# Influence of microhabitat on bryophyte diversity in Ontario mixedwood boreal forest

**Heather A. Cole, Steven G. Newmaster, F. Wayne Bell, Doug Pitt, and Al Stinson**

**Abstract:** As forest management intensifies, the conservation of forest biodiversity is a growing concern. Bryophytes are known to represent a considerable portion of plant diversity within northern forests. This is because bryophyte diversity is closely associated with microhabitat diversity. In this study, the influence of microhabitats on bryophyte diversity was investigated by comparing eight different boreal mixedwood microhabitats. The results indicate that bryophyte diversity (species richness, abundance, and evenness) is quite variable among microhabitats. The accumulation of species richness with microhabitat quantity within a forest stand also varies among microhabitats. $\beta$-diversity analyses indicate that the variety of microhabitats has considerable influence on community structure. Frequency analysis identified bryophytes that are restricted to or prefer particular microhabitats. Although all microhabitats are important to bryophyte diversity, decayed logs and rocks supported the greatest number of microhabitat-specific species, and rock microhabitats supported the largest total number of species. Recommendations for forest management, one of which emphasizes the need to recognize and manage the natural variety of microhabitats, such as downed woody material, found within the forests to conserve or restore bryophyte diversity are provided.

**Résumé :** À mesure que l'aménagement forestier s'intensifie, la conservation de la biodiversité forestière est de plus en plus préoccupante. On sait que les bryophytes représentent une portion considérable de la diversité végétale des forêts nordiques. Cela est dû au fait que la diversité des bryophytes est étroitement associée à la diversité des microhabitats. Dans cette étude, l'influence des microhabitats sur la diversité des bryophytes a été évaluée en comparant huit microhabitats différents dans la forêt boréale mixte. Nos résultats indiquent que la diversité des bryophytes (richesse, abondance et équitabilité) est plutôt variable entre les différents microhabitats. L'accumulation de la richesse en espèce en fonction de la quantité de microhabitats à l'intérieur d'un même peuplement varie aussi entre les microhabitats. L'analyse de la diversité bêta indique que la variété de microhabitats a une influence considérable sur la structure des communautés. Une analyse de fréquences a permis d'identifier les bryophytes qui préfèrent ou sont limités à certains microhabitats. Même si tous les microhabitats sont importants pour la biodiversité des bryophytes, les billes décomposées et les affleurements rocheux supportent le plus grand nombre d'espèces limitées à certains microhabitats et les affleurements rocheux supportent au total le plus grand nombre d'espèces. Une de nos recommandations pour l'aménagement forestier souligne la nécessité de reconnaître et d'aménager la variété naturelle de microhabitats qu'on retrouve en forêt, comme les débris ligneux au sol, de façon à conserver ou restaurer la diversité des bryophytes.

[Traduit par la Rédaction]

## Introduction

As the demand for forest resources continues to increase, efforts are being directed towards developing methods to increase forest yield and productivity, which in turn is prompting concern for the conservation of biodiversity. The potential elimination of native forest flora through these intensifying forestry operations is a growing issue in many developed countries (Wikström and Eriksson 2000). Research on the impacts of forest management on plant diversity has identified bryophytes as one of the most diverse forest groups and the group that is most vulnerable to forest silvicultural treatments (Newmaster and Bell 2002; Ross-Davis and Frego 2002).

Microhabitats are important for understanding bryophyte diversity patterns. Microhabitat has been claimed to be more important than mesohabitat (Vitt and Belland 1997) or stand for predicting bryophyte species richness at the ecosystem scale (Mills and Macdonald 2004). Recent research indicates that distribution and availability of microhabitats influence bryophyte diversity and community composition (Newmaster et al. 2005; Lõhmus et al. 2007). For over a century, habitat specificity has been documented for many bryophyte flora; however, quantitative evidence for habitat specificity is lacking. If some bryophyte species are microhabitat specific, then those critical microhabitats need to be managed accordingly (Økland et al. 2003).

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Forest management affects forest microhabitats and, consequently, bryophyte diversity. The consequences of intensive forest management are highly variable and range from increasing microhabitats and increasing bryophyte diversity (Newmaster et al. 2006) to removing microhabitats and decreasing bryophyte diversity (Newmaster et al. 2007). Forest management practices can also reduce habitat heterogeneity at local scales. These can disrupt the stand age and the distribution of microhabitats, which in turn negatively affects bryophyte community composition (Newmaster and Bell 2002; Roberts and Zhu 2002). Most of these studies are either based on a chronosequence of stands (Newmaster et al. 2003) or on short, (<20 years) post-treatment studies (Newmaster and Bell 2002; Newmaster et al. 2007). The long-term effects of forest management on bryophyte diversity are unknown.

Ideally, this study would predict the long-term effects of forest management practices on bryophyte diversity and identify treatments that might lead to localized plant extinctions. This would require an understanding of the relationship between microhabitat disturbance and the habitat requirements of particular species. Identifying the existence of habitat specificity is critical because species may be able to exist on other habitats, which act as refugia following a forest disturbance. An understanding of how bryophyte diversity relates to microhabitat specificity is the first step in developing models that implement silvicultural techniques that conserve bryophyte diversity.

