ASSESSING THE EFFICACY OF BUFFER STRIPS IN SUSTAINING BRYOPHYTE DIVERSITY IN MONTANE FORESTS IN THE BRITISH COLUMBIA INTERIOR

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DEDICATION

To David R. Williams and Dr. Lyn Baldwin who made me realize the beauty, value and importance of plants in our world.

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ABSTRACT

Small mountain streams are neglected under current BC forestry regulations. Debate exists over buffer widths necessary to maintain floristic diversity. The effectiveness of canopy treatments (clear-cut, one-sided or two-sided buffers and continuous forest) and buffer width in maintaining riparian bryophyte diversity and promoting community reassembly in adjacent harvested uplands was examined using 30 Interior Montane Spruce sites. Analysis found frequency and richness of old-growth associated groups (liverworts, perennial stayers, closed canopy, humus or log species) was maintained with buffers (one sided and two-sided). Disturbance associated groups (colonists, open canopy and mineral soil/rock species) were more abundant in clear-cut riparian sites. Ordination found buffer width and canopy cover within 50 m radius affected bryophytes in riparian sites with buffers, whereas disturbance variables affected composition in clear-cut riparian sites. Regressions showed the importance of habitat quality variables (soft CWD and concavity). A buffer had no effect on community reassembly in the uplands.

Keywords: small stream, riparian, buffer, bryophyte, functional groups

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Chapter One

INTRODUCTION AND LITERATURE REVIEW: RIPARIAN ZONES AND BUFFER STRIPS

Riparian zones, the boundaries between water and land, are environmentally complex ecosystems and contain large, often unique, assemblages of species (Salo et al. 1986, Gregory et al. 1991, Naiman et al. 1993, Naiman and Decamps 1997, Sabo et al. 2005). Past riparian studies have examined the effect of different environmental parameters (e.g. area and height of river edge, substrate heterogeneity, soil pH) on overall biodiversity (Renöfält et al. 2005). Few studies have focused on small first order or headwater streams (Moore and Richardson 2003, Richardson et al. 2005); yet, collectively these smaller streams make up a large portion of the watershed. As dynamic systems, small order riparian zones influence downstream ecosystems through debris flow, sediment deposition, and the storage and transport of organic matter (Gomi et al. 2002). All streams are ecologically important for nutrient cycling (N and P), and provide valuable habitat for vertebrates, invertebrates and terrestrial plants, including bryophytes (Naiman and Decamps 1997, Hagg and Dickinson 2000, Meyer and Wallace 2001, Vesely and McComb 2002, Moore and Richardson 2003, Cockle and Richardson 2003, Lees and Peres 2008).

To protect and maintain these important riparian areas, North American logging companies have been required to leave standardized buffer strips of trees around streams depending on stream channel size, fish presence and whether the streams are part of the community watershed (FEMAT (Forest Ecosystem Management Assessment Team) 1993, Riparian Management Area Guidebook - Forest Practice Code of British Columbia Act 1995, Community Watershed Guidebook - Forest Practices Code 1996, BC Ministry of Forests and Range 2004 Practices Act). Brosofske et al. (1997) confirmed the riparian microclimate was affected by buffer width and found that some of the prescribed dimensions may not be enough to protect the original environmental conditions. A review by Castelle et al. (1994) also recommended a buffer of at least 15 m to maintain stream water quality itself which in turn may alter neighbouring plant communities. However Hibbs and Bower (2001) found no significant difference in the composition and structure of the vascular plant community in forested riparian buffer strips compared with the intact riparian forest in the Oregon Coast Range. In British Columbia, the efficacy of riparian buffer strips in various ecosystems has been evaluated in primarily coastal environments with larger stream sizes (Brosofske et al. 1997, Jonsson 1997, Hibbs and Bower 2001, Richardson et al. 2005). The application of these findings may not be appropriate for the rest of the province (Bird et al. 2004). Overall, there is increasing concern and disagreement over the efficacy of different riparian forestry practices in maintaining ecological diversity (Swanson and Franklin 1992, Brosofske et al. 1997, Blinn C.R. and Kilgore M.A. 2001, Hibbs and Bower 2001, Moore and Richardson 2003, Richardson et al. 2005, Lees and Peres 2008).

Plants, particularly bryophytes, are sensitive to changes in the environment and are valuable indicators of overall riparian health (Naiman et al. 1993, Berglund and Jonsson 2001, Frego 2007). Bryophytes are an important component of many forest ecosystems (Jonsson 1993, Baldwin and Bradfield 2005), accounting for a significant amount of overall species diversity and understory biomass, particularly around stream banks (Schofield 1976). They are also involved in nutrient cycling (Glime 2001, Turetsky 2003). These small nonvascular plants include liverworts (Hepatophyta), mosses (Bryophyta) and hornworts (Anthocerophyta) (Goffinet 2000). Many studies have looked at the influence of biotic and abiotic variables on bryophyte diversity i.e. aspect, relative humidity, temperature, wind, light, coarse woody debris (CWD), harvesting disturbance, elevation, substrate type, pH and vascular plant canopy cover (Brosofske et al. 1997, Jonsson 1997, Haeussler et al. 1999, Pharo et al. 1999, Rambo 2001, Ross-Davis and Frego 2002, Humphrey et al. 2002, Fenton et al. 2003, Mills and Macdonald 2004, Hylander 2005, Hylander et al. 2005, Hylander and Dynesius 2006). Due to their poikilohydric nature (they have little control of water loss), bryophytes are sensitive to changes in their immediate environment (Hylander et al. 2002). Thus, due to their ubiquitous and sensitive nature bryophytes have been suggested as potential environmental indicators or phytometers (Hylander et al. 2002, Frego 2007). Certain bryophyte species can also be used as indicators of red listed bryophyte species which is important for conservation purposes in Swedish forests (Gustafsson et al. 2004). The potential use of bryophytes as indicators is tempered by the acknowledged difficulty in accurate field identification for many species.

The use of plant functional types or functional group classification (rather than phylogeny) has been recommended when examining plant response to environmental change such as disturbance and increasing landscape fragmentation (Bates 1998, Rusch et al. 2003, Verheyen et al. 2003a, Baldwin and Bradfield 2005, 2007, 2010). Bryophytes can be categorized into *a priori* functional groups based on life history strategies, canopy preferences, growth forms and substrate affinity derived from current literature and expert knowledge (Table 1 adapted from Baldwin and Bradfield 2005). Several of these functional groups (i.e. colonists and open canopy species versus perennial stayers and closed canopy species) can be expected to respond differently in terms of frequency and richness to changing environmental factors such as disturbance, moisture and light (During 1992, however see Bates 1998). Harvesting of riparian areas will alter the environment directly and indirectly along the artificial edge (Brosofske et al. 1997); functional groups (rather than specific species) will be useful in understanding overall bryophyte community response to these perturbations (Baldwin and Bradfield 2005, 2007, 2010).

Riparian areas have very high bryophyte species richness (Jonsson 1997, Berglund and Jonsson 2001) thus there is concern over the effectiveness of standardized buffer strips in maintaining this diversity (Fenton and Frego 2005, Dynesius and Hylander 2007). Given the impacts of disturbance on bryophytes, how effective are buffer strips in maintaining bryophyte diversity? Two forms of disturbance may be associated with any kind of forest harvesting: altered microclimate and physical disturbance (Ross-Davis and Frego 2002). Disturbance (for example logging, cattle grazing, and fire) may result in differing responses by various functional groups and overall bryophyte diversity. Disturbance such as harvesting may negatively or positively affect bryophyte diversity in forests (Åström et al. 2005). In particular, changes caused by harvesting to the amount and type of CWD, water pH or soil pH, soil moisture, light, and temperature (Vitt et al. 1995, Mills and Macdonald 2004, Hylander and Dynesius 2006) often have significant negative effects on bryophyte species richness. However, habitat heterogeneity also strongly influences species diversity (Vitt et al. 1995). Increased wind throw due to gaps from harvesting maintains high bryophyte diversity (Jonsson and Esseen 1998, Baldwin and Bradfield 2005). Shields et al. (2007) concluded that forest openings result in shifts in community composition due to changes in microclimate and substrate availability. They suggest openings are valuable for the maintenance of disturbance - adapted bryophytes.

Table 1.1. Bryophyte functional grouping based on taxonomic group, reproductive strategies (life-history based on During 1992), canopy preferences, growth form and substrate affinity (from Table 1 in Baldwin and Bradfield 2005).

Category	Characteristics
Taxonomic group:	moss (M) or liverwort (LW)
Reproductive strategies (life-history):	
Colonists (Co)	spore size < 20 µm: high sporophyte production; life span of few years. Vegetative reproduction common; open short turfs and thalloid mat growth forms
Short-lived shuttles (Ss)	spore size > 20 µm: low sporophyte production; life span of few years; vegetative reproduction rare or absent; short turf or thalloid mat growth forms
Long-lived shuttles (Sl)	spore size > 20 µm: low sporophyte production; life span of many years; vegetative reproduction common; cushions, rough mat, smooth mat, or tuft growth form
Perennial stayers (Ps)	spore size < 20 µm: low sporophyte production; life span of many years. Vegetative reproduction common; weft, dendroid, mats, and large cushion growth forms
Canopy preference:	
Open canopy	shade intolerant
Closed canopy	shade tolerant
Canopy generalist	shade indifferent

Growth form:	
Turfs	erect main shoots
Open turfs (OT)	main shoot 0.1 – 1.0 cm high
Short turfs (ST)	main shoot 0.5 – 3.0 cm high
Tall turfs (TT) and sphagnoid (Tsp)	main shoot > 3.0 cm high
Cushions (CU)	erect main shoots from a central point
Mats	main shoot horizontal, descending, or ascending
Thalloid (TM) and smooth (SM)	main shoots 0.1 – 1.0 cm long
Thread (TH) and rough (RM)	main shoots 0.5 – 3.0 cm long
Wefts (WE) and dendroid (DE)	main shoots > 3.0 cm long
Substrate affinity:	
Substrate generalist	
Humus	
Litter	
Mineral soil/rock	
Logs	

Ross-Davis and Frego (2002) compared forest bryophyte communities found in naturally regenerating clear cuts with plantations. They found that the more disturbed sites (managed plantations) did not have the predicted increase in pioneer species (colonists) but had more perennial stayers such as *Pleurozium schreberi* (Brid.) Mitt. compared to natural regeneration. Their explanation for this apparent discrepancy was the more rapid spread by these perennial stayers which likely outcompeted the slower growing pioneer species – whoever get there first wins. The existence of competition among bryophytes has been suggested by During and van Tooren (1987) and Rydin (1997). However, Jonsson and Esseen (1998), using experimentally disturbed patches to mimic uprooting seen in boreal forests, found recolonization occurred rapidly over four years with forest-associated bryophytes such as perennial stayers (*Hylocomium splendens*, *Pleurozium schreberi* and *Barbilophozia lycopodiodes*) as well as disturbance-associated bryophytes such as colonists (*Pohlia nutans*, *Polytrichum juniperinum* and a few liverworts such as *Marchantia polymorpha*). They attributed this rapid response by both functional groups to the different regeneration methods: detached fragments, gemmae and spores in the mineral soil.

Fenton et al. (2003) compared bryophyte richness across several different disturbance regimes: an undisturbed riparian buffer (greater than 30 m), undisturbed forest, and two increasing disturbed cut areas (indirect – selective logging with minimal machinery and direct – clear-cut with all trees removed, machinery, slash plies, scarification and also herbicide). Using a before and after field technique, they found increased forest floor disturbance due to machinery (mechanical harvest) resulted in an initial reduction in bryophytes due to changes in microclimate and substrate availability. Within four years total bryophyte cover and richness recovered, yet species composition changed amongst the three guilds: liverworts and "forest habitat moss" (defined as those living on trunks, woody debris and humus) decreased while colonist species increased. Liverworts, the most sensitive guild to changes in moisture (Söderström 1988), were lost and will likely not recover (Ross-Davis and Frego 2002). Bryophyte diversity has also been shown to be affected by patches of disturbance (both logging and fire) at the landscape level (Pharo et al. 1999). Mature forest and harvested areas are often used as range/pasture for livestock (Sharrow 2007). Another form of disturbance, continuous grazing within forests can have either a negative effect (Humphrey and Patterson 2000, Virtanen et al. 2002) or a positive effect (Väre et al. 1995, Vare et al. 1996) on bryophyte diversity.

Microclimate changes across ecotones in forested ecosystems have been well studied for vascular plants (Chen et al. 1999, Whitman and Hagan 2000). An ecotone is an area or boundary across which there is a change in conditions, a phenomenon also known as edge effect (Murcia 1995). These ecotones can be natural such as a transition from riparian areas to uplands or artificial such as the ecotones between clear-cuts and remnant forest patches. Riparian forests have a natural ecotone break between the water and the land (Gregory et al. 1991, Hagan et al. 2006). With harvesting close to the stream, the microclimate in riparian buffers shifts from conditions similar to an interior forest to those more similar to a clear-cut. The most notable changes within the remaining forest edge are a decrease in relative humidity and an increase in air temperature at the stream (Brosofske et al. 1997). Other resulting microclimate changes can be both abiotic (pH, light) and biotic (species composition, diversity, competition, substrate type, seed dispersal) (Gehlhausen et al. 2000, Harper and Macdonald 2001). Much research has looked at these edge effects in forests from harvesting, especially in an increasingly fragmented landscape (Brosofske et al. 1997, Chen et al. 1999). The edge effect on species richness was more pronounced for bryophytes than conifers (Hylander et al. 2002, Fenton et al. 2003, Baldwin and Bradfield 2005, Stewart and Mallik 2006). The riparian buffer width over which the edge effects persist (depth of edge influence) can be greater than 74 m (Chen et al. 1999). In contrast, Hibbs and Bower (2001) found no edge effect when comparing riparian buffer strips of variable width adjacent to a clear-cut with an intact riparian forest; they point out their study did not sample sites with significant wind throw generated CWD which can be an important factor for long term stability.

Bryophyte response to edge effects can vary across spatial scales in both natural riparian ecotones and across artificial ecotones created by clear-cut harvesting (Hylander et al. 2002, Hylander and Dynesius 2006, Stewart and Mallik 2006, Dynesius and Hylander 2007). In coastal Oregon, distance from stream edge, size of the stream and the elevation affects bryophyte species composition at the site level (Jonsson 1997). Species richness was lower for sites of small streams with increasing lateral slopes and high canopy cover, whereas sites with increasing rock (gravel and boulders) had higher species richness; at the plot level, the amount of CWD was positively correlated with species richness. In conifer dominated boreal forests, Mills and Macdonald (2004) found that the most important predictor of bryophyte diversity was the substrate type at the micro site level (logs, stumps, tree bases, undisturbed or disturbed 1 m^2 forest floor patches) rather than the environmental variables at the stand (mesosite) level. The results of these studies indicate that spatial scale must be considered when managing riparian buffers. Most forest managers focus at the landscape and stand level and often do not consider the smaller scale where bryophytes exist (however see Huggard and Vyse 2002, BC Ministry of Forests and Range 2004 Practices Act). Multiple management scales are needed for conservation and resource management of the various taxa in a landscape (Lindenmayer et al. 2008).

Microclimate gradients have been detected from the stream edge up into the uplands of various forest types (Brosofske et al. 1997, Danehy and Kirpes 2000, Stewart and Mallik 2006, Brooks and Kyker-Snowman 2008). These microclimate gradients include soil moisture, pH and temperature, as well as, light, humidity and air temperature, and have been shown to influence bryophyte composition (Hylander and Dynesius 2006, Stewart and Mallik 2006). Jonsson (1997) also found significant changes in bryophyte species richness with distance from the stream. Microclimate gradients are influenced by the presence of a riparian buffer (Brosofske et al. 1997). However, more information is needed regarding the effect of differing riparian buffers (buffer widths, position relative to stream – one sided, two-sided) on the bryophyte compositional gradient from stream to uplands.

Recent riparian studies (Hylander et al. 2005, Hylander and Dynesius 2006, Dynesius and Hylander 2007) found there were fewer lost mature forest bryophyte species within a 10 m wide riparian buffer strip on each side of a small stream compared to clear-cut stream side forests. Both Haeussler et al. (1999) and Stewart and Mallik (2006) determined a 20 m buffer was sufficient for maintaining a microclimate suitable for bryophytes, especially at the fine spatial scale. Relative to clear-cut riparian areas, buffer strips may act as refugia for the maintenance of forest moss and liverwort species, though a 10 m buffer may not be adequate to mitigate edge effects (Dynesius and Hylander 2007). Other studies suggest standardized buffer widths or homogenous harvesting techniques but these may not maintain necessary habitat heterogeneity for bryophyte diversity (Rambo 2001, Hylander et al. 2005). The use of variable harvesting techniques with minimal disturbance and a range of buffer widths may be more appropriate (Hylander et al. 2002, Fenton and Frego 2005). However, a recent meta-analysis review (Rosenvald and Löhmus 2008) of green tree retention cutting (GTR) studies in both North America and Europe found that GTR maintained overall biodiversity across most taxa, especially lichens, fungi, birds and small mammals, but was less effective for bryophytes and vascular plants. Using small retention patches in high elevation forests, edge effects were seen on both plants and animals; bryophytes showed a negative edge effect at least 28 m into the intact forest particularly on the north side due to increased exposure and desiccation (Huggard and Vyse 2002). Overall, due to the complex dynamics between species and their environment, Lindenmayer et al. (2008) stressed the importance of using adaptive management strategies in order to improve our understanding of ecosystems and how they should be successfully managed. Adaptive management is an iterative decision making approach involving hypotheses testing and evaluation of uncertainty.

Previous studies of plant communities in fragmented habitats have identified, but do not agree on, several important abiotic and biotic factors which influence the resulting community dynamics (Pharo and Zartman 2007). Bryophyte community persistence and/or colonization within riparian buffers may depend on the “patch” size and degree of isolation from each other (MacArthur and Wilson 1967, Levins 1969, Hanski and Ovaskainen 2000). Fewer bryophyte species may occur in small and/ or more isolated patches due to more extinction and less immigration (biogeographic dynamics – *sensu* Saunders et al. 1991). Pharo et al. (2004) found, however, that substrate was a stronger predictor of bryophyte diversity rather than patch or fragment isolation or size; they also found that the shape of the patch was influential with strips (long and narrow canopy remnants) having more similar bryophyte composition to continuous forests than patches (rounder canopy remnants). Environmental effects, either directly due to physical disturbance or indirectly through altered microclimate, may also play a role in changing the bryophyte communities (Saunders et al. 1991). Previous research of vascular plant communities in fragmented riparian habitats has shown that abiotic and biotic factors influence plant communities at different spatial scales (Holl and Crone 2004).

Fenton and Frego (2005) looked at the role of remnant canopy patches on bryophyte persistence. They found microclimate changes were significantly different between these remnant canopies and clear-cuts (increased temperature, increased photosynthetically active radiation and decreased vapour pressure deficit (synonym for moisture). The remnant canopies contained different bryophyte species (liverwort and forest habitat types) than the clear-cuts (pioneer- colonist species) which the authors suggested was related to the environmental conditions (mean precipitation, mean and maximum temperature) and refugia characteristics (tree size, tree species, tree density, and overall patch size). Fenton and Frego (2005) propose patches may act as refugia for the original forest species and a potential source for recolonization when the harvested areas re-grow (Franklin et al. 1997, Fenton et al. 2003).

Baldwin and Bradfield (2005) also looked at forest patches and the maintenance of bryophyte diversity in fragmented landscapes in coastal B.C. They found a 45 m distance of edge influence in these patches. The bryophyte species composition changed from interior forest functional groups (liverwort, perennial stayers, closed canopy species) to species associated more with clear-cuts (colonists, open canopy species, open turf and tall turf growth forms and terricolous species). Though the actual species richness (number of different species) increased with proximity to the edge, the species themselves were functionally different with more pioneer type bryophytes such as *Ceratodon purpureus* (Hedw.) Brid. and *Polytrichum juniperinum* (Hedw.). This was attributed to the disturbance of substrates resulting in less CWD, more mineral soil and boulders, and decreased canopy cover. They concluded that a smaller patch (1.0 ha square) with an edge effect of 45 m will result in very little unaltered interior habitat; there is a size limit to these small patches below which they are unable to support the appropriate forest bryophyte diversity and thus will not act a refugia. Similar supporting results and conclusions were seen in 0.2 ha patches in coastal Washington (Nelson and Halpern 2005). This has implications for narrow (less than 10m) riparian buffers which also exhibit edge effect (Hylander and Dynesius 2006).

Dynesius and Hylander (2007), using paired riparian sample sites, inferred a reduction in liverworts and moss forest species would remain for 30- 50 years after clear cutting, especially on convex surfaces and woody substrates; the continuing success of these refugia, however, needs further long term study. The long term effect of disturbance on species richness (time influence) was found to be significant for sphagna and bog liverworts but not for true mosses and forest liverworts in boreal *Picea mariana* forests; true mosses and forest liverworts were mainly influenced by habitat variables (Fenton and Bergeron 2008). On the other hand, forest age (time since disturbance) and soil texture (fine-textured versus coarse textured) was found to be important for liverwort diversity and abundance in sub boreal spruce forests (Botting and Fredeen 2006). Overall these previous studies have identified several important abiotic and biotic factors (substrate characteristics, patch size and/or shape, environmental or microclimate variables such as temperature, radiation and moisture, canopy characteristics, amount and persistence of disturbance) which influence the resulting community dynamics of plant communities in fragmented habitats, although these factors are not consistent among the studies.

From a management perspective, not only is it important to know what factors are influencing bryophyte communities within riparian buffer strips, but it is also important to know if riparian buffer strips could affect community dynamics in adjacent harvested areas. Few studies, however, have looked at whether the presence of a riparian buffer has any mitigating effects on the shift in bryophyte composition in the clear-cut uplands themselves. Schmida and Wilson's (1985) "mass effects" suggests that forest bryophyte propagules from the nearby riparian buffers (remnant patches) might move from their normal core habitat out into the unfavourable areas (logged uplands) simply due to spill over. Retention patches including riparian buffer strips , depending on size and shape, may act as potential refugia ("lifeboats") for bryophytes and lichens in managed forests by allowing species to survive long enough to recolonize the harvested areas, although, sensitive liverworts may not survive the long regeneration time (Perhans et al. 2009). More studies are needed to understand the plant population dynamics occurring between retention patches (remnant canopies) and the recovering harvested areas (Pharo and Zartman 2007).

The current literature is contradictory on the main drivers of bryophyte community reassembly suggesting either dispersal limitations (Rambo 2001, Fenton et al.

2003, Sundberg 2005, Kimmerer 2005), propagules sources (Ross-Davis and Frego 2004), competition (Rydin 1997) or habitat heterogeneity (Fenton et al. 2003). However, testing the hypothesis of dispersal limitations, Hylander (2009) found that closer proximity to a propagule source (mature forest) did not result in a higher forest bryophyte colonization rate in nearby clear cuts; only a partial recovery (lower richness and frequency) was seen in the clear cut compared to mature forest unrelated to distance from edge. Suggested reasons for these inconclusive results included: a higher regional background level of spores may have masked the local spore source, *in situ* survival and subsequent reproduction in mesic depressions in the clear cut, or microsite limitations such as substrate availability and microclimate changes. For many bryophyte taxa, asexual reproduction by vegetative fragments (propagules) was more successful in maintaining populations rather than sown spores (During and van Tooren 1987). In a boreal spruce forest, Jonsson and Esseen (1990) proposed four causes of high bryophyte diversity in the disturbed forest floor patches caused by tree uprooting: 1) new space free of competitors, 2) higher habitat heterogeneity, 3) continued disturbance of patches by erosion, and 4) easier diaspore dispersal across small patch size. They found succession of both early and late bryophyte species occurred soon after the disturbance which implied that no facilitation by the earlier species was necessary (see however Økland 1994, Fenton and Bergeron 2006). Facilitation has been considered an important factor in community reassembly of most plants (Callaway 1995). Bryophytes seem to share similar community organization, other than evenness, with vascular plants (Steel et al. 2004). In a subalpine bryophyte study, Bradfield and Sadler (2006) introduced a concept called "transient assemblage dynamics" (TAD) to attempt to describe the relationship between the assembly of bryophyte communities and habitat heterogeneity at a fine spatial and temporal scale. They found a higher level of TAD in plots with increased disturbance (higher stochasticity) and less TAD in plots with more stability. Dynesius et al. (2008) found the retention of logging residues (CWD) in the center of clear-cuts resulted in better bryophyte survival due to microclimate buffering, although it had no effect near the forest edge. Little is known about community reassembly of bryophytes in harvested uplands with respect to the type of riparian buffers strips (Ross-Davis and Frego 2004).

Currently, little is known about riparian and upland bryophyte community response to buffer strips of differing widths and arrangement in the BC interior. The intent of my research is to fill this knowledge gap and provide forest managers with a variety of harvest options. The purpose of my research is twofold: to evaluate the potential environmental influences of buffer strips on bryophyte diversity first in riparian areas and second in the associated uplands around small streams in the B.C. Interior Montane Spruce forests. The second chapter of my thesis focuses on riparian areas and asks the following questions:

1. Within riparian areas, does species richness and abundance of different bryophyte functional groups vary with different canopy treatments (clear-cut, one-sided buffer strips, two-sided buffer strips and continuous forest and/ or buffer width)?
2. Within these differing canopy treatments, what are the environmental influences or physical effects, such as vegetation cover, grazing, coarse woody debris or substrate type, on bryophyte species richness and abundance across the various functional groups?
3. At the landscape level, what is the effect of increased fragmentation of the surrounding forested areas (biogeographic effect) on bryophyte species richness and frequency in the riparian area?

The third chapter of my thesis focuses on the adjacent uplands and asks the following questions:

1. Does the canopy treatment influence the natural gradient of bryophyte distribution from the stream edge up to the uplands?
2. At the site level, what effect does differing canopy treatments (including buffer strips) have on bryophyte community composition (species richness and abundance) in the uplands?

3. Does having a certain canopy treatment affect the resilience of bryophytes in the uplands (measured as changes in functional group representation and species composition)?

Lastly, the fourth chapter of my thesis is a summary of the overall findings and a synthesis indicating the applied significance to a broader environmental context.

Chapter Two

ASSESSING THE EFFICACY OF BUFFER STRIPS IN SUSTAINING BRYOPHYTE DIVERSITY AROUND SMALL MOUNTAIN STREAMS.

Introduction

Small mountain streams make up a large portion of a watershed and provide important ecosystem services such as water, nutrient cycling (N and P), sediment deposition, storage and transport of organic matter, and habitat for invertebrates, vertebrates such as fish, birds and amphibians, and terrestrial plants (Naiman and Decamps 1997, Hagg and Dickinson 2000, Meyer and Wallace 2001, Vesely and McComb 2002, Gomi et al. 2002, Moore and Richardson 2003, Cockle and Richardson 2003, Lees and Peres 2008). In particular, riparian areas contain high levels of bryophyte diversity and abundance (Schofield 1976, Hylander et al. 2005). Bryophytes are an important component of many forest ecosystems (Jonsson 1997, Baldwin and Bradfield 2005), accounting for a significant amount of overall species diversity and understory biomass, particularly around stream banks (Schofield 1976). They are also involved in nutrient cycling (Glime 2001, Turetsky 2003). Bryophytes, sensitive to changes in the environment due to their poikilohydric nature, are considered good indicators of overall riparian health (Naiman et al. 1993, Hylander et al. 2002, Frego 2007). Disturbance processes such as logging have been shown to drastically alter the bryophyte community particularly around streams (Ross-Davis and Frego 2002, Fenton and Frego 2005, Dynesius and Hylander 2007).

Forest canopy cover is an important aspect of the microhabitat affecting plant growth and survival within a forest (Jennings et al. 1999). The retention of strips of trees adjacent to a stream (hereafter referred to as a buffer) has been suggested as a valuable management practice to protect both instream biota and adjacent riparian communities (Swanson and Franklin 1992, Cockle and Richardson 2003). Yet small, non fish-bearing streams such as those found within high elevation forests are neglected under the current BC forestry practice codes (Forest and Range Practices Act - BC Ministry of Forests and

Range 2004). Furthermore, debate exists over the riparian buffer widths necessary to protect the environment and maintain floristic diversity (Castelle et al. 1994, Brosofske et al. 1997, Jonsson 1997, Lee et al. 2004, Hylander et al. 2005). In Sweden, buffer strips of 10 - 15 m (on each side of stream) have been found to mitigate the negative effects of clear cuts and preserve riparian bryophytes (liverworts and mosses) (Hylander 2004, Dynesius and Hylander 2007). Stewart and Mallik (2006) determined a 20 m buffer was sufficient for maintaining a microclimate suitable for bryophytes, especially at the fine spatial scale.

Increased fragmentation of forests due to harvesting practices can result in two main effects on local populations and communities: the "biogeographic" effects of fragmentation whereby populations are divided up into smaller groups (sensu Saunders et al. 1991, Baldwin and Bradfield 2007) and the environmental or "physical" effects of increasing fragmentation through disturbance. Increased stochastic extinctions and decreased recolonization (immigration) due to smaller isolated populations can result in decreased richness in smaller fragments (Levins 1969). The surrounding "mainland" of intact forest may also influence the "islands" of riparian buffers by acting as a source of diaspores, although this is likely distance dependent due to the known dispersal limitations of bryophytes (MacArthur and Wilson 1967, Tangney et al. 1990, Fenton et al. 2003, Holl and Crone 2004, Lindenmayer et al. 2008). Of course, the potential of intact forest to supply diaspores depends on the persistence of bryophytes within forest fragments. Undisturbed canopy may act as refugia especially for liverworts, the most sensitive group (Söderström 1988), and forest mosses (Fenton and Frego 2005), however there seem to be size limitations associated with these retention patches (Baldwin and Bradfield 2007, Perhans et al. 2009). The effects of disturbance itself can be "direct" through the physical destruction of bryophytes or changes in substrate availability caused by harvesting practices (Ross-Davis and Frego 2002, Fenton et al. 2003, Rydgren et al. 2004), or "indirect" through altered microclimate along the artificial anthropogenic ecotone or edge ("edge effect") (Hylander et al. 2002, Hylander and Dynesius 2006, Stewart and Mallik 2006, Dynesius and Hylander 2007). Edge effect is a change in environmental conditions due to proximity to a natural (Brosofske et al. 1997) or artificial boundary (Baldwin and Bradfield 2005). The width over which the edge effects persist can be substantial (greater than 74 m) in coniferous forests of western North America (Chen et al. 1999).

The direct mechanical disturbance of harvesting, altered microclimate (moisture and light), and reduction in appropriate substrate can potentially alter the suite of bryophytes around the stream edge up to the artificial ecotone. However, previous studies have shown that bryophyte responses to increasing forest canopy can be inconsistent, with both increases and decreases in overall bryophyte richness and abundance observed (Jonsson 1997, Fenton and Frego 2005, Hylander and Dynesius 2006). Although responses to disturbance may be species-specific, detailing the impacts on all species may be too time-consuming or costly (Gitay and Noble 1997, *sensu* Saunders et al. 1991). However, functional classification of plants has been increasingly used to understand ecosystem response to large scale environmental perturbations (Diaz and Cabido 1997). Bryophyte functional groups have been used previously to document the response of the bryophyte community to altered microclimate and increased disturbance from logging (Fenton et al. 2003, Baldwin and Bradfield 2005, 2007, though see Bates 1998). Based on the expected consequences of increasing fragmentation, it is possible to group riparian bryophytes into *a priori* bryophyte functional groups that can be expected to respond differently to decreasing levels of canopy cover and increase in substrate disturbance. The use of defined functional groups derived from current bryological literature and expert knowledge rather than using the response of species observed in our study avoids the possibility of a circular argument (Baldwin and Bradfield 2005, Pharo and Lindenmayer 2009). These functional groupings are based on taxonomy, life history strategies (During 1992), and canopy preference, substrate affinity and growth form (Baldwin and Bradfield 2005, 2007). Thus in my study, forest-associated bryophyte species include liverworts, perennial stayers (long life span, small spores, low sporophyte production and frequent vegetative reproduction), closed canopy species and epixylics (species preferring logs), whereas, disturbance-associated bryophytes include colonists (short life span, small spores, high sporophyte production and frequent vegetative reproduction), open canopy species, and species with an affinity for mineral soil/rock.

