradients of age, elevation or disturbance over time. An understanding of habitat specificity has been impeded by the fact that this type of sampling is too coarse; sampling stands instead of microhabitats *within* stands and lacking replication within stands. It is useful to know if a species is common on one type of microhabitat and rare on another in order to describe its distribution in the ecosystem. This helps describe diversity in the forest and contributes to the development of silvicultural techniques that help conserve this diversity. By including quantitative information of compositional diversity in my investigations, my work will provide a more robust description of bryophyte diversity in Ontario mixedwood boreal forest.

Microhabitat Specificity

3a. Are there bryophyte species that occur on only one type of microhabitat?

The presence of bryophyte species were investigated on eight microhabitats in Ontario mixedwood boreal forest.

3b. Are there bryophyte species that have a preference for one type of microhabitat?

The frequency and abundance at which bryophyte species occurred and indicator values for species were compared on eight microhabitats in Ontario mixedwood boreal forest.

Predictions- It is predicted that some species of bryophytes sampled will be found to show specificity to a particular type of microhabitat. It is also predicted that some species will show a preference for one microhabitat type over another, occurring frequently or in large abundance on one type and only rarely or in low abundance on others. Certain combinations of microhabitat attributes may provide optimal environments for the establishment and growth of certain bryophyte species. Some species may even be restricted to the environmental conditions that occur on a specific type of microhabitat. If there are species of liverworts specific to one type of microhabitat it is predicted that those microhabitats will be well-decayed woody microhabitats because they hold more moisture than the other microhabitat types. Liverworts are much more susceptible to desiccation than mosses (Shaw and Goffinet 2000) therefore if well-decayed woody microhabitats are moister, they will provide more optimal environments than drier microhabitat types. It is predicted that logs in mid stages of decay will have the most microhabitat specific species as they are most likely to provide the conditions unavailable on the other microhabitat types. It is predicted that species that share specificity for a

particular type of microhabitat will share morphological or reproductive characteristics. Traits such as sexuality (monoicous, dioicous), spore size, or setae length may dictate which combination of microhabitat attributes provide an acceptable environment for particular bryophyte species.

Justification- Many field guides and bryophyte floras include microhabitat affinities with their description of species however, research on the subject of microhabitat specificity is conflicting with some reporting no preference and others reporting species specific to only one type of microhabitat. As with richness and abundance investigations, most studies have a narrow focus on either a particular microhabitat or a particular species. Quantitative work that compares species on all available microhabitats is needed to more accurately describe the microhabitats on which bryophyte species occur. My work will provide frequency and abundance data to indicate species that are microhabitat specific. It will also identify species with a strong preference for, or strong indicators of, a particular type of microhabitat. In addition I will explore the life-history strategies for any species that is restricted to or shows a preference for a particular type of microhabitat.

MATERIALS AND METHODS

Study Site

The microhabitat dynamics of bryophytes were examined in the Thunder Bay site of an existing project entitled the NEBIE Plot Network (Bell et al. 2003). The Intensive Forest Management Science Partnership established the NEBIE Plot Network (dubbed NEBIE) in 2001. This stand-level, multi-agency research project was designed to compare natural disturbances with a full range of silvicultural practices in the Boreal and Great Lakes-St. Lawrence forest regions of Ontario. NEBIE stands for the management treatments being compared: **N**atural disturbance, **E**xtensive, **B**asic, **I**ntensive and **E**lite silviculture. The Thunder Bay site (Figure 1) chosen for sampling is an eighty year old boreal mixedwood stand with fine loam-clay soil, dominated by trembling aspen (*Populus tremuloides*) and balsam fir (*Abies balsamea*).

Experimental Design

The NEBIE project was established using a randomized complete block design for the placement of the experimental components at eight sites (Figure1). Each site is comprised of four blocks that independent floristic analyses have shown to have the same plant diversity. Each block contains the five, previously-mentioned, NEBIE treatments. At the Thunder Bay site, the Natural treatments (100m x 200m) in each block were used as experimental units for this study. To sample each experimental unit, five co-ordinates were randomly chosen from a pre-existing NEBIE grid layout. A circular (5m radius) plot was established at each co-ordinate, providing a total of twenty subsamples (five in each experimental unit) (Figure 2). The terms 'microhabitat' and 'microhabitat type' will be used to describe the eight different forest substrates being investigated, the term

‘microhabitat representative’ will be used to describe the samples of individual specimens of each microhabitat type (tree, rock etc.). To compare bryophyte communities, two criteria had to be met. The first was that each microhabitat type be equally sampled relative to their overall abundance at the site. Second, that bryophyte sampling reached saturation (plateau on richness-area curve) on each microhabitat type being compared. The first criterion was met by sampling the same proportion of each microhabitat type. Time constraints did not allow for sampling all representatives of each microhabitat type. It was assumed that the plots chosen for sampling were representative of the site, therefore, half of the representatives of each microhabitat type in each plot were sampled (see below). The second criterion was addressed by creating species-area curves to ensure that the subsampling (five plots within each experimental unit (100x200m)) adequately captured the bryophyte community. If the species area curve for each experimental unit levelled off, five plots were assumed adequate.

Sampling

Microhabitats

Sampling took place July-August 2006. The microhabitat representatives in each plot were divided into eight types consisting of ground, logs in an early stage of decay (early logs), logs in a middle stage of decay (mid logs), logs in a late stage of decay (late logs), rocks, stumps, snags and trees. Log microhabitats were subdivided into three decay stages based on previous research that identified decay stage as an important variable in explaining patterns of bryophyte community structure (Söderström 1988a; Newmaster 2000; Rambo 2001; Ódor and van Hees 2004). Stages of log decay have been characterized many different ways. The method of Chambers and Lee (1993) assigns logs

to one of five decay categories using several characteristics including the presence/absence of bark and twigs, as well as log texture and shape. For this study, decay categories one and two were defined as early decay, category three was defined as mid decay, and the fourth and fifth categories were defined as late decay. These definitions were based on previous work that has shown the categories grouped together to be similar (Newmaster 2000). Logs of all three types with a minimum diameter of 10cm and a minimum length of 1m were considered eligible for sampling. All above ground log surfaces were sampled. Trees, snags and stumps eligible for sampling had a minimum diameter at breast height of 10cm. Trees were defined as upright woody plants with a single bole. Snag representatives were defined as standing dead woody debris 1.5m tall or higher, while stumps were defined as standing dead woody debris less than 1.5m tall. Tree and snag representatives were sampled from the base to 1.5m up the bole. The entire above-ground surface of stumps was sampled. Eligible rocks sampled were detached stone (not shield) with a minimum above-ground surface area of 500cm². The entire above-ground surface of rocks was considered eligible for sampling. If a portion of the surface of a rock chosen for sampling was covered by debris (soil, coarse woody, leaf litter) at a depth greater than 5cm, then that area was excluded from sampling. Ground considered eligible for sampling was defined as the forest floor that was not occupied by any of the other microhabitats.

At each plot, the total number of eligible microhabitat representatives of each type was determined and, due to time constraints, half were randomly chosen for sampling, rounding up when the remainder was not a whole number. Ground within the plot was split into four quadrats, two of which were randomly chosen for sampling.

Figure 1. Map of Ontario, Canada showing NEBIE sites including the study location; Thunder Bay, indicated in red.

Figure 2. Experimental design and layout, showing site (Thunder Bay), blocks (4), natural treatment (1 per block =4), plots (5plots x 4 blocks =20) and microhabitat representatives within plots.

Bryophytes

On each of the microhabitat representatives chosen for sampling, bryophyte species presence and abundance was investigated. A flexible twine grid composed of 10x10cm squares was used to sample the entire eligible surface of each chosen microhabitat representative. The abundance (surface area) of each species in each square was recorded (cm^2) for the whole eligible surface. The grid was moved along the microhabitat representative until the entire eligible surface had been sampled, therefore total area sampled varied with the size of each microhabitat representative. Species were named through a combination of field identification and collection of specimens that were identified later in the laboratory; 85 802 specimens were collected and identified. Species nomenclature followed the Flora Ontario (Newmaster and Ragupathy 2005) and vouchers of each species collected are deposited in the OAC Herbarium. Some liverwort species collected did not conform to any existing species descriptions and were therefore suffixed with numbers to describe them for analysis.

Analysis

Structural Diversity

1. Species-area relationships

Species-area relationships describe the change in total species richness (cumulative) with increasing amount of area sampled. Species-area curves were plotted to explore the relationship between cumulative area of microhabitat sampled and total species richness of each microhabitat type. The relationship between the dependent value (species richness; y-axis) and independent value (area of microhabitat; x-axis) was explored on a scatter graph for each of the experimental units. For analysis,

measurements from microhabitat representatives within plots were averaged for each microhabitat to provide data for the experimental units (n=4). The x-axis (area) was log-transformed and linear regression, forced through the origin, was used to generate the slope of the species-area relationship of each microhabitat from the experimental units. The slope of species-area relationship represents how species accumulate with area and was compared among microhabitat types using the slopes of the regression equations.

2. Species Richness

Total species richness was recorded on each microhabitat representative sampled. Mean richness was compared among all eight microhabitat types (n=4) using the means from each plot to calculate a mean for each experimental unit to describe each microhabitat type.

3. Diversity

Several diversity measures were used to quantify bryophyte diversity and abundance on the microhabitats investigated. Total species richness was recorded for each microhabitat representative sampled (n=4). To estimate species diversity on each microhabitat the Shannon-Wiener function and Simpson's index were calculated.