The objective of this study is to address the claim of bryophyte microhabitat specificity and to examine $\alpha$- and $\beta$-diversity among different forest microhabitats. The effects of species $\alpha$-diversity (species richness, abundance, and evenness) on microhabitats as well as the differences in $\beta$-diversity (community) among microhabitats are investigated. More specifically, the following research questions are a focal point of this study: (*i*) Do bryophyte species accumulate in the same way on different microhabitats?; (*ii*) Is there variation in bryophyte $\alpha$-diversity among different microhabitats?; (*iii*) Is there variation in bryophyte $\beta$-diversity among different microhabitats?; and (*iv*) Are there bryophytes that prefer, or are restricted to, a particular 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. The plot network 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 (see OMNR 2007 for more details). The Thunder Bay installation is located 63 km northwest (48°48′ 4″N, 89°53′ 34″W) of the Thunder Bay, Ontario, airport. The site chosen for sampling is an 80-year-old boreal mixedwood forest with fine loam-clay soil dominated by trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), and balsam fir (*Abies balsamea* (L.) Mill.). The forest floor is dominated by trembling aspen and balsam fir litter.

### Experimental design

The installation set contains four blocks (10 ha each) that independent floristic analyses have shown to have similar plant diversity — species richness, abundance, and community composition. The blocks are an average of 2 km apart and an average of 3 km from the nearest paved road; all blocks are accessible by logging roads. In each 10 ha block, one experimental unit (100 m × 200 m) was randomly selected to be the "natural treatment," which implies that it remains a natural, mature forest. These experimental units (4 in total) each represent a typical forest stand with typical forest microhabitats that are evaluated with respect to the dynamics of bryophyte $\alpha$- and $\beta$-diversity. To sample each experimental unit, a, alpha-numeric 20 m × 20 m grid was established in each experimental unit and five coordinates were randomly chosen for study. A circular (5 m radius) plot was established at each co-ordinate, providing a total of 20 subsamples (five in each experimental unit). For this study, the term "microhabitat" is used to describe the eight different forest substrates being investigated; components of the environment upon which bryophytes grow, such as rocks and trees, are considered microhabitats. The term "microhabitat representative" refers to the physical microhabitat structure. For example, if a plot has six trees, there are six tree microhabitat representatives.

### Sampling

Sampling took place in July–August 2006. The microhabitat representatives in each plot were categorized into eight microhabitats, including 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 these decay stages based on previous research that identified decay stage as an important variable for explaining patterns of bryophyte community structure (Newmaster 2000; Ódor and van Hees 2004). The method of Chambers and Lee (1993) was used to assign logs to decay categories. This method uses the general structure of the logs for classification; a solid log with bark intact supported off the ground by its branches is called early decay, while late-decay logs have no bark, are no longer solid boles, and are flattened into the ground. For this study, Chambers and Lee decay categories one and two were defined as early decay, category three was defined as mid decay, and categories four and five were defined as late decay. Grouping the two early and two late decay categories is justified based on previous work that has shown these categories to have similar community structures (Newmaster 2000).

Ground was included as a microhabitat, as it is a substrate upon which bryophytes are found and, based on visual inspection, it was considered to be a contributing component of the bryophyte community. Criteria used to characterize each microhabitat are described in Table 1. All aboveground surfaces of logs, stumps, and rocks were sampled. Tree and snag representatives were sampled from the base to 1.5 m up the bole. Trees were not further categorized by species or height. For rock sampling, if a portion of the surface of a rock chosen for sampling was covered by debris (soil, coarse woody, or leaf litter) at a depth >5 cm, then that

**Table 1.** Criteria used to define and characterize the eight microhabitats investigated.

| Microhabitat | Min. height or length | Min. diameter or area | Additional criteria |
|---|---|---|---|
| Ground | na | na | Forest floor not occupied by other microhabitats |
| Early log | 1 m | 10 cm | — |
| Mid log | 1 m | 10 cm | — |
| Late log | 1 m | 10 cm | — |
| Rock | na | 500 $cm^2$ | Detached stone (not bedrock) |
| Stump | na | 10 cm (measured at top) | Standing dead woody debris <1.5 m tall |
| Snag | 1.5 m | 10 cm | Standing dead woody debris >1.5 m tall |
| Tree | na | 10 cm | Upright woody plants with a single bole |

**Note:** na, not applicable.

area was excluded from sampling. At each plot, the total number of eligible microhabitat representatives of each microhabitat was determined, and half of the eligibile microhabitat representatives were randomly chosen for sampling to ensure the same proportion of each available microhabitat in the forest was sampled. Ground within the 5 m radius plot was split into four equal quadrats, two of which were randomly chosen for sampling. As the presence of other microhabitats varied among plots, total ground sampled varied proportionately.

On each of the eight microhabitat representatives chosen for sampling, bryophyte species presence and abundance was determined using a grid composed of 10 cm × 10 cm squares. The abundance (surface area) of each species in each square was recorded ($cm^2$). 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 follows Anderson et al. (1990) for mosses and Stotler and Crandall-Stotler (1977) for hepatics. Vouchers of each species collected are deposited in the Ontario Agricultural College Herbarium, Biodiversity Institute of Ontario.

