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Conservation and ecology of bryophytes in partially harvested boreal mixed-wood forests of west-central Canada

by

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Abstract

This thesis examined the efficacy of residual forest structure for the preservation and recovery of bryophytes five to six years after partial canopy harvest in boreal mixed-wood forests of northwestern Alberta, Canada. Bryophytes were sampled in two forest types that differed in pre-harvest abundance of broadleaf (primarily *Populus tremuloides* Michx. and *P. balsamifera* L.) and coniferous (primarily *Picea glauca* (Moench) Voss) canopy trees. In Chapter 2, epiphytic bryophytes growing on aspen (*P. tremuloides*) were characterized by species viability and nearest-neighbour relationships. Epiphyte assemblage structure showed increasing impact with declining retention owing to degradation of growing conditions for species on trees. Chapter 3 provided an analysis of species richness and abundance patterns in relation to residual canopy structure. Bryophytes generally benefitted from higher canopy retention; however, epixylic and epiphytic species were more sensitive to partial harvesting than species on other substrates, and liverworts were more sensitive than mosses. Liverworts exhibited higher among-site differences in richness as retention declined, which partly resulted from increasing numbers of local species extinctions. In an analysis of species-environment relations in partially-harvested forests in Chapter 4, forest moisture was reduced with any degree of harvesting in both forest types. Lower canopy retention and forest moisture levels were associated with reduced abundances of species with particular biological traits, such as limited reproduction and dispersal capacities. Their re-establishment after harvesting may be impeded because of biological and environmental limitations. Coniferous-dominated forests supported higher abundances of liverworts and species with greater moisture requirements than did mixed-wood broadleaf-coniferous forests, and are potentially important refuges of bryophyte source populations. Chapter 5 examined the capacity for bryophyte species to germinate from diaspore banks in forest soils. Species germinated readily from mineral soil samples obtained from harvested sites, including several perennials characteristic of intact forests. Diaspore banks may serve as a persistent source for species colonization at post-disturbance sites, but

only under appropriate growing conditions and not for species that were most sensitive to harvesting. Overall, both amount and composition of forest structure retained after partial harvesting are important management considerations for ensuring conservation of the wide variety of bryophyte species in mixed-wood landscapes.

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Chapter 1: Introduction

The conservation of biological diversity in circumpolar boreal forests is essential for maintaining the world's terrestrial biodiversity (UNCED 1992). Boreal forests account for approximately one third of the world's total forested area and the majority of remaining intact and unmanaged forests worldwide (UNEP 2002). These forests perform many important ecological roles, including carbon sequestration (Kasischke and Stocks 2000) and regulation of global climate (Bonan et al. 1992). The boreal forest is a disturbance-adapted biome that experiences perturbations at a range of spatial and temporal scales, as a consequence of fire, insect outbreaks, and canopy gap-formation processes (Shugart et al. 1992). Natural disturbances help maintain forest ecological processes (Zackrisson et al. 1996), and promote forest regeneration (Fenton and Bergeron 2006; Lecomte et al. 2006) and the structural complexity of forests (Kuuluvainen 2009). Commercial logging is currently the dominant form of human disturbance in boreal landscapes (SCBD 2002). Forest harvesting has been shown to affect landscape scale patterns of forest age, composition, and structure (Bergeron et al. 1998, 2001; Cyr et al. 2009), and may have detrimental consequences for maintaining biota that depend on features and processes found in unmanaged forests (Kuuluvainen 2009).

Bryophytes, which include mosses (Bryophyta), liverworts (Marchantiophyta), and hornworts (Anthocerotophyta), can constitute a substantial proportion of the plant diversity in boreal forests. Bryophytes often occur at high cover and biomass on the forest floor (Longton 1992), and influence a number of essential ecosystem processes, including litter decomposition (Uchida et al. 2001), nutrient cycling (Chapin et al. 1987), nitrogen fixation (DeLuca et al. 2007; Gundale et al. 2009), regulation of forest floor temperature and moisture (Bonan and Korzuhin 1989; Fenton and Bergeron 2006), and development of understory vegetation (Parent et al. 2003). Bryophytes also provide habitat for a variety of fungi, protozoa, and invertebrates (Gerson 1982; Döbbeler 2002).

Bryophytes are predominantly poikilohydric, having limited capacity to regulate the uptake and loss of water (Proctor 2009). They lack the root systems and well-developed external cuticle found in vascular plants, but instead have evolved varying levels of desiccation tolerance to facilitate survival during periods of low moisture (Proctor et al. 2007). This permits some species to establish in habitats where vascular plants are generally excluded, such as on rocks and the bark of trees. Despite having mechanisms to cope with low moisture, many forest species typically grow under stable conditions beneath closed forest canopies and are susceptible to prolonged exposure and moisture loss. Forest bryophytes have demonstrated positive density-dependence to increase the growth of colonies under periods of moisture stress (Pedersen et al. 2001), and some species exhibit a colonial growth form in which individual shoots can provide protection for their immediate neighbours, improving their survival under desiccation (Sollows et al. 2001). These adaptations reflect the importance of moisture for forest species, and may account for the large number of positive species associations detected among boreal bryophytes (Økland 1994).

1.1 Factors influencing bryophyte diversity in boreal forests

Regional distributions of bryophyte species are closely related to the availability of suitable habitats and the capacity for species to disperse among them (Vitt and Belland 1997; Söderström and During 2005). In boreal forests, the abundance and properties of substrates available for colonization on the forest floor are strong predictors of bryophyte species composition (McAlister 1995; Crites and Dale 1998; Mills and Macdonald 2004, 2005). Large-diameter pieces of decayed wood are particularly important substrates that can support a large number of species (Söderström 1988). Species diversity at a location is related to habitat heterogeneity (Huston 1994; Weibull and Rydin 2005), and older forests are shown to be important for the development of a variety of forest habitats to support different species (Ohlson et al. 1997; Boudreault et al. 2000). The bark of some tree species becomes increasingly furrowed with age to provide a greater surface area, moisture-retaining capacity, and number of microhabitats for establishment of epiphytes (McGee and Kimmerer 2002; Boudreault et al. 2008). Older forest stands may also provide a greater length of time for species to arrive and become established. However, bryophyte species occurrences in boreal forests may depend more on habitat availability and factors that influence species dispersal and establishment than forest age per se (Ohlson et al. 1997; Fenton and Bergeron 2008; Fritz et al. 2008). In fact, older forests can contain fewer species than younger forests if essential habitats are absent (Fritz et al. 2008). The preservation of forest habitats important to bryophytes is a primary consideration for species conservation in boreal forests.

The capacity to disperse and colonize new substrates is necessary for maintenance of populations and species persistence in boreal forests (Snäll et al. 2004, 2005). Many of the substrates colonized by forest bryophytes have limited duration: standing trees eventually die and fall (e.g., Lõhmus and Lõhmus 2010), and wood on the forest floor can decompose rapidly (Edman et al. 2007). Successful colonization of habitat patches will depend on the distances between habitats (degree of connectivity), habitat longevity, and habitat size (Herben 1994; Heegaard and Hangelbroek 1999; Boudreault et al. 2000; Laaka-Lindberg et al. 2006; Edman et al. 2007). The potential for bryophytes to disperse among habitats also depends on the number of asexual and sexual propagules produced by a species, how efficiently the propagules disperse, and how readily they become established (Ojala et al. 2000; Snäll et al. 2004; Wiklund and Rydin 2004).

Although dispersal is an important factor affecting bryophyte species distributions and population dynamics, its role in the successful establishment of different species remains poorly understood. Some species appear to have few limitations to disperse over longer distances (Ross-Davis and Frego 2002; Hylander 2009), whereas other species exhibit limited capacities for dispersal (Söderström 1987; Laaka-Lindberg et al. 2006). Dispersal limitation is most likely to occur when distances among habitats are large and when a species has high variation in the probability of successful establishment (Laaka-Lindberg et al. 2000; Snäll et al. 2004). Low reproductive output (Laaka-Lindberg et al. 2000) and the relatively large size of many asexual propagules (Kimmerer 1994) can also limit the distances over which species disperse. Asexual propagules are generally considered to be a mechanism for colony maintenance and expansion (Laaka-Lindberg et al. 2000), whereas spores can facilitate the establishment of new colonies by dispersing over longer distances (Miles and Longton 1990). Species life history strategies characterize the relationships between spore size and number, reproductive effort, and plant longevity (During 1979, 1992), and have been used to effectively relate the capacity for species to disperse and persist, with habitat conditions at a site (Jonsson 1993; Frisvoll 1997; Baldwin and Bradfield 2007).

Bryophyte diaspore banks are a mechanism by which species can disperse not only spatially, but also through time. Diaspore banks are repositories of sexual (spores) and asexual (e.g., plant fragments, tubers, gemmae) reproductive propagules that occur naturally in forest soils. Buried propagules that remain viable over an extended period of time may be important for the development of forest floor vegetation following small- and large-scale disturbances that expose mineral soil (Jonsson 1993; During 2001; Ross-Davis and Frego 2004; Kimmerer 2005). Diaspore banks allow species to survive unfavourable periods by dispersing temporally, facilitate rapid colonization after disturbance, and influence the species composition and diversity of post-disturbance sites (Jonsson 1993). They may also have important roles in accumulating and storing genetic diversity for species (Hock et al. 2008).

1.2 Effects of forest harvesting on bryophytes

The unique physiology and often specialized habitat requirements of bryophytes make them susceptible to the effects of forest harvesting. Many species are adversely affected in the first few years after intensive harvesting practices such as clear-cutting or low levels of canopy retention (Quinby 2000; Newmaster and Bell 2002; Ross-Davis and Frego 2002; Fenton et al. 2003; Fenton and Frego 2005; Hylander et al. 2005). Direct effects of forest harvesting on bryophytes include the physical destruction or damage of bryophyte habitat and colonies. Removal of standing trees eliminates habitat for epiphytic bryophytes, which can affect epiphyte persistence within stands (Lõhmus et al. 2006) and across landscapes (Snäll et al. 2004) through altered growing conditions and reduced habitat connectivity. Studies from managed European forests show that the removal of large-diameter coarse woody material in advanced stages of decay results in the loss of bryophyte diversity (Andersson and Hytteborn 1991; Kruys et al. 1999; Ódor and Standovár 2001). The abundance of decayed wood, especially larger size classes, is often reduced in managed as compared to natural forests (Siitonen et al. 2000), with implications for maintaining species affiliated with this substrate type.

Indirect effects of harvesting on bryophytes are more varied. Understory light availability, ground temperatures, and regeneration of broadleaf trees and shrubs can increase with harvesting intensity (Prévost and Pothier 2003; Heithecker and Halpern 2006; Macdonald and Fenniak 2007). Changes in light availability can alter biomass accumulation and growth rates in bryophytes (Rincón 1993), and high light intensities have been shown to cause damage to the photosynthetic apparatus of some mosses (Heber et al. 2001). Greater abundances of regenerating broadleaf trees and shrubs results in increased leaf litter and the chances of smothering bryophyte colonies (Longton 1992). Perhaps most notably, forest harvesting can increase evaporative loss and reduce ground level moisture for bryophytes (Fenton and Frego 2005; Hylander et al. 2005; Heithecker and Halpern 2006; Stewart and Mallik 2006). The species most affected by harvesting are often those with greater moisture requirements, such as epixylic species that are restricted to decayed wood (Fenton et al. 2003; Hylander et al. 2005). Epiphytic species also demonstrate high rates of species mortality in the years immediately following harvest, and slow rates of recovery (Lõhmus et al. 2006; Lõhmus and Lõhmus 2010). In selectively-cut hardwood forests, epiphytic bryophyte communities were dominated by xerophytic bryophytes, whereas intact old-growth forests contained a greater representation of calcioles and mesophytic species (McGee and Kimmerer 2002).

The impacts of forest harvesting on bryophytes will depend on multiple interacting factors, including the attributes of habitat retained and suitability of growing conditions in the harvested matrix, and the sensitivity and resilience (i.e., capacity to absorb disturbance without substantial change; sensu Holling 1973) of bryophyte species to forest modification. Retention of mesic forest floor habitats after harvesting will be important for preserving species with high moisture requirements and sensitivity to canopy removal (Hylander et al. 2005). Upland forest sites can have fewer mesic habitats than topographically lower sites and can exhibit slower rates of species recovery after harvesting (Dynesius et al. 2009). Furthermore, site slope and aspect influence bryophytes through their effects on habitat diversity and moisture retention following harvest (Økland et al. 2003; Åström et al. 2007). The pronounced effects of clear-cutting on some bryophytes and their potential for recovery warrant an examination of forest management practices that may offer a greater capacity to support species persistence and recovery following harvest.

1.3 Potential benefits of partial canopy retention after harvesting

The predominant method of forest harvesting in many boreal regions has been clear-cutting (SCBD 2002); however, there is growing recognition that intensive forest management practices such as clear-cutting do not mimic the variability and structural complexity of unmanaged forests (e.g., Cyr et al. 2009), and will be unsuccessful at maintaining forest biodiversity that depends on natural forest conditions (Kuuluvainen 2009). The conservation of biological diversity is accepted as a fundamental principle of sustainable forest management (Lindenmayer and Franklin 2002) and has led to the adoption of forestry practices in North America and parts of Eurasia that retain greater forest heterogeneity after harvesting (Vanha-Majamaa and Jalonen 2001; Lindenmayer and Franklin 2002; Work et al. 2003; CCFM 2006). In western Canada, green tree retention is perceived by some forestry professionals and companies as an important coarse-filter (sensu Lindenmayer and Franklin 2003) strategy for preserving biodiversity following harvest (Work et al. 2003).

Management practices that retain some level of forest structure after harvesting are generally referred to as variable retention harvesting systems, and vary widely in their application, from the retention of dispersed living ("green") trees to patches of intact forest (Franklin et al. 1997; Lindenmayer and Franklin 2002). Variable retention preserves forest structures in the form of standing trees and fallen wood that were present at the time of harvest (biological legacies, Pharo and Lindenmayer 2009), and is assumed to increase the structural complexity of secondary forests and to "life-boat" (Franklin et al. 1997) species following disturbance. Residual forest structure is thought to create refugia for species by preserving habitats, increasing habitat connectivity, and moderating growing conditions for species in the harvested matrix (Franklin et al. 1997; Vanha-Majamaa and Jalonen 2001; Lindenmayer and Franklin 2002; Rosenvald and Lõhmus. 2008). Furthermore, retention is thought to facilitate forest development towards closed canopy conditions and provide a source of fallen wood as substrata for species establishment in future years. Variable retention practices may, therefore, promote ecosystem resilience by improving species survival and the chances of local dispersal and establishment after harvesting (Turner et al. 1998).

Variable retention harvesting may be particularly beneficial for bryophytes given the documented sensitivity of many species to canopy removal. However, few studies have examined the effectiveness of canopy retention for bryophytes in boreal forests and, of these, the majority have examined the effects of low retention or a single management treatment (e.g., Hannerz and Hånell 1997; Fenton and Frego 2005; Hylander et al. 2005; Lõhmus and Lõhmus 2010). Studies examining the responses of boreal bryophytes along a range of canopy retention levels and across forests of differing canopy composition have not been examined (but see Dovčiak et al. 2006 and Aubry et al. 2009 for forests of the Pacific Northwest). Furthermore, the majority of studies have examined the effects of harvesting on species immediately following canopy removal, but the effects of harvesting on bryophytes in subsequent years may provide a better indication of the potential for future species recovery.

The overarching goal of this thesis was to assess the effectiveness of retained forest canopy structure after partial harvesting for the preservation of bryophytes in managed boreal mixed-wood forests of continental western Canada. Mixed-wood forests in the region comprise stands that occur along a continuum of canopy composition, from purely broadleaf (predominantly *Populus tremuloides* Michx. and *P. balsamifera* L.) to purely coniferous (predominantly *Picea glauca* (Moench) Voss). A forest stand is defined for the purposes of this thesis as an area of forest that is distinct in composition or structure or both from adjacent areas (sensu Lindenmayer and Franklin 2002). Field research was conducted at the Ecosystem Management Emulating Natural Disturbance (EMEND) research site, located in the Lower Boreal–Cordilleran Ecoregion (Strong and Leggat 1992) in northwestern Alberta, Canada. The site marks the transition between boreal and cordilleran vegetation and climatic conditions. The EMEND experiment is a landscape-scale study that was designed, in part, to test the effects of residual forest structure after partial harvesting as a coarse-filter strategy for the conservation of biological diversity (cf. Spence et al. 1999; Work et al. 2004). The large scale of the EMEND experiment (100 stands that comprise > 1,000 ha) allows researchers to make assessments about the effects of harvesting at the forest stand level and inferences to the larger mixed-wood landscape.

For this thesis, the effects of partial harvesting on bryophytes were examined in forests of differing canopy composition along a range of canopy retention levels. Bryophytes were examined in two boreal mixed-wood forest types: mixed broadleaf-coniferous (35–65% broadleaf canopy cover) and coniferous-dominated (> 70% coniferous canopy cover). Within each forest type, stands (each approximately 10 ha in size) were systematically harvested along a range of dispersed green-tree retention levels (unharvested stands as controls) by systematic removal of canopy trees (refer to Spence et al. 1999 for further details of experimental design and protocols, or to individual chapters in this thesis). Stands were previously unmanaged and originated after fire, and within a forest type were similar in pre-harvest ecological site classification, canopy cover and composition, understory vegetation composition, and date of fire-origin. Bryophytes were sampled during the growing seasons of 2004–2005 (i.e., five to six years following harvest) in three replicate stands per retention level per forest type, for a total of 24 sampled stands. The following studies were undertaken to meet the above-stated goal of the thesis.

Chapter 2 – *Responses of boreal epiphytic bryophytes to different levels of partial canopy harvest* – examined the persistence of epiphytic bryophytes that grow on trembling aspen (*P. tremuloides*) along a range of partial harvesting intensities. Epiphytes were sampled using the nearest-neighbour relationships of plants to assess the effects of harvesting intensity on epiphyte community structure. Furthermore, the abundance, richness, and composition of epiphytes on aspen were related to differences in forest structural features and moisture conditions after harvesting to evaluate the most important factors influencing species viability.

Chapter 3 – *Bryophyte community recovery after partial forest harvesting depends on residual canopy structure* – assessed the effectiveness of partial harvesting in forests of differing canopy composition for maintaining natural patterns of bryophyte composition and diversity. Mosses were compared to liverworts, and species with different substrate requirements were compared to one another in terms of their responses to forest canopy retention level and composition. In addition, the effects of harvesting intensity on regional patterns of moss and liverwort diversity were examined through an analysis of species diversity at within plot (alpha) and among plot and among stand (beta) hierarchical levels.

Chapter 4 – *Biological traits of boreal bryophytes reflect species sensitivity to habitat change after partial harvesting* – investigated the effects of partial harvesting on abiotic and biotic forest conditions, and how alteration of forest conditions after harvesting affected different groups of species. First, analyses were conducted to determine the factors that were important drivers of bryophyte species composition after harvesting. Second, bryophyte species with differing biological traits were related to the abundance and composition of retained forest structure, and forest moisture conditions, after partial harvesting, in order to reveal the traits most affected by forest harvesting and the implications for species persistence and recovery. Bryophyte traits included the morphology, habitat requirements, and reproduction and dispersal characteristics of species, considered to be important determinants of species persistence in boreal forests.

Chapter 5 – *Recolonization potential of bryophyte diaspore banks in harvested boreal mixed-wood forest* – examined the capacity for bryophytes to germinate from forest soils to assess the potential role of diaspore banks in the establishment of species after forest harvesting. Mineral soil samples were obtained from forest stands of differing canopy composition that were partially harvested at different intensities. Samples were cultivated in growth cabinets under different light intensities. Germinated species were compared to light regime during cultivation, field soil physical and chemical properties, forest harvesting intensity and canopy composition, and geographic location of the sample site.

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Chapter 2: Responses of boreal epiphytic bryophytes to different levels of partial canopy harvest[1]

Abstract – Epiphytic mosses and liverworts contribute substantially to the bryophyte diversity of circumpolar boreal forests but are susceptible to altered growing conditions after forest harvesting. Management practices that retain some trees after harvest may enhance epiphyte survival; however, the effectiveness of this emerging method needs to be assessed. We examined the survival, composition, and nearest neighbour relationships of epiphytic bryophytes on trembling aspen (*Populus tremuloides* Michx.) across a range (10%–100%) of dispersed green-tree retention 5 years after harvest in boreal mixed-wood forest. Growth of the forest floor moss *Hylocomium splendens* (Hedw.) Schimp. in B.S.G. was used as an indicator of changes in moisture availability for epiphytes following harvesting. Epiphyte richness and abundance increased with canopy retention and were positively correlated with local abundance of coniferous trees. Positive associations among neighbouring species in intact forest demonstrated that interspecies relationships form naturally. However, there was a shift in species composition after harvesting and fewer interspecific associations with declining retention. These trends were accompanied by reduced *Hylocomium splendens* growth, which implies that moisture may be an important driver of epiphyte response. Although different levels of canopy retention were similarly capable of maintaining some epiphytes, the loss of species associated with intact forest will require consideration of alternative management practices for their conservation.

Key words: corticolous, *Hylocomium splendens*, liverwort, moss, poikilohydric, variable retention.

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2.1 Introduction

Forest management practices that retain a greater volume of standing trees after harvest are gradually becoming more widely accepted in place of traditional clearcut methods in North American and Eurasian boreal forests (Lindenmayer and Franklin 2002; Mielikäinen and Hynynen 2003; Canadian Council of Forest Ministers 2006). Variable retention harvesting has been adopted in an effort to maintain habitat heterogeneity in cutover forests to preserve biodiversity (Franklin et al. 2002; Matveinen-Huju et al. 2006). Species may also benefit from improved connectivity among habitat patches within harvested forests (Lindenmayer and Franklin 2002) and landscapes (Snäll et al. 2003, 2004a; Löbel et al. 2006). However, the effectiveness of tree retention for the conservation of forest biota needs to be tested to infer the consequences of this emerging practice.

Bryophytes that grow epiphytically on trees are an important subset of the bryophyte diversity in boreal forests. Many epiphytic bryophytes respond closely to changes in humidity and light intensity as a function of elevation and aspect along the trunk (Smith 1982; John and Dale 1995; Thomas et al. 2001). This suggests that epiphytes may be affected by changes in local growing conditions after harvesting practices that modify the structural attributes of forests. Removal of canopy trees can increase ground-level temperature, incident solar radiation, and air movement, resulting in decreased forest moisture (Chen et al. 1999; Heithecker and Halpern 2006). Diminished forest moisture is implicated in the loss of bryophyte diversity (Fenton and Frego 2005; Hylander et al. 2005). Retaining sufficient forest structure after harvest may, therefore, enhance the vitality (sensu Hazell and Gustafsson 1999) of epiphytes by attenuating extremes in forest climate.

Living trees are an important substrate for obligate and facultative (sensu Smith 1982) epiphytic bryophytes in boreal forests (e.g., Boudreault et al. 2000; Mills and Macdonald 2005; Lõhmus et al. 2006). Obligate epiphytes are usually restricted to the trunks of trees, whereas facultative epiphytes can often establish on other substrate types, including decayed logs and stumps and forest floor (cf.

Andersson and Hytteborn 1991). Host tree specificity of epiphytes is related to bark chemistry and texture (Gustafsson and Eriksson 1995; McGee and Kimmerer 2002), which can affect the germination of bryophyte diaspores (Wiklund and Rydin 2004). In the circumpolar boreal biome, trembling aspen (*Populus tremuloides* Michx.) and Eurasian aspen (*Populus tremula* L.) are particularly important hosts for bryophytes. Aspen bark has a high pH and nutrient status (Gustafsson and Eriksson 1995) and becomes increasingly furrowed with age, providing a greater surface area, roughness, moisture-retaining capacity, and variety of microhabitats for bryophyte establishment (Snäll et al. 2004b; Boudreault et al. 2008b).

There are several means by which residual trees could facilitate bryophyte conservation after forest harvest. Trees colonized by bryophytes might serve as sources for new epiphyte colonization after harvest (Hazell and Gustafsson 1999; Hedenås and Hedström 2007). Epiphytes with limited dispersal capacity may benefit from increased availability of host tree substrates (e.g., Snäll et al. 2003, 2005; Löbel et al. 2006). Moreover, epiphytes may buffer adverse environmental conditions for their immediate neighbours (Pedersen et al. 2001), enhancing species survival and maintenance of species assemblages after harvesting. The effectiveness of these mechanisms may be commensurate with abundance and composition of canopy trees retained. Several studies have examined the influence of forest harvesting on epiphytic lichens (e.g., Esseen and Renhorn 1998; Hedenås and Hedström 2007; Boudreault et al. 2008a) but studies on epiphytic bryophytes in harvested boreal forests are limited and have focused on the response of one or a few species in forests with low retention or a single management treatment (e.g., Hazell et al. 1998; Hazell and Gustafsson 1999; Ojala et al. 2000; Lõhmus et al. 2006). Studies that incorporate a range of disturbance intensities are necessary to better understand the tolerance of individual species and species assemblages, and to assess the consequences of alternative forest management practices on biodiversity conservation.

In this study, our goal was to determine whether or not dispersed canopy retention could support epiphytic bryophytes. We examined epiphytes growing on trembling aspen across a range of different canopy retention levels (10%–100%) after systematic tree removal at the stand level in boreal mixed-wood forest. Epiphytes were sampled using the nearest neighbour relationships of plants (Yarranton 1966; John and Dale 1995; Dale 1999), an approach that has seldom been applied to bryophytes. The method considers a plant to be a point from which its closest neighbouring species is located and recorded (cf. John and Dale 1995). The benefit of using this method is that sampling is conducted at the scale of the plant (Dale 1999), providing a "plant's eye view" (Turkington and Harper 1979) of epiphyte assemblages. Nearest neighbour relationships may provide valuable insight into potential factors influencing epiphyte assemblages in harvested forest ecosystems. Associations between neighbouring pairs of species are defined as either positive or negative depending on whether species are associated more or less frequently than expected by chance. Positive associations can form when species share similar preferences for microhabitat conditions or when one or both species experience some benefit from the relationship. Negative associations can occur when species have differing microhabitat preferences or experience unfavourable interactions (e.g., competition) (cf. John and Dale 1995).

We also used the recent shoot growth of the weft-forming, forest floor moss *Hylocomium splendens* (Hedw.) Schimp. in B.S.G. as a surrogate measure of forest moisture after harvesting. *Hylocomium splendens* is perennial with a modular growth form, adding new segments to existing shoots each year by ramification of the main axis (Økland 1995). Growth of this species corresponds closely to prevailing forest moisture availability (Busby et al. 1978; Hylander 2005) and may reflect the responses of epiphytes to changes in growing conditions after harvesting.

Our objectives were as follows: (*i*) to examine the composition and nearest neighbour relationships of epiphytic bryophytes along a range of canopy retention levels after harvesting, (*ii*) to determine whether an optimal level of retention can be defined to promote epiphyte persistence after harvesting, and (*iii*) to assess the potential for *Hylocomium splendens* to indicate epiphyte response to harvesting.

2.2 Methods

Study area

Our study was located in the Lower Boreal–Cordilleran Ecoregion (Strong and Leggat 1992) in northwest Alberta, Canada (56°46′N, 118°22′W), at the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental area. The region experiences a continental climate with a mean daily temperature of 1.2 °C and mean total precipitation of 402 mm, approximately three-quarters of which falls as rain (Environment Canada 2008). Forests are dominated by varying amounts of broadleaf (*Populus tremuloides* and *Populus balsamifera* L.) and coniferous (*Picea glauca* (Moench) Voss) canopy cover, with lower abundances of *Abies balsamea* (L.) Mill., *Betula papyrifera* Marsh., *Picea mariana* (Mill.) B.S.P., and *Pinus contorta* Dougl. ex Loud. Topographic relief is moderate (elevation ranges from 677 to 880 m above sea level). Most forests in the vicinity originated after fire approximately 100 years ago, but industrial harvesting is becoming an increasingly prevalent form of disturbance on the landscape (Schneider et al. 2003).

Site selection

In the winter of 1998–1999, harvesting treatments of 10%, 50%, 75%, and 100% (unharvested control) dispersed green-tree retention were applied to randomly selected fire-origin stands (each approximately 10 ha in size) of mixed forest (35–65% broadleaf canopy cover). Harvesting was conducted using a modified uniform shelterwood pattern of 5 m wide machine corridors (oriented in a north–south direction, perpendicular to prevailing winds) alternated with 15 m wide retention strips. Retention strips were partially harvested by systematic removal of trees to achieve the desired level of retention for the stand while accounting for the timber removed from the corridors. Machine corridors accounted for 25% of all trees removed from a stand; therefore, no trees were removed from retention strips in stands with 75% retention. Machinery was restricted to the corridors to minimize disturbance to the forest floor and remaining forest structure. Bryophyte sampling was conducted during the 2004 growing season in 12 forest stands (three replicates per harvesting treatment). Replicates were similar in preharvest ecological site classification, understory vegetation composition, and age (Work et al. 2004).

Six 50 m^2 circular plots were randomly established in each forest stand to obtain the following measures of stand structure: percent cover of broadleaf and coniferous trees (assessed at 1 m height by convex spherical densiometer); cover of graminoids, forbs, dominant forest floor mosses (*Hylocomium splendens*, *Pleurozium schreberi* (Brid.) Mitt., and *Ptilium crista-castrensis* (Hedw.) De Not.), dead forest floor mosses, and exposed mineral soil using visual estimates; basal area and density of broadleaf and coniferous trees and shrubs ≥ 2 m height (separately for stems < 5 and ≥ 5 cm DBH (diameter at 1.3 m height)) and cover and density of broadleaf and coniferous trees and shrubs < 2 m height (assessed in a central 10 m^2 circular subplot); aspect (degrees from north); slope (degrees); and depth (centimetres) of the litter-fermented humus layer.

Several shoots of *Hylocomium splendens* were arbitrarily selected from 1 m × 1 m plots located at the centre of each 50 m^2 plot. If *Hylocomium splendens* was not found in the 1 m × 1 m plot, then it was collected elsewhere within the larger 50 m^2 plot. The species was either absent or dead in three plots. Sampled shoots were collected and air dried, and length of the mature segment from the previous growing season was measured under a dissecting microscope to within 0.4 mm. Shoots were not measured if they were dead or damaged, exhibited a monopodial growth form (continuous growth of the shoot with poorly defined annual segments; Økland 1995), or had recent branching along the stem within 1 year of the segment being measured. A total of 1,464 shoots were used for analysis (mean of $n = 21$ per plot).

Epiphyte sampling

Between six and eight aspen trees were sampled for epiphytic bryophytes in each of the three stands of each harvesting treatment for a total of 80 sampled trees. The closest aspen tree to each of the established 50 m^2 circular plots was sampled if it met the following criteria: minimum diameter = 27 cm DBH, alive, healthy (did not show signs of disease or mortality), vertical (not noticeably leaning), and lacking physical damage as a result of mechanical or animal activity. Occasionally, one or two extra trees were randomly selected and sampled in a stand if they met these criteria to increase sample size. Large-diameter trees were used to standardize by size and because epiphyte colonization often depends on large trees, which tend to be older, thereby providing more time and surface area for species establishment (Snäll et al. 2004b; Ranius et al. 2008). Diameter of sampled trees was not significantly different among retention levels ($F_{[3,8]} = 0.54$, $P = 0.665$; mean DBH = 40.48 cm). Sampling dates were randomized among treatments to reduce temporal influence on species composition or response.

Trees meeting the above criteria were sampled using nine horizontal, circumferential line transects around the trunk (cf. John and Dale 1995). One transect was placed every 20 cm from 5 to 165 cm height above the ground. Starting on the north side of each tree, points were located every 10 cm along each transect. The distance between the last and first points on each transect was recorded to calculate stem circumference. The species at each point was recorded along with the closest neighbouring species that was contacting or overlapping it. When the species at a point was not in contact with a neighbour, then the next closest species within a 5 cm radius was recorded (John and Dale 1995). Points and neighbours were not allowed to be the same species unless the area within the 5 cm radius boundary was occupied by a single species. Dead bryophytes and uncolonized bark were often abundant at higher harvesting intensities and were used as a "species" category for a point or nearest neighbour. Plants were classified as dead if they were bleached and discoloured or lacked chlorophyllous tissue when examined with a hand lens. A total of 10,346 point–neighbour pairs were recorded and used for analysis (mean of $n = 129$ per tree).

Species that could not be identified in the field were collected and subsequently determined in the laboratory. Nomenclature follows Anderson et al. (1990) for mosses and Stotler and Crandall-Stotler (1977) for liverworts. Voucher specimens are deposited at the Devonian Botanic Garden (ALTADBG) and Department of Biological Sciences (ALTA) herbaria, University of Alberta.

Analysis of epiphyte response to retention level

Composition of epiphytes on aspen trunks was compared among retention levels by ordination using a matrix of mean relative abundance per species for each forest stand. For each species, relative abundance was calculated as the proportion of all samples (transect points plus neighbours) at which it occurred on each tree. We used mean relative abundance per species for each forest stand because individual trees are nonindependent subsamples. Data were arcsine square root transformed (Sokal and Rohlf 1995) and analyzed by principal component analysis (PCA) (assumes linear responses of species along gradients) because the longest gradient length detected by detrended correspondence analysis was short at 0.95 SD units (ter Braak and Šmilauer 2002). Indicator species analysis (Dufrêne and Legendre 1997) was performed in PC-ORD 5.06 (McCune and Mefford 2006) to detect if species were significantly affiliated with a particular retention level. Data were arcsine square root transformed and tested for significance using 9,999 permutations.

Differences in species composition among harvesting treatments were tested by multivariate analysis of variance (MANOVA) in a distance-based redundancy analysis (db-RDA) (Legendre and Anderson 1999) using a matrix of mean relative abundance per species for each forest stand. The method allows users to choose a measure of species resemblance that is appropriate for the data and uses permutation tests to assess significance, which do not require the assumption of multivariate normality. RDA was used to analyze the principal coordinates obtained from a principal coordinate analysis of species data that were arcsine square root transformed and represented using Bray-Curtis dissimilarity (Legendre and Legendre 1998) after correcting for negative eigenvalues (ter Braak and Šmilauer 2002). Harvesting treatments were coded as orthogonal environmental variables. Pairwise comparisons of harvesting treatments were conducted using 9,999 permutations for tests of significance and assessed after sequential Bonferroni correction for multiple tests (Holm 1979). Analyses were performed using CANOCO 4.5 (ter Braak and Šmilauer 2002).

Epiphyte richness was calculated as the total number of species sampled on each tree using all samples (transect points plus neighbours); abundance of all living epiphytes and uncolonized tree surfaces (bark) was calculated as the proportion of all transect points (excluding neighbours) on each tree. Comparisons among harvesting treatments were made for tree "bases" (transects 1 and 2, 5 and 25 cm height, respectively), "trunks" (transects 3–9, 45–165 cm height), and bases and trunks combined (transects 1–9, 5–165 cm height). The two height classes account for the strong vertical zonation (sensu Trynoski and Glime 1982) in terms of species composition and richness on trees.

We conducted nested analysis of variance (ANOVA) using PROC MIXED in SAS 9.1 (SAS Institute Inc., Cary, North Carolina) to compare epiphyte richness and abundance, abundance of uncolonized bark, and *Hylocomium splendens* growth to retention level. Nested ANOVA was also used to compare the abundance of the two most frequent epiphytes, *Pylaisiella polyantha* (Hedw.) Grout and *Orthotrichum obtusifolium* Brid., to retention level. Tests were conducted using forest stand nested within harvesting treatment as a random factor, which considered trees within each forest stand as subsamples (plots within each forest stand as subsamples for analysis of *Hylocomium splendens* growth). Data were transformed when appropriate before analysis and pairwise comparisons were conducted using Tukey-Kramer's tests when the overall *F* test was significant.

The relationship between forest structure variables (e.g., canopy cover) and epiphyte richness and abundance was examined by Spearman rank correlation using PROC CORR (SAS Institute Inc., Cary, North Carolina). Correlations were only examined for tree bases and were based on mean values per stand ($n = 12$). Forest structure variables were also compared with site scores obtained from PCA axes 1 and 2 to explore factors influencing species compositional change along these gradients. All statistical tests were considered significant at $\alpha = 0.05$.

Analysis of epiphyte neighbour relationships

Neighbour data obtained from sampled trees were analyzed separately for each of the four harvesting treatments. Only data from tree bases were used because the richness and abundance of species on tree trunks were noticeably reduced; their inclusion would have obscured assessments of species relationships.

For each harvesting treatment, data were kept in "unfolded" form, with point and neighbour samples left as distinct from each other (de Jong et al. 1983). Data consisting of k species were arranged in a $k \times k$ contingency table, with each cell in the table, O_{ij}, representing the observed number of times point species i had species j as its neighbour (Dale 1999). The method can therefore distinguish among three types of species associations (Dale 1999): (*i*) when two species, e.g., A and B, are associated with each other, (*ii*) when A is associated with B but B is not associated with A, and (*iii*) when B is associated with A but A is not associated with B. Expected values, E_{ij}, in the table were based on the hypothesis of independence (i.e., no relationship among the row and column categories of the contingency table; Sokal and Rohlf 1995). The entire table was tested for independence using the G statistic, which is compared with the χ^2 distribution on $(k - 1)(k - 1)$ degrees of freedom (Sokal and Rohlf 1995): $G = 2\Sigma\Sigma O_{ij} \ln(O_{ij}/E_{ij})$.