The Shannon-Weiner function

$$H' = -\sum_{i=1}^s (P_i)(\ln(P_i))$$

where H' is the Shannon-Weiner index of species diversity, s is the total number of species, P_i is the proportion of the total sampled belonging to the i th species (Krebs 1999). The Shannon-Weiner function assumes that individuals are randomly sampled from and "indefinitely large" population and that all species are represented in the sample

(Magurran 1988). It is also sensitive to the abundance of rare species in the community.

The Shannon-Weiner function typically ranges from zero to five when examining biological communities, with increasing values indicating higher species diversity.

Simpson's index provides the probability that any two individuals selected at random from an infinitely large community are different species. Simpson's index

$$1-\lambda = 1 - \sum (N_i^*(N_i-1)/(N*(N-1))$$

where $1-\lambda$ is Simpson's index of diversity and N_i is total proportion of the i th species.

Simpson's index is heavily weighted towards abundant species and less sensitive to species richness. This index ranges from zero, indicating low diversity to almost 1, indicating high diversity (Krebs 1999). The combination of both the Shannon-Weiner function and Simpson's index provide independent measures of bryophyte diversity on each of the microhabitats investigated. Finally, evenness, the relative equitability of species within a community, was estimated using Pielou's Evenness.

$$J' = H' / \log(S)$$

where J' is Pielou's measure of Evenness, H' is the Shannon-Wiener index of diversity and S is total number of species. Pielou's measure of evenness describes the degree to which species are evenly distributed within a community (Pielou 1966). Evenness is high when all species are present in approximately the same abundance, while low evenness occurs when some species are much more abundant than others in the same community. This measure provides further description of the communities being investigated. As with all measures of evenness, it assumes that the total number of species in the whole community is known.

4. Statistical Analysis

The log-transformed species-area regression coefficients of each microhabitat were compared using t-tests (Zar 1984),

$$t = \frac{b_1 - b_2}{\left(\frac{(s^2_{Y \cdot X})_p}{(\sum x^2)_1} + \frac{(s^2_{Y \cdot X})_p}{(\sum x^2)_2} \right)^{1/2}} \quad \text{where } (s^2_{Y \cdot X})_p = \frac{(\text{residual SS})_1 + \text{Residual SS})_2}{(\text{residual DF})_1 + \text{Residual DF})_2}$$

where t is the test statistic, $b_{1,2}$ are the regression coefficients (slopes), $(s^2_{Y \cdot X})_p$ is the pooled residual mean square, SS is the sums of squares and DF is the degrees of freedom. T-tests were chosen for their ability to analyze the raw regression data and provide a direct test among the microhabitat types. Degrees of freedom varied among comparisons and significant differences for specific comparisons were adjusted for an overall error of 0.05. Richness and all three indices (Shannon-Weiner, Simpson's and Pielou's) were compared among microhabitats. Means and standard errors were calculated using SAS statistical software (SAS Statistical Analysis Systems, version 8.02, SAS Institute Inc., Cary, NC) (Figure 3). The comparisons were analyzed using a stratified random block design and analysis of variance (ANOVA) assuming a type I error rate of 0.05 in all statistical analyses. A sequential Bonferroni procedure (Holm 1979) and Tukey-Kramer procedure for multiple comparisons were used to control experimentwise error that increases as a result of the numerous comparisons being performed (Sokal and Rohlf 1995). The Tukey-Kramer test is often found to be too conservative, often reporting all significant differences found in the initial analysis as insignificant (Rice 1989). For this reason, the less conservative sequential step-down Bonferroni procedure was used for reporting the results of all analyses. Significant differences for specific comparisons were

adjusted for an overall error of 0.05. In all analyses, unadjusted p-values are presented, with Bonferroni and Tukey-Kramer significances reported.

Compositional Diversity

1. Beta-diversity

In addition to structural diversity measures of each microhabitat type, bryophyte beta diversity, or the diversity among microhabitats was also investigated using two different methods. Whittaker's measure of beta-diversity (β_w) and the Morisita-Horn index of similarity were calculated. Whittaker's beta-diversity was estimated

$$\beta_w = (S/\alpha) - 1$$

where S is the total number of species recorded on the two microhabitats being compared and α is mean richness of the microhabitats. The Morisita-Horn index of similarity (Horn

1966)

$$C_{mH} = (2\sum(an_i * bn_i)) / (da + db)aN * bN$$

where aN is the total number of individuals on microhabitat A and an_i is the abundance of i th species on A. $da = \sum an_i^2 / aN^2$. The Morisita-Horn index combines each species' presence and abundance on the microhabitats being compared to measure the similarity between them. This identifies how similar or different bryophyte diversity is on the investigated microhabitats. The Morisita-Horn index ranges from zero, indicating no similarity, to one, indicating complete similarity. These beta-diversity measures help identify which microhabitats have bryophyte communities that are more (or less) similar to each other.

2. Ordination analysis

Multivariate analysis was used to explore patterns in community organization among all the different microhabitats studied. A principal component analysis

Figure 3. Experimental SAS model used for statistical comparison of mean species richness, Shannon-Wiener and Simpson's diversity indices and Pielou's evenness.

```
proc mixed data=all;
  class BLOCK MICROHABITAT PLOT;
  model RESPONSE=MICROHABITAT /outp=CHECK6;
  random BLOCK MICROHABITAT*BLOCK PLOT(SUBSTRATE BLOCK);
  lsmeans MICROHABITAT /ADJUST=tukey pdiff; run;
proc plot data=CHECK6;
  plot RESID*PRED / vref=0;
proc univariate data=CHECK6 normal plot;
  var RESID;
  run;
```

(PCA, ter Braak 1998) was used to identify the length of the ordination axis and the need for either a linear or unimodal ordination technique. Unimodal, indirect ordination (Detrended Correspondence Analysis (DCA) was used to explore variation in species and site scores. DCA creates a matrix that describes how similar microhabitats are based on species presence and abundance. The matrix is presented on the two axes that best describe the relationships. The units of each axis are standard deviations (SD), where points one SD apart are 68.3% different, 2 SD apart are 95.5% different, 3 SD apart are 99.7% different and 4 SD apart are 99.9% different, with virtually nothing in common. Patterns in community composition were identified on the ordination of species and plots as either clusters or gradients along respective axes in the context of the specific types of microhabitats.

In order to provide an independent check to the ordination, discriminant function analysis was used. The object of discriminant function analysis (DFA) is to predict multivariate responses that best discriminates the subjects in different groups (Ramsey & Schafer 1997). Discriminant analyses were used to classify the eight a-priori microhabitats using the site scores from the DCA analysis while considering any variation in the experimental blocks. The cluster groups from the DCA site scores and the eight microhabitats for each experimental unit was used as input for a discriminant analysis which 1) determined if the classification was accurate, 2) provided discriminant functions for the classification of microhabitat types and, 3) indicates if DCA site scores or experimental units are important variables that define microhabitat clusters. This provided an independent check of the clusters identified in the DCA ordination.

Microhabitat specificity

1. Microhabitat specificity or preference

The occurrence of each species on each microhabitat was examined in order to investigate if there were any bryophyte species that were specific to, or seemed to have a preference for, a particular microhabitat. First, the presence or absence of each species was recorded for each microhabitat sampled. Second, the number of times a given species was recorded in a sample square (10x10cm) of a given microhabitat was recorded in order to better describe how frequently any given species occurred on a particular microhabitat. Species with a frequency of 80-99% on one microhabitat are defined here as having a strong preference for that type of microhabitat. The relative importance of a microhabitat was estimated using the method of Dufrêne and Legendre (1997) in PC-ORD software (McCune & Mefford 1997), which provides indicator values for each species for each type of microhabitat. The indicator value assigns each species a “percent of perfect indication” for each microhabitat type. The value (expressed as a percentage) calculates relative abundance by dividing the average abundance of a given species in a given microhabitat by the average abundance of that same species in all microhabitats. The percentage quantitatively describes the relative importance of a microhabitat with respect to the species’ that occur on each type of microhabitat. Species with an indicator value of $\geq 80\%$ on one microhabitat will be defined as being strong indicators for that type of microhabitat. Microhabitat specificities or preferences of species with S-rankings of S3 (common) or higher with fewer than ten total records were not reported. Microhabitat specificities or preferences of species with a S1 (very rare) or S2 (rare) ranking were reported regardless of the total number of records.

2. Functional diversity

I did not directly investigate bryophyte functional diversity in the field. However, the functional information available was compiled for all the species that a) showed microhabitat specificity, b) showed strong microhabitat preference, or c) were identified as strong indicators for a particular type of microhabitat. In addition to S-ranks (rarity) and floristic affinities (Appendix 1), growth form (pleurocarp vs. acrocarp), sexual orientation (monoicous, dioicous, etc), plant height, setae length, capsule length, spore size and the ability to reproduce vegetatively were investigated. The investigation was carried out by grouping species which share specificity or preference for a particular microhabitat and looking for trends in the aforementioned traits that may distinguish the groups from one other. A DCA was also used here to explore patterns of species distributions. Species showing microhabitat specificities and preferences were indicated on the ordination to provide insight into the bryophyte community.

Relevance to boreal forests

As this research was conducted entirely in one boreal forest site (Thunder Bay), efforts were made to determine if this site was representative of boreal forests at a larger scale. Comparisons were made between (1) rank-abundance curves of forest tree species, (2) the distribution and type of coarse woody debris, (3) the merchantable volume and gross total volume of timber of all eight NEBIE sites. Ordination analysis was also used to compare the distribution of 463 forest species from my research site among the other seven NEBIE sites and eighty Forest Ecosystem Classification (FEC) boreal mixedwood sites (Sims 1989).