## Analyses

### *Species–area relationships on microhabitats*

To examine the manner in which species accumulate on microhabitat representatives, species–area curves were plotted for each microhabitat. Species–area curves were generated from the raw microhabitat data (10 cm × 10 cm squares) using the mean value derived from 100 random shufflings using SAS statistical software (SAS Statistical analysis systems, Version 8.02, SAS Institute Inc., Cary, North Carolina) and EstimateS software (Colwell 2005). Linear regression was used to generate the slope of the species–area curve of each microhabitat from the experimental units ($n$ = 4). The slope of the species–area curve represents how species accumulate with microhabitat area sampled and was compared among microhabitats using the slopes of the regression equations.

### *Species richness*

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

Species–area curves were plotted to explore the relationship between total species richness and total sampled area with reference to the number of microhabitat representatives sampled. The experimental units for each microhabitat were plotted in random order using all microhabitat representatives. Two methods were used to model the species accumulation curves from the Thunder Bay data. Coleman rarefaction (CR) (Coleman 1981) was used to approximate the species accumulation curves within the range of sampled data and Michaelis–Menton (MM) (Colwell and Coddington 1994) algorithms were used for extrapolation models; both were calculated using EstimateS software (Colwell 2005). CR estimates the number of species expected at a given level of sampling within the range of data available (Colwell et al. 2004). MM extrapolation uses randomized data to generate a mean species accumulation curve over the units of observation, then the MM function fits an asymptotic value to estimate total species number (Colwell and Coddington 1994). Species richness data from three other pre-existing boreal mixedwood NEBIE installation sets were plotted ($\alpha$) to assess the extrapolations from the Thunder Bay data and to provide a reference point for species richness in these types of stands. The three sites (Dryden (49°38′27″N, 92°46′22″W), Timmins (48°21′06″N, 81°18′09″W), and Kapuskasing (49°09′06″N, 82°27′58″W)) have similar forest ecosystems to the Thunder Bay installation. The extrapolations provide estimates for the number of microhabitat representatives that may support total species richness in the stands. Rank–abundance curves of forest tree species, distribution and type of coarse woody material, merchantable volume of timber, and the distribution of forest plant species were compared among these NEBIE installation sets, confirming that they are similar forest ecosystems (F.W. Bell, unpublished data).

### *Diversity indices*

Total species richness was recorded for each microhabitat representative sampled. To estimate species diversity on each microhabitat, the Shannon–Wiener diversity index was calculated (Krebs 1999). Evenness, the relative equitability of species within a community, was estimated using Pielou's evenness (Krebs 1999).

### *Statistical analyses*

The species–area regression coefficients of each microhabitat were compared using $t$-tests (Zar 1984); $t$-tests were chosen for their ability to analyze the raw regression data and to provide a direct test among the microhabitats. Degrees of freedom varied among comparisons and signifi-

cant differences for specific comparisons were adjusted for an overall error of 0.05. Species richness, Shannon–Wiener, and Pielou's evenness measures were compared among microhabitats. Means and standard errors were calculated using SAS statistical software. 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 test (Holm 1979) 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 significances reported.

### *β-diversity*

$\beta$-diversity was assessed using both a $\beta$-diversity measure and multivariate analyses of community composition. The Morisita–Horn index of similarity (Horn 1966) was calculated. This $\beta$-diversity measure helps identify which microhabitats have bryophyte communities that are more (or less) similar to each other.

### *Multivariate ordination analysis*

Multivariate analysis was used to explore patterns in community organization among all microhabitats studied. Principal component analysis (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)) of 189 microhabitat representatives and 105 species was used to explore variation in species and site scores. Patterns in community composition were identified on the ordination of microhabitat representatives in species space as either groupings or gradients along respective axes in the context of the specific microhabitats.

### *Microhabitat specificity*

The occurrence of each species on each microhabitat was examined to determine whether there were 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 observed in a sample square (10 cm × 10 cm) of a given microhabitat was recorded, to better describe how frequently any given species occurred on any particular microhabitat. Species with a frequency of 100% on one microhabitat are defined as microhabitat specific. Species with a frequency of 80%–99% on one microhabitat are defined here as having a strong preference for that microhabitat. The *Flora of Ontario* (Newmaster and Ragupathy 2005) provincial ranking was used to categorize species from S1 (very rare) to S5 (very common). Microhabitat specificities or preferences of species with S-rankings of S3 (common) or higher with fewer than ten total records were not reported. This was to avoid making conclusions about species that the sampling method did not sufficiently capture. Microhabitat specificities or preferences of species with a S1 (very rare) or S2 (rare) ranking were reported regardless of the total number of times a species was observed.

## Results

### Species–area relationships on microhabitats

Species accumulation within individual microhabitats is variable among the eight microhabitats compared. Species accumulation slope coefficients (SC) range from 0.85 on early logs to 6.36 on late logs. $R^2$ values range from 0.75 (early logs) to 0.98 (stumps), indicating that there is a strong relationship between cumulative species richness and total area sampled for all microhabitats sampled. The microhabitats with the smallest change in species accumulation are early logs (SC = 0.85) and ground (SC = 0.89). The slopes of both species–area curves are much less steep than the curves for the majority of the other microhabitats; both being less than half of the values on all other microhabitats. Snag and tree microhabitats show intermediate species accumulation (SC = 3.32–3.62). Rock, stump, mid log, and late log microhabitats have the greatest change in species accumulation (SC = 4.40–6.36) (Fig. 1).