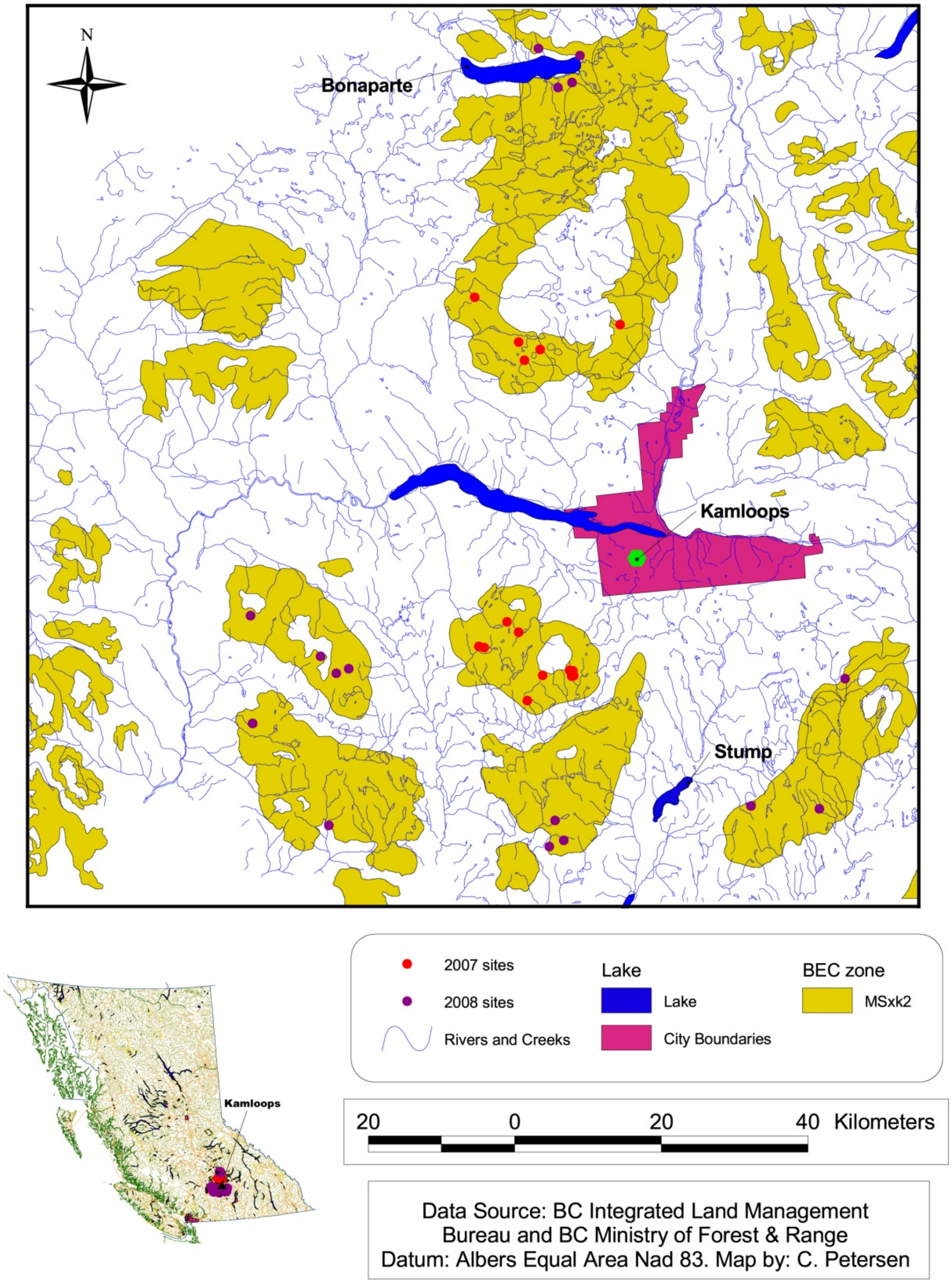
However, in addition to the effects of fragmentation, bryophyte diversity has been shown to be highly correlated with habitat characteristics, especially at the local scale. In particular, many bryophyte species are influenced by substrate availability of coarse woody debris in late decay stages (Rambo 2001, Åström et al. 2005, Hylander et al. 2005). These decaying logs act as "biological legacies" (Rambo and Muir 1998, Rambo 2001, Pharo and Lindenmayer 2009) by providing habitat and thus allowing the continued survival of forest bryophytes in the face of disturbance and landscape fragmentation (Pharo et al. 2004). The amount and type (decay class) of retained coarse woody debris varies with different silvicultural approaches (green tree retention, thinning, variable canopy retention) and may lead to a differential response by sensitive bryophytes such as liverworts (Haeussler et al. 1999, Åström et al. 2005, Fenton and Frego 2005, Nelson and Halpern 2005). The amount of deciduous trees has also been shown to be important for bryophyte survival (Gustafsson et al. 1992).

The primary purpose of my research was to examine the effectiveness of different riparian canopy treatments (continuous, one-sided buffer, two-sided buffer and clear-cut) and buffer width for maintaining the riparian bryophyte community around small mountain streams at the landscape level. Using a functional group approach, I expect forest-associated species (liverworts, perennial stayers, closed canopy species and epixylics (species preferring logs) to be maintained with increasing canopy cover and buffer width. As continuous forest, two-sided buffer, one-sided buffer, and clear-cut represent an increasing disturbance gradient, I would expect disturbance-associated bryophytes (colonists, open canopy species, and species with an affinity for mineral soil/rock) to increase with no canopy cover (clear-cut). A second objective was to determine which substrate, stand structure and habitat variable was the most influential in affecting the riparian bryophyte community at the local scale.

Methods

Study area

Study areas were located within the Montane Spruce BEC (Biogeoclimatic Ecosystem Classification) Zone (Meidinger and Pojar 1991) which occurs between 1100 – 1600 m in Interior British Columbia. The Montane Spruce climate is typified by cold winters with moderate snowfall, and short warm summers. The main conifer species present are lodgepole pine (*Pinus contorta*), hybrid white spruce (*Picea engelmannii x glauca*), and subalpine fir (*Abies lasiocarpa*). Common vascular plants include grouseberry (*Vaccinium scoparium*), birch-leaved spirea (*Spiraea betulifolia*), Utah honeysuckle (*Lonicera utahensis*), twinflower (*Linnaea borealis*) and one-sided wintergreen (*Orthilia secunda*). The study areas were located in the British Columbia Interior Plateau and included sites on the Bonaparte Plateau approximately 50 km northwest of Kamloops, Chuwels Mountains approximately 30 km southwest of Kamloops, and Greenstone Mountain approximately 70 km southwest of Kamloops (Figure 2.1). Additional sites were located west of Barrière north of Kamloops, between Logan Lake and Merritt south of Kamloops, and around Stump Lake also south of Kamloops.



Data Source: BC Integrated Land Management Bureau and BC Ministry of Forest & Range
Datum: Albers Equal Area Nad 83. Map by: C. Petersen

Figure 2.1. Map of study area of riparian sites sampled 2007 and 2008 (n=30).

Site Selection

From the study areas, 30 sampling sites were randomly selected using digital ortho-rectified aerial colour photographs and GIS coverage analysis to limit potential sites to those within the Montane Spruce subtype (MSxk2 - very dry cool)(Field Manual for Describing Terrestrial Ecosystems - BC Ministry of Environment Lands and Parks and BC Ministry of Forests- Research Branch 1998). Forest history maps were used to limit potential sites to those harvested within the past five to 25 years in order to limit the influence of stand age on the bryophyte response. Potential sites were also identified to minimize location bias and encompass riparian site heterogeneity (Table 2.1). Stream cover class was added to the maps to identify small streams. Ground-truthing of potential sites was done to limit the stream type to 1 – 2 m wide and free flowing in June with a distinct channel (S5 or S6 stream channel according to Forest Planning and Practices in Coastal Areas Streams – Technical Report (Forest Practices Board 1997)); wet meadows and fens (type of wetland) were not sampled due to inherent vegetation differences. A buffer was defined as the original conifer stands and not alder re-growth.

Final site selections were made to minimize environmental variation in aspect, elevation, BEC zone, stream class and incorporated various conifer buffer widths (0 - >30 m) including continuous (uncut) forest. In order to sample the full gradient and spatial arrangement of forest cover currently found within Montane Spruce forests, I examined four canopy treatments: clear-cut, one-sided buffer, two-sided buffer and continuous (Figure 2.2). Clear-cut treatment had no conifer trees on either side of the stream. In comparison, one-sided buffers had continuous forest on the non-sampled side and were either cut or had a buffer of trees remaining on the sampled side. Two-sided buffers had two strips of trees remaining around the stream after logging. Finally, as a comparison, I looked at continuous forests that were fully intact on both sides of the stream (no logging). Effort was made to generally restrict buffer strip sites to warm aspects (~165° – 285°) and to sample separate stream drainages with a minimum distance of 1km between sites.

Table 2.1. Location, canopy treatment and harvest date of all sites sampled in 2007 and 2008 (n=30).

Site	Location	Coordinates (UTM)	Canopy Treatment	Harvest Date
4	G-branch Watching	671529 5643806	2-sided	1996
7	Strachen Lake	669347 5642418	clear-cut	1990
12	Heller Creek	662911 5651304	2-sided	1995
34	Dominic Lake Spur 400	661375 5603767	1-sided	pre1990
36	Dominic Lake	662144 5603565	clear-cut	pre1990
39	Chuwels	673430 5600231	clear-cut	pre1990
40	Chuwels	674139 5599168	2-sided	pre1990
41	Chuwels	673634 5599924	clear-cut	pre1990
42	Chuwels	673884 5599120	continuous	none
60	Dominic Lake	665448 5606829	continuous	none
61	Grace Lake	666883 5605428	continuous	none
62	Haybrook	667702 5596073	1-sided	1997
63	Mabel Lake	669913 5599389	1-sided	1998
64	Tranquille	668651 5644932	1-sided	1999
70	Upper Jamieson	677489 5679950	1-sided	2001
71	Jamieson	675559 5679369	continuous	none
73	Chataway	639867 5580234	2-sided	2003
74	Helmer	670749 5579561	clear-cut	1992
75	Mabel Lake	671793 5576794	continuous	none
76	Mabel Lake	669821 5576054	2-sided	1995
77	Bose	643524 5601464	2-sided	1995
78	Bose	639749 5603319	continuous	none
79	Hook	630424 5609298	clear-cut	1990
80	Woods Creek	641786 5600928	2-sided	2002
81	Laura Lake	630063 5594581	2-sided	2002
83	Bonaparte Hills	673131 5684788	clear-cut	1995
84	Jamieson-Bonaparte	678699 5683536	2-sided	2003
85	Frisken	697547 5580368	1-sided	1997
86	Monroe	706870 5579590	1-sided	1999
87	Jewel	711193 5597128	2-sided	2004

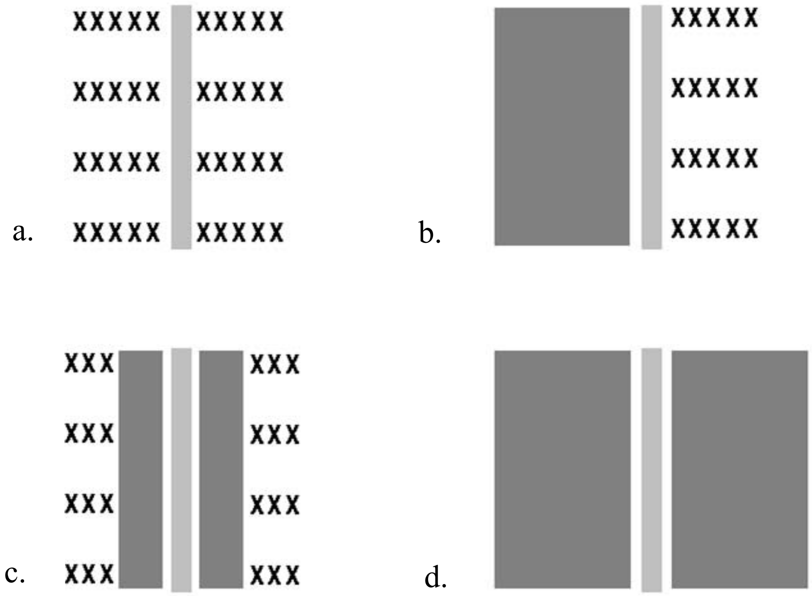


Figure 2.2. Four different canopy treatments (a. = clear-cut, b. = one-sided buffer, c. = two-sided buffer, and d. = continuous) showing the spatial arrangement of intact forest (■) and harvested area (**X**) relative to the stream position (░). Note: one-sided buffer may also have a narrow strip of trees on the right hand side of the steam (not shown).

Study Design and Analysis

To capture the peak phenology in the MS forest ecotype, vegetation sampling occurred during July and August during 2007 and 2008. The sampling protocol was based on a similar one used by Hibbs and Bower (2001). At each study site, three sample lines were placed 30 m apart and were located at least 25 m from the clear-cut edge. Each sample line started at the stream edge and extended 10 m upslope perpendicular to the stream edge. Environmental data, including GPS coordinates, aspect and slope of stream and sample line, elevation, stream and sample line bearing and buffer width, were recorded along each sample line. Along each sample line, bryophytes, shrubs, stand structure and microhabitat variables were sampled in three (10 x 2 m wide) belt transect lines placed perpendicular to each sample line at 1, 5, and 10 m from the stream edge (Figure 2.3).

Bryophyte species presence was sampled within 10 alternately placed microplots (0.1 x 0.3 m) along each belt transect (Figure 2.3) and the entire belt transect was checked for any additional species (McCune and Lesica 1992). In order to quantify habitat heterogeneity, substrate type, floor type and decay class of log (Maser et al. 1979, 1988) were noted for bryophyte microplots. In five shrub plots (2 x 2 m) both species and cover class were determined. Shrubs were classified as either short shrubs (≤1 m) or tall shrubs (> 1 m) using average height from the USDA plant data base and EFlora online database (Klinkenberg 2007, USDA 2009) similar to Dovčiak et al (2006). Percent cover of substrate (disturbed and undisturbed forest floor, mineral soil, coarse woody debris, damp ground, boulder and rocks) and cover type (bryophyte, tree, saplings and seedlings) were recorded at the belt transect level. Within the entire belt transect the species and cover class of conifers and deciduous trees were recorded. Cover classes used were: 0 = 0%, 1 = 0.1 – 1%, 2 = 1 – 5 %, 3 = 5 – 25%, 4 = 25 – 50%, 5 = 50 – 75%, and 6 = 75 – 100%. The diameter at breast height (DBH) and decay class were measured for conifers only. The diameter and decay class of coarse woody debris (CWD) were sampled along a 30 m x 30 m triangle (Van Wagner 1982) with one edge randomly set along each sample line, located at 1 m from stream edge (riparian). Decay classes follow the classification used by B.C. Ministry of Environment, Lands, and Parks, and the B.C. Ministry of Forests (Figure 2.4) (Maser et al. 1979, BC Ministry of Environment Lands and Parks and BC Ministry of Forests- Research Branch 1998). Soil bulk density samples were taken at 1m from stream edge for each sample line to determine effects of grazing on soil compaction. Soil bulk density was determined by measuring the mass of the dry soil per unit volume (g/cc) (GLOBE 2005).

Voucher samples of the bryophytes were collected and identification was confirmed based on Lawton (1971), Koponen (1974) and Godfrey (1977). Problematic species identification was confirmed by Dr. Lyn Baldwin, Michael Ryan and Dr. W. B. Schofield. Identification was limited to the genus level for some bryophytes due to a lack of reproductive characters necessary for identification to the species level (i.e. *Brachythecium* spp. and *Lophozia* spp.). Voucher specimens are stored in the author's herbarium and TRU herbarium. Bryophytes were sorted into functional groups based on taxonomic group, reproductive strategies (life-history), canopy preferences, growth form and substrate affinity (Table 2.2 adapted from Baldwin and Bradfield 2005 and Appendix A).

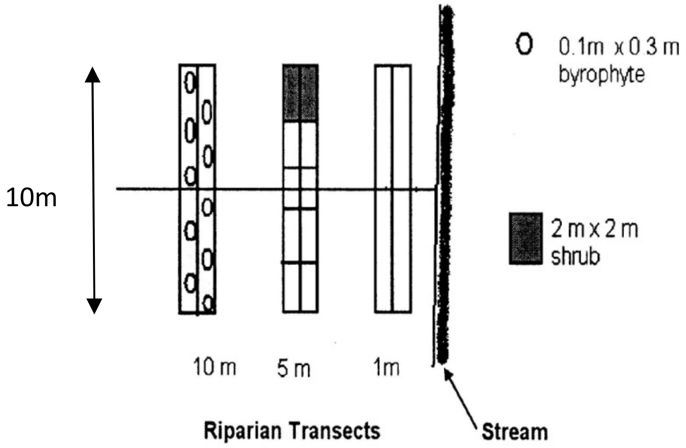


Figure 2.3 A typical sample line (one of three located at each site) showing three 10 m riparian transects with microplots for each vegetation type. For clarity the symbols are not overlaid or repeated in each belt transect (based on Hibbs and Bower 2001).

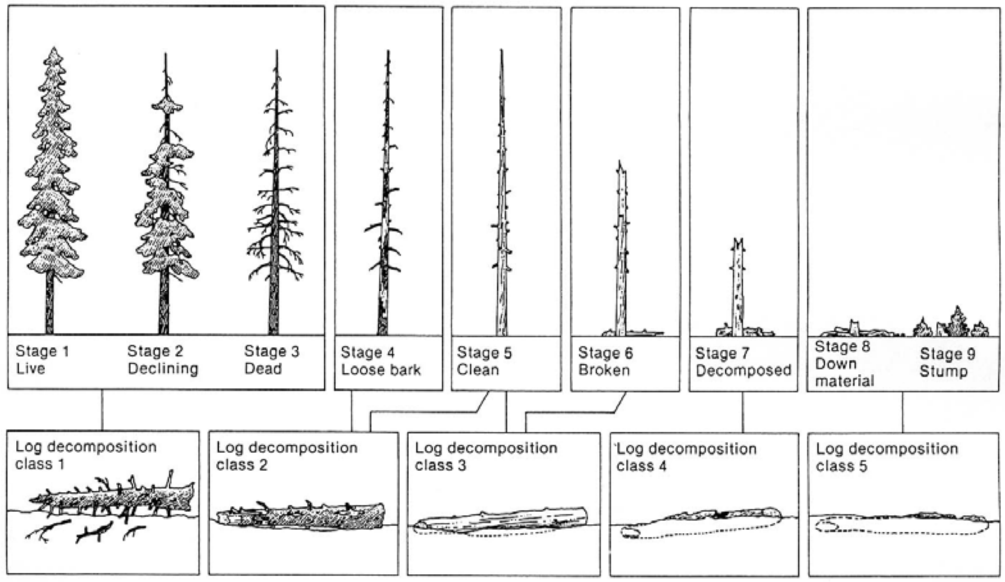


Figure 2.4. Coarse woody debris decay classification (Maser et al. 1979).

I also recorded evidence of disturbance in each site. Harvesting disturbance varied from zero harvesting impact up to 30 m from the stream to full harvesting with a 15 m 'no machine zone', to full machine harvesting directly over the stream channel. Other notable disturbances observed included cattle grazing and 'pugging' (hoof prints), invasive species, grass seeding, and upstream influences due to road building and erosion.

As aspect and slope of the stream bank sample line or the stream itself is highly variable due to its serpentine nature, an "aspect favourability index" (Beers et al. 1966) was calculated as: $A' = \cos(A_{max} - A) + 1.0$ where A' is the aspect favorability index , which varies from 0.0 to 2.00, A_{max} is the aspect with the highest favorability, set at 225° (Baldwin and Bradfield 2005), and A is the actual measured site aspect.

In order to quantify landscape structure and its potential influence on the bryophyte community, I used GIS analysis of the surrounding conifer cover and the riparian buffer sites (ArcView 3.2, ESRI, Redlands, CA). Concentric circles (50 m, 250 and 500 m radii) were added to digital ortho-rectified aerial photographs to calculate the total hectares of forest surrounding each of the 30 sites (Figure 2.5). The amount of forested area in each circle was termed “buffering capacity” and this index was examined as another variable in influencing bryophyte species richness and frequency.

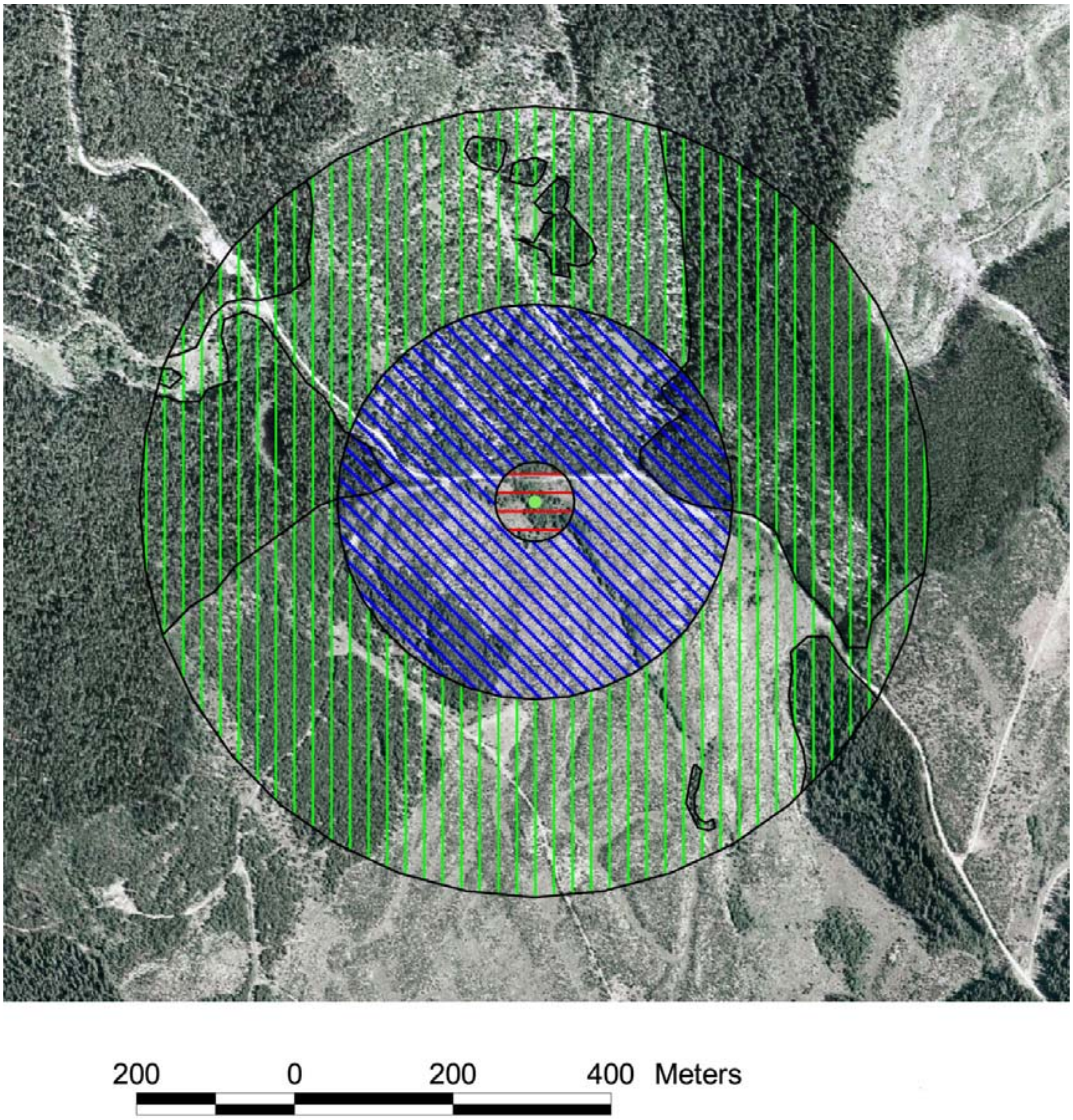


Figure 2.5. Concentric circles (50, 250 and 500 m radii) were used to calculate the amount of forested area in hectares surrounding each site which is termed “buffering capacity”.

Table 2.2. Bryophyte functional grouping with taxonomic group, reproductive strategies (life-history based on During 1992), canopy preferences, growth form and substrate affinity (based on Table 1 in Baldwin and Bradfield 2005).

Category	Characteristics
Taxonomic group:	moss (M) or liverwort (LW)
Reproductive strategies (life-history):	
Colonists (Co)	spore size < 20 µm: high sporophyte production; life span of few years. Vegetative reproduction common; open short turfs and thalloid mat growth forms
Short-lived shuttles (Ss)	spore size > 20 µm: low sporophyte production; life span of few years; vegetative reproduction rare or absent; short turf or thalloid mat growth forms
Long-lived shuttles (Sl)	spore size > 20 µm: low sporophyte production; life span of many years; vegetative reproduction common; cushions, rough mat, smooth mat, or tuft growth form
Perennial stayers (Ps)	spore size < 20 µm: low sporophyte production; life span of many years. Vegetative reproduction common; weft, dendroid, mats, and large cushion growth forms
Canopy preference:	
Open canopy	shade intolerant
Closed canopy	shade tolerant
Canopy generalist	shade indifferent
Growth form:	
Turfs	erect main shoots
Open turfs (OT)	main shoot 0.1 – 1.0 cm high
Short turfs (ST)	main shoot 0.5 – 3.0 cm high
Tall turfs (TT) and sphagnoid (Tsp)	main shoot > 3.0 cm high
Cushions (CU)	erect main shoots from a central point
Mats	main shoot horizontal, descending, or ascending
Thalloid (TM) and smooth (SM)	main shoots 0.1 – 1.0 cm long
Thread (TH) and rough (RM)	main shoots 0.5 – 3.0 cm long
Wefts (WE) and dendroid (DE)	main shoots > 3.0 cm long
Substrate affinity:	
Substrate generalist	
Humus	
Litter	
Mineral soil/rock	
Logs	

Data analysis

Associations between canopy treatments and riparian bryophyte diversity, richness and frequency of bryophyte functional groups, as well as with habitat, stand structure and substrate variables were examined using either one-way ANOVA or Kruskal-Wallis test and their respective post-hoc tests (pairwise t-test using holm correction factor or Wilcoxon rank sum). Habitat, stand structure or substrate variables were either recorded directly at site level or averaged to site level from the nine riparian belt transects. Both richness and frequency were amalgamated from microplot and transect level estimates to provide overall site-level estimates. Shannon-Weiner index (H′) was calculated as a measure of diversity and the Pielou's evenness index (J) was calculated to measure evenness (McCune and Grace 2002). To satisfy the assumptions of normality for ANOVA, some of the variables were log transformed; otherwise, the nonparametric Kruskal-Wallis test was used.

Nonmetric multidimensional scaling (NMS), a method of indirect ordination, was used to summarize patterns in riparian bryophyte species composition based on site level frequencies in relation to canopy treatments. NMS, a form of multivariate data reduction, is a widely accepted approach which essentially is a graphical representation of community structure (McCune and Grace 2002). Using PC-ORD version 4, the Sorensen (Bray-Curtis) distance measure and autopilot mode was selected to run the NMS (McCune and Medford 1999). Joint plots were used to show relationships between the ordination axes and riparian habitat, stand structure and substrate variables. However, due to the minimal association of the 250 and 500 m buffer capacity with the bryophyte community, these variables were not included in the joint plot. Multi-response permutation procedures (MRPP) were performed on the same NMS matrix and tested the null hypothesis that the riparian bryophyte communities were similar among the different canopy treatments.

Regression analysis was used to characterize the association between riparian species richness and frequency of bryophyte functional groups with the amount of forest within 50 m of the stream (50 m buffering capacity). Different generalized linear models

(GLMS) were used depending on the nature of the data and degree of dispersion: a Poisson or quasi-poisson error term and logarithmic link function for count data, or a quasi-binomial error term and logit link for non-count data (species frequency) (Quinn and Keough 2002). Dendroid growth form species richness required the use of a binomial GLM. In all models, 50 m buffering capacity was square root transformed to improve linearity of the relationship. The slope direction of the regression line was noted as a positive or negative association between species richness (or frequency) and 50 m buffering capacity.

Given the known influence of ecological factors working at different spatial scales, I used multiple regression analyses to determine the relative influence of landscape, stand structure, and microhabitat variables on the richness and abundance of bryophyte functional groups. For the multiple regression analyses, I established *a priori* hypotheses based on ecological factors (immigration and extinction, microclimate and habitat quality) previous research has identified as being influential in determining bryophyte richness and abundance in harvested or forested landscapes (Table 2.3). These hypotheses were then used to identify potential predictor variables (other than canopy treatment) to include in 12 candidate models that were evaluated through multiple regression. The predictor variables included in the candidate models included 50 m buffering capacity, *Alnus* species percent cover, slope, mineral soil/rock percent cover, volume of logs in decay class 4 and 5 and concavity. The percent cover of mineral soil/rock was standardized and log transformed (base *e*) to satisfy normality and linearity assumptions of the predictor variables. A GLM with a Poisson error term and logarithmic link function was used for count data (species richness). Due to difficulties with overdispersion for the riparian species frequency data, a GLM with a quasi-binomial error term and logit link was used along with a quasi-likelihood modification to AIC_c ($qAIC_c$) (Quinn and Keough 2002, Anderson and Burnham 2002, Burnham and Anderson 2004).

From a set of 12 candidate models, the top models were determined based on the information-theoretic approach using a selection criterion, Akaike information criterion

(AIC) (Anderson and Burnham 2002, Burnham and Anderson 2004, Canham and Uriarte 2006, Mazerolle 2006). Unlike using a null hypothesis and p values to judge statistical significance, AIC approach looks at the "strength of evidence" or likelihood that a model explains the pattern observed in the data. AIC also encourages parsimony and penalizes a model if there are too many parameters for the number of observations. The model with the lowest AIC value is considered the "best" from the set of models chosen. To correct for small-sample bias (sample size/number of parameters <40), the second order Akaike Information Criterion (AIC_c) is recommended and was used routinely for the subsequent analysis (Anderson and Burnham 2002, however see Richards 2005).

Table. 2.3. Select variables, ecological factors and candidate models for generalized linear models with riparian species richness and frequency of various functional groups. See text for more details.

Select Variables	**Ecological Factors**
50 m buffer capacity	Immigration & Extinction
Alnus spp. percent cover	Microclimate
Slope	Microclimate
Mineral soil/rock percent cover	Habitat quality
Decay class 4 & 5	Habitat quality
Concavity	Habitat quality
Candidate models	
Immigration & Extinction + Microclimate + Habitat quality	
Immigration & Extinction + Microclimate	
Immigration & Extinction + Habitat quality	
Microclimate + Habitat quality	
Immigration & Extinction	
Microclimate*	
Habitat quality*	

Note: *each select variable also run alone for microclimate and habitat quality hence 12 models were run.

Comparison of AIC values is only as good as the set of models chosen therefore the models must be first examined for goodness of fit. The fit of the global or most complex model with all the predictor variables is determined using an adjusted D^2 statistic which measures the drop in deviance and takes into account the number of observations and predictors in a model (Guisan and Zimmermann 2000). Adjusted D^2 ranges from 0 – 1 where 1 equals perfect fit. If the global model fit is fine then the fit of any simpler models is considered acceptable. The log-likelihood (logLik) of a given model also reflects the overall fit where larger values indicate better fit.

Several measures are employed to compare the top models: delta AIC (ΔAIC), Akaike weight (w) and the evidence ratio. Delta AIC is the difference between each model's AIC value and the model with the lowest AIC value. Models with a ΔAICc value of ≤ 2 are considered to have support and inference in explaining most of the variation seen in the data. The Akaike weight (w) is the probability of a model being the best model from a set of candidate models. For instance, a w of 0.75 means there is a 75% chance of a model being the best. Lastly, the evidence ratio compares the number of times the best model is more likely than another model (highest w/ w_i). More than one candidate model of a set may have a ΔAIC of ≤ 2, or equivalently, evidence ratios of < 2.7, and thus those are all equally possible. When using this approach it is important to not make conclusions based on only one model with the lowest AIC value and highest Akaike weight unless $w \geq 0.90$ (Burnham and Anderson 2002). In addition, as a result of several top models with different nested variables, more than one variable maybe involved in explaining the pattern seen in the data. Burnham and Anderson (2004) recommend assessing the relative importance of these top variables separately by summing their Akaike weights from all the models containing them (Σw). The predictor variable with the largest Σw is estimated to be the most important in explaining the variation in the response variable (Anderson and Burnham 2002).