RESULTS

Structural Diversity

Species-area relationships among microhabitats

Species accumulation was variable among the eight microhabitats compared. Species accumulation ranged from 0.85 species/10cm² on early logs to 6.36 species/10cm² on late logs (Table 1). R² values ranged from 0.75 (early logs) to 0.98 (stumps) indicating that there was a strong relationship between cumulative species richness and total area sampled for all microhabitats sampled (Table 1). Species accumulation on ground microhabitats was found to be significantly ($p < 0.05$) less than on all other microhabitats except early logs (Figure 4, Table 1,2). Species accumulation on early log microhabitats was found to be significantly less ($p < 0.05$) than all other microhabitats except ground. In addition to the differences from ground and early logs, species accumulation on mid log microhabitats was significantly greater ($p < 0.05$) than on snags and trees. In addition to the differences from ground and early logs, species accumulation on late logs was significantly greater ($p < 0.05$) than on stumps, snags and trees. In addition to the differences from ground and early logs, species accumulation on rock microhabitats was significantly greater ($p < 0.05$) than on snags and trees. In addition to the differences from ground and early log, species accumulation on stumps was found to be significantly ($p < 0.05$) less than on late logs. As mentioned, accumulation on both snag and tree microhabitats was found to be significantly greater than on ground and early logs, and significantly less than on mid logs, late logs, and rocks. The microhabitats with the shallowest change in species accumulation were early logs (0.85 sp/10cm²) and ground (0.89 sp/10cm²). The slopes of both species-area relationships were much

shallower than those found on the majority of the other microhabitats; the slope on both being less than half of the values on all other microhabitats (Table 1). Snag and tree microhabitats showed intermediate species accumulation (3.32-3.62 sp/10 cm²). Rock, stump, mid log and late log microhabitats had the greatest change in species accumulation (4.40-6.36 species/10cm²) (Figure 4, Table 1).

Species Richness

Species richness in the site totalled 106 species; 74 mosses (M), 32 liverworts (L). The local bryoflora was dominated by boreal species (58%) with some cosmopolitan species (29%) and few temperate (13%) species. Less than a third (29%) of the species had distributions limited to North America (App. 1). The *Flora of Ontario* (Newmaster and Ragupathy 2005) provincial ranking was used to categorize species as S1 (very rare) ranking to S5 (very common). Most (75%) of the species were common (S4, S5) with a considerable portion of uncommon (15% -S3) and rare (13% S1, S2). Total species richness on the microhabitats was as follows: ground 34(28M, 6L), early log 20 (14M, 6L), mid log 74 (52M, 23L), late log 70 (50M, 20L), rock 83 (63M, 20L), stump 49 (36M, 13L), snag 42 (32M, 10L), Tree 58 (45M, 13L). Mean species richness differed among the different microhabitats (Table 3). Late log microhabitats were found to have significantly ($p<0.05$) higher species richness than ground, early log, rock, stump, snag and tree microhabitats (Table 4). Mid log microhabitats were found to have significantly ($p<0.05$) higher mean species (25.3) richness than ground (9.4), early log (6.7) and tree microhabitats (14.9) (Table 4).

Table 1. Slope coefficient, slope standard error and R^2 from linear regressions of log-transformed data for eight microhabitats.

	Slope coefficient	Std. error of slope	R^2
Ground	0.89	0.003	0.85
Early log	0.85	0.017	0.75
Mid log	5.51	0.043	0.95
Late log	6.36	0.062	0.95
Rock	6.15	0.078	0.98
Stump	4.10	0.035	0.89
Snag	3.62	0.053	0.89
Tree	3.32	0.041	0.92

Figure 4. Species-area curves for eight microhabitats, showing regression curves, mean and standard deviation of bryophyte species accumulation. Logarithmic equations of curve, R^2 values, number of representatives (n) and standard error of regression curves are shown. Regression curves plotted to the mean sample unit of each respective microhabitat. Significant differences ($\neq$) ($p < 0.05$) are as follows: a $\neq$ cdefgh, b $\neq$ cdefgh, c $\neq$ abgh, d $\neq$ abfgh, e $\neq$ abgh, f $\neq$ abd, g $\neq$ abcde, h $\neq$ abcde.

Table 2. Significance values from t-test comparisons of the species-area regression lines among all microhabitats. * indicates unadjusted significant difference and ° indicates significant differences after sequential Bonferroni adjustment.

		t value
Ground	Early log	0.165
Ground	Mid log	25.401*°
Ground	Late log	24.327*°
Ground	Rock	26.957*°
Ground	Stump	54.129*°
Ground	Snag	10.970*°
Ground	Tree	11.737*°
Early log	Mid log	12.776*°
Early log	Late log	13.831*°
Early log	Rock	12.683*°
Early log	Stump	14.158*°
Early log	Snag	7.259*°
Early log	Tree	6.983*°
Mid log	Late log	1.515
Mid log	Rock	1.161
Mid log	Stump	1.994*
Mid log	Snag	3.302*°
Mid log	Tree	4.405*°
Late log	Rock	0.317
Late log	Stump	3.284*
Late log	Snag	4.314*
Late log	Tree	5.398*
Rock	Stump	2.607*
Rock	Snag	3.781*°
Rock	Tree	4.940*°
Stump	Snag	1.443
Stump	Tree	2.093*
Snag	Tree	0.530

Table 3. Total richness, mean and standard error values of structural diversity measures for eight microhabitats. *indicates highest value and ° indicates lowest value for each measure.

	Total Species Richness	Mean Richness Mean ± standard error	Shannon- Weiner Index	Simpson's Index	Pielou's Evenness
Ground	34	9.40 ± 2.14	°0.89 ± 0.11	°0.43 ± 0.03	°0.41 ± 0.03
Early log	°20	°6.66 ± 3.01	1.08 ± 0.17	0.60 ± 0.05	*0.63 ± 0.04
Mid log	74	25.31 ± 2.01	1.81 ± 0.10	0.74 ± 0.03	0.59 ± 0.02
Late log	70	*27.55 ± 2.15	*1.88 ± 0.11	*0.74 ± 0.04	0.58 ± 0.03
Rock	*83	17.80 ± 1.93	1.71 ± 0.09	0.71 ± 0.03	0.61 ± 0.02
Stump	49	17.02 ± 2.33	1.60 ± 0.12	0.67 ± 0.04	0.56 ± 0.03
Snag	42	16.69 ± 2.42	1.59 ± 0.13	0.70 ± 0.04	0.58 ± 0.03
Tree	58	14.93 ± 1.93	1.49 ± 0.09	0.56 ± 0.03	0.56 ± 0.02

Table 4. Significance values from comparisons of structural diversity measures among eight microhabitats. * indicates significant difference after sequential Bonferroni test and ° indicates significant difference after Tukey-Kramer adjustment.

		Mean Richness	Shannon- Wiener	Simpson's	Pielou's Evenness
Ground	Early log	0.4663	0.3313	0.0141	0.0004*°
Ground	Mid log	<0.0001*°	0.0001*°	<0.0001*°	0.0002*°
Ground	Late log	<0.0001*°	0.0001*°	<0.0001*°	0.0001*°
Ground	Rock	0.0085	0.0001*°	<0.0001*°	0.0001*°
Ground	Stump	0.0258	0.0004*°	<0.0001*°	0.0014*°
Ground	Snag	0.0352	0.0005*°	0.0001*°	0.0008*°
Ground	Tree	0.0696	0.0004*°	<0.0001*°	0.0002*°
Early log	Mid log	<0.0001*°	0.0007*°	0.0398	0.3982
Early log	Late log	<0.0001*°	0.0013*°	0.0353	0.4702
Early log	Rock	0.0054	0.0033*	0.0770	0.7510
Early log	Stump	0.0131	0.0221	0.2960	0.2666
Early log	Snag	0.0171	0.0244	0.1625	0.3863
Early log	Tree	0.0315	0.0438	0.2457	0.2091
Mid log	Late log	0.4560	0.6414	1.0000	0.8279
Mid log	Rock	0.0139	0.4946	0.9976	0.4772
Mid log	Stump	0.0139	0.2020	0.8542	0.5285
Mid log	Snag	0.0125	0.2063	0.9892	0.7690
Mid log	Tree	0.0013*°	0.0309	0.7354	0.4098
Late log	Rock	0.0030*°	0.2660	0.5401	0.3781
Late log	Stump	0.0034*	0.1082	0.9818	0.6796
Late log	Snag	0.0032*	0.1119	0.1974	0.9228
Late log	Tree	0.0003*°	0.0147	0.429	0.5945
Rock	Stump	0.7968	0.4584	0.3934	0.2165
Rock	Snag	0.7226	0.4587	0.7583	0.3851
Rock	Tree	0.3040	0.1027	0.3199	0.0966
Stump	Snag	0.9240	0.9877	0.6432	0.7747
Stump	Tree	0.4977	0.5050	0.9774	0.9824
Snag	Tree	0.5745	0.5262	0.6171	0.7196

Diversity

There was no difference in diversity between most of the microhabitats (Table 3). The Shannon-Wiener function shows the ground microhabitat to be significantly different (lower) than all of the other microhabitats except early log. The function also shows early log microhabitats to be significantly different from mid and late log microhabitats. There was no significant differences ($p < 0.05$) in the Shannon-Wiener index in any of the other microhabitat comparisons (Table 4).

Simpson's index also shows the ground microhabitat to be significantly different (lower) than all the other microhabitats except for early logs. There was no significant differences ($p < 0.05$) in Simpson's index between any of the other microhabitats (Table 4).

Pielou's measure of evenness shows the ground microhabitat to be significantly (lower) different than all of the other microhabitats including early logs. There were no significant differences ($p < 0.05$) in Pielou's evenness in any of the other microhabitat comparisons (Table 4).