### Species richness

Bryophyte species richness on the site totals 105 species; 73 mosses (M) and 32 liverworts (L). The local bryoflora is dominated by boreal species (58%) with some cosmopolitan species (29%) and few temperate (13%) species. Less than a third (29%) of the species have distributions limited to North America. Most (75%) of the species are classified as common (S4 and S5) with a considerable portion of uncommon (15% S3) and rare (13% S1 and S2). Total species richness on the microhabitats is as follows: ground 34 (28M and 6L), early log 20 (14M and 6L), mid log 74 (52M and 22L), late log 70 (50M and 20L), rock 82 (62M and 20L), stump 49 (36M and 13L), snag 42 (32M and 10L), and tree 58 (45M, 13L). Mean species richness differs among the different microhabitats (Table 2). Late log microhabitats were found to have significantly ($p < 0.05$) higher species richness than ground, early log, rock, stump, snag, and tree microhabitats. Mid log microhabitats were found to have significantly ($p < 0.05$) higher mean species richness (25.3) than ground (9.4), early log (6.7), and tree (14.9) microhabitats.

For all microhabitats, total species richness increased quickly within 8 ha of sampling. CR closely follows the field data for all microhabitats and provides a predictive species richness model for various quantities of microhabitat sampled within 8 ha of forest. The MM extrapolation curves provide a predictive species richness model for the number of species expected in sampling up to 24 ha of forest. Most of the extrapolations are accurate when compared with the actual species richness totals ($\alpha$) from other NEBIE sites (Fig. 2). Microhabitats with greater sample sizes resulted in more accurate estimated species richnesses for both the CR interpolation and MM extrapolation curves (Fig. 2).

### Diversity indices

There was no difference in $\alpha$-diversity among most microhabitats (Table 2). The Shannon–Wiener diversity index shows the ground microhabitat to be significantly less than all other microhabitats except early log. This index also shows early log microhabitats to be significantly different from mid and late log microhabitats. There was no signi-

**Fig. 1.** Species–area curves for the eight microhabitats investigated, showing regression curves with logarithmic equations of curve, $R^2$ values, number of representatives ($n$), and standard error (se). Regression curves are plotted to the mean number of units sampled on 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, and h $\neq$ abcde. Data points are back-transformed, with $R^2$ values demonstrating the fit to the transformed data.

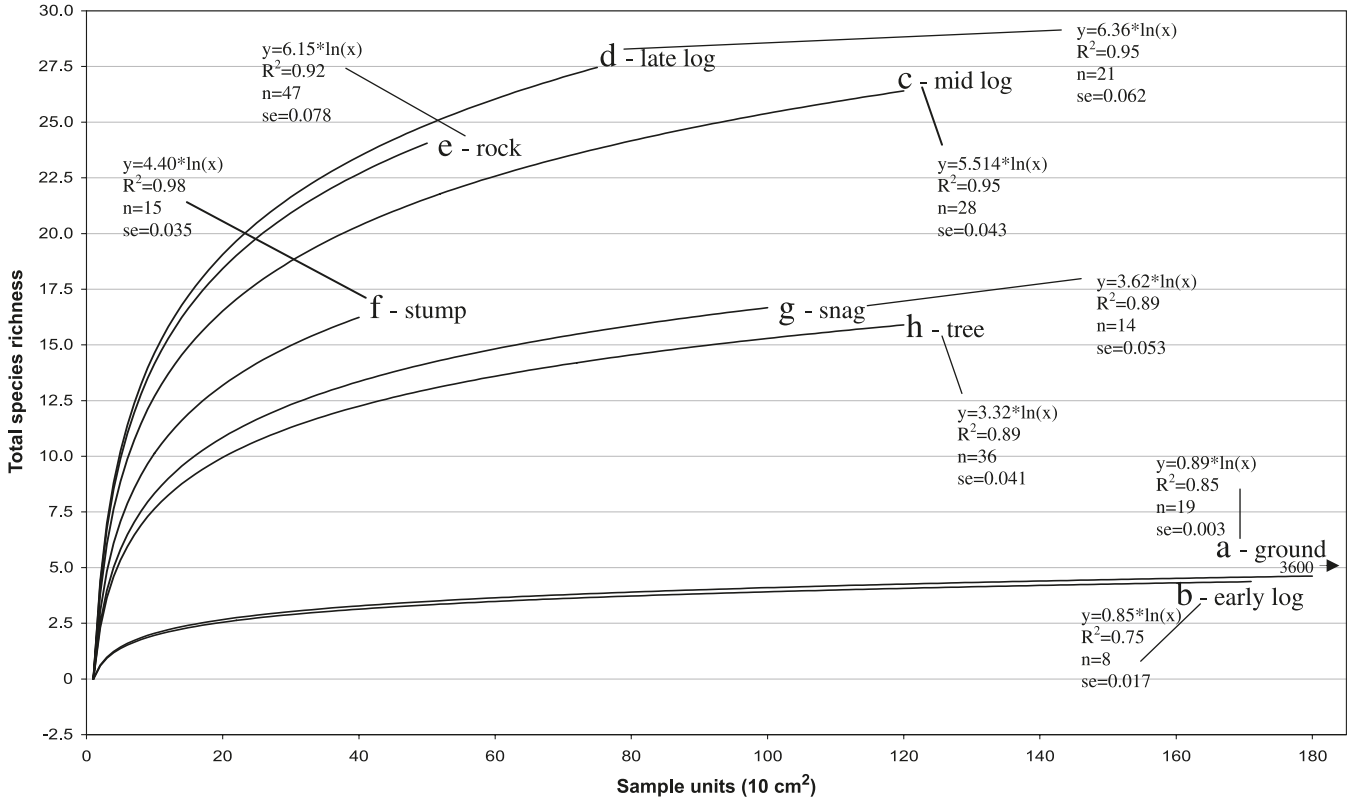



**Table 2.** Total species richness, mean ± 1 standard error, of $\alpha$-diversity measures for the eight microhabitats investigated.

