

# Bryophyte (moss and liverwort) conservation under remnant canopy in managed forests

Nicole J. Fenton<sup>1</sup>, Katherine A. Frego<sup>\*</sup>

*Department of Biology, University of New Brunswick, P.O. Box 5050, Saint John, NB, Canada E2L 4L5*

Received 5 February 2004

## Abstract

Management of forest for timber values presents potential threats for forest floor bryophytes, as localized disturbances are applied across landscapes. Dispersal limitation may exacerbate local extirpation, by preventing recolonization within a cut-block rotation period. Populations of forest floor bryophytes that persist under those patches of tree canopy remaining after clear-cutting could reduce dispersal distances and thereby contribute to conservation of species across the landscape. We examined bryophyte guilds (liverworts, forest-habitat mosses and colonist–pioneer mosses) and community composition in relation to habitat quality (microclimate and substrate) in five treatment classes in New Brunswick Acadian forest, 4 years after harvest. Four potential refugium classes with intact substrate were examined: three were characterized by remnant canopy height, one was treeless. These were compared to clear-cut areas with substrate disturbance. Microclimate (temperature, total daily photosynthetically active radiation and vapour pressure deficit) differed significantly between areas with and without remnant canopy, but differed little among refugium classes. This suggests that any remnant canopy moderates microhabitat relative to treeless areas. Liverworts and forest-habitat mosses were more frequent under remnant canopy than in open and clear-cut areas, with 25 species present only under remnant canopy. Environmental variation explained approximately 24% of bryophyte pattern, highlighting the potential influence of the pre-harvest community, which we could not document. In the absence of substrate disturbance, patches of remnant canopy provide potential refugia for some forest-habitat bryophytes. Characteristics of effective refugia (size and shape) should be determined by assessments of their impacts on: (i) change in bryophyte communities in refugia relative to natural dynamics and (ii) recolonization of adjacent areas.

© 2004 Elsevier Ltd. All rights reserved.

**Keywords:** Bryophytes; Forest management; Refugia; Microclimate; Disturbance

## 1. Introduction

Replacement of natural disturbance regimes by disturbance regimes created by forest management for commercial timber values represents a potential threat to forest organisms. Organisms respond to habitat alter-

ation at local and landscape levels, and small organisms such as forest floor bryophytes (mosses and liverworts) may be particularly vulnerable to local extirpation (Frisvoll and Prestø, 1997; Gustafsson and Hallingbäck, 1988). Local reduction in bryophyte diversity (Fenton et al., 2003; Ross-Davis and Frego, 2002) after forest management treatments such as clear cutting may result from: (i) altered temperature and humidity regimes (Renhorn et al., 1997; Saunders et al., 1991) where fluctuations exceed the tolerance limits of some species (Söderström, 1988; Busby et al., 1978), or (ii) reduction in quantity or quality (especially humidity) of substrates

<sup>\*</sup> Corresponding author. Tel.: +1 506 648 5566; fax: +1 506 648 5811.

E-mail address: [frego@unbsj.ca](mailto:frego@unbsj.ca) (K.A. Frego).

<sup>1</sup> Present address: URDFAT UQAT-UQAM, Université du Québec en Abitibi-Témiscamingue, 445 Boul. de l'Université, Rouyn-Noranda, Que., Canada J9X 1C5.

such as rotting wood that are required by some species (Rambo and Muir, 1998; Frisvoll and Prestø, 1997; Le-sica et al., 1991).

Loss of species immediately after harvest may be exacerbated by the role of recruitment events in structuring many bryophyte communities (Haig et al., 2000; Kimmerer and Driscoll, 2000; Frego, 1996). These recruitment events may be rare in undisturbed forests, and are the result of the interaction between meta-population dynamics of individual species (Söderström and Herben, 1997) and chance events of disturbance that create free space favourable for colonization (Hurt and Pacala, 1995). Metapopulation dynamics are dependant on propagule dispersal and establishment, which is poorly understood for bryophytes. However, the apparent vulnerability of early lifestages (i.e., spores and protonemata), and low germination rates (Miles and Longton, 1990), are likely to slow or prevent recolonization of extirpated species if rotation times of cut blocks are short (Ross-Davis and Frego, 2004; Söderström et al., 1992; Herben et al., 1991; Söderström, 1988; Söderström, 1987). The result may be an extinction debt (sensu Tilman et al., 1994), as the most sensitive species are lost and do not return.

The most effective way to promote bryophyte survival across a managed landscape may be to conserve populations within harvested stands, thus minimizing dispersal distances to, and recolonization times of, harvested areas. Patches of retained canopy that escape substrate disturbance constitute a potential type of refugium. In the context of a variety of harvest operations, including selection, shelterwood and partial harvests, as well as variable retention, stands of mature merchantable trees are removed. The resulting mosaic of remnant canopy varies in crown closure, height and species. The remnant patches are interspersed with more or less discrete paths of harvest machinery (e.g., feller-bunchers and skidders) in which all canopy is removed or crushed, and the substrate is disrupted by scouring, crushing and/or compression. Using definitions modified from White and Pickett (1985), these trails receive direct disturbance, where plants are lethally damaged or removed by physical impact, whereas remnant patches receive indirect disturbance, i.e., environmental change related to canopy removal (increased temperature and incident photosynthetically active radiation (PAR), decreased humidity; Nyland, 1996) but negligible physical impact. It is not surprising that all bryophyte vegetation is removed on directly disturbed areas, however, we have documented survival of much of the bryophyte community in parts of the cutover that received only indirect disturbance (Fenton et al., 2003). Many other species found in mature closed-canopy forest persist in residual forest patches in Maine, including birds (Hagan and Grove, 1999), ground beetles (Jennings et al., 1986), vascular plants and lichens (Whitman and Hagan, 1999).

Do patches of remnant canopy between machinery trails have the potential to act as refugia for forest floor bryophytes within a clear-cut? What characteristics define conservation potential of remnant canopy patches? In order to function as refugia, such areas: (i) must not experience the extreme habitat changes associated with clear-cuts and (ii) must contain, and preserve, forest floor bryophyte species at risk. Our objectives were therefore:

1. to compare bryophyte communities in remnant patches to those in adjacent directly disturbed areas of the cutover,
2. to compare bryophyte communities among remnant patches of different characteristics and
3. to relate differences in these communities to environmental features of the patch types.

## 2. Methods

### 2.1. Study site

This study took place within the Hayward Brook Watershed, New Brunswick (45°52'N, 65°11'W), as part of a monitoring study from 1995-present, where localized impacts of forest harvest are well-documented (Fenton et al., 2003; Roberts and Zhu, 2002). The site is found in the Continental Lowlands Ecoregion, Anagance Ridge Ecodistrict (Department of Natural Resources and Energy, 1997). Daily mean temperatures range from −13.9 to 18.5 °C. Average annual precipitation is 1228 mm, falling mostly in late autumn and early spring. Approximately 30% of total annual precipitation falls as snow, which may exceed 300 cm (Environment Canada, 2003).

The Acadian forest region is characterized by *Picea rubens* (red spruce) along with species of the boreal and deciduous forests (e.g., *Abies balsamea*, balsam fir, and *Acer saccharum*, sugar maple, respectively; Rowe, 1972). Historically, the region experienced both stand-replacing (fire, widespread outbreaks of spruce budworm, *Choristoneura fumiferana*) and gap-replacing (lightning or isolated spruce budworm) disturbances, depending on stand type (Woodley and Forbes, 1997). The stands of interest were most likely initiated by a fire between 1900 and 1920 (Methven and Kendrick, 1995).

Stands used in this study were dominated by *Abies balsamea* and *Picea* spp. before they were harvested in fall 1995 by the landowner, J.D. Irving Ltd, according to their operational plan at that time. While some portions of the watershed were scarified and planted, a variable-retention approach was applied to the study area, i.e., advanced regeneration (young trees of merchantable species), non-merchantable trees (any age and low mar-

Table 1

Refugium class defined by substrate and canopy characteristics, corresponding to degrees of indirect and direct disturbance

Refugium class	Substrate disturbance	Tree species	# patches	# quadrats	Mean area (m <sup>2</sup> )	tree density (trees m <sup>-2</sup> )	Basal area (cm <sup>2</sup> m <sup>-2</sup> )
<i>Indirect disturbance</i>							
Tall	None	<i>Picea</i> spp. (42%) <i>Abies balsamea</i> (45%) trees > 5 m in height	7	71	37.49b ± 8.47	1.69a ± 0.30	42.92 c ± 4.05
Medium	None	<i>Abies balsamea</i> (66%) trees 1.5–5 m in height	8	57	14.60a ± 2.56	2.66a ± 0.65	30.93b ± 2.36
Low	None	<i>Abies balsamea</i> (75%) trees < 1.5 m in height	6	43	10.20a ± 4.00	3.79a ± 1.42	8.45a ± 1.62
Open	None	None	9	62	9.01a ± 1.35	NA	NA
<i>Direct disturbance</i>							
Machinery track	Compressed, disrupted, or slash	None or <i>Populus</i> spp. saplings (>4 years)	22	120	NA	NA	

Patches were sample units of at least 25 m<sup>2</sup>, sampled using a transect of contiguous 0.25 m<sup>2</sup> quadrats.