Compositional Diversity

Beta-diversity

Beta-diversity is an important component of diversity often reported in diversity studies because it helps to quantify differences among microhabitats. Whittaker's measure of beta-diversity (β_w) describes how different the bryophyte community is between microhabitats. High values indicate large community differences and therefore low species similarity. β_w shows ground microhabitats to be most like late logs and snags, and least like rocks, early logs and trees (Figure 5, Table 5). Early logs were found

to be most like late log and snag microhabitats and least like rock and tree microhabitats. Mid log microhabitats are most like late logs, stumps and snags, and least like rocks and trees. Late logs are like early log, late log, stump and snag microhabitats and least like rock and tree microhabitats. Rock microhabitats are most like mid and late logs, and least like ground and trees. Stumps and snags are both most like late logs, mid logs and each other, and both stumps and snags are least like ground, rock and tree microhabitats. Tree microhabitats are most like late logs and snags, and least like ground and rocks (Figure 5, Table 5).

The Morisita-Horn index uses species identity and relative abundance to estimate similarity among microhabitats, high values indicate high similarity. The index indicates that ground microhabitats are most similar to rock microhabitats and dissimilar to early log and tree microhabitats (Figure 6, Table 6). Early logs are most similar to snag microhabitats, and least similar to rock microhabitats. Mid log microhabitats are similar to late logs and stumps, and least like early logs. Late logs are similar to mid log and stump microhabitats, and least like early log microhabitats. Rock microhabitats are most similar to stumps and least like early logs. Stumps are similar to mid and late log microhabitats and least like early log microhabitats. Snags and trees are most similar to each other and both are least like ground microhabitats (Figure 6, Table 6). Although it seems that data for all microhabitat types is available after calculating beta-diversity for one microhabitat type to all others, beta-diversity must be calculated for each microhabitat combination. The beta-diversity values are relative to the microhabitat types whose data is used for the calculation, making it invalid to make a rock-tree comparison from rock-ground and tree-ground values.

Figure 5. Whittaker's beta-diversity, showing relative differences among microhabitat types.

Table 5. Values of Whittaker's beta-diversity for each microhabitat comparison. * indicates most similar microhabitat and ° indicates least similar microhabitat for each comparison.

	Ground	Early log	Mid log	Late log	Rock	Stump	Snag	Tree
Ground	---	3.75	3.19	*2.85	°4.10	3.33	3.02	3.84
Early log	°3.75	---	2.57	*2.26	3.65	3.01	2.49	3.37
Mid log	3.19	2.57	---	*2.29	°3.47	2.50	2.44	3.25
Late log	2.85	2.26	2.29	---	°3.33	*2.23	2.26	3.10
Rock	°4.10	3.65	3.47	*3.33	---	3.62	3.50	3.84
Stump	3.33	3.01	2.50	*2.23	°3.61	---	2.49	3.22
Snag	3.02	2.49	2.44	*2.26	°3.50	2.49	---	3.10
Tree	3.84	3.37	3.25	3.10	°3.84	3.22	*3.10	---

Figure 6. Morisita-Horn values, showing relative similarities among microhabitat types.

Table 6. Values of Morisita-Horn similarity index for each microhabitat comparison. * indicates most similar microhabitat and ° indicates least similar microhabitat for each comparison.

	Ground	Early log	Mid log	Late log	Rock	Stump	Snag	Tree
Ground	---	°0.12	0.28	0.28	*0.36	0.25	0.20	0.12
Early log	0.12	---	0.13	0.09	°0.07	0.13	*0.20	0.18
Mid log	0.28	°0.13	---	*0.96	0.40	0.88	0.33	0.26
Late log	0.28	°0.09	*0.96	---	0.37	0.86	0.29	0.22
Rock	0.36	°0.07	0.40	0.37	---	*0.51	0.29	0.23
Stump	0.25	°0.13	*0.89	0.86	0.51	---	0.41	0.37
Snag	°0.20	0.20	0.33	0.29	0.29	0.41	---	*0.98
Tree	°0.12	0.18	0.26	0.22	0.23	0.37	*0.98	---

Ordination analysis

Patterns in community organization were apparent among different types of microhabitat. Detrended Correspondence Analysis (DCA) analyses of 189 microhabitat representatives and 106 species resulted in ordinations that display distinct relationships between species and microhabitats well defined on two ordination axes as indicated by high eigenvalues (X axis 0.6911; Y axis 0.5045) and long theoretical gradients (X axis 4.430 SD; Y axis 3.277 SD) (Figure 7). Tree microhabitats were split into two clusters positioned at the extreme ends of the first axis, indicating that the community structure is very different. Further investigation revealed that aspens were tightly clustered on the right end of the gradient, while birch and balsam fir were clustered at the left. Separating these tree groups for analysis was not possible as the sampling technique used did not differentiate among tree species. Stump and snag microhabitats were distributed along the first axis, between the two clusters of tree microhabitats. Mid-decay and late-decay stage logs were found spread from the middle of the axis, to the left-side near the cluster of tree (balsam-birch) microhabitats. Rock and ground microhabitats were separated along the Y-axis (2 SD). Ground microhabitats were clustered (1SD, 2 outliers) at the bottom of the ordination while rock microhabitats were more variable (2SD) along the rest of the axis. Early log microhabitats were spread out along both axis, with some grouping with the tree microhabitats (aspen cluster) along the x-axis and others spread along the y-axis between rock and ground microhabitats.

The discriminant analysis successfully used 8 microhabitats to classify heterogeneity in bryophyte community composition. The canonical correlation from the discriminant functions is the ratio of the between groups sums of squares to the total

sums of squares. Thus, the first discriminant function is responsible for 71.6 % of the between group differences (variability in the discriminant scores). The second function is responsible for 43.0 % of the between group variance. Wilk's Lambda was used to test the hypothesis that in the population there are no differences between the groups (SPSS 1999). There were significant differences ($p < 0.001$) for first two DCA axes scores, but no significant ($p = 0.080$) differences attributed to the experimental units (blocks). The eight microhabitat groups explained 54.5 % of the observed variability (between the groups) in the DCA axis 1 scores and 39.7% in the DCA axis 2 scores. The final discriminant model uses two discriminant functions (DCA axis 1 and 2 scores) to explain 82.3 % of the variation between the groups of microhabitats.

Microhabitat specificity

Ground

One species (*Polytrichum commune* (M-S5)) was found only on ground microhabitats (Appendix 1). There were no other species with a strong preference ($\geq 80\%$ frequency) or with high indicator values (indicator value ≥ 80) for ground microhabitat (Appendix 1).

Early log

There were no species found to occur exclusively on early log microhabitats (Appendix 1). There were no species with a strong preference for early log microhabitats, however, two species (*Leskea polycarpa* (M;S4-5); *Orthotrichum speciosum* (M;S1)) were identified as strong indicators (indicator value $> 80\%$) of early logs (Appendix 1).

Mid log

Two species (*Lophozia heterocolpos*3 (L); *Weissia controversa* (M;S5)) were found to be specific to mid log microhabitats (Appendix 1). Two more species (*Nowellia curvifolia* (L;S4); *Hypnum pratense* (M;S5)) had a strong preference for mid logs. In addition to these four, one additional species (*Ceratodon purpureus* (M;S5)) was found to be a strong (indicator value >80%) indicator of mid log microhabitats (Appendix 1).

Late log

Three species of liverworts (*Lophozia badensis*2 (S3), *Lophozia sp*2 (S2), *Lophozia sp*3 (S2)) were found only on late log microhabitats (Appendix 1). There were no other species with a strong preference for late log microhabitats. Two additional species (*Cephaloziella hampeana*2 (L;S2); *Dicranum polysetum* (M;S5)) were identified as strong indicators for late log microhabitats (Appendix 1).

Rock

Rocks supported the highest number of specific species, with five species of moss (*Brachythecium plumosum* S5, *Dicranum scoparium* S5, *Fissidens taxifolius* S4, *Hedwigia ciliata* S5, *Pseudoleskeella tectorum* S2) and two species of liverworts (*Barbilophozia barbata* S3, *Lophozia capitata* S3) found exclusively on this microhabitat (Appendix 1). Fourteen additional species (*Lophozia capitata*1 (L;S2); *Anomodon attenuatus* S5, *Brachythecium populeum* S5, *Homalia trichomanoides* S5, *Homomallium adnatum* S3, *Leskeella nervosa* S5, *Loeskeobryum brevirostre* S1, *Mnium marginatum* S5, *Neckara pennata* S5, *Paraleucobryum longifolium* S5, *Plagiothecium laetum* S5, *Schistidium apocarpum* S5, *Thuidium delicatulum* S5, *Tortella tortuosa* S5 (M)) showed

Figure 7. DCA microhabitat ordination of 106 species on 189 microhabitat representatives to explore relationships between species and microhabitat types. Eigenvalues: axis 1 = 0.6911, axis 2 = 0.5045.

a strong preference for rocks. In addition to these, three more species (*Radula complanata* (L;S4); *Mnium spinulosum*, *Rhytidiadelphus triquetrus* (M;S5)) were found to be strong (indicator value >80%) indicators of rock microhabitats. Four of these non-specific species had indicator values of 100% (Appendix 1).

Stump

One species (*Mnium thomsonii* (M;S2)) was found only on stump microhabitats (Appendix 1), it was only observed in one sampling grid, however due to its S2 ranking its microhabitat preference is reported. There were no species that showed a strong preference for stumps. In addition, one species (*Forsstroemia nitans* (M;S1)) was found to be a strong indicator (indicator value = 85%) of stump microhabitats (Appendix 1).