| Microhabitat | Total species richness | Species richness | Shannon–Weiner diversity index | Pielou's evenness |
|---|---|---|---|---|
| Ground | 34 | 9.40±2.14 | 0.89±0.11† | 0.41±0.03† |
| Early log | 20† | 6.66±3.01† | 1.08±0.17 | 0.63±0.04* |
| Mid log | 74 | 25.31±2.01 | 1.81±0.10 | 0.59±0.02 |
| Late log | 70 | 27.55±2.15* | 1.88±0.11* | 0.58±0.03 |
| Rock | 82* | 17.80±1.93 | 1.71±0.09 | 0.61±0.02 |
| Stump | 49 | 17.02±2.33 | 1.60±0.12 | 0.56±0.03 |
| Snag | 42 | 16.69±2.42 | 1.59±0.13 | 0.58±0.03 |
| Tree | 58 | 14.93±1.93 | 1.49±0.09 | 0.56±0.02 |

*Highest value for each measure.
†Lowest value for each measure.

ficant differences ($p < 0.05$) among Shannon–Wiener diversity index values in any other microhabitat comparisons.

Pielou's evenness measure shows the ground microhabitat to be significantly less even than all other microhabitats including early logs. There were no significant differences ($p < 0.05$) among Pielou's evenness values in any other microhabitat comparisons.