Some species occurred infrequently in a particular harvesting treatment, resulting in small expected values in the contingency table. To correct for this problem, data for some species were pooled into larger taxonomic categories (John and Dale 1995; Sokal and Rohlf 1995) to produce expected values > 1 (Legendre and Legendre 1998). Species belonging to the family Mniaceae and genus *Brachythecium* were pooled into single categories because of their similar habitat preferences in mixed-wood forest (Koponen 1974; Crum and Anderson 1981). A category of "live bryophytes" combined several species that occurred too infrequently in the data set to be analyzed separately. Each harvesting treatment contained a unique set of species abundances; therefore, the number of categories used for each treatment and the species contained within each category are slightly different.

If the hypothesis of independence for the entire table was rejected, then Freeman-Tukey deviates were calculated for each cell (Sokal and Rohlf 1995): $Z_{ij} = (O_{ij})^{0.5} + (O_{ij} + 1)^{0.5} – (4E_{ij} + 1)^{0.5}$. The significance of each cell was then determined by comparison with the following critical value (Sokal and Rohlf 1995): $(v\chi^2_{[1,\alpha/\#\text{cells}]}/\#\text{cells})^{0.5}$, where v is degrees of freedom and #cells is the number of cells in the contingency table, which incorporates the recommended Bonferroni correction for multiple tests (Legendre and Legendre 1998). Parameter E_{ij} is significantly different from O_{ij} when the absolute value of the test statistic is larger than the critical value. However, tests of significance can be too liberal (i.e., increase the rate of Type I error) if species sampled along transects exhibit positive spatial autocorrelation (Dale 1999). Therefore, the effects of spatial autocorrelation were accounted for in tests of significance for neighbour relationships. For each harvesting treatment, the G statistic and Freeman-Tukey deviates were adjusted by the effective sample size, which is smaller than the actual sample size in the presence of positive autocorrelation and correctly modifies the power of the tests. Effective sample size was determined using the formulae presented in Dale and Fortin (2009) for goodness-of-fit tests. The effects of autocorrelation for each harvesting treatment and the sizes of the applied corrections were small, likely because values of positive and negative autocorrelation were fairly balanced. Significance of G statistics and Freeman-Tukey deviates were not affected by the applied corrections.

2.3 Results

Response of epiphytes to retention level

A total of 23 bryophyte species was recorded on aspen trees even though the chosen sampling method (nearest neighbour relationships) does not capture as many species as, for example, full surveys of trees. Indeed, unsampled species observed at the base of trees remain unaccounted for. Most sampled species were pleurocarpous mosses (65.2%) followed by acrocarpous mosses (21.7%) and liverworts (13.0%) (Appendix 2.1). Facultative epiphytes (91.3%) were better represented than obligate epiphytes (8.7%), which consisted solely of the acrocarpous mosses *Orthotrichum obtusifolium* and *Orthotrichum speciosum* Nees in Sturm.

A substantial proportion of the variation in epiphyte composition was explained by PCA (axis 1 = 61.9%, axes 1–4 = 89.1%). Axis 1 represents a gradient of harvesting intensity, with intact (control) forest exhibiting positive scores and forests with 10% and 50% retention exhibiting negative scores (Figure 2.1). High-retention (75%) forest had both positive and negative scores along this axis. Species with > 25% explained variation along the plotted axes tended to have positive loadings on axis 1, in close association with intact or high-retention (75%) forests. The obligate epiphyte *Orthotrichum obtusifolium* had the greatest eigenvector weight on axis 1. All other species with positive eigenvector weights on axis 1 were facultative epiphytes, comprising the pleurocarpous mosses (in order of decreasing eigenvector weights) *Sanionia uncinata* (Hedw.) Loeske, *Eurhynchium pulchellum* (Hedw.) Jenn., *Brachythecium campestre* (C. Müll.) Schimp. in B.S.G., *Thuidium recognitum* (Hedw.) Lindb., *Brachythecium erythrorrhizon* Schimp. in B.S.G., *Pylaisiella polyantha*, *Brachythecium albicans* (Hedw.) Schimp. in B.S.G., and *Hylocomium splendens*, and the acrocarpous mosses (in order of decreasing eigenvector weights) *Mnium spinulosum* Bruch & Schimp. in B.S.G., *Plagiomnium drummondii* (Bruch & Schimp.) T. Kop., *Oncophorous wahlenbergii* Brid., and *Plagiomnium cuspidatum* (Hedw.) T. Kop. Few species had negative eigenvector weights on axis 1 but included the pleurocarpous moss *Brachythecium salebrosum* (Web. & Mohr) Schimp. in B.S.G., acrocarpous moss *Orthotrichum speciosum*, and liverwort *Ptilidium pulcherrimum* (G. Web.) Hampe.

Most species experienced declining abundance with loss of canopy retention (Figure 2.1; Appendix 2.1) resulting in the detection of significant indicator species for intact forest only: *Mnium spinulosum* (indicator value (IV) = 71.4, *P* = 0.038), *Brachythecium erythrorrhizon* (IV = 49.6, *P* = 0.020), *Brachythecium campestre* (IV = 46.9, *P* = 0.030), *Orthotrichum obtusifolium* (IV = 41.4, *P* = 0.020), *Eurhynchium pulchellum* (IV = 37.1, *P* = 0.041), and *Pylaisiella* *polyantha* (IV = 28.8, $P = 0.037$). Changes in epiphyte abundance along the retention gradient also influenced the composition of epiphyte assemblages. Results of MANOVA using db-RDA confirmed that epiphyte composition differed among the four harvesting treatments ($F\# = 2.76$, $P = 0.007$), with pairwise comparisons revealing a significant difference between low-retention (10% and 50%) and intact forests (10% versus 100%: $F\# = 4.98$, $P = 0.001$; 50% versus 100%: $F\# = 3.50$, $P = 0.006$). Composition did not differ between remaining treatment pairs but a disparity was evident between 75% and 100% retention (10% versus 50%: $F\# = 0.82$, $P = 0.541$; 10% versus 75%: $F\# = 1.45$, $P = 0.192$; 50% versus 75%: $F\# = 0.433$, $P = 0.895$; 75% versus 100%: $F\# = 2.22$, $P = 0.056$).

Epiphyte richness and abundance and abundance of uncolonized bark responded to harvesting (Figure 2.2). Mean richness was greatest in intact forest and decreased with declining retention for tree bases ($F_{[3,8]} = 11.89$, $P = 0.003$), trunks ($F_{[3,8]} = 5.88$, $P = 0.020$), and also for both tree segments combined ($F_{[3,8]} = 12.72$, $P = 0.002$). In all cases, richness in intact forest was significantly different from the lowest (10% and 50%) retention levels. Epiphyte abundance was also greatest in intact forest, which was significantly different from all harvested retention levels for tree bases ($F_{[3,8]} = 11.77$, $P = 0.003$), trunks ($F_{[3,8]} = 32.51$, $P < 0.001$), and both tree segments combined ($F_{[3,8]} = 31.65$, $P < 0.001$). Abundance of uncolonized bark showed the opposite response. There was significantly less uncolonized bark in intact forest than in the lowest retention level for tree bases and trunks combined ($F_{[3,8]} = 5.40$, $P = 0.025$). Although not significant, strong trends were observed among retention levels for tree bases ($F_{[3,8]} = 3.80$, $P = 0.058$) and trunks ($F_{[3,8]} = 3.79$, $P = 0.059$).

Epiphyte richness and abundance at the base of trees were also related to prevailing forest structure (Table 2.1). Richness and abundance were positively correlated with total canopy cover and coniferous density (both ≥ 5 and < 5 cm DBH), and negatively correlated with cover of graminoids and dead forest floor feather moss and (for richness only) density of small (< 5 cm DBH) broadleaf trees and shrubs. Intercorrelations revealed that epiphyte richness was positively correlated with abundance for tree bases only, and abundance was negatively correlated with uncolonized bark for tree bases, trunks, and both tree segments combined (Table 2.2).

Changes in species composition along PCA axes 1 and 2 were also related to forest structure (Table 2.1). Increasing site scores along PCA axis 1 represented a gradient of increasing total canopy cover and coniferous density (both ≥ 5 and < 5 cm DBH) and cover of *Hylocomium splendens* on the forest floor, and decreasing cover of graminoids, forbs, and dead forest floor feather mosses. Increasing site scores along PCA axis 2 represented a gradient of increasing broadleaf density (< 5 cm DBH) and decreasing cover of coniferous canopy and forest floor feather mosses.

Epiphyte richness and abundance, abundance of uncolonized bark, and changes in species composition (PCA) were related to changes in forest moisture as detected by *Hylocomium splendens* growth. Growth of *Hylocomium splendens* decreased with canopy harvest ($F_{[3,8]} = 10.74$, $P = 0.004$) but exhibited no significant difference among harvested treatments (Figure 2.3). *Hylocomium splendens* growth was positively correlated with epiphyte richness at the base of trees and with abundance for tree bases, trunks, and both tree segments combined; it was negatively correlated with bark at the base of trees (Table 2.2). Moreover, growth was positively correlated with PCA axis 1, representing a trend of increasing forest moisture with species compositional change along the gradient of increasing retention (Table 2.1).

The two most frequently sampled epiphytes, *Pylaisiella polyantha* and *Orthotrichum obtusifolium*, varied in abundance with height along the trunk and each responded differently to harvesting. Abundance of *Pylaisiella polyantha* was greatest toward the base of trees (Figure 2.4) and exhibited a significant response to retention level ($F_{[3,8]} = 5.06$, $P = 0.030$). Pairwise comparisons indicated that abundance of *Pylaisiella polyantha* in intact forest was greater than in 10% and 50% retention forests. Abundance of *Orthotrichum obtusifolium* was lowest toward the base of trees (Figure 2.4) but also responded to retention level ($F_{[3,8]} = 12.74$, $P = 0.002$). Abundance of *Orthotrichum obtusifolium* dropped abruptly with any level of harvest; pairwise comparisons indicate that abundance in intact forest was greater than for all harvested treatments.

Epiphyte neighbour relationships

Nearest neighbour relationships provided a unique perspective on factors influencing epiphyte assemblages. Overall *G* tests for each harvesting treatment were significant and subsequent analyses revealed that interspecific relationships were strongly structured (Table 2.3). Intact forest had a greater number of positive and negative associations than harvested forest and fewer associations that included “dead” or “bark” categories. In intact forest, positive associations were found among *Brachythecium*, *Eurhynchium pulchellum*, and Mniaceae categories but these relationships were absent from harvested treatments. Instead, the “live bryophytes” category in harvested treatments was positively associated with Mniaceae (10% and 50% retention) and *Brachythecium* (75% retention). Mniaceae occurred too infrequently to be included as a category in the 75% retention treatment and was therefore included in the category for live bryophytes. Fewer positive associations between neighbouring species in harvested forests likely resulted from decreased abundances of species with declining retention (Appendix 2.1). Species that were negatively affected by harvesting tended to be less frequently sampled as a point and more frequently sampled as a neighbour. In comparison, abundance of dead bryophytes and uncolonized bark increased noticeably with decreasing retention and these were thus more likely to be sampled as points. Dead bryophytes were negatively associated with *Brachythecium* and Mniaceae in intact forest and negatively associated with live bryophytes at 75% retention. Dead bryophytes exhibited positive associations with *Eurhynchium pulchellum* and live bryophytes at 75% and 50% retention, respectively. Uncolonized bark was negatively associated with *Brachythecium* and *Eurhynchium pulchellum* (75% retention), Mniaceae (10% and 50% retention), and live bryophytes (all harvested treatments), and was positively associated with dead bryophytes (all harvested treatments).

Although *Pylaisiella polyantha* was one of the most frequently sampled species at the base of trees, it formed few positive associations with other epiphytes, instead forming positive associations with dead bryophytes in all treatments and negative associations with *Brachythecium* and *Eurhynchium pulchellum* in intact forest. However, the species formed a positive association with Mniaceae at 10% retention.

2.4 Discussion

Amount and composition of canopy retention had a considerable influence on the persistence of epiphytic bryophytes in boreal mixed-wood forest 5 years after harvest. These factors need to be considered in managed forests for the conservation of epiphytes. Partial harvesting reduced epiphyte richness and abundance and shifted the composition and nearest neighbour relationships of epiphyte assemblages. These responses were associated with changes in forest structure after harvest and concomitant changes in forest moisture as detected by the growth of *Hylocomium splendens*.

Intact forest was consistently the most effective at maintaining epiphytic bryophytes. Richness declined with canopy removal and was significantly reduced at low levels (10% and 50%) of retention (Figure 2.2). Epiphyte abundance exhibited the same trend but was significantly reduced even at high (75%) retention. Several species were less abundant at low retention (e.g., *Orthotrichum obtusifolium*, *Sanionia uncinata*, and *Eurhynchium pulchellum*), whereas other species such as *Brachythecium salebrosum*, *Orthotrichum speciosum*, and *Ptilidium pulcherrimum* were apparently not as strongly affected (Figure 2.1). The impact of decreasing retention on some species led to significant differences in epiphyte composition between intact and low-retention (10% and 50%) forests and the detection of significant indicator species for intact forest only.

Species varied in their tolerance to harvesting, preferred habitat conditions, and nearest neighbour associations. For example, the response of *Orthotrichum obtusifolium* to declining retention was more pronounced than that of *Pylaisiella* *polyantha* (Figure 2.4). The different responses of these two species may be partly explained by their microhabitat preferences. *Orthotrichum obtusifolium* was significantly more abundant in intact forest than in harvested forests. This could reflect a preference for more shaded conditions (Snäll et al. 2003; Friedel et al. 2006) that may increase moisture availability (Chen et al. 1999) in intact forest. In addition, the increased connectivity of habitat (i.e., tree trunks) in intact forest might improve the chances of local colonization for *Orthotrichum obtusifolium*, which has been shown to have limited dispersal capacity (Snäll et al. 2004a). In intact forest, *Orthotrichum obtusifolium* is most abundant at greater heights along the trunk and is thought to have a higher tolerance to moisture loss than *Pylaisiella polyantha*, which prefers more mesic conditions at the base of trees (Hazell et al. 1998). However, the more exposed habitat of *Orthotrichum obtusifolium* may make it more susceptible to changes in growing conditions after harvesting. The rapid decline in abundance of this species with canopy removal suggests that it may be near the limits of tolerance for moisture availability and that its resilience to habitat perturbation is low. The more mesic habitat of *Pylaisiella polyantha* at the base of trees may buffer it from the effects of harvesting and subsequent forest moisture loss.

Facultative epiphytes such as *Pylaisiella polyantha* may have an adaptive advantage to disturbances that create stressful growing conditions because of their ability to colonize alternative forest floor substrates like fallen wood (Andersson and Hytteborn 1991). This might increase their chances of survival following harvest through avoidance of extreme conditions found at elevated positions on trees. In comparison, obligate epiphytes such as *Orthotrichum obtusifolium* are typically confined to trees and may be more prone to local extirpation after harvesting. This could have important consequences for the distribution of obligate epiphytes over large areas of managed landscapes (e.g., Snäll et al. 2003, 2004b).

The mortality of epiphytes that are susceptible to changes in growing conditions after harvesting could, in turn, affect the response of remaining species and their neighbour relationships. Forest floor (Økland 1994) and epiphytic (Thomas et al. 2001) bryophytes have been characterized as having many positive but few negative interspecific associations. However, studies of nearest neighbour relationships among bryophytes have revealed the presence of negative associations as a result of differences in species habitat preferences or competitive abilities (John and Dale 1995; Dale 1999). This study examined the nearest neighbour relationships of epiphytic bryophytes to provide a detailed look at epiphyte community structure along a range of harvesting intensities. Although a limited number of relationships could be examined statistically (several uncommon species needed to be pooled into larger categories), we found both positive and negative associations among species categories, indicating that bryophytes at the base of aspen are not distributed arbitrarily.

The numbers and types of associations among epiphytes differed between intact and harvested forests. The direction and magnitude of these associations reflected growth form (e.g., wefts, tufts, and mats), microhabitat preferences, size and abundances of species involved, and changes in forest structure after harvesting. The comparatively large size of plants belonging to *Brachythecium*, *Eurhynchium pulchellum*, and Mniaceae categories and their greater abundances and tendency to grow as mats (Hill et al. 2007) in intact forest resulted in their being more frequently detected as point and neighbour samples than other species. *Amblystegium serpens* (Hedw.) Schimp. in B.S.G. and *Isopterygiopsis pulchella* (Hedw.) Iwats., for example, are smaller and less abundant, and commonly grow as single plants among other bryophytes (personal observation).

Brachythecium, *Eurhynchium pulchellum*, and Mniaceae categories were positively associated with one another but were negatively associated with themselves in intact forest (Table 2.3). This implies that species belonging to these categories tended to occur in mixture rather than in isolation. Their common preference for mesic microhabitat conditions at the base of aspen and tendency to occur together suggest that multispecies colonies of epiphytes develop naturally in intact forest. The colonial nature of these relationships may help protect species from stressful conditions like low moisture (Pedersen et al. 2001; Sollows et al. 2001). Bryophytes are most likely to have facilitative effects when plant growth is limited by moisture availability (cf. Pedersen et al. 2001). Facilitation may be particularly important for epiphyte assemblages situated in exposed positions above the forest floor. Under these circumstances, species might provide protection for their immediate neighbours by decreasing air movement or increasing shade, which may improve fine-scale humidity levels.

Fewer significant neighbour relationships were detected with declining retention. This is in part a reflection of decreased abundances of several species with harvest (Appendix 2.1). The survival of epiphytes and their potential to form interspecific relationships on trees are likely affected by changes in microclimate after harvesting. Species mortality may further affect neighbouring species by intensifying the effects of microclimatic change through loss of protective colonial relationships. Indeed, the increased abundance of uncolonized bark and dead bryophytes with declining retention and their positive association with one another in all harvested treatments may signify a more extreme microclimate for epiphytes in harvested forests (Lõhmus et al. 2006). Uncolonized bark and dead bryophytes were negatively associated with *Brachythecium*, *Eurhynchium pulchellum*, Mniaceae, and live bryophytes in all treatments, suggesting that these latter species categories either avoid areas of uncolonized bark on the trunk or experience increased mortality under more severe microclimatic conditions.

In contrast with the colonial relationships formed by species belonging to the *Brachythecium*, *Eurhynchium pulchellum*, and Mniaceae categories, *Pylaisiella polyantha* formed few associations with other species. *Pylaisiella polyantha* exhibited positive associations with dead bryophytes in all treatments and negative associations with *Brachythecium* and *Eurhynchium pulchellum* in intact forest. At 10% retention, the positive association between *Pylaisiella polyantha* and dead bryophytes shifted from *Pylaisiella polyantha* being sampled as either a point or a neighbour to occurring as a neighbour only. The loss of *Pylaisiella polyantha* as a point sample for this association likely resulted from the drop in abundance and associated increase in abundance of dead bryophytes. The mats formed by *Pylaisiella polyantha* at the base of aspen in mature forest are often dense and may prevent the establishment of other species through competitive exclusion. This is likely the cause of the negative associations between *Pylaisiella* *polyantha* and *Brachythecium* and *Eurhynchium pulchellum* in intact forest. *Pylaisiella polyantha* formed a positive association with Mniaceae at 10% retention, possibly reflecting its preference for more mesic microsite conditions under more stressful growing conditions and loss of the mat growth form, which may promote the development of associations with other species.

Hylocomium splendens is well documented in terms of its life history and population biology (e.g., Økland 1995; Økland and Bakkestuen 2004; Rydgren et al. 2006) and has been successfully used as a surrogate measure of moisture availability in boreal forest (Hylander 2005). Busby et al. (1978) found that growth rate of *Hylocomium splendens* was highly correlated with evaporation stress and the length of time that mosses were in a wet state, whereas light intensity and air temperature were poor predictors of growth. In this study, *Hylocomium splendens* growth was significantly correlated with abundance and richness of epiphytes and epiphyte composition (PCA) on trees (Table 2.1). These trends strengthen the argument that changes in forest moisture after harvesting influence the response and persistence of epiphytes in boreal forest. This is also supported by evidence in harvested stream-side boreal forests where concave habitats with greater moisture-retaining capacity on the forest floor were important for bryophyte conservation (Hylander et al. 2005). We demonstrated that *Hylocomium splendens* growth responded to retention level with significant growth reductions in any harvested treatments (Figure 2.3). These findings indicate that various levels of forest perturbations, even seemingly small ones, can influence the response of this species and potentially other poikilohydric bryophytes by reducing available moisture. Furthermore, retention level may act in combination with canopy composition to drive changes in forest moisture. In particular, coniferous trees may be more effective at moderating ground-level microclimate than broadleaf trees. This is suggested by the positive relationships detected between coniferous tree density and epiphyte composition (PCA axis 1), richness, and abundance, and similar positive relationships between *Hylocomium splendens* growth and the same response variables (Table 2.1). Boreal forests with a greater coniferous component are, therefore, expected to provide more favourable growing conditions for epiphytic bryophytes on aspen and increased capacity for epiphyte preservation after harvesting.

Epiphyte survival in the harvested matrix will influence patterns of their recolonization after harvesting and, consequently, the development of forest biota during secondary forest succession. A relatively large number of epiphytic bryophytes (especially facultative ones) have been documented in boreal forest (e.g., Boudreault et al. 2000; Mills and Macdonald 2005; Lõhmus et al. 2006), including 23 species in this study. Populations that persist on residual trees after disturbance may function as centres for re-establishment in the surrounding forest (Andersson and Hytteborn 1991) through a process of "nucleation" whereby initial colonists increase in abundance by expansion from the point of establishment (Yarranton and Morrison 1974). Nucleated succession has been previously inferred for trees in tropical forest (Hooper et al. 2004; Schlawin and Zahawi 2008) and understory vegetation in boreal forest (Kembel and Dale 2006). Remnant trees in boreal clearcuts are thought to provide a temporary link between old and young forests for some lichens (Hazell and Gustafsson 1999; Hedenås and Hedström 2007). However, the same trends have not been observed for epiphytic bryophytes (Rosenvald and Lõhmus 2008), which typically exhibit reduced vitality in low-retention systems (Hazell and Gustafsson 1999; Lõhmus et al. 2006), as revealed in this study.

Management implications

Abundance and composition of retained forest structure after harvesting influenced the persistence of epiphytic bryophytes. Epiphyte richness, abundance, and composition were positively related to total retention and the abundance of coniferous trees. These results underscore the importance of canopy closure for epiphytes and imply that conifers may be more effective at moderating forest microclimate for epiphytes than broadleaf trees. Growth of *Hylocomium splendens* was also positively related to epiphyte richness, abundance, and composition, suggesting that moisture is an important driver of epiphyte responses to harvesting. *Hylocomium splendens* is an effective indicator of epiphyte viability in boreal mixed-wood forest.

Nearest neighbour relationships of species provided unique insight into the structure of epiphyte assemblages. Several species shared positive associations with one another in intact forest, suggesting that mixtures of species form naturally and share similar preferences for habitat conditions. In harvested forests, dead bryophytes and uncolonized bark were positively associated with each other and were accompanied by few positive associations among epiphytes. These trends reflect more extreme growing conditions for epiphytes (Lõhmus et al. 2006) and the degradation of epiphyte community structure with any level of partial harvesting.

Epiphyte richness, abundance, and composition did not differ significantly among the different levels of canopy retention after harvesting. This implies that harvested stands in this study offer similar growing conditions for epiphytes. Indeed, growth of *Hylocomium splendens* did not differ among harvested treatments but differed between harvested and intact forest. For some species, low retention (e.g., 10%) could provide as effective protection for epiphytes as does higher retention (e.g., 50% or 75%). However, any level of harvesting will be detrimental for some species that are closely associated with intact forest. Obligate epiphytes (e.g., *Orthotrichum obtusifolium*) may be more affected by harvesting than facultative species because of their restricted occurrence on trees and inability to avoid extreme growing conditions after harvesting.

Effective conservation of epiphytic bryophytes will require the preservation of forest conditions that support species with low tolerance to tree harvest. Retention of forest patches has been recommended as an approach to conserve epiphytic lichens (Hazell and Gustafsson 1999; Boudreault et al. 2008a) and should be more thoroughly tested as an option for epiphytic bryophytes (Perhans et al. 2009). Forest canopy composition and structure are important factors influencing the response of epiphytic bryophytes and need to be considered for the maintenance of these species in managed boreal landscapes.

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Table 2.1. Spearman rank correlations between measures of forest structure and epiphyte richness and abundance and site scores along PCA axes 1 and 2.

	Epiphyte richness	Epiphyte abundance	PCA 1	PCA 2
Forest canopy				
Canopy cover				
Broadleaf	0.452	0.462	0.315	0.259
Coniferous	0.406	0.343	0.573	**–0.657***
Total	**0.820****	**0.895*****	**0.860*****	–0.231
Stem density (> 2 m), DBH ≥ 5 cm				
Broadleaf	0.088	0.269	0.244	0.332
Coniferous	**0.747****	**0.627***	**0.841*****	–0.522
Total	**0.632***	**0.687***	**0.823****	–0.336
Stem density (> 2 m), DBH < 5 cm				
Broadleaf	**–0.775****	–0.504	–0.550	**0.623***
Coniferous	**0.580***	**0.703***	**0.743****	–0.466
Total	**–0.695***	–0.458	–0.371	**0.825*****
Forest floor				
Hylocomium splendens growth	**0.701***	**0.636***	**0.671***	0.154
Graminoid cover	**–0.907*****	**–0.685***	**–0.727****	0.308
Forb cover	–0.329	–0.210	**–0.664***	**0.601***
Forest floor feather moss cover				
Hylocomium splendens	**0.606***	0.315	**0.601***	**–0.685***
Pleurozium schreberi	0.487	0.021	0.336	**–0.601***
Ptilium crista-castrensis	0.242	–0.140	0.084	**–0.741****
Dead forest floor feather moss cover	**–0.701***	**–0.871*****	**–0.714****	0.138

Notes: Analyses were based on mean values per stand ($n = 12$). Results for epiphyte richness and abundance are for tree bases only. Epiphyte abundance was calculated as the mean proportion of samples on trees for each stand (see Methods). Significant correlations are in bold: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2.2. Spearman rank correlations among epiphyte richness and abundance, abundance of uncolonized bark, and *Hylocomium splendens* growth for tree bases, trunks, and both tree segments combined.

	Epiphyte abundance	Epiphyte richness	*Hylocomium splendens* growth
Tree bases			
Epiphyte richness			**0.701***
Epiphyte abundance		**0.651***	**0.636***
Bark abundance	**–0.860*****	–0.557	**–0.594***
Tree trunks			
Epiphyte richness			0.270
Epiphyte abundance		–0.102	**0.727****
Bark abundance	**–0.839*****	0.137	–0.399
Tree bases and trunks			
Epiphyte richness			0.552
Epiphyte abundance		0.224	**0.699***
Bark abundance	**–0.853*****	–0.203	–0.490

Notes: Analyses were based on mean values per stand ($n = 12$). Epiphyte and bark abundance were calculated as the mean proportion of samples on trees for each stand (see Methods). Significant correlations are in bold: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2.3. Positive and negative associations between species categories for each level of canopy retention based on the chances of a particular neighbour category (to the right of each arrow) being associated with a particular point category (to the left of each arrow).

Positive associations	Negative associations
100% retention (*G*-statistic = 351.7, *P* < 0.001)	
Brachy → Eurpul	**Brachy → Brachy**
Brachy → Mniaceae	*Brachy → Dead*
Dead → Pylpol	Brachy → Pylpol
Eurpul → Mniaceae	Dead → Brachy
Mniaceae → Brachy	**Dead → Dead**
Pylpol → Dead	Dead → Mniaceae
	Eurpul → Eurpul
	Eurpul → Pylpol
	Mniaceae → Mniaceae
	Pylpol → Brachy
	Pylpol → Pylpol
75% retention (*G*-statistic = 406.1, *P* < 0.001)	
Bark → Dead	Bark → Brachy
Brachy → Live	**Bark → Eurpul**
Dead → Eurpul	Bark → Live
Dead → Pylpol	**Dead → Dead**
Pylpol → Dead	*Live → Dead*
	Pylpol → Pylpol
50% retention (*G*-statistic = 315.2, *P* < 0.001)	
Bark → Dead	**Bark → Live**
Dead → Live	**Bark → Mniaceae**
Dead → Pylpol	**Dead → Dead**
Live → Mniaceae	**Pylpol → Pylpol**
Mniaceae → Live	
Pylpol → Dead	

Positive associations	Negative associations
10% retention (*G*-statistic = 376.2, $P < 0.001$)	
Bark → Dead	*Bark → Live*
Dead → Pylpol	**Bark → Mniaceae**
Live → Mniaceae	**Dead → Dead**
Pylpol → Mniaceae	**Mniaceae → Mniaceae**
	Pylpol → Pylpol

Notes: In the positive associations column for 100% retention, Brachy → Eurpul means that *Eurhynchium pulchellum* was found as a neighbour of *Brachythecium* spp. more often than expected by chance (cf. Dale 1999). Only significant associations are presented, with significance level indicated by different fonts: regular, $P < 0.05$; italic, $P < 0.01$; bold, $P < 0.001$. Categories used in the analysis include the following: Bark, uncolonized tree surfaces; Brachy, *Brachythecium* spp.; Dead, dead bryophytes or other (e.g., non-bryophyte); Eurpul, *Eurhynchium pulchellum*; Live, live bryophytes; Mniaceae, species belonging to the family Mniaceae; Pylpol, *Pylaisiella polyantha*. See Appendix 2.1 for details.

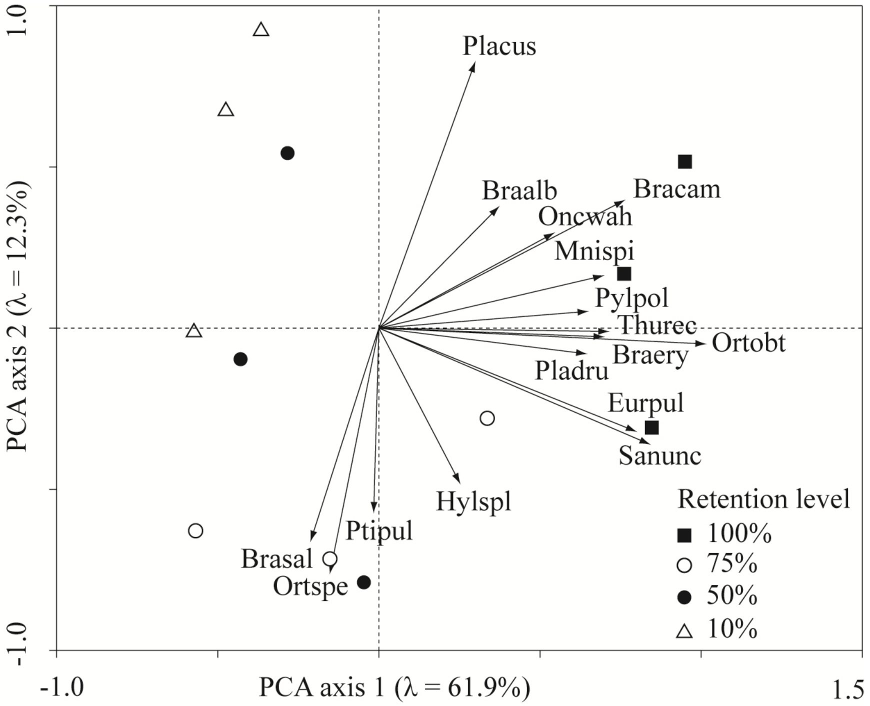

Figure 2.1. Results of PCA on 23 species in 12 forest stands for four levels of canopy retention (10%–100%). The analysis is based on epiphyte composition using the full range of transect heights on trees and the mean relative abundance per species for each stand. Locations in ordination space of species with > 25% explained variation are displayed. Braalb, *Brachythecium albicans*; Bracam, *Brachythecium campestre*; Braery, *Brachythecium erythrorrhizon*; Brasal, *Brachythecium salebrosum*; Eurpul, *Eurhynchium pulchellum*; Hylspl, *Hylocomium splendens*; Mnispi; *Mnium spinulosum*; Oncwah, *Oncophorous wahlenbergii*; Ortspe, *Orthotrichum speciosum*; Ortobt, *Orthotrichum obtusifolium*; Placus, *Plagiomnium cuspidatum*; Pladru, *Plagiomnium drummondii*; Ptipul, *Ptilidium pulcherrimum*; Pylpol, *Pylaisiella polyantha*; Sanunc, *Sanionia uncinata*; Thurec, *Thuidium recognitum*.

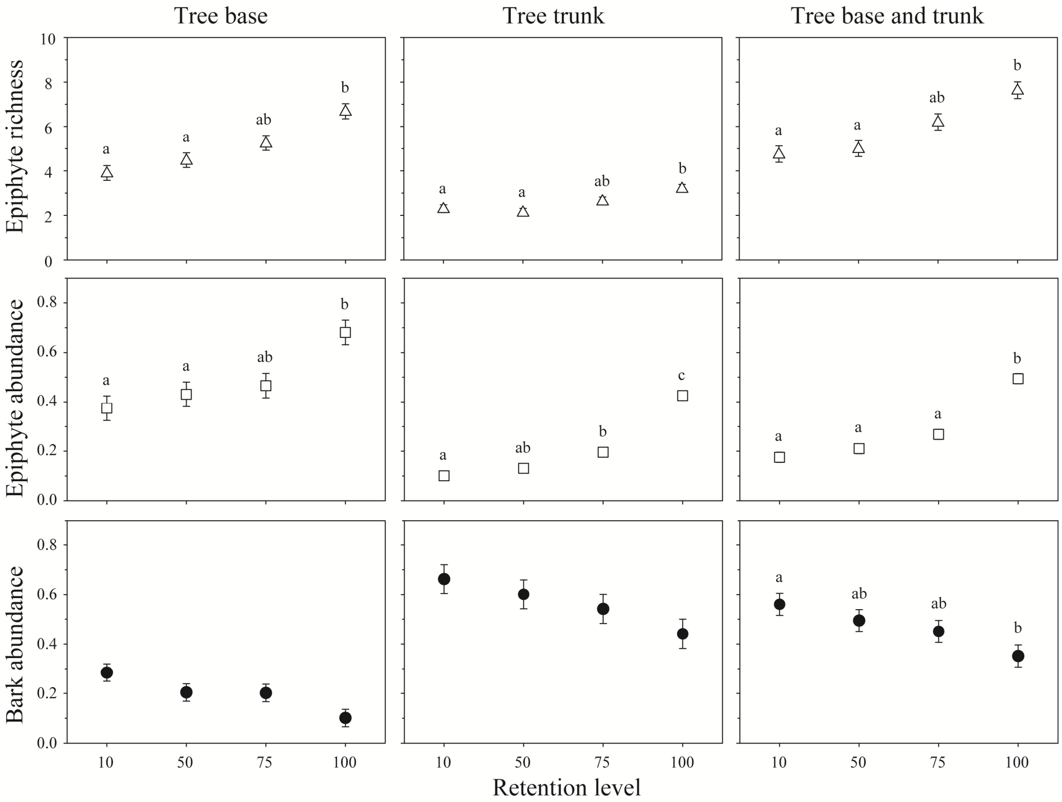

Figure 2.2. Mean ± 1 SE for epiphyte richness and abundance and abundance of uncolonized bark for each level of canopy retention (*n* = 3 forest stands per retention level). Abundance of epiphytes and uncolonized bark was calculated as the mean proportion of samples on trees for each stand (see Methods). Separate analyses were conducted for tree bases (left panels), trunks (centre panels), and bases and trunks combined (right panels). Means with different letters were significantly different based on nested ANOVA.

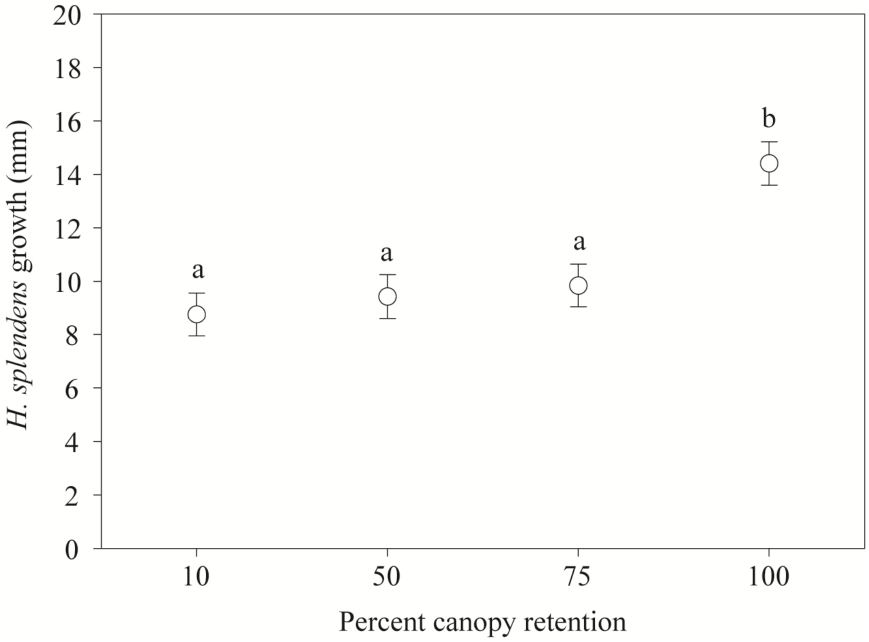

Figure 2.3. Mean ± 1 SE for *Hylocomium splendens* growth at each level of canopy retention ($n = 3$ forest stands per retention level). Means with different letters were significantly different based on nested ANOVA.