Means followed by the same letter in the same column are not significantly different.

Letters also indicate rank a &lt; b &lt; c.

ket value), wildlife trees (nest habitat for cavity-nesting birds) and seed trees (large individuals of *Pinus* spp.) were left in strips between tracks of machinery. Patches of remnant canopy between machinery tracks experienced indirect disturbance; four visually distinct refugium classes (Table 1) were assigned, based on amount of canopy removed and height of the tallest tree canopy remaining. A fifth class, henceforth termed machinery tracks, received direct disturbance, and was expected to have no refugium potential, while the four categories of remnant canopy were predicted to offer different degrees of protection with tree height and density. For ease, the refugium classes will be called open (no trees), low (trees < 1.5 m in height), medium (trees 1.5–5 m) and tall (trees > 5 m).

## 2.2. Sampling design

In 1999, 11 transects were placed through randomly chosen 50 m sections of remnant canopy patches according to the following criteria: (i) pre-harvest canopy dominated by coniferous trees, (ii) no evidence of anthropogenic substrate disturbance, and (iii) ≥ 5 m of each of two refugium classes represented per transect. Transects were also chosen to balance replicates of patch types, and to represent the range of vegetation variability previously described for the area (Fenton et al., 2003). Transects ranged from 13 to 20 m long, and 67 to 87 masl in elevation.

## 2.3. Data collection

Bryophyte and environmental data were collected in summers, 1999 and 2000. Vegetation was sampled using contiguous 0.5 × 0.5 m quadrats from one machinery track through remnant canopy to the next track. Percent cover and substrate were recorded for each bryophyte

species, including those on slash to 1 m above the ground surface and on trunks to 0.5 m. In each quadrat, % covers of available substrates (not colonized by bryophytes) were also recorded. Vouchers of bryophytes remain in the herbarium at the University of New Brunswick, Saint John. Taxonomy follows Ireland (1982) and Crum and Anderson (1981) for the mosses and Schuster (1969, 1974, 1980) for the liverworts.

Bryophyte species were assigned to one of the three guilds: liverworts, colonist–pioneer mosses and forest-habitat mosses. Liverworts are believed to be sensitive to changes associated with forest harvest (Moen and Jonsson, 2003; Frisvoll and Prestø, 1997; Söderström, 1988). Colonists sensu stricto and pioneers (During, 1992) have small spore sizes (<20 µm), colonize disturbed habitats and are uncommon in undisturbed forests (Jonsson and Esseen, 1998; Rydgren et al., 1998; Sims, 1996). Forest-habitat mosses are typically found in interior forests, on substrates such as trunks, woody debris and humus. This category also includes species (e.g., *Brachythecium rutabulum*) that are found in many habitats but unlike the colonists and pioneers, are not specifically associated with soil disturbance.

Data-loggers recorded temperature, relative humidity and PAR using probes 207, HMP45C, and L190SB, respectively (Campbell Scientific, Logan, UT). Temperature and relative humidity probes were shielded from direct sunlight and all probes were installed 10–15 cm above the forest floor. Incident precipitation was recorded in millilitres. Data were collected June–September 1999 and April–September 2000, with some data loss in 1999 when rodents damaged probe wires.

One set of probes was permanently located in a treeless area of the clear-cut, where it functioned as the control for seasonal and diurnal fluctuations. Two pairs of two probes each were rotated through four replicates of each refugium class at weekly intervals to capture

spatial and seasonal variability. Temperature, relative humidity and PAR density ( $\mu\text{mol s}^{-1} \text{m}^{-2}$ ; a measure of photon density) were recorded as hourly averages, as well as daily maxima and minima. In 2000, PAR was also recorded as daily totals ( $\mu\text{mol m}^{-2} \text{day}^{-1}$ ).

#### 2.4. Analysis

Species' frequencies among refugium classes were examined using  $\chi^2$  analysis ( $\alpha = 0.05$  in all tests). The expected frequency for an individual species in each refugium class was determined as the total number of the species' occurrences in all classes, as a proportion of the total number of quadrats in that refugium class.

Comparisons of individual species abundances (% cover) among refugium classes were limited to quadrats in which the species were present. The non-parametric Kruskal–Wallis test was chosen to accommodate the resulting unequal sample sizes among treatments.

In order to compare the frequencies of species too infrequent to be assessed (<10 occurrences) individually, their pooled occurrences were compared among guilds and classes. Presence of these species in a given guild was summed overall and for each class. Expected values were calculated by multiplying the total number of occurrences of that guild across all classes by the proportion of quadrats each class represented. The total number of occurrences per class was then compared to expected values by  $\chi^2$ .

Four community indices were calculated for each quadrat using PC-Ord (McCune and Mefford, 1999): total bryophyte cover, richness, evenness and Simpson's Diversity Index, which emphasizes dominant species rather than rare species (Krebs, 1989). ANOVA and Tukey's test were used to compare indices among refugium classes; Kruskal–Wallis test was used for those with non-homogeneous variances. Total bryophyte cover was log-transformed before analysis.

Detrended Correspondence Analysis (DCA) with no downweighting of rare species was used to explore species and quadrat patterns (CANOCO; ter Braak and Šmilauer, 1998). Quadrats with <5 species, and 20 quadrats that contained only the five most common species (thus creating a "tongue", sensu Økland, 1990), were passively inserted into the pattern.

Relative humidity was converted to vapour pressure deficit (VPD in hPa) by the following formula:

$$\text{VPD} = (6.1078) \{ \exp[17.269T / (237.3 + T)] \} (1 - \text{RH}), \quad (1)$$

where  $T$  is temperature in Celsius and RH is relative humidity as a decimal (modified from Tanner, 1972).

Mean, maximum and minimum values of precipitation, total daily PAR, temperature and VPD were calculated for each class. Because both frequency and

duration of extreme values of PAR density, temperature and VPD may be more biologically important than mean values, daily durations (in hours) of extreme values were also calculated. In the absence of known ranges of tolerance for these species, readings were classified as extreme if they exceeded the median value of all readings:  $>100 \mu\text{mol s}^{-1} \text{m}^{-2}$  for PAR density,  $>20^\circ \text{C}$  for temperature and  $>10 \text{ hPa}$  for VPD. One-way ANOVA and Tukey's test were used to compare mean values and mean durations of extremes of total daily PAR, PAR density, temperature and VPD among refugium classes. Frequency distributions for temperature and total daily PAR were plotted in five pentile groups for all refugium classes over the sampling season.

Environmental variables were related to the bryophyte pattern using partial Canonical Correspondence Analysis (pCCA) (CANOCO, ter Braak and Šmilauer, 1998). A subset of uncorrelated environmental variables was chosen by Forward Selection procedure applied to each of four sets of variables separately, using the default settings of CANOCO and Monte Carlo test to establish probability of significance for each variable. Seventeen variables were selected: (i) substrates: humus, stump, rock, needle, trunk, scat, fine and coarse woody debris, and leaves; (ii) refugium characteristics: mean tree circumference, size of patch, dominant tree species (balsam-fir or spruce), total number of trees and tree density; (iii) microclimate: mean precipitation, mean temperature, and maximum temperature and (iv) canopy: total herbaceous cover. Contributions of categories and their interactions to bryophyte community variation were approximated as a proportion of the sum of Canonical Eigenvalues.

### 3. Results

#### 3.1. Comparison of bryophyte communities

Overall 93 species, comprising 68 mosses and 25 liverworts, were found in 363 quadrats. Twenty-five species (14 mosses and 11 liverworts) were found only in refugium classes (Appendix A). Nineteen species, including seven liverworts, were found only in treed refugium classes, including four rare liverwort species for the region (Ireland, 1982; Schuster, 1969, 1974, 1980): *Anastrophyllum hellerianum*, *Lophozia bicrenata*, *Lophozia capitata* and *Scapania apiculata*.

At the patch scale, tall and medium refugium classes displayed the highest richness (57 and 55 species, respectively), with 66 species in tracks. At the quadrat scale, total bryophyte cover, richness, evenness, and Simpson's diversity were consistently higher in medium and low classes than on tracks, while tall and open classes were intermediate (Fig. 1).