Results

Comparisons among the canopy treatments

Riparian habitat characteristics, stand structure and substrate availability

In terms of riparian habitat characteristics, only buffer width and buffering capacity differed among sites (Table 2.4), indicating that the site selection protocol was effective in minimizing potential confounding differences in slope, aspect favourability, elevation, or soil bulk density. The range of buffer widths and buffer positions (one-sided and two-sided) encompassed local variation found within the Montane Spruce landscape in the study areas. The average buffer widths for one-sided and two-sided sites ranged from 9.79 m ± 5.22 (SE) to 15.54 m ± 1.84 (SE). Overall, one-sided and two-sided buffer sites did not have significantly different buffer widths, or 50 m and 250 m buffering capacity. In comparison, clear-cut sites had significantly lower 50 m and 250 m buffering capacity than other canopy treatments and continuous sites had significantly higher values of 50 m and 250 m buffering capacity than the other canopy treatments.

In terms of stand structure and substrate variables, the four canopy treatments displayed obvious differences related to the disturbance intensity of harvesting (Table 2.4). Not surprising, stand basal area, conifer percent cover, bryophyte percent cover, and undisturbed forest floor showed significantly increasing values with increasing canopy cover (i.e., lowest values found in clear-cuts, intermediate values in one- and two-sided buffers, and highest values in continuous forest, Table 2.4). CWD in decay classes 1 and 2 peaked in two-sided buffers and had significantly lower values in clear-cuts. Both the percent cover of disturbed forest floor and associated mineral soil substrate were highest in clear-cuts and lowest in continuous forests. However, concavity, pugging (hoof prints from ungulates), and damp ground percent cover were not significantly different among the four canopy treatments.

Table 2.4. Comparison of environmental variable means by canopy treatments in the riparian forest.

Canopy treatment:	**clear-cut (n=7)**	**one sided (n=7)**	**two sided (n=10)**	**continous (n=6)**	**X^2 (F^c)**	**p**
Habitat variables						
AFI [€]	1.58±0.23	0.98±0.35	1.27±0.22	0.96±0.30	1.05[c]	0.388
Buffer width (m)	0.00±0.00**a**	9.79±5.22**b**	15.54±1.84**b**	54.56±10.99**c**	22.00	**0.000**
Elevation (m)	1537.57±33.99	1407.00±72.41	1468.50±34.69	1508.33±54.92	1.23[c]	0.318
Stream aspect °*	213.00±37.68	191.57±46.73	315.90±175.45	157.50±50.01	0.31[c]	0.817
Site bearing°	212.58±24.77	131.28±35.64	206.29±27.68	181.95±41.47	1.31[c]	0.293
Buffering capacity (ha)¥						
50 m	0.003±0.003**a**	0.446±0.088**b**	0.378±0.068**b**	0.773±0.009**c**	21.64	**0.000**
250 m	4.082±1.291**a**	9.973±1.174**b**	9.315±1.201**b**	15.178±1.014**c**	17.35	**0.001**
500 m	37.325±6.097	51.095±5.189	55.153±2.298	56.514±2.529	5.36	0.147
SBD[b] (g/cc)*	0.61±0.18	0.75±0.32	0.61±0.13	0.48±0.15	0.05[c]	0.984
Slope %*	9.62±3.22	8.64±2.73	9.72±2.25	8.22±3.82	0.25[c]	0.864
Stand structure variables						
Stand basal area (m^2/ha)$	0.001±0.001**a**	0.007±0.003**b**	0.010±0.002**bc**	0.018±0.001**c**	11.45[c]	**0.000**
Volume of CWD[a] (m^3/ha)	51.26±14.08	62.37±10.11	67.17±8.29	44.13±10.23	0.97[c]	0.424
Decay class 1-2 logs	1.67±1.67**a**	20.36±9.53**b**	34.39±7.49**b**	12.48±4.67**b**	12.45	**0.006**
Decay class 3 logs	22.76±6.69	29.46±7.9	14.82±3.76	11.80±5.69	4.74	0.192
Decay class 4 logs	24.92±8.24	11.87±3.76	9.45±2.76	17.02±8.18	3.31	0.347
Decay class 5 logs	1.91±1.26	0.68±0.68	8.02±3.50	2.83±1.35	3.97	0.265

Table 2.4. Continued.

Percent cover						
Alnus spp#	14.03±8.71	8.33±4.68	16.42±4.25	2.98±1.53	1.96^{c}	0.145
Boulder/Rock	0.36±0.2	0.43±0.29	0.17±0.14	0.02±0.01	6.66	0.083
Bryophyte	7.05±1.47**cd**	12.06±1.44**ab**	10.31±1.3**ad**	15.25±0.83**b**	12.22	**0.007**
Conifer	0.18±0.14**c**	1.3±0.46**a**	2.55±0.55**ad**	3.73±0.84**bd**	15.10	**0.002**
Decidious*	3.23±1.84	2.42±1.29	4.02±0.89	0.86±0.25	5.96	0.113
Large shrub*	25.26±11.22	28.95±7.48	31.03±5.21	12.81±2.95	2.26^{c}	0.105
Sapling	2.09±0.38	1.18±0.26	2.07±0.69	1.3±0.34	2.02	0.569
Seedling	1.71±0.98	0.72±0.36	0.71±0.25	0.73±0.42	1.31	0.727
Shrub	40.65±10.56	47.34±7.22	50.93±6.73	37.84±7.44	0.57	0.640
Small shrub*	12.41±3.82	13.62±1.61	14.84±3.86	20.43±4.73	0.89^{c}	0.459
Stand basal area (m^{2}/ha)\$	0.001±0.001**d**	0.007±0.003**a**	0.010±0.002**ab**	0.018±0.001**b**	11.45^{c}	**0.000**
Substrate Variables						
Concavity	2.86±0.74	3.00±0.72	2.70±1.07	2.50±1.18	1.31	0.727
Percent cover						
Disturbed forest floor#	8.37±2.65**a**	4.00±1.16**b**	2.24±0.66**b**	1.51±0.87**b**	7.93	**0.047**
Mineral soil	1.00±0.45**a**	0.23±0.15**a**	0.09±0.04**a**	0.00±0.00**b**	11.56	**0.009**
Pugging	1.16±0.46	1.14±0.52	0.67±0.29	1.00±0.92	2.28	0.516
Undisturbed forest floor	7.38±2.43**a**	8.04±1.37**a**	12.55±1.15**b**	14.77±1.03**b**	11.01	**0.012**
Damp ground*	1.11±0.36	2.89±0.96	2.01±0.61	0.87±0.20	6.10	0.107

Table 2.4. Continued.

Note: Values for the riparian locations are means (± SE) averaged to the site level from the appropriate nine belt transects. Other values are recorded at the site level. [a] Coarse woody debris, [b] Soil bulk density, [c] Anova F statistic with associated P-value in column to right.

€ = AFI refers to "aspect favourablilty index" (Beers et al. 1996) using $A' = \cos(A_{max}-A) + 1.0$ where A' =AFI

¥ = no site 84 due to lack of available ortho photo (n = 9), $ = squareroot transformation

= standardization (+ 0.01 or 0.1) & $\log_e$ transformation, * = $\log_e$ transformation

Post hoc tests were either pairwise t-test (holm correction factor) for ANOVA or Wilcoxon for Kruskal-Wallis; means followed by the same letter are not significantly different. Values of $p < 0.05$ are bolded.

Riparian bryophyte community characteristics: species diversity, richness and frequency

In general, the richness and frequency of bryophyte functional groups found in clear-cut sites differed significantly from continuous forest sites (Tables 2.5 and 2.6). In comparison the richness and frequency of bryophyte functional groups in one-sided and two-sided buffers were intermediate between clear-cuts and continuous forest sites, and were significantly different from values found in clear-cuts but not significantly different from values observed in continuous forests. However, the response of individual bryophyte functional groups differed among the canopy treatments. The richness of forest-associated functional groups (liverworts, perennial stayers, closed canopy species, species with growth forms of either smooth mat or weft, species with an affinity for humus and epixylics) were not statistically different among sites with continuous forests and any type of buffer (one-sided and two-sided). Only when there was no buffer (clear-cut) did the forest-associated species richness exhibit a significant decline. Surprisingly, disturbance-associated bryophyte species richness (colonists, open canopy species, open turf species and mineral soil/rock associated species), as well as moss species richness, Shannon-Weiner's diversity index, and Pielou's evenness index, showed no statistically significant difference among the four canopy treatments.

The species richness of short- and long-lived shuttles showed mixed responses in sites with different canopy treatments. Only the richness of long lived shuttles in clear-cuts and continuous forests were significantly different when canopy treatments were compared, whereas the richness of short-lived shuttles showed no significant differences among canopy treatments (Table 2.5). The richness of canopy generalists was significantly lower in clear-cuts as compared to one-sided and continuous forests sites, but was not significantly different than the richness found in two-sided buffers. Other functional groups (rough mat, short turf/cushion, thread, thalloid and tall turf/sphagnoid growth forms, substrate generalists and species preferring litter/scat) showed no statistical difference in richness among the four canopy treatments.

While the frequency of bryophytes, specifically mosses, was not significantly different among the four canopy treatments, the frequency of liverworts was significantly higher in one-sided buffers and continuous forests compared to the other canopy treatments (Table 2.6). Overall, the frequency of forest-associated bryophytes (perennial stayers, closed canopy species, smooth mat or weft species, liverworts, species associated with logs or humus) showed no statistical difference among sites with any canopy. Only when there was no buffer (clear-cut) did the forest-associated species frequency exhibit a significant decline. Not surprisingly, disturbance-associated bryophytes (colonists and mineral soil/rock species) were most frequent in clear-cut sites. The frequency of colonists in one-sided buffer sites was statistically similar to clear-cuts, whereas the frequency of colonists in two-sided buffer sites was statistically similar to continuous forests. Thalloid species had a statistically similar frequency in the clear-cut sites as the continuous forest and were most frequent in one-sided buffers (thalloid growth forms include the disturbance-associated colonist *Marchantia polymorpha*). All other functional groups (open turf, rough mat, short turf/cushion, thread, and tall turf/sphagnoid growth forms, substrate generalists and species preferring litter/scat) showed no difference in frequency among the four canopy treatments (Table 2.6).

Table 2.5. Comparison of diversity indices and species richness of various functional groups by canopy treatments (clear-cut, one-sided buffer, two-sided buffer and continuous) in the riparian forest.

Canopy treatment:	**clear-cut (n=7)**	**1-sided buffer (n=7)**	**2 sided buffer (n=10)**	**continuous (n=6)**	χ^2 (F^c)	**p value**
Shannon diversity index	2.34±0.35	2.73±0.17	2.47±0.32	2.49±0.38	5.66	0.129
Pielou's Evenness index	0.72±0.07	0.75±0.04	0.69±0.05	0.69±0.06	5.36	0.147
Species richness						
Taxonomic groups						
Bryophyte	25.86±2.55**a**	37.86±2.09**b**	34.8±2.68**ab**	36.83±3.66**b**	9.92	**0.019**
Moss	21.29±1.92	27.57±1.27	26.4±1.98	25.5±1.98	5.15	0.161
Liverwort	4.57±1.02**a**	10.29±0.97**b**	8.4±1.31**b**	11.33±1.86**b**	10.81	**0.013**
Life-history strategy groups						
Perennial stayers	9.57±1.13**a**	15.43±1.09**b**	14.6±1.38**b**	16.83±1.38**b**	5.33^c	**0.005**
Colonists	7.00±0.44	7.43±0.57	6.20±1.00	5.33±1.17	2.81	0.422
Short-lived shuttles	5.29±0.89	6.86±0.51	6.80±0.44	5.67±0.84	1.47^c	0.245
Long-lived shuttles	4.00±0.95**a**	8.14±1.01**ab**	7.20±1.25**ab**	9.00±1.21**b**	3.16^c	**0.041**
Canopy Preference						
Closed	8.57±1.86**a**	19.43±1.78**b**	18.3±1.63**b**	19.83±1.70**b**	8.59^c	**0.000**
Generalist	5.86±0.94**a**	9.00±0.72**b**	7.70±0.54**ab**	8.83±0.87**b**	3.46^c	**0.031**
Open	10.00±0.44	9.43±0.61	8.80±1.46	8.17±1.74	0.36^c	0.786
Growth form groups						
Dendroid	0.14±0.14**a**	0.14±0.14**a**	0.40±0.16**ab**	0.83±0.17**b**	8.40	**0.038**
Open Turf	2.29±0.36	2.29±0.36	2.70±0.54	2.67±0.42	0.25^c	0.862
Rough mat	2.57±0.61	3.71±0.78	3.00±0.39	3.83±0.60	2.61	0.456
Smooth mat	1.86±0.67**a**	4.57±0.43**b**	4.20±0.65**b**	5.00±1.00**b**	3.73^c	**0.024**
Short Turf/Cushion	9.29±1.04	11.57±0.61	10.90±0.77	11.17±1.17	1.17^c	0.339

Table 2.5. continued.

Thread	1.71±0.42	3.14±0.46	3.10±0.50	2.67±0.71	1.55^{c}	0.224
Thalloid	0.57±0.30	1.57±0.30	1.00±0.26	1.17±0.48	4.44	0.218
Tall turf/Sphagnoid	5.57±0.37	8.00±0.53	6.70±0.60	6.50±0.85	2.55^{c}	0.077
Weft	1.86±0.46**a**	2.86±0.26**ab**	2.80±0.49**ab**	3.50±0.22**b**	8.25	**0.041**
Substrate-affinity groups						
Generalists	2.71±0.61	3.57±0.53	2.50±0.27	3.00±0.37	1.16^{c}	0.342
Humus	9.86±1.56**a**	17.00±0.82**b**	16.20±1.15**b**	17.00±1.39**b**	7.06^{c}	**0.001**
Litter/Scat	4.43±0.53	5.14±0.55	5.20±0.83	5.50±0.76	0.35^{c}	0.789
Log	2.86±0.70**a**	6.57±0.72**b**	6.50±0.82**b**	7.17±0.95**b**	5.40^{c}	**0.005**
Mineral soil/Rock	6.00±0.31	5.57±0.48	4.40±0.83	4.17±0.91	5.01	0.171

Note: Values at the site level averaged across all microplots in transects (± 1 SE). c ANOVA F statistic with associated P-value in column to right. Bolded values are p<0.05. Letters represent post hoc results for Wilcoxon Rank Sum (Kruskal-Wallis test) or pairwise t-test (holm correction factor) (ANOVA) where same letter = no significant difference.

Table 2.6. Comparison of species frequency of various functional groups by canopy treatments (clear-cut, one-sided buffer, two-sided buffer and continuous) in the riparian forest.

Canopy treatment:	**clear-cut (n=7)**	**1-sided buffer (n=7)**	**2 sided buffer (n=10)**	**continuous (n=6)**	**χ^2 (F^c)**	**p value**
Species frequency						
Taxonomic groups						
Bryophyte	61.71±5.55	71.14±3.08	65.90±2.70	77.00±2.62	2.95^c	0.051
Moss	61.57±5.49	70.43±3.08	65.60±2.66	76.67±2.70	2.88^c	0.055
Liverwort	6.71±2.43**a**	23.00±3.90**b**	8.90±1.80**a**	17.67±2.86**ab**	7.72^c	**0.001**
Life-history strategy groups						
Perennial stayers	45.14±5.9**a**	63.29±3.61**b**	60.70±3.58**b**	74.50±2.25**b**	7.53^c	**0.001**
Colonists	30.29±5.42**a**	21.14±5.71**ab**	9.30±1.91**b**	6.67±1.96**b**	13.25	**0.004**
Short-lived shuttles	14.71±4.25	19.43±2.83	18.60±3.30	16.17±2.94	0.38^c	0.767
Long-lived shuttles	9.86±3.40	19.43±4.37	10.80±2.03	15.00±3.68	3.72	0.293
Canopy Preference						
Closed	39.43±5.85**a**	61.86±4.16**b**	57.20±3.83**b**	71.33±3.66**b**	7.93^c	**0.001**
Generalist	15.86±2.54**a**	32.14±3.45**b**	23.70±2.6**ab**	26.50±6.79**ab**	3.02^c	**0.048**
Open	44.00±5.92	28.86±7.03	22.20±5.96	27.17±8.12	2.02^c	0.135
Growth form groups						
Dendroid	0.00±0.00	0.71±0.71	1.00±0.70	4.00±2.67	7.42	0.060
Open Turf	6.71±3.47	5.86±1.84	4.20±1.14	2.83±1.05	1.39	0.709
Rough mat	33.57±5.50	48.43±3.09	42.70±4.50	49.50±5.05	2.20^c	0.112
Smooth mat	2.14±0.88**a**	11.71±2.01**b**	7.80±1.02**b**	6.83±1.92**b**	14.79	**0.002**
Short Turf/Cushion	34.14±4.10	39.43±3.84	26.4±3.62	27.50±5.18	2.21^c	0.111
Thread	3.57±0.75	5.57±1.15	4.00±1.05	4.50±2.05	1.59	0.661

Table 2.6. continued.

Thalloid	1.14±0.99**a**	6.00±2.41**b**	0.60±0.27**a**	1.00±0.52**ab**	7.85	**0.049**
Tall turf/Sphagnoid	29.00±7.62	33.00±2.69	24.6±5.14	37.00±4.69	0.98^c	0.416
Weft	8.57±4.19**a**	23.86±7.73**b**	18.50±3.87**b**	33.83±8.06**b**	8.27	**0.041**
Substrate-affinity groups						
Generalists	8.29±4.10	20.86±8.55	16.90±4.38	30.67±9.14	5.91	0.116
Humus	42.71±5.48**a**	56.71±2.11**ab**	51.90±4.64**ab**	63.67±4.67**b**	3.28^c	**0.037**
Litter/Scat	10.43±1.66	17.86±3.19	15.10±1.89	12.00±2.44	1.91^c	0.153
Log	3.14±1.16**a**	12.00±2.23**b**	8.20±1.38**b**	12.17±3.47**b**	10.40	**0.015**
Mineral soil/Rock	35.43±4.33**a**	15.71±5.35**b**	6.90±1.68**b**	6.33±2.43**b**	15.44	**0.001**

Note: Values are means at the site level averaged across all microplots in riparian transects (± 1 SE). ^{c} ANOVA F statistic with associated P-value in column to right. Bolded values are $p<0.05$. Letters represent post hoc results either Wilcoxon Rank Sum for Kruskal-Wallis test or pairwise t-test (holm correction factor) for ANOVA . Same letter = no significant difference.

NMS ordination of riparian bryophyte species composition revealed that while bryophyte composition in the clear-cut and continuous forests represent ends of a gradient, the one-sided and two-sided buffers occupied intermediate positions between clear-cut and continuous forests (Figure 2.6). Joint plots of environmental variables overlaid on the ordination identified that mineral soil/rock percent cover, disturbed forest floor percent cover and elevation were strongly correlated with bryophyte composition found in clear-cut, one-sided and two-sided buffers (Figure 2.6). Canopy cover variables (50 m buffer capacity, stand basal area, buffer width, tree and undisturbed forest floor percent cover), bryophyte percent cover, and slope were associated with bryophyte composition found in continuous and some one-sided and two-sided buffer sites. The effect of canopy type on bryophyte composition illustrated through the NMS ordination was corroborated by the MRPP results which identified significant differences in riparian bryophyte species composition between continuous sites and clear-cut sites and no significant difference in riparian bryophyte species composition between the continuous forest sites and sites with either one-sided or two-sided buffers (Table 2.7).

Table 2.7 Comparison of bryophyte species composition between canopy treatments in riparian areas using MRPP.

	Riparian	
Group comparisons of canopy treatments	A	p value
continuous (6)/ clearcut (7)	0.085	**0.0012**
continuous (4)/ one-sided buffer (7)	0.004	0.3293
continuous (6)/two-sided buffer (10)	-0.002	0.4562
clearcut (7)/ one-sided buffer (7)	0.049	**0.0407**
clearcut (7)/ two-sided buffer (10)	0.047	**0.0032**
one-sided buffer (7)/ two-sided buffer (10)	-0.007	0.5888

Note: number in parentheses indicates the number of sites in each group, A = Chance-corrected within-group agreement. P values <0.05 are listed in bold.

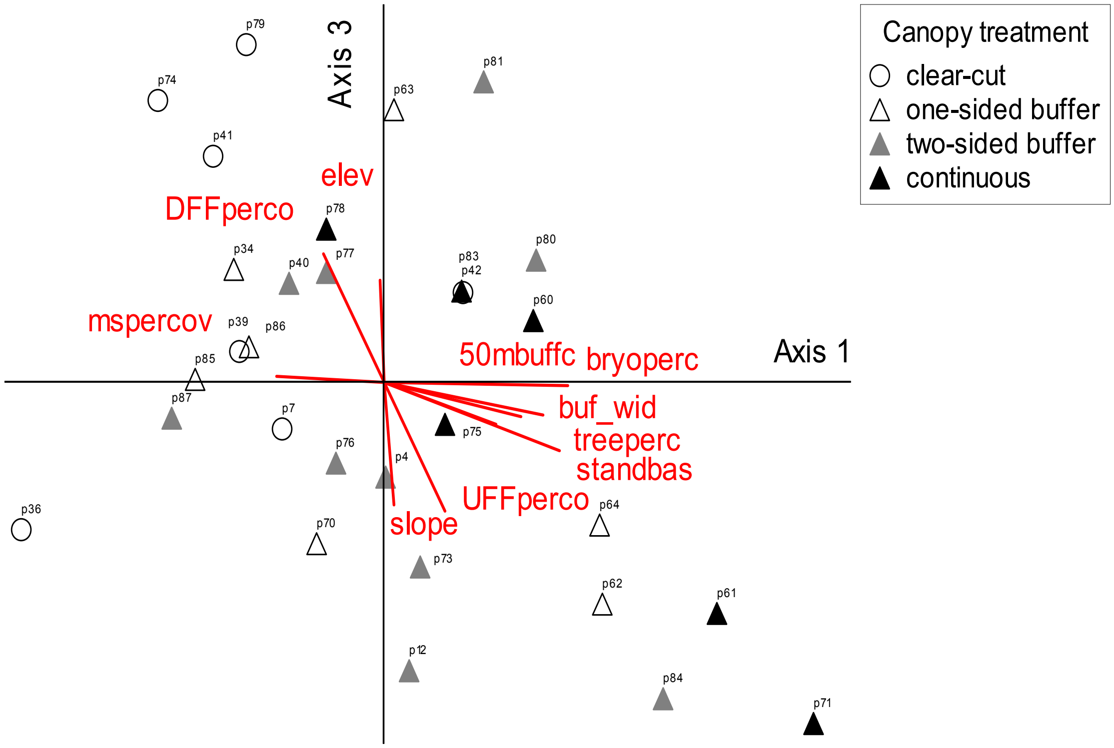


Figure 2.6. Joint plot of NMS ordination of bryophyte species composition in different canopy treatments: clear-cut (open circles) one-sided (open triangles), two-sided (grey triangles) and continuous (black triangles) overlain with stand structure, habitat and substrate variables with R^2 values of 0.20 in the riparian forests based on species frequency data (95 species). Axis 1 accounts of 51.0% of the variation in the data while the third axis accounts for 25.4% (total=76.4%). Ordination is based on a three dimensional solution, 62 iterations with a final stress of 11.42664 and final instability of 0.00010. The strength of the correlation is represented by the length of correlation vectors. standbas = stand basal area; UFFperco = percent cover of undisturbed forest floor; buf_wid = buffer width; 50mbuffc = 50m buffer capacity; treeperc = tree percent cover; bryoperc = bryophyte percent cover; elev = elevation; slope = slope; mspercov = mineral soil percent cover; DFFpercov = disturbed forest floor percent cover.

Site level modelling of various predictor variables and bryophyte species richness and frequency in the riparian forests.

When the amount of forest cover within a 50 m radius of each site was used as a predictor variable in simple linear regression models, the richness of most forest-associated functional groups (liverworts, perennial stayers, closed canopy species, dendroids, wefts, species preferring humus, and epixylics) was significantly positively associated with increasing 50 m buffer capacity (Table 2.8). Other functional groups' species richness such as bryophytes, moss, long-lived shuttles and tall turfs also exhibited positive associations with increasing 50 m buffer capacity. No disturbance-associated bryophyte (colonist, open canopy species, and mineral soil/rock species) richness exhibited a significant association (positive or negative) with 50 m buffer capacity.

Overall, while the frequency of bryophyte functional groups exhibited fewer significant associations, some disturbance-associated bryophytes (colonist and mineral soil/rock species) did show a negative relationship with 50 m buffer capacity. Forest-associated functional group frequency (liverworts, perennial stayers, closed canopy species, wefts, and epixylics) and substrate generalist's frequency were significantly positively associated with increasing 50 m buffer capacity.

Table 2.8. Regression analysis summary relating riparian species richness and frequency of bryophyte functional groups to 50 m buffer capacity.

Functional Groups	**Species Richness**			**Species Frequency**		
Taxonomic	**slope**	**z value**	**p value**	**slope**	**t value**	**p value**
Bryophytes (57)	+	4.29	**0.000**	+	1.796	0.083
Mosses (43)	+	2.523	**0.012**	+	1.752	0.091
Liverworts (14)	+	4.168	**0.000**	+	2.642	**0.013**
Life-history strategy						
Colonists (12)	-	-1.046	0.296	-	-3.972	**0.000**
Perennial stayers (25)	+	4.204	**0.000**	+	3.468	**0.002**
Long-lived shuttles (12)	+	3.366	**0.001**	+	1.56	0.130
Short-lived shuttles (8)	+	1.127	0.260	-	-0.121	0.904
Canopy preference						
Closed (24)	+	5.643	**0.000**	+	3.399	**0.002**
Generalist (12)	+	2.205	**0.028**	+	1.913	0.066
Open (21)	-	-0.519	0.604	-	-1.8	0.083
Growth form						
Dendroid (1)	+	2.197	**0.028**	+	1.774	0.087
Open turf (3)	+	0.554	0.580	-	-1.237	0.226
Rough mat (7)	+	1.613	0.107	+	1.239	0.226
Smooth mat (6)	+	3.389	**0.001**	+	2.434	**0.022**
Short turf/Cushion (19)	+	1.171	0.242	-	-1.124	0.270
Thread mat (4)	+	1.184	0.236	+	0.464	0.646
Thallose Mat (1)	+	0.877	0.380	+	0.255	0.800
Tall turf (12)	+	2.184	**0.038**	+	0.677	0.504
Weft (4)	+	3.093	**0.004**	+	3.375	**0.002**
Substrate affinity						
Generalists (6)	+	0.623	0.533	+	2.657	**0.013**
Humus (20)	+	3.89	**0.000**	+	1.886	0.070
Litter/Scat (7)	+	1.559	0.119	+	1.082	0.289
Log (11)	+	3.302	**0.001**	+	2.974	**0.006**
Mineral soil/Rock (12)	-	-1.236	0.216	-	-5.587	**0.000**

Note: Regression models depended on data type: Poisson log-linear model for all species richness (except binomial model for dendroid bryophytes, quasi-poisson models for Tall turf & Weft due to underdispersion); quasi-binomial log-linear model for all species frequency due to overdispersion. In all models 50 m buffering capacity was square root transformed. p values < 0.05 are bolded. Number of total species in each functional group provided in parentheses immediately following each group name. The slope of regression is noted as positive (+) or negative (-).

Most influential predictor variables affecting the riparian bryophyte community

Many of the candidate regression models were considered top models for explaining the variation seen in the species richness data of various functional groups (Appendix B). The top regression models had reasonable fit (global D^2 adj. >0.10); a ΔAICc ≤ 2 and high Akaike weights (*w*) indicating the probability that they were the best from the set of candidate models (Anderson and Burnham 2002). However, it is important to note that the richness of several functional groups (colonists, open and general canopy species, and species with an affinity for general substrates or mineral soil/rock) and the frequency of other functional groups (liverworts, perennial stayers, short-lived shuttles, general canopy species, and species with an affinity for litter substrates) had invalid models due to poor fit (Appendix C).

Based on summed Akaike weights (Σw), the richness of bryophyte functional groups largely conformed to initial expectations that forest-associated functional groups would show the greatest association with the 50 m buffer capacity (Table 2.9). The 50 m buffer capacity had a strong positive association with species richness of forest-associated groups such as liverworts, mosses, perennial stayers, closed canopy species and species preferring a humus substrate as well as with overall richness of bryophytes and general canopy species (Σw ranging from 0.79 – 0.94). Furthermore, the association of the 50 m buffer capacity with the richness of long-lived shuttles, short-lived shuttles, and species preferring litter or log substrates was only moderately positive (Σw ranging from 0.32 – 0.54). In comparison, the association of the 50 m buffer capacity and the frequency of bryophyte functional groups exhibited surprising results (Table 2.10). Not only did the 50 m buffer capacity have a strong positive association with the frequency of disturbance-associated groups (colonists, open canopy species (Σw ranging from 0.61 – 1.00)), the association with 50 m buffering capacity was paradoxically moderately to strongly negative on the frequency of forest-associated closed canopy species, as well as long-lived shuttles and substrate generalists (Σw ranging from 0.39 – 0.77).

Based on the summed Akaike weights (Σw), the richness of bryophyte functional groups did not conform to initial expectations that disturbance-associated functional groups would show the greatest association with microclimate variables, *Alnus* species percent cover and slope (Table 2.9). *Alnus* species percent cover had a moderate positive association with the richness of bryophytes, mosses, short-lived shuttles, and species preferring humus, litter or log (Σ*w* ranging from 0.27 – 0.56) but no association with any disturbance-associated functional groups. Slope had a moderate positive association with the richness of bryophytes and species preferring litter (Σ*w*= 0.31 – 0.33), whereas it had a moderate but negative association with mosses, short-lived shuttles, and forest-associated species preferring humus, and logs (Σ*w* ranging from 0.27 – 0.54). On the other hand, the frequencies of bryophyte functional groups did conform to expectations that disturbance-associated bryophytes would be strongly associated with *Alnus* species percent cover and slope (Table 2.10). *Alnus* species percent cover and slope had similar associations with species frequency depending on the functional groups. *Alnus* species percent cover had a strong positive association with the frequency of disturbance-associated functional groups: colonists, open canopy species, and species preferring general or mineral soil/rock substrates (Σ*w* ranging from 0.76 – 1.00), whereas it had moderately negatively association with the frequency of long-lived shuttles (Σ*w* = 0.42). Slope also had a strong positive association with the frequency of disturbance-associated bryophytes: colonists, open canopy species and species preferring mineral soil/rock (Σ*w* = 0.98 – 1.00), whereas it had a moderate but negative association with long-lived shuttles and substrate generalists (Σ*w* = 0.61 – 0.78).

Reflecting habitat quality, mineral soil/rock percent cover, DC 4/5 (soft CWD) and concavity had varying associations with the richness of different functional groups. Based on summed Akaike weights (Σ*w*), the richness of bryophyte functional groups did conform to initial expectations that forest-associated functional groups would show the greatest negative association with mineral soil/rock percent cover and greatest positive association with concavity, but did not conform to initial expectations that forest-associated functional groups would show the greatest positive association with DC 4/5 (Table 2.9). Mineral soil/rock percent cover had a strong to moderate negative association with species richness of bryophytes, long-lived shuttles, as well as forest-associated functional groups: liverworts, closed canopy species, and species preferring logs or humus (Σ*w* ranging from 0.34 – 1.00). On the other hand, mineral soil/rock percent cover had a moderate positive association with moss species richness (Σ*w* = 0.36). Surprisingly, DC 4/5 had a moderate to strong negative association with species richness of bryophytes, mosses, long-lived shuttles, as well as forest-associated functional groups: liverworts, closed canopy species, and species preferring humus or logs (Σ*w* = 0.25 – 0.99). Lastly, concavity had a moderately to strongly positive association with species richness of bryophytes, mosses, long-lived shuttles, as well as forest-associated functional groups: liverworts, closed canopy species, and species preferring humus or logs (Σ*w* = 0.26 – 0.99).