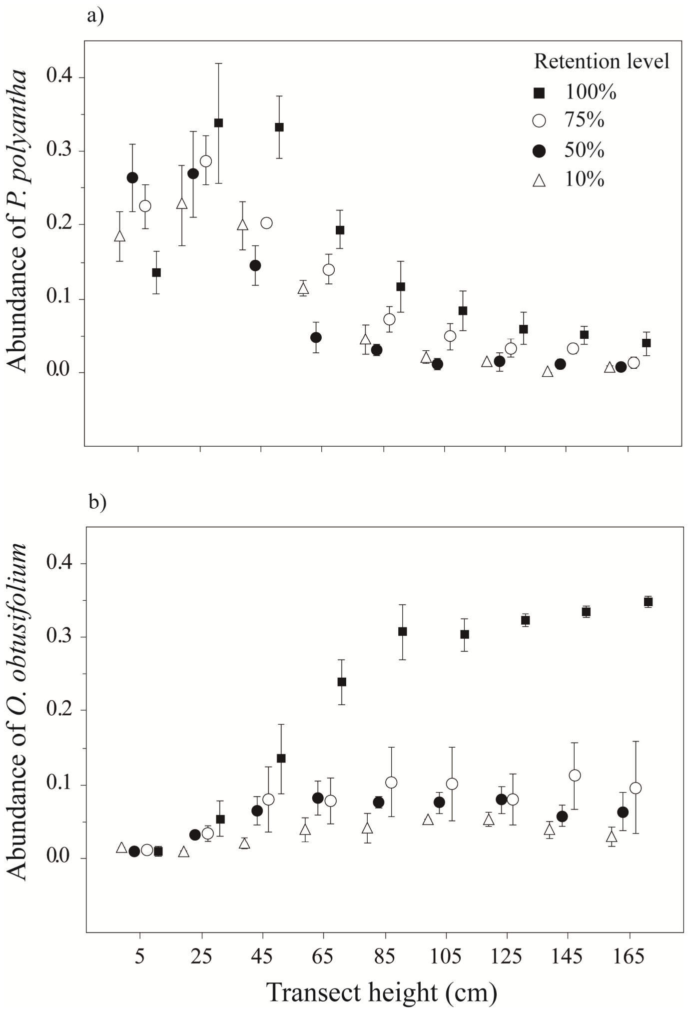

Figure 2.4. Mean ± 1 SE for abundance of (*a*) *Pylaisiella polyantha* and (*b*) *Orthotrichum obtusifolium* along the full range of transect heights on trees for each level of canopy retention (*n* = 3 forest stands per retention level). Abundance was calculated as the mean proportion of samples on trees for each stand (see Methods). Pairwise comparisons indicate that abundance of *Pylaisiella polyantha* in intact forest was significantly different from that for 10% and 50% retention and abundance of *Orthotrichum obtusifolium* in intact forest was significantly different from that for all retention levels. Results are based on nested ANOVA.

Appendix 2.1. Abundance (proportion) of epiphytic bryophytes and substrates sampled at the base of trembling aspen (*Populus tremuloides*) as either the point (Pt) or neighbour (Nb) for the different levels of canopy retention.

			100% retention (*n* = 19 trees, 607 sample pairs)[a]			75% retention (*n* = 20 trees, 713 sample pairs)			50% retention (*n* = 21 trees, 714 sample pairs)			10% retention (*n* = 20 trees, 741 sample pairs)		
Species	Tendency[b]	Plant type[c]	Pt	Nb	Category	Pt	Nb	Category	Pt	Nb	Category	Pt	Nb	Category
Amblystegium serpens	F	P	0.005	0.025	Live	0.003	0.007	Live	0.006	0.008	Live	0.003	0.018	Live
Bark			0.185	0.013	Dead	0.359	0.060	Bark	0.366	0.042	Bark	0.472	0.094	Bark
Brachythecium albicans	F	P	0.002	0.003	Brachy		0.001	Brachy					0.003	Live
Brachythecium campestre	F	P	0.046	0.049	Brachy	0.006	0.014	Brachy	0.001	0.008	Live	0.007	0.026	Live
Brachythecium erythrorrhizon	F	P	0.048	0.068	Brachy	0.008	0.010	Brachy	0.015	0.014	Live	0.004	0.018	Live
Brachythecium salebrosum	F	P	0.008	0.008	Brachy	0.024	0.017	Brachy	0.006	0.031	Live	0.004	0.003	Live
Campylium hispidulum	F	P											0.003	Live
Dead bryophytes			0.216	0.208	Dead	0.332	0.290	Dead	0.364	0.273	Dead	0.336	0.320	Dead
Dead *Orthotrichum* sp.			0.002	0.015	Dead	0.010	0.029	Dead	0.028	0.056	Dead		0.012	Dead
Dicranum fragilifolium	F	A				0.001		Live		0.001	Live			
Eurhynchium pulchellum	F	P	0.157	0.104	Eurpul	0.056	0.076	Eurpul	0.017	0.049	Live	0.018	0.043	Live
Hylocomium splendens	F	P	0.003	0.008	Live	0.004	0.004	Live	0.006	0.006	Live		0.001	Live
Isopterygiopsis pulchella	F	P	0.002	0.002	Live									
Lophozia ventricosa	F	L	0.002	0.002	Live		0.001	Live						
Mnium spinulosum	F	A	0.020	0.016	Mniaceae	0.001		Live		0.001	Mniaceae	0.001	0.001	Mniaceae
Oncophorous wahlenbergii[d]	F	A												
Orthotrichum obtusifolium	O	A		0.021	Live	0.004	0.038	Live	0.006	0.035	Live	0.003	0.020	Live
Orthotrichum speciosum	O	A	0.007	0.030	Live	0.003	0.014	Live	0.001	0.006	Live		0.001	Live
Other (non-bryophyte)						0.003		Dead	0.004		Dead	0.011		Dead
Plagiomnium cuspidatum	F	A	0.100	0.114	Mniaceae	0.021	0.043	Live	0.039	0.066	Mniaceae	0.065	0.097	Mniaceae
Plagiomnium drummondii	F	A	0.007	0.013	Mniaceae									
Ptilidium pulcherrimum	F	L		0.003	Live	0.006	0.004	Live	0.003	0.003	Live			

Species	Tendency[b]	Plant type[c]	100% retention (n = 19 trees, 607 sample pairs)[a]			75% retention (n = 20 trees, 713 sample pairs)			50% retention (n = 21 trees, 714 sample pairs)			10% retention (n = 20 trees, 741 sample pairs)		
			Pt	Nb	Category	Pt	Nb	Category	Pt	Nb	Category	Pt	Nb	Category
Ptilium crista-castrensis	F	P					0.001	Live						
Pylaisiella polyantha	F	P	0.185	0.264	Pylpol	0.153	0.373	Pylpol	0.137	0.396	Pylpol	0.077	0.339	Pylpol
Radula complanata	F	L					0.001	Live						
Sanionia uncinata	F	P	0.008	0.028	Live	0.006	0.014	Live	0.001	0.004	Live		0.001	Live
Thuidium recognitum	F	P		0.007	Live									

Notes: Species abundance was calculated as a proportion and was determined separately for all point samples and all neighbour samples for each treatment. The following categories were assigned to each species for the nearest neighbour analysis: Bark, uncolonized tree surfaces; Brachy, *Brachythecium* spp.; Dead, dead bryophytes or other (e.g., non-bryophyte); Eurpul, *Eurhynchium pulchellum*; Live, live bryophytes; Mniaceae, species belonging to the family Mniaceae; Pylpol, *Pylaisiella polyantha*.

[a] Sample pairs is the total number of samples for points and for neighbours recorded on tree bases for each retention level.

[b] Tendency denotes facultative (F) or obligate (O) epiphytes.

[c] Plant type denotes pleurocarpous moss (P), acrocarpous moss (A), or liverwort (L).

[d] *Oncophorous wahlenbergii* was sampled higher up on the trunk (100% retention) and was not included.

Chapter 3: Bryophyte community recovery after partial forest harvesting depends on residual canopy structure

Abstract – Forest harvesting practices designed to conserve biodiversity require further insight into the relationship between species habitat requirements and how these are preserved after harvest. We examined the effects of different levels (10%, 50%, and 75%) of dispersed green-tree retention (unharvested stands as controls) on the diversity and composition of bryophytes five to six years after partial harvesting, in boreal mixed-wood forest types with contrasting abundances of broadleaf and coniferous trees. Bryophytes were sampled in large (> 0.1 ha) plots in 24 forest stands (each 10 ha) using a factorial experimental design with replication at the stand level. Mosses and liverworts both responded to retention level and forest type but liverwort response was more pronounced. Liverwort richness and diversity were reduced at low (10% and 50%) retention, and composition differed between all harvested levels and the control. In comparison, mosses did not differ in richness or diversity among retention levels but shifted in composition from intact forest at low retention. Bryophyte responses to harvesting were partly explained by species substrate preferences: epixylics on decayed wood and epiphytes on bark experienced declines in richness with any level of harvesting, whereas trends for species on other substrates were not as apparent. Furthermore, harvesting influenced regional patterns of species diversity, as revealed by additive partitioning of diversity into within-plot (alpha) and among-plot and among-stand (beta) components. For both mosses and liverworts, total beta diversity explained the greatest proportion of total diversity for each retention level, signifying that multiple sites and stands are important for species representation at any disturbance level. The substantial contribution of beta diversity within each harvesting treatment resulted partly from species differences between forest types. However, total beta diversity of liverworts increased substantially with harvesting, reflecting greater among-site differentiation with increasing disturbance. Results highlight the importance of canopy retention and composition for maintaining bryophytes in managed forests. Although several species persisted at low retention, intact forest is required for the conservation of numerous species sensitive to harvest. Implementation of conservation strategies for bryophytes in managed boreal forests should consider species diversity at local scales and also among sites and entire stands.

Key words: *additive partitioning*, *beta diversity*, *disturbance*, *epiphytic*, *epixylic*, *liverwort*, *moss*, *variable retention*

3.1 Introduction

Habitat loss and declines in habitat quality can have profound consequences for maintaining the structure and dynamics of biotic communities across landscapes (Hanski 1998; Velland et al. 2006). In harvested forests, measures to protect biodiversity are increasingly being integrated into management practices and policies to balance both economic and ecological values in the forest matrix (Lindenmayer and Franklin 2002). Variable retention harvesting is one such approach that has been gaining acceptance in place of clear-cut practices in regions of North America and Eurasia (Franklin et al. 1997; Vanha-Majamaa and Jalonen 2001; Lindenmayer and Franklin 2002; Canadian Council of Forest Ministers 2006). Variable retention preserves biological legacies (sensu Pharo and Lindenmayer 2009) in the form of standing live trees and coarse woody material on the forest floor, and is presumed to reduce the magnitude of change in biotic communities following harvesting by “life-boating” species through the post-disturbance period and facilitating more rapid recovery of forests during secondary succession (Lindenmayer and Franklin 2002). However, the effectiveness of such retention for the conservation of many species groups remains poorly understood, requiring knowledge of the ways target organisms respond along the range of forest conditions that develop after harvesting.

Variable retention harvesting systems may be particularly beneficial for mosses and liverworts (bryophytes), organisms that lack physiological features to regulate their internal water balance (Proctor 2009). Bryophytes are a conspicuous and ecologically important component of boreal forests. Forest floor feather mosses commonly attain high biomass in intact stands and have the capacity to influence ecosystem processes, including regulation of forest soil moisture and temperature, nitrogen fixation and nutrient sequestration, and tree regeneration (Chapin et al. 1987; DeLuca et al. 2002; Parent et al. 2003; Lavoie et al. 2005; Nilsson and Wardle 2005). Uncommon species may also provide important ecosystem functions (Lyons et al. 2001), and are often the focus of conservation efforts because of their restricted occurrences on landscapes and greater susceptibility to extirpation resulting from stochastic events (Matthies et al. 2004). At fine scales, bryophytes may buffer the effects of adverse environmental conditions for their immediate neighbours to enhance species survival and the integrity of bryophyte assemblages (Sollows et al. 2001).

Forest harvesting can affect the abundance and survival of bryophytes through direct and indirect changes to forest conditions following canopy removal (Hylander et al. 2005; Aubry et al. 2009). Past research has demonstrated that clear-cutting can have residual effects on bryophytes that last for decades (Dynesius and Hylander 2007; Dynesius et al. 2009). Direct effects include the physical disruption of bryophyte populations or habitat; whereas indirect effects include modification of local microclimate and habitat quality. Forestry practices may disrupt natural patterns of species occupancy through local extinctions and increasingly isolated occurrences. The extirpation of species from harvested sites can reduce their chances of recovery during secondary forest development because some species reputedly have limited dispersal beneath intact forest canopies (Söderström 1987; Laaka-Lindberg et al. 2006), or across harvested or fragmented forest (Snäll et al. 2004). Few studies have examined the benefits of canopy retention through partial harvesting in boreal forests, for bryophyte survival and to maintain natural patterns of species diversity (but see Aubry et al. 2009 for forests of the Pacific Northwest).

Variable retention harvesting could benefit bryophytes through moderation of microclimatic conditions and the retention of substrates for colonization. Such benefits will depend on the density and composition of the retained canopy and habitat requirements of individual species. Many forest bryophytes are adapted to shaded conditions and may benefit from greater levels of canopy cover. The relative abundances of broadleaf and coniferous canopy trees retained will also influence understory microclimate conditions (Chen et al. 1999; Heithecker and Halpern 2006) and the types of substrates available for colonization (Mills and Macdonald 2005). Bryophytes are considered to be a paraphyletic group of plants, with mosses and liverworts forming separate lineages of distinct evolutionary origin (Shaw and Renzaglia 2004). Liverworts commonly grow as epixylics on decayed wood in boreal forests and are sensitive to canopy removal (Fenton et al. 2003; Nelson and Halpern 2005). We might, therefore, expect them to be more affected by changes in forest structure and composition than mosses, but this requires further exploration.

Understanding the effects of variable retention harvesting on patterns of species diversity may provide insight about the potential for species recovery. Changes in within-site (alpha) and among-site (beta) diversity (Whittaker 1972) from intact forest with harvesting intensity may reflect the impacts of habitat modification and local species extirpations. Community assembly theory predicts that environmentally similar sites will exhibit low beta diversity under conditions including high disturbance and high species dispersal capacity (Chase 2003). In comparison, environmentally similar sites that exhibit high beta diversity should occur under opposite conditions. Whether bryophytes exhibit higher or lower beta diversity with increasing disturbance (partial canopy harvest) remains unexplored, yet the answer could reveal the consequences of forestry practices at different hierarchical levels.

We examined how bryophyte diversity and composition were patterned in boreal mixed-wood forests in relation to intensity of variable retention harvesting and canopy composition, to provide information about the species most susceptible to harvesting and the implications of different management scenarios for bryophyte conservation. Specific study objectives were 1) to assess the importance of canopy retention level and composition on bryophytes; 2) to compare the responses of mosses and liverworts and determine the species most susceptible to local extirpation along a range of canopy retention levels; and 3) to determine differences in bryophyte diversity at different hierarchical levels with changes in canopy retention and composition, and the implications this has for species conservation at the landscape scale.

3.2 Methods

Study area

Research was conducted at the EMEND (Ecosystem Management Emulating Natural Disturbance) experiment in northwest Alberta, Canada (56º 46' N, 118º 22' W), within the Lower Boreal–Cordilleran Ecoregion (Strong and Leggat 1992). EMEND was established in part to test the effects of residual forest structure on biodiversity conservation at the forest stand level. The region has a continental climate with a mean daily temperature of 1.2 °C and mean total precipitation of 402 mm, approximately three-quarters of which falls as rain (Environment Canada 2009). On average, 71.2 days per year have rainfall > 0.2 mm (17.2 days with rainfall > 5.0 mm). Forests in the study area are dominated by varying amounts of broadleaf (mostly *Populus tremuloides* and *Populus balsamifera* L.) and coniferous (mostly *Picea glauca* (Moench) Voss) canopy cover, with lower abundances of *Abies balsamea* (L.) Mill., *Betula papyrifera* Marsh., *Picea mariana* (Mill.) B.S.P., and *Pinus contorta* Dougl. *ex* Loud. Topographic relief ranges from 677 to 880 m above sea-level.

Site selection

We used a replicated, factorial design with a nested sampling structure to test the effects of forest type and retention level treatments on bryophytes. During the winter of 1998/1999, harvesting treatments were randomly applied to forest stands (each approximately 10 ha in size) of mixed broadleaf-coniferous ("mixed", 35–65% broadleaf canopy cover) and coniferous-dominated ("coniferous", > 70% coniferous canopy cover) composition. Harvesting treatments consisted of 10%, 50%, and 75% dispersed green-tree retention (unharvested stands as controls). Harvesting was conducted using a modified uniform shelterwood pattern of 5 m wide machine corridors (oriented in a north-south direction, perpendicular to prevailing winds) that alternated with 15 m wide retention strips. Retention strips were partially harvested by systematic removal of trees to achieve the desired level of retention for the stand, while accounting for the timber removed from the corridors. Machinery was restricted to corridors to minimize disturbance to standing trees and forest floor organic substrates.

Bryophytes and forest structure were sampled during the 2004–2005 growing seasons in three replicate stands per harvesting treatment per forest type, for a total of 24 sampled stands. Prior to harvesting, stands were unmanaged and had established after fire approximately a century ago. Replicates of each forest type were similar in pre-harvest ecological site classification, composition of understory vegetation, and age (Work et al. 2004). Stands frequently included small, intermittent watercourses but did not contain perennial streams, rock outcrops, or large boulders.

Forest structure measurements

Six sampling points were randomly established in each stand. Each point was then repositioned by the shortest distance required to fall on the centerline of a retention strip. This was done to standardize the type of habitat (retention strip or machine corridor) sampled within each stand. A 50 m^2 circular plot was centered on each sampling point and within each we obtained the following measures of forest structure: crown closure of broadleaf and coniferous trees (assessed at 1 m height by convex spherical densiometer); cover of graminoids, forbs, bryophytes (separately for mosses and liverworts), and exposed mineral soil, using visual estimates; basal area and density of trees (broadleaf and coniferous) and shrubs ≥ 2 m height (separately for stems < 5 cm and ≥ 5 cm DBH (diameter at 1.3 m height)); and diameter and decay stage (1–4, Mills and Macdonald 2005) of natural and harvested tree stumps. Within a central 10 m^2 circular sub-plot we estimated the cover and density of trees (broadleaf and coniferous) and shrubs < 2 m height; aspect (degrees from north); slope (degrees); and depth of the litter-fermented humus (LFH) layer (cm). Along two perpendicular line transects that bisected each 50 m^2 plot we enumerated the diameter and decay stage (1–7, Mills and Macdonald 2005) of logs ≥ 5 cm and diameter of fine woody material < 5 cm diameter. Logs in decay stages 1–2 (stumps in decay stages 1–2) were classified as "hard"; logs in decay stages 3–7 (stumps in decay stages 3–4) were classified as "soft".

Bryophyte sampling

We estimated the abundance of each bryophyte species in 20 m radius circular plots (1,256 m^2) centered on each sampling point. The large size of these plots precluded precise assessments of percent cover; therefore, we recorded the relative abundance of each species per plot using the following scale (modified from Newmaster et al. 2005): 1 = one (including trace amounts) to a few occurrences; 2 = several occurrences to frequent in one or some areas of the plot; 3 = frequent throughout the plot. The large size of these plots captured more unique habitats and associated species as compared to smaller plot sizes (R. Caners, unpublished data), and provided the best representation of species composition at the stand level.

The substrates on which each species was growing were recorded for each plot. Each species was subsequently assigned to a single substrate category based on the most frequent substrate on which it was found in the study area or from the literature (Crum and Anderson 1981; Schuster 1966–1992) if few specimens were encountered. We used the following substrate categories: dung (animal excrement and bones); epigeic (forest floor and humus); epiphytic (bark of living trees and recently fallen wood; includes facultative and obligate epiphytes); epixylic (decayed wood); generalist (consistently found on a variety of substrate types); and mineral soil.

Species that could not be identified in the field by hand lens were collected and subsequently identified in the laboratory. We collected 3,957 samples, each containing multiple species. Nomenclature follows Anderson (1990) for *Sphagnum*, Anderson et al. (1990) for mosses, and Stotler and Crandall-Stotler (1977) for liverworts. The liverwort, *Lophozia ciliata*, was recently described

(Söderström et al. 2000) and is included as a distinct species. We combined *Rhizomnium pseudopunctatum* + *R. gracile* and *Cephalozia lunulifolia* + *C. affinis* because identification was sometimes ambiguous. *Calliergon obtusifolium* is considered to be synonymous with *Calliergon richardsonii* following Hedenäs (1993). Voucher specimens are deposited at the Devonian Botanic Garden (ALTADBG) and Department of Biological Sciences (ALTA) herbaria, University of Alberta.

Statistical analyses

Bryophyte responses to forest type and retention level

We examined differences in richness, diversity, and evenness of mosses and liverworts among retention levels and forest types. Richness was calculated as the number of unique taxa per plot. Diversity was calculated as "effective number of species" using the exponential of Shannon entropy (N_1, Hill 1973), $\exp(H)$, where $H = -\Sigma P_i(\ln P_i)$. P_i is the proportional abundance of each species, and the summation term is from i to S, where S is the total number of species per plot. The exponential of Shannon entropy provides a "true measure" of diversity, and can be interpreted as the number of species in the sample had all species been equally common (Jost 2006). The measure attains a maximum value equal to the total number of species in the community. We also calculated Heip's (1974) evenness, $E_{\mathrm{Heip}} = (\exp(H) - 1)/(S - 1)$, which is fairly insensitive to species richness and does not overemphasize rare species (Magurran 2004). We tested for the effect of forest type and retention level and their interaction with nested analysis of variance (ANOVA), using PROC MIXED in SAS 9.2 (SAS Institute Inc., Cary, NC). Forest stand nested within harvesting treatment by forest type was a random factor; plots within each forest stand were sub-samples. Data were Box-Cox transformed (Sokal and Rohlf 1995) before analysis, when required, to meet the assumptions of normality and homogeneity of variances of the residuals, and pair-wise comparisons were conducted using Tukey-Kramer tests when the overall F-test was significant.

Differences in species richness for each substrate category and differences in measured forest structure variables were also tested for the effects of retention level and forest type and their interaction. Because data could not always be transformed to achieve normality or homogeneity of variances, we used the Scheirer-Ray-Hare extension of the Kruskal-Wallis test to perform two-factor ANOVA on ranked data (Sokal and Rohlf 1995). Analyses were performed on mean values per stand. For each analysis, *H*-statistics were calculated separately for each main effect and the interaction term using output from PROC GLM in SAS 9.2 (SAS Institute Inc., Cary, NC), and tested for significance as chi-squared values (Sokal and Rohlf 1995). When the main effect of retention level was significant, pair-wise comparisons were conducted using Wilcoxon signed-rank tests in PROC NPAR1WAY and assessed after sequential Bonferroni correction (Holm 1979) for multiple tests.

Differences in species composition among forest types and retention levels were examined by principal coordinate analysis (PCoA) in CANOCO 4.5 (ter Braak and Šmilauer 2002) using a matrix of mean relative species abundance per forest stand. PCoA is a variant of principal component analysis (PCA) but allows users to choose a measure of species resemblance that is appropriate for datasets like ours with several uncommon species. The method portrays sites in ordination space while preserving the distance relationships among them, but unlike PCA does not produce weights of species along axes. This analysis uses PCA to analyze the principal coordinates obtained from a PCoA on species data represented by Bray-Curtis dissimilarity (Legendre and Legendre 1998) after correcting for negative eigenvalues (ter Braak and Šmilauer 2002). All species were retained for analysis.

We tested for differences in species composition among treatments using permutational multivariate analysis of variance (PERMANOVA 1.6, Anderson 2005). The method assumes independence among sample units but does not require the assumption of normality, as significance is assessed by permutation. PERMANOVA was used to perform a two-factor ANOVA on a matrix of mean relative species abundance per stand represented using Bray-Curtis dissimilarity.

Tests of significance were performed using 9,999 unrestricted permutations of raw data (Anderson 2001) and assessed using Monte Carlo asymptotic *P*-values (Manly 1997), recommended for small data sets (Anderson 2005). When *F*-tests were significant, pair-wise comparisons were conducted using 9,999 unrestricted permutations of raw data, and examined after sequential Bonferroni correction of Monte Carlo *P*-values. PERMANOVA is sensitive to differences among groups in the dispersion of samples in multivariate space; therefore, rejection of a null hypothesis may result from differences in composition or dispersion of samples, or both (Anderson 2005, 2006). We used permutational analysis of multivariate dispersions (PERMDISP, Anderson 2004), a multivariate analogue to Levene's test (Levene 1960), to assess the influence of sample dispersion on results obtained from PERMANOVA. The same options were used as those for PERMANOVA.

To determine if certain species were associated with a particular forest type or retention level we conducted indicator species analysis (ISA, Dufrêne and Legendre 1997). Analyses were performed in PC-ORD 5.06 (McCune and Mefford 2006), using mean species abundance per stand and significance tested using 9,999 permutations.

Additive partitioning of bryophyte diversity

Additive partitioning of species diversity (Lande 1996, Crist et al. 2003) provides a statistical framework for testing the relative contributions of within-plot (alpha, α), and among-plot and among-stand (beta, β), to total (gamma, γ) diversity in studies with hierarchically nested sampling designs. Total diversity is calculated as the sum of alpha and beta diversity (i.e., $\gamma = \overline{\alpha} + \beta$), where alpha is the mean diversity within sampling units and beta is the mean diversity among sampling units (Crist et al. 2003; Gering et al. 2003). Whittaker (1960) used a multiplicative relationship to define regional diversity (i.e., $\gamma = \overline{\alpha} \text{ x } \beta$) but the units of alpha and beta diversity are not equivalent when partitioned across more than one spatial scale. Additive partitioning represents diversity components in the same units, thereby facilitating direct comparisons among them (Lande 1996).

For this study, total diversity for each forest type and retention level treatment was partitioned into mean diversity within plots (alpha) + among plots ($beta_1$) + among stands ($beta_2$). Diversity was represented as species richness. Analyses were performed in PARTITION 3.0 (Veech and Crist 2009) using 9,999 individual-based randomizations for tests of significance, which randomly reassigns individuals among samples based on species abundances while retaining original species-abundance and sample-size distributions (Crist et al. 2003). Since my estimates of species abundance were relative numbers of occurrences, the data is well-suited to individual-based randomization (T. Crist, personal communication). Tests were performed separately for mosses and liverworts to assess if they differed in diversity patterns among treatments and hierarchical levels.

3.3 Results

Bryophyte responses to forest type and retention level

Our sampling included 135 bryophyte species among the forest types and retention levels, consisting of 96 mosses and 39 liverworts (Appendix 3.1). Species were predominantly epiphytic on bark (27.4% of species), epixylic on decayed wood (24.4%), and epigeic on forest floor and humus (23.7%), with fewer species on mineral soil (17.8%), dung or animal remains (5.2%), or generalists (1.5%).

Several forest attributes differed among retention levels and between forest types (Table 3.1). There were no interactions between these main effects for any of the measured attributes. Total canopy cover and total basal area decreased incrementally with declining retention. This was mostly attributable to reduced cover and basal area of coniferous trees. Declining retention was also related to increased cover of graminoids, shrubs, and abundance of fine woody material and harvested stumps. There was no difference among retention levels in terms of forb cover or abundance of hard or soft logs, or hard stumps. Soft stumps decreased in abundance with greater harvesting intensity, likely as a result of decomposition or being colonized by understory vegetation. Cover of liverworts and mosses declined with harvesting intensity, with significantly lower cover in low (10%) retention as compared to intact forest.

Mixed forest had a higher total canopy cover than coniferous forest, resulting from a greater cover and basal area of broadleaf trees. Mixed forest also had a higher forb cover, whereas coniferous forest had a greater abundance of hard logs and hard natural stumps, and exposed soil.

Retention level and forest type influenced bryophyte species richness, diversity (exponential of Shannon entropy, Hill 1973), and evenness, but mosses and liverworts responded differently. Liverwort richness was significantly lower at the lowest retention levels (10% and 50%) than in the control, and was significantly lower in mixed as compared to coniferous forest (Table 3.2, Figure 3.1). The same trends among retention levels were observed for diversity of liverworts, but diversity did not differ between forest types. Evenness had the opposite response for liverworts, increasing with declining retention, but again did not differ between forest types (Table 3.2, Figure 3.2). Mosses, in comparison, did not differ in richness, diversity, or evenness among retention levels or between forest types (Table 3.2, Figures 3.1–3.2).

Species with different substrate preferences responded differently to retention level after harvesting (Table 3.3). There were no differences between forest types and no interaction between forest type and retention level for any substrate categories. Epixylic and epiphytic species experienced the greatest declines in richness with declining retention (Figure 3.3). All levels of harvesting had significantly lower richness than the control. Richness of epigeic species also declined with increasing harvesting intensity; although the overall test for retention level was significant, none of the subsequent pair-wise comparisons were significant. Generalist species showed the opposite response, increasing in richness with declining retention. Richness of species on soil exhibited strong trends, whereas dung specialists were apparently not as affected by harvesting.

PCoA explained a large proportion of the variation in species composition among the 24 stands (axes 1–2 = 57.1%, axes 1–4 = 70.9%; Figure 3.4). Axis 1 represents a gradient of canopy openness associated with a progressive shift in species composition. Axis 2 represents a weak separation of broadleaf and coniferous forest types. The majority of species are closely associated with stands of intact forest at the positive end of axis 1. These consisted mostly of epixylic liverworts, including (in order of decreasing centroid weights) *Lophozia ascendens*, *Anastrophyllum hellerianum*, *Ptilidium pulcherrimum*, *Blepharostoma trichophyllum*, and *Lophozia longidens*. Mosses with the strongest loadings on axis 1 include (in order of decreasing centroid weights) *Dicranum fuscescens*, *Mnium spinulosum*, *Oncophorous wahlenbergii*, *Dicranum fragilifolium*, and *Herzogiella turfacea*. The forest floor mosses, *Hylocomium splendens*, *Ptilium crista-castrensis*, and *Pleurozium schreberi*, had positive loadings on axis 1 and negative loadings on axis 2, in association with intact coniferous forests. In comparison, some species had negative loadings on axes 1 and 2, as they occurred more frequently in harvested coniferous stands. These included (in order of increasing centroid weights) *Ceratodon purpureus*, *Bryum lisae* var. *cuspidatum*, *Pohlia nutans*, *Marchantia polymorpha*, *Polytrichum commune*, *Polytrichum strictum*, and *Aulacomnium palustre*. The moss, *Plagiomnium cuspidatum*, had a strong positive loading on axis 2 in association with mixed forests.

Results of PERMANOVA revealed compositional differences in mosses and liverworts among retention levels and between forest types, with no interactions between these main effects (Table 3.4). Liverworts had a pronounced response to harvesting: differences in composition were observed between intact forest and all harvested treatments, and between 10% and 75% retention. For mosses, species composition of intact forest differed from the lowest (10% and 50%) retention levels; other pair-wise comparisons were not significantly different. PERMDISP did not detect any differences in multivariate dispersion among retention levels or forest types (or their interactions), for mosses, liverworts, or all bryophytes. Results of PERMANOVA can thus be largely attributed to shifts in species composition (Anderson 2004).

ISA detected several species that were significant indicators of a particular retention level or forest type (Appendix 3.2). Thirty species were indicators of intact forest, including both mosses (12 species) and liverworts (18 species). Most mosses were epiphytic (8 species), with fewer species being epigeic (3 species) or epixylic (1 species). In comparison, the majority of liverworts were epixylic (17 species) with one epigeic species. Only two species were found to be indicators of low (10%) retention: one epiphytic moss and one generalist moss. Indicator species were also detected for the two forest types: mixed forest indicators consisted of three mosses and one liverwort, and coniferous forest indicators consisted of four mosses and three liverworts.

Additive partitioning of bryophyte diversity

The proportions of total (gamma) diversity explained by within-plot (alpha), among-plot ($beta_1$), and among-stand ($beta_2$) diversity differed among retention levels and forest types, and between mosses and liverworts (Table 3.5). Separate analyses for each retention level and forest type revealed that observed levels of alpha diversity were consistently less than expected ($P < 0.001$), and observed levels of $beta_1$ and $beta_2$ diversity were consistently greater than expected ($P < 0.001$), for both mosses and liverworts. In addition, the contribution of alpha to gamma diversity was consistently larger than either $beta_1$ or $beta_2$ diversity.

For liverworts, the contribution of within-plot to total diversity decreased, and the contributions of among-plot and among-stand diversity increased, with declining retention levels. In comparison, trends for mosses were less pronounced. Mosses exhibited little variation among retention levels in the contribution of within-plot to total diversity, whereas the contribution of among-plot diversity increased slightly, and contribution of among-stand diversity decreased slightly with declining retention.

3.4 Discussion

Retained forest canopy structure drives bryophyte community response

Forest harvesting is a prevalent form of disturbance on the boreal landscape and has the potential to influence species persistence over large areas. Effects of clear-cutting (Dynesius and Hylander 2007; Dynesius et al. 2009) and habitat fragmentation (Snäll et al. 2004) on bryophytes can last for decades, warranting a detailed investigation into the benefits of structural retention for protecting species and preserving natural species patterns. Our findings demonstrate that both retention level and forest type influenced bryophyte diversity and composition, and these factors did not interact for any analyses. Furthermore, mosses and liverworts were affected differently, as were species with dissimilar substrate preferences. Forest management practices can therefore have a substantial influence on bryophytes, with different consequences for different species groups.

The distinct phylogenetic groups, mosses and liverworts, showed appreciable differences in their responses to retention level and forest type treatments. Liverwort richness and diversity were reduced but evenness increased at the lowest retention levels. Increased evenness likely resulted from the reduced abundances of several common species with declining retention, creating a greater proportion of species with similarly low abundance. Reduced diversity was attributable to the increased evenness and reduced richness of liverworts with declining retention. Liverwort richness was higher in coniferous than mixed forest, implying that conifer dominance provides more favourable habitat conditions for this species group. Mosses, in comparison, did not differ in richness, diversity, or evenness among retention levels or forest types. These findings imply that mosses are not as sensitive to changes in local habitat conditions as liverworts; however, results may also be attributable to species turnover among retention levels that was generally not observed for liverworts. Namely, whereas some moss species decreased in abundance with declining retention levels, other species increased in abundance. Results highlight the importance of recognizing differences between mosses and liverworts in examining factors influencing their response in boreal forests.

The observed shift in moss composition between intact and low retention forests resulted partly from the loss of species associated with intact forest, including those that were obligately or facultatively epiphytic (e.g., *Dicranum fragilifolium*, *Dicranum fuscescens*, *Mnium spinulosum*, *Oncophorous* *wahlenbergii*, *Orthotrichum speciosum*), epixylic (e.g., *Herzogiella turfacea*, *Tetraphis pellucida*), and epigeic (e.g., *Brachythecium erythrorrhizon*, *Brachythecium starkei*, *Hylocomium splendens*, *Plagiomnium medium*, *Pleurozium schreberi*, *Ptilium crista-castrensis*) (PCoA, Figure 3.4). Several of these species were significant indicators of intact forest. Reduced abundances of the feather mosses, *Hylocomium splendens*, *Ptilium crista-castrensis*, and *Pleurozium schreberi* after harvest may impair their abilities to perform important ecological functions (e.g., Nilsson and Wardle 2005). Compositional change of mosses among retention levels also resulted from species that increased in abundance with harvesting intensity, such those preferring epigeic (*Aulacomnium palustre*) and soil (*Ceratodon purpureus*, *Polytrichum commune*, *Polytrichum strictum*) substrates, or generalists (*Bryum lisae* var. *cuspidatum*, *Pohlia nutans*). Effects of harvesting on liverwort composition were more pronounced; any level of harvesting resulted in species compositional change.

Variation in forest canopy is important for maintaining natural variation in bryophyte communities. The mosses, *Plagiomnium cuspidatum*, *Sanionia uncinata*, and *Brachythecium salebrosum* were associated with mixed forests, whereas, *Hylocomium splendens*, *Ptilium crista-castrensis*, and *Pleurozium schreberi*, and several colonists (s. str., During 1979, 1992), were associated with coniferous forests. Colonists were most abundant in harvested coniferous forests, which had more exposed soil resulting from occasional windthrow of residual canopy white spruce. Species compositional differences reflect inherent differences in growing conditions and substrates between forest types. First, stands with coniferous-dominated canopies may support more shaded, cooler, and humid forest floor conditions than broadleaf-dominated stands to provide more optimal growing conditions for many bryophytes, especially liverworts. Second, different forest types support distinctive substrates for colonization. For example, the liverworts *Cephalozia lunulifolia* and *Tritomaria exsectiformis* were indicators of coniferous forest and prefer decayed coniferous wood (personal observation), whereas *Chiloscyphus pallescens* was an indicator of mixed forest and favours decayed broadleaf wood (personal observation). Greater habitat heterogeneity within stands is more likely to support greater numbers of species (Mills and Macdonald 2005; Økland et al. 2008). At larger scales, variation in canopy composition among stands provides a range of substrate types and growing conditions to support a greater diversity of species on the landscape.

Bryophytes with different substrate preferences had dissimilar responses to harvesting, implying that changes in environmental conditions can have a controlling influence over species responses (Whittaker 1956). Epixylic and epiphytic species declined in richness in all harvested treatments, demonstrating acute sensitivity to habitat change. These results were also reflected in the indicator species analysis, where the majority (93.8%) of indicators were found for intact forest, and these consisted of epixylic (60%), epiphytic (26.7%), and epigeic (13.3%) species. Decayed wood can support large numbers of species in boreal forests (Söderström 1988) and is often the focus of restoration and species conservation efforts (Vanha-Majamaa et al. 2007). This substrate is elevated above the ground and may lose moisture more rapidly after harvesting than sheltered habitats such as mesic forest floor depressions (Hylander et al. 2005). The loss of species associated with this substrate type suggests the function of decayed wood as bryophyte habitat may be diminished after harvesting.