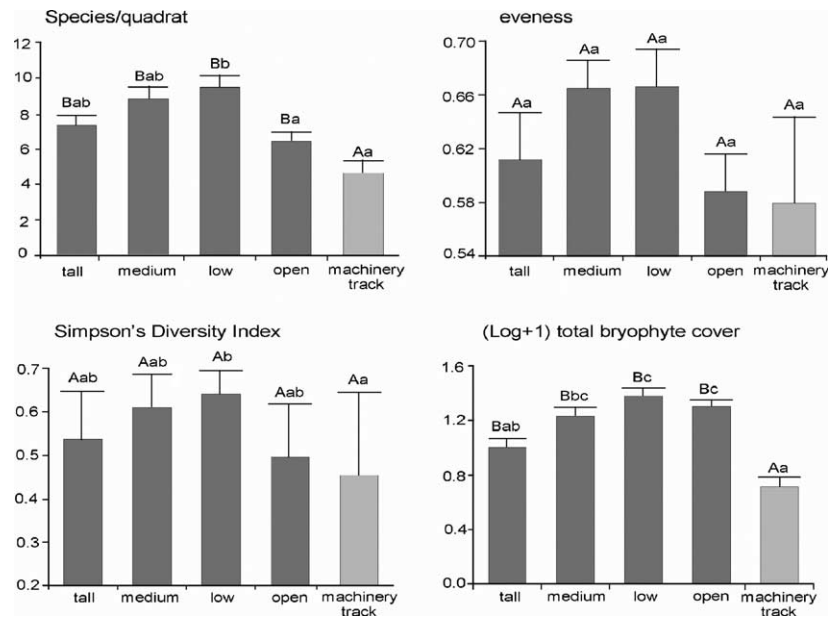


Fig. 1. Community indices by refugium class. Bars are means with standard errors. Different upper case letters indicate significant differences between all refugium classes (tall, medium, low and open) vs. machinery track; different lower case letters indicate significant differences among all classes. Letters also indicate rank of the mean ( $a < b < c$ ).

Table 2

Number of frequent species (>20 occurrences) of 3 species guilds (liverworts, forest-habitat mosses and colonist-pioneer mosses) differing significantly (tested with  $\chi^2$ ) in frequency (# of quadrats) and abundance (% cover when present) among refugium classes

Species	Guild		
	Liverworts	Forest-habitat mosses	Colonist-pioneer mosses <sup>a</sup>
Total	6	17	6
With differences among classes in:			
Frequency	6 [100%]	10 [59%]	3 [50%]
Abundance	2 [33%]	1 [5.9%]	4 [67%]

% of total displaying differences are in square brackets.

<sup>a</sup> Includes *Polytrichum commune* and *Polytrichum juniperinum* that are not strictly pioneer species in terms of life-strategy, but colonize machinery tracks (Fenton pers. obs.).

All frequent (in >20 quadrats) liverworts and  $\geq 50\%$  of frequent forest-habitat mosses and colonist-pioneers showed significant differences in frequency among refugium classes (Table 2). A far smaller proportion of liverworts and forest-habitat mosses showed significant differences in abundance, however abundances of two-thirds of the colonist-pioneers differed with refugium class.

Although infrequent species may be of greater concern because they are inherently rare, low numbers preclude statistical inference. Infrequent (<10 occurrences) liverworts and forest-habitat mosses showed significantly higher than expected richness in treed vs. treeless quadrats (Table 3), whereas few species of infrequent colonist-pioneers occurred in refugia, regardless of canopy height.

Table 3

Numbers of infrequent species (<10 occurrences) among refugium classes by species guild; total 82 species

Guild	Refugium class				Machinery track	$\Sigma$
	Tall	Medium	Low	Open		
Liverworts	<b>6+</b>	<b>7+</b>	<b>4+</b>	<b>2–</b>	<b>4–</b>	<b>24</b>
Forest-habitat mosses	<b>11+</b>	<b>13+</b>	<b>9+</b>	<b>6–</b>	<b>8–</b>	<b>47</b>
Colonist-pioneer mosses	1	0	1	2	7	11

Expected values were derived from total number of occurrences of each guild and the proportion of quadrats in each class; significant differences from expected (tested with  $\chi^2$ ,  $P < 0.05$ ) are **bold**; + or – indicates whether the observed frequency was greater or lesser than expected.



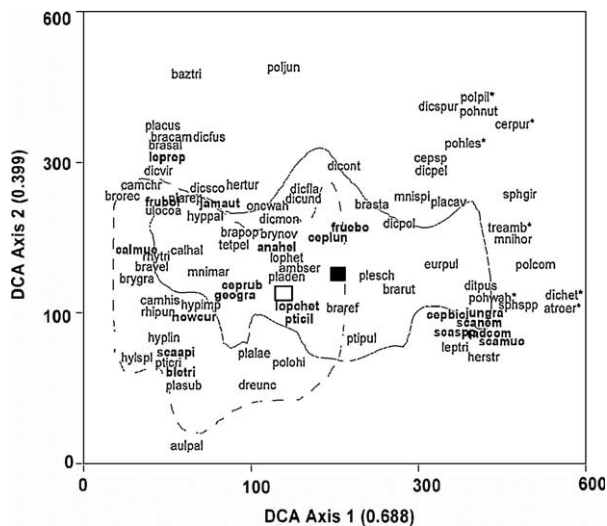


Fig. 2. Bryophytes and quadrats in refugium and track classes: scatterplot of first and second axes of species scores in detrended correspondence analysis (DCA), with eigenvalues in brackets. Ellipses encompass quadrats within refugia (dashed) and machinery tracks (solid). Rectangles mark the centroids of the ellipses (open = refugia, solid = machinery tracks). Total inertia = 10.06. Species codes are in Appendix A. Liverworts are in **bold**, species found only in potential refugia are in *italics* and species found only in nonrefugia are marked with \*.

The first DCA axis clearly separated colonist–pioneer species common in areas that received direct disturbance (e.g., *Ceratodon purpureus*, *Atrichum oerstedianum* and *Dichodontium pellucidum*) from forest-habitat mosses (e.g., *Brotherella recurvans*, *Bryhnia graminicolor* and *Campyllum chrysophyllum*) and liverworts (e.g., *Lophocolea heterophylla*) in quadrats that received minimal indirect disturbance (treed refugium classes, Fig. 2). DCA Axis 2 appeared to represent a moisture gradient: species common in moist to wet areas (e.g., *Aulacomnium palustre* and *Polytrichum commune*) were found at central and low positions, while colonists–pioneers that are more commonly found in dry areas (e.g., *Ceratodon purpureus* and *Polytrichum juniperinum*) had high scores.

A second DCA omitted track quadrats to clarify differences among refugium classes. Colonist–pioneer species scored high on DCA Axis 1 (Fig. 3(a)), while species common in moist to wet areas were high on Axis 2. In the centre of the ordination, between 0 and 200 on both axes, were species that are common on rotting wood and humus (e.g., *Tetraphis pellucida* and *Nowellia curvifolia*).

Community composition differed among refugium classes in both central tendency and diversity (Fig. 3(b)). The tall class had the greatest spread of quadrats and was influenced by species common on rotting wood (between 0 and 200), while medium and low classes had reduced spread on both axes, with centroids higher on Axis 2. The open class extended higher on Axis 1, reflecting the abundance of pioneer species. Overall,

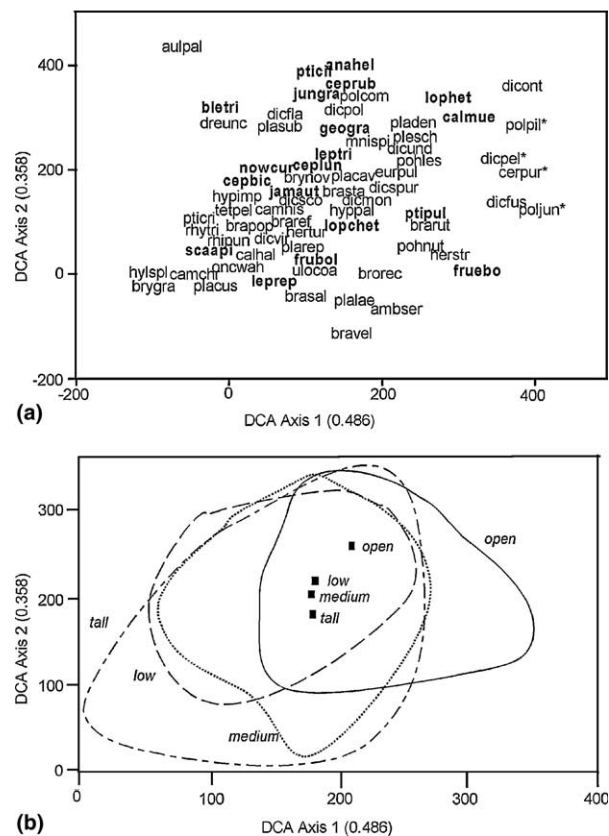


Fig. 3. (a) Bryophytes and (b) quadrats within remnant canopy classes: scatterplot of first and second axes of species in detrended correspondence analysis (DCA), with eigenvalues in brackets. (a) Liverworts are in **bold**, colonist–pioneer species are marked with \*. (b) Ellipses encompass the spread of quadrats of each refugium class (tall dash-dot-dash, medium dotted, low dashed, and open solid). Total inertia = 7.71. Species codes are in Appendix A.

class centroids and ranges of quadrat scores on both axes increased with increased canopy removal, i.e., from tall to open.