In comparison, the association of the mineral rock/soil and the frequency of bryophyte functional groups exhibited surprising results (Table 2.10). Mineral soil/rock percent cover had a moderately to strongly positive association with the frequency of bryophytes, mosses, and disturbance-associated colonists but also forest-associated closed canopy species, and species preferring humus or logs (Σ*w* ranging from 0.50 – 0.90), and a paradoxically strong negative association with the frequency of disturbance-associated functional groups: open canopy species and species preferring mineral soil/rock (Σ*w* = 087 – 0.92). DC 4/5 had a moderately positive association with the frequency of bryophytes and species preferring logs but also a paradoxically moderately positive association with the frequency of colonists (Σ*w* = 0.26 – 0.50). However, DC4/5 did have a strong negative association with the frequency of other disturbance-associated functional groups: open canopy species and species with an affinity for mineral soil/rocks (Σ*w* = 0.89 – 0.92). Lastly the association of concavity was moderately to strongly negative with the frequency of bryophytes and species preferring logs, and disturbance-associated functional groups: colonists, open canopy species, and species preferring mineral soil/rock (Σ*w* = 0.26 – 0.92).

By averaging the summed Akaike weights of each top predictor variable for the six groups considered to be forest-associated bryophytes (liverwort, moss, perennial stayer, closed canopy, and species preferring humus or log) for both species richness and frequency one can get a sense of their relative importance (Table 2.11). Guided by ecological processes, several factors explaining forest-associated bryophyte composition in riparian areas are listed in decreasing importance: immigration and extinction (approx. 73% for species richness and approx.16% for species frequency), habitat quality (approx. 54% for species richness and approx. 45% for species frequency), and microclimate (approx. 21% for species richness but zero for species frequency).

Table 2.9. Relative importance of top predictor variables using summed Akaike weights (Σω) and coefficient sign on riparian bryophyte species richness.

	Taxonomic						**Life History Strategy**					
	Bryophyte		**Liverwort**		**Moss**		**Perennial stayer**		**Long-lived shuttle**		**Short-lived shuttle**	
Variable	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**
50 buffer capacity (ha)	pos	0.94	pos	0.44	pos	0.86	pos	0.92	pos	0.39	pos	0.32
Alnus spp.cover (%)	pos	0.33			pos	0.56					pos	0.56
slope	pos	0.33			neg	0.54					neg	0.35
mineral soil/rock cover (%)	neg	0.92	neg	0.98	pos	0.36			neg	0.85		
DC4/5	neg	0.92	neg	0.92	neg	0.36			neg	0.76		
concavity	pos	0.92	pos	0.92	pos	0.36			pos	0.76		

	Canopy Preference						**Substrate affinity**			
	General		**Closed**		**Humus**		**Litter**		**Log**	
Variable	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**
50 buffer capacity (ha)	pos	0.92	pos	0.79	pos	0.84	pos	0.54	pos	0.54
Alnus spp.cover (%)					pos	0.27	pos	0.40	pos	0.41
slope					neg	0.27	pos	0.31	neg	0.41
mineral soil/rock			neg	1.00	neg	0.34			neg	0.62
DC4/5			neg	0.99	neg	0.25			neg	0.62
concavity			pos	0.99	pos	0.26			pos	0.62

Note: Coefficient sign (positive or negative) and summed Akaike weights (Σω) are listed for all variables retained in the best models; blank cells indicate excluded variables due to poor fit of the models. Results for Colonists, Open Canopy, Substrate Generalists & Mineral soil/rock groups were all invalid and not shown.

Table 2.10. Relative importance of top predictor variables using summed Akaike weights (Σω) and coefficient sign on riparian bryophyte species frequency.

	Taxonomic				**Life History Strategy**			
	Bryophyte		**Moss**		**Colonist**		**Long-lived shuttle**	
Variable	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**
50 buffer capacity (ha)					pos	1.00	neg	0.47
Alnus spp.cover (%)					pos	1.00	neg	0.42
slope					pos	1.00	neg	0.61
mineral soil/rock cover (%)	pos	0.90	pos	0.89	pos	0.50		
DC4/5	pos	0.26			pos	0.50		
concavity	neg	0.26			neg	0.50		

	Canopy Preference				**Substrate affinity**							
	Open		**Closed**		**General**		**Humus**		**Log**		**Mineral soil/rock**	
Variable	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**	**coefficient sign**	**Σω**
50 buffer capacity (ha)	pos	0.61	neg	0.39	neg	0.77			neg	0.59	pos	1.00
Alnus spp.cover (%)	pos	1.00			pos	0.76					pos	0.98
slope	pos	1.00			neg	0.78					pos	0.98
mineral soil/rock cover (%)	neg	0.92	pos	0.67			pos	0.77	pos	0.57	neg	0.87
DC4/5	neg	0.92							pos	0.30	neg	0.89
concavity	neg	0.92							neg	0.28	neg	0.89

Note: Coefficient sign **(**positive or negative**)** and summed Akaike weights (Σω) are listed for all variables retained in the best models; blank cells indicate excluded variables (poor fit). Results for Liverwort, Perennial stayer, Short-lived shuttle, Canopy Generalist and Litter groups were invalid and not shown.

Table 2.11. Averaged summed Akaike weights of top predictor variables for species richness and frequency of old growth-associated bryophyte functional groups.

	Predictor variables					
Functional group	Immigration & Extinction		Habitat quality		Micro-climate	
	SR Σw	SF Σw	SR Σw	SF Σw	SR Σw	SF Σw
Liverwort	0.44	NA	0.95	NA	0	NA
Moss	0.86	0	0.36	0.89	0.55	0
Perennial stayer	0.92	NA	0	NA	0	NA
Closed canopy	0.79	0.39	1.00	0.67	0	0
Humus	0.84	0	0.30	0.77	0.27	0
Log	0.54	0.59	0.62	0.38	0.41	0
average	0.73	0.16	0.54	0.45	0.21	0
Note: SR= species richness, SF= species frequency, Σw = summed Akaike weights.						

Table 2.12. Averaged summed Akaike weights of top predictor variables for species richness and frequency of disturbance-associated bryophyte functional groups.

	Predictor variables						
Functional group	Immigration & Extinction		Habitat quality		Micro-climate		
	SR Σw	SF Σw	SR Σw	SF Σw	SR Σw	SF Σw	
Colonists	NA	1.00	NA	0.50	NA	1.00	
Open canopy	NA	0.61	NA	0.92	NA	1.00	
Mineral soil/rock	NA	1.00	NA	0.88	NA	0.98	
average	NA	1.00	NA	0.77	NA	0.99	
Note: SR= species richness, SF= species frequency, Σw = summed Akaike							
weights, NA= model not valid due to poor fit.							

Discussion

The relative influence of ecological processes operating at different spatial scales has been an important question in efforts to effectively manage fragmented habitats (Holl and Crone 2004, Pharo et al. 2004, Pharo and Zartman 2007). While the use of buffer strips may provide an operational tool to mitigate the immediate effects associated with harvesting (Brosofske et al. 1997, Dynesius and Hylander 2007), long-term maintenance of plant diversity within riparian areas will require understanding the relative influence of ecological processes on the plant community. The results of this study clearly demonstrate that riparian buffers had a significant influence on the understory bryophyte community adjacent to small streams in the B.C. Interior Montane Spruce forest. However, the results of this study have provided evidence that landscape-level variables such as the 50 m buffer capacity demonstrate stronger association with the maintenance of forest-associated species than smaller-scale microhabitat variables such mineral soil percent cover or concavity.

The influence of canopy treatments on bryophyte functional group representation

One of the most important results of this study was that, in general, riparian sites with any canopy cover (one-sided, two-sided and continuous), supported both higher richness and abundance of forest-associated bryophytes. Use of a plant functional group approach demonstrated that both the richness and abundance of forest-associated groups was similar among sites with any canopy as compared to the richness and abundance of forest-associated bryophyte in clear-cuts. In comparison, the frequency, but not the richness, of disturbance-associated groups (mineral soil/rock species and to some extent, colonists) was significantly higher in clear-cuts than in sites with canopy cover. The sensitivity of forest-associated bryophyte to anthropogenic disturbances caused by clear-cut harvesting, edge effects and declining patch size has been clearly demonstrated (Fenton et al. 2003, Baldwin and Bradfield 2005, 2007). In particular, previous work has documented declines in both liverwort richness and abundance in clear-cuts (Söderström

1988, Ross-Davis and Frego 2002, Fenton et al. 2003, Fenton and Frego 2005, Dovčiak et al. 2006), second-growth stands and variable retention harvests (Botting and Fredeen 2006, Dovčiak et al. 2006).

In contrast to the clear-cut: continuous forest comparison, I found little difference in either the richness or abundance of forest-associated species when buffers (one-sided or two-sided) were compared with continuous forest sites. While the capacity of buffers to protect floristic diversity may vary (Brosofske et al. 1997, Hibbs and Bower 2001, Stewart and Mallik 2006), the average buffer widths for one-sided and two-sided buffer sites observed in this study (9.79 – 15.54 m ± SE) appeared sufficient to protect the rich riparian bryophyte diversity in the sampled Montane Spruce forests. Similarly, narrow two-sided buffer strips of 10 m on each side of a stream (Hylander et al. 2002, 2005, Hylander and Dynesius 2006, Dynesius and Hylander 2007) maintained forest bryophyte diversity in Sweden. Remnant canopy moderates microclimate (Fenton and Frego 2005), specifically humidity and soil moisture, which could offset the anthropogenic edge effect created by harvesting (Hylander et al. 2002). In my study, both buffers and continuous forests had some similar habitat, stand structure and substrate characteristics (amount of disturbed and undisturbed forest floor, stand basal area, conifer percent cover, 50 m buffering capacity, and hard CWD (decay class 1 – 2)) consequently the microclimate and habitat quality probably did not differ substantially between them resulting in a similar bryophyte community. Hylander et al. (2002), Pharo et al. (2004, 2009), and Saunders et al. (1991) have suggested that variation in the buffer type (i.e., differences in remnant shape, pattern, size, and or landscape position) may influence bryophyte conservation; however in my study, neither the richness nor abundance of forest-associated species differed in one-sided and two-sided buffers. Likewise, overall bryophyte composition was little influenced by the position of the overall buffer relative to the stream (Table 2.7). It is important to note that given the current state of harvesting and forestry regulations in BC, one-sided buffer sites may well become two-sided buffer sites during future salvage harvesting.

Many of the same studies that have documented the effect of harvesting on forest-associated bryophytes have also recorded a positive association with harvesting and disturbance-associated species (Jonsson and Esseen 1990, Rydgren et al. 2004, Baldwin and Bradfield 2005, 2007, 2010, Fenton and Frego 2005). Similar to Rydgren et al. (2004), this study found increasing disturbance was associated with an increase in the abundance of disturbance-associated bryophytes (colonists such as *Ceratodon purpureus, Polytrichium juniperinum* or *Pohlia nutans*) though not species richness. Disturbed mineral soil is a known source of colonists' diaspores (Jonsson 1993). In contrast, Baldwin and Bradfield (2010) found that both the richness and abundance of many of the same disturbance-associated groups significantly increased in clear-cuts in temperate rainforest, but only richness increased in forest habitats influenced by edge effects (Baldwin and Bradfield 2005, 2007). The contrasting results between this study and Baldwin and Bradfield (2010) may have arisen as a result of baseline disturbance levels present in the riparian forests. It is important to note that none of the bryophyte species sampled are exotic species, rather they are species that naturally occur in disturbed microsites within the Montane Spruce forest (Schofield 1976). Similar to many previous studies (Jonsson and Esseen 1998, Fenton et al. 2003, Åström et al. 2005), the ordination and regression results both indicate that increased mineral/soil substrate and amount of disturbed ground (habitat quality) were strongly correlated with the increased abundance of disturbance-associated species (Figure 2.6 and Table 2.12). If baseline disturbances in riparian forests maintain the full complement of disturbance-associated species pool, then the effects of harvesting is likely to have only increased abundance rather than richness (Rydgren et al. 2004, Hylander et al. 2005).

The different canopy treatments (continuous, one-sided, two-sided and clear-cut) examined in my study represent an increasing disturbance gradient due to harvesting pressure; however, the pattern of overall bryophyte richness did not support the Intermediate Disturbance Hypothesis as richness did not increase with intermediate disturbance (Connell 1978). Similarly, Haeussler et al. (1999) found with increasing disturbance there was varying response by the overall cryptogam community – in some cases diversity decreased or remained the same. Rather than intermediate levels of disturbance allowing non-dominant, disturbance-associated species to invade and increase overall bryophyte richness (Connell 1978), the impacts of harvesting appear to be primarily diminishing the overall richness and abundance of forest-associated species with a concurrent increase in the abundance but not diversity of disturbance-associated bryophytes.

Relative influence of habitat, substrate and stand structure variables

At the landscape level, the presence of intact forest within 50 m radius of small streams (50 m buffering capacity) was strongly linked to forest-associated bryophyte diversity (Table 2.8). The relationship between the retention of overstory and increased bryophyte conservation (maintenance of diversity and abundance) has been previously documented (Rambo and Muir 1998, Fenton and Frego 2005, Nelson and Halpern 2005, Dovčiak et al. 2006, however see Jonsson 1997). In this study both the simple and multiple regression analysis supported the strong positive association of the 50 m buffer capacity with both the richness and abundance of forest-associated bryophytes (Tables 2.8 and 2.9). Nearby intact forest within 50 m radius of small streams may serve as a source of diaspores or reproductive propagules of forest-associated bryophytes such as *Hylocomium splendens* (however see Jonsson 1993). This surrounding "mainland" of intact forest may influence the "islands" of riparian buffers through metapopulation dynamics of immigration and extinction, although this is likely distance dependent due to the known dispersal limitations of bryophytes (MacArthur and Wilson 1967, Tangney et al. 1990, Holl and Crone 2004, Fenton and Frego 2005, Lindenmayer et al. 2008). Recently, however, Hylander (2009) found that the colonization rate of boreal forest bryophytes in harvested stands showed no relationship with increasing proximity to mature forests. Little is still known about the process of dispersal and establishment of bryophytes to new locations (Ross-Davis and Frego 2004, Kimmerer 2005, Hylander 2009).

However, it is also important to note that proximity to intact forest could also have influenced microclimate at individually sampled sites by slowing the wind and possibly shading the site (Chen et al. 1995). Hylander (2004) looked at the effect of edge orientation and prevailing wind (wind effect) on the growth of *Hylocomiastrum umbratum* (a forest bryophyte) and concluded that best microclimate would be obtained by establishing an "asymmetric buffer" with most of the trees on the south side of the stream opposite to the clear-cut (similar to the one-sided buffers).

Many of the adverse influences of harvesting on bryophyte communities have resulted from changes in stand structure influencing the microclimate (Rambo and Muir 1998, Fenton and Frego 2005, Stewart and Mallik 2006). I selected *Alnus* cover as predictor variable in the multiple regression analyses as total shrub cover, including *Alnus* species, has been suggested to be important in creating a suitable microclimate for bryophyte species due to relative size differences (Stewart and Mallik 2006, Dovčiak et al. 2006). Interesting, the ordination and regression analyses found that the amounts of *Alnus* species percent cover were positively associated with disturbance- associated bryophytes rather than with forest-associated bryophytes (Figure 2.6 and Table 2.12). *Alnus* species may have reduced insolation or increased soil moisture due to fallen leaves thus altering the microclimate which allowed for the germination of the colonists' spores. Availability of deciduous trees has been shown to be an important substrate for epiphytic bryophyte survival (Rambo and Muir 1998, Perhans et al. 2009) and provide shade and higher humidity for sensitive bryophytes particularly on slopes (Gustafsson et al. 1992). As my site selection process specifically selected "warm sites" (~165° – 285° - southern aspect), it is not surprising that both the ordination and regression analyses found that the slope angle (average 9 %) was negatively associated with the richness and abundance of forest-associated bryophytes found on humus and logs; however slope was moderately positively associated with species richness of all "bryophytes" and those species preferring litter. Similarly in the upper montane tropical forests of Southern Ecuador, Mandel et al. (2009) found on ridges with an average slope of 14% and sunny exposure the overall bryophyte, especially liverwort, species richness decreased compared to shaded sites; they suggested microclimate differences due to exposure levels and slope affected bryophyte diversity patterns.

The quality of microhabitat (both its diversity and the abundance of specific types) has been identified as an important factor controlling the response of bryophyte communities in harvested landscapes (Rambo and Muir 1998, Hylander et al. 2005, Fenton and Frego 2005, Botting and Fredeen 2006). Certainly the amount and specific decay classes of CWD has been identified for maintenance of epixylic bryophytes typically found on decaying CWD (Jonsson 1997, Rambo and Muir 1998, Rambo 2001). Although my study found an inconsistent response to the presence of soft coarse woody debris for the richness of most forest-associated functional groups, the abundance of epixylic species did increase supporting the notion of these biological legacies in maintaining riparian bryophytes (Rambo and Muir 1998, Rambo 2001, Pharo and Lindenmayer 2009). Habitat heterogeneity and local complexity in substrate form is also important for bryophyte diversity (Hylander 2004, Pharo and Zartman 2007, Pharo and Lindenmayer 2009). The results of this study support this contention as the multiple regression models found that bryophyte species richness (though not abundance) of both liverwort and moss species, were strongly positively associated with the presence of concave surfaces (Tables 2.9 and 2.10). Not surprisingly the presence of mineral soil had a negative association with forest-associated bryophyte species richness and abundance (Mills and Macdonald 2004); however, mineral soil had an inconsistent association with the frequency of disturbance-associated functional groups. Colonists had an expected positive but only moderate association with mineral soil/rock whereas other disturbance-associated functional groups (open canopy species and species preferring mineral soil/rock) had paradoxically unexpected strong negative association with mineral soil/rock. This inconsistent result may have occurred due to basing the inference on a single “best” quasi-binomial likelihood model with several variables despite an excellent goodness of fit (Appendix C) rather than from several possible models (Burnham and

Anderson 2004). By using only a single model with several variables (global) there is less precision (more spurious effects) compared to a model with fewer variables; multi-model inference or MMI is thus recommended (Burnham and Anderson 2001). The averaged Akaike weights of the models for open canopy species and species preferring mineral soil/rock was ≤ 0.90 and it is recommended to not make conclusions based on only one model with the lowest AIC value and highest Akaike weight unless $w \geq 0.90$ (Burnham and Anderson 2002). Models only approximate reality given the data and no single model can explain the "whole truth" (Mazerolle 2006).

While numerous studies have investigated the influence of either landscape (Campbell et al. 2003, Verheyen et al. 2003b), stand structure (Berger and Puettmann 2000, Brose 2001) or microhabitat variables (Guo 1998, Yu et al. 2009) on plant communities in fragmented habitats, relatively few have compared the relative influence of factors operating at different spatial scales. Fenton and Frego (2005) found that the overall bryophyte community pattern can be attributed to several environmental variables in differing amounts such as substrate (approx. 50%), refugia characteristics (approx. 20%), microclimate (approx. 10%) and canopy itself (approx. 5%). In comparison, Holl and Crone (2004) found that local biotic and abiotic variables (overstorey cover, exotic plant cover, bare ground, elevation, and soil texture) explained much of the variance seen in richness and cover of riparian understorey vascular plant communities, whereas landscape scale variables (distance to river, distance to forest, percentage of surrounding forest or fallow land) and variables related to island biogeography theory (patch size and time since restoration) explained very little variance. Based on ecological processes, this study found that riparian forest-associated bryophyte community composition (species richness and frequency) is largely controlled by the remaining intact forest within 50 m (immigration and extinction), and habitat quality with minor contributions by microclimate (Table 2.11). The potential influences affecting disturbance-associated bryophyte species richness were inconclusive due to the limitations of the models used. However, their abundance was strongly affected by immigration and extinction, habitat quality, and microclimate (Table 2.12). Several studies have suggested that local factors such as habitat and microclimate strongly regulate bryophyte communities due to their small size and poikilohydric nature rather than dispersal limitations (Pharo et al. 2004, Fenton and Bergeron 2008). However, the overall effects of fragmentation on bryophyte communities are likely to be hierarchical, with multiple ecological processes influencing their survival and regrowth (Pharo and Zartman 2007). While the results of this study clearly identify the overall importance of landscape level factors like the 50 m buffer capacity, factors operating at smaller spatial scales appear to also contribute to the overall response of the bryophyte community.

Overall, my study found narrow strip shaped buffers with an average width of 10 – 15 m regardless of position (one-sided versus two-sided) largely mitigated the effects of clear-cutting on the riparian community around small, high-elevation streams. This study contributes to the growing body of evidence indicating the value of buffers for bryophytes in other ecosystems (Hylander et al. 2002) as well as for other taxa such as small mammals (Cockle and Richardson 2003). Small streams are very sensitive to canopy removal and even small buffers help to reduce the overall changes (Richardson et al. 2010). Although the narrow buffers sampled in this study maintained the richness and abundance of forest-associated bryophytes, I did not record their vitality by recording the proportion of green shoots per plant (Hylander et al. 2002, Stewart and Mallik 2006), nor did I record their growth or reproductive rates. The effectiveness of riparian buffer strips may depend in large part on how bryophytes reproduce in small buffer strips (Saunders et al. 1991, Hylander et al. 2002). Certainly the edge effects found within buffer strips (Saunders et al. 1991) may be further exasperated by the combined anthropogenically created edge owing to logging and the natural riparian upland ecotone along the existing microclimate gradient (Brosofske et al. 1997, Stewart and Mallik 2006). While the narrow buffer widths sampled in this study maintained forest-associated bryophyte richness and abundance, it is unclear if this would be true in all landscapes. With steep terrain and certain regional climates the recommended buffer width on each side of the stream can be up to 45 m or more (Brosofske et al. 1997).

Chapter Three

THE INFLUENCE OF RIPARIAN CANOPY TREATMENTS ON UPLAND COMMUNITY REASSEMBLY: WHAT HAPPENS TO THE NATURAL GRADIENT OF BRYOPHYTE COMPOSITION FROM STREAM TO UPLAND WHEN BUFFERS ARE PRESENT?

Introduction

Riparian areas, zones connecting aquatic and terrestrial habitats, are ecosystems supporting a diverse assemblage of plants, invertebrates, amphibians, birds and mammals (Gregory et al. 1991, Richardson et al. 2005, Meyer et al. 2007). All habitats are patchy and the ecological gradients linking one habitat patch to another (Harper and Macdonald 2001, Richardson et al. 2005) contribute to overall biological diversity (Stehli et al. 1969). In riparian areas, gradients of soil moisture, pH, and temperature, as well as, light, humidity and air temperature extend from the stream bank up into surrounding uplands (Brosofske et al. 1997, Danehy and Kirpes 2000, Stewart and Mallik 2006, Brooks and Kyker-Snowman 2008). Species-environment relationships (Hawkins et al. 2003, Francis and Currie 2003, Field et al. 2009) have long been recognized as important forces structuring plant communities, and abiotic gradients are often strongly correlated with gradients in plant composition and richness (Gregory et al. 1991, Stewart and Mallik 2006, Tinya et al. 2009). Bryophytes are an important component of many riparian ecosystems and both composition and richness may vary with distance from stream edge (Jonsson 1997, Hylander and Dynesius 2006, Stewart and Mallik 2006). Strong gradients appear to even influence plant communities adjacent to small headwater streams (Hagan et al. 2006). While the existence of ecological gradients between riparian areas and the surrounding uplands has long been recognized (Brosofske et al. 1997, Stewart and Mallik 2006), it is difficult to predict the effect that large-scale anthropogenic disturbance, such as large-scale forest harvesting, will have on the ecological gradients surrounding small, high-elevation streams. Riparian buffer strips have been suggested as a means to mitigate the effects of harvesting on in-stream biota (Swanson and Franklin 1992, Cockle and Richardson 2003) and are known to influence abiotic gradients surrounding streams

(Brosofske et al. 1997), but it is unclear what effect these superimposed anthropogenic edges will have on the ecological gradient surrounding small, high elevation streams.

Disturbances, both small and large-scale, are major factors structuring plant communities (Connell 1978). In forested ecosystems such as the boreal spruce forests, treefall disturbance is important for maintaining bryophyte diversity (Jonsson and Esseen 1998). In high-elevation Montane Spruce forests in British Columbia, the natural disturbance regimes are fire (Smith 1978), drought, and pests such as mountain pine beetle (Ebata 2004). In the past 100 years however, human activities such as fire suppression and logging, coupled with a drier warmer climate (Carroll et al. 2004), has altered the natural pattern of renewal. This has led to vast areas of lodgepole pine forests of similar stand age which has increased their vulnerability to attack from pine beetle (Taylor and Carroll 2004). Widespread salvage logging over the past six years (Forest Practices Board 2009) has led to increased disturbance which may homogenize the species-environment relationships in Southern Interior BC landscape (Vellend et al. 2007, however see the description of regeneration, Vyse et al. 2009).

Forest harvesting often creates a matrix of “nonhabitat” where bryophyte species composition is drastically different from that in non-harvested forest areas. Numerous studies have documented the effect of clear-cut logging on the bryophyte communities in both upland (Fenton et al. 2003, Nelson and Halpern 2005, Dovčiak et al. 2006, Dynesius and Hylander 2007, Dynesius et al. 2008, 2009) and riparian forest (Hylander et al. 2002, Dynesius and Hylander 2007). While riparian buffers have been to shown to mitigate the effects of clear-cut harvesting on bryophytes, questions remain about not only what constitutes the best buffer management practices (i.e. size of buffer, arrangement of buffers, and timing of buffer creation (Castelle et al. 1994, Hylander et al. 2002, Moore and Richardson 2003), but also if buffers can influence community reassembly in adjacent uplands.

Worldwide there is more matrix than intact habitats (remnant patches) and the maintenance or improvement of matrix habitats through adaptive management is important for conserving and maintaining biological diversity (Elmqvist et al. 2003, Prugh et al. 2008, Franklin and Lindenmayer 2009). Specifically, the existence of mass effects (Schmida and Wilson 1985), whereby immigration from nearby sources of favourable habitat help maintain the species diversity in less favourable or disturbed habitats, has been part of the ecological theory underpinning the use of variable retention as a means of providing potential refugia (or "lifeboats") that can allow disturbance sensitive species to survive long enough to recolonize the harvested areas. More studies are needed to understand the plant population dynamics occurring between retention patches such as riparian buffer strips and the recovering harvested areas (Pharo and Zartman 2007). Franklin and Lindenmayer (2009) stress that in fragmented landscapes the matrix surrounding isolated habitat patches may still allow the survival and reproduction of specific organisms.

Depending upon the specific ecological needs of a species, the clear-cut matrix can act as a sink or a source (Pulliman 1988). Logged uplands may be considered a sink if populations of former forest bryophyte species are maintained by the continued immigration from the nearby more productive forest riparian buffer (Schmida and Wilson 1985). Regardless of the immediate impact of disturbance on bryophytes, mountain pine beetle salvage harvesting has profoundly altered the proportion of disturbed versus undisturbed habitat in pine forests in BC (Taylor and Carroll 2004). In high-elevation forests such as the Montane Spruce forests, there is minimal riparian management around small streams, yet these small streams account for a large portion of the overall watershed (Forest Practice Code of British Columbia Act 1995, BC Ministry of Forests and Range 2004, Richardson et al. 2005). Retention patches including riparian buffer strips, depending on size and shape, may act as potential refugia ("lifeboats") for bryophytes and lichens in managed forests by allowing species to survive long enough to recolonize the harvested areas (Perhans et al. 2009). If riparian buffer strips encompass enough of the abiotic gradient extending out from streams, they may provide habitats in which an assortment of bryophyte species can survive (Elmqvist et al. 2003).

The degree to which riparian buffer strips represent an important management technique for the long-term conservation of upland bryophyte communities will depend upon the resilience of bryophyte communities in adjacent uplands (Holling 1973, Halpern 1988, Gunderson 2000). The "engineering resilience" of Holling (1973) has been evaluated by comparing species composition in disturbed areas to species composition in undisturbed areas (Dynesius et al. 2009, Baldwin and Bradfield 2010). While Dynesius and Hylander (2007) demonstrated that a buffer prevented the short term loss of low resilience species near small streams, no studies, to date, have looked at whether the presence of a riparian buffer confers bryophyte resilience in the clear-cut uplands.

The influence of riparian buffer strips on bryophyte community reassembly in the uplands, as well as on the nature of the bryophyte community gradient extending from the stream into the upland, was examined in my study using a natural field "experiment" (Diamond 1983). In the Montane Spruce forests of interior BC, harvesting practices have resulted in buffer strips of variable width (0 ->30 m) and spatial arrangement (hereafter called one-sided, two-sided and clear-cut canopy treatments) surrounding small, high-elevation streams. Studies addressing the overall impact of increasing forest canopy on bryophytes have documented variable responses among different bryophyte species (Jonsson 1997, Fenton and Frego 2005, Hylander and Dynesius 2006). Although responses to disturbance may be species-specific, detailing the impacts on all species may be too time-consuming or costly (Gitay and Noble 1997, *sensu* Saunders et al. 1991). However, functional classification of plants has been increasingly used to understand ecosystem response to large scale environmental perturbations (Diaz and Cabido 1997). In order to account for species-specific responses to the disturbance associated with forest harvesting, bryophytes were assigned to functional groups based on an approach similar to Baldwin and Bradfield (2005, 2007, 2010) which was based on a classification system proposed by During (1992). The use of *a priori* defined functional groups derived from current bryological literature and expert knowledge rather than using the response of species observed in my study avoids the possibility of a circular argument. Determining functional groups is considered an important step in assessing relative resilience (Allen et al. 2005).

The objectives of this study were to evaluate the influence of buffers differing in spatial arrangement and width, both on the bryophyte gradient extending from the stream edge into the upland and on the community reassembly found in the uplands. Firstly, to assess the influence of canopy treatment on the natural bryophyte gradient from stream edge out to the uplands, the relative change in select environmental variables as well as the richness and frequency of various bryophyte functional groups (taxonomic, life-history, canopy type, and substrate affinity) were compared. It is unclear what effect the combined ecotonal and clear-cut edges will have on the ecological gradient surrounding small, high elevation streams, although Stewart and Mallik (2006) found a dual edge effect on bryophyte growth. It is also unclear what the position of the buffer relative to the stream will have on the ecological gradient surrounding small-high elevation streams, although Hylander (2005) suggested an optimal microclimate at the stream may be maintained by establishing an asymmetric buffer with most trees retained on the northern aspect.

Secondly, to assess the influence of riparian buffer strips on bryophyte community reassembly in the uplands, I specifically compared the functional group representation and species composition in upland continuous, undisturbed forest with bryophyte functional group representation and composition in uplands adjacent to streams surrounded by clear-cuts, one-sided buffers and two-sided buffers. If riparian canopy treatment influences bryophyte community resilience in adjacent uplands, then I would expect to observe differences in the richness and abundance of bryophyte functional groups in uplands adjacent to different canopy treatments. Based on Hollings' (1973) definition of resilience as the persistence of relationships in the face of change, the maintenance of pre-disturbance levels of forest-associated species (liverworts, perennial stayers, closed canopy, epixylics (log dwelling species) would indicate high resilience and the loss or decline of these species would indicate lower resilience. Conversely, an increase in disturbance associated species (colonists, open canopy and mineral soil/rock associated species) indicates the degree of change to the environment (succession).

Methods

Study area

Study areas were located within the Montane Spruce BEC (Biogeoclimatic Ecosystem Classification) Zone (Meidinger and Pojar 1991) which occurs between 1100 – 1600 m. The montane spruce climate is typified by cold winters with moderate snowfall, and short warm summers. The main conifer species present are lodgepole pine (*Pinus contorta*), hybrid white spruce (*Picea engelmannii x glauca*), and subalpine fir (*Abies lasiocarpa*). Common vascular plants include grouseberry (*Vaccinium scoparium*), birch-leaved spirea (*Spiraea betulifolia*), Utah honeysuckle (*Lonicera utahensis*), twinflower (*Linnaea borealis*) and one-sided wintergreen (*Orthilia secunda*). The study areas were located in the British Columbia Interior Plateau and included the Bonaparte Plateau approximately 50 km northwest of Kamloops; Chuwels Mountains approximately 30 km southwest of Kamloops, and Greenstone Mountain approximately 70 km southwest of Kamloops (Figure 3.1). Additional study areas were located west of Barrière north of Kamloops, between Logan Lake and Merritt south of Kamloops, and around Stump Lake also south of Kamloops.