Although many species were affected by harvesting, few were completely eliminated from harvested sites. Even low levels of structural retention may provide protection from excessive exposure (Fenton and Frego 2005). However, reduced abundance after harvesting may make species more susceptible to local extirpation, as small populations are vulnerable to stochastic demographic, genetic, and especially environmental events (Matthies et al. 2004). Large temporal fluctuations in decayed wood abundance (Edman et al. 2007) may create corresponding fluctuations in populations associated with this habitat. Short-lived species may be particularly affected because their survival depends on frequent recruitment events (Matthies et al. 2004). Smaller populations, creating fewer reproductive propagules for dispersal, can reduce rescue effects and result in the loss of species over time (Snäll et al. 2004; Löbel et al. 2006). Some species with highly diminished abundances after disturbance may therefore represent the "living dead" (Hanski 1998) to be lost in future years (Berglund and Jonsson 2005).

The loss of sensitive species from harvested sites requires an understanding of potential mechanisms for species recovery. Bryophyte diaspore banks in the uppermost mineral soil horizons contain a source of reproductive propagules that might facilitate species establishment after forest floor disturbances that expose mineral soil (Caners et al. 2009). Pleurocarpous mosses germinated frequently from soil samples obtained from the centre of sample plots used in this study. Many of these species are characteristic of intact forest where they preferentially colonize epigeic and epiphytic substrates, some of the most sensitive moss species in this study. In comparison, liverworts germinated infrequently and were poorly represented in mixed-wood diaspore banks. The sensitivity of some liverworts to even low levels of forest modification may have important consequences for their representation after harvesting. Protecting extant liverwort populations is needed because re-establishment after local extirpation may be hindered for several reasons, including the generally low abundance of liverworts in mixed-wood forests, their specific substrate requirements (dead wood) and rapid substrate turnover (Edman et al. 2007), dispersal limitations (Söderström 1987; Laaka-Lindberg et al. 2006), and poor representation in diaspore banks (Caners et al. 2009).

Harvesting influences hierarchical partitioning of bryophyte diversity

Additive partitioning of diversity showed that for both mosses and liverworts, total beta diversity (among-plot and among-stand combined) explained the greatest proportion of total diversity for all retention levels except for liverworts in intact forest (Table 3.5). This demonstrates that differences among plots and stands are important for capturing more species in both harvested and intact forests. Lower than expected alpha and higher than expected beta diversity components for each retention level may be attributable to intraspecific aggregation, which occurs when individuals are associated with other individuals of the same species (Veech 2005). Further research is needed to elucidate the factors influencing aggregation, and its implications for biodiversity conservation.

Harvesting intensity influenced the relative contributions of alpha and beta to total diversity, and can therefore affect regional patterns of species diversity. Changes were pronounced for liverworts but were more equivocal for mosses. In intact forest, the comparatively high alpha diversity for liverworts suggests that closed canopy conditions provide favourable conditions to increase local numbers of species. Large numbers of local species can, in turn, reduce species differences among locations (Gering et al. 2003). Beta diversity of liverworts in intact forest was substantially lower (44.5%) than the most intensively harvested forests (61.1%), but still comprised nearly half of total diversity. Intact forests are thus important for supporting large numbers of liverwort species at local scales, and also for maintaining species differences at among-plot and among-stand scales.

In the most intensively harvested forests, the low proportion of alpha and high proportion of beta diversity for liverworts represents a shift from patterns in intact forest. These trends are opposite to those predicted by community assembly theory (Chase 2003). Sites with greater levels of disturbance are expected to have reduced among-site variability in species composition (beta diversity) because 1) fewer species can persist at disturbed sites, 2) disturbance increases the time it takes for species to re-establish, and 3) species that colonize after disturbance are often poor competitors (Chase 2003). For liverworts, greater among-site variability at low retention may result from stochastic processes such as colonization/extinction dynamics and dispersal limitation, which are thought to create highly divergent communities among similar habitats (Chase et al. 2009). Dispersal of some liverworts is presumed to be limited over longer distances (Söderström 1987; Laaka-Lindberg et al. 2006), and may be restricted across inhospitable environments after forest harvesting resulting in part from reduced abundance and quality of suitable substrates (Longton 1992; Hylander et al. 2005; Nelson and Halpern 2005). This may perpetuate the high levels of beta diversity for an indefinite period after harvesting. This pattern was not observed for mosses. Mosses may be more likely to persist at harvested sites as compared to liverworts, or may have greater dispersal capacities to facilitate re-establishment after harvesting. Lack of observed changes in diversity for mosses may also be attributed to species turnover among retention levels, warranting further investigation.

Implications for species conservation and forest management

Bryophyte conservation in managed boreal mixed-wood forests requires the consideration of species responses at local (within-plot) and larger (among-plot and among-stand) scales. We found that canopy retention level and composition had significant influences on the short-term (five to six year) responses of mosses and liverworts, even though stands were harvested with minimal disturbance to forest floor habitats. The absence of significant interactions between retention level and forest type for all analyses suggests their effects are, to a great extent, mutually exclusive. Both factors need to be considered when implementing management strategies for bryophyte conservation.

Mosses and liverworts should be recognized for their distinctive responses to harvesting and canopy composition. Results of analyses that combined these groups lacked resolution as they were driven largely by the response of liverworts. Liverworts composed nearly one-third of all bryophyte species in the study and were affected even at low levels of canopy removal. Greater harvesting intensities created more heterogeneous diversity patterns for liverworts, but of lower local and total diversity. This heterogeneity may persist if species that were extirpated from harvested sites are unable to re-establish.

In comparison, mosses had a more subtle response to intensity of harvesting, although several species affiliated with epixylic, epiphytic, and epigeic substrates were detrimentally affected by canopy loss. As seen for liverworts, total beta diversity explained the majority of total diversity for each retention level, implying that multiple sites are important for regional species representation in both harvested and intact systems. High beta diversity for mosses and liverworts may be partly attributable to variation in species composition between forest types. Forest canopies of dissimilar composition are expected to foster divergent growing conditions and substrates to support different species.

The survival of several species even at low retention implies that partial canopy preservation can support species with high tolerance to habitat alteration. However, species that experience sharp declines in abundance with harvesting and may be at increased risk of future extirpation (Hanski 1998). Intact coniferous and mixed forests should be recognized for their capacity to support high levels of local diversity and for their importance as potential species refugia (Perhans et al. 2009). Appreciable beta diversity in intact forest emphasizes the need to also consider variation among habitats at different hierarchical levels when implementing management strategies that attempt to maintain regional patterns of species diversity.

3.5 Acknowledgements

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Table 3.1. Mean (± 1 SE) measures of forest structure for each retention level and forest type.

	Retention level				Forest type	
	10%	50%	75%	100%	Mixed	Coniferous
Canopy						
Total canopy (% cover)	33.60 (6.41)a	59.72 (5.46)b	68.35 (4.92)b	78.93 (4.33)b	70.31 (5.22)a	49.99 (5.56)b
Coniferous canopy (% cover)	14.58 (4.04)a	42.20 (5.23)b	47.47 (3.40)bc	57.8 (3.12)c	40.19 (5.23)	40.84 (5.81)
Broadleaf canopy (% cover)	18.79 (4.96)	17.07 (6.84)	20.88 (6.06)	20.89 (7.09)	29.78 (3.86)a	9.03 (1.42)b
Total basal area (m^2 ha^{-1})	18.83 (4.05)a	57.08 (6.22)b	65.34 (4.65)b	60.15 (3.83)b	48.47 (4.94)	52.23 (7.58)
Coniferous basal area (m^2 ha^{-1})	9.04 (3.04)a	42.05 (4.69)b	49.5 (7.00)b	46.54 (6.65)b	29.07 (3.93)	44.50 (7.06)
Broadleaf basal area (m^2 ha^{-1})	9.78 (2.72)	15.02 (4.01)	15.84 (3.74)	13.60 (4.99)	19.39 (2.47)a	7.73 (1.68)b
Understory						
Graminoids (% cover)	38.2 (5.95)a	11.39 (2.32)b	11.25 (3.68)b	2.68 (1.33)b	14.19 (4.99)	17.57 (4.44)
Forbs (% cover)	53.75 (4.43)	37.11 (7.70)	44.06 (4.83)	36.46 (7.24)	50.11 (4.67)a	35.58 (3.54)b
Shrubs (% cover)	86.35 (12.56)a	57.78 (12.99)ab	47.70 (7.38)ab	30.95 (7.08)b	64.92 (9.14)	46.48 (8.52)
Total bryophytes (% cover)	18.81 (6.07)a	58.63 (14.01)b	67.27 (9.69)b	87.23 (5.59)b	56.06 (10.05)	59.90 (9.60)
Mosses (% cover)	18.73 (6.05)a	58.12 (13.89)b	66.51 (9.60)b	86.00 (5.54)b	55.62 (9.97)	59.06 (9.43)
Liverworts (% cover)	0.07 (0.03)a	0.51 (0.18)ab	0.75 (0.30)ab	1.22 (0.17)b	0.44 (0.14)	0.84 (0.19)
Forest floor substrates						
Hard natural stumps (m^2 ha^{-1})	6.22 (3.15)	11.38 (3.70)	10.60 (2.84)	10.25 (3.01)	6.20 (1.32)a	13.03 (2.48)b
Soft natural stumps (m^2 ha^{-1})	1.47 (0.77)a	4.54 (1.57)ab	6.12 (1.68)ab	12.04 (2.97)b	5.30 (1.67)	6.78 (1.76)
Harvested stumps (m^2 ha^{-1})	68.23 (5.50)a	18.68 (4.79)b	0.00 (0.00)c	0.00 (0.00)c	21.70 (8.52)	21.75 (9.00)
Hard logs (cm)	47.27 (7.61)	48.61 (12.28)	38.12 (7.00)	21.35 (3.91)	28.10 (4.81)a	49.57 (6.28)b
Soft logs (cm)	71.53 (9.30)	60.39 (14.55)	44.83 (12.34)	64.10 (11.71)	51.25 (7.87)	69.18 (8.61)
Fine woody material (cm)	75.80 (8.76)a	63.46 (7.91)a	51.37 (7.88)ab	26.00 (4.09)b	58.97 (8.18)	49.35 (6.32)
Mineral soil (% cover)	0.85 (0.63)	0.27 (0.13)	0.15 (0.07)	0.07 (0.06)	0.02 (0.02)a	0.64 (0.31)b

Notes: Two-factor ANOVA was performed on ranked data using the Scheirer-Ray-Hare extension of the Kruskal-Wallis test to determine the effects of retention level and forest type and their interaction on each forest structure measure (n = 6 per retention level; n = 12 per forest type). No interactions were detected for the main effects. When the main effect of retention level was significant, pair-wise comparisons were calculated using Wilcoxon signed-rank tests. Means of retention levels with different letters were significantly different after sequential Bonferroni correction of *P*-values.

Table 3.2. Results of two-factor nested ANOVA to test the effects of retention level and forest type and their interaction on species richness (S), diversity (exponential of Shannon entropy, $\exp(H)$), and Heip's evenness (E_{Heip}).

		S			$\exp(H)$			E_{Heip}		
		DF	*F*	*P*	*DF*	*F*	*P*	*DF*	*F*	*P*
Bryophytes	Forest	1	4.79	0.044	1	3.49	0.080	1	4.40	0.052
	Retention	3	8.76	0.001	3	7.41	0.003	3	2.73	0.078
	Forest x Retention	3	1.02	0.410	3	0.98	0.425	3	0.75	0.540
Mosses	Forest	1	3.49	0.080	1	2.45	0.137	1	4.07	0.061
	Retention	3	2.11	0.139	3	1.54	0.243	3	2.44	0.102
	Forest x Retention	3	1.21	0.340	3	1.15	0.361	3	0.81	0.505
Liverworts	Forest	1	4.66	0.046	1	3.78	0.070	1	3.59	0.077
	Retention	3	21.11	< 0.001	3	16.80	< 0.001	3	36.64	< 0.001
	Forest x Retention	3	0.75	0.540	3	0.61	0.618	3	1.59	0.231

Notes: Tests were performed separately for mosses, liverworts, and all bryophytes. See Figures 3.1–3.2.

Table 3.3. Results of two-factor ANOVA to test the effects of retention level and forest type and their interaction on species richness for the different substrate categories.

Substrate category		*DF*	*H*	*P*
Dung	Forest	1	1.11	0.293
	Retention	3	2.34	0.505
	Forest x Retention	3	2.62	0.453
Epigeic	Forest	1	1.03	0.311
	Retention	3	8.65	0.034
	Forest x Retention	3	0.59	0.899
Epiphytic	Forest	1	0.01	0.931
	Retention	3	14.15	0.003
	Forest x Retention	3	0.41	0.938
Epixylic	Forest	1	0.52	0.470
	Retention	3	18.63	< 0.001
	Forest x Retention	3	0.45	0.929
Generalist	Forest	1	0.06	0.814
	Retention	3	17.68	0.001
	Forest x Retention	3	0.50	0.920
Soil	Forest	1	1.34	0.247
	Retention	3	7.73	0.052
	Forest x Retention	3	3.32	0.344

Notes: Tests were performed on ranked data using the Scheirer-Ray-Hare extension of the Kruskal-Wallis test. See Figure 3.3.

Table 3.4. Results of PERMANOVA for A) the effects of retention level and forest type and their interaction on species composition, and B) pair-wise comparisons of species composition among retention levels.

A)

		DF	*F*	*P*[a]
Bryophytes	Forest	1	3.01	0.022
	Retention	3	5.01	< 0.001
	Forest x Retention	3	0.91	0.525
Mosses	Forest	1	3.02	0.015
	Retention	3	3.78	< 0.001
	Forest x Retention	3	0.92	0.542
Liverworts	Forest	1	2.90	0.045
	Retention	3	8.45	< 0.001
	Forest x Retention	3	1.11	0.352

[a] Monte Carlo *P*-values based on unrestricted permutation of raw data.

B)

	Bryophytes		Mosses		Liverworts	
	t	*P*[a]	*t*	*P*[a]	*t*	*P*[a]
Test pair						
10, 50	1.06	0.336	0.91	0.512	1.43	0.089
10, 75	1.96	**0.005**	1.71	0.021	2.64	**0.001**
10, 100	3.46	**< 0.001**	2.93	**< 0.001**	4.56	**< 0.001**
50, 75	1.17	0.231	1.08	0.323	1.41	0.096
50, 100	2.53	**0.001**	2.18	**0.003**	3.27	**0.001**
75, 100	1.83	**0.011**	1.68	0.021	2.15	**0.004**

Notes: Tests were performed separately for mosses, liverworts, and all bryophytes using a matrix of mean species abundance per stand, and represented with Bray-Curtis dissimilarity. Bolded *P*-values for pair-wise tests are significant after sequential Bonferroni correction.

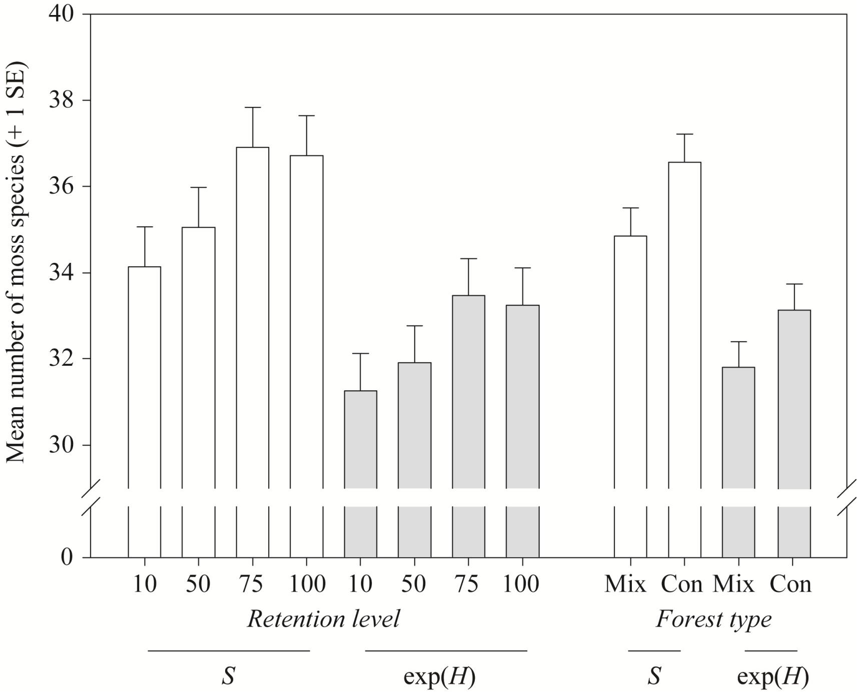
[a] Monte Carlo *P*-values based on unrestricted permutation of raw data.

Table 3.5. Results of additive partitioning of species diversity for the retention level and forest type treatments.

		Retention level								Forest type			
		10%		50%		75%		100%		Mixed		Coniferous	
	Diversity fraction	*O*	*E*	*O*	*E*	*O*	*E*	*O*	*E*	*O*	*E*	*O*	*E*
Bryophytes	α (within plot)	44.6	78.3	46.1	79.3	47.4	78.5	49.5	79.5	40.3	70.2	42.9	72.9
	β_1 (among plot)	25.2	19.2	23.8	18.2	23.4	18.6	19.6	17.4	31.2	26.9	28.8	24.7
	β_2 (among stand)	30.2	2.5	30.1	2.5	29.2	2.8	30.9	3.0	28.6	2.9	28.3	2.4
Mosses	α (within plot)	46.7	77.8	48.1	79.5	47.3	76.7	47.1	78.2	40.9	69.4	43.1	71.9
	β_1 (among plot)	22.9	19.6	22.2	18.0	21.0	20.0	19.4	18.7	29.9	27.9	27.5	25.8
	β_2 (among stand)	30.4	2.7	29.7	2.7	31.7	3.3	33.6	3.0	29.2	2.8	29.4	2.4
Liverworts	α (within plot)	38.9	78.9	41.3	78.7	47.7	82.9	55.5	82.6	38.2	71.5	42.4	74.7
	β_1 (among plot)	31.5	18.9	27.7	19.3	29.0	15.2	20.3	14.2	34.7	25.0	32.1	22.4
	β_2 (among stand)	29.6	2.2	31.0	2.0	23.2	1.6	24.2	3.2	27.1	3.5	25.6	2.9

Notes: Values are the contribution (%) of α (within-plot), β_1 (among-plot), and β_2 (among-stand) in relation to γ (total) diversity for each retention level and forest type. Diversity was measured as species richness. Tests were performed separately for mosses, liverworts, and all bryophytes. In all cases, observed (*O*) levels of alpha diversity were significantly lower than expected (*E*) ($P < 0.001$) and observed levels of beta diversity (both among plot and among stand) were significantly greater than expected ($P < 0.001$) by individual-based randomization.

A)


Mean number of moss species (+ 1 SE)
40
38
36
34
32
30
0
10
50
75
100
10
50
75
100
Mix
Con
Mix
Con
Retention level
Forest type
S
exp(*H*)
S
exp(*H*)

B)

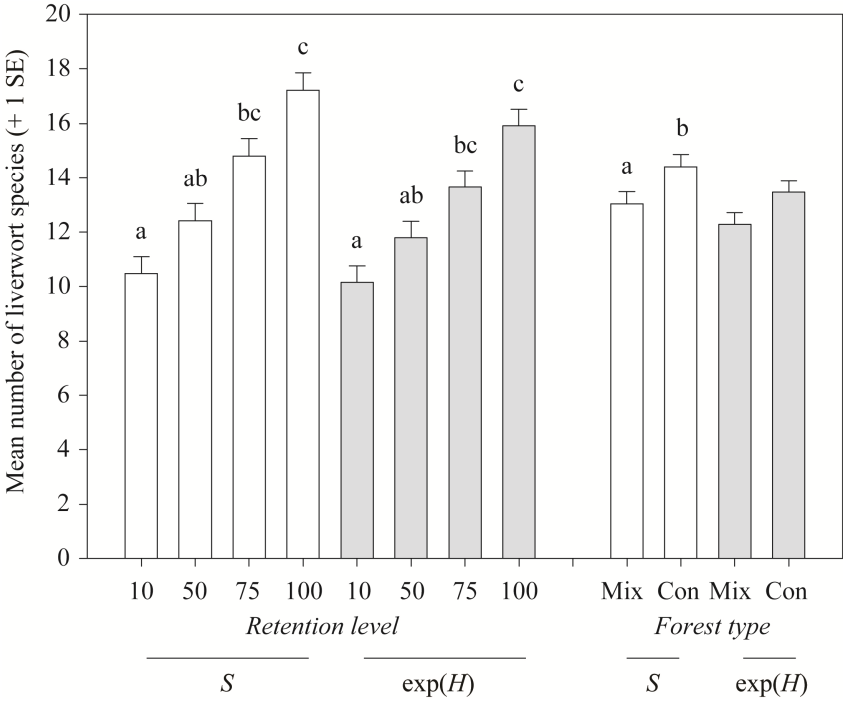

Mean number of liverwort species (+ 1 SE)
20
18
16
14
12
10
8
6
4
2
0
a
ab
bc
c
a
ab
bc
c
a
b
10
50
75
100
10
50
75
100
Mix
Con
Mix
Con
Retention level
Forest type
S
exp(*H*)
S
exp(*H*)

Figure 3.1. Mean (+ 1 SE) species richness (*S*) and diversity (exponential of Shannon entropy, exp(*H*)) per plot for each retention level and forest type for A) mosses and B) liverworts. The effects of retention level and forest type and their interaction were calculated separately for richness and diversity using nested ANOVA (Table 3.2). No interactions were detected for the main effects. Pair-wise comparisons of retention levels were calculated when the main effect was significant. Bars of retention levels or forest types with different letters were significantly different.

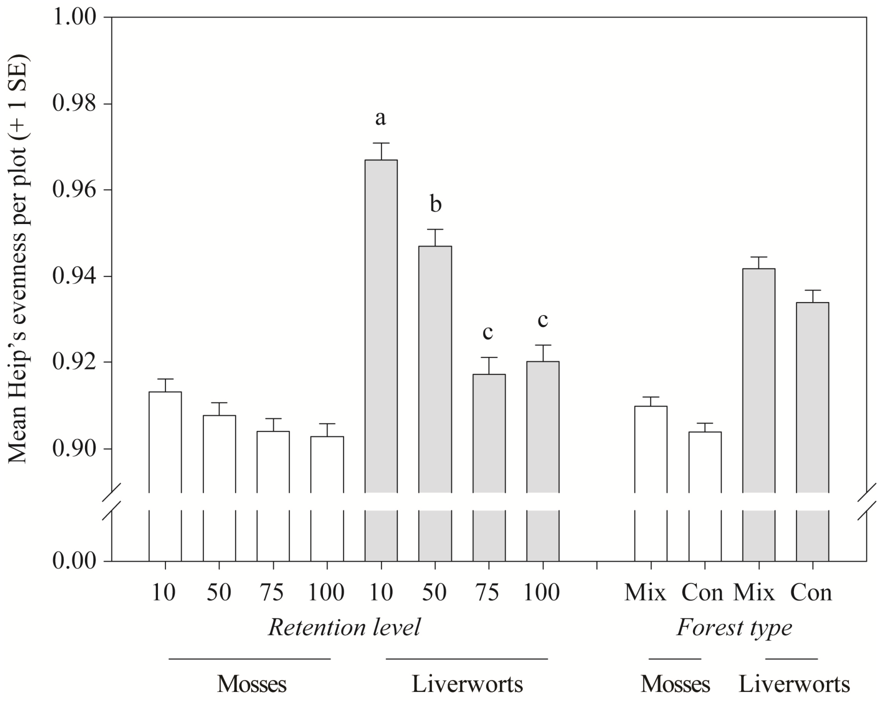


Figure 3.2. Mean (+ 1 SE) Heip's evenness (E_{Heip}) per plot for each retention level and forest type for mosses (M) and liverworts (L). The effects of retention level and forest type and their interaction were calculated separately for mosses and liverworts using nested ANOVA (Table 3.2). No significant interactions were detected. Pair-wise comparisons of retention levels were calculated when the main effect was significant. Bars of retention levels or forest types with different letters were significantly different.

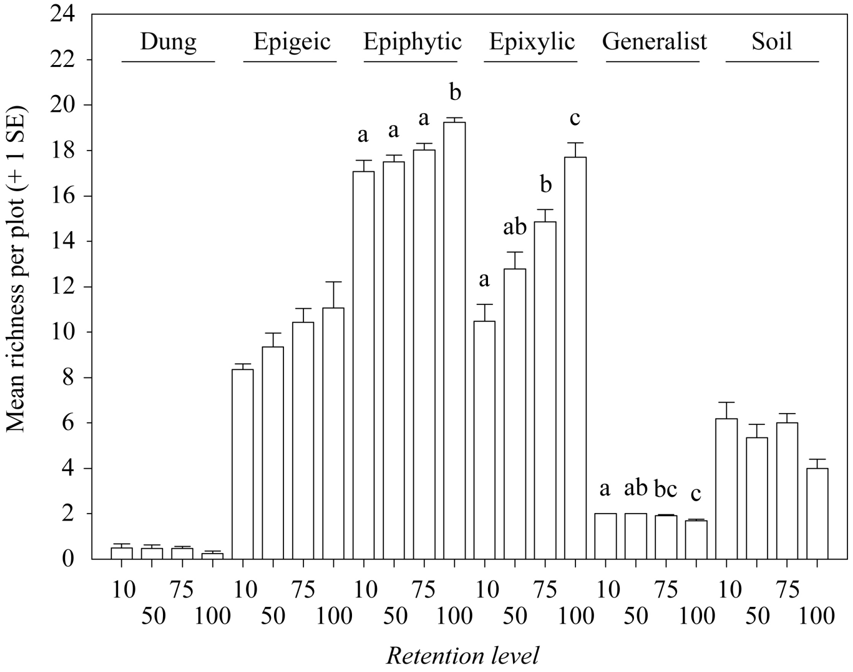
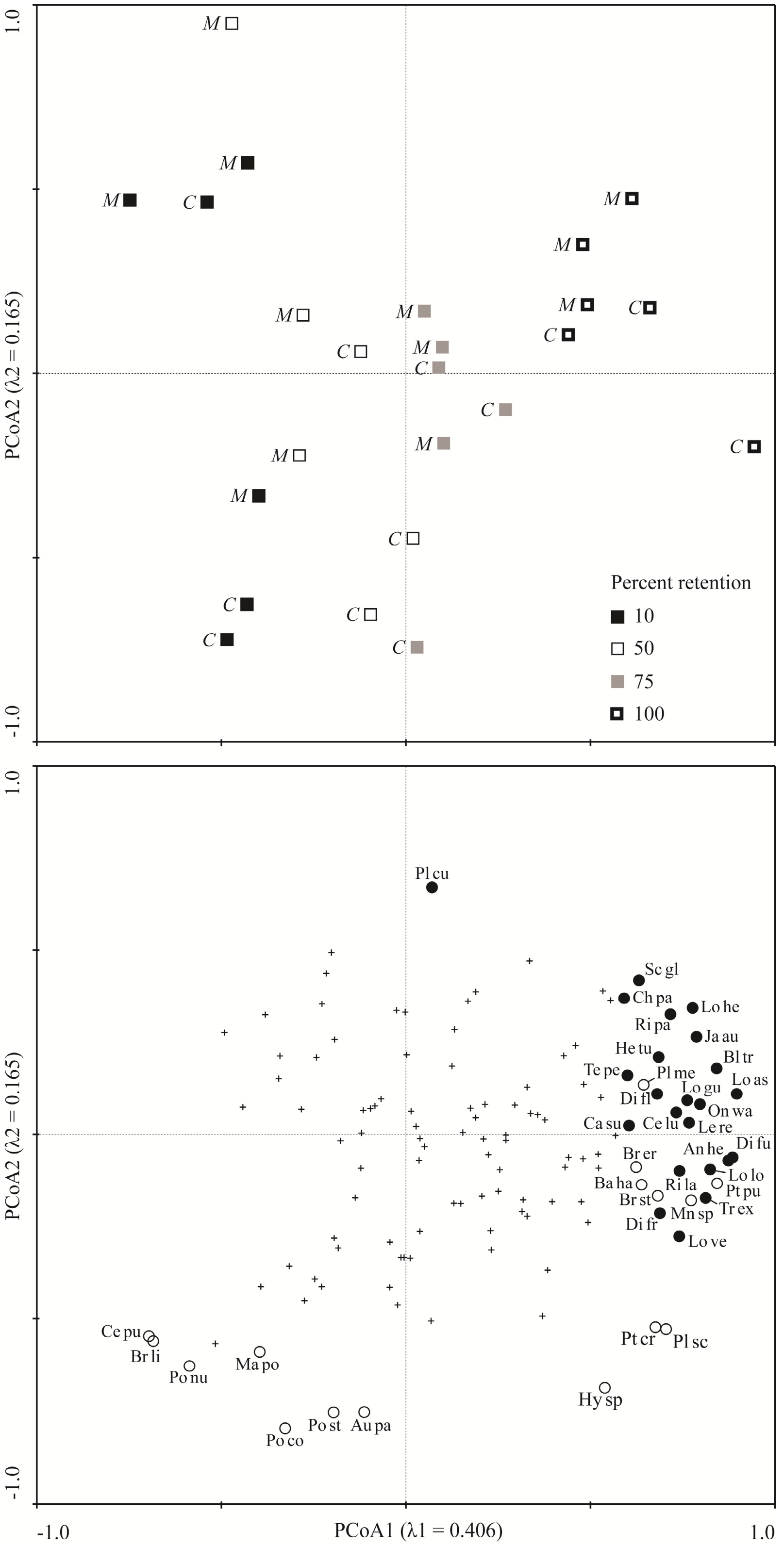


Figure 3.3. Mean (+ 1 SE) richness per plot of bryophytes with different substrate preferences for each retention level. The effects of retention level and forest type and their interaction were calculated separately for each substrate group using the Scheirer-Ray-Hare extension of the Kruskal-Wallis test (Table 3.3). Pair-wise comparisons of retention levels were calculated when the main effect was significant. Bars for a substrate category with different letters were significantly different.



1.0
PCoA2 (λ2 = 0.165)
-1.0
M
C
Percent retention
■ 10
□ 50
▨ 75
⊡ 100
1.0
PCoA2 (λ2 = 0.165)
-1.0
Pl cu
Sc gl
Ch pa
Lo he
Ri pa
Ja au
He tu
Bl tr
Te pe
Pl me
Lo as
Di fl
Lo gu
On wa
Ca su
Ce lu
Le re
Br er
An he
Di fu
Lo lo
Ba ha
Ri la
Pt pu
Br st
Mn sp
Tr ex
Di fr
Lo ve
Ce pu
Br li
Po nu
Ma po
Pt cr
Pl sc
Hy sp
Po co
Po st
Au pa
-1.0
PCoA1 (λ1 = 0.406)
1.0

Figure 3.4. Results of PCoA on 135 species and 24 stands using Bray-Curtis dissimilarity. A) Plot of stands coded by retention level (10%, closed boxes; 50%, thin open boxes; 75%, shaded boxes; 100%, thick open boxes) and forest type (*M*, mixed; *C*, coniferous forest). B) Plot of species centroids. Species with > 60% explained variation along the two plotted axes are depicted as circles and are coded by species name. Species codes are the first two letters of the genus and species (Appendix 3.1). Filled circles are species with epixylic or epiphytic substrate preferences. All other species are depicted as "+" symbols.

Appendix 3.1. Mean relative abundance per plot of bryophytes sampled within each level of canopy retention.

	Phylogenetic group	Substrate preference	Retention level			
			10%	50%	75%	100%
Species						
Anastrophyllum hellerianum	L	Ex	0.67	0.86	1.11	1.75
Barbilophozia hatcheri	L	Eg	0.03	0.11	0.22	0.39
Barbilophozia kunzeana	L	Eg	0.00	0.00	0.03	0.00
Blasia pusilla	L	So	0.19	0.06	0.08	0.03
Blepharostoma trichophyllum	L	Ex	0.42	0.81	1.00	1.42
Calypogeia suecica	L	Ex	0.06	0.06	0.31	0.44
Cephalozia connivens	L	Ex	0.00	0.00	0.06	0.03
Cephalozia connivens var. *compacta*	L	Ex	0.00	0.00	0.00	0.03
Cephalozia leucantha	L	Ex	0.03	0.00	0.00	0.00
Cephalozia lunulifolia + C. affinis	L	Ex	0.33	0.47	0.64	0.97
Cephalozia pleniceps	L	So	0.00	0.00	0.00	0.03
Cephaloziella rubella	L	Ex	0.76	0.58	0.61	0.58
Cephaloziella rubella var. *bifida*	L	Ex	0.00	0.00	0.03	0.08
Chiloscyphus pallescens	L	Ex	0.33	0.50	0.72	1.19
Geocalyx graveolens	L	Ex	0.14	0.28	0.22	0.58
Harpanthus drummondii	L	Ex	0.06	0.00	0.00	0.00
Jamesoniella autumnalis	L	Ex	1.06	1.44	1.78	2.11
Lepidozia reptans	L	Ex	0.25	0.33	0.56	0.82
Lophozia ascendens	L	Ex	0.81	1.03	1.43	2.08
Lophozia ciliata	L	Ex	0.00	0.03	0.00	0.00
Lophozia excisa	L	Ex	0.06	0.00	0.11	0.03
Lophozia guttulata	L	Ex	0.11	0.08	0.28	0.86
Lophocolea heterophylla	L	Ex	0.69	0.78	1.15	1.92
Lophozia incisa	L	Ex	0.00	0.08	0.06	0.03
Lophozia longidens	L	Ex	0.31	0.51	0.69	1.53
Lophocolea minor	L	Ex	0.50	0.56	0.67	1.08
Lophozia ventricosa	L	Ex	0.14	0.22	0.44	0.67
Lophocolea sp.	L	Ex	0.00	0.03	0.00	0.00
Lophozia sp.	L	Ex	0.00	0.06	0.00	0.00
Marchantia polymorpha	L	So	0.86	0.58	0.69	0.25
Plagiochila porelloides	L	Eg	0.00	0.11	0.17	0.44
Ptilidium ciliare	L	Ep	0.03	0.08	0.08	0.14
Ptilidium pulcherrimum	L	Ex	1.57	2.14	2.79	2.94
Radula complanata	L	Ep	0.00	0.00	0.03	0.00
Riccardia latifrons	L	Ex	0.82	1.00	1.14	1.29
Riccardia palmata	L	Ex	0.14	0.31	0.25	0.82
Scapania glaucocephala	L	Ex	1.11	1.32	1.50	1.90
Scapania irrigua	L	Ex	0.00	0.03	0.00	0.00

	Phylogenetic group	Substrate preference	Retention level			
			10%	50%	75%	100%
Tritomaria exsectiformis	L	Ex	0.31	0.47	0.58	1.08
Amblystegium serpens	M	Ep	1.88	2.03	1.83	2.31
Amblystegium varium	M	Ep	0.06	0.00	0.00	0.00
Aulacomnium palustre	M	Eg	1.75	1.54	1.53	1.31
Barbula convoluta	M	So	0.03	0.00	0.00	0.00
Barbula unguiculata	M	So	0.00	0.00	0.06	0.00
Brachythecium albicans	M	Ep	0.39	0.47	0.36	0.44
Brachythecium campestre	M	Ep	2.50	2.15	2.10	2.00
Brachythecium cf. calcareum	M	Ep	0.00	0.00	0.03	0.00
Brachythecium erythrorrhizon	M	Eg	0.76	0.78	1.57	1.63
Brachythecium reflexum	M	Ep	0.00	0.00	0.00	0.03
Brachythecium rutabulum	M	Ep	0.08	0.11	0.08	0.15
Brachythecium salebrosum	M	Ep	1.43	1.36	1.31	1.24
Brachythecium starkei	M	Eg	1.26	1.19	1.79	2.01
Brachythecium velutinum	M	Ep	0.00	0.00	0.03	0.19
Bryohaplocladium microphyllum	M	Ep	0.25	0.19	0.00	0.03
Bryum argenteum	M	So	0.14	0.06	0.11	0.00
Bryum caespiticium	M	So	0.03	0.08	0.03	0.03
Bryum lisae var. *cuspidatum*	M	Ge	2.01	1.71	1.46	0.72
Bryum pseudotriquetrum	M	So	0.22	0.28	0.44	0.33
Calliergon cordifolium	M	Eg	0.00	0.08	0.03	0.00
Calliergon giganteum	M	Eg	0.03	0.06	0.00	0.14
Calliergon richardsonii	M	Eg	0.00	0.00	0.00	0.14
Campylium cf. *radicale*	M	Eg	0.00	0.00	0.00	0.03
Campylium chrysophyllum	M	Ep	0.47	0.44	0.44	0.63
Campylium hispidulum	M	Ep	1.68	1.90	1.83	1.54
Campylium stellatum	M	So	0.25	0.22	0.28	0.28
Ceratodon purpureus	M	So	2.58	2.47	2.26	0.86
Climacium dendroides	M	Eg	0.06	0.08	0.08	0.14
Cratoneuron filicinum	M	So	0.00	0.03	0.00	0.00
Dicranum acutifolium	M	Ep	0.00	0.00	0.03	0.06
Dicranum cf. *bonjeanii*	M	Ep	0.00	0.03	0.00	0.03
Dicranum flagellare	M	Ep	0.53	0.75	0.83	1.13
Dicranum fragilifolium	M	Ep	1.43	1.47	1.88	2.25
Dicranum fuscescens	M	Ep	0.61	1.03	1.42	2.47
Dicranum groenlandicum	M	Ep	0.03	0.00	0.00	0.00
Dicranum polysetum	M	Eg	0.61	0.78	0.75	1.00
Dicranum scoparium	M	Ep	0.06	0.14	0.28	0.36
Dicranum tauricum	M	Ep	0.03	0.00	0.00	0.03
Dicranum undulatum	M	Eg	0.50	0.96	0.94	1.24
Distichium capillaceum	M	So	0.03	0.00	0.03	0.00
Drepanocladus aduncus	M	Eg	0.08	0.22	0.03	0.25
Eurhynchium pulchellum	M	Ep	2.44	2.68	2.79	2.78
Funaria hygrometrica	M	So	0.72	0.44	0.50	0.22

	Phylogenetic group	Substrate preference	Retention level			
			10%	50%	75%	100%
Helodium blandowii	M	Eg	0.03	0.06	0.03	0.06
Herzogiella turfacea	M	Ex	0.69	0.92	1.03	1.29
Hylocomium splendens	M	Eg	2.36	2.64	2.94	2.99
Hypnum pallescens	M	Ep	0.00	0.06	0.03	0.03
Hypnum pratense	M	Eg	0.31	0.28	0.28	0.19
Isopterygiopsis pulchella	M	Ep	0.22	0.19	0.47	0.36
Leptodictyum riparium	M	Eg	0.00	0.03	0.03	0.00
Leptobryum pyriforme	M	So	1.39	1.19	1.17	0.56
Mnium spinulosum	M	Ep	1.22	1.78	1.88	2.68
Oncophorous wahlenbergii	M	Ep	1.36	1.79	1.90	2.31
Orthotrichum obtusifolium	M	Ep	1.22	1.56	1.97	2.03
Orthotrichum speciosum	M	Ep	0.89	1.08	1.39	1.72
Plagiomnium cuspidatum	M	Ep	1.97	1.94	2.29	2.17
Plagiomnium drummondii	M	Ep	0.94	0.78	1.14	1.76
Plagiomnium ellipticum	M	Eg	0.28	0.47	0.56	0.83
Plagiomnium medium	M	Eg	0.28	0.44	0.89	1.11
Plagiothecium denticulatum	M	Ep	0.17	0.17	0.22	0.47
Plagiothecium laetum	M	Ep	0.08	0.11	0.14	0.11
Platygyrium repens	M	Ep	0.11	0.14	0.03	0.06
Pleurozium schreberi	M	Eg	1.81	2.17	2.81	2.99
Pohlia cruda	M	So	0.06	0.00	0.08	0.06
Pohlia nutans	M	Ge	2.01	2.08	1.99	1.07
Pohlia proligera	M	So	0.00	0.03	0.00	0.03
Pohlia wahlenbergii	M	So	0.06	0.00	0.00	0.00
Polytrichum commune	M	So	1.06	0.81	0.86	0.33
Polytrichum juniperinum	M	So	0.92	0.94	0.94	0.56
Polytrichum longisetum	M	So	0.06	0.03	0.03	0.03
Polytrichum piliferum	M	So	0.03	0.03	0.03	0.00
Polytrichum strictum	M	So	0.83	0.69	0.53	0.25
Ptilium crista-castrensis	M	Eg	1.82	2.33	2.67	2.99
Pylaisiella polyantha	M	Ep	1.68	2.01	2.13	2.14
Rhizomnium pseudopunctatum + R. gracile	M	So	0.00	0.11	0.28	0.33
Rhytidiadelphus triquetrus	M	Eg	0.06	0.08	0.19	0.28
Sanionia uncinata	M	Ep	1.96	1.81	2.04	2.21
Sarmenthypnum sarmentosum	M	Eg	0.00	0.00	0.00	0.03
Sphagnum angustifolium	M	Eg	0.00	0.03	0.03	0.00
Sphagnum capillifolium	M	Eg	0.08	0.00	0.08	0.06
Sphagnum girgensonii	M	Eg	0.00	0.00	0.06	0.00
Sphagnum squarrosum	M	Eg	0.03	0.00	0.11	0.00
Sphagnum warnstorfii	M	Eg	0.00	0.03	0.08	0.22
Splachnum ampullaceum	M	Du	0.00	0.03	0.00	0.06
Splachnum luteum	M	Du	0.00	0.00	0.03	0.00
Splachnum rubrum	M	Du	0.25	0.22	0.19	0.06
Splachnum sp.	M	Du	0.03	0.00	0.00	0.00

	Phylogenetic group	Substrate preference	Retention level			
			10%	50%	75%	100%
Splachnum sphaericum	M	Du	0.17	0.17	0.14	0.03
Tetraphis pellucida	M	Ex	0.28	0.47	0.53	0.75
Tetraplodon angustatus	M	Du	0.06	0.03	0.06	0.11
Tetraplodon mnioides	M	Du	0.00	0.03	0.06	0.00
Thuidium recognitum	M	Ep	0.69	0.67	0.94	1.13
Tomentypnum nitens	M	Eg	0.33	0.39	0.39	0.44
Tortula ruralis	M	So	0.00	0.00	0.00	0.03
Warnstorfia exannulata	M	Eg	0.06	0.00	0.06	0.06
Warnstorfia fluitans	M	Eg	0.00	0.00	0.00	0.03

Notes: Refer to Methods for species relative abundance calculations. Phylogenetic group: L = liverworts; M = mosses. Substrate preference: Du, animal excrement and bones; Eg, epigeic on forest floor and humus; Ep, epiphytic on bark; Ex, epixylic on dead wood; Ge, generalist on various substrate types; So, mineral soil. Species were assigned to substrate categories based on the most frequent substrate on which it was sampled or from the literature (Crum and Anderson 1981; Schuster 1966–1992).