### 3.2. Comparison of environments

Presumably uninfluenced by any trees, controls experienced the highest means and extremes of incident precipitation, PAR, temperature and VPD (Table 4). Over 60% of total daily PAR values recorded in the clear-cut were between 30,000 and 60,000  $\mu\text{mol}^{-1} \text{m}^{-2} \text{day}^{-1}$  (Fig. 4), with the highest frequency of extreme temperatures, and durations of extreme PAR and temperatures (Table 5). Mean VPD ranged from 2.52 to 35.98 hPa in control patches (Table 4), with >15% of readings over 30 hPa (Fig. 4).

Microclimatic conditions in the open refugium class generally fell between those of control patches vs. low, medium and tall patches. Mean temperature and PAR (Table 4) and durations of extremes of PAR (Table 5) were significantly different from both the treed refugia and the control. Half of total daily PAR values were

Table 4  
Microclimatic variables for refugium classes over 5 months (25 April to 26 September 2000)

Microclimatic variable	Refugium class				Control
	Tall	Medium	Low	Open	
<i>Precipitation</i>					
Total for sampling period <sup>a</sup>	2021.2	6112.8	3153.6	3621.2	3456.4
Mean/sampling period	135.2	203.7	210.2	241.7	265.7
SE	34.3	51.9	55.5	50.9	60.2
<i>N</i> (recordings)	12	12	12	12	12
<i>Total PAR</i>					
Mean	1663a	1371a	1544a	14,166b	34,776c
SE	90	88	92	916	1248
Minimum	84	150	272	172	8833
Maximum	4868	4501	4406	47,165	56,544
<i>N</i> (days)	128	113	121	128	119
Temperature					
Mean	14.6a	14.8a	14.9a	15.8b	17.5c
SE	0.2	0.2	0.1	0.2	0.2
Minimum	3.6	3.9	4.0	5.9	5.8
Maximum	35.2	34.5	33.1	44.0	46.0
VPD					
Mean	8.21a	12.10b	11.62b	13.16b	17.58c
SE	0.11	0.11	0.12	0.18	0.27
Minimum	0	0	0.04	0	2.52
Maximum	40.09	42.85	35.28	58.32	95.98

Total precipitation (ml), total PAR ( $\mu\text{mol}^{-2} \text{m}^{-2} \text{day}^{-1}$ ), temperature ( $^{\circ}\text{C}$ ) and vapour pressure deficit (VPD in hPa).

N for temperature and VPD for each refugium class varied from 2922 to 3347 recordings.

Means followed by the same letter in a row are not significantly different at  $P < 0.05$ ; letters also indicate ranking (i.e:  $a < b < c < d$ ).

SE: standard error.

<sup>a</sup> Sampling periods varied from 1–3 weeks.

between 30,000 and 60,000  $\mu\text{mol}^{-1} \text{m}^{-2} \text{day}^{-1}$ , with 50% of temperature readings over 17  $^{\circ}\text{C}$  (Fig. 4). Mean VPD was higher only in tall patches (Table 4).

Tall, medium and low refugium classes were similar in means, ranges and durations of extremes of PAR and temperature (Tables 4 and 5). Mean VPD and duration of high VPD were significantly lower in the tall class. VPD values of 5–20 hPa were most frequent, with few or no values greater than 30 hPa (Fig. 4).

Refugium classes differed in % covers of individual substrates related to disturbance (Table 6). Percent covers of bare mineral soil, humus, roots, rocks, twigs and woody debris were highest in directly disturbed areas, reflecting mechanical damage to the forest floor and deposition of slash. Open and low classes also had high values of deposited woody debris. Frequent available substrates in the refugium classes included trunks and needles, from a maximum in tall to minimum values in open. Substrate richness was significantly greater in medium and low classes.

### 3.3. Relationship between bryophyte communities and environmental features

In total, 24.4% of the variability captured in the bryophyte communities could be directly related to environ-

mental and refugium characteristics. Of this, substrates accounted for 50%, followed by refugium characteristics (19.9%) and microclimate (10.2%), with minor contributions from interactions (Fig. 5).

## 4. Discussion

While confined to retrospective assessment of a clear-cut harvest that was not designed to create refugia, this study confirmed previous suggestions (Fenton et al., 2003; Whitman and Hagan, 2003; Beese and Bryant, 1999) that patches of retained canopy that escape substrate disturbance may serve as refugia to preserve bryophyte communities. Furthermore, it identified environmental features of the remnant patches that are most likely to contribute to their conservation value.

### 4.1. Remnant patches vs. direct disturbance

Four years after harvest, bryophyte communities in the remnant patches differed from communities on the machinery tracks in richness, total cover and species composition. While these communities shared a core group of relatively common species, they supported different suites of less frequent species: colonist–pioneer

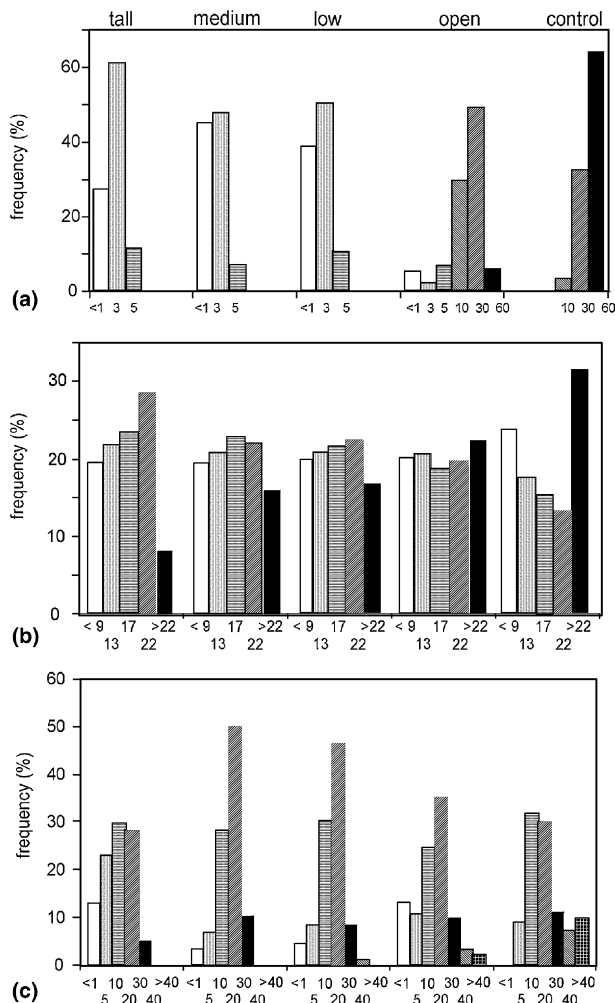


Fig. 4. Microclimate of refugium classes compared to treeless control. Frequencies of (a) total daily PAR ( $\mu\text{mol s}^{-1} \text{ day}^{-1}$ ) ( $\times 10^3$ ), (b) temperature ( $^{\circ}\text{C}$ ) and (c) vapour pressure deficit (VPD, hPa).

mosses were more prominent on machinery tracks, and liverworts and forest-habitat mosses were more prominent in remnant patch communities. Tracks differed significantly from remnant patches in terms of both

substrates and microclimate. Tracks were characterized by greater cover of mineral soil and slash, higher mean PAR, temperature and VPD as well as more frequent extremes of longer durations. While the initial disturbance effect was presumably direct, the ensuing habitat conditions represent a potential barrier to colonization of the tracks by species from the pre-harvest community if the conditions they offer are beyond the ecological tolerance of propagules or juveniles of these species.

#### 4.2. Comparison of potential refugium classes

Central to this study was the comparison of bryophyte communities of remnant canopy patches four years after harvest, from which we might infer their potential effectiveness as refugia. There were clear differences in the bryophyte communities of refugium classes with and without trees. The bryophyte community in the open class was less rich, contained fewer liverwort and forest-habitat moss species, with more frequent and more abundant pioneer moss species than did treed remnant canopy classes. We attribute this to microclimatic differences: although moderated compared to the control, the open class was significantly warmer, drier, and higher in PAR than treed refugia.