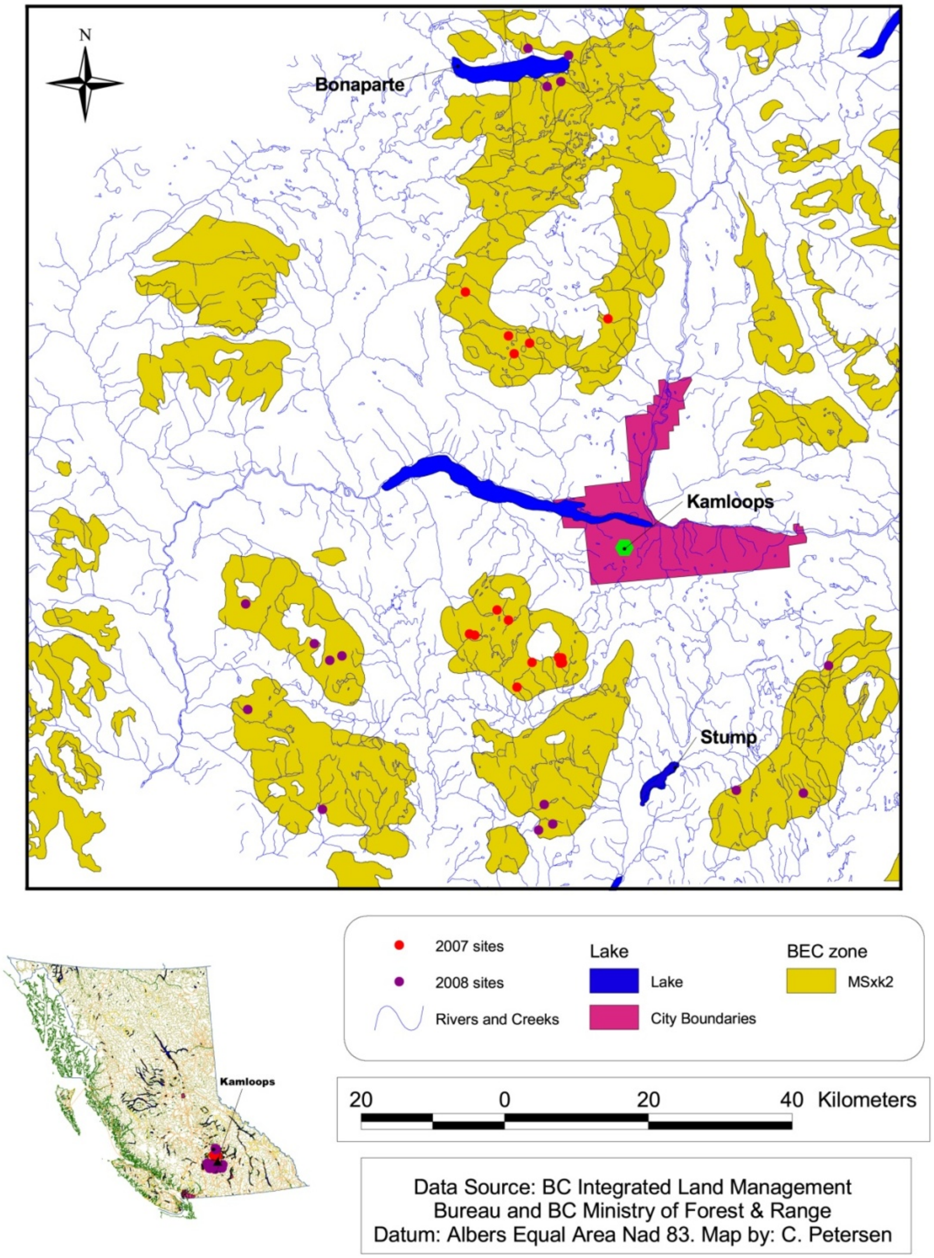


Figure 3.1. Map of study area for quantification of riparian buffers showing all sites sampled Summers 2007 and 2008 (n=30).

Site Selection

From the study areas, 30 sampling sites were selected using digital ortho-rectified aerial colour photographs and GIS coverage analysis to limit potential sites to those within the Montane Spruce subtype (MSxk2 - very dry cool) (Field Manual for Describing Terrestrial Ecosystems - BC Ministry of Environment Lands and Parks and BC Ministry of Forests- Research Branch 1998). Forest history maps were also used to limit some of the sites to those harvested within the past five to 25 years in order to limit the influence of stand age on the bryophyte response. Potential sites were also identified to minimize location bias and encompass riparian site heterogeneity (Table 3.1). Stream cover class was added to the maps to identify small streams. Ground-truthing of potential sites was done to limit the stream type to 1 – 2 m wide and free flowing in June with a distinct channel (S5 or S6 stream channel according to Forest Planning and Practices in Coastal Areas Streams – Technical Report (1997)); wet meadows and fens (type of wetland) were not sampled due to inherent vegetation differences. A buffer was defined as the original conifer stands and not alder re-growth.

Final site selections were made to minimize environmental variation in aspect, elevation, BEC zone, stream class and incorporated various conifer buffer widths (0 - >30 m) including continuous (uncut) forest. In order to sample the full gradient and spatial arrangement of forest cover currently found within the local Montane spruce forests, I examined four cover treatments: clear-cut, one-sided buffer, two-sided buffer and continuous (Figure 3.2). Clear-cut treatment had no conifer trees on either side of the stream. In comparison, one-sided buffers had continuous forest on the un-sampled side and were either clear-cut or had a buffer of trees remaining on the sampled side. Two-sided buffers had two strips of trees remaining around the stream after logging. Finally as a comparison, I looked at continuous forests that were fully intact on both sides of the stream (no logging). Effort was made to generally restrict buffer strip sites to warm aspects (~165° – 285°) and to sample separate stream drainages with a minimum distance of 1 km between sites.

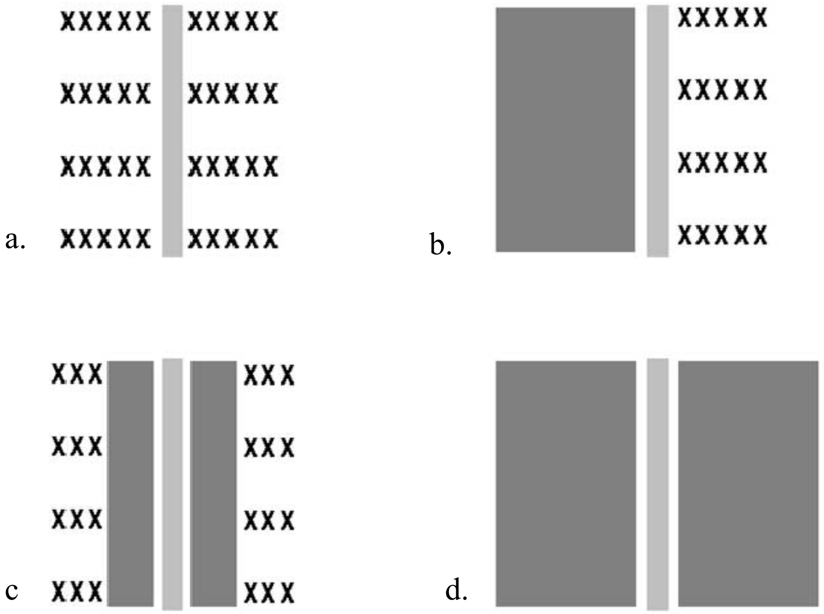


Figure 3.2. Four different canopy treatments (a. = clear-cut, b. = one-sided buffer, c. = two-sided buffer, and d. = continuous) showing the spatial arrangement of intact forest (■) and harvested area (**X**) relative to the stream position (□). Note: one-sided buffer may also have a narrow strip of trees on the right hand side of the steam (not shown).

Table 3.1. Location, canopy treatment, and disturbance date of all sites sampled in Summers 2007 and 2008 (n=30).

Site	Location	Coordinates	Canopy Treatment	Disturbance Date
4	G-branch Watching	671529 5643806	2-sided	1996
7	Strachen Lake	669347 5642418	clear-cut	1990
12	Heller Creek	662911 5651304	2-sided	1995
34	Dominic Lake Spur 400	661375 5603767	1-sided	pre1990
36	Dominic Lake Spur 400	662144 5603565	clear-cut	pre1990
39	Chuwels	673430 5600231	clear-cut	pre1990
40	Chuwels	674139 5599168	2-sided	pre1990
41	Chuwels	673634 5599924	clear-cut	pre1990
42	Chuwels	673884 5599120	continuous	none
60	Dominic Lake Spur 400	665448 5606829	continuous	none
61	Grace Lake	666883 5605428	continuous	none
62	Haybrook	667702 5596073	1-sided	1997
63	Mabel Lake	669913 5599389	1-sided	1998
64	Tranquille	668651 5644932	1-sided	1999
70	Upper Jamieson	677489 5679950	1-sided	2001
71	Jamieson	675559 5679369	continuous	none
73	Chataway	639867 5580234	2-sided	2003
74	Helmer	670749 5579561	clear-cut	1992
75	Mabel Lake	671793 5576794	continuous	none
76	Mabel Lake	669821 5576054	2-sided	1995
77	Bose	643524 5601464	2-sided	1995
78	Bose	639749 5603319	continuous	none
79	Hook	630424 5609298	clear-cut	1990
80	Woods Creek	641786 5600928	2-sided	2002
81	Laura Lake	630063 5594581	2-sided	2002
83	Bonaparte Hills	673131 5684788	clear-cut	1995
84	Jamieson-Bonaparte	678699 5683536	2-sided	2003
85	Frisken	697547 5580368	1-sided	1997
86	Monroe	706870 5579590	1-sided	1999
87	Jewel	711193 5597128	2-sided	2004

Study Design and Analysis

To capture the peak phenology in the MS forests, vegetation sampling occurred during July and August 2007 and 2008. The sampling protocol was based on a similar one used by Hibbs and Bower (2001). At each study site, three sample lines were placed 30 m apart and were located at least 25 m from the clear-cut edge. Each sample line started at the stream edge and extended 10 m upslope perpendicular to the stream edge. Environmental data, including GPS coordinates, aspect and slope of stream and sample line, elevation, stream and sample line bearing and buffer width, were recorded along each sample line. Along each sample line, bryophytes, shrubs, stand structure and microhabitat variables were sampled in six (10 m long and 2 m wide) belt transect lines placed perpendicular to each sample line at specific distances from the stream edge (Figure 3.3). In order to compare bryophyte communities from stream edge up to the upland, three belt transects were located in the "riparian area" at 1, 5, 10 m from stream edge and three others were located in the "uplands" at 5, 15 and 25 m intervals depending on the riparian buffer size. This resulted in three sampling scenarios:

1. With buffer strip ≥ 10 m to ≤ 30 m: upland transects set at 5, 15 and 25 m from actual buffer edge (actual distance from stream edge therefore varies and mean distance was based on average width of buffer strips (9.79 – 15.54 m ± SE).
2. No buffer strip (clear-cut and one-sided buffer): upland transects set at 5, 15 and 25 m from the last riparian transect (i.e. fourth transect at 15 m from stream edge, fifth transect at 25 m from stream edge, sixth transect at 35 m from stream edge).
3. Intact forest (continuous): upland transects set at 5, 15 and 25 m from largest buffer (30 m) (i.e. fourth transect at 35 m, fifth transect at 45 m and sixth transect at 55 m).

Bryophyte species presence was sampled within 10 alternately placed microplots (0.1 x 0.3 m) along each belt transect (Figure 3.3) and the entire belt transect was checked for any additional species (McCune and Lesica 1992). In order to quantify habitat heterogeneity, substrate type, floor type and decay class of logs (Maser et al. 1979, 1988) were noted for bryophyte microplots. In five shrub plots (2 x 2 m) both species and cover class were determined. Shrubs were classified as either short shrubs (≤1 m) or tall shrubs (> 1 m) using average height from the USDA plant data base and EFlora online database (Klinkenberg 2007, USDA 2009) similar to Dovčiak et al. (2006). Percent cover of substrate (disturbed and undisturbed forest floor, mineral soil, coarse woody debris, damp ground, boulder and rocks) and cover type (bryophyte, tree, saplings and seedlings) were recorded at the belt transect level. Within the entire belt transect the species and cover class (0 = 0%, 1 = 0.1 – 1%, 2 = 1 – 5 %, 3 = 5 – 25%, 4 = 25 – 50%, 5 = 50 – 75%, and 6 = 75 – 100%) of conifers and deciduous trees were recorded. Diameter at breast height (DBH) was measured for conifers only. The diameter and decay class of coarse woody debris (CWD) were sampled along a 30 m x 30 m triangle (Van Wagner 1982) with one edge randomly set along each sample line, located at 1 m from stream edge, and 5 m from the first upland transect. Decay classes follow the classification used by B.C. Ministry of Environment, Lands, and Parks, and the B.C. Ministry of Forests (Figure 3.4) (Maser et al. 1979, BC Ministry of Environment Lands and Parks and BC Ministry of Forests- Research Branch 1998). Soil bulk density samples were taken at 1 m from stream edge and 5 m from the first upland transect for each sample line to determine effects of grazing. Soil bulk density was determined by measuring the mass of the dry soil per unit volume (g/cc) (GLOBE 2005).

Voucher samples of the bryophytes were collected and identification was confirmed based on Lawton (1971), Koponen (1974) and Godfrey (1977). Problematic species identification was confirmed by Dr. Lyn Baldwin, Michael Ryan and Dr. W.B. Schofield. Identification was limited to the genus level for some bryophytes due to a lack of reproductive characters necessary for identification to the species level (i.e. *Brachythecium* spp. and *Lophozia* spp.). Voucher specimens are stored in the author's herbarium and TRU herbarium. Bryophytes were sorted into functional groups based on taxonomic group, reproductive strategies (life-history), canopy preferences, growth form and substrate affinity (Table 3.2 adapted from Baldwin and Bradfield (2005) and Appendix A).

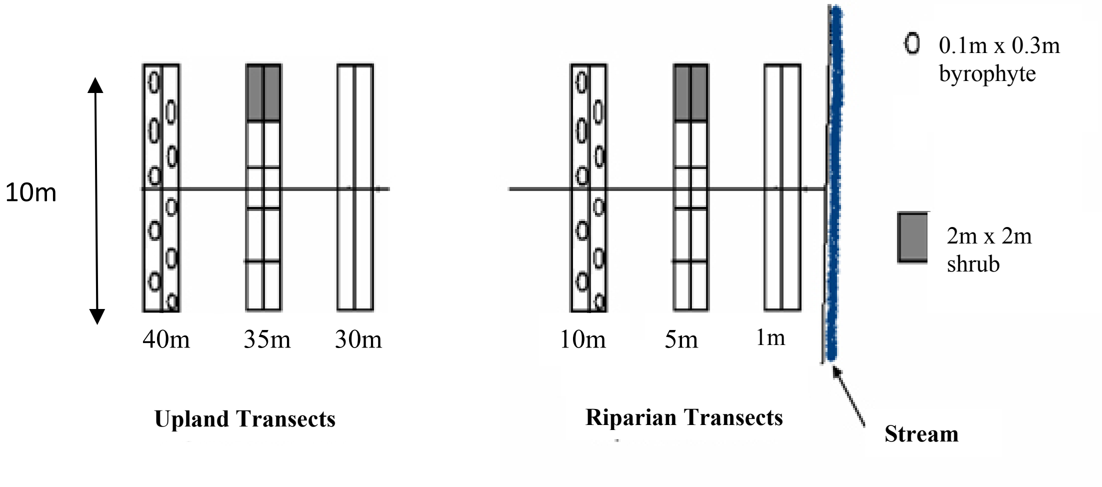


Figure 3.3. A typical sample line (one of three located at each site) showing six 10 m transects (riparian and upland) with the microplots for each vegetation type. For clarity the symbols are not overlaid or repeated in each belt transect (based on Hibbs and Bower 2001).

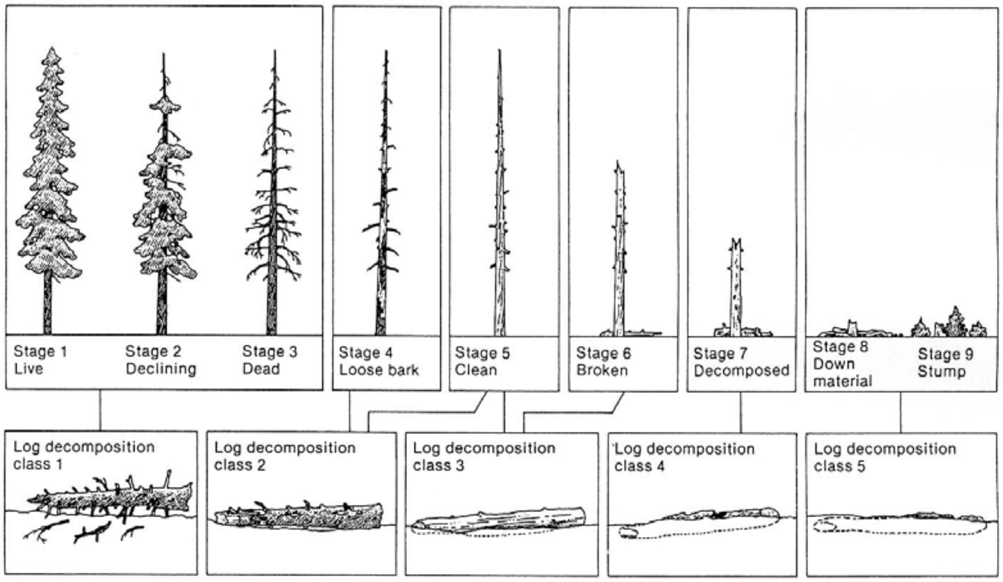


Figure 3.4. Coarse woody debris decay classification (Maser et al. 1979).

I also recorded evidence of disturbance in each site. Harvesting disturbance varied from zero harvesting impact up to 30 m from the stream to full harvesting with a 15 m ‘no machine zone’, to full machine harvesting directly over the stream channel. Other notable disturbances were cattle grazing and ‘pugging’ (hoof prints), invasive species, grass seeding, and upstream influences due to road building and erosion.

As aspect and slope of the stream bank sample line or the stream itself is highly variable due to its serpentine nature, an “aspect favourability index” (Beers et al. 1996) is calculated as: $A' = \cos(A_{max} - A) + 1.0$ where A' is the aspect favorability index , which varies from 0.0 to 2.00, A_{max} is the aspect with the highest favorability, set at 225° (Baldwin and Bradfield 2005), and A is the actual measured site aspects.

In order to quantify landscape structure and its potential influence on the bryophyte community, I used GIS analysis of the surrounding conifer cover and the riparian buffer sites (ArcView 3.2, ESRI, Redlands, CA). I added concentric circles (50, 250 and 500 m radii) to digital ortho-rectified aerial photographs to calculate the total hectares of forest surrounding each of the 30 sites (Figure 3.5). The amount of forested area in each circle was termed “buffering capacity” and this index was examined as another variable in influencing bryophyte species richness and frequency.

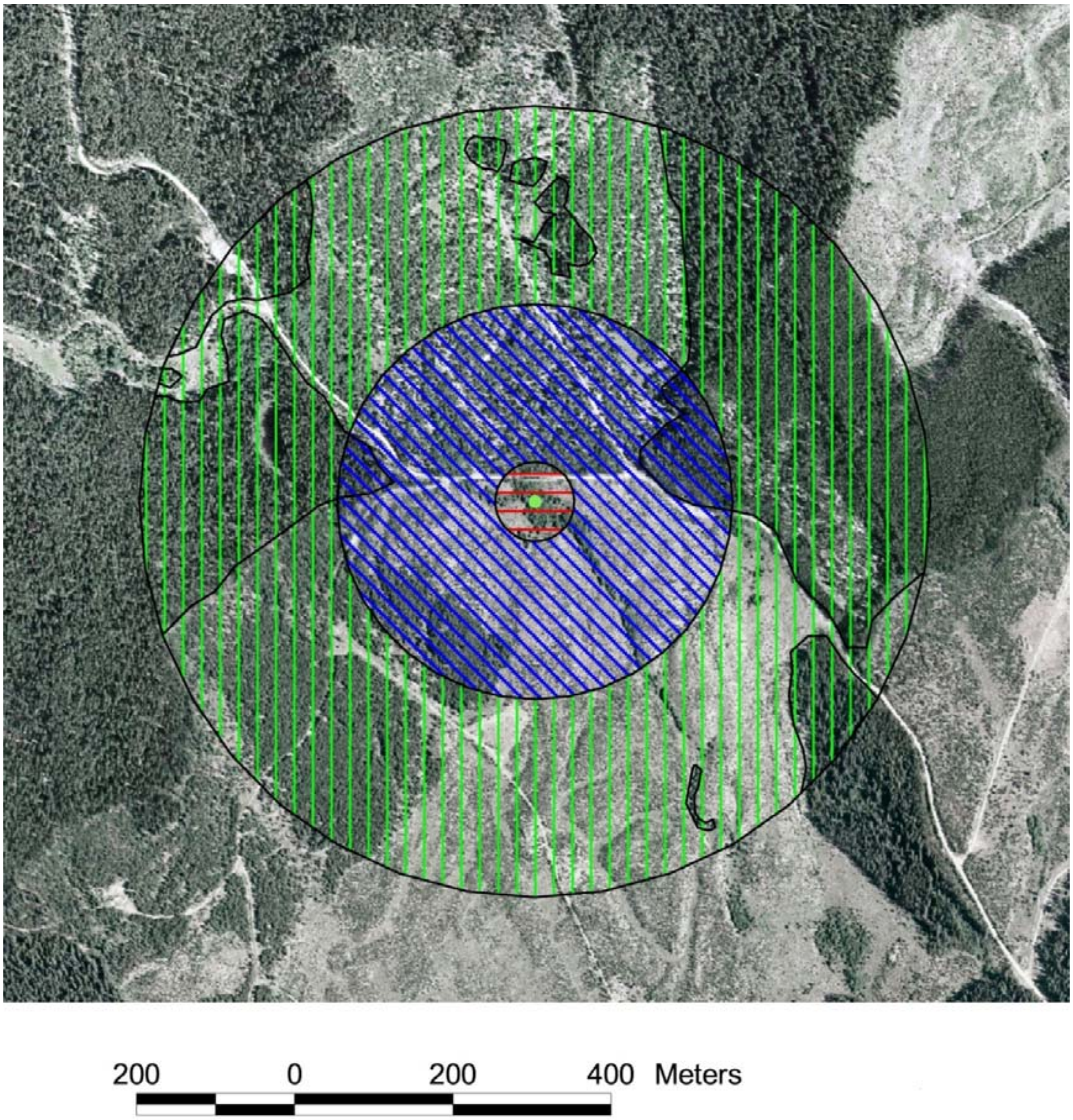


Figure 3.5. Concentric circles (50, 250, and 500 m radii) were used to calculate the amount of forested area in hectares surrounding each site which is termed “buffering capacity”.

Table 3.2. Bryophyte functional grouping with taxonomic group, reproductive strategies (life-history based on During 1992), canopy preferences, growth form and substrate affinity (from Table 1 in Baldwin and Bradfield 2005).

Category	Characteristics
Taxonomic group:	moss (M) or liverwort (LW)
Reproductive strategies(life- history):	
Colonists (Co)	spore size < 20 µm: high sporophyte production; life span of few years. Vegetative reproduction common; open short turfs and thalloid mat growth forms
Short-lived shuttles (Ss)	spore size > 20 µm: low sporophyte production; life span of few years; vegetative reproduction rare or absent; short turf or thalloid mat growth forms
Long-lived shuttles (Sl)	spore size > 20 µm: low sporophyte production; life span of many years; vegetative reproduction common; cushions, rough mat, smooth mat, or tuft growth form
Perennial stayers (Ps)	spore size < 20 µm: low sporophyte production; life span of many years. Vegetative reproduction common; weft, dendroid, mats, and large cushion growth forms
Canopy preference:	
Open canopy	shade intolerant
Closed canopy	shade tolerant
Canopy generalist	shade indifferent
Growth form:	
Turfs	erect main shoots
Open turfs (OT)	main shoot 0.1 – 1.0 cm high
Short turfs (ST)	main shoot 0.5 – 3.0 cm high
Tall turfs (TT) and sphagnoid (Tsp)	main shoot > 3.0 cm high
Cushions (CU)	erect main shoots from central point
Mats	main shoot horizontal, descending, or ascending
Thalloid (TM) and smooth (SM)	main shoots 0.1 – 1.0 cm long
Thread (TH) and rough (RM)	main shoots 0.5 – 3.0 cm long
Wefts (WE) and dendroid (DE)	main shoots > 3.0 cm long
Substrate affinity:	
Substrate generalist	
Humus	
Litter	
Mineral soil/rock	
Log	

Effect of stream distance and/or canopy treatment on gradients from stream edge into the uplands

Transect values (stand structure, habitat and substrate) sampled at 1, 5, 10 and 35 m (or approximately 35 m for two-sided buffers due to protocol difference) from stream edge up into the uplands were averaged across each distance from the stream (10 microplots per belt transect, 3 belt transects per distance = 30 microplots per transect) (Figure 3.3). In this analysis, a hypothesis testing approach was used with planned comparisons between the canopy treatments and select environmental variables (stand structure, habitat and substrate) after accounting for the distance to stream. A generalized linear model (GLM) with a normal error term and identity link (quassian) function was employed for non-count variables (stand structure and habitat variables); a GLM with a quasi-binomial logistic link was used for frequency data (substrate variables) due to over-dispersion. In both cases canopy treatment was entered as a categorical variable. GLMs were also run to assess the influence of stream distance on stand structure, habitat and substrate variables after accounting for canopy treatments. Variables were appropriately transformed to satisfy the assumptions of the regression models: distance to stream, concavity, slope standard deviation and stand basal area were log *e* transformed; percent cover variables were converted to proportions of one, then arcsine-square root transformed (Quinn and Keough 2002).

The overall importance of stream distance or canopy treatment in the models was assessed by the significance of the drop in deviance residual (a measure of the lack of model fit) seen when each term was added using the F statistic distribution (Ramsey and Schafer 1997). Significant results comparing the canopy treatments were reported even if the overall effect of stream distance was not significant as planned comparisons were made versus all possible pairwise comparisons (Ramsey and Schafer 1997). To see if the responses were similar among the canopy treatments the GLMs were rerun to include the interaction between stream distance and canopy treatment. Alder percent cover values were non-parametric despite transformations and were analyzed at each transect position using Kruskal-Wallis to compare between the canopy treatments instead of GLM's.

To evaluate the influence of canopy treatments on the natural gradient of the richness and frequency of bryophyte functional groups existing from the stream edge up into the uplands, I compared each non-continuous canopy treatment (clear-cut, one-sided and two-sided buffers) separately with continuous sites, after accounting for the distance to stream in the model. A GLM with a quasi-poisson error term and log-linear link function was employed for count variables (species richness); a GLM with a quasi-binomial logistic link was used for species frequency data due to over-dispersion (Quinn and Keough 2002). In both cases canopy treatment was entered as a categorical variable. Variables were appropriately transformed to satisfy the assumptions of the regression models: distance to stream was log *e* transformed. The overall importance of stream distance or canopy treatment in the models was assessed by the significance of the drop in deviance residual (a measure of the lack of model fit) seen when each term was added using X^2 for count data and the F statistic distribution for frequency (Ramsey and Schafer 1997). Significant results comparing the canopy treatments were reported even if the overall effect of stream distance was not significant as planned comparisons were made versus all possible pairwise comparisons (Ramsey and Schafer 1997). To see if the responses were similar among the canopy treatments the models were rerun to include the interaction between stream distance and canopy treatment.

Finally, I plotted each functional group's mean species richness and frequency, in addition to the frequency of empty microplots, as a function of the distance from stream (1, 5, 10 and 35 m) for each of the four canopy treatments. These plots were not derived from the GLM's themselves but are representative of the interaction between distance from stream and canopy type for each functional group's averaged richness and frequency. Due to variable two-sided buffer widths, the closest transect position to 35 m was used (between 33 and 37 m).

Statistical analysis was done using Excel (Microsoft 2002) and R (R Development Core Team 2009). Generalized linear models were run using R whereas both MRPP and NMS were carried out with PC-ORD (McCune and Medford 1999).

Effect of canopy treatments on adjacent uplands

I used univariate analyses to determine the effect of canopy treatment on the richness and frequency of bryophyte functional groups as well as various substrate, stand structure and abiotic variables in the upland areas. First, species richness and frequency were averaged to site level from the nine upland belt transects, each with 10 microplots (total = 90 microplots per site). Environmental variables were recorded directly at site level or averaged to site level. Simple one-way ANOVA models or Kruskal-Wallis test and their respective post-hoc tests (pairwise t-test using holm correction factor or Wilcoxon rank sum) were used to compare the richness and frequency of bryophyte functional groups or environmental variables amongst the canopy treatments. To satisfy the assumptions of normality for ANOVA some of the variables were transformed (square root or $\log_e$). Alpha diversity was measured using Shannon-Weiner index (H′) and Pielou's evenness index (J) (McCune and Grace 2002).

Second, given the fact that upland transects in different canopy treatments were located at different distances from the stream, I reran the above analysis using only data that was collected with transects located at 35 m. Sampling in all canopy treatments included a transect located at 35 or approx 35 m (31.2-37.8 m) and by repeating this analysis, I effectively removed the influence of distance from the comparison of canopy treatments.

To further investigate the impact of canopy treatment on the riparian bryophyte communities nonmetric multidimensional scaling (NMS) was used to summarize and look for patterns in upland bryophyte species composition (site level frequencies) in relation to canopy treatments. NMS, a method of indirect ordination, is a widely accepted approach of multivariate data reduction and produces graphical representations of community structure (McCune and Grace 2002). Using PC-ORD version 4, the Sorensen (Bray-Curtis) distance measure and autopilot mode was selected to run the NMS (McCune and Medford 1999). To improve the reliability of the ordination, rare species occurring in fewer than 2 out of 30 sites (20 out of 71 species or 28%) were omitted. Joint plots were used to show relationships between the ordination axes and habitat, stand structure and substrate variables. However, due to the minimal association of the 250 and 500 m buffer capacity with the bryophyte community, these variables were not included in the joint plot. Multi-response permutation procedures (MRPP) were performed on the same NMS matrix and tested the null hypothesis that the bryophyte communities were similar among the different canopy treatments.

Results

Transect level effect of stream distance

Stand structure, habitat and substrate variables

After accounting for the influence of canopy treatment, increasing distance from stream was significantly associated with declining stand basal area and significantly associated with increasing sapling percent cover (Table 3.3). Most substrate variables (general, litter and mineral soil/rock microplot frequencies) showed a significantly positive association with distance from stream, in comparison, frequency of humus within microplots showed a significantly negative association with distance from stream. The frequencies of microplots sampled on log and concave substrates, as well as the standard deviation in belt transect slopes showed no significant association with distance from stream.

Bryophyte diversity and composition

After accounting for the influence of canopy treatment, the strongest trend observed for bryophyte community diversity and composition was a significant negative association between the richness of most individual functional groups and increasing distance from stream, with a distinct ecotone around 5 - 10 m (Table 3.5, Figures 3.6 a-aa). This was true not only for all bryophytes, mosses and many forest-associated groups (liverworts, perennial stayers, closed canopy, species found on humus, litter (marginally significant) and log), but also for canopy generalists and long-lived shuttles. Some disturbance-associated groups (colonist and open canopy) also showed a significant decline in species richness with increasing distance from the stream, whereas other groups such as species found on mineral soil/rock and substrate generalists showed a significant increase with distance from stream. Only short-lived shuttles richness showed no significant association with distance from stream.

Similarly, the frequency of all bryophytes, mosses, and many forest-associated functional groups (liverworts, perennial stayers, closed canopy, species found on humus, and log), as well as for canopy generalists and long-lived shuttles, was significantly negatively associated with increasing distance from the stream after accounting for the influence of canopy treatment (Table 3.5, Figures 3.6 a-bb). The frequency of most disturbance-associated groups (colonist and species found on mineral soil/rock) and substrate generalists showed a significantly positive association with distance from stream, except species found in open canopy which were significantly negatively associated. Only the frequencies of species found on litter and short-lived shuttles showed no significant association with distance from stream. Finally, as a measure of overall bryophyte abundance, the frequency of microplots devoid of all bryophytes, "empty microplots", increased significantly with increasing distance from stream (Table 3.5 and Figure 3.6 ee). Interestingly, there is a change in the frequency of empty microplots around 5 – 10 m which suggests the natural riparian/upland transition.