Appendix 3.2. Results of indicator species analysis (ISA) conducted separately for A) retention level and B) forest type treatments.

	Phylogenetic group	Substrate preference	ISA		
			Group	IV	*P*
A) Retention level					
Lophozia guttulata	L	Ex	100	64.6	0.001
Riccardia palmata	L	Ex	100	54.1	< 0.001
Lophozia longidens	L	Ex	100	50.2	< 0.001
Geocalyx graveolens	L	Ex	100	47.7	0.008
Lophozia ventricosa	L	Ex	100	45.3	0.030
Tritomaria exsectiformis	L	Ex	100	44.3	0.001
Chiloscyphus pallescens	L	Ex	100	43.4	0.004
Barbilophozia hatcheri	L	Eg	100	43.2	0.048
Lophocolea heterophylla	L	Ex	100	42.2	< 0.001
Lepidozia reptans	L	Ex	100	41.8	0.005
Cephalozia lunulifolia + C. affinis	L	Ex	100	40.2	0.012
Anastrophyllum hellerianum	L	Ex	100	39.9	< 0.001
Lophozia ascendens	L	Ex	100	39.0	< 0.001
Blepharostoma trichophyllum	L	Ex	100	38.9	< 0.001
Jamesoniella autumnalis	L	Ex	100	33.0	0.005
Scapania glaucocephala	L	Ex	100	32.6	0.002
Ptilidium pulcherrimum	L	Ex	100	31.2	0.003
Riccardia latifrons	L	Ex	100	30.4	0.039
Brachythecium velutinum	M	Ep	100	58.3	0.015
Dicranum fuscescens	M	Ep	100	44.7	< 0.001
Plagiomnium medium	M	Eg	100	40.8	0.043
Plagiomnium drummondii	M	Ep	100	38.1	0.012
Mnium spinulosum	M	Ep	100	35.5	< 0.001
Dicranum flagellare	M	Ep	100	34.8	0.040
Orthotrichum speciosum	M	Ep	100	33.9	0.024
Bryum lisae var. *cuspidatum*	M	Ge	10	33.8	0.049
Herzogiella turfacea	M	Ex	100	32.9	0.013
Dicranum fragilifolium	M	Ep	100	32.0	0.036
Oncophorous wahlenbergii	M	Ep	100	31.3	0.004
Pleurozium schreberi	M	Eg	100	30.6	0.016
Ptilium crista-castrensis	M	Eg	100	30.5	0.016
Brachythecium campestre	M	Ep	10	28.6	0.019
B) Forest type					
Lophozia ventricosa	L	Ex	Con	71.7	0.006
Cephalozia lunulifolia + C. affinis	L	Ex	Con	63.2	0.030
Chiloscyphus pallescens	L	Ex	Mix	63.1	0.042
Tritomaria exsectiformis	L	Ex	Con	62.5	0.047
Bryum pseudotriquetrum	M	So	Con	76.1	< 0.001

	Phylogenetic group	Substrate preference	ISA		
			Group	IV	*P*
Polytrichum strictum	M	So	Con	69.8	0.021
Brachythecium salebrosum	M	Ep	Mix	68.5	< 0.001
Polytrichum commune	M	So	Con	67.3	0.027
Plagiothecium denticulatum	M	Ep	Con	64.4	0.032
Plagiomnium cuspidatum	M	Ep	Mix	55.6	0.035
Sanionia uncinata	M	Ep	Mix	54.8	0.011

Notes: Only species with significant indicator values (IV) are presented. Phylogenetic group: L = liverworts; M = mosses. Substrate preference: Eg, epigeic on forest floor and humus; Ep, epiphytic on bark; Ex, epixylic on dead wood; Ge, generalist on various substrate types; So, mineral soil. Species are ordered by decreasing IV within each phylogenetic group. ISA group is the particular retention level or forest type (Mix = mixed forest; Con = coniferous forest) for which a species is a significant indicator.

Chapter 4: Biological traits of boreal bryophytes explain species sensitivity to habitat change after partial harvesting

Abstract - Biological traits are potentially important for understanding plant species responses to local habitat conditions, and may also provide insight regarding how species respond to natural and anthropogenic disturbance. Forest harvesting is a particularly important form of disturbance in the circumpolar boreal biome, influencing stand and landscape scale patterns of forest structure and biodiversity. We examined a range of variable retention harvesting intensities in terms of their effectiveness for maintaining mosses and liverworts (bryophytes) with differing biological traits. Bryophytes were sampled five to six years after application of 10%, 50%, and 75% dispersed green-tree retention harvesting (unharvested stands as controls), in 24 forest stands (each 10 ha) of two forest types (broadleaf-coniferous mixed-wood, coniferous-dominated). We first examined the environmental factors that were the strongest predictors of species composition across the forest types and retention levels. We then used fourth-corner analysis to examine how differences in forest structure and growing conditions among harvesting treatments influenced species with differing traits. Selected traits included phylogeny and life form, habitat requirements, and reproduction and dispersal characteristics of species, all thought to be important determinants of bryophyte species occupancy in boreal forests. The strongest predictors of species composition were forest moisture and degree of canopy closure. Fourth-corner analysis showed that forest type, retention level, and their associated moisture conditions, were closely related to the abundances of species characterized by different sets of biological traits. Species with rare sporophyte production, larger spores, dioicous sexuality, and which require greater moisture and shade, were affiliated with higher retention and forest moisture. Reduced abundances of species with these traits after harvesting may detrimentally affect their capacity to disperse and re-establish, and suggests that moisture limitation is an important environmental filter that may further reduce their representation at harvested sites. Coniferous-dominated forests supported higher abundances of liverworts and species with greater moisture requirements than mixed broadleaf-coniferous forests. This conveys the importance of coniferous forests for bryophyte preservation in mixed-wood landscapes, and the influence of canopy composition on regional species distributions. Understanding the tolerances of species exhibiting particular traits to habitat conditions after harvesting may improve predictions about species extirpation risk and ways to ensure their continued survival.

Key words: environmental filter, epiphytic, epixylic, *Hylocomium splendens*, life form, regression tree, moss, liverwort, fourth-corner analysis, variable retention

4.1 Introduction

Species responses to prevailing abiotic and biotic habitat conditions are important determinants of both local and regional patterns of diversity (Whittaker 1956; Whittaker and Levin 1975; Huston 1979, 1994). Species differ in biological attributes (traits) that are evolutionarily adapted to a range of conditions (Levins 1968; Kassen 2002). The biological traits of a species characterize its capacity to reproduce, disperse, and become established, and to persist in a habitat. Alteration of habitat conditions (e.g., microclimate) may detrimentally affect the persistence of a species at a location, or the potential for a species to arrive and establish, if the changed environment is beyond the range of tolerance for a species' traits to successfully perform (Lynch and Gabriel 1987; Chapin et al. 1993). Species with different traits may respond in dissimilar ways to habitat modification to influence the biodiversity represented at a site (Keddy 1992; Lavorel et al. 2002; Hewitt et al. 2005). Biological traits of species are, therefore, potentially meaningful descriptors of species responses to habitat change, and may provide insights into effects of human disturbance on species persistence and recovery.

Forest harvesting is a prevalent form of disturbance in the circumpolar boreal biome. Although boreal forests are adapted to recurrent natural disturbances, including fire, insect outbreaks, and canopy gap-formation processes, harvesting can differ substantially as an agent of disturbance (Niemelä 1999; Haeussler and Kneeshaw 2003). Recent studies have documented the effects of forest management regimes on landscape scale patterns of forest structure and composition (Bergeron et al. 1998; Cyr et al. 2009) and how changes in these factors affect biodiversity (Kuuluvainen 2009). This has been accompanied by growing interest in the development of forest harvesting practices that retain structural features characteristic of unmanaged forests (Lindenmayer et al. 2006). Variable retention harvest systems are increasingly being used to preserve elements of forest structure (biological legacies) in the hopes of maintaining ecosystem processes and enhancing species survival or recovery after harvesting (Lindenmayer and Franklin 2002; Lindenmayer et al. 2006). Variable retention is assumed to preserve species by moderating growing conditions, retaining important habitat features, and enhancing habitat connectivity in the harvested matrix (Lindenmayer and Franklin 2002). However, we are just beginning to understand the effects of variable retention harvesting on different forest biota (Lindenmayer et al. 2006; Kuuluvainen 2009).

Biological traits may indicate important aspects of species responses to variable retention practices. Species with particular traits may become locally extirpated if habitat conditions are unsuitable after forest harvesting. Furthermore, re-establishment may be limited when species have ineffective reproduction and/or dispersal capacities, or if inhospitable conditions in the forest matrix impede species colonization. Plant species seed size, fecundity, and dispersal vectors can influence recruitment (McEuen and Curran 2004), and plant life form is often associated with environmental conditions to which a species is adapted (Raunkiaer 1934; Bates 1998). The biological traits of species may better explain the effects and consequences of harvesting than by examining species using taxonomy alone, yet traits have infrequently been used to test these relationships for some groups of organisms.

The unique physiology and habitat requirements of boreal mosses and liverworts (bryophytes) make them well suited to study the effects of habitat change on species. Bryophytes can attain high abundance on the forest floor and influence several ecosystem processes, including nutrient cycling, nitrogen fixation, regulation of ground temperature and moisture, and understory vegetation development (e.g., Chapin et al. 1987; Nilsson and Wardle 2005). The internal moisture content of forest bryophytes is at equilibrium with their surroundings, and many species have some level of desiccation tolerance allowing them to grow in habitats that are not readily colonized by vascular plants, including fallen logs and tree bark. However, some species are negatively affected by prolonged desiccation and exposure following intensive forest harvesting such as clear-cutting (e.g., Hylander et al. 2005). Thus, bryophytes stand to benefit from retained forest structure, canopy cover, and habitat heterogeneity provided by variable retention harvesting. Currently, the factors influencing the response of bryophyte species to forest harvesting remain poorly understood. The responses of species with different biological traits to retained forest structure may provide insights about the effects of disturbance intensity on different species groups and their propensity for post-disturbance recovery.

Our objective herein, is to determine whether the biological traits of bryophyte species help to explain their abundances across variation in forest structure and composition resulting from a range of partial harvesting intensities in boreal mixed-wood forests. We first examined relationships between measured forest structure/environmental variables and species abundances to determine the abiotic and biotic factors that most influenced species assemblages five to six years post-harvest. We then used fourth-corner analysis (Legendre et al. 1997; Dray and Legendre 2008) to examine how species with different traits responded to habitat conditions after partial harvesting. The method has been used to examine factors influencing community structure (e.g., Roy and de Blois 2006; Besemer et al. 2009; Gallardo et al 2009) and succession (e.g., Hooper et al. 2004; Aubin et al. 2009; Lacourse 2009), and less frequently to relate the effects of disturbance intensity to species recovery (but see Little 2000). We selected a limited number of traits describing bryophyte species phylogeny and life form, habitat requirements, and reproduction and dispersal characteristics, which are considered to be important determinants of species persistence in boreal forests (e.g., Söderström and During 2005). Abundances of species with particular traits after harvesting may reflect their sensitivity to altered habitat conditions and the possibilities for their continued survival.

4.2 Methods

Study area

Research was conducted at the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental site in northwestern Alberta, Canada (56º 46' N, 118º 22' W). EMEND was established in part to examine the effects of residual forest structure on biodiversity conservation. The site is situated in the Lower Boreal–Cordilleran Ecoregion, marking the transition between boreal and cordilleran climatic conditions, and between the deciduous boreal and coniferous cordilleran vegetation (Strong and Leggat 1992). Regional climate is continental with a mean daily temperature of 1.2 ºC and mean total annual precipitation of 402 mm, of which approximately three-quarters falls as rain (Environment Canada 2010). Forest stands originated after fire approximately a century ago, and are dominated by varying amounts of broadleaf (primarily *Populus tremuloides* Michx. and *Populus balsamifera* L.) and coniferous (primarily *Picea glauca* (Moench) Voss) canopy cover, with lower abundances of *Abies balsamea* (L.) Mill., *Betula papyrifera* Marsh., *Picea mariana* (Mill.) B.S.P., and *Pinus contorta* Dougl. ex Loud. Topography is undulating with moderate relief, ranging from 677 to 880 m above seal-level.

Study design

We examined the influence of forest canopy composition and retention level on bryophytes using a factorial design with replication at the forest stand level. During the winter of 1998/1999, harvesting treatments were randomly applied to forest stands (each approximately 10 ha in size) in two different forest canopy types: mixed broadleaf-coniferous ("mixed", 35–65% broadleaf canopy cover) and coniferous-dominated ("coniferous", > 70% coniferous canopy cover) composition.

Harvesting treatments consisted of 10%, 50%, and 75% dispersed green-tree retention (unharvested stands as controls). Harvesting was conducted using a modified shelterwood pattern in which machine traffic was restricted to 5 m wide corridors (oriented in a north-south direction, perpendicular to prevailing winds) that alternated with 15 m wide retention strips. Retention strips were partially harvested by systematic tree removal to achieve the desired level of retention for the stand, while accounting for the timber removed from corridors.

Bryophytes and measures of forest structure were sampled during the 2004–2005 growing seasons in three replicate stands per harvesting treatment per forest type, for a total of 24 sampled stands. Replicate stands of each forest type were similar in pre-harvest ecological site classification, canopy cover and composition, composition of understory vegetation, and age (e.g., Work et al. 2004). Stands frequently contained small, intermittent watercourses, but did not contain perennial streams, rock outcrops, or large boulders.

Forest structure measurements

Within each stand we randomly established six sampling points which were placed along the centre line of retention strips to standardize the type of habitat (retention strip or machine corridor) that was sampled. A 50 m^2 circular plot was centered on each sampling point and the following measures of forest structure were obtained: percent cover of broadleaf and coniferous trees (assessed at 1 m height by convex spherical densiometer); cover of graminoids, forbs, dead forest floor feather mosses, and exposed mineral soil (visual estimates); basal area and density of broadleaf and coniferous trees and shrubs ≥ 2 m height (separately for stems < 5 and ≥ 5 cm DBH (diameter at 1.3 m height)); aspect; degrees slope; depth of the litter-fermented humus (LFH) layer (cm); and diameter and decay stage (1–4; Mills and Macdonald 2005) of natural and harvested tree stumps. Within a central 10 m^2 circular sub-plot we measured the cover and density of broadleaf and coniferous trees and shrubs < 2 m height. We used two perpendicular line transects bisecting each plot to measure the diameter and decay stage (1–7; Mills and Macdonald 2005) of all intercepted pieces of downed wood ≥ 5 cm and fine woody material < 5 cm diameter.

Hylocomium splendens sampling and growth measurements

We used the recent shoot growth of the forest floor moss *Hylocomium splendens* (Hedw.) Schimp. in B.S.G. as a surrogate measure of local forest moisture. *Hylocomium splendens* is perennial with a modular growth form, adding new segments to existing shoots each year by ramification of the main axis (Tamm 1953; Økland 1995). Segment lengths correspond closely with local forest moisture availability (Busby et al. 1978; Hylander 2005; Stewart and Mallik 2006), making the species a potentially meaningful biological indicator of local habitat quality for bryophytes.

We arbitrarily selected several shoots of *Hylocomium splendens* from 1 m x 1 m plots located at the centre of each 50 m^2 plot. The species was sometimes absent from the 1 m x 1 m plot and was collected elsewhere within the larger 50 m^2 plot. The species was either dead or absent in three plots of mixed and two plots of coniferous forest. Sampled shoots were air dried, and the length of the mature segment from the previous growing season was measured under a dissecting microscope to within 0.4 mm. Shoots were not measured if they were dead, had branching along the stem within one year of the segment being measured, or exhibited a monopodial growth form (continuous growth of the shoot with poorly defined annual segments) (Økland 1995). A total of 4,628 shoots were used for analysis (mean of $n = 33$ shoots per plot).

Bryophyte sampling

Bryophytes were sampled in 20 m radius (1,256 m^2) circular plots centered on each 50 m^2 plot. The large plot size ensured the capture of uncommon habitats and associated species, and provided the best estimate of species occurrences at the stand level. Species abundance was estimated for each plot on a three-point scale of relative abundance (modified from Newmaster et al. 2005), where 1 = one (including trace amounts) to a few occurrences, 2 = several occurrences to frequent in one or some areas of the plot, and 3 = frequent throughout the plot. Species abundances were averaged for each forest stand prior to analysis.

We recorded the substrates on which each species was growing in each plot. Each species was subsequently assigned to a single substrate category based on the most frequent substrate it was associated with, or based on the literature (e.g., Crum and Anderson 1981; Schuster 1966–1992) if few specimens were encountered in the field. The following substrate categories were used: 1) dung (animal excrement and bones), 2) epigeic (forest floor and humified organic matter), 3) epiphytic (bark of living trees and recently fallen wood), 4) epixylic (decayed wood), 5) generalist (species were consistently found on a variety of substrate types), and 6) mineral soil.

Species that could not be identified in the field were collected and subsequently identified in the laboratory. A total of 3,957 samples were collected, each containing multiple species. Nomenclature follows Anderson (1990) for *Sphagnum*, Anderson et al. (1990) for mosses, and Stotler and Crandall-Stotler (1977) for liverworts. The liverwort *Lophozia ciliata* was recently described (Söderström et al. 2000) and is included in our dataset. We combined *Rhizomnium pseudopunctatum* + *R. gracile* and *Cephalozia lunulifolia* + *C. affinis* because identification was sometimes ambiguous. *Calliergon obtusifolium* is considered to be synonymous with *Calliergon richardsonii* following Hedenäs (1993). Voucher specimens are deposited at the Devonian Botanic Garden (ALTADBG) and Department of Biological Sciences (ALTA) herbaria, University of Alberta.

Bryophyte traits

We took advantage of a recently published dataset of bryophyte species traits (Hill et al. 2007) as a starting point to compile trait information for individual species. A limited number of traits that were relevant to this study and that pertained to species from our region were selected from the database. Traits were organized into three categories: 1) species phylogeny and life form (sensu Bates 1998); 2) reproduction and dispersal capacity (phenology, type of specialized asexual propagules produced, sexuality, frequency of sexual reproduction, spore size); and 3) habitat requirements (substrate, light, and moisture conditions). For reproduction and dispersal traits, only specialized asexual propagules that are known to develop into new plants were considered. Non-specialized gametophyte fragments were not considered, oweing to a lack of information on establishment success for different species. Studies have found these traits to be closely related to species occurrences in boreal forests (e.g., Ross-Davis and Frego 2004; Hylander et al. 2005; Mills and Macdonald 2005; Laaka-Lindberg et al. 2006; Hylander 2009; Löbel et al. 2009). These traits may be important predictors of the species distributions in harvested forests. Traits consisted of nominal, ordinal, and continuous data and are summarized in Table 4.1. Values of traits associated with each species are presented in Appendix 4.1.

The selected traits are mostly descriptive ("soft", Lavorel and Garnier 2002) and the majority of our species have a circumpolar distribution, making the selected traits generally applicable to species from our study area (M.O. Hill, personal communication). However, some species can display variation in the frequency of sexual reproduction, production of asexual propagules, and substrate affinity over their range (e.g., Sagmo Solli et al. 2000; Crum and Anderson 1981; Schuster 1966–1992). Therefore, values of each selected trait in the dataset were modified when appropriate based on the literature for the region (Lawton 1971; Flowers 1973; Crum and Anderson 1981; Crum 1984; Spence 1988; Schofield 1992; Schuster 1966–1992; Söderström et al. 2000; Damsholt 2002; Flora of North America Editorial Committee 2007), as well as expert advice and personal knowledge. Spore size was based solely on Crum and Anderson (1981) and Crum (1984) for mosses, and Schuster (1966–1992) for liverworts, except *Lophozia ciliata*, which was based on Söderström et al. (2000). Species substrate requirements were based solely on our field data. Three species that could only be identified to the genus level were omitted from the final table of species traits.

Statistical analysis

A variety of analytical tools were used to determine the most important factors influencing bryophyte species composition after partial harvesting, and how forest habitat (structure/environment) conditions after harvesting affected the abundances of species with differing biological traits. First, we conducted a constrained ordination using distance-based redundancy analysis (db-RDA, Legendre and Anderson 1999) to relate forest habitat variables to bryophyte species composition. These variables described the structure and composition, forest floor substrates, and moisture (using *Hylocomium splendens* growth) conditions of sampled stands. Db-RDA is closely related to redundancy analysis (RDA) but allows users to select a measure of species resemblance that is appropriate for the data. The analysis uses RDA to analyze the principal coordinates obtained from a principal coordinate analysis of species data based on the chosen resemblance measure, after accounting for negative eigenvalues (ter Braak and Šmilauer 2002). We performed db-RDA using Bray-Curtis dissimilarity (Legendre and Legendre 1998) in CANOCO 4.5 (ter Braak and Šmilauer 2002). Significance of the first axis and all axes combined were assessed using 9,999 unrestricted permutations. We obtained a reduced set of forest habitat variables to enter into the db-RDA using the program DISTLM forward (Anderson 2003). This program conducts a forward selection of explanatory variables on the basis of a user-selected measure of species resemblance, with tests of significance by permutation. The selection criterion for this method is the proportion of the total sum of squares explained by the individual variables, conditional on the variables already included in the model. Forward selection was conducted using forest habitat variables on species data represented by Bray-Curtis dissimilarity and 9,999 permutations for tests of significance.

Second, since forest moisture (detected by *Hylocomium splendens* growth) was found to be an important predictor of species composition (see Results) we wanted to determine how it was influenced by the harvesting treatments and by forest habitat. To this end, we examined differences in *Hylocomium splendens* growth among retention levels for each forest type separately. Direct comparisons between forest types and the interaction between forest type and retention level were not examined because shoots were sampled in the different forest types in different years. Shoot segments on a plant are considered to be physiologically independent (Callaghan et al. 1978) in terms of their growth response, making direct comparisons among different years potentially problematic. Tests were conducted by nested analysis of variance (ANOVA) using PROC MIXED in SAS 9.2 (SAS Institute Inc., Cary, NC). For each forest type, stand was nested within retention level as a random factor, which considered plots within each forest stand as sub-samples. Shoot growth was averaged for each plot prior to analysis. Data were transformed when appropriate to meet the assumptions of normality (Kolmogorov-Smirnov tests) and homogeneity of variances (Levene's tests), and pair-wise comparisons among retention levels for each forest type were conducted using Tukey-Kramer tests when the overall *F*-test was significant.

We also examined the influence of forest habitat (predictor variables) on *Hylocomium splendens* growth (dependent variable) for each forest type separately using regression tree analysis (Brieman et al. 1984). Regression tree analysis is a non-parametric technique that is capable of summarizing complex data structures and interactions among predictor variables. At each division in the tree the response variable is split into two well-defined groups based on the level of a particular explanatory variable (Brieman et al. 1984). The technique can incorporate nominal, ordinal, and continuous data, and is robust to non-linearity, heteroscedasticity, and multicollinearity in the data (Piramuthu 2008). Removing inter-correlated variables can lead to poor model fit (Zuur et al. 2007; Piramuthu 2008). The optimal tree size was ascertained by the recommended 10-fold cross-validation and "1-SE rule" (Brieman et al. 1984; Zuur et al. 2007). The analysis was performed in rpart 3.1-45 in R 2.10.1 (R Development Core Team 2010).

Third, we examined the effects of forest habitat conditions after partial harvesting on the abundances of species with different biological traits using a recently modified version of fourth-corner analysis (Dray and Legendre 2008). The analysis calculates the relationships between species traits and habitat variables through a link provided by a dataset of species abundances. The original version of the method could incorporate only species presence-absence data (Legendre et al. 1997). The analysis required three datasets: table **Q** (p x s) contained data on s traits for p bryophyte species, table **L** (n x p) contained the abundances for each of the p species at n sample sites, and table **R** (n x m) contained m environmental variables measured at each of the n sample sites. We used the mean relative abundance of each species per stand. The fourth-corner analysis then calculates the relationship between each pair of trait and environmental variables. An appropriate test statistic is returned depending on the type of data being analyzed. When both variables are quantitative (ordinal or continuous data), a correlation coefficient, r, provides the strength of the relationship. When one variable is nominal and the other quantitative, an F-statistic is returned for the global association between the pair of variables. The relationship between each level of the nominal variable and the quantitative variable is provided by a correlation coefficient. The magnitude and direction of the correlation coefficient for each trait level provides the relative trend in relation to all species (S. Dray, personal communication). When both variables are nominal, a G-statistic is provided for the global relationship, and tests for each trait level are performed by chi-squared tests. The significance of each test was assessed by permutation using model 1 (environmental control model, Legendre et al. 1997) to test the null hypothesis that individual species are equally likely to be found at any site. Permutation is performed by exchanging the values of species among sample units in table **L**, while preserving the number of sites at which a species was found (Legendre et al. 1997). P-values were adjusted for multiple tests by Holm correction (1979) when the overall test was significant.

We used three environmental variables in the fourth-corner analysis: 1) forest type as nominal variable with 2 levels; 2) retention level (%) after partial harvesting as a quantitative variable with 4 levels, and 3) *Hylocomium splendens* growth (mm) as a continuous quantitative variable. Forest type and retention level were main effects in our experimental design and *Hylocomium splendens* was a strong predictor of species composition in the db-RDA (see Results). Analyses were performed in ADE4 1.4-14 in R 2.10.1 (R Development Core Team 2010) using 9,999 permutations for tests of significance. For all of the above statistical tests we used alpha = 0.05.

4.3 Results

Relationships between forest habitat conditions and species composition

We sampled a total of 135 bryophyte species, consisting of 39 liverworts (28.9% of species) and 96 mosses (71.1%). Db-RDA summarized the variation in species composition (represented using Bray-Curtis dissimilarity) among the retention level and forest type treatments (Figure 4.1). Four environmental variables were significant descriptors of species composition. In order of selection, these were forest moisture (measured as *Hylocomium splendens* growth), total shrub cover, total canopy cover, and LFH depth. Total shrub cover included all residual and regenerating trees and shrubs < 2 m in height. The first axis (F-ratio = 9.66, $P < 0.001$) and all axes combined (F-ratio = 5.47, $P < 0.001$) were significant descriptors of species data, with the first two axes accounting for 44.8% of variation in species data (Table 4.2). Species-environment correlations along the first two axes were strong, especially for axis 1 ($r = 0.924$).

Forest environmental conditions shifted incrementally from intact forest with increasing harvesting intensity. Intact stands had high weights along db-RDA axis 1, in association with higher moisture, higher total canopy cover, and lower total shrub cover. Forest stands with lower levels of canopy retention generally had lower weights along axis 1, characterized by lower total canopy cover, lower moisture, and greater total shrub cover. Mixed forests had mostly positive scores on axis 2, in association with greater values of total shrub cover, LFH depth, and total canopy cover. Coniferous forests, in comparison, generally had negative scores on axis 2, with lower total shrub cover, LFH depth, and total canopy cover.

The importance of forest moisture as a driver of species composition in the db-RDA warranted a separate analysis of the factors affecting this environmental parameter. For both forest types *Hylocomium splendens* growth declined with any level of harvesting as compared to intact forest (Table 4.3). In mixed forest, *Hylocomium splendens* growth did not differ among the harvesting levels, whereas in coniferous forest there were incremental reductions in growth with declining retention (Table 4.3). These trends were consistent with output from the regression tree analysis performed on plot level data for each forest type (Figure 4.2). The most parsimonious tree for mixed forests had a single split between harvested and intact forests, which explained 50.8% of the variation in *Hylocomium splendens* growth. For coniferous forests, the final tree had three splits with four terminal nodes that together explained 70.7% of variation in growth. The first split (alone explaining 47.6% of variation) separated lower (10% and 50%) and higher (75% and 100%) retention. The split within lower retention indicated that plots with < 23.8% coniferous canopy cover had reduced *Hylocomium splendens* growth as compared to plots with greater coniferous cover. The split within the higher retention was based on the division between 75% retention and intact forest (Figure 4.2).

Relationships between forest habitat conditions and species traits

Fourth-corner analysis revealed that retention level, forest type, and variation in forest moisture (as indicated by *Hylocomium splendens* growth), were closely related to abundances of species with traits pertaining to phylogeny and life form, reproduction and dispersal capacity, and habitat requirements.

Retention level – Global tests of significance between retention level and each species trait were significant. In terms of phylogenetic group (Table 4.4), liverworts were more abundant at greater levels of canopy retention, whereas both pleurocarpous and acrocarpous mosses were comparatively more abundant at lower retention. Species with smooth mat, solitary creeping, and thread life forms were also more abundant at higher retention, while species having rough mats and turfs were associated with lower retention. For traits pertaining to reproduction and dispersal capacity (Table 4.5), species with a perennial phenology, dioicous sexuality, and rare sporophyte production were more abundant at greater retention levels. In comparison, species with annual phenology, monoicous sexuality, and abundant reproduction were more abundant at lower retention. Spore size was positively related to retention level, indicating that species with larger spores were more abundant with higher remnant canopy. Regarding habitat requirements (Table 4.6), epixylic and epigeic species were the only substrate groups to be affiliated with higher retention; species occupying dung and soil, and generalist species, were more abundant at lower retention. Furthermore, species that typically grow under lower light conditions and species that occupy wetter forest habitats were found to be more abundant at higher retention.

Forest type – Forest type was commonly related to species traits but fewer significant global tests were detected than for retention level. Coniferous forests harboured greater abundances of some species than mixed forests; there was no evidence that species with any traits were significantly more abundant in mixed forests. Liverworts and acrocarpous mosses were more abundant in coniferous forests (Table 4.4); pleurocarpous mosses did not differ in abundance between the two forest types. Species with a turf life form were also more abundant in coniferous than mixed stands. No difference was detected between forest types for species with monoicous sexuality, but dioicous (and predominantly or sometimes dioicous) species were more abundant in coniferous forests (Table 4.5). Species with rare or occasional sexual reproduction were also more dominant in coniferous forests. Moreover, coniferous forests supported greater abundances of species that colonize forest floor and soil substrates and that have higher moisture requirements (Table 4.6).

Forest moisture – Results of fourth-corner analysis for relationships between moisture (*Hylocomium splendens* growth) and species traits were similar to relationships between retention level and species traits (Tables 4.4–4.6). This likely resulted from the close relationship between forest moisture and retention (Table 4.3).

4.4 Discussion

The effectiveness of variable retention harvesting systems for maintaining natural patterns of bryophyte diversity will largely depend on species tolerances to habitat conditions generated by retained forest canopy. We demonstrated that partial harvesting resulted in the alteration of habitat structure and growing conditions, and these factors were closely related to bryophyte species composition and the representation of species with different biological traits. Species with differing traits pertaining to phylogeny and life form, reproduction and dispersal capacity, and habitat requirements, often had dissimilar responses to abiotic and biotic conditions after harvesting. In particular, diminished forest moisture (as detected by *Hylocomium splendens* growth) after harvesting was an important driver of species responses. These findings show that bryophyte species can differ in their capacities to persist and recover following disturbance, with consequences for maintaining populations at local and larger scales. The examination of species traits provided insight into the effects of residual forest structure and growing conditions after partial harvesting that are not readily discernable from assessments of species taxonomic data alone.

Partial harvesting modifies habitat conditions important to bryophytes

There were pronounced differences in forest structure and growing conditions among retention levels and between forest types. More intensive partial harvesting resulted in greater divergence of the forest environment from that of intact forest. These differences occurred along a gradient of decreasing forest canopy cover, accompanied by decreasing moisture, and increasing dominance of understory shrubs. Mixed forests (both intact and harvested stands) were associated with a higher total canopy cover and understory shrub cover as compared to coniferous forests. Forest stands of differing pre-harvest canopy composition differed in habitat conditions and bryophyte species composition after harvesting. Variation in forest canopy composition will, therefore, provide distinctive habitats for bryophytes, and may influence regional patterns of bryophyte species composition and development during secondary succession.