In the absence of direct disturbance, general trends in total bryophyte cover, diversity indices, and frequency and abundance of several species with increasing remnant canopy height (Fig. 1) are likely related to patterns of indirect disturbance. Neither substrate variables indicative of direct disturbance (e.g., stumps and mineral soil), nor frequency or abundance of colonizer–pioneer species, display trends that parallel canopy height. Our canopy height classes, which represent a reciprocal of canopy removal, present a complex microclimate gradient. Medium and low remnant canopy create light, temperature and humidity regimes similar to those under layered canopy in the tall class, yet intercept less incident precipitation. Some uniformly tall canopy

Table 5

Duration (h) of high values of PAR density, temperature and VPD by refugium class, defined as high at:  $>100 \mu\text{mol m}^{-2} \text{ s}^{-1}$  PAR density,  $>20^{\circ}\text{C}$  and VPD  $>10 \text{ hPa}$

Microclimatic variable	Refugium class				Control
	Tall	Medium	Low	Open	
PAR density					
Mean	0.71a	0.53a	0.83a	10.98b	11.53c
SE	0.095	0.70	0.10	0.02	0.15
Temperature					
Mean	5.00a	5.54ab	5.46ab	6.60b	8.37c
SE	0.37	0.37	0.38	0.35	0.36
VPD					
Mean	7.78a	13.87b	12.80b	11.86b	13.64b
SE	0.62	0.66	0.67	0.63	0.51

Means followed by the same letter in a row are not significantly different at  $P < 0.05$ ; letters also indicate ranking (i.e.:  $a < b < c < d$ ).

SE = standard error.



Table 6

Available substrates grouped by refugium class. Values are means  $\pm$  standard errors; means followed by the same letter in a row are not significantly different at  $P < 0.05$

Substrates	Refugium class				Machinery track
	Tall	Medium	Low	Open	
Rocks	0.24a $\pm$ 0.22	0.009a $\pm$ 0.009	0.07a $\pm$ 0.052	0.20a $\pm$ 0.10	0.26a $\pm$ 0.083
Live trunks	1.64b $\pm$ 0.30	0.98ab $\pm$ 0.18	0.90ab $\pm$ 0.35	0.41a $\pm$ 0.241	0.26a $\pm$ 0.097
Stumps	0.21a $\pm$ 0.21	1.20a $\pm$ 0.90	0.00a $\pm$ 0.00	0.12a $\pm$ 0.16	1.88a $\pm$ 0.81
Mineral soil	0.02b $\pm$ 0.02	0.18a $\pm$ 0.18	0.12b $\pm$ 0.095	0.21a $\pm$ 0.14	1.11a $\pm$ 0.26
Humus	0.70a $\pm$ 0.31	0.67a $\pm$ 0.24	0.72a $\pm$ 0.30	1.15a $\pm$ 0.47	2.43a $\pm$ 0.66
Loose bark	2.36a $\pm$ 1.03	1.93a $\pm$ 0.69	2.92a $\pm$ 0.74	1.49a $\pm$ 0.32	3.10a $\pm$ 0.46
Cones	0.39a $\pm$ 0.098	0.12a $\pm$ 0.043	0.86 b $\pm$ 0.29	0.15a $\pm$ 0.053	0.22a $\pm$ 0.073
Scats	0.63a $\pm$ 0.10	0.64a $\pm$ 0.10	0.68a $\pm$ 0.10	0.63a $\pm$ 0.088	0.17a $\pm$ 0.05
Needles	52.56d $\pm$ 0.103.92	45.56cd $\pm$ 4.40	32.25bc $\pm$ 4.64	21.56ab $\pm$ 3.69	15.95a $\pm$ 1.78
Deciduous leaves	25.86b $\pm$ 2.40	18.85ab $\pm$ 2.60	14.13a $\pm$ 1.69	28.53b $\pm$ 3.36	29.08b $\pm$ 2.51
Exposed woody roots	0.42a $\pm$ 0.14	0.73a $\pm$ 0.44	0.99a $\pm$ 0.50	0.78a $\pm$ 0.43	1.92a $\pm$ 0.47
Twigs (diameter <1 cm)	7.23a $\pm$ 0.83	11.44a $\pm$ 1.82	11.25a $\pm$ 1.25	11.81 $\pm$ 1.66	12.62a $\pm$ 1.33
Woody debris (coniferous or deciduous wood with diameter >5 cm)	10.71a $\pm$ 2.23	14.59ab $\pm$ 2.00	17.20abc $\pm$ 2.23	24.37 bc $\pm$ 2.68	25.13 c $\pm$ 2.12
Substrate richness	4.99ab $\pm$ 0.14	6.42c $\pm$ 0.24	5.74bc $\pm$ 0.30	4.87a $\pm$ 0.17	4.67a $\pm$ 0.14

Letters also indicate ranking (i.e.: a < b < c < d).

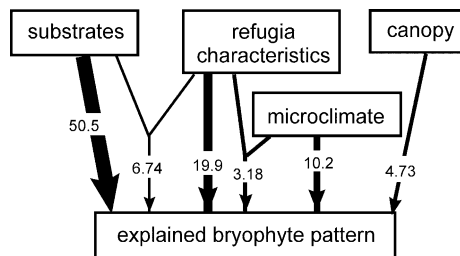


Fig. 5. Contribution of environmental variables to observed bryophyte pattern, as determined by partial Canonical Correspondence Analysis. Boxes represent categories of environmental variables included in the analysis. Arrow width and numbers indicate percent of the explained variation in the bryophyte community corresponding to each category or interactions between categories. Variables, chosen by Forward Selection ( $P = 0.05$ ), are (i) substrates: humus, stumps, rocks, needles, trunks, scat, fine and coarse woody debris, and leaves; (ii) refugium characteristics: mean circumference of trees, size of refugium patch, dominant tree species (spruce or fir), total number of trees and tree density; (iii) microclimate: mean precipitation, mean temperature, and maximum temperature and (iv) canopy: total herbaceous cover.

lacked an intermediary layer, likely resulting in greater exposure to wind. Furthermore, an intermediate level of shading may be more hospitable than either heavy shade or high light intensity of tall vs open respectively (Peterson, 1999; Olsson and Staaf, 1995). Together, these interactions are likely to influence bryophyte hydration time, a key factor in growth and establishment (Päivänen, 1966; in Økland et al., 1999; Tamm, 1950).

In view of our previous study, in which we found that the pre-harvest community was the largest determining factor of post-harvest bryophyte community composition (Fenton et al., 2003), the legacy of pre-harvest community and habitat features not documented in this study should not be overlooked. For example, low and

medium classes were dominated by young *Abies balsamea* (Table 1), which is abundant in canopy gaps (Kneeshaw and Bergeron, 1998) such as those created by tip ups, which in turn favour high bryophyte diversity (Jonsson and Esseen, 1990). This is supported by the significantly higher substrate diversity in medium and low classes, and low correspondence between bryophyte composition and current environmental variables (Fig. 5). The residual influence of the pre-harvest community may indicate that the community is in transition, adjusting to the changes created by the disturbance event. Alternatively, it may reflect the over-riding importance of propagule availability in community assembly.

#### 4.3. Implications for conservation

This study should be seen as a preliminary assessment of the potential bryophyte conservation value of remnant canopy areas within a clear-cut. This is in part because this study was undertaken 4 years after harvest; we cannot be sure that the pre-harvest bryophyte communities were identical throughout the area. However, given the nature of bryophyte diversity documented in this study area (Fenton et al., 2003; Ross-Davis and Frego, 2002) and elsewhere (e.g., Økland, 1990), it is likely that the greatest variability was at a fine scale (e.g., m<sup>2</sup>), hence multiple samples from a wide range of areas within the stands are likely to have adequately summarized the potential at the stand scale.

This study also cannot address the issue of edge effects (all patches were far below the minimum diameters at which edge effects have been detected; e.g., Moen and Jonsson, 2003). However, it shows that even small (<50 m<sup>2</sup>) patches of remnant canopy may be important for population preservation within a harvested forest. Three categories of remnant canopy patches, typically left in

areas with abundant advanced tree regeneration, provide environmental conditions sufficiently similar to unharvested forest to allow populations of some forest floor bryophyte species to persist. It is particularly worthy of note that this included seven species (four mosses and three liverworts found only in refugia) shown to have been extirpated from adjacent quadrats four years after clear-cut (Fenton et al., 2003). Given that some liverworts have been shown to be sensitive to microclimate changes up to 50 m from the edge of the forest islands (Moen and Jonsson, 2003), it is remarkable that many species, including four rare species, survived in these treed patches. If presence of propagules and colonization events are key elements in structuring bryophyte communities (Kimmerer and Driscoll, 2000; Hurtt and Pacala, 1995), then persistence of these populations may be even more critical as sources of propagules to recolonize the regenerating forest.

We propose that the conditions governing the conservation potential of a bryophyte refugium, in order of decreasing importance, are: absence of direct disturbance, presence of remnant canopy, height and closure of remnant canopy, and microsite (especially substrate) diversity. The role of initial bryophyte diversity remains to be tested but is likely to be critical.