Snag

There were no species found to occur exclusively on, or have a strong preference for, snag microhabitats (Appendix 1). Similarly, there were no species identified as strong indicators of snag microhabitats (Appendix 1).

Tree

One species (*Bazzania trilobata* (L;S4)) was found to be specific to tree microhabitats (Appendix 1). There were no other species with a strong preference or with high indicator values for tree microhabitats (Appendix 1).

Nineteen species were excluded from these results due to low occurrences, all except three species were microhabitat specific (Appendix 1).

Functional Diversity

Patterns in community organization among microhabitat types were apparent in the DCA ordination used to explore patterns of species distribution (Figure 8). The DCA of 106 species on 189 microhabitat representatives showed relationships between species and microhabitat type well defined on two ordination axes as indicated by high eigenvalues (X axis 0.6911; Y axis 0.5045) and long theoretical gradients (X axis 6.2725; Y axis 6.4837). Some patterns observed corresponded to microhabitat affinities. In particular, rock, late log, and mid log species formed obvious clusters with only two or three outliers. S-ranks, floristic affinities (Appendix 1), growth form (pleurocarp vs. acrocarp), sexual orientation (monoicous, dioicous, etc), plant height, setae length, capsule length, spore size and the ability to reproduce vegetatively were compared among groups of bryophyte species that shared a microhabitat specificity or preference. There were no apparent trends in any of the functional traits examined that would explain or characterize the groups (or clusters) of species that share a preference for a particular type of microhabitat.

Relevance to boreal forests

The comparisons I made between rank-abundance curves of forest tree species showed the relative percent cover values of woody species in the Thunder Bay site to be close to, and overlapping with the values of the other NEBIE boreal mixedwood forest sites. The distribution and type of coarse woody debris, the merchantable volume of timber and the gross total volume of timber in the Thunder Bay site were also consistent with the other boreal mixedwood NEBIE sites. In the ordination analysis performed

comparing the distribution of forest species from my research site among the other NEBIE and FEC sites (Sims 1989), the Thunder Bay data overlaps with the boreal mixedwood NEBIE sites and the FEC boreal mixedwood sites. These investigations indicate that the Thunder Bay installation of NEBIE is an appropriate representation of mixedwood boreal forests in Ontario.

DISCUSSION

This research shows the influence that forest microhabitats have on the diversity of the local bryophyte community. Although the influence of microhabitat has been studied extensively in vascular plants, this study is the first of its kind pertaining to bryophyte communities. Of over four hundred journal articles on bryology reviewed over the course of this study, only two (Mills and Macdonald 2004; Pharo and Beattie 2002) incorporate comparisons of multiple microhabitats, however, both only estimate species richness and only one (Mills and Macdonald) is relevant to boreal forest environments. This study contributes to a better understanding of forest bryophyte diversity by showing that bryophytes species richness does not accumulate the same way on different types of microhabitats, quantifying microhabitat diversity and identifying species that are specific to, or have preferences for particular microhabitat types. This type of information describes the natural patterns of diversity that are critical to forest management for creating guidelines and regulations to implement techniques that conserve forest diversity with respect to bryophyte diversity and forest microhabitats. Bryophyte diversity on microhabitats is different for both the structural and compositional components of diversity. These levels need to be taken into joint consideration when describing diversity in order to not only identify “how many species are there” but also “how do species co-exist” (Lindenmayer et al. 2000).

Structural Diversity

Species diversity on microhabitats in the boreal forest is not all the same; bryophyte species accumulation, richness and diversity vary among the eight microhabitats investigated. Variation in bryophyte diversity within microhabitats was

observed in all aspects of this study. This variation especially influenced the comparison of species accumulation. Microhabitats with low species richness such as ground and early logs have extremely patchy occurrences of bryophytes (Frego and Carlton 1995a,b). Tree microhabitats have definitive patterns of bryophyte richness and abundance with few species occurring infrequently higher (1-1.5m) on the trunk and greater species richness and abundance occurring at the base. This scattered pattern of bryophyte occurrence combined with random and unbalanced sampling result in large within microhabitat variation. This variation is typical of boreal forest communities (Mills and Macdonald 2004). Although it makes significant differences among microhabitats difficult to identify, this variation reflects the naturally occurring differences in size, structure, frequency and orientation in the forest that occurs in all the microhabitats studied. Further studies should consider further subdivisions of the microhabitats such as tree base and bole, or acidic and basic rocks to address the within-microhabitat variation.

Despite the within microhabitat variation, differences among microhabitats were identifiable. Late log microhabitats showed the steepest increase of total species richness with area. Mid logs, which were predicted to have the steepest relationship came in third, after late logs and rocks. Ground was predicted to have the shallowest slope, however the species-accumulation relationship on early logs was found to have a slightly more shallow slope. A possible reason that late log microhabitats showed the steepest species area relationship is that they are the most variable and distinctive microhabitat type, providing habitat for a wide range of bryophyte preferences. It was thought that the species-area relationship on rocks would be shallower than all the biotic microhabitats. A possible reason for this unexpected result is that rocks in the boreal forest are more

variable than predicted. There is variation in the amount of leaf litter, coarse woody debris and even plants that cover rocks in the forest. Also, temperatures on rocks would likely differ from those on woody microhabitats, it is possible that they maintain different ambient temperatures which some bryophyte find preferable for establishment, growth or reproduction. It is possible that microhabitat heterogeneity is not the driving factor for diversity, other characteristics such as pH and surface texture may influence bryophyte establishment and growth.

It was surprising to observe early logs microhabitats showing a species-area relationship most similar to ground. It was predicted that early logs would be similar to other woody microhabitats. It appears that patchy bryophyte occurrences and low species richness are common to both ground and early log microhabitats, resulting in both having shallow species area relationships. Forest management should consider these patterns, particularly if they occur in other types of forests and at broader scales on the landscape. If, as this study indicates, bryophyte species accumulate differently on different microhabitats, then forest management techniques must take this into consideration. One of the restoration goals in forest management is to provide habitat that influences species diversity. How much habitat to leave or provide is a critical piece of information within forest silvicultural guides (OMNR 2001). Microhabitats that require larger areas to reach total species richness would need to be more available than microhabitats that accumulate their total species over less area. These differences may be a result of the different dispersal and establishment requirements of species (Cleavitt 2001; Wiklund and Rydin 2004) and that the more variable a microhabitat, the more acceptable it is to a wider range

of bryophyte species. Further research is necessary to assess the number of microhabitat representatives of each type needed to support mean and total species richness.

Richness is one of the most tangible aspects of structural diversity. It provides an indication of how species are distributed in their environment. Measures of richness can also help identify which features of an ecosystem contribute most to its diversity. As predicted, richness was lowest on ground microhabitats. However, late log microhabitats were found to have the highest mean species richness, closely followed by mid-log which was predicted to be higher. With the exception of rock microhabitats which had higher species richness than predicted, the results follow what was predicted, with decayed woody microhabitats being more species rich. The analysis revealed several significant differences (Table 4) but did not adequately reflect the contrasts in total species richness among microhabitats (Table 3). Mean species richness on rock was fourth highest of the microhabitats examined, however, total species richness was by far the highest with eighty-three species (Table 3). Similarly, *total* species richness on trees was higher than on stumps and snag microhabitats which both had higher *mean* species richness. Mills and MacDonald (2004) also showed similar mean richness patterns on the microhabitats they investigated. Their study of conifer-dominated boreal mixedwood stands estimated logs to have the highest mean species richness and undisturbed ground to have the lowest. The mean values are necessary for summary descriptions of the microhabitats, but total species richness must be examined as well to help describe the microhabitats for management and conservation. If conservation efforts only acknowledged microhabitats with the highest mean values of richness, many valuable microhabitat resources would be lost.

The patterns of structural diversity among microhabitats showed similar trends based on the diversity indices. Both Simpson's index and Shannon-Wiener function were highest on late log microhabitats and lowest on ground microhabitats (Table 3). The significant differences ($P < 0.05$) observed in both indices between ground and all other microhabitats (except early log) are a result of the low species richness characteristic of the ground microhabitat. Similarly, the additional significant differences ($p < 0.05$) between early logs and both late and mid log microhabitats identified by the Shannon-Wiener function also separate the most species-poor microhabitat (ground) from the two with the overall highest species richness (mid and late log). Pielou's estimate of evenness showed similar trends with ground microhabitats (lowest value=0.4068) being significantly different ($p < 0.05$) than all of the other microhabitats. Early log microhabitats were found to have the highest evenness, indicating that despite low species richness (Table 3) species are most evenly distributed on this microhabitat.

Compositional Diversity

Compositional diversity is an important aspect of diversity to consider because all species do not occur equally in an ecosystem (Tilman et al. 1997). Species that are common on one microhabitat and rare on another need to be considered differently than species common on all available microhabitats. Beta-diversity describes these differences in order to indicate similarities and differences among microhabitats. The beta-diversity comparisons somewhat follow the predictions. All the woody microhabitats were more similar to woody microhabitats than to rock or ground. Early logs were found to be more like late logs or snags than trees. Stumps and snags were not found to be most similar to each other, but were more similar to the other woody microhabitats than to rocks. There

does not seem to be a pattern in either measure to explain the community similarities and differences among microhabitat types. The different values obtained for the two values of beta-diversity calculated are a result of the fact that the Morisita-Horn index uses species identity in its calculation. Whittaker's is commonly used because the abundance data needed for Morisita calculations is not available. As the Morisita-Horn index compares each individual species and their relative abundance between the microhabitats it is believed to be the more useful measure. Used in conjunction with values of structural diversity, compositional diversity also aids in determining methods for effective management. Beta-diversity was variable among the microhabitat comparisons, with some microhabitats appearing to have very similar bryophyte communities (trees and snags) while others appearing very dissimilar (rocks and early logs). Other research has compared beta-diversity within microhabitat types (Pharo and Beattie 2002; Mills and Macdonald 2004; Weibull and Rydin 2005). This work identified tree base microhabitats as having the highest differences (most variable/dissimilar) and logs as having the lowest. This helps quantify the aforementioned variability *within* microhabitats, but doesn't address community differences among microhabitat types. Identifying the differences both within and among microhabitats provides knowledge to better describe the local bryophyte populations.