Forest moisture is an important factor influencing bryophyte survival at harvested sites (e.g., Hylander et al. 2005). The most important factor affecting moisture at our sampled stands was harvesting as shown by the significant differences in *Hylocomium splendens* growth between intact forest and all other harvested levels for both forest types. In turn, changes in bryophyte species composition corresponded to reductions in forest moisture (detected by

Hylocomium splendens growth) associated with increasing harvesting intensity. *Hylocomium splendens* has been previously identified as a sensitive biological indicator (phytometer, sensu Stewart and Mallik 2006) of microclimate conditions, which can effectively discern changes in moisture in relation to distance from forest edge and edge aspect after harvesting (Hylander et al. 2005), and ecotonal changes from intact riparian and upland to harvested forest (Stewart and Mallik 2006). Growth of the species is closely related to light conditions and especially vapour pressure deficit (Tamm 1964; Busby 1978; Stewart and Mallik 2006). In this study, we further demonstrate that *Hylocomium splendens* growth was related to the effects of partial harvesting and was a strong predictor of bryophyte species composition in harvested forests.

There were no differences in moisture among the different partial retention levels for harvested mixed forests, whereas moisture loss was incremental with harvesting intensity in coniferous forest. Stands with greater coniferous canopy cover may be more effective at moderating forest floor moisture loss following harvest. Coniferous-dominated stands have cooler forest floor temperatures than broadleaf-dominated stands, and retain cooler forest floor temperatures at higher harvesting intensities (Macdonald and Fenniak 2007). Stands with a greater coniferous component may also occur on naturally wetter sites. In the regression tree analysis for coniferous forests the best discriminator of moisture measured at the plot level for lower (10% and 50%) retention was coniferous canopy cover. This implies that a higher local abundance of conifers can be important for buffering near-ground forest moisture loss after harvesting (cf. Fenton and Frego 2005). Overall, these results suggest that forests of differing canopy composition can support different moisture conditions after harvesting and that this may have implications for bryophyte species persistence. Epiphytic bryophytes that grow on aspen trees, for example, can benefit from higher local abundance of conifers (Hazell et al. 1998; Caners et al. 2010).

Understory shrubs can also moderate growing conditions for bryophytes by reducing moisture loss near the ground (Busby 1978; Stewart and Mallik 2006). Although the increased cover of shrubs at greater harvesting intensities in this study was a consequence of canopy removal, and could actually be indicative of more extreme growing conditions for bryophytes, high local shrub dominance might also provide protection for some species. Indeed, many epixylic and epiphytic species sensitive to canopy removal (Hylander et al. 2005; Caners et al. 2010) were sometimes documented on protected substrates beneath a dense shrub cover at intensively harvested sites (personal observation). The role of shrubs in protecting bryophytes after forest harvesting requires further examination.

Species biological traits explain responses to partial harvesting

Fourth-corner analysis revealed that species responded differently to partial harvesting intensity and associated forest moisture conditions depending on the traits they exhibit. These results conform to a model of environmental control (Whittaker 1956, 1975) in which species are not equally likely to be found across the full range of forest conditions after harvesting. Forest harvesting may create particular abiotic and biotic conditions that act as a filters (sensu Keddy 1992; Lavorel et al. 2002), which exclude certain species from harvested sites. This has potential consequences for their persistence and re-establishment during post-harvest forest development.

There is growing recognition that bryophyte traits can provide information about species distributions and population dynamics (Laaka-Lindberg et al. 2000; Söderström and During 2005; Hedderson and Longton 1996, 2008). Bryophytes with different life forms are affiliated with specific moisture and light conditions (Gimingham and Birse 1957; Bates 1998). Our study showed that different life forms were also uniquely affected by forest structure and growing conditions along a range of harvesting intensities. Species with smooth mat, solitary creeping, and thread life forms were more abundant at higher retention levels, whereas species with other life forms were either unrelated to retention level (e.g., cushions, tufts, wefts) or more abundant at lower retention (rough mats, turfs). The smooth mat life form included several liverwort species, which were also more closely related to higher retention than species in other phylogenetic groups. The affinity of species with these life forms and phyogeny for greater retention suggests they may be particularly sensitive to harvesting and may require additional conservation measures for their protection.

The intensity of partial harvesting also affected the abundances of species with differing substrate, moisture, and light requirements. Species that grow at lower light (e.g., *Tetraphis pellucida*, *Lophozia guttulata*) and high moisture (e.g., *Calliergon richardsonii*, *Chyloscyphus pallescens*) were less abundant at lower retention. This trend detected by fourth-corner analysis corresponds closely with results of the constrained ordination, in which species compositional change was detected along gradients of decreasing moisture and canopy closure with increasing harvesting intensity (Figure 4.1, Table 4.2). Epixylic and epigeic bryophytes were most abundant at greater retention levels, whereas species that grow on dung or mineral soil, or were generalists, were more abundant at lower retention. As retention decreases, decayed wood and forest floor substrates may become drier and therefore less effective at supporting species because of reduced moisture content. Dung specialists may increase in abundance after harvesting when regenerating broadleaf trees and shrubs attract higher densities of ungulate herbivores that deposit fecal substrates (personal observation). However, the comparatively high moisture requirements of many coprophilous species (Koponen 1990) implies they would require sheltered microhabitats with sufficient moisture at harvested sites. Although other studies have documented detrimental effects of harvesting on tree-colonizing epiphytes (Hazell et al. 1998; Caners et al. 2010), this study showed that epiphytic species that grow on tree bark and recently fallen wood were unrelated to retention level. This can be explained by the fact that epiphytes in this study also included species on fallen wood, which may not be as strongly impacted by canopy removal as species that grow at more exposed positions on trees.

Bryophyte reproduction and dispersal characteristics are important factors influencing the maintenance of populations (Söderström and Herben 1997; Söderström 2002) and in this study they provided insights about the effects of forest harvesting on species persistence. Our study showed that species with a shorter (annual) lifespan, monoicous sexuality, abundant sporophyte production, smaller spores, or that reproduced asexually by tubers were more abundant at lower retention levels. These trends are consistent with studies that have documented increases in disturbance-adapted species under more extreme conditions (e.g., Fenton and Frego 2005). In addition, results revealed that species with a longer (perennial) lifespan, dioicous sexuality, rare sporophyte production, and larger spores were more abundant at higher retention. Diminished abundances of species with these attributes at greater harvesting intensities may not only limit their persistence but also their capacity to disperse and colonize new habitats. Dioicous species generally do not reproduce as frequently as monoicous species (Bates 1988; Söderström and During 2005) and larger spores are thought to disperse over shorter distances than smaller spores (Miles and Longton 1992). Species with low reproductive output are also more likely to be dispersal limited (Laaka-Lindberg et al. 2000). The dynamic nature of many boreal forest substrates (Edman et al. 2007) may create further impediments to establishment. Although some species with infrequent sporophyte production can also reproduce asexually (e.g., *Anastrophyllum hellarianum*, *Dicranum fragilifolium*), the large size of many asexual propagules can limit the distances over which they disperse (Laaka-Lindberg et al. 2006). Generally, asexual propagules are considered to be a mechanism for maintaining colonies (Laaka-Lindberg et al. 2006), whereas spores are thought to be more important in the establishment of new colonies than in population maintenance (Miles and Longton 1990). However, decreased forest moisture after harvesting may exaggerate establishment limitations for some species that are susceptible to mortality during early developmental stages (e.g., Phojamo and Laaka-Lindberg 2004).

Significant relationships observed between forest types and species traits provided further evidence that canopy composition can influence species distributions in mixed-wood forests. Coniferous forest had greater abundances of turf species and species that grow on epigeic and soil substrates; the majority of turf-forming species in our study were sampled on these substrate types. Coniferous forests were also associated with greater abundances of species that require higher moisture levels. Intact coniferous forests often contained areas of wet forest floor and occasionally had intermittent streams that support wet-adapted species. Species with dioicous sexuality and infrequent sporophyte production may also benefit from wetter site conditions in this forest type.

Plant communities are the product of biotic (e.g., competition) and abiotic (e.g., climate) filters that limit from a regional pool the species and traits that can persist at a location (Lavorel et al. 2002). Such filters can selectively exclude the traits or combinations of traits that are not adapted to a particular environment (Keddy 1992). Observed relationships between forest conditions after partial harvesting and species traits may indicate the presence of one or more limiting factors for some species. In particular, the strong link between species traits and forest moisture shows moisture to be an important environmental filter in harvested forests. Habitat heterogeneity is closely related to species diversity (Huston 1994; Weibull and Rydin 2005) but moisture limitation following harvest may have a homogenizing effect by reducing the number of mesic microsites for bryophytes. The loss of wet-adapted species from harvested sites may constrain recovery if these species are biologically limited in terms of reproduction and dispersal.

Despite the numerous relationships detected by fourth-corner analysis, the method can presently only test pair-wise combinations of traits and environmental variables. Pair-wise tests limit the inferences that can be made about species responses because many traits are interrelated (Hedderson and Longton 1996). Monoicous species, for example, generally produce sporophytes more abundantly than dioicous species because of self-fertilization (e.g., Söderström and During 2005). Further research that defines relationships among bryophyte traits and generates groups of species with similar responses to environmental variation (response groups, Lavorel et al. 1997) would improve the accuracy of predictions about the effects of disturbance in general and forest harvesting in particular on species.

Conclusions

Our results demonstrate that the abundance and composition of retained canopy trees after partial harvesting affected abiotic and biotic forest conditions, with implications for regional patterns of bryophyte species composition. Furthermore, species with distinctive phylogeny and life form, reproduction and dispersal characteristics, and habitat requirements responded differently to forest type and retention level, and trends in forest moisture. The varied responses of species along forest structure and microclimate gradients imply that some traits are adapted to a limited range of suitable habitat conditions. Several species apparently depend on higher moisture and more intact forest canopies. Dioicous species, for example, may require greater moisture to facilitate the gamete transfer required for sporophyte production and dispersal. On the other hand, intraspecific variation among populations in the expression of some traits (e.g., spore size, reproductive effort) can occur for certain species because of differences in population genetics and the influence of environmental conditions on gene expression (Hedderson and Longton 2008). Local disturbances may have consequences for maintaining inter-population variation over larger spatiotemporal scales.

Considering that forest moisture was strongly affected by partial harvesting, forest management practices are likely to have the most pronounced effects on species that respond closely to this environmental filter. The effectiveness of partial harvesting for preserving bryophytes will depend on the tolerances of species to the magnitude of habitat change following canopy removal. The greater capacity of coniferous over mixed forests to support liverworts, turfs, and species with infrequent sporophyte production, dioicous sexuality, and higher moisture requirements, demonstrates the importance of coniferous habitats for harbouring a variety of bryophytes. Coniferous forests may have an important role as refuges of bryophyte source populations in mixed-wood forests. Understanding the ways in which bryophyte species traits and combinations of traits respond to forest management practices can provide meaningful information about the species at greatest risk of extirpation following harvest, and the forest conditions required to ensure their continued representation in harvested boreal landscapes.

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Table 4.1. Summary of species biological traits used in fourth-corner analysis. Traits have been assigned to one of three categories: A) phylogeny and growth form, B) reproduction and dispersal capacity, and C) habitat requirements.

Trait category	Data type	Trait level	Trait level abbreviations	#Species	Trait level description
A) Phylogeny and life form					
Phylogenetic group	Nominal	Liverwort	L	37	Thalloid and leafy liverworts
		Moss, pleurocarpous	Mp	43	Sporophytes produced laterally; plants usually prostrate, freely branched
		Moss, acrocarpous	Ma	52	Sporophytes produced terminally; plants usually erect, sparsely branched
Life form[a]	Nominal	Cushion	Cu	2	Dome-shaped colonies
		Dendroid	De	1	Stolons and erect shoots
		Mat, rough	Mr	22	Creeping, lateral branches erect
		Mat, smooth	Ms	32	Creeping, branches lying flat
		Mat, thalloid	Mt	3	Creeping, thalli forming a layer
		Solitary, creeping	Sc	2	Creeping, solitary shoots
		Solitary, thalloid	St	1	Rosette-forming patch, not mat
		Turf	Tf	33	Vertical stems with little or no branching
		Thread	Thread	1	Solitary, thread-like creeping stems
		Tuft	Tuft	21	Loose cushions, not dome-shaped
		Weft	We	14	Intertwining, branched layers
B) Reproduction and dispersal capacity					
Phenology	Nominal	Annual (Perennial)	A(P)	1	Normally annual but can sometimes be perennial
		Annual	A	6	Plant completes life cycle within one year
		Perennial	P	117	Plant completes life cycle over more than one year
		Perennial (Annual)	P(A)	8	Normally perennial but can sometimes complete life cycle within one year
Vegetative propagules	Nominal	Branches		2	Produces deciduous, modified or unmodified branches
		Bulbils		1	Produces bulbils
		Gemmae		39	Produces gemmae
		Leaves		2	Produces fragmenting leaves
		None		86	No record of vegetative propagule production
		Tubers		2	Produces tubers

Trait category	Data type	Trait level	Trait level abbreviations	#Species	Trait level description
Sexuality	Nominal	Dioicous	D	70	Sexes on different plants; includes pseudo-monoicous condition
		Dioicous (Monoicous)	D(M)	6	Normally dioicous, rarely monoicous
		Dioicous or Monoicous	DM	3	Plants can be either dioicous or monoicous
		Monoicous	M	51	Sexes on same plant; includes autoicous, synoicous, paroicous, and polyoicous conditions
		Monoicous (Dioicous)	M(D)	2	Normally monoicous, rarely dioicous
Sporophyte production	Nominal	Abundant	A	23	Well-developed colonies produce sporophytes in most years
		Frequent	F	35	Well-developed colonies produce sporophytes frequently, but not consistently in most years
		Occasional	O	41	Well-developed colonies produce sporophytes occasionally; commonly found without
		Rare	R	33	Well-developed colonies produce sporophytes rarely
Spore diameter	Continuous	µm		132	Midpoint of reported minimum and maximum spore diameters
C) Habitat requirements					
Substrate type	Nominal	Dung	Du	6	Animal bones and excrement
		Epiphytic	Ep	39	Bark of living trees and recently fallen wood
		Epixylic	Ex	29	Decayed wood
		Epigeic	Eg	33	Forest floor and humus
		Generalist	Ge	2	Found on different substrate types
		Soil	So	23	Mineral soil
Light conditions[a]	Ordinal	0		0	Plant in darkness
		1		0	Plant in deep shade
		2		0	Between 1 and 3
		3		7	Shade plant, mostly < 5% relative illumination, seldom > 30%
		4		17	Between 3 and 5
		5		25	Semi-shade plant, rarely in full light but usually > 10% relative illumination
		6		36	Between 5 and 7
		7		29	Plant usually in well-lit places but also occurring in partial shade
		8		17	Light-loving plant, rarely found when relative illumination < 40%
		9		1	Plant in full light, found mostly in full sun

Trait category	Data type	Trait level	Trait level abbreviations	#Species	Trait level description
<u>Moisture conditions</u>[a]	Ordinal	1		0	Indicator of extreme dryness, restricted to substrates that are often dry
		2		0	Between 1 and 3
		3		3	Dry-site indicator, more often on dry than moist substrates
		4		15	On well-drained terrestrial substrates, or bark with some shelter
		5		25	On moderately moist soils, or bark in moderately humid places
		6		34	On moist soils, or bark in humid places
		7		14	On constantly moist or damp, but not permanently saturated substrata
		8		25	Between 7 and 9
		9		11	In waterlogged sites, either in streams or flushes
		10		5	In pools and by streams that may intermittently lack water
		11		0	On surface of still water, or submerged in moving water; sometimes above normal water level
		12		0	Normally submerged

[a] Trait level descriptions adapted from Hill et al. (2007).

Table 4.2. Results of constrained ordination (distance-based redundancy analysis) examining the relationship between bryophyte species composition (represented using Bray-Curtis dissimilarity) and forest structural and environmental variables chosen by forward selection. Given are A) results summary and B) inter-set correlations of environmental variables with axes.

A)

Axes	1	2	3	4
Eigenvalues	0.337	0.111	0.066	0.022
Species-environment correlations	0.924	0.846	0.924	0.718
Cumulative percentage variance				
of species data	33.7	44.8	51.4	53.5
of species-environment relation	63.0	83.6	95.9	100.0

B)

Axes	1	2	3	4
Moisture (*Hylocomium splendens* growth)	**0.877**	0.052	–0.209	–0.151
Total canopy cover	**0.689**	0.357	**0.431**	0.157
Total shrub cover	**–0.638**	**0.587**	–0.154	–0.086
LFH depth	0.177	**0.458**	–0.368	**0.513**

Notes: Variables are listed in order of forward selection. Correlation coefficients in bold were significant at $P < 0.05$.

Table 4.3. Results of nested ANOVA testing for differences in *Hylocomium splendens* growth. A) Global tests conducted separately for mixed and coniferous forest types. B) Pair-wise comparisons among retention levels conducted separately for mixed and coniferous forest types. Mean growth measures followed by a different letter within each forest type were significantly different.

A)

	Num DF	Den DF	Mixed forest *F*	Mixed forest *P*	Coniferous forest *F*	Coniferous forest *P*
Retention level (%)	3	8	11.01	0.003	42.18	< 0.001

B)

	Mixed forest		Coniferous forest	
Retention level (%)	Growth (mm)	SE[a]	Growth (mm)	SE[a]
10	8.75a	0.811	6.79a	0.678
50	9.42a	0.823	10.73b	0.645
75	9.84a	0.802	12.82b	0.645
100	14.40b	0.802	17.01c	0.645

[a] SE is based on estimates of least squares means from nested ANOVA.

Table 4.4. Results of fourth-corner analysis between forest structural and environmental variables and species traits pertaining to phylogeny and life form. Global tests of significance are provided for each trait and environmental variable pair. For each level of a trait and an environmental variable the direction of a test (positive or negative) indicates whether the relationship is greater or less than expected based on permutation. Significant values are in bold: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Forest type		Retention level (%)	*Hylocomium splendens* growth (mm)
	Coniferous	Mixed		
Phylogenetic group	**$G = 2.29$, $P = 0.005$**		**$F = 9.12$, $P < 0.001$**	**$F = 9.33$, $P < 0.001$**
Liverwort	**+***	**–***	**0.097*** **	**0.099*** **
Moss, pleurocarpous	–	+	**–0.029** **	**–0.031*** **
Moss, acrocarpous	**+** **	**–** **	**–0.056*** **	**–0.055*** **
Life form	**$G = 8.18$, $P < 0.001$**		**$F = 2.49$, $P < 0.001$**	**$F = 2.40$, $P < 0.001$**
Cushion	–	+	0.016	0.006
Dendroid	–	+	0.006	0.000
Mat, rough	–	+	**–0.039** **	**–0.033** **
Mat, smooth	+	–	**0.079** **	**0.082** **
Mat, thalloid	+	–	–0.007	–0.005
Solitary, creeping	+	–	**0.035***	**0.042** **
Solitary, thalloid	+	–	–0.026	**–0.028***
Turf	**+** **	**–** **	**–0.065** **	**–0.061** **
Thread	+	–	**0.028***	**0.025***
Tuft	+	–	–0.017	–0.016
Weft	+	–	0.019	0.010

Notes: *G*-statistics are given for analyses involving a nominal trait and nominal environmental variable. The abundances of species characterized by each level of a nominal trait are indicated as being greater than (+) or less than (–) expected for each level of the environmental variable. *F*-statistics are given for analyses involving a nominal trait and quantitative environmental variable. Fourth-corner correlation coefficients indicate the relationship between the abundances of species having each level of a nominal trait and the environmental variable. Significance of all relationships were determined by permutation under a model of environmental control.

Table 4.5. Results of fourth-corner analysis between forest structural and environmental variables and species reproduction and dispersal capacity traits. Global tests of significance are provided for each trait and environmental variable pair. For each level of a trait and an environmental variable the direction of a test (positive or negative) indicates whether the relationship is greater or less than expected based on permutation. Significant values are in bold: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Forest type		Retention level (%)	*Hylocomium splendens* growth (mm)
	Coniferous	Mixed		
Phenology	$G = 0.28$; $P = 0.769$		**$F = 5.18$, $P < 0.001$**	**$F = 4.58$, $P < 0.001$**
Annual (Perennial)	–	+	**–0.038****	**–0.040*****
Annual	+	–	**–0.022***	–0.017
Perennial	+	–	**0.090*****	**0.083*****
Perennial (Annual)	+	–	**–0.078*****	**–0.072*****
Vegetative propagules	$G = 1.70$, $P = 0.129$		**$F = 1.54$, $P < 0.001$**	**$F = 1.84$, $P < 0.001$**
Branches	+	–	0.007	0.016
Bulbils	–	+	–0.021	**–0.022***
Gemmae	+	–	**0.038****	**0.042****
Leaves	+	–	0.006	0.010
None	+	–	**–0.026***	**–0.032****
Tubers	+	–	**–0.048*****	**–0.050*****
Sexuality	**$G = 9.51$, $P < 0.001$**		**$F = 2.27$, $P < 0.001$**	**$F = 2.20$, $P < 0.001$**
Dioicous	**+*****	**–*****	**0.052*****	**0.052*****
Dioicous (Monoicous)	**+***	**–***	**–0.052*****	**–0.045****
Dioicous or Monoicous	**+***	**–***	–0.001	–0.005
Monoicous	–	+	**–0.034****	**–0.038*****
Monoicous (Dioicous)	+	–	0.016	0.024
Sporophyte production	**$G = 3.12$, $P = 0.003$**		**$F = 6.00$, $P < 0.001$**	**$F = 5.56$, $P < 0.001$**
Abundant	+	–	**–0.082*****	**–0.078*****
Frequent	–	+	**0.022***	0.015
Occasional	**+*****	**–*****	–0.004	0.001
Rare	**+***	**–***	**0.067*****	**0.067*****
Spore diameter[a]	$F = 0.15$, $P = 0.454$		**0.041*****	**0.029****
	–0.009	0.009		

[a] Similar results and identical significance levels were obtained when analyses were performed using minimum spore diameter.

Notes: *G*-statistics are given for analyses involving a nominal trait and nominal environmental variable. The abundances of species characterized by each level of a nominal trait are indicated as being greater than (+) or less than (–) expected for each level of the environmental variable. *F*-statistics are given for analyses involving a nominal trait and quantitative environmental variable. Fourth-corner correlation coefficients indicate the relationship between the abundances of species having each level of a nominal trait and the environmental variable. The global test of significance between two quantitative variables is provided only by a fourth-corner correlation coefficient. Significance of all relationships were determined by permutation under a model of environmental control.

Table 4.6. Results of fourth-corner analysis between forest structural and environmental variables and species habitat requirements traits. Global tests of significance are provided for each trait and environmental variable pair. For each level of a trait and an environmental variable the direction of a test (positive or negative) indicates whether the relationship is greater or less than expected based on permutation. Significant values are in bold: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Forest type		Retention level (%)	*Hylocomium splendens* growth (mm)
	Coniferous	Mixed		
Substrate type	**$G = 6.37$, $P < 0.001$**		**$F = 10.61$, $P < 0.001$**	**$F = 10.19$, $P < 0.001$**
Dung	+	–	**–0.022***	–0.017
Epiphytic	–	+	–0.005	–0.007
Epixylic	+	–	**0.102*****	**0.106*****
Epigeic	**+****	**–****	**0.031****	**0.024***
Generalist	+	–	**–0.077*****	**–0.071*****
Soil	**+****	**–****	**–0.119*****	**–0.117*****
Light conditions	$F = 0.28$, $P = 0.290$		**–0.098*****	**–0.101*****
	0.012	–0.012		
Moisture conditions	**$F = 1.68$, $P = 0.007$**		**0.033****	**0.033****
	0.030**	**–0.030****		

Notes: G-statistics are given for analyses involving a nominal trait and nominal environmental variable. The abundances of species characterized by each level of a nominal trait are indicated as being greater than (+) or less than (–) expected for each level of the environmental variable. F-statistics are given for analyses involving a nominal trait and quantitative environmental variable. Fourth-corner correlation coefficients indicate the relationship between the abundances of species having each level of a nominal trait and the environmental variable. The global test of significance between two quantitative variables is provided only by a fourth-corner correlation coefficient. Significance of all relationships were determined by permutation under a model of environmental control.

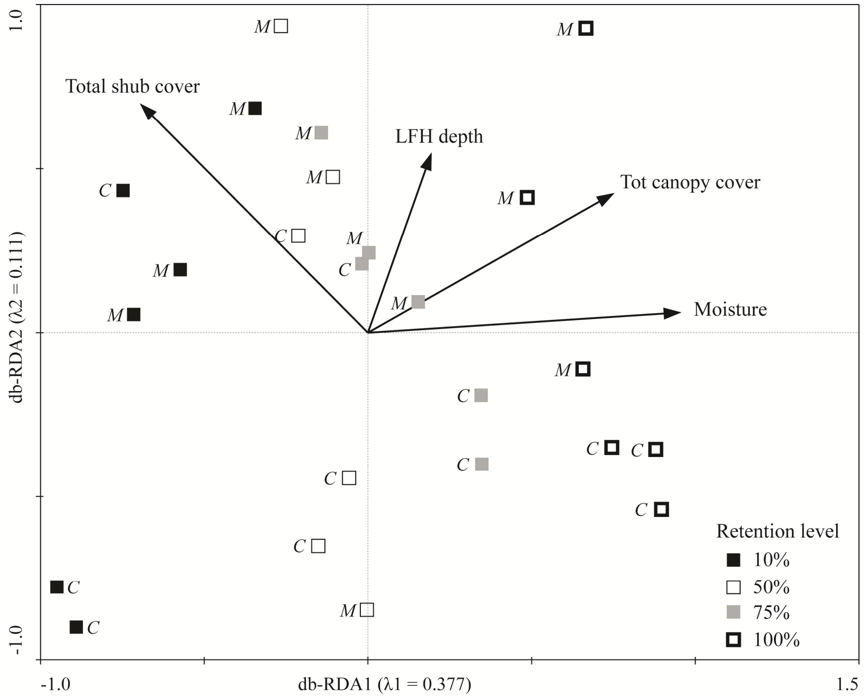
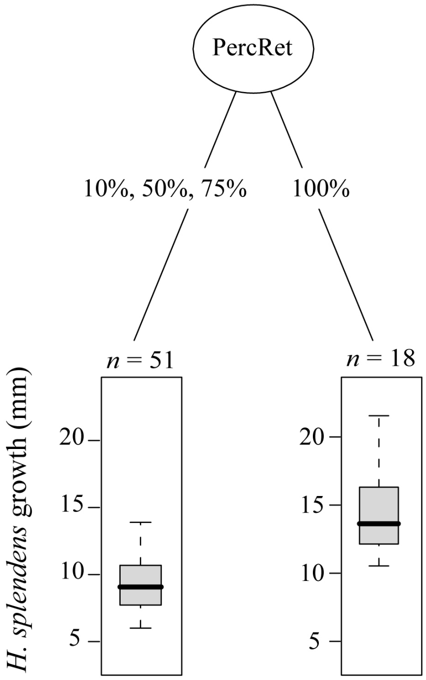


Figure 4.1. Results of constrained ordination (distance-based redundancy analysis, db-RDA) examining the relationship between bryophyte species composition (represented using Bray-Curtis dissimilarity) and forest structural and environmental variables chosen by forward selection. See Table 4.2 for details. The symbols are stands coded by retention level (10%, closed boxes; 50%, thin open boxes; 75%, shaded boxes; 100%, thick open boxes) and forest type (*M*, mixed; *C*, coniferous forest). The arrows show the magnitude and direction of significant habitat variables along the ordination axes.

A) Mixed forest



B) Coniferous forest

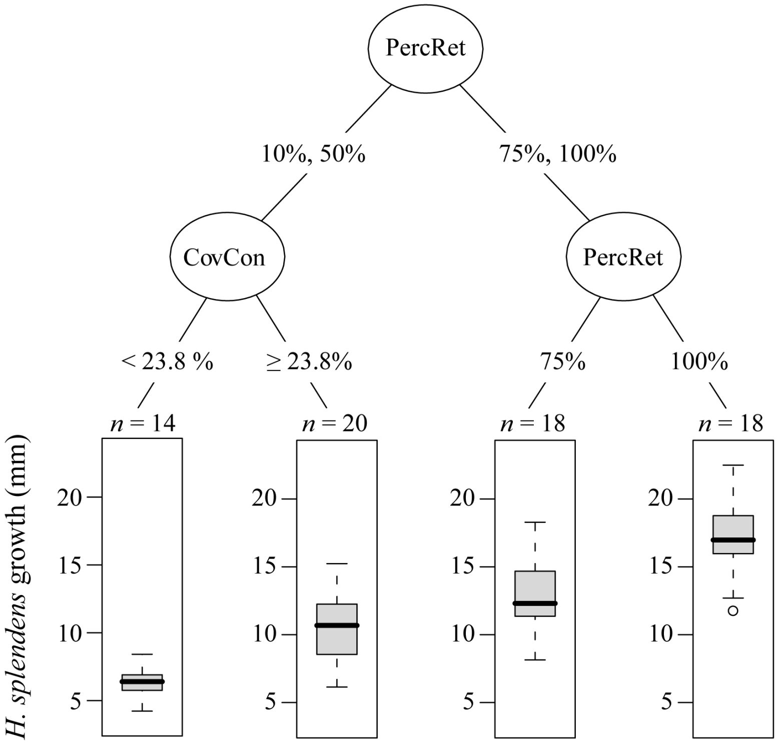


Figure 4.2. Results of regression tree analysis of *Hylocomium splendens* growth (shoot length in the most recent growing season, mm) as a function of predictor variables for A) mixed and B) coniferous forests. Circles are nodes with predictor variable indicated. Values assigned to branch pairs are levels of the corresponding predictor variable that best discriminated growth. Abbreviations for nodes: PercRet = canopy retention level (%); CovCon = coniferous canopy cover (%). Boxplots of *Hylocomium splendens* growth at each terminal branch show median (dark horizontal bar), upper and lower quartile (ends of box), upper and lower extremes (whiskers), and outlying (points outside whiskers) values. Sample size (*n*) is the number of replicate plots in which growth was measured.

Appendix 4.1. Values of species biological traits used in fourth-corner analysis. Traits are ordered by categories to which they were assigned: phylogeny and growth form, reproduction and dispersal capacity, and habitat requirements.

Species name	Phylogeny and life form		Reproduction and dispersal capacity						Habitat requirements		
	Phylogeny	Life form	Phenology	Propagules	Sexuality	Frequency	Spore diam. (mid., µm)	Spore diam. (min., µm)	Substrate	Light	Moisture
Amblystegium serpens	Mp	Mr	P(A)	None	M	A	14.5	11.0	Ep	5	6
Amblystegium varium	Mp	Mr	P	None	M	O	12.0	9.0	Ep	5	9
Anastrophyllum hellerianum	L	Ms	P	Gemmae	D	R	11.0	10.0	Ex	4	7
Aulacomnium palustre	Ma	Tf	P	Gemmae	D	O	12.0	11.0	Eg	7	8
Barbilophozia hatcheri	L	We	P	Gemmae	D	R	14.8	14.0	Eg	6	5
Barbilophozia kunzeana	L	Ms	P	Gemmae	D	R	12.0	10.0	Eg	6	5
Barbula convoluta	Ma	Tf	P(A)	Tubers	D	O	8.0	7.0	So	7	4
Barbula unguiculata	Ma	Tf	P	None	D	F	11.0	9.0	So	7	5
Blasia pusilla	L	St	P(A)	Gemmae	D	F	42.5	40.0	So	6	8
Blepharostoma trichophyllum	L	Thread	P	Gemmae	M	F	10.5	8.0	Ex	4	8
Brachythecium albicans	Mp	Mr	P	None	D	R	13.5	11.0	Ep	8	3
Brachythecium campestre	Mp	Mr	P	None	M	O	16.5	13.0	Ep	5	6
Brachythecium cf. calcareum	Mp	Mr	P	None	D	O	11.0	11.0	Ep	5	6
Brachythecium erythrorrhizon	Mp	Mr	P	None	D	O	17.0	14.0	Eg	8	4

Species name	Phylogeny and life form		Reproduction and dispersal capacity						Habitat requirements		
	Phylogeny	Life form	Phenology	Propagules	Sexuality	Frequency	Spore diam. (mid., µm)	Spore diam. (min., µm)	Substrate	Light	Moisture
Brachythecium reflexum	Mp	Mr	P	None	M	O	13.5	11.0	Ep	5	6
Brachythecium rutabulum	Mp	Mr	P	None	M	A	16.5	13.0	Ep	6	6
Brachythecium salebrosum	Mp	Mr	P	None	M	O	15.5	13.0	Ep	5	6
Brachythecium starkei	Mp	Mr	P	None	M	O	14.0	12.0	Eg	6	7
Brachythecium velutinum	Mp	Mr	P	None	M	F	11.5	10.0	Ep	4	5
Bryohaplocladium microphyllum	Mp	Mr	P	None	M	A	10.0	9.0	Ep	6	5
Bryum argenteum	Ma	Tf	P	Bulbils	D	O	12.5	10.0	So	8	4
Bryum caespiticium	Ma	Tf	P	None	D	A	13.0	11.0	So	7	4
Bryum lisae var. *cuspidatum*	Ma	Tf	P	None	M	A	15.5	11.0	Ge	7	5
Bryum pseudotriquetrum	Ma	Tf	P	Gemmae	DM	O	15.5	11.0	So	8	9
Calliergon cordifolium	Mp	Tf	P	None	M	R	15.5	13.0	Eg	5	10
Calliergon giganteum	Mp	Tf	P	None	D	R	15.0	13.0	Eg	7	10
Calliergon richardsonii	Mp	Tf	P	None	M	R	18.5	15.0	Eg	5	10
Calypogeia suecica	L	Sc	P	Gemmae	D	R	9.5	8.0	Ex	3	7
Campylium cf. *radicale*	Mp	Mr	P(A)	None	M	A	10.0	9.0	Eg	5	9
Campylium chrysophyllum	Mp	Mr	P	None	D	R	13.5	13.0	Ep	5	6
Campylium hispidulum	Mp	Mr	P	None	M	A	11.0	9.0	Ep	6	5
Campylium stellatum	Mp	We	P	None	D	R	16.5	15.0	So	8	8

Species name	Phylogeny and life form		Reproduction and dispersal capacity						Habitat requirements		
	Phylogeny	Life form	Phenology	Propagules	Sexuality	Frequency	Spore diam. (mid., µm)	Spore diam. (min., µm)	Substrate	Light	Moisture
Cephalozia connivens	L	Ms	P	Gemmae	M	F	12.5	12.0	Ex	6	8
Cephalozia connivens var. *compacta*	L	Ms	P	Gemmae	M	F	12.5	12.0	Ex	6	8
Cephalozia leucantha	L	Ms	P	Gemmae	D	O	10.0	8.0	Ex	3	7
Cephalozia lunulifolia + C. affinis	L	Ms	P	Gemmae	D	O	10.0	8.0	Ex	5	8
Cephalozia pleniceps	L	Ms	P	Gemmae	M	F	12.8	11.5	So	4	8
Cephaloziella rubella	L	Ms	P	Gemmae	M	F	8.5	6.0	Ex	6	5
Cephaloziella rubella var. *bifida*	L	Ms	P	Gemmae	M	F	7.5	7.0	Ex	6	5
Ceratodon purpureus	Ma	Tf	P(A)	Gemmae	D	A	13.0	11.0	So	7	4
Chiloscyphus pallescens	L	Ms	P	None	M	F	16.0	13.0	Ex	6	9
Climacium dendroides	Mp	De	P	None	D	R	17.5	13.0	Eg	7	7
Cratoneuron filicinum	Mp	We	P	None	D	O	16.5	15.0	So	6	8
Dicranum acutifolium	Ma	Tuft	P	None	D	R	21.0	14.0	Ep	8	8
Dicranum cf. *bonjeanii*	Ma	Tuft	P	None	D	R	21.0	14.0	Ep	7	7
Dicranum flagellare	Ma	Tuft	P	Branches	D	R	17.5	14.0	Ep	4	4
Dicranum fragilifolium	Ma	Tuft	P	Leaves	D	R	22.5	18.0	Ep	4	4
Dicranum fuscescens	Ma	Tuft	P	None	D	O	24.0	16.0	Ep	6	5

Species name	Phylogeny and life form		Reproduction and dispersal capacity						Habitat requirements		
	Phylogeny	Life form	Phenology	Propagules	Sexuality	Frequency	Spore diam. (mid., µm)	Spore diam. (min., µm)	Substrate	Light	Moisture
Dicranum groenlandicum	Ma	Tuft	P	None	D	R	19.5	16.0	Ep	8	5
Dicranum polysetum	Ma	Tuft	P	None	D	O	21.5	16.0	Eg	5	5
Dicranum scoparium	Ma	Tuft	P	None	D	O	19.0	14.0	Ep	6	5
Dicranum tauricum	Ma	Tuft	P	Leaves	D	R	14.0	10.0	Ep	4	4
Dicranum undulatum	Ma	Tuft	P	None	D	R	19.5	16.0	Eg	8	8
Distichium capillaceum	Ma	Tuft	P	None	M	F	20.5	16.0	So	6	6
Drepanocladus aduncus	Mp	We	P	None	D	R	16.0	16.0	Eg	7	10
Eurhynchium pulchellum	Mp	Mr	P	None	D	O	12.0	11.0	Ep	6	4
Funaria hygrometrica	Ma	Tuft	A(P)	None	M	A	17.5	11.0	So	7	5
Geocalyx graveolens	L	Sc	P	None	M	F	11.5	8.0	Ex	4	6
Harpanthus drummondii	L	Ms	P	Gemmae	D	R	8.3	8.0	Ex	4	6
Helodium blandowii	Mp	Tf	P	None	M	A	13.0	11.0	Eg	7	8
Herzogiella turfacea	Mp	Mr	P	None	M	F	10.0	9.0	Ep	5	6
Hylocomium splendens	Mp	We	P	None	D	O	15.5	13.0	Eg	6	5
Hypnum pallescens	Mp	Mr	P	None	M	F	12.5	12.0	Ep	5	6
Hypnum pratense	Mp	Mr	P	None	D	O	11.5	10.0	Eg	7	7
Isopterygiopsis pulchella	Mp	Mr	P	Gemmae	M	A	11.0	9.0	Ep	3	6
Jamesoniella autumnalis	L	Ms	P	None	D	F	13.0	11.0	Ex	4	6
Lepidozia reptans	L	We	P	None	M	F	13.0	11.0	Ex	3	6
Leptobryum pyriforme	Ma	Tuft	P(A)	Tubers	M	F	11.0	9.0	So	7	6