Future studies should utilize a BACI (Before-After-Control-Impact, e.g., Underwood, 1991) design, incorporating pre- and post-harvest comparisons in order to assess species responses, i.e. changes over time, and nat-

ural community dynamics in areas not subjected to disturbances such as canopy removal or substrate disruption. In order to assess the long-term functions of bryophyte refugia, it is essential to determine (i) the influence of refugium size and shape, both in terms of contributions of initial species composition and microclimatic edge effects and (ii) the contribution of persistent populations within refugia to the assembly of regenerating bryophyte communities in surrounding disturbed areas.

## Acknowledgements

The authors acknowledge the field assistance of Jennifer Delaney, Chris Norfolk and Amy Ross-Davis, and assistance with taxonomic determinations by Mary Sims and Bruce Bagnell. The bryophyte collection at the New Brunswick Museum and the assistance of curator Stephen Clayden were invaluable. Discussions with Drs. G. Forbes, J. Kieffer and D. MacLean, and constructive comments from an anonymous reviewer, were very helpful and improved the manuscript. Financial support was provided by the Natural Science and Engineering Research Council of Canada, Fundy Model Forest, Summer Career Placement, the School of Graduate Studies and the Department of Biology, University of New Brunswick, Saint John. J.D. Irving Ltd. allowed us to work on their landbase.

## Appendix A

Abundance (% cover) and % frequency of bryophyte species by refugium class in remnant canopy

Species	Spp code	Refugium class								Machinery track	
		Tall		Medium		Low		Open		Cover	Frequency
		Cover	Frequency	Cover	Frequency	Cover	Frequency	Cover	Frequency		
Liverworts											
<i>Anastrophyllum hellerianum</i>	anahel	0.000	0	0.000	0	0.001	2.3	0.000	0	0.000	0
<i>Bazzania trilobata</i>	baztri	0.000	0	0.000	0	0.000	0	0.000	0	0.001	1.5
<i>Blepharostoma trichophyllum</i>	bletri	0.002	4.2	0.002	5.3	0.000	0	0.000	0	0.000	0
<i>Calypogeia muelleriana</i>	calmue	0.001	2.8	0.000	0	0.000	0	0.000	0	0.000	0
<i>Cephalozia bicuspidata</i> <sup>a</sup>	cepbic	0.004	8.5–	0.008	14+	0.010	27.9+	0.003	8.1–	0.009	0.8–
<i>Cephalozia lunulifolia</i>	ceplun	0.002	5.6	0.003	8.8	0.003	9.3	0.000	0	0.001	0.7
<i>Cephalozia</i> spp.	cepspp	0.000	0	0.000	0	0.001	4.7	0.000	0	0.001	0.7
<i>Cephaloziella rubella</i>	ceprub	0.000	0	0.001	3.5	0.001	2.3	0.000	0	0.000	0
<i>Frullania bolanderi</i>	frubol	0.001	1.4	0.000	0	0.000	0	0.000	0	0.000	0
<i>Frullania eboraensis</i>	fruebo	0.006	2.8	0.000	0	0.000	0	0.006	1.6	0.000	0
<i>Geocalyx graveolens</i> <sup>a,b</sup>	geogra	0.004b	4.2–	0.007a	17.5+	0.007a	18.6+	0.000	0	0.002a	3.1–
<i>Jamesoniella autumnalis</i> <sup>a, b</sup>	jamaut	0.057b	23.9+	0.050b	24.6+	0.043b	27.9+	0.009a	9.7–	0.006a	8.5–
<i>Jungermannia gracillima</i>	jungra	0.000	0	0.001	1.7	0.000	0	0.000	0	0.008	1.5

## Appendix A (continued)

Species	Spp code	Refugium class								Machinery track	
		Tall		Medium		Low		Open		Cover	Frequency
		Cover	Frequency	Cover	Frequency	Cover	Frequency	Cover	Frequency		
<i>Jungermannia</i> spp.	junspp	0.000	0	0.000	0	0.000	0	0.000	0	0.001	0.7
<i>Lepidozia repens</i>	leprep	0.000	0	0.000	0	0.001	2.3	0.000	0	0.000	0
<i>Lophocolea heterophylla</i> <sup>a</sup>	lopchet	0.037	49.3+	0.056	49.1+	0.039	46.5+	0.017	27.4–	0.008	15.4–
<i>Lophozia bicrenata</i>	lopbic	0.000	0	0.000	0	0.000	0	0.000	0	0.001	0.7
<i>Lophozia heterocolpos</i>	lophet	0.000	0	0.001	1.7	0.000	0	0.000	0	0.000	0
<i>Nowellia curvifolia</i> <sup>a</sup>	nowcur	0.010	8.5+	0.008	10.5+	0.015	14+	0.001	1.6–	0.001	0.7–
<i>Ptilidium ciliare</i>	ptcil	0.002	1.4	0.017	7	0.001	4.7	0.015	4.8	0.000	0
<i>Ptilidium pulcherrimum</i> <sup>a</sup>	ptipul	0.314	69+	0.147	70.2+	0.145	83.7+	0.208	66.1+	0.070	31.5–
<i>Radula complanata</i>	radcom	0.000	0	0.000	0	0.000	0	0.000	0	0.001	0.7
<i>Scapania apiculata</i>	scaapi	0.000	0	0.001	1.7	0.000	0	0.000	0	0.000	0
<i>Scapania mucronata</i>	scamuc	0.000	0	0.000	0	0.000	0	0.000	0	0.005	0.7
<i>Scapania nemorosa</i>	scanem	0.000	0	0.000	0	0.000	0	0.000	0	0.001	0.7
<i>Scapania</i> spp.	scaspp	0.000	0	0.000	0	0.000	0	0.000	0	0.001	0.7
Forest-habitat mosses											
<i>Amblystegium serpens</i>	ambser	0.001	1.4	0.001	3.5	0.000	0	0.003	6.45	0.001	1.5
<i>Aulacomnium palustre</i>	aulpal	0.010	11.2	0.143	10.5	0.004	7	0.014	1.6	0.005	1.5
<i>Brachythecium campestre</i>	bracam	0.075	5.6	0.001	1.7	0.002	2.3	0.010	4.8	0.004	1.5
<i>Brachythecium populeum</i>	brapop	0.003	5.6	0.002	3.5	0.001	2.3	0.000	0	0.014	1.5
<i>Brachythecium reflexum</i> <sup>a</sup>	braref	0.033	12.6+	0.043	19.3+	0.074	18.3+	0.013	6.5–	0.020	2.3–
<i>Brachythecium rutabulum</i> <sup>a</sup>	brarut	0.030	21.1+	0.139	24.6+	0.046	30.2+	0.049	17.7–	0.010	10–
<i>Brachythecium salebrosum</i>	brasal	0.006	5.6	0.000	0	0.023	7	0.001	3.2	0.001	2.3
<i>Brachythecium starkei</i>	brasta	0.259	45.1	0.293	54.4	0.283	53.5	0.181	41.9	0.120	46
<i>Brachythecium velutinum</i>	bravel	0.000	0	0.000	0	0.000	0	0.010	1.6	0.000	0
<i>Brotherella recurvans</i>	brorec	0.015	2.8	0.000	0	0.001	2.3	0.000	0	0.004	0.7
<i>Bryhnia graminicolor</i>	brygra	0.001	1.4	0.000	0	0.000	0	0.000	0	0.000	0
<i>Bryhnia novae-angliae</i>	brynov	0.001	1.4	0.006	5.3	0.000	0	0.000	0	0.000	0
<i>Callicladium haldanianum</i> <sup>a</sup>	calhal	0.139	25.3+	0.075	17.5+	0.083	25.6+	0.008	8.1–	0.019	11.5–
<i>Campylium chrysophyllum</i>	camchr	0.002	1.4	0.000	0	0.000	0	0.000	0	0.000	0
<i>Campylium hispidulum</i>	camhis	0.011	1.4	0.000	0	0.000	0	0.000	0	0.001	0.7
<i>Climacium dendroides</i>	cliden	0.000	0	0.001	1.7	0.000	0	0.000	0	0.000	0
<i>Dicranum flagellare</i> <sup>a</sup>	dicfla	0.070	18.3–	0.165	36.8+	0.092	53.5+	0.084	25.8–	0.070	31.5
<i>Dicranum fuscescens</i>	dicfus	0.000	0	0.023	3.5	0.000	0	0.045	6.5	0.001	0.7
<i>Dicranum montanum</i> <sup>a</sup>	dicmon	0.012	18.3–	0.064	35.1+	0.026	34.9+	0.040	22.6	0.017	14.6–
<i>Dicranum ontariense</i>	dicont	0.018	2.8	0.019	7	0.070	16.3	0.097	9.7	0.010	10

(continued on next page)