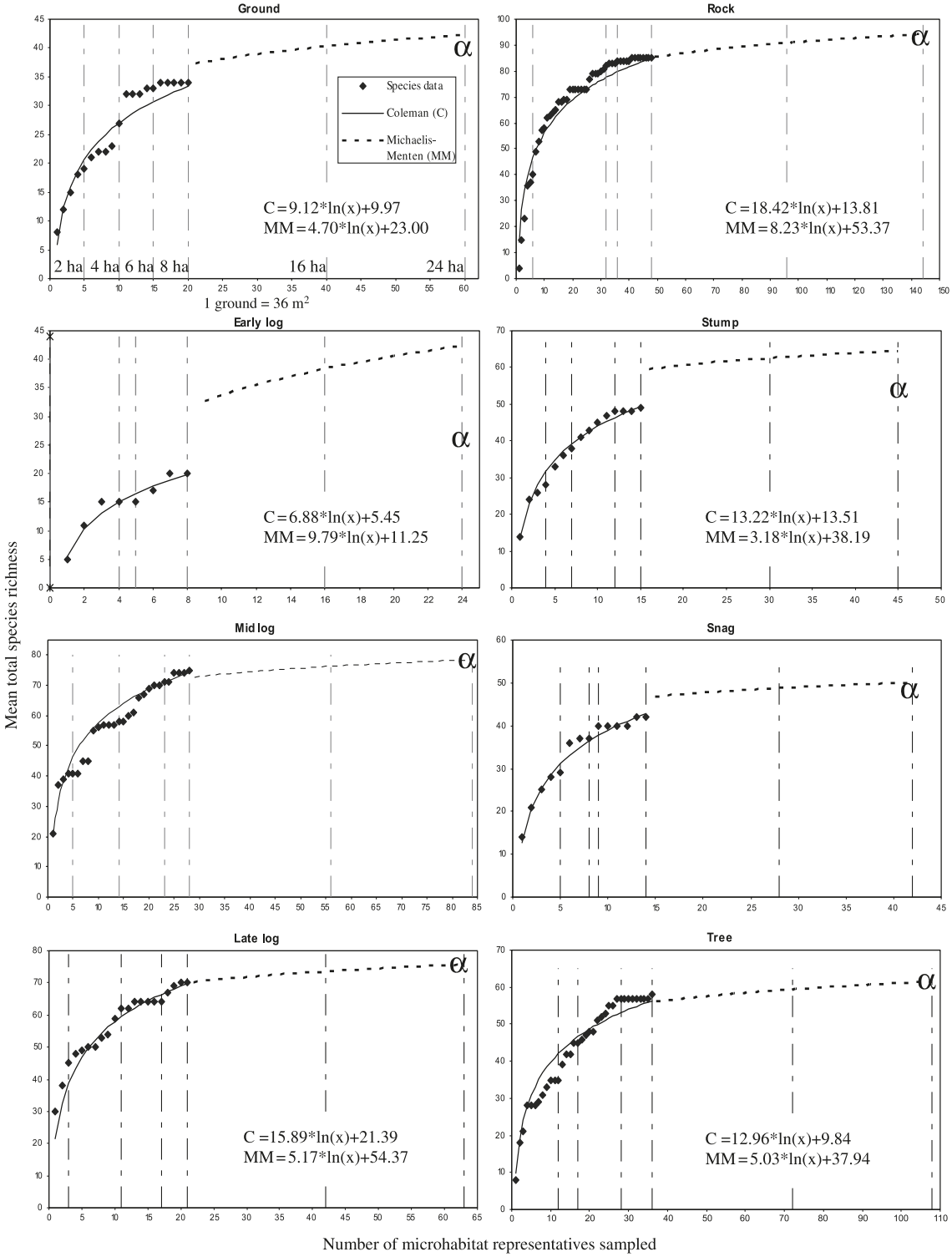
### $\beta$-diversity

The Morisita–Horn index uses species identity and relative abundance to estimate similarity among microhabitats. The highest Morisita–Horn value was found between tree and snag microhabitats, indicating high similarity. The lowest value was found between rock and early log microhabitats (Table 3).

### Ordination analysis

Patterns in community organization were apparent among microhabitats. DCA analyses of 189 microhabitat representatives and 105 species resulted in ordinations that display well-defined relationships between species and microhabitats on two ordination axes, as indicated by high Eigenvalues (axis 1 = 0.6911; axis 2 = 0.5045) and long gradients (axis 1 SD = 4.430; axis 2 SD = 3.277). Tree microhabitats were split into two groups positioned at the extreme ends of axis 1, indicating that the community structure of these two

**Fig. 2.** Estimates of total species accumulation with increasing microhabitat representative quantity and stand size for the eight microhabitats investigated. Michaelis–Menton (MM) extrapolated species richness estimates for each type of microhabitat are qualified with actual $\alpha$-diversity ($\alpha$ = total number of species) estimates at 24 ha using three other NEBIE sites (Dryden, Timmins, and Kapuskasing) with similar forest ecosystems.




groups is very different. Stump and snag microhabitats were distributed along axis 1, between the two groups of tree microhabitats. Mid-decay and late-decay log microhabitats were spread from the middle of the axis to the left side near the group of tree (balsam – white birch) microhabitats. Rock and ground microhabitats were separated along axis 2 (2 SDs). Ground microhabitats were grouped (1 SD, 2 outliers) at the bottom of the ordination; whereas, rock microhabitats were more variable (2 SD) along the rest of the axis (Fig. 3).

## Microhabitat specificity

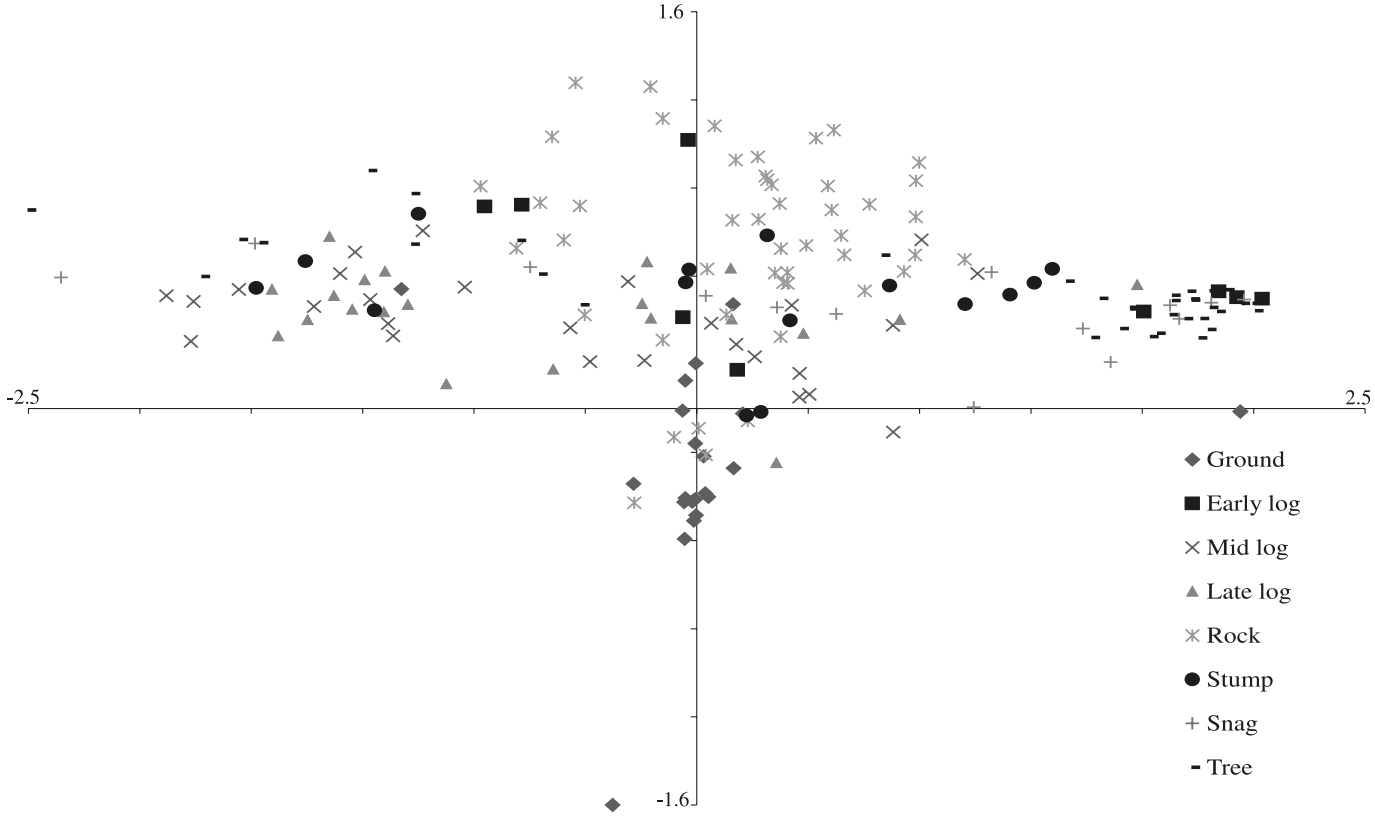
Some bryophytes observed on the site appear to have