Species name	Phylogeny and life form		Reproduction and dispersal capacity						Habitat requirements		
	Phylogeny	Life form	Phenology	Propagules	Sexuality	Frequency	Spore diam. (mid., µm)	Spore diam. (min., µm)	Substrate	Light	Moisture
Leptodictyum riparium	Mp	Mr	P	None	M	F	11.0	9.0	Eg	6	9
Lophocolea heterophylla	L	Ms	P	Gemmae	M	A	9.5	8.0	Ex	4	5
Lophocolea minor	L	Ms	P	Gemmae	D(M)	R	10.0	10.0	Ex	4	5
Lophozia ascendens	L	Ms	P	Gemmae	D	R	10.0	9.5	Ex	5	6
Lophozia ciliata	L	Ms	P	Gemmae	D	O	13.0	12.0	Ex	5	6
Lophozia excisa	L	Ms	P	Gemmae	M	F	14.5	12.0	Ex	7	5
Lophozia guttulata	L	Ms	P	Gemmae	D	F	9.0	8.0	Ex	3	7
Lophozia incisa	L	Ms	P	Gemmae	D	O	12.5	10.0	Ex	6	6
Lophozia longidens	L	Ms	P	Gemmae	D	R	11.5	10.0	Ex	5	6
Lophozia ventricosa	L	Ms	P	Gemmae	D	O	13.0	10.0	Ex	5	6
Marchantia polymorpha	L	Mt	P	Gemmae	D	O	11.5	8.0	So	7	8
Mnium spinulosum	Ma	Tf	P	None	M	F	20.0	18.0	Ep	4	6
Oncophorous wahlenbergii	Ma	Tf	P	None	M	F	22.0	14.0	Ep	7	8
Orthotrichum obtusifolium	Ma	Cu	P	Gemmae	D	F	17.0	16.0	Ep	6	4
Orthotrichum speciosum	Ma	Cu	P	None	M	A	19.5	13.0	Ep	6	4
Plagiochila porelloides	L	Tf	P	None	D	R	18.0	15.0	Eg	4	6
Plagiomnium cuspidatum	Ma	Ms	P	None	M	F	27.5	24.0	Ep	6	6
Plagiomnium drummondii	Ma	Ms	P	None	M	F	21.0	18.0	Ep	6	6
Plagiomnium ellipticum	Ma	Tf	P	None	D	O	27.5	26.0	Eg	7	8
Plagiomnium medium	Ma	Ms	P	None	M	F	26.5	24.0	Eg	6	7

Species name	Phylogeny and life form		Reproduction and dispersal capacity						Habitat requirements		
	Phylogeny	Life form	Phenology	Propagules	Sexuality	Frequency	Spore diam. (mid., µm)	Spore diam. (min., µm)	Substrate	Light	Moisture
Plagiothecium denticulatum	Mp	Ms	P	Gemmae	M(D)	A	10.0	9.0	Ep	4	6
Plagiothecium laetum	Mp	Ms	P	Gemmae	M	F	10.5	9.0	Ep	3	5
Platygyrium repens	Mp	Ms	P	Branches	D	R	13.0	11.0	Ep	4	4
Pleurozium schreberi	Mp	We	P	None	D	O	15.5	11.0	Eg	6	5
Pohlia cruda	Ma	Tuft	P	None	DM	O	18.5	13.0	So	5	6
Pohlia nutans	Ma	Tuft	P	None	M	A	18.5	16.0	Ge	5	5
Pohlia proligera	Ma	Tf	P(A)	Gemmae	D	O	17.0	16.0	So	7	6
Pohlia wahlenbergii	Ma	Tf	P(A)	None	D	O	17.5	15.0	So	6	8
Polytrichum commune	Ma	Tf	P	None	D(M)	F	8.0	8.0	So	6	7
Polytrichum juniperinum	Ma	Tf	P	None	D(M)	F	8.5	8.0	So	8	5
Polytrichum longisetum	Ma	Tf	P	None	D(M)	F	24.5	17.0	So	5	6
Polytrichum piliferum	Ma	Tf	P	None	D(M)	F	10.5	8.0	So	9	3
Polytrichum strictum	Ma	Tf	P	None	D(M)	O	8.5	8.0	So	8	7
Ptilidium ciliare	L	We	P	None	D	R	30.0	27.0	Ep	6	5
Ptilidium pulcherrimum	L	We	P	None	D	O	26.0	25.0	Ex	6	4
Ptilium crista-castrensis	Mp	We	P	None	D	O	14.0	12.0	Eg	5	6
Pylaisiella polyantha	Mp	Mr	P	None	M	A	13.0	9.0	Ep	6	4
Radula complanata	L	Ms	P	Gemmae	M	A	32.5	25.0	Ep	5	4
Rhizomnium pseudopunctatum + R. gracile	Ma	Tf	P	None	M	F	39.0	28.0	So	7	9

Species name	Phylogeny and life form		Reproduction and dispersal capacity						Habitat requirements		
	Phylogeny	Life form	Phenology	Propagules	Sexuality	Frequency	Spore diam. (mid., µm)	Spore diam. (min., µm)	Substrate	Light	Moisture
Rhytidiadelphus triquetrus	Mp	We	P	None	D	R	22.0	20.0	Eg	6	6
Riccardia latifrons	L	Mt	P	Gemmae	M	F	15.5	14.0	Ex	7	8
Riccardia palmata	L	Mt	P	Gemmae	D	F	15.0	15.0	Ex	4	7
Sanionia uncinata	Mp	We	P	None	M	F	13.0	10.0	Ep	6	6
Sarmenthypnum sarmentosum	Mp	Tf	P	None	D	R	18.0	16.0	Eg	8	9
Scapania glaucocephala	L	Ms	P	Gemmae	D	O	11.0	10.0	Ex	5	6
Scapania irrigua	L	Ms	P	Gemmae	D	R	10.5	9.0	Ex	7	8
Sphagnum angustifolium	Ma	Tf	P	None	D	O	24.5	22.0	Eg	7	9
Sphagnum capillifolium	Ma	Tf	P	None	DM	O	25.5	22.0	Eg	7	7
Sphagnum girgensonii	Ma	Tf	P	None	M(D)	R	20.0	18.0	Eg	6	8
Sphagnum squarrosum	Ma	Tf	P	None	M	O	22.0	17.0	Eg	6	9
Sphagnum warnstorfii	Ma	Tf	P	None	D	O	19.5	17.0	Eg	7	8
Splachnum ampullaceum	Ma	Tuft	A	None	D	A	8.3	7.0	Du	8	8
Splachnum luteum	Ma	Tuft	A	None	D	A	8.0	7.0	Du	8	8
Splachnum rubrum	Ma	Tuft	A	None	D	A	12.0	11.0	Du	8	8
Splachnum sphaericum	Ma	Tuft	A	None	D	A	9.5	7.0	Du	8	8
Tetraphis pellucida	Ma	Tf	P	Gemmae	M	O	11.5	10.0	Ep	3	6
Tetraplodon angustatus	Ma	Tuft	A	None	M	A	9.5	9.0	Du	7	8
Tetraplodon mnioides	Ma	Tuft	A	None	M	A	10.5	9.0	Du	7	7

Species name	Phylogeny and life form		Reproduction and dispersal capacity						Habitat requirements		
	Phylogeny	Life form	Phenology	Propagules	Sexuality	Frequency	Spore diam. (mid., µm)	Spore diam. (min., µm)	Substrate	Light	Moisture
Thuidium recognitum	Mp	We	P	None	D	R	13.5	11.0	Ep	6	5
Tomentypnum nitens	Mp	Tf	P	None	D	R	15.0	13.0	Eg	7	9
Tortula ruralis	Ma	Tf	P	None	D	O	10.0	7.0	Eg	8	3
Tritomaria exsectiformis	L	Ms	P	Gemmae	D	R	11.6	10.5	Ex	5	5
Warnstorfia exannulata	Mp	We	P	None	D	O	19.5	15.0	Eg	8	9
Warnstorfia fluitans	Mp	Ms	P	None	M	O	22.0	17.0	Eg	7	10

Notes: Abbreviations are defined as follows: **Phylogeny**: L = liverwort, Mp = pleurocarpous moss, Ma = acrocarpous moss; **Life form**: Cu = cushion, De = dendroid, Mr = rough mat, Ms = smooth mat, Mt = thalloid mat, Sc = solitary creeping, St = solitary thalloid, Tf = turf, We = weft; **Phenology**: P(A) = perennial but sometimes annual, P = perennial, A = annual, A(P) = annual but sometimes perennial; **Propagules** = type of asexual propagules produced; **Sexuality** = sexual condition of gametophyte: D = dioicous, D(M) = dioicous but sometimes monoicous, DM = dioicous or monoicous, M = monoicous, M(D) = monoicous but sometimes dioicous; **Frequency** = frequency of sexual reproduction: A = abundant, F = frequent, O = occasional, R = rare; **Spore diam. (mid.)** = midpoint of reported minimum and maximum spore diameters; **Spore diam. (min.)** = minimum of reported spore diameter; **Substrate** = substrate affinity: Du = dung, Eg = epigeic, Ep = epiphytic, Ex = epixylic, Ge = generalist, So = soil; **Light** = light conditions (ordinal scale from 0 = plant in darkness to 9 = plant in full light); **Moisture** = moisture conditions (ordinal scale from 1 = indicator of extreme dryness to 12 = normally submerged).

Chapter 5: Recolonization potential of bryophyte diaspore banks in harvested boreal mixed-wood forest[2]

Abstract – Bryophyte diaspore banks are a potential source of reproductive propagules that may be able to colonize newly available habitat after forest harvesting. However, their role and the factors influencing the successful establishment of species remain poorly understood. To investigate these aspects of diaspore banks, we obtained mineral soil samples from mixed and coniferous stands of boreal mixed-wood forest in northern Alberta, Canada, which had recently experienced a range of harvesting intensities. Samples were germinated in growth cabinets under two light regimes. The composition of germinated bryophyte species was compared among forest types, harvesting intensities, and light levels, and also related to edaphic conditions and geographic location of the sample site. Germinated species composition was not related to forest type or harvesting intensity, but was associated with measured edaphic variables and geographic space, indicating that similarity in species composition reflected similarity in edaphic conditions and spatial proximity. This was partly because of spatial dependence of edaphic variables. Light intensity had a significant influence on the development of species assemblages and individual species responses. Richness and cover of acrocarpous mosses (fugitive, colonist, and shuttle life-history strategies) were significantly reduced under low light conditions, but pleurocarpous mosses (perennial strategy) were not affected. Shannon diversity and the frequency of reproduction were significantly greater with high light. Pleurocarpous mosses that are characteristic of intact forests germinated frequently, suggesting that diaspore banks may influence their recovery after disturbance. Diaspore banks are a repository of species at sites affected by forest harvesting; however, diaspore germination and establishment will be constrained by the local environment, including edaphic conditions and light intensity.

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Key words: disturbance, germination, liverwort, Mantel test, moss, variable retention

5.1 Introduction

Bryophytes constitute a substantial proportion of the plant diversity in boreal forests and provide key ecosystem functions (Nilsson and Wardle 2005); however, forest harvesting has been shown to affect their persistence through direct and indirect changes to habitat conditions (Økland et al. 2003; Åström et al. 2005; Fenton and Frego 2005; Dynesius and Hylander 2007). The conservation of biological diversity on harvested landscapes is an increasingly important component of forest management, and is mandated in the Canadian Biodiversity Strategy (Environment Canada 1995) in response to the United Nations Convention on Biological Diversity (UNEP 1992). The successful re-establishment of bryophytes is necessary for the maintenance of species diversity at harvested sites, yet the factors influencing bryophyte colonization remain poorly understood.

Bryophytes can establish after disturbance by clonal expansion of surviving populations, deposition of aerial diaspore rain, or germination from mineral soil diaspore banks (Rydgren and Hestmark 1997). Diaspores are any structures that can produce a plant, including sexually derived spores and asexually derived diaspores (Schofield 2001). The wide variety of diaspore types produced by bryophytes (Imura 1994; Laaka-Lindberg et al. 2003) have assorted roles in establishing and maintaining populations (Newton and Mishler 1994) and different capacities for dispersal and germination (Kimmerer 1996).

Diaspore banks are a means of temporal dispersal whereby species avoid unsuitable conditions and germinate when the greatest chances for successful establishment arise (Thompson and Grime 1979). This allows plants to avoid competition (Hyatt and Evans 1998) by disseminating diaspores that remain in a dormant and viable condition for undetermined periods as part of a well-adapted “resting” strategy (Furness and Hall 1981). Diaspore banks also accumulate genetic variation for species with long-lived diaspores that colonize temporary microsites; this may help maintain the genetic diversity of above-ground populations (Hock et al. 2008). Past studies have used ex situ experiments (Rydgren and Hestmark 1997; Ross-Davis and Frego 2004) and experimentally (During and ter Horst 1987; van Tooren and During 1988; Jonsson 1993; Frego 1996) or naturally cleared (Jonsson and Esseen 1990; Jonsson 1993; von Oheimb et al. 2007) patches of forest floor to show that bryophyte diaspore banks in forests often contain diverse assemblages of species. Forest floor disturbances that expose mineral soil create important microsites for bryophyte colonization. Treefall mounds, for example, stimulate diaspore germination to form "local centers" of high species diversity (Jonsson and Esseen 1990; Jonsson 1993).

The general lack of correspondence between diaspore bank composition and the extant flora (Rydgren and Hestmark 1997; Ross-Davis and Frego 2004) is largely attributable to differences in the life-history strategies of species (During 1997), which summarize trade-offs between reproductive effort and life span, and spore size and number (During 1979, 1992). Forest diaspore banks commonly contain species having colonist or short-lived shuttle strategies (Jonsson 1993) that have a life-span of only a few years and grow on habitats with short longevity, like exposed patches of mineral soil. Extant bryophyte communities of intact forests are dominated by perennial stayers, which live for many years on stable substrates.

Diaspore banks are potentially important in the maintenance of species diversity, influencing the development of forest floor species assemblages (van Tooren and During 1988; Jonsson and Esseen 1990; Rydgren et al. 2004) and promoting secondary succession and site restoration (Grime 1989; Poschlod 1995; Rydgren et al. 1998; Campbell et al. 2003; Hautala et al. 2008). Forest harvesting may affect the viability, composition, and germination of buried diaspores and, therefore, the future establishment of species. Diaspore viability may be reduced through direct and indirect changes to forest floor conditions (e.g., temperature, moisture) beyond the natural range of variation of intact forests. Moreover, harvesting may act in combination with forest type and fine-scale variation in soil conditions to influence diaspore availability. Past studies have focused on spatial (Ross-Davis and Frego 2004) and temporal (During and ter Horst 1987; van Tooren and During 1988; Jonsson 1993; Rydgren et al. 2004) turnover of diaspore bank composition, but we know little about the effects of harvesting and local edaphic and light environments on species recovery.

We examined the effects of variable retention harvesting on the composition of bryophyte diaspore banks in boreal mixed-wood forest. Our objectives were to assess the effects of forest type and harvesting intensity, and the influence of light intensity, soil conditions, and geographic space, on germination from bryophyte diaspore banks.

5.2 Methods

Study design

Research was conducted at the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental area, in the Lower Boreal–Cordilleran Ecoregion (Strong and Leggat 1992) in northwest Alberta, Canada (56°46′ N, 118°22′ W). The region is characterized by a continental climate with cold winters (mean January –17.5 °C), warm summers (mean July 15.9 °C), and an average annual total precipitation of 402 mm, approximately three-quarters of which falls as rain (Environment Canada 2007). Forests are dominated by varying amounts of broadleaf (predominantly *Populus tremuloides* Michx. and *P. balsamifera* L.) and coniferous (predominantly *Picea glauca* (Moench) Voss) canopy cover, with an elevation range of 677 to 880 m a.s.l. Parent material is fine-textured glacial till or glaciolacustrine deposit with few coarse fragments, and soils are primarily well drained and Luvisolic with restricted occurrences of Brunisolic, Gleysolic, and Solonetzic soils (Kishchuk 2004).

We examined diaspore bank composition in 12 mixed (35–65% broadleaf canopy cover) and 12 coniferous (> 70% coniferous canopy cover) forest stands (each approximately 10 ha). Replicate stands in each forest type were similar in pre-harvest ecological site classification, understory vegetation composition, and stand age (Work et al. 2004). Harvesting treatments were randomly applied to three stands in each forest type during the winter of 1998/1999 as 10%, 50%, 75%, and 100% (unharvested controls) dispersed green-tree retention. A modified uniform shelterwood pattern was implemented, whereby 5 m wide machine corridors (oriented in a north–south direction, perpendicular to prevailing winds) alternated with 15 m wide retention strips. Retention strips were partially harvested by systematic tree removal to achieve the desired level of retention for the stand, while accounting for the timber removed from the corridors. Machinery was restricted to the corridors, thereby minimizing disturbance to the forest floor.

Mineral soil samples were obtained in July and August from six plots that were randomly established along the centerline of retention strips in each forest stand for mixed (2004, $n = 72$) and coniferous (2005, $n = 72$) forest types. Sampling dates were randomized among the harvesting treatments. At each sampling location, a 25 × 25 cm section of litter-fermented humus (LFH) was carefully removed, its depth measured, and the sample retained. The exposed mineral soil surface was cleaned of gametophores and the uppermost 5 cm was sampled five times using a 7.2 cm diameter core. The five samples were combined to obtain a total sample volume of 1,018 cm^3. Lower soil depths were not sampled as richness of buried diaspores decreases with depth (Bisang 1996; Rydgren and Hestmark 1997). Soil and LFH samples were immediately refrigerated and kept in darkness.

Germination

Each soil sample was manually homogenized, cleaned of roots and stones, and divided into two portions, each of which was spread to a depth of 2.5 cm over sterile, silica-based perlite in a plastic pot (12.3 × 9.7 × 5.0 (depth) cm). The paired pots for each sample were placed in separate plastic trays and covered with transparent lids. The remaining soil volume and the LFH samples were air dried and analyzed for physical and chemical properties: soil base cations (Ca, K, Mg, Na); soil particle size; soil and LFH pH; soil and LFH electrical conductivity; and soil charcoal abundance (0 = absent, 1 = minor, 2 = abundant).

One set of samples was placed in a growth cabinet with a mean light intensity (Photosynthetic Photon Flux Density) of 275 ± 3.8 μmol s^{-1} m^{-2} ("high light") and the other set in a cabinet with 25 ± 1.3 μmol s^{-1} m^{-2} ("low light"). Illumination was provided by 160 and 20 W cool white fluorescent bulbs. Trays were repositioned every 7 days to reduce the effects of variation in light intensity. Each cabinet received 16 h of light at 18 °C and 8 h of darkness at 12 °C each day, and samples were kept consistently moist by watering every few days. Heat-sterilized soil samples were placed in each cabinet as controls. The high light cabinet had some contamination by *Leptobryum pyriforme*, likely because of sporophyte development in samples in the cabinet. The species frequently colonizes disturbed forest floor in the study area (Mills and Macdonald 2005; R. Caners, unpublished data) and is expected in the diaspore bank and was, therefore, retained for all analyses. There were no germinants in the control pots under low light, where sporophyte density of *L. pyriforme* was greatly reduced.

Emergence of new bryophyte species was assessed every two weeks by hand lens, and after 32 weeks the samples were air-dried. Each species was identified by microscope, its percent cover was measured, and the presence of asexual or sexual reproduction noted; *Sphagnum* coloration and the frequency of deciduous innovations of *Pohlia nutans* (cf. *P. nutans* fo. *decipiens*, Crum and Anderson 1981) were also recorded.

Nomenclature is according to Anderson et al. (1990) for mosses except Sphagnaceae (Anderson 1990), and Stotler and Crandall-Stotler (1977) for liverworts. The species *Brachythecium campestre* includes *B. salebrosum*, and *Bryum lisae* var. *cuspidatum* includes *B. caespiticum*. Voucher specimens are deposited at the Devonian Botanic Garden (ALTADBG) and Department of Biological Sciences (ALTA) herbaria, University of Alberta.

Statistical analyses

We applied Mantel tests and linear ordination to describe the relationships between germinated species abundance, edaphic variables, geographic space (UTM coordinates of samples), and the forest type, harvesting intensity, and light treatments. Space reflects the combined influence of several underlying abiotic and biotic community processes (Borcard et al. 1992). No difference in species composition was detected for forest type (Mantel tests, Results) so data were pooled for subsequent tests. We used alpha = 0.05 for all the statistical tests.

Simple Mantel tests were used to test the null hypothesis of no correlation, r_M, between two independently derived empirical or model (dummy) resemblance matrices (Legendre and Legendre 1998). Partial Mantel tests were used to calculate the (partial) correlation between two resemblance matrices after removing the effects of a third matrix. Log-transformed species abundance data were represented using Bray-Curtis dissimilarity (D14, Legendre and Legendre 1998). Edaphic variables and geographic space were represented using Euclidean distance (Legendre and Legendre 1998) after edaphic variables were standardized to z-scores with zero mean and unit variance to make the different measurements more comparable (Legendre and Legendre 1998). The forest type, harvesting intensity, and light treatments were coded as dummy variables (0, 1) and represented using Euclidean distance. Analyses were performed in the vegan package 1.8-6 (Oksanen et al. 2007) of R 2.4.1 (R Development Core Team 2006) using 10,000 permutations (Jackson and Somers 1989).

Indirect gradient analysis using principal component analysis (PCA) was used to examine the variation in species composition as related to light treatments (288 samples), while direct gradient analysis (constrained ordination) using redundancy analysis (RDA) (Legendre and Legendre 1998) was used to determine if edaphic variables were an important descriptor of germinated species composition. Species cover values were averaged for the high and low light samples at each site prior to analysis by RDA (144 samples). PCA and RDA were chosen over unimodal methods because beta diversity was relatively low; the longest gradient lengths detected by detrended correspondence analysis were 2.2 and 2.3 SD units, respectively (ter Braak and Šmilauer 2002). Edaphic variables were Box-Cox transformed (SAS 9.1; SAS Institute Inc., Cary, NC) to maximize normality (Sokal and Rohlf 1995) and were entered into RDA by forward selection. Only those found to be significant were used in the final model. RDA axes were tested for significance using 999 permutations. Species cover values were log-transformed to reduce the influence of the most abundant species. Analyses were performed using CANOCO 4.5 (ter Braak and Šmilauer 2002) using inter-species correlations and post-transformation of species scores by their standard deviation (to make species scores more comparable; ter Braak and Šmilauer 2002), and centering by species (analyses based on a covariance matrix).

Mann-Whitney *U*-tests (Sokal and Rohlf 1995) were used to test individual species responses to forest type after averaging the values of the sub-samples for each forest stand (*n* = 24 stands). Alpha values were not adjusted to correct for multiple species tests, to reduce the probability of Type II statistical error. Wilcoxon signed-rank tests (Sokal and Rohlf 1995) were used to examine differences in species richness, cover, Shannon diversity (H′, Magurran 2004), number of reproductive species, and species-specific growth responses between paired light treatments. Species belonging to the family Mniaceae were combined for this analysis because they each germinated too infrequently to be analyzed separately but share similar habitat preferences in boreal forests (Koponen 1974) allowing for a biologically meaningful combined response. Trends for individual species were similar to those for all species combined. Analyses were performed using SAS 9.1 (SAS Institute Inc., Cary, NC).

5.3 Results

Composition of germinated species

A total of 56 species (54 mosses and two liverworts) representing 35 genera and 21 families germinated from the mixed-wood diaspore bank (Table 5.1), with similar representation of monoicous (42.3%) and dioicous (58.0%) forms of sexuality. The majority of germinated species were characterized as preferring mineral soil substrates (39.6%), although species that grow on wood (28.3%), humus (13.2%), forest floor (11.3%), and dung (1.9%) were represented, as well as generalist (3.8%) and aquatic (1.9%) species. Species having perennial (36.5%) and colonist (32.7%) life-history strategies were more frequent than fugitive

(1.9%), and short- (13.5%) and long-lived (15.4%) shuttle strategies. Several species adapted to growth under hygric conditions were present (Table 5.1).

Forest type and harvesting intensity

Forest types did not differ in diaspore bank composition (Table 5.2), but differed in measured edaphic variables; however, some species exhibited a greater abundance within a particular forest type: *Philonotis fontana* ($Z = 2.520$, $P = 0.012$), *Brachythecium velutinum* ($Z = 2.482$, $P = 0.013$), and *Plagiomnium drummondii* ($Z = 2.043$, $P = 0.041$) were more abundant in samples from mixed stands, whereas *Herzogiella turfacea* ($Z = -2.663$, $P = 0.008$) was more abundant in samples from coniferous stands.

Diaspore bank composition was not related to harvesting intensity, even after accounting for the effects of the edaphic variables and geographic space. Harvesting intensity was unrelated to measured edaphic variables both before and after accounting for geographic space.

Light treatments

The composition of germinated species differed significantly between the two light intensity treatments (Table 5.2). PCA axes 1 and 2 accounted for 55.5% of the explained variation in species composition (70.2% for axes 1–4), with samples from the low and high intensity cabinets tending to have positive and negative scores along axis 2, respectively (Figure 5.1).

Samples germinated in the high light cabinet exhibited a greater total richness and total cover of bryophytes (Table 5.3). Richness and cover of acrocarpous mosses was greater under high light, but pleurocarpous mosses did not show the same effects. Shannon diversity and the number of species producing sporophytes and asexual diaspores were greater for the high light cabinet. *Pohlia nutans* developed deciduous innovations more frequently under high ($F = 0.60$) as compared to low ($F = 0.04$) light intensity ($S = 1707$, $P < 0.001$).

Some species responded to the light treatments by germinating more frequently under high or low light intensity (Table 5.4).

Edaphic conditions

The first RDA canonical axis (*F*-ratio = 47.286, $P = 0.001$) and all axes combined (*F*-ratio = 8.188, $P = 0.001$) were significant descriptors of the relationship between samples and edaphic variables (Figure 5.2). Axis 1 explained 25.8% of the variation in the model and had the largest species–environment correlation (0.753) (Table 5.5), whereas remaining axes exhibited negligible explained variance. RDA selected seven edaphic variables as significant descriptors of the species data: Ca, pH, Na, charcoal, K, and LFH depth were positively correlated with axis 1, whereas silt was negative (Table 5.5). A summary of significant edaphic variables is presented in Table 5.6. Linear regression of RDA axis 1 site scores averaged for each forest stand ($n = 24$) and mean richness of germinated species (Figure 5.3) showed a relationship of increasing richness with decreasing site scores ($R^2 = 0.52$, $F = 23.351$, $P < 0.001$). This suggests that forests differ in their capacity for diaspore germination along the gradient of edaphic conditions.

Using the same edaphic variables as those selected in RDA, Mantel tests confirmed that species composition was significantly related to the edaphic variables, even after accounting for the effects of geographic space (Table 5.2). Species composition was spatially autocorrelated, even after accounting for the effects of edaphic variables. Edaphic variables exhibit significant spatial dependence, reflecting the edaphic similarity of proximal forest stands.

5.4 Discussion

Germinated diaspore bank composition

Mixed-wood diaspore banks show a strong capacity for regeneration and may be important for the maintenance of species diversity in harvested forests. Total richness of germinated bryophytes was comparable to that found in other studies of forest ecosystems (During et al. 1987; Jonsson 1993; Peterson 1993; Rydgren and Hestmark 1997; Ross-Davis and Frego 2004). Although a relatively small total surface area was used for germination (3.44 m^2, $n = 288$), species with a variety of life-history strategies, substrate preferences, and phylogenetic relationships were recorded (Table 5.1). The appearance of species with perennial life-history strategies (e.g., *Hylocomium splendens*, *Sanionia uncinata*, *Pleurozium schreberi*) alongside colonist and shuttle strategists suggests that facilitation through initial habitat modification (Connell and Slatyer 1977) is not required for establishment of perennials (cf. Jonsson and Esseen 1990) under growth cabinet conditions. Perennial strategists typically dominate the above-ground flora of mature, intact boreal forests but are cited as being infrequent in diaspore banks (Jonsson 1993; During 1997, 2001). However, perennials germinated readily in this study, suggesting that under some situations diaspore banks can provide a notable role in their storage and establishment. This study underscores the significance of diaspore banks as a potential propagule source for the development and diversity of forest floor vegetation (e.g., van Tooren and During 1988; Jonsson and Esseen 1990).

The presence of several species that are adapted to hygric conditions (e.g., *Campylium stellatum*, *Fontinalis* cf. *novae-angliae*, *Helodium blandowii*, *Leptodictyum riparium*, *Philonotis fontana*, *Sphagnum squarrosum*) was surprising, given that the sampled forests are comparatively dry. These species may have effective dispersal capabilities, prolonged viability in the diaspore bank, or both. The viability of *Sphagnum* spores (Sundberg and Rydin 2000) and diaspores of other peatland mosses (Poschlod 1995) is thought to be the highest under wet storage, yet, we found them in the sampled mixed-wood stands. Wetland species were not often observed growing on mineral soil in the study area; their establishment may be limited by moisture availability under natural conditions (Hylander et al. 2005; Benscotter 2006).

Species germinated that were unknown to the extant flora of the study area, including *Atrichum* cf. *tenellum*, *Bartramia ithyphylla*, *Fontinalis* cf. *novae-angliae*, *Pohlia bulbifera*, and *Saelania glaucescens* (Mills and Macdonald 2005; R. Caners, unpublished data); these may have dispersed over extended distances. *B. ithyphylla* is generally restricted to montane and subalpine regions in the province and is absent from the lower foothills where the study area was located;

A. tenellum is undocumented in the province and *P. bulbifera* is considered to be provincially rare (Gould 2006).

Few liverworts germinated, which contrasts with previous studies (Jonsson and Esseen 1990; Jonsson 1993; Rydgren and Hestmark 1997; Ross-Davis and Frego 2004). This may be attributable to unsuitable growth cabinet conditions, poor viability, or the fact that few liverwort species in the study area are adapted for growth on mineral soil, instead preferring wood-based substrates (Mills and Macdonald 2005; R. Caners, unpublished data). Given that liverworts are rapidly lost from harvested sites because of changes in microclimate and the quality and abundance of substrates (Fenton and Frego 2005; Hylander et al. 2005; Nelson and Halpern 2005) their under representation in the diaspore bank calls for the conservation of extant populations to ensure their persistence in harvested mixed-wood landscapes.

Biotic and abiotic factors affecting diaspore bank composition

Germinated species composition was not affected by forest type or harvesting intensity, but responded to light intensity during cultivation, edaphic conditions, and geographic space. The compositional similarity of diaspore banks between forest types suggests that diaspore dispersal or viability is not influenced by prevailing canopy composition. The sampled forest types are often in close proximity on the mixed-wood landscape and many germinated species grow naturally on substrates found in both forest types. However, some species exhibited differences in abundance between forest types and this may reflect their abundance in the extant flora. *Herzogiella turfacea* is preferential to coniferous forests (Crum and Anderson 1981) and was significantly more abundant in our samples from conifer forest. *Brachythecium velutinum* is occasional and *Plagiomnium drummondii* occurs frequently in mixed forests (R. Caners, unpublished data) and were more abundant in those diaspore bank samples. The relationship between the composition of diaspore banks and the above-ground flora will be further considered in a subsequent article, which will focus on patterns of variation in the above-ground flora and response to variable harvesting intensity.

The compositional similarity among harvesting treatments suggests diaspore viability is not affected by this type of disturbance (Ghorbani et al. 2003). In contrast, numerous studies on vascular plant seed banks have shown compositional change in response to management (Decocq et al. 2004; Roovers et al. 2006). Long-term effects of management on diaspore bank composition may occur as a result of changes in abundance of extant species that serve as source populations (Handlová and Münzbergová 2006).

Light intensity influenced the composition of the germinated diaspore bank, suggesting that changes in ground-level insolation after harvesting can influence the development of species assemblages at disturbed forest floor microsites. Acrocarpous mosses, largely represented by colonist and shuttle strategies (Table 5.1), had a greater richness, cover, and frequency of reproduction under high light. Increased light may provide an advantage to acrocarpous mosses by allowing them to develop rapidly at microsites with limited permanence, providing increased opportunity for reproduction and dispersal (Rydgren and Økland 2002). Kimmerer (2005) found that establishment success of acrocarpous moss fragments on treefall mounds was limited to canopy gaps and was absent under limiting light. Pleurocarpous mosses, represented here by a perennial life-history strategy, were not affected by light treatments. The morphological plasticity of many pleurocarpous species allows them to actively "forage" for limited resources, including light (Rincon and Grime 1989; Grime et al. 1990), providing an adaptive advantage for establishment at microsites with limited light availability.

Species that exhibited a greater abundance under high light (Table 5.4) often grow naturally in open habitats (e.g., *Polytrichum strictum*, *Ceratodon purpureus*). In contrast, species belonging to the family Mniaceae, which are common beneath closed mixed-wood canopies, had reduced germination in the high light cabinet. *Mnium spinulosum* is intolerant of high light because of physiological limitations; its preferred habitat is shaded coniferous forest (Cleavitt 2002). *Brachythecium* *velutinum* is frequently found beneath closed forest canopies (Mills and Macdonald 2005) and was significantly less abundant in the high light cabinet, possibly reflecting a preference for reduced light levels. The increased abundance of *Leptobryum pyriforme* under low light may reflect its wide ecological amplitude in combination with reduced competition from other acrocarpous mosses.

The significant relationship between diaspore bank composition and edaphic variables remained after accounting for spatial dependence. The position of species in the RDA biplot reflected their affinity for substrates. For example, *Barbula convoluta* and *Campylium stellatum* are calciphiles and are associated with samples having high values of pH and Ca (Figure 5.2). In comparison, *Hylocomium splendens*, *Pleurozium schreberi*, *Pohlia nutans*, and *Polytrichum strictum* grow on acidic substrates in boreal forests and were associated in this study with samples having low pH. Substrate conditions are an important determinant of species abundance (Vitt et al. 1995) and provide valuable insight into the establishment success of diaspores.

The lowest species richness was observed in samples loading to the high end of RDA axis 1; these were associated with the highest values of LFH depth, charcoal, cation concentrations, and pH, and the lowest values of silt (Figure 5.3). The greater LFH depth at these sites suggests that diaspores have been buried for periods beyond their maximum viability, or it may prevent the downward movement of diaspores through the LFH profile. Samples with the lowest richness also had the greatest abundance of the colonist *Leptobryum pyriforme*. The higher nutrient status of these soils may allow *L. pyriforme* to germinate quickly and displace other species through the exclusion of space and light resources, a pattern that may be accentuated under low light availability. The highest species richness was observed in samples loading to the lower end of RDA axis 1 and which often had acidic and silty, eluviated soil horizons. These samples had lower abundances of *L. pyriforme*, reflecting its reduced viability, germination potential, or presence under these site conditions, or reduced capacity to colonize in samples with higher richness (Tilman 1997).

Diaspore bank composition exhibited significant spatial autocorrelation (Table 5.2). The compositional similarity of proximate forest stands suggests diaspore production and dispersal may be spatially restricted. This supports previous studies in which bryophyte diaspore banks exhibit compositional differences between more distant sites (Bisang 1996; Ghorbani et al. 2003; Ross-Davis and Frego 2004). Dispersal limitation of diaspores can influence patterns of bryophyte colonization in forests (Söderström 1987; Økland et al. 2003; Kimmerer 2005) and may regulate diaspore bank composition.

Management implications

The loss of bryophyte diversity from harvested forests (Fenton et al. 2003; Hylander et al. 2005) necessitates a better understanding of the mechanisms regulating species colonization after disturbance. Bryophyte diaspore banks can facilitate the recruitment of species on the forest floor, but successful species establishment will depend on both the availability of diaspores and suitable microsite conditions.

Mixed-wood diaspore banks can provide a source of viable propagules for establishment at the harvested sites. The frequent germination of perennial strategists characteristic of mature forest conditions suggests that they can readily germinate after disturbance. Germinated species composition was not affected by forest type or harvesting intensity five to six years after disturbance. However, species responded to light intensity and edaphic conditions; thus, these factors will influence their development at forest floor microsites after disturbance. Variation in species responses to these factors may also provide a mechanism for coexistence (regeneration niche, Grubb 1977) and help maintain fine-scale patterns of diversity (Olano et al. 2002). The effects of prevailing growing conditions on species germination, in combination with the spatial autocorrelation of diaspore bank composition, have resulted in forests with different capacities for colonization and recovery after disturbance.

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Table 5.1. Summary of species germinated under high (*n* = 144) and low (*n* = 144) light intensity.