## Appendix A (continued)

Species	Spp code	Refugium class								Machinery track	
		Tall		Medium		Low		Open		Cover	Frequency
		Cover	Frequency	Cover	Frequency	Cover	Frequency	Cover	Frequency		
<i>Dicranum polysetum</i> <sup>a</sup>	dicpol	0.217	35.2–	0.540	56.1+	0.537	83.7+	1.075	72.6+	0.194	38.5–
<i>Dicranum scoparium</i> <sup>a</sup>	dicsco	0.249	57.7+	0.176	47.4+	0.133	44.2+	0.029	30.6–	0.045	26.2–
<i>Dicranum spurium</i>	dicspur	0.000	0	0.000	0	0.000	0	0.001	1.6	0.000	0
<i>Dicranum undulatum</i>	dicund	0.000	0	0.001	1.7	0.043	4.7	0.000	0	0.000	0
<i>Dicranum viride</i>	dicvir	0.000	0	0.000	0	0.002	2.3	0.000	0	0.000	0
<i>Drepanocladus uncinatus</i> <sup>a</sup>	dreunc	0.128	21.1	0.283	38.6+	0.032	18.6	0.150	25.8+	0.070	8.5–
<i>Eurhynchium pulchellum</i>	eurpul	0.000	0	0.008	5.3	0.001	2.3	0.000	0	0.000	0
<i>Herzogiella striatella</i>	herstr	0.001	1.4	0.000	0	0.001	2.3	0.001	1.6	0.001	0.7
<i>Herzogiella turfacea</i> <sup>b</sup>	hertur	0.139	45.1+	0.167	59.6+	0.138	62.7+	0.057	35.5–	0.108	26.2–
<i>Hylocomium splendens</i>	hylspl	0.152	4.2	0.036	5.3	0.001	2.3	0.001	1.6	0.014	3.1
<i>Hypnum imponens</i>	hypimp	0.002	4.2	0.001	3.5	0.000	0	0.001	3.2	0.001	1.5
<i>Hypnum lindbergii</i>	hyplin	0.000	0	0.003	1.7	0.000	0	0.000	0	0.000	0
<i>Hypnum pallescens</i> <sup>a</sup>	hyppal	0.012	12.7	0.015	21.1+	0.015	23.3+	0.010	11.3–	0.017	6.2–
<i>Leptodictyum trichopodium</i>	leptri	0.001	1.4	0.002	5.3	0.001	2.3	0.001	1.6	0.001	1.5
<i>Mnium hornum</i>	mnihor	0.000	0	0.000	0	0.000	0	0.000	0	0.007	0.7
<i>Mnium marginatum</i>	mnimar	0.001	1.4	0.001	1.7	0.001	2.3	0.000	0	0.000	0
<i>Mnium spinulosum</i>	mnispi	0.000	0	0.001	1.7	0.000	0	0.000	0	0.001	0.7
<i>Oncophorus wahlenbergii</i>	oncwah	0.013	14.1	0.001	3.5	0.002	7	0.001	3.2	0.002	5.4
<i>Plagiomnium cuspidatum</i>	placus	0.055	14.1	0.027	8.8	0.000	0	0.000	0	0.002	4.6
<i>Plagiothecium cavifolium</i>	placav	0.017	8.5	0.005	7	0.003	2.3	0.002	4.8	0.010	4.6
<i>Plagiothecium denticulatum</i>	pladen	0.000	0	0.000	0	0.000	0	0.006	1.6	0.001	0.7
<i>Plagiothecium laetum</i> <sup>a</sup>	plalae	0.047	28.2+	0.046	33.3+	0.051	23.5+	0.025	5–	0.007	14.6–
<i>Platydictya subtile</i>	plasub	0.000	0	0.001	1.7	0.000	0	0.000	0	0.000	0
<i>Platygyrium repens</i>	plarep	0.011	9.9	0.003	3.5	0.000	0	0.003	3.2	0.006	4.6
<i>Pleurozium schreberi</i> <sup>b</sup>	plesch	1.047b	77.5	1.280b	87.7	1.729b	100	2.151b	92	0.277a	64.6
<i>Prilium crista-castrensis</i>	pticri	0.023	7	0.035	8.77	0.000	0	0.002	3.2	0.001	0.7
<i>Rhizomnium punctatum</i>	rhipun	0.001	1.4	0.003	1.7	0.000	0	0.000	0	0.000	0
<i>Rhytidadelphus triquetrus</i>	rhytri	0.011	1.4	0.003	1.7	0.000	0	0.000	0	0.001	0.7
<i>Sphagnum girgensohnii</i>	sphgir	0.000	0	0.000	0	0.000	0	0.000	0	0.008	2.3
<i>Sphagnum</i> spp.	sphspp	0.000	0	0.000	0	0.000	0	0.000	0	0.001	1.5
<i>Tetraphis pellucida</i>	tetpel	0.008	8.5	0.006	10.5	0.001	4.7	0.000	0	0.004	4.6
<i>Ulota coarctata</i>	ulocoa	0.001	1.4	0.000	0	0.000	0	0.001	1.6	0.000	0
Colonists–pioneers											
<i>Atrichum oerstedianum</i>	atroer	0.000	0	0.000	0	0.000	0	0.000	0	0.001	0.7
<i>Ceratodon purpureus</i> <sup>b</sup>	cerpur	0.001a	2.8	0.000a	0	0.002a	7	0.034b	11.3	0.121b	12.3

## Appendix A (continued)

Species	Spp code	Refugium class								Machinery track	
		Tall		Medium		Low		Open		Cover	Frequency
		Cover	Frequency	Cover	Frequency	Cover	Frequency	Cover	Frequency		
<i>Dicranella heteromalla</i>	dichet	0.000	0	0.000	0	0.000	0	0.000	0	0.072	2.3
<i>Dichodontium pellucidum</i>	dicpel	0.000	0	0.000	0	0.000	0	0.001	1.6	0.000	0
<i>Ditrichum pusillum</i>	ditpus	0.000	0	0.000	0	0.000	0	0.000	0	0.084	1.5
<i>Pohlia lescuriana</i> <sup>b</sup>	pohles	0.001a	1.4	0.003a	5.3	0.018a	16.3	0.016a	9.7	0.030b	7.7
<i>Pohlia nutans</i> <sup>a,b</sup>	pohnut	0.003a	2.8–	0.004a	7–	0.028a	16.3	0.029a	17.7+	0.078b	20.8+
<i>Pohlia wahlenbergii</i>	pohwah	0.000	0	0.000	0	0.000	0	0.000	0	0.017	4.6
<i>Polytrichum commune</i> <sup>a</sup>	polcom	0.003	2.8–	0.296	12.3	0.021	9.3–	0.059	8.1–	0.650	6.9+
<i>Polytrichum juniperinum</i> <sup>a,b</sup>	poljun	0.005a	2.8–	0.001a	1.7–	0.013a	14+	0.065a	11.3	0.136b	15.4+
<i>Polytrichum ohioense</i>	polohi	0.001	1.4	0.000	0	0.000	0	0.000	0	0.002	1.5
<i>Polytrichum piliferum</i>	polpil	0.000	0	0.000	0	0.000	0	0.001	1.6	0.001	0.7
<i>Trematodon ambiguus</i>	treamb	0.000	0	0.000	0	0.000	0	0.000	0	0.001	0.7

Mean % cover followed by the same letter in the same row are not significantly different; letters also indicate rankings, i.e. a < b.

<sup>a</sup> Indicates species that differ significantly in frequency among refugium classes + or – indicate whether the observed frequency was greater or lesser than expected; values with no sign showed no significant difference.

<sup>b</sup> Indicates species that differ significantly in % cover when present among refugium classes ( $P < 0.05$ ).