**Table 3.** Comparison of Morisita–Horn index values among the eight microhabitats investigated.

| | 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† | 0.88* | 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* | — |

*Most similar microhabitats for each comparison (as read across each row).
†Least similar microhabitats for each comparison (as read across each row).

**Fig. 3.** Detrended correspondence analysis (DCA) microhabitat ordination of 105 species on 189 microhabitat representatives to explore relationships between species and microhabitats. Eigenvalues: axis 1 = 0.6911, axis 2 = 0.5045.




specific microhabitat requirements. One species was found only on ground microhabitats. There were no species with a strong preference (≥80% frequency) for ground microhabitat. There were no species found to occur exclusively on or have a preference for early log microhabitats. Two species were found to be specific to mid log microhabitats. Two additional species had a strong preference for mid log microhabitats. Three L species were found only on late log microhabitats. Rocks supported the highest numbers of specific species, with six species found exclusively on this microhabitat. Fourteen additional species showed a strong preference for rocks. One species was found only on stump microhabitats; however, it was only observed in one sampling grid. Owing to its S2 ranking (rare), it is included as having microhabitat specificity. There were no species that showed a strong preference for stumps. There were no species found to occur exclusively on or have a strong preference for snag microhabitats. One species was found to be specific to tree microhabitats (Table 4).

## Discussion

This research supports the claim that forest microhabitats influence the diversity of the local bryophyte community (Newmaster et al. 2003; Lõhmus et al. 2007). The results indicate that bryophytes species richness does not accumulate in the same manner on different microhabitats and that bryophyte diversity is variable among microhabitats. Additionally, this study identifies species that are specific to or have preferences for particular microhabitats within boreal mixedwood forests in northern Ontario.

Species diversity on microhabitats in the boreal forest is

**Table 4.** Bryophyte species found to be specific to or have a preference for a particular microhabitat.

| Microhabitat | Specific species | Species with a preference |
|---|---|---|
| Ground | *Polytrichum commune* M-S5 | — |
| Early log | — | *Leskea polycarpa* M, S4–5 |
| | — | *Orthotrichum speciosum* M, S1 |
| Mid log | cf. *Lophozia heterocolpos* var. 3 L | *Nowellia curvifolia* L-S4 |
| | *Weissia controversa* M, S5 | *Hypnum pratense* M-S5 |
| Late log | cf. *Lophozia badensis* var. 2 L | — |
| | *Lophozia* sp. 2 L | — |
| | *Lophozia* sp. 3 L | — |
| Rock | *Brachythecium plumosum* M-S5 | cf. *Lophozia capitata* var. 1 L |
| | *Dicranum scoparium* M-S5 | *Anomodon attenuatus* M-S5 |
| | *Fissidens taxifolius* M-S4 | *Brachythecium populeum* M-S5 |
| | *Hedwigia ciliata* M-S5 | *Homalia trichomanoides* M-S5 |
| | *Barbilophozia barbata* L-S3 | *Homomallium adnatum* M-S3 |
| | *Lophozia capitata* L-S3 | *Leskeella nervosa* M-S5 |
| | — | *Loeskeobryum brevirostre* M-S1 |
| | — | *Mnium marginatum* M-S5 |
| | — | *Neckara pennata* M-S5 |
| | — | *Paraleucobryum longifolium* M-S5 |
| | — | *Plagiothecium laetum* M-S5 |
| | — | *Schistidium apocarpum* M-S5 |
| | — | *Thuidium delicatulum* M-S5 |
| | — | *Tortella tortuosa* M-S5 |
| Stump | *Mnium thomsonii* M-S2* | — |
| Snag | — | — |
| Tree | *Bazzania trilobata* L-S4 | — |

**Note:** M, moss class; L, liverwort class; S, rarity ranking.
*One record only.

not uniform; bryophyte species accumulation, richness, and diversity each vary among the eight microhabitats investigated. Despite the within-microhabitat variation in this study, differences among microhabitats were identifiable. A possible reason that late log microhabitats showed the steepest species–area curve is that they are the most variable and distinctive microhabitat, providing a range of environmental conditions accommodating a wide range of bryophyte species preferences. Research conducted in Sweden indicated that the available area of late decay logs was strongly correlated with the presence of rare, red-listed species (Hylander and Dynesius 2006). In support of previous work (Frego and Carleton 1995), it appears that patchy bryophyte occurrence and low species richness are common to both ground and early log microhabitats, resulting in both microhabitats having less steep species–area curves.