Species	Family	High light		Low light		Sexuality	Substrate preference[a]	Lifehistory strategy[b]
		F	Repro.	*F*	Repro.			
Mosses								
Acrocarpous								
Leptobryum pyriforme	Bryaceae	0.99	c.fr	0.99	c.fr	Mo	Soil	C
Pohlia nutans	Bryaceae	0.93	c.fr	0.78	c.fr	Mo	Generalist	Ss
Sphagnum squarrosum[c]	Sphagnaceae	0.83		0.85		Mo	Humus	Sl
Ceratodon purpureus	Ditrichaceae	0.67	c.fr	0.25		Di	Soil	C
Polytrichum strictum[c]	Polytrichaceae	0.57		0.18		Di	Soil	C
Bryum lisae var. *cuspidatum* agg.	Bryaceae	0.52	c.fr	0.28		Mo	Generalist	C
Pohlia cruda	Bryaceae	0.40		0.33		Di	Soil	Ss
Aulacomnium palustre[c]	Aulacomniaceae	0.27	c.ge	0.08	c.ge	Di	Humus	C
Philonotis fontana[c]	Bartramiaceae	0.18		0.08		Di	Soil	Ss
Funaria hygrometrica	Funariaceae	0.13	c.fr	0.04		Mo	Soil	F
Polytrichum juniperinum	Polytrichaceae	0.10		0.06		Di	Soil	C
Pohlia proligera	Bryaceae	0.10	c.ge	0.06	c.ge	Di	Soil	C
Sphagnum spp.[c]	Sphagnaceae	0.09					Humus	
Barbula convoluta	Pottiaceae	0.06		0.06		Di	Soil	C
Polytrichum commune	Polytrichaceae	0.06				Di	Soil	C
Bryum argenteum	Bryaceae	0.02				Di	Soil	C
Dicranum polysetum	Dicranaceae	0.02		0.01		Di	Forest floor	Sl
Polytrichum cf. *longisetum*	Polytrichaceae	0.02				Di	Soil	Ss
Saelania glaucescens	Ditrichaceae	0.02				Mo	Soil	C
Bartramia ithyphylla	Bartramiaceae	0.01				Mo	Soil	Sl
Pohlia wahlenbergii[c]	Bryaceae	0.01		0.01		Di	Soil	C
Dicranum fuscescens	Dicranaceae	0.01		0.01		Di	Wood	Sl
Dicranum scoparium	Dicranaceae	0.01				Di	Wood	Sl
Plagiomnium drummondii	Mniaceae	0.01		0.03		Mo	Wood	Sl
Pohlia bulbifera	Bryaceae	0.01	c.ge			Di	Soil	C
Polytrichum piliferum	Polytrichaceae	0.01				Di	Soil	C
Splachnum ampullaceum	Splachnaceae	0.01	c.fr			Di	Dung	Ss
Tetraphis pellucida	Tetraphidaceae	0.01	c.ge	0.01	c.ge	Mo	Wood	C
Atrichum cf. *tenellum*	Polytrichaceae			0.01		Di	Soil	Ss
Mnium spinulosum	Mniaceae			0.01		Mo	Wood	Ss
Plagiomnium cuspidatum	Mniaceae			0.03		Mo	Wood	Sl
Plagiomnium ellipticum	Mniaceae			0.01		Di	Forest floor	Sl
Plagiomnium spp.	Mniaceae			0.02				
Polytrichum sp.	Polytrichaceae			0.01		Di		
Pleurocarpous								
Hylocomium splendens	Hylocomiaceae	0.22		0.20		Di	Forest floor	Ps
Sanionia uncinata	Amblystegiaceae	0.16		0.10		Mo	Wood	Ps
Pleurozium schreberi	Hylocomiaceae	0.10		0.05		Di	Forest floor	Ps
Campylium hispidulum	Amblystegiaceae	0.08	c.fr	0.08	c.fr	Mo	Wood	Ps
Herzogiella turfacea	Hypnaceae	0.06		0.07		Mo	Wood	Ps
Brachythecium campestre agg.	Brachytheciaceae	0.05		0.03		Mo	Wood	Ps
Brachythecium starkei	Brachytheciaceae	0.04		0.01		Mo	Forest floor	Ps
Amblystegium serpens	Amblystegiaceae	0.04		0.07	c.fr	Mo	Wood	Ps
Brachythecium velutinum	Brachytheciaceae	0.03		0.08		Mo	Wood	Ps

Species	Family	High light		Low light		Sexuality	Substrate preference[a]	Lifehistory strategy[b]
		F	Repro.	*F*	Repro.			
Campylium stellatum[c]	Amblystegiaceae	0.03		0.01		Di	Soil	Ps
Plagiothecium laetum	Plagiotheciaceae	0.01		0.01		Mo	Wood	Ps
Eurhynchium pulchellum	Brachytheciaceae	0.01		0.01		Di	Wood	Ps
Fontinalis cf. *novaeangliae*[c]	Fontinalaceae	0.01		0.01		Di	Aquatic	Ps
Helodium blandowii[c]	Helodiaceae	0.01		0.01		Mo	Humus	Ps
Isopterygiopsis pulchella	Hypnaceae	0.01		0.01		Mo	Wood	Ps
Leptodictyum riparium[c]	Amblystegiaceae	0.01				Mo	Humus	Ps
Tomentypnum nitens[c]	Brachytheciaceae	0.01		0.01		Di	Humus	Ps
Brachythecium erythrorrhizon	Brachytheciaceae			0.01		Di	Forest floor	Ps
Brachythecium sp.	Brachytheciaceae			0.01				
Hypnum pratense[c]	Hypnaceae			0.01		Di	Humus	Ps
Liverworts								
Marchantia polymorpha	Marchantiaceae	0.24	c.ge	0.07	c.ge	Di	Soil	C
Cephalozia cf. *pleniceps*	Cephaloziaceae			0.01		Mo	Soil	C

Notes: Data for mixed and coniferous forest types are combined. *F* = establishment frequency; reproduction (Repro.): c.fr = sporophyte(s) produced, c.ge = asexual diaspores produced; life-history strategy: C = colonist, F = fugitive, Ps = perennial stayer, Ss = short-lived shuttle, Sl = long-lived shuttle.

[a] Substrate preference is based on personal observation for extant vegetation in the study area, or from published descriptions (Crum and Anderson 1981).

[b] Life-history strategy classification is based on During (1979, 1992).

[c] Species characteristic of hygric habitats.

Table 5.2. Results of simple and partial Mantel tests for the correlation, r_M, between two resemblance matrices with (partial) or without (simple) the removal of the effects of a third matrix: species abundance, Y (56 species, Bray-Curtis dissimilarity); edaphic variables, X (7 variables, standardized Euclidean); geographic space, Z (UTM E and N, Euclidean); forest type, F (1 dummy variable, Euclidean); harvesting intensity, H (3 dummy, Euclidean); light intensity, L (1 dummy, Euclidean).

	n	r_M	*P*
Forest type			
YF	24	–0.023	0.659
XF	24	0.159	0.002
Harvesting intensity			
YH	24	–0.022	0.619
YH.X	24	–0.041	0.764
YH.Z	24	0.017	0.352
XH	24	0.016	0.378
XH.Z	24	0.046	0.208
Light intensity			
YL	288	0.102	< 0.001
Edaphic variables and space			
YX	24	0.639	< 0.001
YX.Z	24	0.611	< 0.001
YZ	24	0.327	0.001
YZ.X	24	0.230	0.004
XZ	24	0.242	0.002

Table 5.3. Differences in mean per-sample species richness, cover, Shannon diversity, and number of species with sexual and asexual reproduction for samples germinated under high (n = 144) and low (n = 144) light intensity (Wilcoxon signed-rank tests, S). Values in parentheses are 95% confidence intervals.

	High light	Low light	S	P
Richness				
Total	7.19 (0.48)	5.01 (0.38)	3367.5	< 0.001
Acrocarpous mosses	6.08 (0.35)	4.17 (0.27)	3464.5	< 0.001
Pleurocarpous mosses	0.87 (0.18)	0.76 (0.17)	241.0	0.224
Cover				
Total	118.71 (3.75)	109.88 (3.51)	2477.0	< 0.001
Acrocarpous mosses	115.05 (3.45)	107.71 (3.30)	2265.0	< 0.001
Pleurocarpous mosses	0.81 (0.35)	1.18 (0.43)	251.0	0.314
Diversity				
Shannon diversity	0.97 (0.08)	0.62 (0.07)	4315.0	< 0.001
Reproduction				
Species with sporophytes	2.10 (0.12)	1.12 (0.07)	2695.0	< 0.001
Species with asexual diaspores[a]	0.47 (0.11)	0.14 (0.06)	629.5	< 0.001

[a] Does not include deciduous innovations of *Pohlia nutans*.

Table 5.4. Species exhibiting a significantly greater rank-abundance under high (n = 144) or low (n = 144) light intensity (Wilcoxon signed-rank tests, S).

	S	P
High light		
Aulacomnium palustre	285.5	< 0.001
Ceratodon purpureus	1811.5	< 0.001
Funaria hygrometrica	90.0	0.012
Marchantia polymorpha	198.5	0.006
Philonotis fontana	164.0	0.005
Pohlia nutans	1047.0	0.011
Polytrichum commune	22.5	0.004
Polytrichum juniperinum	63.5	0.020
Polytrichum strictum	1894.0	< 0.001
Sphagnum spp.	45.5	< 0.001
Low light		
Brachythecium velutinum	–38.0	0.027
Leptobryum pyriforme	–1431.0	< 0.001
Mniaceae[a]	–45.5	< 0.001

[a] Includes *Plagiomnium cuspidatum*, *P. drummondii*, *P. ellipticum*, *P.* spp., and *Mnium spinulosum*.

Table 5.5. Results of the RDA including inter-set correlations of edaphic variables (chosen by forward selection) on each axis.

RDA summary	Axis 1	Axis 2	Axis 3
Eigenvalues[a]	0.258	0.020	0.008
Species-environment correlations	0.753	0.496	0.389
Cumulative percent variance explained			
of species data	25.8	27.8	28.6
of species-environment relationship	87.0	93.8	96.5
Inter-set correlations[b]			
Ca	**0.651**	–0.104	0.083
pH	**0.580**	–0.052	**–0.201**
Na	**0.465**	0.164	0.115
Charcoal	**0.205**	0.151	0.127
K	**0.310**	**–0.367**	0.100
Silt[c]	–0.117	0.102	–0.160
LFH depth	**0.401**	**0.189**	0.156

[a] Axis 1 and all combined axes are significant at $P = 0.001$.

[b] Edaphic variables are ordered from the most to the least significant as determined by forward selection. Significant correlations are in bold ($P < 0.05$).

[c] Silt is significantly correlated with axis 4.

Table 5.6. Mean (95% confidence intervals in parentheses) and range of significant edaphic variables (chosen by forward selection in the RDA) for mixed (*n* = 72) and coniferous (*n* = 72) forest types.

	Mixed forest		Coniferous forest	
Edaphic variables	Mean	Range	Mean	Range
Ca ($mg \cdot L^{-1}$)	442.81 (58.75)	70.67–1736.81	417.66 (89.34)	33.87–2356.36
pH	4.92 (0.12)	3.89–7.16	5.28 (0.13)	4.45–6.47
Na ($mg \cdot L^{-1}$)	12.24 (0.93)	8.16–29.49	10.64 (1.22)	7.19–47.04
Charcoal (0 – 2)	1.1 (0.2)	0.0–2.0	1.4 (0.1)	1.0–2.0
K ($mg \cdot L^{-1}$)	60.27 (7.82)	19.42–208.23	44.32 (4.33)	16.23–86.06
Silt (%)	50.33 (1.05)	39.13–60.57	49.40 (1.12)	40.16–60.14
LFH depth (cm)	8.5 (1.0)	3.5–35.5	7.7 (1.3)	1.5–31.5

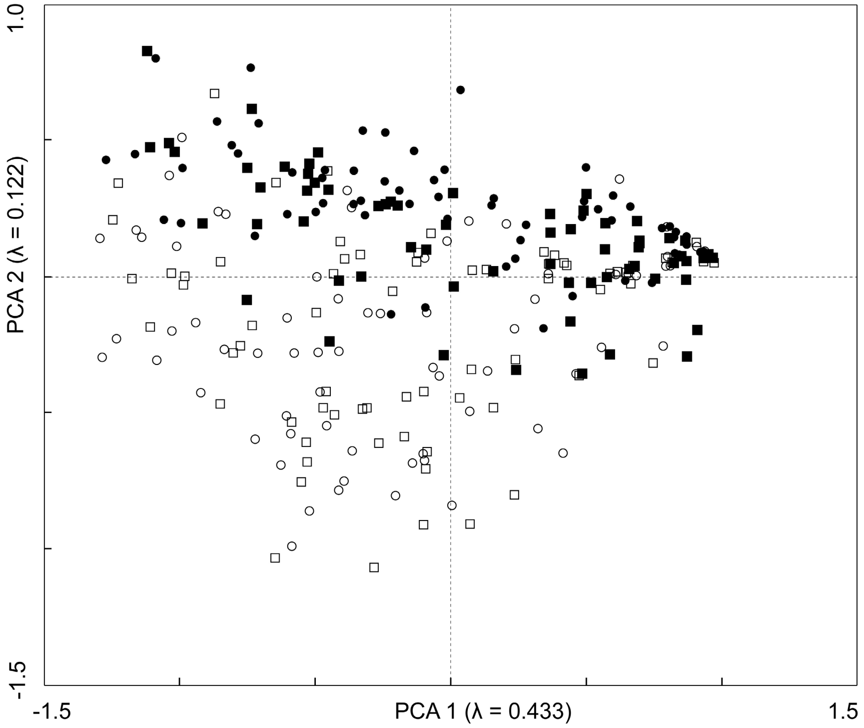
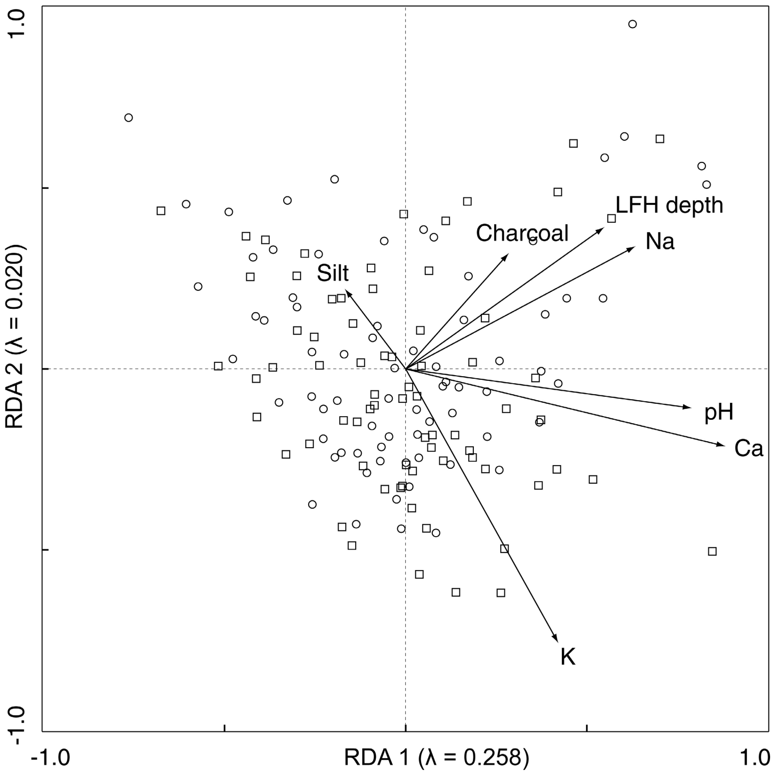


Figure 5.1. Results of PCA of species composition for samples germinated under high (open symbols) and low light intensity (closed symbols) for mixed and coniferous forest types: mixed forest–high light, □ (*n* = 72); mixed forest–low light, ■ (*n* = 72); coniferous forest–high light, ○ (*n* = 72); coniferous forest–low light, ● (*n* = 72).

(a) Samples biplot



(b) Species plot

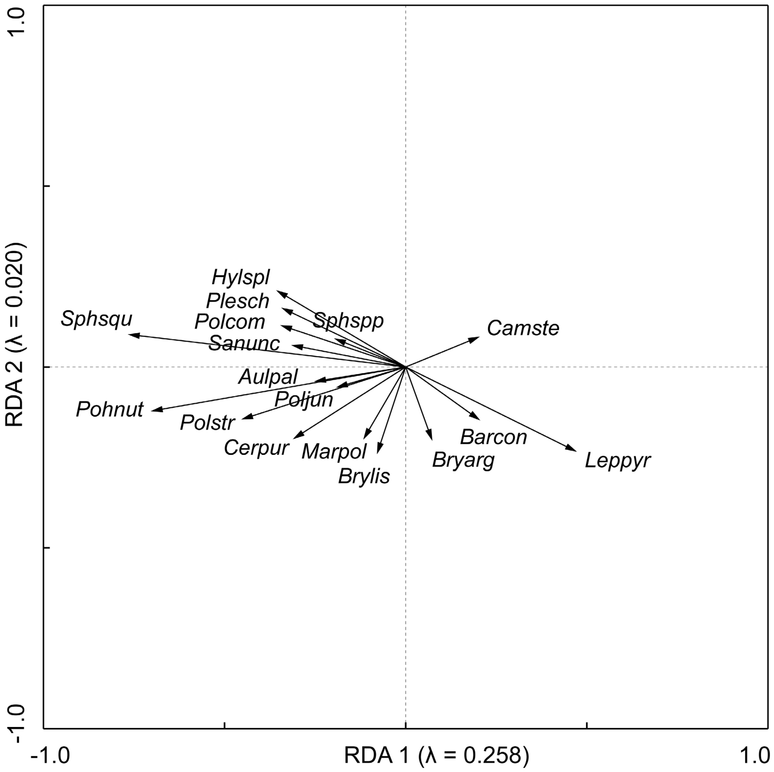


Figure 5.2. Results of RDA of 144 samples (combined composition for high and low light treatments). a Biplot of samples and significant edaphic variables (chosen by forward selection): pH = soil pH; Ca = calcium concentration; Charcoal = charcoal abundance; K = potassium concentration; LFH depth = depth of the organic layer; Na = sodium concentration; Silt = silt content. Samples from mixed (□, *n* = 72) and coniferous (○, *n* = 72) forest types are indicated. b Species plot, displaying those with the greatest explained variance. Species codes are the first three letters of genus and species (see Table 5.1). Vector lengths for species and edaphic variables represent the strength of each relationship along the displayed axes (see Table 5.5).

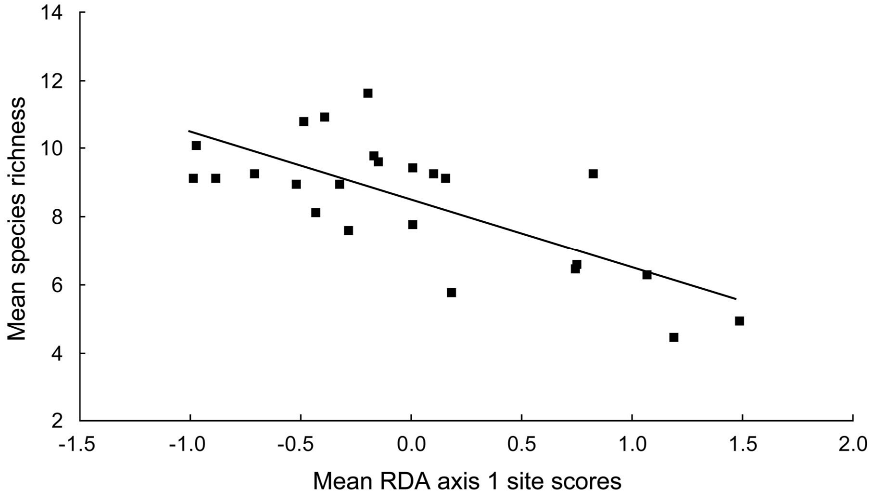


Figure 5.3. Linear regression of mean richness of germinated species on mean RDA axis 1 scores; samples were averaged for each forest stand ($R^2 = 0.52$, $n = 24$, $P < 0.001$).

Chapter 6: Summary and implications

An emerging objective in forest management policy is the maintenance of biological diversity in harvested landscapes (Mielikäinen and Hynynen 2003; Work et al. 2004; CCFM 2006). Whether or not this goal can be achieved will depend on the extent to which natural habitat features and dynamics can be retained at different spatial and temporal scales for a range of forest biota (Lindenmayer and Franklin 2002; Kuuluvainen 2002, 2009). In many regions of the boreal forest the dominant model of forest harvesting has been clear-cutting. This method can result in forest homogenization (Cyr et al. 2009; Kuuluvainen 2009) and biodiversity loss (Hylander et al. 2005; Niemelä et al. 2007; Paillet et al. 2010) at stand and landscape scales. Although forest management practices that preserve some level of forest structure are being more widely implemented with the goal of species preservation, in many cases these practices remain as untested scientific hypotheses (Spence 2001). A major goal will be to assess the efficacy of these practices for maintaining species and the forest features and processes they require.

This thesis provides several insights about relationships between residual forest structure and the preservation and potential recovery of boreal mixed-wood bryophytes in the short-term (five to six years) following partial canopy harvest. The original hypothesis at the outset of this thesis that residual forest structure could provide protection for bryophytes was based on an assessment of past studies, which found that 1) intensive forest harvesting practices such as clear-cutting or low canopy retention resulted in the loss of species with high sensitivity to harvest (e.g., Newmaster and Bell 2002; Ross-Davis and Frego 2002; Fenton and Frego 2005; Hylander et al. 2005); and 2) greater levels of residual forest structure were beneficial for preserving some forest-dwelling biota (e.g., Work et al. 2004) and might enhance the preservation of bryophytes (e.g., Hannerz and Hånnell 1997; Jalonen and Vanha-Majamaa 2001; see also Dovčiak et al. 2006 and Aubry et al. 2007 for forests of the Pacific Northwest). Results from my research demonstrated that the level and composition of forest canopy retained after partial harvesting were important drivers of bryophyte species richness and abundance in the harvested matrix. Chapter 3 established that residual forest structure had distinctive effects on different groups of bryophyte species and influenced regional patterns of species diversity at multiple hierarchical levels. Chapter 2 focused on one group of species, epiphytic bryophytes that grow on the bark of trembling aspen (*Populus tremuloides*). Through an analysis of nearest-neighbour relationships of individual plants this study showed that partial harvesting intensity impacted species viability with consequences for maintaining the structure and possible functioning of epiphyte assemblages. Chapters 4 and 5 were fundamentally concerned with the capacity for bryophyte species to disperse and establish in forest stands that had experienced a range of partial harvesting intensities. Chapter 5 provided an assessment of species establishment potential from bryophyte diaspore banks in forest soils, and Chapter 4 examined the effects of habitat change after partial harvesting on species with different biological attributes. Ultimately, this thesis contributes new perspectives on a number of topics that relate to evolving approaches to sustainable forest management and its role in biodiversity conservation.

6.1 Effectiveness of residual forest structure for maintaining bryophytes

Species responses

The number of bryophyte species detected after partial harvesting, and the compositional similarity of bryophytes to intact forests, were positively associated with canopy retention level. However, harvesting effects were more prominent for some species groups than others: epixylic species that are restricted to decayed wood and epiphytic species that colonize tree bark and recently fallen wood were more sensitive to partial canopy harvest than species on other substrate types (Chapters 2 and 3), and liverworts were more sensitive than mosses (Chapter 3).

Epixylic and epiphytic species had reduced plot-level richness with any degree of partial harvesting as compared to intact forest, which likely resulted from a combination of more extreme growing conditions after canopy removal and/or reduced abundances or quality of substrates on which these species grow. Indeed, forest moisture declined significantly in all harvested forests as compared to intact forest for both forest types (Chapter 4). Although harvesting was conducted with minimal disruption to forest floor substrates, the direct loss of habitat in the form of decayed logs and stumps, and standing trees, from machine corridors (occupying approximately 25% of forest floor area in all harvested stands) may have partly contributed to the reduced numbers of epixylic and epiphytic species even at high (75%) retention. The separate study of epiphytic bryophytes on aspen (Chapter 2) provided additional insights for this species group. These epiphytes declined in richness and shifted in species composition from intact forest at lower (10% and 50%) retention, and the abundance of living epiphytes decreased with any level of partial harvesting. In the same study, an analysis of epiphyte nearest-neighbour relations revealed that lower retention levels resulted in the degradation of epiphyte assemblage structure. Epiphytes were associated with fewer neighbours of differing species at lower retention and inter-species relationships became increasingly dominated by dead bryophytes and uncolonized bark. Other researchers found that epiphytic bryophytes on residual trees in clear-cuts had high initial mortality following harvest and slow rates of recovery (Lõhmus et al. 2006; Lõhmus and Lõhmus 2006). In my study, higher levels of residual forest structure after harvesting provided only minor improvements over low retention for epiphyte protection, but further research may reveal an influence of retention on rates of species recovery over longer time periods.

Liverworts, most of which colonize decayed wood, had reduced richness per plot at lower (10% and 50%) retention as compared to intact forest but species differed significantly in composition from intact forest with any level of partial harvesting. These trends were accompanied by a substantial increase in beta diversity (measured as species richness) among plots and among stands with increasing harvesting intensity for liverworts (Chapter 3). In essence, partial harvesting created greater among-site differentiation in liverwort richness with increasing disturbance intensity likely as a result of increased numbers of local species extinctions at harvested sites. Epigeic species that inhabit forest floor were also detrimentally affected by harvesting, and decreased in richness and abundance with declining retention (Chapters 3 and 4). Reduced cover of the dominant mosses *Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis* may limit the functional roles they provide in boreal forests (Nilsson and Wardle 2005; DeLuca et al. 2007). In comparison, species that grow on mineral soil, animal bones and excrement, and species that were generalists, were not as detrimentally affected by harvesting, and often increased in richness and abundance with declining retention. Partial harvesting may be effective for the preservation of some bryophyte species with high tolerance to canopy removal; however, liverworts and several epixylic and epiphytic bryophytes may require areas of intact forest to preserve the habitat conditions found in unmanaged forests.

In a comparable study in forests of the Pacific Northwest, Dovčiak et al. (2006) found that all bryophyte species combined had reduced richness and frequency at low levels (either 40% or 15% retained basal area) of dispersed canopy retention as compared to intact forests, three to four years after harvesting. In the same study, patches of aggregated retention were generally comparable to dispersed retention in terms of effectiveness for supporting bryophytes. However, findings from my research in boreal mixed-wood forests demonstrated that some species groups were detrimentally affected at any level of canopy removal. Species with differing phylogenies (e.g., mosses, liverworts) and substrate requirements should be examined separately from one another in studies of forest harvesting (Chapters 3 and 4), since combining them can obscure meaningful differences in their responses.

Studies examining the effects of harvesting on bryophytes have often used small sample plots (≤ 1 m^2; e.g., Hannerz and Hånell 1997; Fenton et al. 2003; Fenton and Frego 2005; Dovčiak et al. 2006; Baldwin and Bradfield 2007; Hart and Chen 2008). Although sampling species at small spatial scales may be important for addressing questions at finer scales, such as species-substrate relationships, the majority of forest bryophytes are infrequent and occur at low abundance (Newmaster et al. 2005). This suggests that results of studies utilizing small plots will generally reflect the responses of only the most common species and may underestimate the effects of anthropogenic disturbance on uncommon specialist species (R. Caners, unpublished data). In this thesis, bryophytes were sampled using large (20 m radius, 1,256 m^2) plots to capture infrequent forest habitats and associated species. By capturing greater numbers of uncommon species, results of this thesis are likely to reflect more closely the responses of bryophytes to harvesting practices at a spatial scale appropriate to forest management.

Maintenance of populations

This research confirms that epixylic and epiphytic species contribute substantially to bryophyte diversity in boreal forests and are sensitive to forest harvesting (Söderström 1988; Fenton et al. 2003; Hylander et al. 2005; Dynesius et al. 2009). My results further demonstrate that even minor forest perturbations can affect the persistence of these species. Reduced abundances or the extirpation of species from partially harvested stands may have detrimental consequences for maintaining populations over larger spatial and temporal scales (Snäll et al. 2004, 2005; Lõhmus and Lõhmus 2010). For species to become re-established after harvesting, reproductive propagules will have to arrive from more distant locations within a harvested stand or from other forested areas. However, some species are thought to have limited dispersal capacities (Laaka-Lindberg et al. 2006) and propagule dispersal may be constrained by having to disperse through inhospitable habitat conditions over large areas of forest matrix.

Small populations are more susceptible to extirpation than larger populations because of the effects of stochastic environmental, demographic, and genetic events (Matthies et al. 2004; Lõhmus and Lõhmus 2010). This suggests that the reduced abundances of several bryophyte species at lower structural retention (Chapters 2–4) may increase their vulnerability to future extirpation from harvested sites. Although several species were able to persist after harvesting, it was not possible to ascertain in this study whether populations were in decline or recovering. Other studies have demonstrated that species continue to be affected in the years following disturbance (Tilman et al. 2002; Velland et al. 2006; Rogers et al. 2009), but whether or not this is the case for extant bryophytes in my study will require further investigation.

Many bryophyte species responded closely to reduced forest moisture after harvesting (Chapters 2 and 4) and forest moisture in all harvested stands remained significantly lower than intact forest five to six years post-harvest. Reduced forest moisture in harvested stands reflects degraded growing conditions for bryophytes and may contribute towards the erosion of extant populations. Furthermore, lower moisture may create a bottleneck that limits the re-establishment of species adapted to mesic conditions or species that have physiological limitations during parts of their life cycle (Cleavitt 2002; Pohjamo and Laaka-Lindberg 2004). Preliminary analyses suggest that high local abundance of regenerating and residual broadleaf shrubs in harvested stands with low canopy retention can buffer ground-level moisture loss (R. Caners, unpublished data; see also Stewart and Mallik 2006). Although broadleaf plants produce leaf litter that can smother bryophyte colonies on the forest floor (Longton 1992), bryophytes that grow in elevated positions on tree bases and logs are often protected from litter fall. Shrubs may, therefore, have an important role in protecting bryophytes and the quality of substrates on which they grow during forest regeneration. Coarse woody material situated beneath dense shrub canopies in intensively harvested stands often supported a larger number of epixylic species than wood in more exposed locations (personal observation). The role of broadleaf shrubs as possible facilitators of bryophyte species recovery following harvest warrants further examination.

6.2 Species dispersal capacity in harvested boreal forests

This thesis provided important insight about the dispersal capacity of bryophytes and implications for species establishment after harvesting. Chapter 4 examined relationships between the forest environment after partial harvesting and species with traits related to reproduction and dispersal. Results indicated that species with potentially limited reproduction and dispersal capacities (e.g., species with infrequent sexual reproduction, dioicous sexuality, large spore size) were less abundant at the more intensively harvested sites. Lower abundances of these species after harvesting may limit their chances of successful dispersal and establishment as compared to species with greater capacities to reproduce and disperse. Future research that classifies species based on suites of traits (response groups, Lavorel et al. 1997) may provide more accurate predictions of species responses to changes in forest environment after harvesting. Moreover, species should be tested experimentally (e.g., using reciprocal transplant or propagule establishment experiments) to determine if certain traits or combinations of traits can limit their establishment or persistence at harvested sites. An experimental approach 1) will reduce the effects of potentially confounding factors under natural settings, and 2) could determine the expression of species traits in response to particular environmental conditions.

Species dispersal and establishment were also examined through an analysis of bryophyte diaspore banks (Chapter 5). This study revealed that soil physical and chemical properties, and light intensity during cultivation, were strong determinants of germinated species composition in a growth cabinet experiment. These findings suggest that the development of species assemblages from exposed soil under natural forest conditions may be influenced by prevailing habitat conditions during germination. Species of the moss family Mniaceae, for example, are common in mesic, close-canopied boreal forests and developed more frequently under low light conditions in the growth cabinets.

Intensity of forest harvesting and forest canopy composition had no effect on the composition of germinated species. This suggests that diaspore banks may serve an important role in the storage of reproductive propagules to influence the establishment of species at harvested sites. Tree fall events are an important form of small scale disturbance in boreal forests and may facilitate species establishment on the forest floor (Jonsson and Esseen 1990; Jonsson 1993). However, the establishment of species from exposed soil after tree fall may be constrained because of reduced forest moisture at harvested sites (personal observation). The development of closed forest canopies and higher moisture levels after harvesting may be required before species can establish successfully from forest floor microsites.

Bryophyte diaspore banks are often dominated by ruderal species that are adapted to disturbed habitat conditions (During 2001). However, results demonstrate that a relatively large number of longer-lived perennial species (sensu During 1979, 1992) that are characteristic of intact forests also germinated frequently from diaspore banks. Perennial species are generally thought to form a minor component of diaspore banks because of the trade-off between adult longevity and diaspore longevity in the soil (During 2001). Furthermore, perennial species are characterized as having small spores (During 1979, 1992), which are thought to persist for shorter periods in the mineral soil than larger spores (Jonsson 1993). The germination of perennials from mixed-wood soils suggests that diaspore banks have a notable role in their conservation at harvested sites. However, the near absence of liverworts from mixed-wood diaspore banks indicates that forest soils are unlikely to provide a supply of propagules for local establishment. The strong sensitivity of liverworts in above-ground communities to forest harvesting and their absence (or poor germination capacity) from diaspore banks will necessitate the development of measures for their preservation in managed forests. Additional research is required to assess the factors influencing diaspore longevity in the soil and the capacity for species to establish from diaspore banks under natural forest conditions.

6.3 Importance of canopy composition for bryophytes

An additional conclusion from this thesis was that forest stands of differing pre-harvest canopy composition commonly supported different bryophyte species after harvesting (Chapter 3). Bryophytes differed in richness, diversity, and composition between the mixed broadleaf-coniferous and coniferous-dominated forest types, while responses to harvesting intensity were similar between forest types. Bryophyte differences between forest types were either a legacy of differences that existed before harvest, or resulted from the post-harvest response of bryophytes within each forest type, or both. These results are noteworthy because they imply that forests of differing canopy composition can influence the development of bryophytes at a location during secondary forest succession. This is an important consideration for conserving species patterns and dynamics across larger areas of managed forest.

Bryophyte differences between the sampled forest types were related in part to differences in substrates (e.g., coniferous and broadleaf tree bases and decayed wood) and forest moisture conditions. Coniferous stands contained greater abundances of coniferous tree bases and coniferous coarse woody material, which supported species with an affinity for these substrate types (e.g., *Cephalozia lunulifolia* agg., *Tritomaria excectiformis*). Coniferous stands also had a greater cover of mineral soil that resulted from windthrow of coniferous canopy trees to support soil specialists (e.g., *Bryum pseudotriquetrum*, *Polytrichum strictum*). Stands with a greater broadleaf canopy component supported species with an affinity for broadleaf bark and decayed wood (e.g., *Chiloscyphus pallescens*, *Plagiomnium cuspidatum*).

Coniferous forests should be recognized for their capacity to support a wide variety of species in boreal mixed-wood forests. Liverworts had greater richness and abundance in coniferous as compared to mixed forests (Chapter 3 and 4). These results are partially consistent with Hart and Chen (2008) who found that boreal forests with a coniferous canopy had higher bryophyte richness than broadleaf-dominated or mixed-composition forests (the authors did not distinguish between liverworts and mosses). Furthermore, my research revealed that coniferous forests supported greater abundances of acrocarpous mosses, and species with a turf life form, infrequent sexual reproduction, dioicous (or commonly dioicous) sexuality, and species that inhabit forest floor and mineral soil substrates. Coniferous forests also had greater abundances of species with higher moisture requirements, confirming other results from this study, that coniferous forests can support wetter conditions than forests with a greater broadleaf component. Vascular plants often attain higher richness and diversity in broadleaf-dominated forests (Macdonald and Fenniak 2007; Hart and Chen 2008); however, bryophytes may benefit from cooler temperatures and increased forest moisture provided by greater conifer abundance. Coniferous forests are valuable habitats for bryophytes and should be examined further in terms of their significance as refuges of source populations in managed mixed-wood landscapes.

6.4 Management considerations

The amount and quality of habitat available in the harvested matrix is an important determinant of species survival, and will impact the capacity for species to sustain population demographic processes within stands and landscapes. In this thesis, boreal mixed-wood forests that were partially harvested along a range of intensities varied considerably in structural features and habitat conditions, and in the species they could support five to six years after harvesting. Species with high sensitivity to habitat modification after forest harvesting will require the implementation of strategies to ensure their continued representation in managed forests.

A large proportion of boreal mixed-wood bryophytes require coarse woody material in different stages of decomposition as habitat, necessitating the preservation of these substrates following harvest. As some species are considered to have limited dispersal capacities, the loss of suitable substrates for colonization may have detrimental consequences for maintaining these species after harvest. Forest management practices that minimize disturbance to forest floor substrates will help retain these habitats and may facilitate species preservation across larger areas of managed forest.

Higher levels of canopy retention in both mixed and coniferous forests generally supported a higher richness and abundance of bryophytes, and more similar species composition to intact forests. Higher canopy retention also supported higher moisture to suggest that many forest bryophytes depend on mesic habitat conditions for their survival. However, forest moisture was significantly reduced with any degree of partial harvesting in both mixed and coniferous forests, and was associated with reduced viability of some species (including several epixylic and epiphytic bryophytes) that are potentially more sensitive to desiccation. From a biodiversity perspective, preserving viable populations of specialist species in managed landscapes is a high priority (Kuuluvainen 2002). For several species, low (10%) retention might be as effective as high (75%) retention for their persistence (cf. Chapters 2–4) by providing comparable habitat conditions. In comparison, several species were sensitive to any canopy removal and will require areas of intact forest to ensure their persistence.

The composition of retained forest structure also needs to be considered when developing management strategies for the preservation of boreal bryophytes at the landscape scale. The mixed and coniferous forest types sampled in this thesis differed in bryophyte species composition, and each contained unique indicator species that reflected the growing conditions and substrates available for colonization within each forest type. Coniferous forests are important habitats for bryophytes in mixed-wood landscapes but maintaining variation in forest canopy composition at the landscape scale will be necessary for supporting species with different habitat requirements. A number of forest attributes not examined in this thesis, but thought to influence bryophyte diversity and distributions at different spatiotemporal scales, including site disturbance history, physiography, and habitat connectivity, should be considered for a more complete understanding of canopy harvesting effects on bryophyte species.

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