## References

- Beese, W., Bryant, A., 1999. Effects of silvicultural systems of vegetation and bird communities in coastal montane forests of British Columbia, Canada. *Forest Ecology and Management* 115, 231–242.
- Busby, J., Bliss, L., Hamilton, C., 1978. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomethypnum nitens* and *Hylocomnium splendens*. *Ecological Monographs* 48, 95–110.
- Crum, H., Anderson, L., 1981. Mosses of North America, vols. I–II. Columbia University Press, New York.
- Department of Natural Resources and Environment, 1997. Ecological Land Classification for New Brunswick: Ecoregion, Ecodistrict and Ecosite levels. Ecosystem Classification Working Group, Department of Natural Resources and Energy, Forest Management Branch. Fredericton, New Brunswick.
- During, H., 1992. Ecological classifications of bryophytes and lichens. In: Bates, J., Farmer, A. (Eds.), *Bryophytes and Lichens in a Changing Environment*. Clarendon Press, Oxford, pp. 1–31.
- Environment Canada. Canadian Climate Normals. Station Moncton A. Available from: <[http://www.climat.meteo.ec.gc.ca/climate\\_normals/stnselect\\_e.html](http://www.climat.meteo.ec.gc.ca/climate_normals/stnselect_e.html)>. Last modified 2003-07-24. Date visited 2003-12-09.
- Fenton, N., Frego, K., Sims, M., 2003. Changes in forest floor bryophyte (moss and liverwort) communities four years after harvest. *Canadian Journal of Botany* 81, 714–731.
- Frego, K.A., 1996. Regeneration of four boreal bryophytes: Colonization of experimental gaps by naturally occurring propagules. *Canadian Journal of Botany* 74, 1937–1942.
- Frisvoll, A., Prestø, T., 1997. Spruce forest bryophytes in central Norway and their relationship to environmental factors including modern forestry. *Ecography* 20, 3–18.
- Gustafsson, L., Hallingbäck, T., 1988. Bryophyte flora and vegetation of managed and coniferous forests in south-west Sweden. *Biological Conservation* 44, 283–300.
- Hagan, J.M., Grove, S.L., 1999. Bird abundance and distribution in managed and old-growth forest in Maine. Manomet Center for Conservation Sciences, Brunswick, ME. Report No. MM-9901.
- Haig, A., Matthes, U., Larson, D., 2000. Effects of natural habitat fragmentation on the species richness, diversity, and composition of cliff vegetation. *Canadian Journal of Botany* 78, 786–797.
- Herben, T., Rydin, H., Söderström, L., 1991. Spore establishment probability and the persistence of the fugitive invading moss *Orthodontium lineare*: a spatial simulation model. *Oikos* 60, 215–221.
- Hurt, G., Pacala, S., 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology* 176, 1–12.
- Ireland, R., 1982. Moss Flora of the Maritime Provinces. National Museum of Natural Science, Ottawa.
- Jennings, D.T., Houseweart, M.W., Dunn, G.A., 1986. Carabid beetles [Coleoptera Carabidae] associated with strip clearcut and dense spruce-fir forests of Maine, USA. *Coleopterists Bulletin* 40, 251–263.
- Jonsson, B., Esseen, P., 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. *Journal of Ecology* 78, 924–936.
- Jonsson, B., Esseen, P., 1998. Plant colonization in small forest-floor patches: importance of plant groups and disturbance traits. *Ecography* 21, 518–526.
- Kimmerer, R., Driscoll, M., 2000. Bryophyte species richness and insular boulder habitats: the effect of area isolation, and microsite diversity. *The Bryologist* 103, 748–756.
- Kneeshaw, D., Bergeron, Y., 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology* 79, 783–794.
- Krebs, C., 1989. *Ecological Methodology*. Benjamin/Cummings, Menlo Park, CA.
- Lesica, P., McCune, B., Cooper, S., 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. *Canadian Journal of Botany* 69, 1745–1755.



- McCune, B., Mefford, M., 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MJM Software Design, Gleneden Beach, OR.
- Methven, I., Kendrick, M., 1995. A Disturbance History Analysis of the Fundy Model Forest Area. Fundy Model Forest, Sussex, New Brunswick.
- Miles, C., Longton, R., 1990. The role of spores in reproduction in mosses. *Botanical Journal of the Linnean Society* 104, 149–173.
- Moen, J., Jonsson, B.G., 2003. Edge effects on liverworts and lichens in forest patches in a mosaic of boreal forest and wetland. *Conservation Biology* 17, 380–388.
- Nyland, R., 1996. *Silviculture: Concepts and Applications*. McGraw-Hill, New York.
- Økland, R., 1990. *Vegetation Ecology, Theory, Methods and Applications with Reference to Fennoscandia*. Sommerfeltia Supplement. Botanical Garden and Museum, University of Oslo, 154.
- Økland, R., Rydgren, K., Økland, T., 1999. Single-tree influence on understorey vegetation in a Norwegian boreal spruce forest. *Oikos* 87, 488–498.
- Olsson, B., Staaf, H., 1995. Influence of harvesting intensity of logging residues on ground vegetation in coniferous forests. *Journal of Applied Ecology* 32, 640–654.
- Päivänen, J., 1966. Sateen jakaantuminen erilaisissa metsiköissä (Eng. summ.: The distribution of rainfall in different types of forest stands). *Silva Fennica* 119, 1–37.
- Peterson, J., 1999. The effects of forest harvest on bryophyte recolonization in a mixed forest in New Brunswick. M.Sc. thesis, Department of Biology, University of New Brunswick. Saint John.
- Rambo, T., Muir, P., 1998. Forest floor bryophytes of *Pseudotsuga menziesii*-*Tsuga heterophylla* stands in Oregon: Influence of substrate and overstory. *Bryologist* 101, 116–130.
- Renhorn, K.-E., Esseen, P.-A., Palmqvist, K., Sundberg, B., 1997. Growth and vitality of epiphytic lichens. I. Responses to microclimate along a forest edge-interior gradient. *Oecologia* 109, 1–9.
- Roberts, M., Zhu, L.-X., 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. *Forest Ecology and Management* 155, 17–31.
- Ross-Davis, A., Frego, K., 2002. Comparison of plantations and naturally regenerated clearcuts in the Acadian forest: forest floor bryophyte community and habitat features. *Canadian Journal of Botany* 80, 21–33.
- Ross-Davis, A., Frego, K., 2004. Propagule sources of forest floor bryophytes: spatiotemporal compositional patterns. *The Bryologist* 107, 88–97.
- Rowe, J., 1972. *Forest Regions of Canada*. Department of the Environment Canadian Forest Service, Ottawa.
- Rydgren, K., Hestmark, G., Økland, R., 1998. Revegetation following experimental disturbance in a boreal old-growth *Picea abies* forest. *Journal of Vegetation Science* 9, 763–776.
- Saunders, D., Hobbs, R., Margules, C., 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5, 18–32.
- Schuster, R., 1969. *The Hepaticae and Anthocerotae of North America, East of the hundredth meridian*, vol. II. Columbia University Press, New York and London.
- Schuster, R., 1974. *The Hepaticae and Anthocerotae of North America, East of the hundredth meridian*, vol. III. Columbia University Press, New York and London.
- Schuster, R., 1980. *The Hepaticae and Anthocerotae of North America, East of the hundredth meridian*, vol. IV. Columbia University Press, New York and London.
- Sims, M., 1996. Distribution of forest floor bryophyte in a north temperate forest. B.Sc. thesis, Department of Biology, University of New Brunswick Saint John.
- Söderström, L., 1987. Dispersal as limiting factor for distribution among epixylic bryophytes. *Symposia Biologica Hungarica* 35, 475–483.
- Söderström, L., 1988. The occurrence of epixylic bryophyte and lichen species in an old and a managed forest stand in northeast Sweden. *Biological Conservation* 45, 169–178.
- Söderström, L., Hallingbäck, T., Gustafsson, L., Cronberg, N., Hedenäs, L., 1992. Bryophyte conservation for the future. *Biological Conservation* 59, 265–270.
- Söderström, L., Herben, T., 1997. Dynamics of bryophyte metapopulations. *Advances in Bryology* 6, 205–240.
- Tamm, C., 1950. Growth and plant nutrient concentration in *Hylocomnium proliferum* (L.) Lindb. in relation to tree canopy. *Oikos* 2, 60–64.
- Tanner, C., 1972. Application of psychometry to micrometeorology. In: Brown, R., VanHaveren, B. (Eds.), *Psychometry in Water Relations Research*. Utah Agricultural Experiment Station, Utah State University, Salt Lake City, UT, pp. 239–247.
- ter Braak, C., Šmilauer, P., 1998. CANOCO for Windows Version 4.2. Center for Biometry Wagenin, CPRO-DLO, Wageningen, The Netherlands.
- Tilman, D., May, R., Lehman, C., Nowak, M., 1994. Habitat destruction and the extinction debt. *Nature* 371, 65–66.
- Underwood, A.J., 1991. Beyond BACI: Experimental designs for detecting human environmental impacts on temporal variations in natural populations. *Australian Journal of Marine and Freshwater Research* 42, 569–588.
- White, P., Pickett, S., 1985. Natural disturbance and patch dynamics: An introduction. In: Pickett, S., White, P. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, pp. 3–13.
- Whitman, A.A., Hagan, J.M., 2003. Legacy retention: A tool for retaining biodiversity in managed forests. Manomet Center for Conservation Sciences, Brunswick, ME. Report No. MM 2003-1.
- Whitman, A.A., Hagan, J.M., S.L. Grove., 1999. Herbaceous plant communities in old growth and partial harvested forest in northern Maine. Manomet Center for Conservation Sciences, Brunswick, ME. Report No. MM-9902.
- Woodley, S., Forbes, G. (Eds.), 1997. *Forest Management Guidelines to Protect Native Biodiversity in the Fundy Model Forest*. University of New Brunswick, Fredericton, NB.