Transect level effect of canopy treatment

Stand structure, habitat and substrate variables

After accounting for differences in the distance from stream, one-sided buffer, two-sided buffer and clear-cut sites had significant differences in many stand, habitat and substrate variables at the transect level compared to continuous canopy sites (Table 3.3). As expected, all three non-continuous canopy treatments (one-sided buffer, two-sided buffer and clear-cut sites) had significantly lower conifer stand basal area compared to continuous canopy sites; in comparison both conifer sapling (Table 3.3) and alder percent cover (Table 3.4) were not significantly different in harvested sites as compared to continuous canopy sites. The standard deviation of the slope measured in the three belt transects at each distance was significantly greater for sites with two-sided or one-sided buffers as compared to continuous forest sites, whereas, the slope standard deviation was not significant for clear-cuts as compared to continuous canopy sites. The frequency of microplots on concave substrates (concavity) showed no significant difference between canopy types after accounting for distance from stream. For all harvested canopy types, the number of microplots with a mixture of several substrates was significantly less in contrast to continuous canopy sites. The frequency of humus-dominated microplots was significantly higher in two-sided buffer and clear-cut sites as compared to continuous canopy sites; in contrast, the frequency of humus-dominated microplots was not significantly different in one-sided buffer sites as compared to continuous canopy sites. Litter-dominated microplot frequency was not significantly different when two-sided or one-sided buffer sites were compared with continuous canopy sites, yet the frequency of litter-dominated microplots was significantly less in clear-cut sites as compared to continuous canopy sites. When the frequency of log microplots was compared between harvested canopy sites and continuous canopy sites, only the frequency of log microplots in one-sided buffer sites was significantly higher compared to continuous canopy sites. Finally, the frequency of microplots with mineral soil/rock was significantly higher for all harvested canopy sites compared to continuous canopy sites.

Table 3.3. Summaries of generalized linear models evaluating the influence of canopy treatment (two-sided buffer (2S), one-sided buffer (1S), clear-cut (CC), and continuous forest (CON)) and distance from the stream (1, 5, 10, and 35 m) on transect level stand structure, habitat and substrate variables.

	Stream Distance effect			**2S:CON**		**1S:CON**		**CC:CON**		**Stream Distance *Canopy type**
Stand structure variables	**relative change**	**F**	**p value**	**relative change**	**p value**	**relative change**	**p value**	**relative change**	**p value**	**p value**[1]
stand basal area (m^2/ha)#	neg	30.91	**0.000**	neg	**0.000**	neg	**0.000**	neg	**0.000**	**0.036**
sapling percent cover	pos	2.98	**0.034**	neg	0.597	neg	0.619	pos	0.058	0.342
Habitat variables										
concavity*	neg	0.53	0.666	pos	0.305	pos	0.314	pos	0.272	0.574
slope standard deviation	pos	2.01	0.117	pos	**0.026**	pos	**0.039**	pos	0.133	0.424
Frequency of microplots of different substrates										
Mixed Substrate	pos	10.24	**0.000**	neg	**0.000**	neg	**0.000**	neg	**0.000**	0.933
Humus	neg	5.72	**0.001**	pos	**0.000**	pos	0.071	pos	**0.010**	0.845
Litter	pos	7.60	**0.000**	pos	0.248	pos	0.338	neg	**0.006**	0.716
Log	neg	2.54	0.060	pos	0.302	pos	**0.010**	pos	0.227	0.897
Mineral Soil/Rock	pos	10.89	**0.000**	pos	**0.038**	pos	**0.012**	pos	**0.001**	0.130

Note: Models run using either linear regression model (for non-count variables) or quasi-binomial logistic regression models (for frequency data) with canopy type entered as a categorical variable. Distance to stream, slope standard deviation and stand basal area were log *e* transformed. Percent cover variables were converted to proportions of one, then arcsine-square root transformed. Overall effect of distance from stream variable in model given by relative change (pos or neg), F statistic (for non-count and frequency data) and p value in first three columns. Relative change indicates whether the mean values for the variables in the two-sided, one-sided and clear-cut sites were greater (pos) or smaller (neg) than the mean values in the continous sites after the effect of distance from stream was accounted for. P values <0.05 are shown in bold.

[1] =p value indicates the significance of the interaction term between stream distance and canopy type when included in the full model. All models re-run with interaction included. # = marginally normal after transformation - results supported by nonparametric analysis, *frequency of microplots.

Table 3.4. Comparison of alder percent cover at different distances (1, 5, 10 and 35 m) from the stream among the four different canopy treatments using a Kruskal-Wallis test.

Alder percent cover			**Canopy types**			
Distance from stream	**clear-cut (n=7)**	**one-sided (n=7)**	**two-sided (n=10)**	**Continous (n=6)**	χ^2	**p**
1	22.2±12.55	12.22±7.09	26.08±6.43	5.18±2.33	5.45	0.141
5	12.13±7.91	9.81±5.7	16.46±5.26	2.57±2.11	4.17	0.243
10	7.76±7.59	2.96±1.62	6.72±3.31	1.23±0.8	2.14	0.543
35	3.59±2.35	0.84±0.81	5.45±2.43	3.38±3.38	1.85	0.604

Notes: Values are means (± SE) averaged to the transect level as a proxy for distance from stream.

Bryophyte diversity and composition

After accounting for the influences of the distance from stream, the richness of most functional groups in harvested canopy sites showed a significant decrease as compared with the richness in continuous canopy sites, (Table 3.5, Figures 3.6 a -aa). Overall, bryophyte species richness was significantly lower in two-sided buffer sites and clear-cut sites (but not one-sided buffer sites) as compared to continuous canopy sites. On the other hand, moss species richness in either two-sided or one-sided buffer sites was not significantly different than moss richness in continuous canopy sites; however moss richness in clear-cuts was significantly lower than moss richness in continuous canopy sites (Table 3.5). The trend lines of both bryophyte and moss richness in one-sided buffer sites (intact canopy mainly on the other side of sampling) are typically higher than two-sided buffer sites which are themselves higher than clear-cuts (Figures 3.6 a and e). Interestingly, the absolute value of bryophyte, moss and liverwort richness immediately adjacent to the stream in continuous forest sites is not greater than richness in harvested canopy treatments; however, the decline in richness appears less steep for continuous forest than for the other three canopy treatments (Figures 3.6 a, c and e).

As expected, forest-associated functional groups (liverworts, perennial stayers, closed canopy species, species found on humus, litter or logs) showed significant declines in species richness in clear-cut sites as compared to continuous forest sites (Table 3.5, Figures 3.6 c, i, q, u and aa). However the response in species richness by forest-associated functional groups varied in sites with two-sided or one-sided buffers when compared to continuous canopy sites (Table 3.5). Overall, two-sided buffer sites had significant declines or no difference in species richness for the forest-associated functional groups (liverworts, perennial stayers, closed canopy species, species found on humus or litter, and epixylics (log dwellers)), whereas, one-sided buffer sites had no significant difference in species richness for the same forest-associated functional groups compared to continuous canopy sites after accounting for distance from stream. Although both one-sided and two-sided buffer sites showed overall declines in richness in most forest-associated functional groups (liverworts, perennial stayers, closed canopy species, and species found on humus or logs) the trend line for one-sided buffer sites was higher than two-sided buffer sites, and below continuous canopy sites (Figures 3.6 c, i, q, u and aa).

In comparison, disturbance-associated bryophytes (colonists, open canopy species, and species typically found on mineral soil/rock) showed significantly higher species richness in clear-cuts as compared to continuous canopy sites (Table 3.5, Figures 3.6 g, o, and cc). The richness of colonists and species typically found on mineral soil/rock was significantly higher in both two-sided and one-sided buffer sites when compared to continuous canopy sites. Another disturbance-associated functional group, open canopy species, had significantly higher richness only in one-sided buffers when buffers were compared with continuous forest sites (Table 3.5, Figure 3.6 o).

Short-lived shuttles (species with typically large spores, short life span and little vegetative reproduction) showed no difference in species richness between any non-continuous canopy sites and continuous canopy sites (Table 3.5, Figure 3.6 k).

Conversely, long-lived shuttles (species with typically large spores, long life span and widespread vegetative reproduction) and both generalists (substrate and canopy) showed a significant decline in species richness for two-sided and clear-cut sites or no difference for one-sided sites versus continuous canopy sites. Substrate generalists' species richness showed variable responses depending on the canopy treatments; the models indicate the richness significantly declined for two-sided buffer sites and clear-cuts, whereas one-sided buffer sites were not significantly different compared to continuous sites (Table 3.5).

The frequency of most functional groups showed an even stronger decline than richness when harvested canopy sites (two-sided and one-sided buffer sites and clear-cuts) were compared with continuous canopy sites (Table 3.5, Figures 3.6 b – dd). As expected, forest-associated groups (liverworts, perennial stayers, closed canopy species, and species found on humus or logs) exhibited significant declines in abundance when clear-cuts were compared with continuous canopy sites. Many of the disturbance-associated groups (colonists, open canopy species, and mineral soil/rock associated species) showed significant increases in abundance in clear-cuts when compared with continuous canopy sites. As with species richness, the response of forest-associated functional groups frequency varied in sites with two-sided or one-sided buffers when compared to continuous canopy sites. Overall, two-sided buffer sites had significant declines in species frequency for the forest-associated functional groups (liverworts, perennial stayers, closed canopy species, species found on humus or logs, whereas, one-sided buffer sites had significant declines or no significant difference in species frequency when compared to continuous canopy sites. The response by disturbance-associated bryophytes (colonists, open canopy species, and species typically found on mineral soil/rock) in general showed significantly higher (or similar) species frequency for both two-sided and one-sided buffer sites when compared to continuous canopy sites. In all non-continuous canopy sites, the frequency of species typically found on litter substrate or short-lived shuttles were not significantly different from continuous canopy sites. Both long-lived shuttles and canopy generalists' frequencies had significant declines for both two-sided and clear-cut sites but no difference for one-sided sites versus continuous canopy sites. Substrate generalists significantly declined for all non-continuous canopy sites versus continuous canopy sites. Not surprisingly, all non-continuous canopy sites exhibited greater patchiness with significantly higher numbers of "empty" microplots than continuous canopy sites (Table 3.5, Figure 3.6 ee).

Interactions between stream distance and canopy treatments

Of the habitat, stand structure, and microhabitat variables, only stand basal area had a significant interaction between distance to stream and canopy treatments in the generalized linear models (Table 3.3). Moreover, there were few significant interactions between distance to stream and canopy treatments in the generalized linear models for most functional group species richness and frequency (Table 3.5, Figures 3.6 a-ee). The majority of the significant interaction terms were observed in the models for the frequency of individual functional groups including the frequency of two disturbance-associated functional groups (open canopy species and mineral soil/rock species) and two forest-associated groups (perennial stayers and closed canopy species). The graphs of the forest-associated functional groups with a significant interaction term indicate that there was a less severe decrease in frequency of these groups in continuous forest than in harvested canopy treatments (Figures 3.6 j and r). Also, the trend lines for both forest-associated groups' frequencies in one-sided and two-sided buffer sites were intermediate between continuous and clear-cut sites. Specifically, continuous canopy sites showed an initial decrease in perennial stayers frequency from the 1 to 5 m transect positions and then an increase at the 10 m transect position (ecotone) followed by a leveling off with increasing distance from the stream. In comparison, the trend line for one-sided and two-sided buffers exhibited no increase at the 10 m transect position and did not completely ameliorate the steady decline in abundance over the distance from the stream post harvest.

In comparison, the graphs for open canopy species and mineral soil/rock species indicate that frequency of these groups declines in continuous forests with increasing distance from the stream (Figures 3.6 p and dd). In general for these disturbance-associated groups, the frequency increases with distance from the stream in the three other canopy treatments with a distinct ecotone around 5 – 10 m (although mineral soil/rock species frequency in clear-cut sites did decline with distance from stream). A significant interaction between stream distance and canopy types was seen for both the models and graphs of the frequency of canopy generalists, and species found on litter or logs. The graphs for both canopy generalists and litter species showed overall increases in frequencies in continuous canopy sites versus harvested sites with distance from the stream (Figures 3.6 t and z).

The models for the richness of a forest-associated group (perennial stayers) and of a disturbance-associated functional group (mineral soil/rock) also showed a significant interaction between distance to stream and canopy treatments. The graph of the perennial stayers indicates that there was a less severe decrease in richness of this group in continuous forest than in harvested canopy treatments (Figure 3.6 i). In comparison, the graph of the mineral soil/rock species shows higher absolute levels of richness for the harvested sites versus continuous canopy sites immediately at the stream edge (1 m) and from 10 m onwards into the uplands (Figure 3.6 cc). Only mineral soil/rock associated species richness showed a more variable pattern depending on the canopy treatment; generally they increased with distance from stream especially for non-continuous canopy sites (Figure 3.6 dd). In continuous canopy sites, some disturbance-associated species richness (colonists and species associated with mineral soil/rock) peaked around 5 m (ecotone) and then decreased with distance from stream; open canopy species decreased with distance from stream for all non-continuous canopy treatments. As expected with direct disturbance from harvesting, the frequency of microplots with mineral soil/rock was significantly higher overall for all harvested canopy sites compared to continuous canopy sites with increasing distance from the stream (Table 3.5, Figure 3.6 dd).

Table 3.5. Summaries of generalized linear models evaluating the influence of canopy treatment (two-sided buffer (2S), one-sided buffer (1S), clear-cut (CC), and continuous forest (CON)) and distance from the stream (1, 5, 10, and 35 m) on transect-level bryophyte functional group richness and frequency.

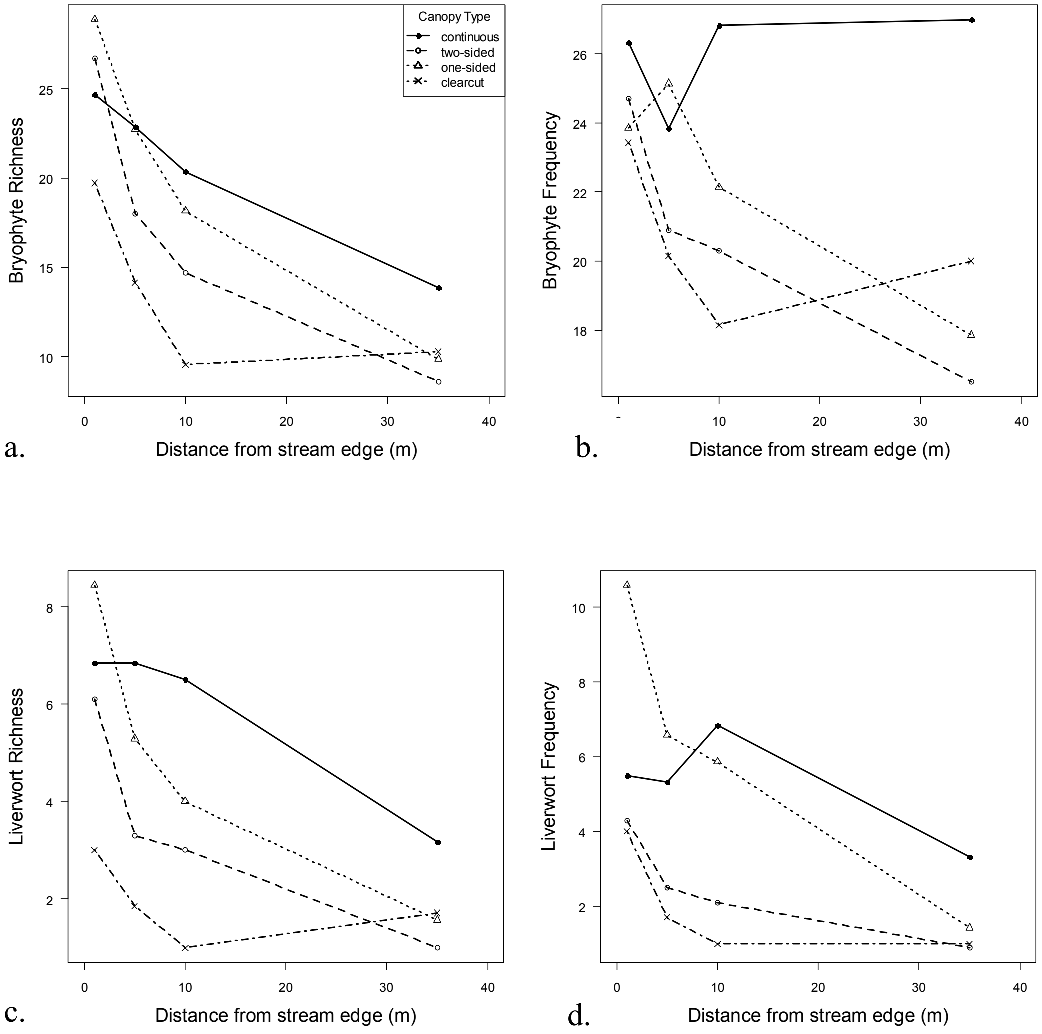
	Stream Distance effect			**2S:CON**		**1S:CON**		**CC:CON**		**Stream Distance*Canopy type**
Functional Groups	**relative change**	**F or χ2**	**p value**	**relative change**	**p value**	**relative change**	**p value**	**relative change**	**p value**	**p value[1]**
Taxonomic groups										
Bryophytes										
Richness	neg	49.30	**0.000**	neg	**0.032**	neg	0.770	neg	**0.000**	0.110
Frequency	neg	9.21	**0.000**	neg	**0.000**	neg	**0.002**	neg	**0.000**	0.101
Liverworts										
Richness	neg	64.59	**0.000**	neg	**0.000**	neg	0.217	neg	**0.000**	0.092
Frequency	neg	14.94	**0.000**	neg	**0.000**	pos	0.366	neg	**0.000**	0.064
Mosses										
Richness	neg	15.19	**0.011**	neg	0.405	pos	0.698	neg	**0.011**	0.220
Frequency	neg	9.80	**0.000**	neg	**0.000**	neg	**0.006**	neg	**0.000**	0.083
Life History Strategy groups										
Colonists										
Richness	neg	16.87	**0.000**	pos	**0.010**	pos	**0.000**	pos	**0.000**	0.683
Frequency	pos	22.69	**0.000**	pos	**0.003**	pos	**0.000**	pos	**0.000**	0.095
Short-lived shuttles										
Richness	neg	6.61	0.122	pos	0.805	neg	0.919	neg	0.074	0.462
Frequency	neg	0.51	0.679	pos	0.825	pos	0.907	neg	0.412	0.753
Long-lived shuttles										
Richness	neg	44.15	**0.000**	neg	**0.002**	neg	0.290	neg	**0.000**	0.103
Frequency	neg	4.51	**0.005**	neg	**0.020**	pos	0.780	neg	**0.019**	0.128
Perennial stayers										
Richness	neg	45.04	**0.000**	neg	**0.001**	neg	0.123	neg	**0.000**	**0.033**
Frequency	neg	20.39	**0.000**	neg	**0.000**	neg	**0.000**	neg	**0.000**	**0.008**

Table 3.5. continued.

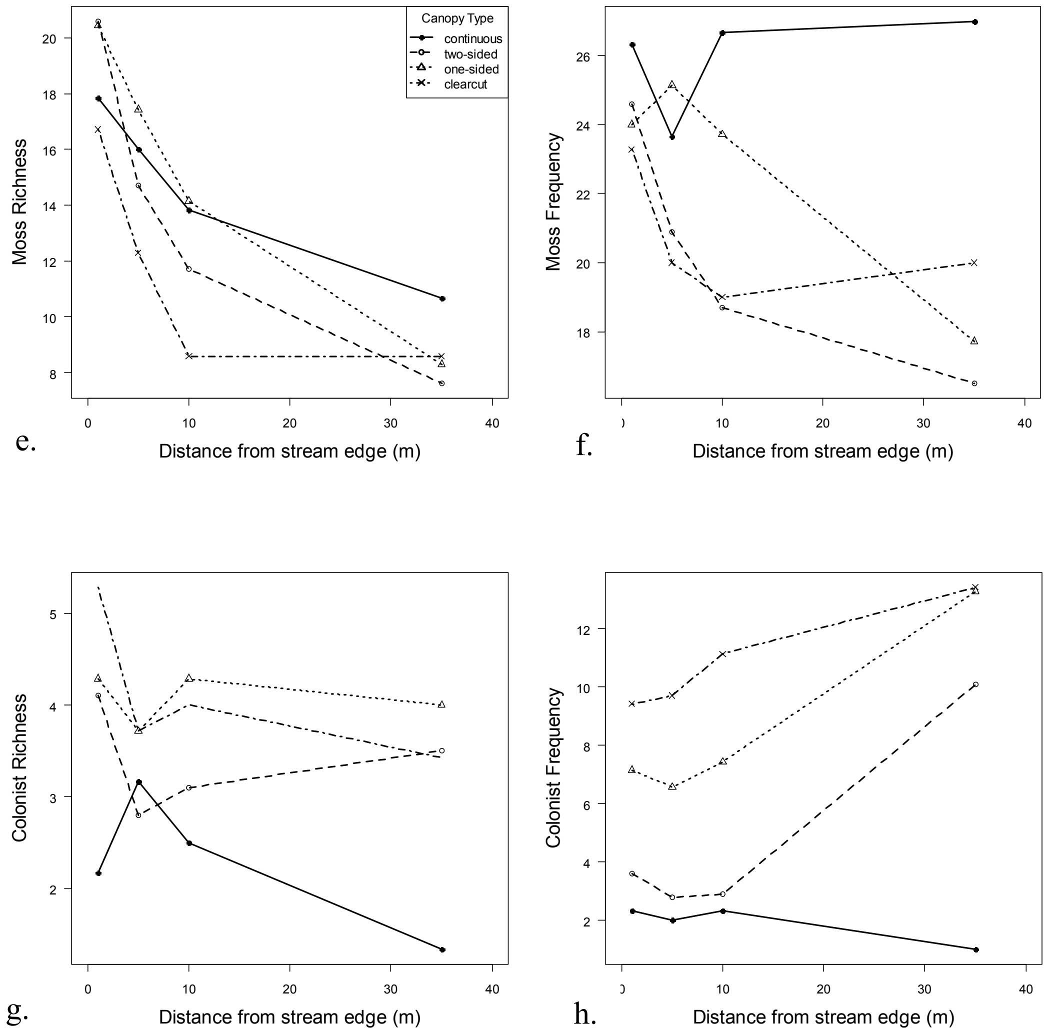
Canopy type groups										
Open										
Richness	neg	13.78	**0.013**	pos	0.206	pos	**0.018**	pos	**0.004**	0.614
Frequency	neg	6.94	**0.000**	pos	0.645	pos	0.063	pos	**0.000**	**0.020**
Closed										
Richness	neg	83.28	**0.000**	neg	0.057	neg	0.427	neg	**0.000**	0.133
Frequency	neg	21.69	**0.000**	neg	**0.000**	neg	**0.000**	neg	**0.000**	**0.011**
Generalist										
Richness	neg	21.06	**0.000**	neg	**0.001**	neg	0.121	neg	**0.000**	0.088
Frequency	neg	5.16	**0.002**	neg	**0.028**	neg	0.648	neg	**0.001**	**0.010**
Substrate Affinity groups										
Generalists										
Richness	pos	10.98	**0.001**	neg	**0.008**	pos	0.959	neg	**0.004**	0.374
Frequency	pos	11.53	**0.000**	neg	**0.000**	neg	**0.001**	neg	**0.000**	0.113
Humus										
Richness	neg	35.06	**0.000**	neg	0.130	neg	0.641	neg	**0.000**	0.107
Frequency	neg	6.42	**0.000**	neg	**0.002**	neg	**0.042**	neg	**0.000**	0.702
Litter										
Richness	neg	6.18	0.051	neg	0.864	neg	0.259	neg	**0.020**	0.336
Frequency	neg	0.82	0.484	neg	0.791	pos	0.909	neg	0.211	**0.028**
Log										
Richness	neg	52.65	**0.000**	neg	**0.018**	neg	0.067	neg	**0.000**	0.168
Frequency	neg	9.45	**0.000**	neg	**0.020**	neg	0.378	neg	**0.000**	0.138
Mineral soil/Rock										
Richness	pos	258.75	**0.000**	pos	**0.012**	pos	**0.000**	pos	**0.000**	**0.000**
Frequency	pos	24.81	**0.000**	pos	**0.017**	pos	**0.000**	pos	**0.000**	**0.000**
"Empty" microplots frequency	pos	9.21	**0.000**	pos	**0.000**	pos	**0.002**	pos	**0.000**	0.101

Note: Models run using either quasi-poisson log-linear models (count variables) or quasi-binomial logistic regression models (frequency data) with canopy type entered as categorical variable. Distance to stream was log e transformed. Overall effect of distance from stream variable in model given by F statistic for frequency data or $\chi 2$ for count data & p value in first two columns. Relative change indicates whether mean values for variables in two-sided, one-sided and clear-cut sites were greater (pos) or smaller (neg) than mean values in continous sites after the effect of distance from stream accounted for.

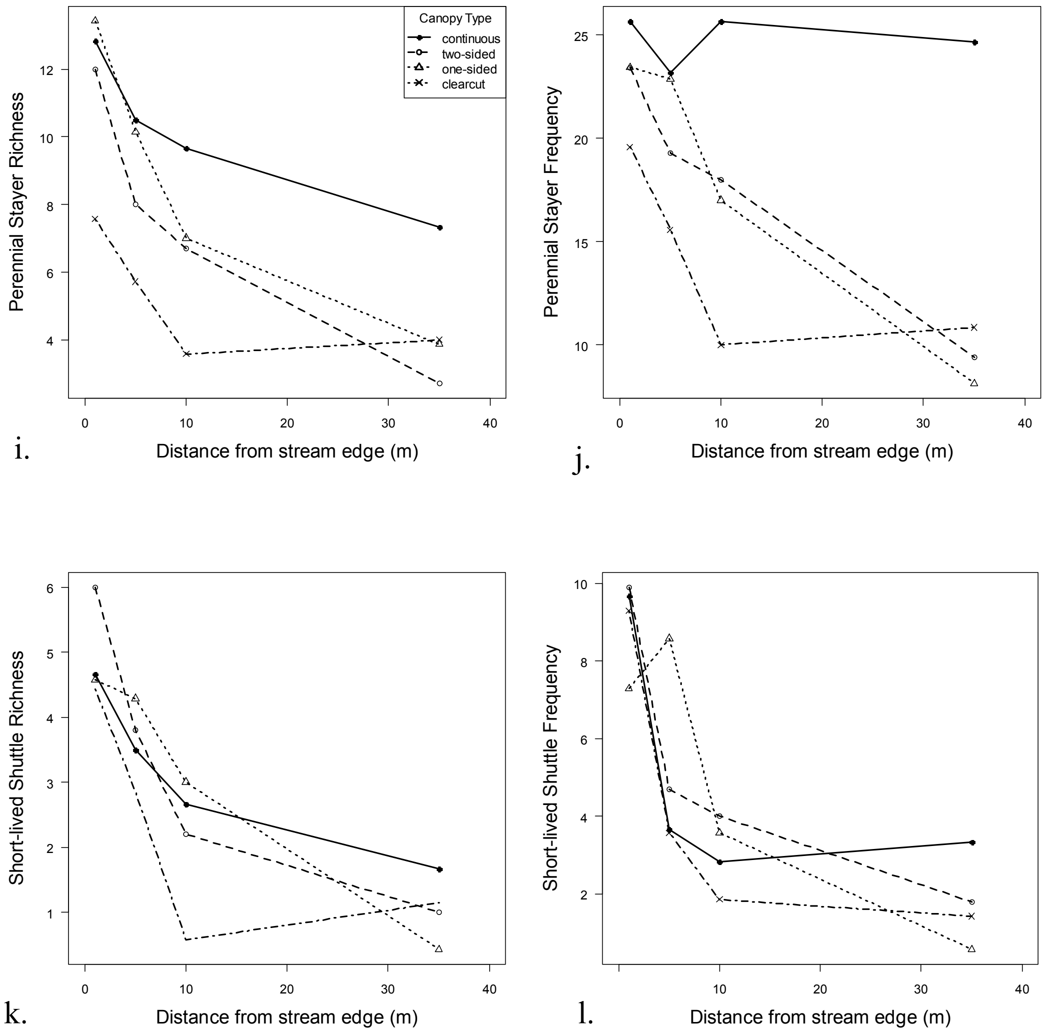
P values <0.05 are shown in bold.[1] p value of interaction term in full model.



Figures 3.6. The effect of distance from the stream (m) on the mean species richness and frequency of various functional groups: taxonomic (a. – f.), life history strategies (g. – n.), canopy preference (o. – t.) and substrate affinity (u. – dd.), and the frequency of empty microplots (ee.) in four canopy treatments. Sampled distances were 1, 5, 10 and 35 m from stream edge for clear-cut, one-sided and continuous forest. Sampled distances for two-sided treatments were 1, 5, 10 and between 33 and 37 m (for clarity plotted here at 35 m).



Figures 3.6 continued.