Bryophyte species show affinities for particular microhabitats. The DCA community analysis indicates that different species prefer particular microhabitat types. Although the tree microhabitat is split at opposite ends of the first axis (Figure 7), review of field notes revealed that all the trees occurring on the right side of the ordination were aspens (*Populus tremuloides*), while the left side was represented by balsam fir (*Abies*

balsamia) and white birch (*Betula papyrifera*). This shows that not only are there species showing a preference for tree microhabitats, but also a preference for a particular type (species) of tree microhabitat. Schmitt and Slack (1990) observed similar preferences in their study of epiphytic bryophytes and lichens in the Adirondack Mountains, New York. The largest differentiation along the second axis of the ordination is between ground and rock microhabitats. Rocks had the highest total species richness and the most (14) microhabitat specific species while ground had the second lowest total species richness and only 1 specific species. These differences contributed to their separation in the ordination, with species only occurring on rock microhabitats clustering from the other microhabitats. The patterns observed in the ordination indicate that there are several groups of bryophyte species that prefer, or are specific to, a particular type of microhabitat. The affinities are possibly due to the matching of establishment requirements with appropriate microhabitat qualities. These trends are supported by the results of the discriminant analysis which indicate that microhabitat type influence bryophyte community structure.

Microhabitat specificity

Excluding the species removed due to low observations, 18% of the species observed in this study were only found on one type of microhabitat, 9% were found on two, 14% were found on three, 4% were found on four types of microhabitat, 8% were found on five, 14% were found on six, 11% were observed on seven and 15% were found on all eight types of microhabitat. Of the 60 species that occurred on more than one microhabitat, 14 showed a strong preference (frequency $\geq 80\%$) for one type of microhabitat (Appendix 1). Among the seven species of liverworts that were found to be

microhabitat specific, four were specific to decaying log microhabitats. These results support the prediction that some bryophyte species, but not all, would be specific to a particular type of microhabitat. They also show that some species have an identifiable preference for one type of microhabitat over another. In the case of the microhabitat specific species, the microhabitats on which they are found are possibly providing an environment that the species can either not find, or not access (disperse to) on other microhabitat types. For the species which show a preference for a particular type of microhabitat, it is thought that the environments on other microhabitat types are acceptable, but growth is more optimal on the preferred microhabitat. In her study of bryophyte host specificity on trees Studlar (1982) observed a similar trend with few species occurring on one tree type (species) but more showing preferences for one type over another. The indicator analysis performed also provides indication of species' preference for microhabitat type. Indicator analysis differs from frequency measurements as it is based on the relative abundances of species on each microhabitat type. Species with low frequency (occur in few grid squares) but high abundance (fill the square) were identified as indicators that would have been missed if frequencies were the only information examined (Appendix 1). These methods provide quantitative measures of microhabitat specificity by individual species. They also help identify species groups that share a preference for the same type of microhabitat. These preferences can be used as a starting point for investigating trends in functional diversity of individual species and species groups.

Functional diversity

Functional differences in diversity are useful in identifying biological

characteristics that may be contributing to species diversity in seed plants. Contrary to the predicted results and in contrast to seed plants, there were no apparent trends in any of the traits examined that would explain or characterize the groups of species that share a preference for a particular type of microhabitat. As the examined characteristics of species do not explain microhabitat preferences, it is perhaps physical characteristics of the microhabitats themselves which contribute to the specificities observed. Not only do the distribution and abundance of microhabitats act as environmental filters that may influence species distribution, but the abiotic features of the environment around microhabitats act in a similar way; exposure to sun, rain and wind contribute to patterns of bryophyte distribution by creating different micro-environments on different microhabitats that fulfill the requirements of various bryophyte species (Ross-Davis and Frego 2002; Fenton et al. 2003; Mills and Macdonald 2004; Wiklund and Rydin 2004; Gignac and Dale 2005). These filters are in place at a *mesohabitat* level, dictated by forest canopy, vegetation and presence of microhabitats. Studies have shown that this mesohabitat level is important to bryophyte communities (Heinlen and Vitt 2003), bryophyte richness quickly declines on forest microhabitats that lose surrounding canopy and other components of forest structure (Newmaster and Bell 2002; Roberts and Zhu 2002; Nelson and Halpern 2005). It has been identified that bryophyte communities are conserved more effectively when patches in which all forest components are retained (Pharo et al. 2004; Fenton and Frego 2005; Gignac and Dale 2005). At a smaller (within mesohabitat) scale, the temperature, humidity and pH of particular microhabitats have been shown to influence bryophyte populations. For example, research on the attributes of microhabitat characteristics has shown bryophyte preferences for a particular position

on a microhabitat. Kimmerer and Young (1996) observed that one species (*Dicranum flagellare*) occurred predominantly on the tops of logs, while another (*Tetraphis pellucida*) preferred the sides. Weibull and Rydin (2005) observed higher bryophyte species richness on rocks under deciduous trees than those under coniferous species. Again, little work has been done that qualitatively compares these characteristics between microhabitats. It would be useful to know if species occurring on several microhabitats were responding to characteristics such as orientation that were independent of the microhabitats on which they occur. An additional confounding component of bryophyte functional diversity is the possibility that function varies with life-stage. In studies of select bryophyte species it has been proposed that microhabitat characteristics may influence bryophyte species differently during different life stages. Research has found tree species (McAlister 1995), mesohabitat (Ódor and van Hees 2004), pH and moisture (Wiklund and Rydin 2004) to influence bryophyte establishment. This may reflect patterns seen here in bryophyte species that occur on several microhabitats, but seem to prefer one in particular. If establishment or growth for a particular species is more optimal on a certain microhabitat, then that microhabitat would be used more effectively than others on which living is more difficult. Although patterns or similarities in bryophyte functional diversity may not explain the community patterns observed, research of this type contributes to our understanding of bryophyte ecology and the factors that may influence their populations.

Conservation and management

There is no doubt that microhabitat plays an important role in bryophyte diversity. Studies examining bryophyte communities consistently report that habitats with high

habitat heterogeneity have both higher species richness and higher species diversity than more homogenous habitats (Vitt et al. 1995, Vitt and Belland 1997; Rambo 2001; Gignac and Dale 2005).

This study provides quantitative evidence to support other qualitative studies that identify woody microhabitats such as logs, stumps and trees to be of particular importance to bryophyte diversity (Söderström 1988b; Berg 1994, 2002; Crites and Dale 1998; Hautala et al. 2004; Ódor and van Hees 2004). These studies identify the combined log microhabitats to be the greatest contributors to bryophyte richness and diversity, with many (14) bryophyte species occurring exclusively on logs and others (8) showing a strong preference for, or being good indicators of these log microhabitats. This work also supports past research that has shown some bryophyte species to prefer and be specific to logs in a particular stage of decay (Söderström 1988a; Rambo 2001; Ódor and van Hees 2004). In addition to supporting distinctive bryophyte communities, coarse woody debris has been shown to be important to other plant (Rasmussen et al. 1998; McGee 2001), insect (Jonsell et al. 1998; Schiegg 2000; Evans et al. 2003), amphibian (Butts and McComb 2000; Young and Yahner 2003), bird (Lohr et al. 2002; Johnson and Freedman 2002) and mammal (Bull and Heater 2000; Butts and McComb 2000; Ucitel et al. 2003) populations. These log microhabitats that are identified as being the most important to forest communities, and the microhabitat most threatened by current forest management regimes. Intensive forest management including clear cuts have an economically driven motive to remove all woody matter with a diameter larger than 10cm is removed from the site, with the remaining debris left in piles or burned; even rocks are often moved by

skidder blades to make way for harvesting machinery. This intensive method of harvesting negatively impacts all of the forest microhabitats examined in this study.

Recommendations

This research has identified the importance of microhabitats to bryophyte communities in Ontario mixedwood boreal forests. In order to conserve bryophyte diversity in support of forest diversity, management techniques that take the importance of microhabitats into consideration and incorporate all levels of diversity must be employed. This study provides quantitative evidence to support work done at larger landscape scales and supplies the microhabitat-level information necessary for effective forest management. I recommend 1) that silvicultural management for forest diversity incorporate leaving representatives of all forest microhabitats intact after harvest, 2) that these remnant microhabitats are both left scattered throughout the cut and also left together in unharvested patches, with buffers of at least 15 meters (Gignac and Dale 2005), 3) these patches contain as many different types of microhabitats as possible and 4) experimental research be performed to optimize ecosystem management protocols which consider each microhabitat type individually. This is based on the premise that unharvested patches will act as refugia for bryophyte communities and upon canopy closure, bryophytes will be able to colonize the microhabitats left scattered in the area (Pharo et al. 2004). Specific research is needed to ascertain the relative volumes, or numbers, of each type of microhabitat retained, as well as to optimize the distances maintained between patches. Further research on the functional diversity of bryophytes in the forest will also contribute to scientific evidence supporting and improving ecosystem management criteria.