### $\alpha$-diversity

One of the restoration goals of forest management is to provide habitat that influences species diversity. How much habitat to leave or to provide is a critical piece of information within forest silvicultural guides (OMNR 2001). As concluded in Kruys and Jonsson's (1999) study of fine and coarse woody material, some microhabitats must be available in larger volumes than others to accommodate total bryophyte species richness. This study provides the first quantitative area estimates for different microhabitats to support mean and total bryophyte species richness. Analysis of species richness must consider both mean and total species richnesses, as they can provide different and even conflicting information. For example, this study showed that mean and total species richness indicators have conflicting results of which microhabitat supports the greatest species richness. Mean species richness on rock was third highest of the microhabitats examined; however, total species richness was by far the highest with 82 species (Table 2). Similarly, total species richness on trees was higher than on stumps and snag microhabitats; whereas, stump and snag microhabitats both had higher mean species richnesses than tree microhabitats. Mills and Macdonald (2004) also found similar mean species richness patterns on the microhabitats they investigated. This has important management implications, as it demonstrates that different microhabitats require different consideration. With high total species richness but lower mean species richness, any given rock microhabitat only supports a subset of the bryophyte community found on rocks; whereas on log microhabitats, high mean species richness but low total species richness indicates that a given log is likely to host most of the bryophyte community found on log microhabitats. Mean species richness values are useful for understanding the amount of local disturbance local of diversity within stands; total diversity is necessary for stand-level management and conservation.

### $\beta$-diversity

Some microhabitats appeared to have very similar bryophyte communities (trees and snags) to each other, whereas others appeared very dissimilar (rocks and early logs). Other research has compared $\beta$-diversity within microhabitats (Pharo and Beattie 2002; Mills and Macdonald 2004). This

work identified tree base microhabitats as having the highest differences (most variable and (or) dissimilar) and logs as having the lowest. This helps quantify the aforementioned variability within microhabitats, but does not address community differences among microhabitats.

DCA community analysis indicates that there are differences among the microhabitats investigated. The tree microhabitat is split at opposite ends of the axis 1 (Fig. 3). Field notes, by providing identification for some of the trees sampled, help illustrate a pattern. All the trees that the notes identified as trembling aspen occurred on the right side of the ordination, while trees identified as balsam fir and white birch occurred on the left. This separation could not be incorporated into the analyses, as species information was not available for all the trees sampled. Schmitt and Slack (1990) observed similar species specific host preferences in their study of epiphytic bryophytes and lichens. The presence of deciduous trees (excluding birch) has also been shown to be positively correlated with bryophyte diversity (Frisvoll and Prestø 1997). The DCA results from this study indicated a large differentiation in bryophyte communities along axis 2 of the ordination between ground and rock microhabitats. This finding supports results observed in Portuguese evergreen forests, in which ordinations also differentiated among rock, soil, and two different tree microhabitats (Gabriel and Bates 2005). The affinities of bryophytes to a particular rock or ground microhabitat are possibly due to the particular environment that a given microhabitat provides; studies have shown that pH and moisture influence bryophyte communities (Söderström 1988; Hylander and Dynesius 2006).

### Microhabitat specificity

This study supports the claim that some species of bryophytes are substrate specific. Almost half of the species in this study were found on three or fewer microhabitats: 18% were found on one microhabitat, 9% were found on two, and 14% were found on three. Less than 15% were found on all eight microhabitats. Of the 60 species that occurred on more than one microhabitat, 14 showed a strong preference (frequency ≥80%) for one microhabitat. These results suggest that some, but not all, bryophyte species are specific to a particular microhabitat. They also show that some species have an identifiable preference for one microhabitat over another. In the case of microhabitat specific species, the microhabitats on which they are found are possibly providing an environment that the species cannot either find or access (disperse to) on other microhabitats. In a study in Tasmanian forests, Turner and Pharo (2005) also found 18% of bryophyte species investigated to have a significant association with a particular substrate. For species that show a preference for a particular microhabitat, it is thought that the environments on other microhabitats are acceptable, but growth is 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 species of tree type but more showing preferences for one species over another. These methods provide quantitative measures of microhabitat specificity by individual species. They also help identify species groups that share a preference for the same microhabitat.

### Recommendations

This research furthered the knowledge and understanding of bryophyte communities in Ontario mixedwood boreal forests by quantifying the relationship between microhabitats and bryophyte species diversity. The results strongly suggest that to conserve bryophyte diversity, forest managers need to be aware of species specificity related to microhabitats and use harvesting and silvicultural practices that will maintain a variety of microhabitats across a landscape (Fig. 2). The following recommendations for forest managers are provided based on this research and previous published studies:

1. Microhabitat retention quantity estimates: that the microhabitat retention models from this study (interpolation) be used within boreal mixedwood stands for estimating the number of microhabitats needed for bryophyte conservation within 2–8 ha cutblocks.
2. Microhabitat spatial requirements: that forest management incorporate leaving representatives of all forest microhabitats intact during harvest operations. This includes remnant microhabitats left scattered throughout the cut (the quantities calculated as in recommendation 1) and also left together in unharvested patches that contain as many different microhabitats as possible. 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 throughout the harvest areas.

Further research is needed to develop microhabitat retention models (interpolation) for other forest ecosystems and to ascertain patch size and distances between patches based on dispersal limitations of bryophytes.

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