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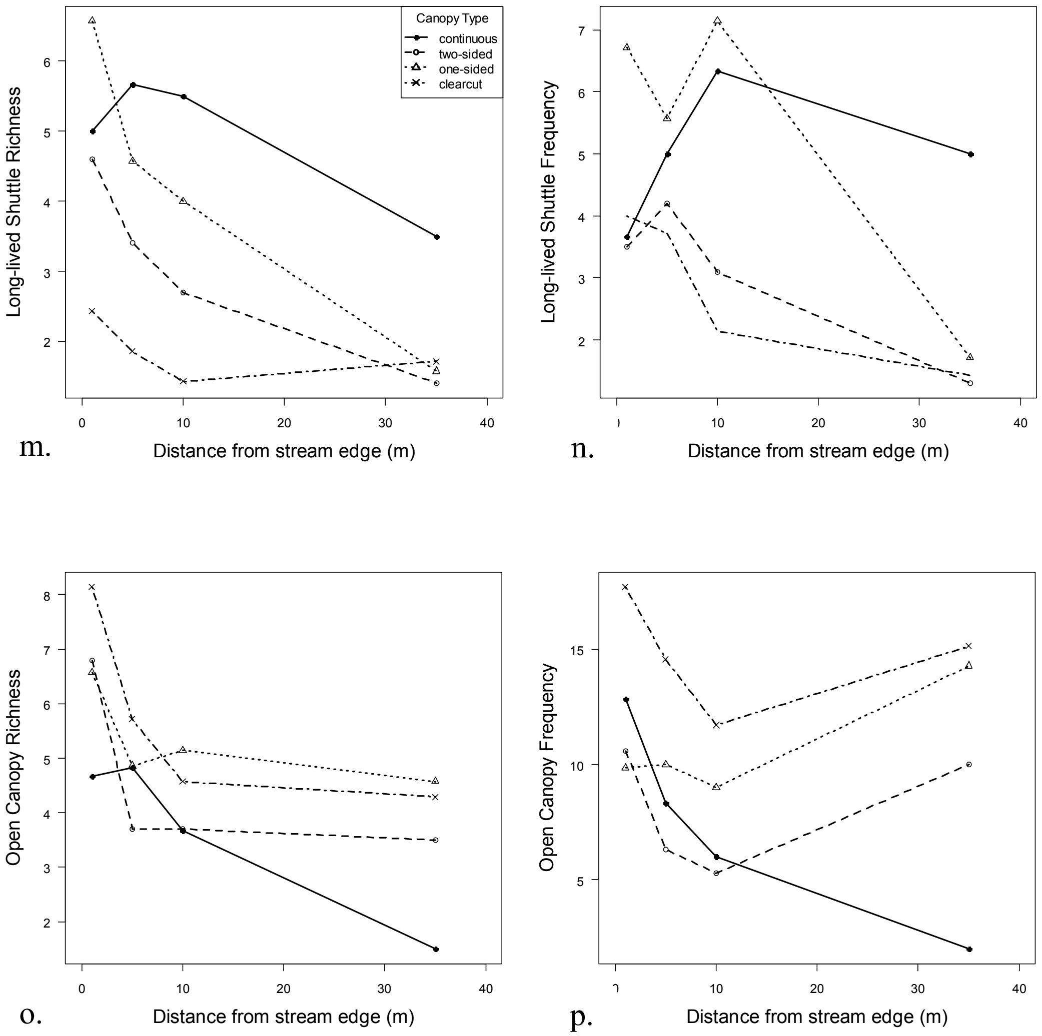

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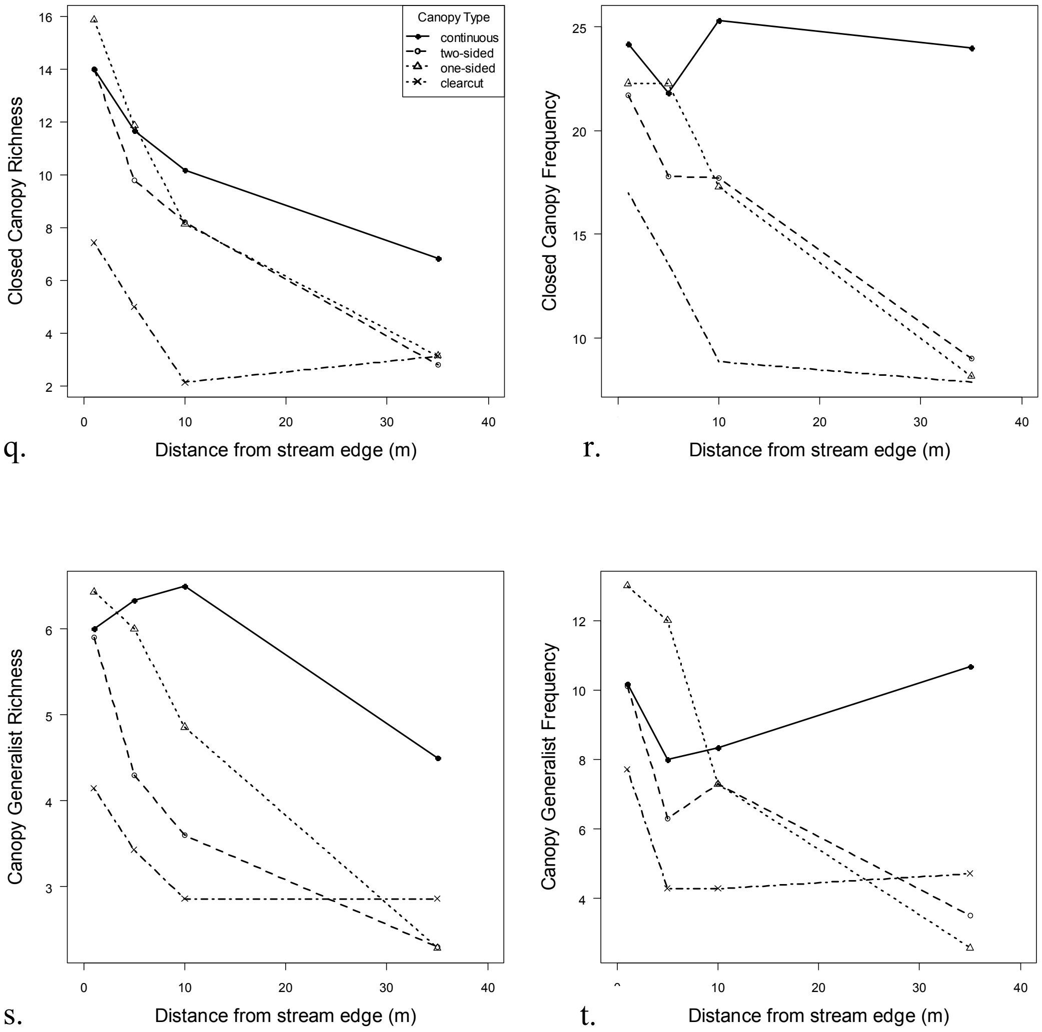

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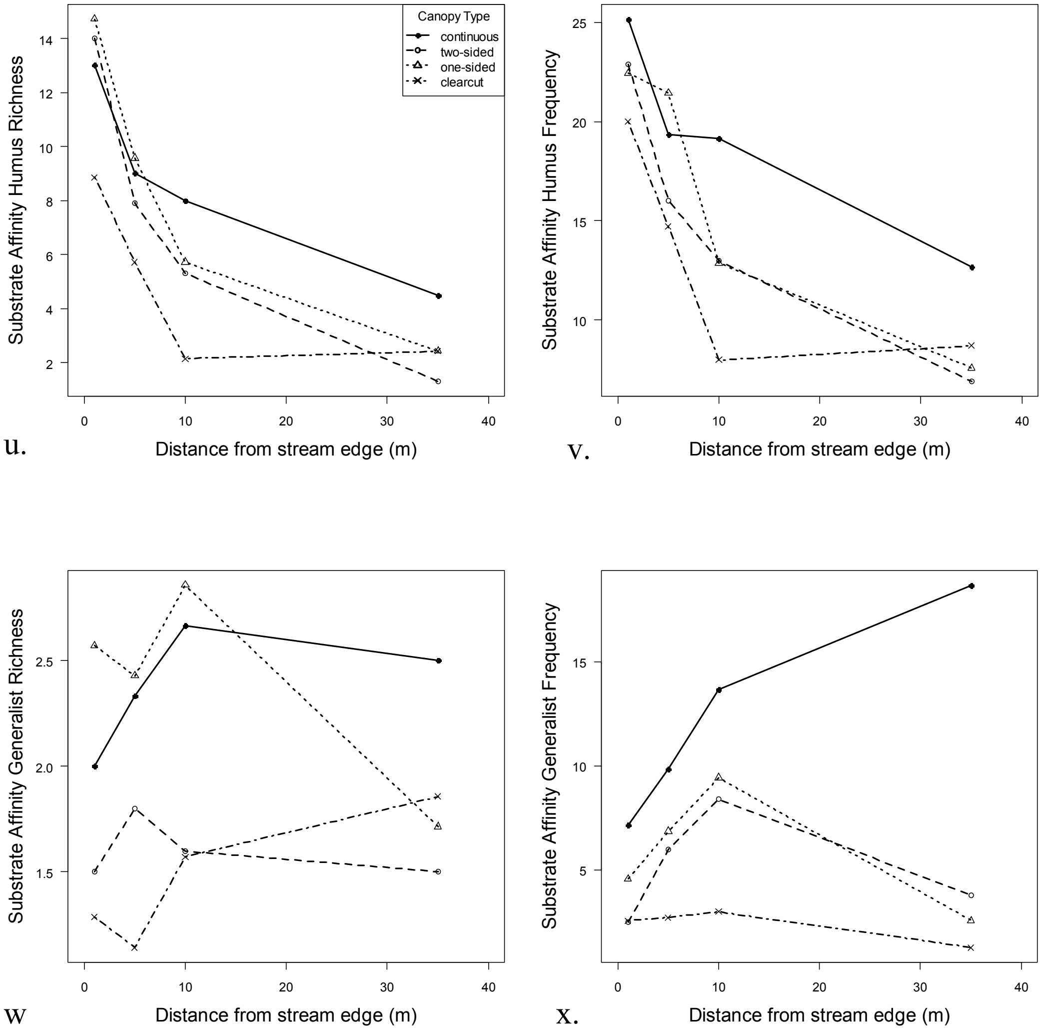

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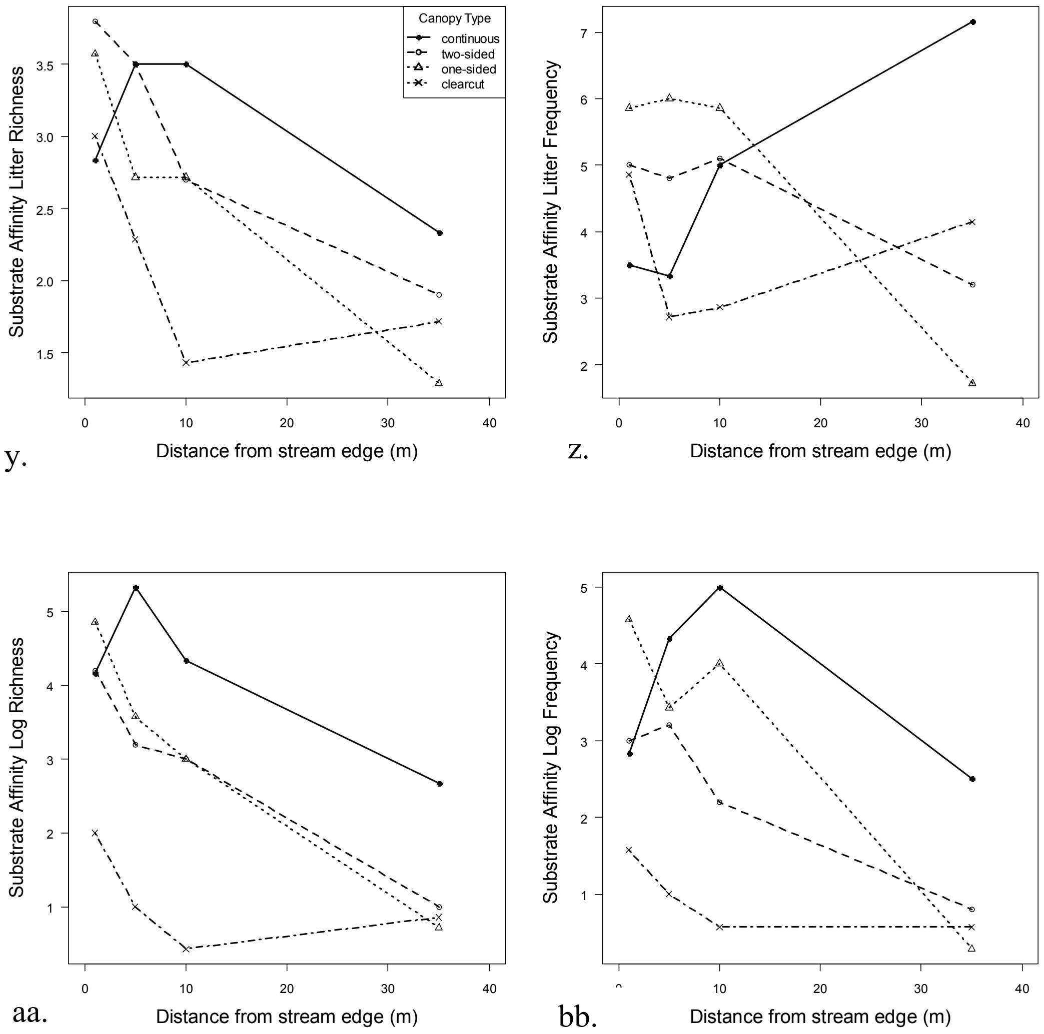

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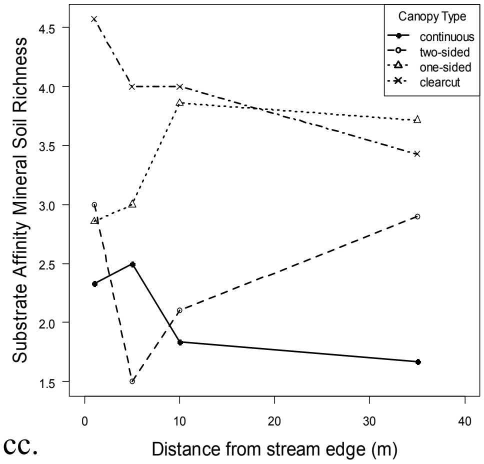
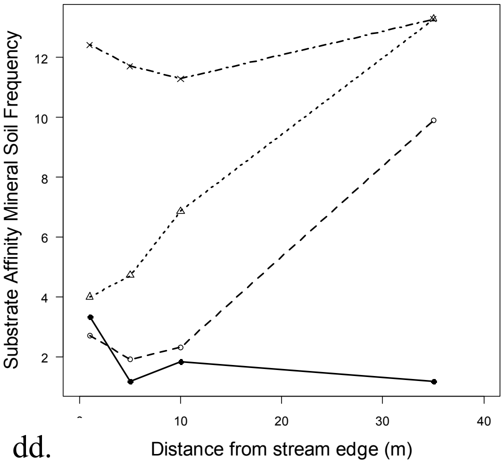
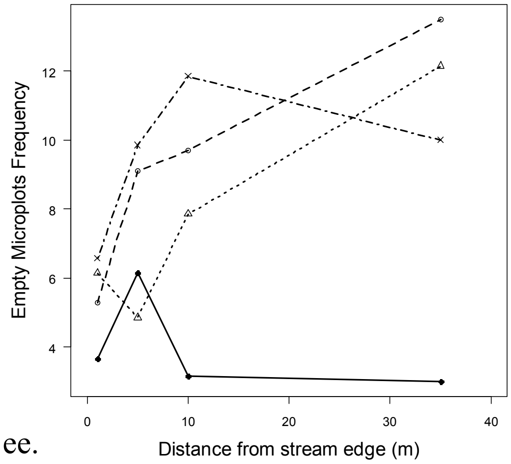


cc.



dd.



ee.

Figures 3.6 continued.

Site level effects of canopy treatments on adjacent uplands

Upland habitat characteristics, stand structure and substrate availability

When comparing the various upland habitat characteristics at the site level only buffer width and buffering capacity (50 m and 250 m) differed between the canopy treatments (Table 3.6), indicating the site selection protocol was effective in minimizing potential confounding factors of this natural experiment. The range of canopy/buffer widths and positions encompassed variation found within the Montane Spruce landscape (C. Petersen - personal observation of unpublished GIS maps). As expected, the buffering capacity (amount of remaining forest within a 50 m or 250 m radius) and the buffer width increased with decreasing levels of disturbance (i.e. lowest in clear-cut sites, intermediate in one- and two-sided buffers, and highest in continuous forest sites). However, one- and two-sided buffers did not have significantly different buffer width or buffering capacity. Also, the 500 m buffering capacity did not differ significantly across the canopy treatments.

Several aspects of stand structure differed significantly between the canopy treatments in the uplands at the site level (Table 3.6); The same trends were also seen for select stand structure variables at the 35 m transect level when distance from stream was taken into consideration thus, it is likely there were no confounding influence due to protocol differences between continuous and non-continuous canopy sites (Table 3.9). Though the overall volume of CWD was similar among the four canopy treatments in the uplands, canopy treatments varied in the availability of CWD in soft (decay class 1-2) or hard decay classes (decay class 5). One-sided sites had significantly lower amounts of hard CWD than continuous forest sites. Interestingly, both clear-cut and continuous forests had the largest amount of the soft CWD (decay class 5) in the uplands. Not surprisingly, continuous forests had the greatest amount of bryophytes and conifers, whereas the remaining canopy treatments had lower but statistically similar levels of bryophyte and conifer cover in the adjacent uplands. Interestingly, the percent covers of *Alnus* species, deciduous trees, large shrubs (> 1 m), saplings, seedlings and shrubs in general were not significantly different among the canopy treatments. Results for *Alnus* species and sapling percent cover results concur at both site and 35 m transect levels (Tables 3.6 and 3.9). Only small shrub percent cover (≤ 1 m) was significantly different, with the highest percent cover observed in the uplands of continuous forest sites and lowest percent cover in the one-sided buffer sites. As expected, overall conifer stand basal area was significantly greatest in the uplands of the continuous sites and negligible in the uplands of the other canopy treatments (site and 35 m transect level results concur – Tables 3.6 and 3.9).

The availability of several substrates exhibited statistically significant differences among the canopy treatments. Boulder/rock percent cover was lowest in the continuous forests and highest in the clear-cuts and one-sided sites. Not surprisingly, the percent cover of disturbed forest floor and mineral soil were significantly lower in continuous forest as compared to any of the harvested sites; however, there was no statistical difference in the percent cover of disturbed forest floor or mineral soil among the three harvested canopy types. Conversely, the percent cover of undisturbed forest floor was significantly higher in continuous forests than in harvested sites, yet showed no significant difference among harvested sites.

Upland bryophyte community characteristics: species diversity, richness and frequency

The species richness of bryophytes, mosses and liverworts did not vary among the four canopy treatments (clear-cut, one-sided, two-sided and continuous) at both the site and 35 m transect levels (Tables 3.7 and Table 3.9). The Shannon-Weiner's diversity index also showed no significant difference among the canopy treatments, whereas the Pielou's evenness index showed the least variation in the clear-cuts and the most in the continuous forests with one-sided and two-sided sites displaying intermediate values. In terms of bryophytes, continuous forests in general were composed of 75% mosses (15 species) and 25% liverworts (5 species). In fact, this proportion of mosses to liverworts remained similar for clear-cut, one-sided and two-sided sites. In general, the richness of bryophyte functional groups differed significantly only when continuous forest was compared with harvested sites; few differences in bryophyte functional group richness were significant when clear-cut, one-sided and two-sided sites were compared with each other at both the site and 35 m transect levels (Tables 3.7 and Table 3.9). While not all comparisons were significant, the overall pattern indicates that continuous forests had higher species richness of forest-associated bryophytes (liverworts, perennial stayers, closed canopy species, wefts, and epixylics) as compared to clear-cuts. Conversely, continuous forests had lower species richness of bryophytes associated with disturbance (colonists, open canopy species, and species typically found on mineral soil/rock) as compared to clear-cuts. Most often, buffers (two-sided and one-sided) had levels of species richness intermediate to that of clear-cuts and continuous for bryophyte functional groups.

Of the life-history functional groups, only the colonists showed a statistical difference in species richness among the canopy treatments; continuous forests had significantly lower richness of colonists than any of the harvested canopy treatments (site level and 35 m transect results concur). Likewise, of the canopy preference functional groups, only bryophytes with closed canopy preferences had a significantly higher richness in continuous forest sites when compared with clear-cut and two-sided sites. Species richness of growth form functional groups was largely similar amongst the buffer sites; only the richness of weft growth forms was significantly higher in continuous forest as compared to clear-cut and two-sided sites.

Table 3.6. Comparison of habitat, stand structure and substrate variables in upland forests at the site level adjacent to different canopy treatments.

		Canopy treatments					
		clear-cut (n=7)	**one sided**	**two sided**	**continuous**	**X^2 (F^c)**	**p**
Habitat variables							
AFI $^€$		1.58±0.23	0.98±0.35	1.27±0.22	0.96±0.30	1.05^c	0.388
Buffer width (m)		0.00±0.00**a**	9.79±5.22**b**	15.54±1.84**b**	54.56±10.99**c**	22.00	**0.000**
Elevation (m)		1537.57±33.99	1407±72.41	1468.5±34.69	1508.33±54.92	1.23^c	0.318
Stream aspect °*		213±37.68	191.57±46.73	315.9±175.45	157.5±50.01	0.31^c	0.817
Site bearing°		212.58±24.77	131.28±35.64	206.29±27.68	181.95±41.47	1.31^c	0.293
Buffering capacity (ha)¥							
	50 m	0.003±0.003**a**	0.446±0.088**b**	0.378±0.068**b**	0.773±0.009**c**	21.64	**0.000**
	250 m	4.082±1.291**a**	9.973±1.174**ab**	9.315±1.201**b**	15.178±1.014**c**	17.35	**0.001**
	500 m	37.325±6.097	51.095±5.189	55.153±2.298	56.514±2.529	5.36	0.147
SBD^b (g/cc)		0.72±0.12	1.05±0.11	0.90±0.08	0.77±0.08	1.94^c	0.148
Slope %		4.62±1.55	8.21±1.60	3.52±0.99	5.40±1.88	2.04^c	0.132
Stand structure variables							
Volume of CWD^a (m3/ha)		51.52±12.50	48.58±7.07	38.21±4.92	60.26±9.85	1.23^c	0.320
Decay class 1-2 logs		0.6±0.6 **ac**	1.62±1.62 **a**	7.04±2.76 **ac**	14.17±3.29 **bc**	13.12	**0.004**
Decay class 3 logs$^\#$		24.76±11.07	37.85±7.41	20.78±2.84	29.51±4.94	5.83	0.120
Decay class 4 logs		22.93±6.75	9.11±5.08	10.19±3.21	13.99±4.25	4.65	0.200
Decay class 5 logs		3.23±2.17 **ab**	0±0 **a**	0.2±0.2 **a**	2.59±0.9 **b**	8.98	**0.030**
Percent cover							
	Alnus spp	2.27±1.51	0.43±0.31	4.87±2.77	3.97±3.96	3.12	0.374
	Bryophyte*	3.94±0.94**a**	4.04±1.24**a**	3.52±1.2**a**	15.65±0.81**b**	14.44	**0.002**
	Conifer	0.35±0.34**a**	0.15±0.14**a**	0.13±0.08**a**	4.15±0.58**b**	16.20	**0.001**
	Decidious	0.32±0.24	0.03±0.02	0.81±0.4	1.18±1.18	4.61	0.203
	Large shrub*	8.6±2.88	10.08±3.14	18.21±5.71	7.82±5.06	3.80	0.284
	Sapling	4.28±1.2	1.01±0.32	2.18±0.87	2.1±0.95	5.15	0.161

Table 3.6. continued.

Seedling*	1.48±0.6	1.44±0.41	1.67±0.64	0.8±0.32	1.59	0.661
Shrub*	28.55±4.42	26.34±4.12	42.83±7.64	48.24±11.08	1.98	0.142
Small shrub*	17.23±3.55 **ce**	13.43±2.45 **ac**	18.96±3.09 **ade**	37.01±6.98 **bd**	8.00	**0.046**
Stand basal area (m^2/ha)	0.001±0.001**bd**	0.001±0.001**ab**	0.001±0.000**ad**	0.018±0.002**c**	18.13	**0.000**
Substrate Variables						
Percent cover						
Disturbed forest floor	7.62±2.79**cd**	11.88±2.02**ac**	12.61±1.92**ad**	0.07±0.05**b**	15.39	**0.002**
Mineral soil	0.96±0.35**cd**	1.06±0.22**ac**	0.95±0.25**ad**	0.01±0.01**b**	12.46	**0.006**
Pugging	0.22±0.2	0.31±0.28	0.04±0.03	0±0	3.20	0.361
Undisturbed forest floor	7.65±2.45**cd**	2.83±1.38**ac**	4.08±1.83**ad**	17.41±0.09**b**	15.66	**0.001**
Damp ground	0.03±0.02	0.01±0.01	0.01±0.01	0.01±0.01	0.62	0.891

Note*:* Values for the upland locations are means (± SE) averaged to the site level from the appropriate nine belt transects. Other values are recorded at the site level. [a] Coarse woody debris, [b] Bulk soil density, [c] Anova F statistic with associated P-value in column to right. € = AFI refers to "aspect favourablilty index" (Beers et al. 1996) using A' = cos(A_{max}-A) + 1.0 where A' =AFI which varies from 0.0 to 2.00, A_{max} is the aspect with highest favouribility, set here at 225°, and A is the recorded aspect in each transect. ¥ = no site 84 due to lack of available ortho photo (n = 9). # = standardization (+ 0.01 or 0.1) & $\log_e$ transformation, * = $\log_e$ transformation. Post hoc tests were either pairwise t-test (holm correction factor) for ANOVA or Wilcoxon for K-W; means followed by the same letter are not significantly different. Values of $p < 0.05$ are bolded.

Table 3.7. Comparison of diversity indices and bryophyte functional group richness at the site level in upland forests adjacent to different canopy treatments.

	Canopy treatments					
	clear-cut (n=7)	**1-sided (n=7)**	**2 sided (n=10)**	**continuous (n=6)**	**χ^2 (F^c)**	**p value**
Shannon diversity index	1.96±0.34	1.94±0.36	1.76±0.5	1.86±0.23	0.92	0.821
Pielou's evenness index	0.71±0.05**a**	0.69±0.05**a**	0.66±0.1**ac**	0.61±0.06**bc**	7.89	**0.048**
Species richness						
Taxonomic groups						
Bryophyte	15.86±2.63	16.14±2.45	14.6±2.06	20.17±1.58	3.06	0.383
Moss	12.43±1.85	12.71±1.38	11.7±1.27	15±1.41	2.42	0.490
Liverwort	3.43±0.97	3.43±1.23	2.9±0.91	5.17±0.31	2.85	0.415
Life-history strategy groups						
Perennial stayers	4.43±0.92	5±1.33	3.9±0.72	6.17±0.83	1.00^c	0.410
Colonists	4.14±0.46**a**	4.86±0.34**a**	4.8±0.63**a**	2.67±0.49**b**	3.17^c	**0.041**
Short-lived shuttles	1.43±0.57	1±0.31	1.3±0.33	2±0.52	2.47	0.480
Long-lived shuttles	2.14±0.7	2.29±0.87	2.2±0.73	4.33±0.49	5.02	0.171
Canopy Preference						
Closed	4.71±1.23**a**	6±1.36**ac**	5.2±0.9**a**	10.33±1.31**bc**	4.16^c	**0.016**
Generalist	4.43±0.78	4.57±0.95	4.2±0.94	5.83±0.6	0.61^c	0.615
Open	6.71±1.06	5.57±0.61	5.2±0.61	4±0.89	1.76^c	0.180
Growth form groups						
Dendroid	0±0	0±0	0±0	0.17±0.17	4.00	0.262
Open Turf	1.86±1.22	1.14±0.26	1.2±0.25	1.17±0.17	0.63	0.889
Rough mat	2.43±0.48	2.71±0.64	1.8±0.39	3.33±0.33	5.73	0.125
Smooth mat	1±0.31	1.29±0.52	1.4±0.37	2.5±0.43	5.28	0.153
Short Turf/Cushion	6.71±0.89	6±0.69	6±0.83	6.67±0.71	0.23^c	0.872
Thread	1±0.38	0.71±0.18	0.6±0.27	1±0.26	1.94	0.586
Thalloid	0±0	0.29±0.18	0.1±0.1	0±0	3.99	0.263
Tall turf/Sphagnoid	3±0.62	2.43±0.43	2.3±0.4	3.17±0.7	1.72	0.632
Weft	0.86±0.26**a**	1.57±0.2**ab**	1±0.15**a**	2.17±0.31**b**	12.33	**0.006**

Table 3.7 continued.

Substrate-affinity groups						
Generalists	3±0.53	2.86±0.51	2.4±0.45	3±0.45	1.35	0.716
Humus	3.14±1.03	4.14±1.14	2.7±0.45	6.5±1.31	7.27	0.064
Litter/Scat	3.14±0.91	2.86±0.59	3±0.54	3.67±0.42	0.26[c]	0.855
Log	2±0.58**a**	1.57±0.57**a**	2.4±0.62**ab**	4±0.45**b**	7.80	**0.050**
Mineral soil/Rock	4.57±0.48**ab**	4.71±0.29**a**	4.1±0.35**ac**	3±0.45**bc**	3.30[c]	**0.036**

Note: Values shown are at the site level averaged across all microplots in riparian transects (± 1 SE).

[c] ANOVA F statistic with associated P-value in column to right. Bolded values are p<0.05. Letters represent post hoc results either Wilcoxon Rank Sum for Kruskal-Wallis test or pairwise t-test (holm correction factor) for ANOVA where same letter means no significant difference. Due to few records the following were combined: cushion with short turf, sphagnoid with tall turf, scat with litter, rock with mineral soil, bark and branches with log.

Table 3.8. Comparison of bryophyte functional group frequency at the site level in upland forests adjacent to different canopy treatments.

	Canopy treatments					
	clear-cut (n=7)	**1-sided (n=7)**	**2 sided (n=10)**	**continuous (n=6)**	**χ^2 (F^c)**	**p value**
Species frequency						
Taxonomic groups						
Bryophyte	60.14±3.49**ab**	61.86±6.03**ac**	49.8±5.65**a**	80±1.61**bc**	5.96^c	**0.003**
Moss	60.14±3.49**ab**	61.57±5.9**ac**	49.7±5.60**a**	80±1.61**bc**	6.13^c	**0.003**
Liverwort	2.71±0.94	4.29±1.73	4.40±1.86	9.83±1.90	7.22	0.065
Life-history strategy groups						
Perennial stayers	31.43±5.17**a**	31.29±4.78**a**	28.5±6.22**a**	73.83±4.08**b**	13.15^c	**0.000**
Colonists	40.43±4.36**a**	45.00±4.21**a**	28.50±3.70**b**	4.67±1.93**c**	18.63^c	**0.000**
Short-lived shuttles	5.57±2.90	3.14±1.06	5.80±1.74	7.50±4.36	1.35	0.718
Long-lived shuttles	4.29±2.00**a**	5.14±1.75**a**	4.90±1.91**a**	13.67±1.74**b**	8.39	**0.039**
Canopy Preference						
Closed	23.57±4.45**a**	29.86±4.58**a**	27.4±5.87**a**	73.17±3.88**b**	14.33	**0.002**
Generalist	11.43±2.97	9.57±3.08	13.0±4.12	23.67±4.78	6.31	0.098
Open	46.71±4.01**a**	46.43±4.77**a**	28.4±3.84**b**	5.00±1.61**c**	21.34^c	**0.000**
Growth form groups						
Dendroid	0.00±0.00	0.00±0.00	0.00±0.00	0.17±0.17	4.00	0.262
Open Turf	3.29±2.02	1.29±0.36	2.10±0.55	4.00±2.44	1.14	0.769
Rough mat	20.57±4.82	23.00±4.95	19.30±4.42	31.00±8.68	1.24	0.743
Smooth mat	1.14±0.55	1.29±0.57	1.60±0.50	3.50±0.89	6.17	0.104
Short Turf/Cushion	38.29±4.40	41.71±4.68	31.20±4.08	22.83±3.89	2.21^c	0.111
Thread	1.14±0.55	0.71±0.18	1.00±0.45	0.83±0.17	0.49	0.921
Thalloid	0.00±0.00	0.57±0.37	0.10±0.10	0.00±0.00	4.26	0.235
Tall turf/Sphagnoid	23.29±6.44	23.43±5.60	12.10±3.62	5.00±1.67	7.59	0.055
Weft	3.43±1.69**a**	9.57±2.41**a**	11.10±3.40**a**	55.33±8.49**b**	16.10	**0.001**

Table 3.8 continued.

Substrate-affinity groups						
Generalists	5.29±1.92**a**	11.86±2.60**a**	13.80±4.08**a**	59.83±6.31**b**	15.60	**0.001**
Humus	25.29±6.13	24.71±5.85	19.90±4.60	32.17±8.66	1.47	0.690
Litter/Scat	10.00±2.74	7.71±2.86	11.00±3.67	17.67±4.40	3.95	0.267
Log**	2.00±0.85**a**	1.57±0.61**a**	3.10±1.22**a**	6.50±1.34**b**	9.04	**0.029**
Mineral soil/Rock	40.86±3.56**a**	44.71±4.14**a**	27.80±3.86**b**	4.67±1.52**c**	20.33[c]	**0.000**

Note: Values shown are at the site level averaged across all microplots in upland transects (± 1 SE). [c] ANOVA F statistic with associated P-value in column to right. Bolded values are p<0.05 . Letters represent post hoc results either Wilcoxon Rank Sum for Kruskal-Wallis test or pairwise t-test (holm correction factor) for ANOVA. Same letter means no significant difference. Due to few records the following were combined: cushion with short turf, sphagnoid with tall turf, scat with litter, rock with mineral soil, bark and branches with log**.

Table 3.9. Comparison of a subset of stand structure variables, and bryophyte functional group species richness and frequency at approximately 35 m transect level in upland forests adjacent to different canopy treatments.

			Canopy Treatments					
			clear cut (n=7)	**one-sided canopy**	**two-sided canopy**	**continuous canopy**	**χ2**	**p value**
Stand structure variables								
		Stand basal area (m^2/ha)	0.02±0.01**a**	0.00±0.00**a**	0.06±0.03**a**	1.12±0.13**b**	19.50	**0.000**
		Alnus spp percent cover	3.59±2.35	0.84±0.81	5.45±2.43	3.38±3.38	1.85	0.604
		Sapling percent cover	0.60±0.09	0.28±0.10	0.33±0.11	0.35±0.12	4.39	0.222
Species Richness								
	Taxonomic groups							
		Bryophyte	10.29±1.86	9.86±1.94	8.60±1.25	13.83±0.98	6.28	0.099
		Moss	8.57±1.15	8.29±1.34	7.60±0.99	10.67±0.88	3.62	0.306
		Liverwort	1.71±0.78	1.57±0.78	1.00±0.37	3.17±0.31	6.55	0.088
	Life-history strategy groups							
		Perennial stayers	4.00±0.69**a**	3.86±1.03**a**	2.70±0.63**a**	7.33±0.80**b**	10.53	**0.015**
		Colonists	3.43±0.30**a**	4.00±0.38**a**	3.50±0.43**a**	1.33±0.42**b**	12.26	**0.007**
Species Frequency								
	Taxonomic groups							
		Bryophyte	20.00±0.49**a**	17.86±2.70**a**	16.50±2.20**a**	27.00±0.89**b**	11.95	**0.008**
		Moss	20.00±0.49**a**	17.71±2.65**a**	16.50±2.20**a**	27.00±0.89**b**	12.11	**0.007**
		Liverwort	1.00±0.44**a**	1.43±0.57**a**	0.90±0.41**a**	3.33±0.56**b**	9.12	**0.028**

Table 3.9 continued.