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Appendix 1. Microhabitat distributions of liverwort (L) and moss (M) species represented by (frequency (Freq.)) and indicator values (IV). Total records indicate the total number of grid squares (10x10cm) in which the species occurred and number of microhabitats indicates the total number of different microhabitats on which the species occurred. Provincial rarity (S rank) and floristic affinities (B=boreal, B-T=boreal-temperate, B-I=boreal-interrupted, cB=circumboreal, cB-T=circumboreal and temperate, cT=circumtemperate, C=cosmopolitan, T=temperate) are included. **Bolded** values represent frequencies or indicator values $\geq 80\%$. Values of 100 in the frequency column, * identifies species occurring on one microhabitat type and shaded font indicates species with S rank of S3-S5 with fewer than ten total records.

Species	Species code	Ground Freq. IV	Early log Freq. IV	Mid log Freq. IV	Late log Freq. IV	Rock Freq. IV	Stump Freq. IV	Snag Freq. IV	Tree Freq. IV	total records	# of different microhabitats	Rarity/ S Rank	Floristic Affinity
<i>Barbilophozia L barbata</i>	BARbar	0 0	0 0	0 0	0 0	100	0 0	0 0	0 0	46	1*	S3	cB
<i>Bazzania trilobata</i>	BAZtri	0 0	0 0	0 0	0 0	0 0	0 0	0 0	100	18	1*	S4	cB
<i>Blepharostoma trichophyllum</i>	BLEtri	3 9	0.6 11	32 29	16 10	33 19	7 9	3 6	7 8	2203	8	S4	cB
<i>Calyptogeja muelleriana</i>	CALmue	0 0	0 0	100	100	0 0	0 0	0 0	0 0	1	1*	S4	cB
<i>Cephalozia lunulifolia</i>	CEPlun	0 0	0 0	100	100	0 0	0 0	0 0	0 0	4	1*	S4	cB
<i>Cephaloziella hampeana</i>	CEPham	0 0	0.2 0	65 60	31 34	2 1	0.9 5	0 0	0.2 0	1041	6	S3	cB
<i>Cephaloziella hampeana2</i>	Cham2	0 0	0 0	2 2	71 84	27 14	0 0	0 0	0 0	48	3	S2	cB
<i>Cephaloziella rubella</i>	CEPrub	0 0	0.3 25	66 44	30 25	4 2	0.7 4	0 0	0.1 0	1077	6	S3	cB
<i>Frullania eboracensis</i>	FRUebo	0 0	1 0	3 12	0 0	44 4	1 0	1 29	48 55	281	6	S4	T
<i>Geocalyx graveolens</i>	GEOgra	23 21	0.6 0	44 39	21 23	7 3	2 10	0.4 0	3 3	1817	8	S4	cB
<i>Jamesoniella autumnalis</i>	JAMaut	0.1 0	0.1 0	43 23	33 42	13 5	3 11	2 12	6 7	2221	8	S4	cB
<i>Lepidozia reptans</i>	LEPrep	0 0	0 0	0 0	100	0 0	0 0	0 0	0 0	5	1*	S4	cB

Species	Species code	Ground										Rock	Late log										Stump	Snag	Tree	total records	# of different microhabitats	Rarity/ S Rank	Floristic Affinity
		Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV		Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV							
<i>Lophocolea heterophylla</i>	LOPhet	2	12	0	0	51	32	20	14	19	31	4	8	0.7	1	4	2	1279	7	S4	cB								
<i>Lophozia badensis</i>	LOPbad	0.2	4	0.2	0	66	51	30	35	2	4	1	6	0.2	0	0.2	0	938	8	S3	cB								
<i>Lophozia badensis2</i>	Lbad2	0	0	0	0	0	0	100	100	0	0	0	0	0	0	0	0	22	1*	S3	B								
<i>Lophozia bicrenata</i>	LOPbic	0	0	0	0	100	100	0	0	0	0	0	0	0	0	0	0	1	1*	S3	cB								
<i>Lophozia capitata</i>	LOPcap	0	0	0	0	0	0	0	0	100	100	0	0	0	0	0	0	124	1*	S3	cB								
<i>Lophozia capitata1</i>	Lcap1	0	0	0	0	0	0	0	0	99	100	0	0	0	0	0.9	0	112	2	S2	cB								
<i>Lophozia heterocolpos</i>	LOPheH	0	0	0.7	42	72	48	26	7	0.3	1	0.7	2	0	0	0.3	0	591	6	S3	cB								
<i>Lophozia heterocolpos2</i>	LheH2	0	0	0	0	68	67	32	33	0	0	0	0	0.2	0	0	0	438	3	S2	cB								
<i>Lophozia heterocolpos3</i>	LheH3	0	0	0	0	100	100	0	0	0	0	0	0	0	0	0	0	45	1*	S2	cB								
<i>Lophozia longidens</i>	LOPlon	0	0	0	0	63	23	32	57	5	20	0	0	0	0	0	0	19	3	S3	cB								
<i>Lophozia sp1</i>	L3	0	0	0	0	69	39	31	61	0	0	0	0	0	0	0	0	118	2	S2	B								
<i>Lophozia sp2</i>	L4	0	0	0	0	0	0	100	100	0	0	0	0	0	0	0	0	1	1*	S2	B								
<i>Lophozia sp3</i>	L5	0	0	0	0	0	0	100	100	0	0	0	0	0	0	0	0	1	1*	S2	B								
<i>Nowellia curvifolia</i>	NOWcur	0	0	0.3	0	92	89	6	4	0	0	2	6	0	0	0	0	340	4	S4	cB								
<i>Plagiochila porelloides</i>	PLApor	0	0	0	0	33	4	0	0	33	51	0	0	33	45	0	0	3	3	S4	cB								
<i>Porella platyphylla</i>	PORpla	0	0	0	0	0	0	0	0	100	100	0	0	0	0	0	0	2	1*	S4	cT								

Species	Species code	Ground	Early log	Mid log	Late log	Rock	Stump	Snag	Tree	total records	# of different microhabitats	Rarity/ S Rank	Floristic Affinity
Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV													
<i>Ptilidium L ciliare</i>	PTlcll	0 0	0 0	25 4	50 95	25 1	0 0	0 0	0 0	4	3	S4	cB
<i>Ptilidium pulcherrimum</i>	PTlpul	0.1 0	2 32	39 18	15 11	15 1	6 5	3 18	18 14	2025	8	S4	cB
<i>Radula complanata</i>	RADco m	0 0	0.2 0	5 0	8 4	65 84	1 6	2 1	18 4	649	7	S4	cB
<i>Riccardia latifrons</i>	RIClat	0 0	0 0	58 32	33 66	0 0	8 2	0 0	0 0	12	3	S3	C
<i>Amblystegium M serratum</i>	AMBser	0 0	0 0	22 6	11 4	40 57	6 3	8 28	13 2	209	6	S3	C
<i>Amblystegium varium</i>	AMBvar	1 4	0 0	10 88	12 0	8 1	0 0	0 0	68 7	73	5	S5	C
<i>Anomodon attenuatus</i>	ANOatt	0 0	0 0	0 0	0 0	99 100	0 0	0 0	1 0	87	2	S5	C
<i>Anomodon viticulosus</i>	ANOVit	0 0	0 0	0 0	0 0	100 100	0 0	0 0	0 0	1	1*	S4	cT
<i>Brachythecium acuminatum</i>	BRAacu	0.2 1	0.3 0	16 6	14 7	26 7	5 28	9 23	30 30	3234	8	S5	T
<i>Brachythecium plumosum</i>	BRApLu	0 0	0 0	0 0	0 0	100 100	0 0	0 0	0 0	227	1*	S5	C
<i>Brachythecium populeum</i>	BRApop	0.4 1	0 0	1 0	5 3	93 94	0 0	0.4 2	0.1 0	1008	6	S5	cT
<i>Brachythecium reflexum</i>	BRAreF	14 19	0 0	11 3	15 10	37 29	5 23	3 7	14 9	4540	8	S4/S5	cT
<i>Brachythecium salebrosum</i>	BRAsal	2 5	0 0	17 10	22 23	27 7	6 18	6 16	19 20	1482	7	S5	C
<i>Bryhnia graminicolor</i>	BRYGra	0 0	0 0	75 30	13 1	0 0	13 69	0 0	0 0	8	3	S3	T
<i>Bryhnia novae-angliae</i>	BRYNov	20 66	0 0	6 2	8 4	50 20	3 2	2 1	11 5	445	7	S5	C
<i>Bryohapllocladum microphyllum</i>	BRYmic	0.7 1	0 0	42 42	33 33	7 4	3 6	5 8	9 7	1424	7	S4	C

Species	Species code	Ground										Late log	Rock	Stump	Snag	Tree	total records	# of different microhabitats	Rarity/ S Rank	Floristic Affinity	
		Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV										
<i>Bryum caespitium</i>	BRYcae	0	0	0	0	100	100	0	0	0	0	0	0	0	0	0	2	1*	S5	C	
<i>Bryum pseudotriquetrum</i>	BRYpse	0	0	0	0	0	0	0	0	100	100	0	0	0	0	0	9	1*	S5	cB	
<i>Bryum sp.</i>	BRYsp	0.8	1	0	0	15	41	9	14	73	42	2	2	0	0	0	123	5			
<i>Callicladium haldanianum</i>	CALhal	3	5	2	2	38	18	28	33	12	5	7	19	4	11	7	7	3865	8	S5	cT
<i>Campyllum hispidulum</i>	CAMhis	16	17	2	27	32	24	17	6	15	5	4	16	4	3	11	2	4033	8	S4/S5	C
<i>Ceratodon purpureus</i>	CERpur	6	10	0	0	35	84	6	1	6	1	0	0	0	0	47	5	17	5	S5	C
<i>Dicranella heteromalla</i>	DICHet	0	0	0	0	0	0	0	0	80	98	0	0	0	0	20	2	5	2	S5	cB
<i>Dicranum flagellare</i>	DICfla	0	0	0	0	49	5	26	6	6	0	3	1	3	73	12	14	833	6	S5	C
<i>Dicranum fuscescens</i>	DICfus	0	0	0	0	25	3	26	24	37	45	6	4	2	8	6	16	778	6	S5	cB
<i>Dicranum montanum</i>	DICmon	0.1	0	0.1	34	29	4	23	5	24	15	10	10	2	9	12	23	1418	8	S5	B-T
<i>Dicranum ontariense</i>	DICont	0	0	0	0	0	0	0	0	100	100	0	0	0	0	0	0	1	1*	S4/S5	B-T
<i>Dicranum polysetum</i>	DICpol	0	0	0	0	31	6	45	85	24	9	0	0	0	0	0	0	71	3	S5	B-T
<i>Dicranum scoparium</i>	DICsco	0	0	0	0	0	0	0	0	100	100	0	0	0	0	0	0	11	1*	S5	cB
<i>Enodon seductrix</i>	ENTsed	0	0	0	0	14	0	0	0	0	0	0	0	0	0	86	100	7	2	S4	T
<i>Eurhynchium pulchellum</i>	EURpul	3	3	0	0	0	0	9	12	42	15	14	39	0	0	32	31	65	5	S5	cB
<i>Fissidens taxifolius</i>	FISStax	0	0	0	0	0	0	0	0	100	100	0	0	0	0	0	0	10	1*	S4	C

Species	Species code	Ground	Early log	Mid log	Late log	Rock	Stump	Snag	Tree	total records	# of different microhabitats	Rarity/ S Rank	Floristic Affinity									
		Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV Freq. IV																				
M	<i>Forstroemia nitans</i>	FORnit	0	0	0	0	1	0	20	2	3	1	13	85	4	3	60	9	209	6	S1	T
	<i>Grimmia rivulare</i>	GRI(riv)	0	0	0	0	0	0	100	100	0	0	0	0	0	0	0	0	3	1*	S5	C
	<i>Hedwigia ciliata</i>	HEDcil	0	0	0	0	0	0	0	0	100	100	0	0	0	0	0	0	533	1*	S5	cB-T
	<i>Homalia trichomanoides</i>	HOMtri	0	0	0	0	0	0	6	1	88	99	0	0	0	0	6	0	17	3	S5	cT
	<i>Homomallium adnatum</i>	HOMadn	0	0	0.7	37	3	6	0.7	1	85	42	0	0	0	0	10	15	137	5	S3	T
	<i>Hygrohypnum sp.</i>	HYGsp	7	31	0	0	6	1	4	1	64	21	5	1	13	46	0.9	0	107	7		
	<i>Hypnum cupressiforme</i>	HYPcup	1	1	1	28	41	19	19	14	14	3	7	13	3	5	14	17	2543	8	S3	C
	<i>Hypnum pratense</i>	HYPpra	0.2	0	0.5	0	88	75	9	10	0	0	0.2	0	2	16	0	0	558	6	S5	cB
	<i>Isopterygiopsis pulchella</i>	ISOpul	1	5	0	0	51	23	33	15	12	37	3	20	0	0	0.6	0	168	6	S3	cB
	<i>Leskea polycarpa</i>	LESpol	0	0	8	87	57	10	26	3	6	0	2	0	0	0	2	0	116	6	S4/S5	cB
	<i>Leskeella nervosa</i>	LESner	0.2	0	0	0	7	0	0.2	0	87	94	0	0	0.2	0	5	6	426	6	S5	C
	<i>Loeskeobryum brevirostre</i>	LOEbre	0	0	0	0	0	0	5	2	95	98	0	0	0	0	0	0	132	2	S1	T
	<i>Mnium marginatum</i>	MNImar	0	0	0	0	0	0	0	0	97	80	3	20	0	0	0	0	31	2	S5	cB
	<i>Mnium sp.</i>	MNIsp	0	0	0	0	18	2	12	9	60	15	8	74	0	0	2	1	60	5		
	<i>Mnium spinulosum</i>	MNIspi	0	0	0	0	33	0	0	0	67	100	0	0	0	0	0	0	18	2	S5	B-I
	<i>Mnium thomsonii</i>	MNItho	0	0	0	0	0	0	0	0	0	0	100	100	0	0	0	0	1	1*	S2	cB

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		Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV		Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV								
<i>Neckera pennata</i>	NECpen	0	0	0	0	0	0	0	0	0	89	92	0	0	1	0	10	8	91	3			S5	B-I				
<i>Oncophorus wahlenbergii</i>	ONCwh	0	0	0	0	75	55	24	45	0.6	1	0.2	0	0	0	0	0.2	0	520	5			S5	C				
<i>Orthotrichum obtusifolium</i>	ORTobt	0	0	21	86	23	8	8	3	0.8	0	0	0	0	14	2	34	1	644	6			S5	cB				
<i>Orthotrichum speciosum</i>	ORTspE	0	0	13	73	17	10	4	6	0.3	0	0.3	1	17	6	48	4	1852	7			S1	cB					
<i>Paraleucobryum longifolium</i>	PARlon	0.1	3	0.1	4	3	0	1	0	93	90	0	0	0.5	3	2	1	732	7			S5	C					
<i>Plagiomnium cuspidatum</i>	PLAcus	0.4	0	0.4	3	19	3	15	9	45	41	5	24	4	15	11	5	2193	8			S5	cB					
<i>Plagiomnium drummondii</i>	PLAdru	0.6	0	0	0	34	7	26	15	19	50	0.9	0	2	6	18	21	348	7			S4/S5	C					
<i>Plagiomnium medium</i>	PLamed	0	0	0	0	46	38	14	4	36	54	0	0	4	3	0	0	28	3			S5	cB					
<i>Plagiothecium denticulatum</i>	PLAden	0	0	0	0	0	0	0	0	100	100	0	0	0	0	0	0	5	1*			S5	cB					
<i>Plagiothecium laetum</i>	PLAlae	4	3	0	0	2	2	2	1	84	83	2	0	1	0	5	10	370	7			S5	B-I					
<i>Platydictya subtilis</i>	PLASub	0.2	1	6	0	14	6	11	14	30	25	3	7	9	22	27	26	495	8			S3	C					
<i>Platygyrium repens</i>	PLAre	0	0	2	58	31	16	14	9	35	3	3	3	5	7	11	4	1341	7			S5	C					
<i>Pleurozium schreberi</i>	PLEsch	2	1	0	0	28	13	35	46	32	35	1	1	0.2	0	2	3	841	7			S5	cB					
<i>Pohlia nutans</i>	POHnut	0	0	0	0	0	0	100	100	0	0	0	0	0	0	0	0	1	1*			S5	cB					
<i>Polytrichum commune</i>	POLcom	100	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32	1*			S5	C					
<i>Polytrichum juniperinum</i>	POLjun	0	0	0	0	0	0	0	0	100	100	0	0	0	0	0	0	1	1*			S5	C					

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		Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV	Freq. IV				
<i>Pseudoleskeella</i>													
<i>M. sibirica</i>	PSEsib	0 0	0 0	28 49	0 0	41 45	3 2	0 0	28 5	29	4	S1	
<i>Pseudoleskeella</i>													
<i>tectorum</i>	PSEtec	0 0	0 0	0 0	0 0	100 100	0 0	0 0	0 0	2	1*	S2	C
<i>Ptilium crista-</i>													
<i>castrensis</i>	PTIcri	0 0	0 0	46 28	31 58	21 14	1 0	0 0	0.5 0	216	5	S5	cB
<i>Pylaisiella</i>													
<i>polyantha</i>	PYLPol	0.7 0	2 11	6 4	3 3	4 0	3 6	17 34	64 42	2989	8	S5	C
<i>Rhizomnium</i>													
<i>punctatum</i>	RHIpun	0 0	0 0	100 100	0 0	0 0	0 0	0 0	0 0	2	1*	S5	C
<i>Rhodobryum</i>													
<i>ontariense</i>	RHOont	0 0	0 0	0 0	0 0	100 100	0 0	0 0	0 0	4	1*	S5	B-T
<i>Rhyidiadelphus</i>													
<i>triquetrus</i>	RHItri	28 10	0 0	0 0	39 4	33 86	0 0	0 0	0 0	18	3	S5	cB
<i>Sanionia</i>													
<i>uncinata</i>	SANunc	3 4	1 0	41 23	19 21	18 4	5 25	2 8	11 16	3019	8	S5	cB
<i>Schistidium</i>													
<i>apocarpum</i>	SCHapo	0 0	0 0	0.5 0	0 0	98 100	0 0	0 0	1 0	653	3	S5	C
<i>Stereocleus</i>													
<i>serrulatus</i>	STEser	27 46	0.9 4	20 9	17 10	17 11	4 8	3 8	11 4	5391	8	S5	C
<i>Tetraphis</i>													
<i>pellucida</i>	TETpel	0 0	0 0	75 66	6 5	7 16	0 0	3 2	9 11	89	5	S5	cB
<i>Thuidium</i>													
<i>delicatulum</i>	THUdel	0 0	0 0	14 2	0 0	86 98	0 0	0 0	0 0	42	2	S5	C
<i>Tortella</i>													
<i>tortuosa</i>	TORTor	0.3 0	0 0	0.5 0	1 0	98 100	0 0	0 0	0 0	366	4	S5	cB
<i>Weissia</i>													
<i>controversa</i>	WEIcon	0 0	0 0	100 100	0 0	0 0	0 0	0 0	0 0	15	1*	S4	C