	Life-history strategy groups							
		Perennial stayers	10.86±1.81**a**	8.14±1.96**a**	9.40±2.00**a**	24.67±1.61**b**	13.97	**0.003**
		Colonists	13.43±1.19**a**	13.29±2.20**a**	10.10±1.70**a**	1.00±0.52**b**	15.54	**0.001**

Note: values shown are at site level averaged across all microplots at approximately 35 m in the uplands (± 1 SE).

Bolded values are p<0.05 . Letters represent post hoc results using Wilcoxon Rank Sum for Kruskal-Wallis test.

Same letter = no significant difference.

Lastly, the richness of bryophytes found growing on downed logs and the richness of bryophytes typically found on mineral soil/rock exhibited opposite trends as disturbance increased. The richness of log bryophytes was significantly higher in continuous forest as compared to clear-cuts and one-sided forests, whereas the richness of mineral soil/rock bryophytes was significantly higher in one-sided sites as compared to continuous forest. No other substrate affinity functional groups exhibited a significant difference in richness in upland forests adjacent to different canopy treatments.

In comparison to pattern of species richness, the response of bryophyte functional group frequency in uplands adjacent to different canopy treatments was very different (Table 3.8). Continuous upland forests had significantly higher frequencies of “bryophytes”, driven by a significant increase in the frequency of mosses, as compared to two-sided buffer sites (similar results at 35 m transect level – Table 3.9). There was no statistical difference for the frequencies of “bryophyte” or moss between any of the non-continuous sites. Continuous forests had significantly higher frequency of forest-associated bryophytes (perennial stayers, closed canopy species, species with weft growth forms, and epixylics) as compared to any of the harvested canopy treatments (similar results for perennial stayers at the 35 m transect level). Long-lived shuttles, similar to perennial stayers in some respects, did occur more frequently in continuous forests compared to the other buffer sites. Interestingly, the frequencies of the forest-associated bryophytes were not significantly different between clear-cuts and either one-sided or two-sided buffer sites. Liverwort frequency, though not significant between treatments at the site level, did exhibit a trend of increasing frequency from clear-cut sites to continuous forest sites, and was significantly different at the 35 m transect level (Table 3.9). Conversely, the abundance of disturbance-associated bryophytes (colonists, open canopy species, and species typically on mineral soil/rock) was significantly higher in the clear-cuts than in continuous forest (similar results for colonists at the 35 m transect level). In fact for all the fore-mentioned functional groups, one-sided and two-sided buffer sites did not have similar or consistent responses in frequency as clear-cut sites in the uplands.

NMS ordination of upland bryophyte species composition at the site level showed clear separation of the continuous forest sites along the first axis from the remaining sites with harvested canopy treatments (Figure 3.7). Furthermore, there was significant overlap in the position of the harvested sites (clear-cuts, one-sided and two-sided buffer sites) along Axis 1. This trend was corroborated by the MRPP results which also showed significant differences in upland bryophyte species composition between continuous sites and non-continuous sites (Table 3.10). In contrast, there was no significant difference in bryophyte species composition in the harvested uplands when the bryophyte composition in clear-cut, one-sided and two-sided canopy treatments was compared. Joint plots of environmental variables indicate correlation between the percent covers of disturbed forest floor and mineral soil, and the uplands of sites with either clear-cut , one-sided or two-sided buffers. Continuous forest and two-sided buffer sites were strongly associated with variables strongly correlated with overall forest canopy cover (50 m buffer capacity, buffer width, stand basal area and conifer tree percent cover), as well as the frequency of hard CWD (DC 1 and 2) and the percent covers of small shrubs, undisturbed forest floor and bryophytes.

Table 3.10. Comparison of bryophyte species composition between canopy treatments in uplands at the site level using MRPP.

	Upland	
Group comparisons of canopy treatments	A	p value
continuous (6)/ clearcut (7)	0.269	**0.0004**
continuous (4)/ one-sided buffer (7)	0.257	**0.0004**
continuous (6)/two-sided buffer (10)	0.175	**0.0004**
clearcut (7)/ one-sided buffer (7)	-0.007	0.6127
clearcut (7)/ two-sided buffer (10)	0.014	0.1894
one-sided buffer (7)/ two-sided buffer (10)	0.006	0.3061

Note: number in parentheses indicates the number of sites in each group, A = Chance-corrected within-group agreement. P values <0.05 are listed in bold.

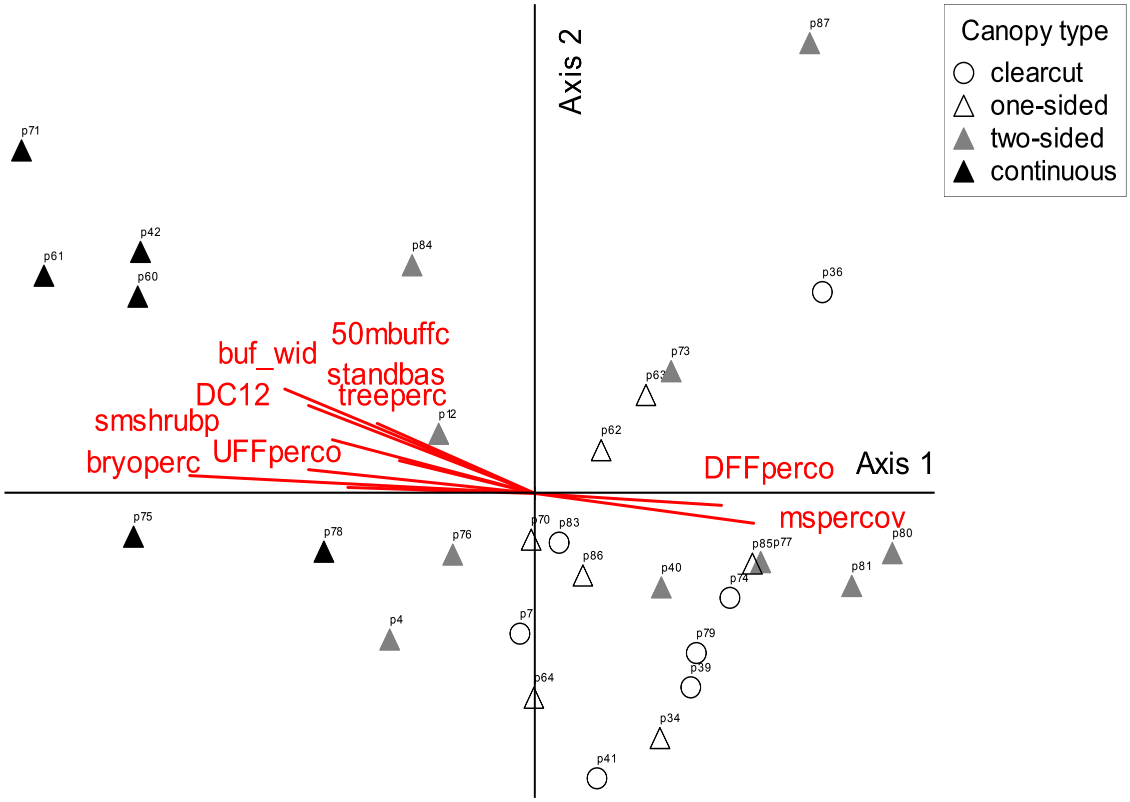


Figure 3.7. Joint plot of NMS ordination of bryophyte species composition in uplands adjacent to different canopy treatments: clear-cut (open circles) one-sided (open triangles), two-sided (grey triangles) and continuous (black triangles) overlaid with stand structure, habitat and substrate variables with R^2 values of 0.20 in the upland forests. Ordination based on species frequency data. Axis 1 accounts of 69.5% of the variation in the data while the second axis accounts for 20.1% (total=89.6%). Ordination is based on a two dimensional solution with a final stress of 13.23 and used 51 out of 71 species present (rare species occurring in less than 2 sites were omitted). The strength of the correlation is represented by the length of correlation vectors. Standbas = stand basal area; UFFpercov = percent cover of undisturbed forest floor; buf_wid = buffer width; 50m buffc = 50m buffer capacity; treeperc = conifer tree percent cover; bryoperc = bryophyte percent cover; DC12 = decay class 1 and 2; smshrubp = small shrub percent cover; mspercov = mineral soil percent cover; DFFpercov = disturbed forest floor percent cover.

Discussion

The results of this study demonstrate that riparian habitats immediately adjacent to small, high elevation streams are centres of bryophyte diversity in Interior British Columbia montane spruce forests. Whereas the retention of a buffer (one-sided or two-sided) appeared to mitigate the decline in species richness and frequency observed across the streamside-upland gradient for some forest-associated groups (Figure 3.6 c,d,i,j,q,r,u,v,aa and bb), riparian buffer strips appeared to have little effect on the bryophyte community reassembly in adjacent harvested uplands. At the site level, I found no evidence that the presence of riparian buffers ameliorates the effect of harvesting disturbance on the upland bryophyte community.

Pre-harvest microclimate gradients from small stream edge to upland have been detected for air temperature, soil temperature, surface air temperature and relative humidity (Brosofske et al. 1997, Danehy and Kirpes 2000, Stewart and Mallik 2006, however see Brooks and Kyker-Snowman 2008). Relative to surrounding uncut uplands, the microclimate immediately adjacent to streams is cooler, moister, less windy and shadier (Brosofske et al. 1997, Danehy and Kirpes 2000, Stewart and Mallik 2006). The higher bryophyte diversity around streams has been attributed to higher stream and soil water pH rather than tree basal area or soil moisture (Hylander and Dynesius 2006). Although these microclimate gradients were not measured directly in my study, expected gradients in microclimate variables may have interacted with both the gradients of alder and conifer sapling percent cover, as well with the gradients in substrate availability observed in this study. Streamside riparian habitats are also more disturbed than upland forest due to intermediate stream flow, debris flow and flooding which results in increased habitat and microclimate heterogeneity (Gomi et al. 2002). Increased habitat and microclimate heterogeneity has been shown to explain differences in species composition around streams (Gregory et al. 1991, Naiman and Decamps 1997). Such stochastic disturbances may result in higher bryophyte diversity (Jonsson 1997). The higher levels of bryophyte diversity adjacent to the stream edge observed in this study are similar to patterns of vascular plant diversity around high elevation streams in Maine (Pelletier 1999) as well as for larger streams at lower elevations (Salo et al. 1986, Gregory et al. 1991, Naiman et al. 1993, Naiman and Decamps 1997, Richardson et al. 2005, Sabo et al. 2005, Hylander et al. 2005, Hylander and Dynesius 2006, Hagan et al. 2006). My results, however, are contradictory to Whitman and Hagan (2000) who, using a functional group approach, found that riparian areas around small headwater streams in Maine did not contain more herbaceous plants species compared to upland forests (similar species diversity). MacNally et al. (2008) also didn't detect a sharp change in vascular plant vegetation between riparian and upland forest for small high elevation streams in Australia which they attributed to ground water availability. Overall, recent studies of plant diversity around small mountain streams have found conflicting results.

The trend of high species diversity adjacent to small high elevation streams exists over many different taxa—birds, invertebrates, small vertebrates such as small mammals, frogs and birds (Hagg and Dickinson 2000, Gomi et al. 2002, Cockle and Richardson 2003, Olson et al. 2007, Richardson et al. 2010). In my study, not only was bryophyte richness higher near the stream edge, but the bryophyte mat was more continuous with fewer empty microplots closer to the stream than further away. Furthermore, the response of forest-associated and disturbance-associated bryophyte groups was very different to the stream-upland gradient, indicating the importance of a functional group approach to monitoring plant communities. Hagan et al. (2006) also detected differences in the proportions of herbaceous species that were forest specialists, wetland specialists and generalists at different distances from the small high elevation stream bank.

Overall, plots of most forest-associated functional groups (liverworts, perennial stayers, closed canopy species, and species found on humus or logs) showed significant declines in richness for all canopy treatments and significant declines in frequency for all non-continuous canopy treatments as distance from stream increased. In comparison, disturbance-associated groups (colonists and open canopy species) richness and abundance was highest in clear-cuts and intermediate in one-sided and two-sided buffers compared to continuous canopy sites, and their frequency increased with distance from the stream edge for all non-continuous canopy treatments. Several of the forest-associated and disturbance-associated functional groups showed distinct changes for both richness and frequency around 5 – 10 m regardless of the canopy treatment which suggest the natural riparian/ upland ecotone for these small mountain streams. This is supported by Hagan et al. (2006) who also found a narrow riparian zone based on herbaceous plants exists on small headwater steams with greatest species richness between 5 to 13 m and contradicts Naiman et al.'s (1993) suggestion that small streams would not have riparian zones.

An important conclusion of this research is that canopy treatment had a significant impact on the characteristics of the bryophyte community gradient from stream to upland. In comparison to continuous forest, the gradients for forest-associated bryophytes in harvested canopy treatments were depressed, especially at distances of 10 m from the stream. For most forest-associated functional groups (liverworts, perennial stayers, closed canopy species, and species found on humus or logs), the relative position of the trend line for canopy treatments was highest for continuous canopy sites followed by one-sided buffer sites, two-sided buffer sites, and then clear-cuts. These findings imply that different harvesting techniques can have different effects on the natural bryophyte gradient existing from stream to upland. Interestingly, most of the graphs plotting bryophyte functional group richness and frequency against distance from the stream indicate that values in one-sided buffer sites were intermediate between values found in continuous forest sites and two-sided buffers (Figure 3.6 a-dd). In fact, whereas liverworts, known to be the most sensitive to disturbance (Söderström 1988, Fenton et al. 2003, Hylander et al. 2005), had significantly lower species richness and frequency in two-sided buffer sites than in continuous forests; there was no difference in liverwort richness and frequency between one-sided and continuous forest sites. In addition to liverworts, six other bryophyte functional groups showed significant richness declines in the two-sided: continuous forest comparisons but not in the one-sided: continuous forest comparison (Table 3.5). This suggests that the type of canopy treatment may be important to mitigate the impact of harvesting on the bryophyte community. Aspect has been shown to modify bryophyte response to harvesting (Hylander 2005, Åström et al. 2007) and the increased resilience (as measured by changes in richness and frequency relative to continuous sites) of the bryophyte community in one-sided buffers suggests that proximity to intact forest community may be as important as the immediate removal of the canopy. In this study, one-sided buffers had intact forest on the northern aspect of the stream side. Unmeasured environmental variables such as humidity, and either air or soil temperature may have had an overall cooling affect on the harvested side (Brosofske et al. 1997). Although one-sided buffers sites seem to offer better resistance to changes from harvesting compared to two-sided buffers, these one-sided canopy types are transitory and will likely be changed to two-sided buffers in the next round of forest harvesting.

Given that the canopy treatments represent a gradient of disturbance severity in both the extent of canopy removal as well as forest floor disturbance, it was difficult to predict the precise interaction between canopy treatment and stream distance. While few habitat, stand structure or substrate variables showed a significant interaction between canopy treatment and stream distance, I found significant interaction terms for the frequency of many functional groups: including both forest-associated bryophytes such as perennial stayers, and closed canopy species as well as disturbance-associated groups such as open canopy species and species found on mineral soil. In comparison, only the species richness of perennial stayers and species found on mineral soil showed interaction between distance from stream and canopy type. One of the most interesting aspects of the "interaction plots" is that while there is great variation in the richness and frequency values of many groups immediately adjacent to the stream, at 35 m from the stream, the values found in the harvested canopy types are much more similar to one another than they are to continuous forest. This similarity in response suggests a spatial homogenization of the bryophyte community in the harvested uplands. This similarity in bryophyte community could be due to similar habitat, substrate and microclimate (environmental conditions) in the uplands once past 35 m and/or due to the dispersal limitations of different species (dispersal filters). Meta-analyses of several studies on plant community reassembly however suggests that homogenization of forest plant communities (lower beta diversity) in former agriculture fields (recent forests) compared to ancient forests was due to dispersal limitations rather than environmental heterogeneity (Vellend et al. 2007).

Several ecological models predict that uplands adjacent to remnant buffer strips could support increased bryophyte diversity relative to uplands adjacent to harvested riparian areas. As stated above, the canopy treatments represent a gradient of disturbance severity, from minimal disturbance in continuous forest to the greatest disturbance within clear-cut. Based on the Intermediate Disturbance Hypothesis, diversity could be expected to be higher in the sites of intermediate disturbance (one-sided and two-sided buffers) relative to sites of high (clear-cuts) or low (continuous forest) disturbance. Previous research on bryophyte diversity has found evidence supporting high levels of plant diversity in areas of intermediate disturbance (Denslow 1980, Fenton et al. 2003, Baldwin and Bradfield 2007). However, at the site level, I found no evidence for significant differences in the richness of bryophyte, moss and liverwort between all four canopy treatments; continuous forest had the same number of species (similar gamma diversity) as non-continuous forests including clear-cut, though the actual species composition and evenness varied (Tables 3.7 and 3.9; Appendix A). As all upland sites sampled were clear-cut areas adjacent to different canopy treatments, the lack of differences may have originated in the same severity of disturbance in each clear-cut. In fact, substrate variables indicative of disturbance (percent of disturbed ground and mineral soil) were statistically indistinguishable (Table 3.6). Interestingly there seems to be a natural ratio of mosses to liverworts regardless of disturbance; most of the bryophytes in either the continuous or non-continuous upland areas are mosses with smaller numbers of liverworts. This higher ecosystem order is maintained despite disturbance and suggests ecological resilience at the landscape or site level (Holling 1973, Gunderson 2000).

Mass effects (Schmida and Wilson 1985) could maintain species diversity in uplands if forest bryophyte propagules from the adjacent riparian buffers disperse from their core habitat out into the adjacent upland. Despite the ordination showing a strong association between the nearby remnant canopy within 50 m (50 m buffer capacity) and bryophytes found in two-sided buffer sites, canopy treatment had little effect on the upland bryophyte species richness including the richness of liverworts (Figure 3.7 and Table 3.7). Bryophytes have been shown to be dispersal limited (Sundberg 2005, Pharo and Zartman 2007, Hylander 2009). In particular, Söderström and Jonsson (1989) found, despite leafy liverwort *Ptilidium pucherrinum* producing many small spores, the spores often only dispersed close to the parent plant and grew mainly on decaying logs (substrate dependent short-lived shuttle). Fenton and Bergeron (2006) also found that spread of *Sphagnum* into young forests was partially limited due to spore dispersal and also the availability of germination substrates. Hylander (2009) found despite proximity to nearby forest there was no increase in colonization rate for forest-associated bryophytes. The same trends in these studies thus support my results – bryophytes are dispersal limited. Furthermore, the results of my research corroborate previous findings by Nelson and Halpern (2005) where proximity to intact forest of 1 ha size did not prevent decline of sensitive liverworts in adjacent harvested areas. Other studies on biodiversity across edges have found only weak mass effects (Kunin 1998). There maybe more important influences such as the reproductive nature of the plant itself and microclimate differences which were not specifically examined in my study.

The use of a functional group approach in this research, however, clearly demonstrated the different responses of forest-associated and disturbance-associated bryophyte functional groups to canopy treatments (Table 3.7). Clear-cut uplands had lower diversity (both species richness and frequency) of forest-associated bryophytes (closed canopy species, wefts and epixylics) and higher diversity (both species richness and frequency) of disturbance-associated bryophytes (colonists, and species typically found on mineral soil/rock) compared to continuous forest sites. This result is supported by previous bryophyte studies looking at regenerating clear-cuts (Fenton and Frego 2005, Nelson and Halpern 2005, Dovčiak et al. 2006, Dynesius and Hylander 2007). The uplands of two-sided and one-sided buffer sites had richness levels similar to clear-cut sites for some functional groups (colonists, species typically found on mineral soil/rock, closed canopy species and weft species). At the site level, the similarity between clear-cut and one- and two-sided buffers may have resulted from the three harvested canopy treatments sharing many similarities in habitat, stand structure and substrate variables. Uplands adjacent to two-sided and one-sided buffers were no different than uplands adjacent to clear-cuts for the following variables: volume of coarse woody debris and stand basal area, and the percent covers of large shrubs (especially *Alnus* species), conifers, damp ground, and disturbed forest floor - factors which have been shown to be detrimental for bryophyte survival (Jonsson 1993, Rambo and Muir 1998, Dovčiak et al. 2006, Dynesius et al. 2008, 2009).

Overall, the results of this study indicate that at the site level, the presence of a nearby forested riparian buffer strip did not confer increased resilience measured as changes in functional group representation and species composition (Allen et al. 2005, Dynesius and Hylander 2007) to the adjacent upland bryophyte community. If resilience is measured as changes in functional group representation and species composition, increased resilience would have resulted in similar levels of forest-associated functional groups (liverworts, perennial stayers, closed canopy, epixylics (log dwelling species) in harvested canopy treatments and the continuous forest treatment. Conversely, increased resilience could have also been detected through a *lack* of an increase in disturbance-associated species (colonists, open canopy and mineral soil/rock associated species) in harvested canopy types. The results of this study clearly indicate that abundance of forest-associated bryophytes in the uplands (including liverworts (albeit with a $p = 0.065$), perennial stayers, closed canopy, and epixylics) declined regardless of any buffer type in the riparian area, while disturbance-associated species (colonists, open canopy and mineral soil/rock species) increased. In comparison, the abundance of groups for which it was difficult to predict their response, such as short- and long-lived shuttles, exhibited variable responses across the canopy treatments. The abundance of short-lived shuttles did not decline in harvested canopy treatments, while the abundance of long-lived shuttles was lower in harvested canopy treatments. This result is not surprising given the nature of short-lived shuttles (During 1992) which are thought to be adapted to microhabitats that are ephemeral and have abundant propagules in the soil bank (Ross-Davis and Frego 2004). In comparison, long-lived shuttles included species often living on branches or logs; their decline in the harvesting uplands is unsurprising.

The maintenance of some forest-associated species (perennial stayers, short or long-lived shuttles) in the uplands, seen as a lack of difference between any of the four canopy treatments, could be due to the presence of the mineral soil. Exposed mineral soil, rather than humus, is considered a rich source of propagules (especially diaspores) and thus may be the source of the persisting bryophytes (Jonsson 1993); mineral soil was highest in the non-continuous buffers. The diaspores of pleurocarpous mosses such as *Pleurozium schreberi* and *Hylocomium splendens* germinated frequently regardless of light conditions and were associated with low pH soils (Caners et al. 2009); perennial stayers such as *Pleurozium schreberi* and *Hylocomium splendens* also use vegetative propagules (detached shoot fragments) and are able to recolonize quickly after disturbance (Jonsson and Esseen 1990).

Similar to other bryophyte studies (Rambo and Muir 1998, Baldwin and Bradfield 2005, 2007, 2010, Botting and Fredeen 2006), my study involved an intense sampling protocol done at the fine spatial scale (0.1 m x 0.3 m) and included full transect searches which would detect the rarer bryophyte species (McCune and Lesica 1992). Thus the presence of some forest-associated species (perennial stayers, short or long –lived shuttles) in the uplands, seen as a lack of difference between any of the four canopy treatments, could be due to better detectability. In comparison other studies comparing forest-associated species in continuous forest and harvested areas only used quadrat sampling and no full transect searches which would have missed species occurring at low levels (Haeussler et al. 1999, Fenton et al. 2003, Fenton and Frego 2005, Nelson and Halpern 2005, Dovčiak et al. 2006, Dynesius and Hylander 2007, Shields et al. 2007, Dynesius et al. 2009). More importantly, however, the decline in abundance rather than richness indicates that harvested areas are not completely devoid of forest-associated species and argues for continued monitoring to determine their long term success.

My natural experiment was a snap shot of bryophyte compositional change relative to canopy treatment (spatial study) rather than a temporal one and included upland forests with a wide range of age from 5 – 25 years (Table 3.1). One could correctly state that we have not accounted for the different ages of the recovering forests. Even in forests not harvested there can be compositional changes in as little as four years although species richness and cover remains stable (Fenton et al. 2003). However, in forests that have been disturbed by logging, the difference in bryophyte composition was more pronounced and remains despite recovery of species richness. While proximity to a riparian buffer did not influence the upland bryophyte community at the site level, the upland is not depauperate of all bryophytes. The decline in abundance rather than richness implies that forest-associated bryophytes still exist in the uplands. Many different bryophytes including several forest species (*Ptillium crista-castrensis, Lophozia ventricosa*, *Pleurozium schreberi, Ptilidium pulcherrimum*) persisted in the upland habitat, although it is unclear if they will reproduce in this upland matrix. Through post harvest site preparation, there are depressions and abundant CWD left on site which likely can provide adequate microclimate for their survival (C. Petersen, personal observation). With reduced abundance of forest species in the clear-cut there may also be reduced competition for limited substrates (Rydin 1997). However, other studies of bryophyte community dynamics such as Dysenius and Hylander (2007) have shown that it takes a long time for forest bryophyte species to fully recover (30 – 50 years). The normal harvest rotation for lodgepole pine forests is 80 – 120 years in the central interior of British Columbia (Wei et al. 2003, Steen et al. 2007). The management of matrix habitats such as clear-cuts are thus considered important for conservation and maintaining biological diversity (Franklin and Lindenmayer 2009).

At the transect level, buffers did appear to ameliorate the decline in forest-associated bryophyte richness across a gradient from the stream out into the harvested uplands. These findings imply that different harvesting techniques can have different effects on the natural bryophyte gradient existing from stream to upland. By maintaining the biological diversity one may maintain functional diversity in a riparian forest ecosystem. Different species may respond differently to environmental change (increase or decrease) but still contribute to the riparian ecosystem functioning and thus provides resilience (response diversity - Elmqvist et al. 2003). Together riparian buffers near clear-cuts may offer insurance with a variety of habitats which promote overall bryophyte diversity and maintain riparian ecosystem functioning (*sensu* Elmqvist et al. 2003).

Chapter Four

RIPARIAN BUFFERS ON SMALL MOUNTAIN STREAMS – SUMMARY, SYNTHESIS AND IMPLICATIONS FOR MANAGEMENT

The purpose of my research was to examine the effectiveness of different riparian canopy treatments (clear-cut, one-sided buffer, two-sided buffer and continuous forest) and buffer width in maintaining riparian bryophyte diversity and functional group representation, as well as, promoting community reassembly post harvest in the adjacent uplands around small high elevation steams in the B.C. Interior Montane Spruce forests. The results of this study indicate that functionally, riparian buffer strips have ecological value for bryophyte communities found immediately adjacent to the stream (<10 m away) and much less value for upland community reassembly. In general, the frequency and richness of forest-associated bryophyte groups (liverworts, perennial stayers, closed canopy species, humus or log associated species) were similar among riparian sites with canopies, including one-sided and two-sided buffers, than without canopies. Hylander et al. (2002), Pharo et al. (2004, 2009), and Saunders et al. (1991) have suggested that variation in the buffer type (i.e., differences in remnant shape, pattern, size, and or landscape position) may influence bryophyte conservation; however in my study, neither the richness nor abundance of forest-associated species in the riparian sites differed in one-sided and two-sided buffers. Disturbance-associated bryophyte groups (colonists, open canopy species, and mineral soil/rock associated species) were significantly more abundant in clear-cut riparian sites than in sites with canopies; however their richness did not vary among the canopy treatments. Thus disturbance-associated bryophytes are present albeit at low levels in unharvested riparian forests and their numbers subsequently increase with harvest.

Based on *apriori* ecological processes, this study found that riparian forest-associated bryophyte community composition (species richness and frequency) was largely controlled at the landscape level by remaining intact forest within 50 m (immigration and extinction), as well as smaller scale microhabitat variables such as habitat quality (mineral rock/rock, soft CWD and concavity) although microclimate (slope and *Alnus* species) made only minor contributions. Interestingly, only the frequency but not species richness of forest-associated functional groups showed a positive association with soft CWD. A variety of decay classes of CWD has been shown to be important to maximize the richness of forest bryophytes (Rambo and Muir 1998). Not surprisingly, some disturbance-associated bryophytes (colonist and mineral soil/rock species) showed a negative relationship with a 50 m buffer capacity. Overall, my study found narrow strip shaped buffers with an average width of 10 – 15 m regardless of position (one-sided versus two-sided) largely mitigated the effects of clear-cutting on the riparian community around small, high-elevation streams. This study provides evidence that for forest-associated bryophytes small narrow buffers are better than no buffer around small headwater streams. This study also contributes to the growing body of evidence indicating the value of buffers for bryophytes in other ecosystems (Hylander et al. 2002) as well as for other taxa such as birds (Hagg and Dickinson 2000, Staicer et al. 2006), frogs (Olson et al. 2007) and mammals (Cockle and Richardson 2003, Martell and Foote 2006, Lees and Peres 2008). However Marczak et al.'s (2010) meta-analysis of 396 papers found most buffer widths used do not maintain the terrestrial fauna at the same levels compared to the undisturbed riparian areas. They also found the response among the different taxa was not consistent; birds (particularly edge-associated species) and arthropods abundance was greater in riparian buffers compared with unharvested riparian sites whereas amphibian abundance decreased.

The results of the upland study however suggest that riparian buffers have no effect on the maintenance of forest-associated bryophytes (liverworts, perennial stayers, closed canopy species and epixylics) in the logged uplands. The uplands consisted largely of disturbance-associated bryophytes (colonists, open canopy species, and species preferring mineral soil/rock) in terms of both species richness and frequency, and very few forest-associated bryophytes (liverworts, perennial stayers, closed canopy species and epixylics) in terms of both species richness and frequency. As with the riparian study, buffer width and remaining canopy cover within 50 m radius strongly affected the bryophytes in the riparian sites with continuous canopy, whereas disturbance appeared to affect species composition in sites with non-continuous canopies (buffers) or clear-cut riparian sites. The management of the matrix (clear-cut) (Franklin and Lindenmayer 2009), and the maintenance of biological legacies (logs) for bryophytes (Pharo and Lindenmayer 2009) in the uplands is considered important for subsequent recovery of the harvested forest. However, studies of bryophyte community dynamics such as Dysenius and Hylander (2007) have shown that it takes a long time for forest bryophyte species to fully recover (30 – 50 years) and the normal harvest rotation for lodge-pole pine forests in the central interior of British Columbia is 80 – 120 years (Wei et al. 2003, Steen et al. 2007).

Microclimate gradients are known to exist from stream edge to uplands and can be influenced by the presence of a riparian buffer (Brosofske et al. 1997). These gradients in turn affect riparian plant life (Gregory et al. 1991, Stewart and Mallik 2006). The results of this study clearly document a decline in bryophyte species richness and frequency with increasing distance from small, high-elevation streams. Conversely, “patchiness”, as measured by the frequency of empty microplots, increased with distance from the stream edge. Whereas a distinct vascular plant community has been detected around high-elevation small streams, my results are the first to document a distinct bryophyte community surrounding high-elevation streams (see Table 3 in Hylander and Dynesius (2006) for a description of bryophyte communities around larger streams). In addition, the functional group approach used in this study detailed the differential response of bryophyte groups to the stream-upland gradient. Forest-associated bryophytes had the highest diversity closest to the stream for all canopy types. In general, forest bryophytes (liverworts, perennial stayers, closed canopy species, and epixylics) showed a marked decline in species richness and frequency regardless of the presence of a buffer as distance from the stream increased. Conversely, disturbance-associated bryophytes (colonists, open canopy, and species preferring mineral soil/rock) increased in richness and abundance with distance from the stream - buffers did not reduce the response to disturbance – one could still see a shift in community composition.

Interestingly, by a distance of 35 m there was little difference in terms of species richness among the bryophyte community in the harvested uplands. More importantly, however, the decline in abundance rather than richness indicates that harvested areas are not completely devoid of forest-associated species and argues for the importance of the matrix (Franklin and Lindenmayer 2009).

Defining riparian zones is an important aspect of forest management around riparian areas (Blinn C.R. and Kilgore M.A. 2001). Riparian areas have a diverse plant community (Gregory et al. 1991, Naiman and Decamps 1997) which is typically used to assess the extent of the riparian zone. In the past it has been assumed that small streams have little or no riparian zone in contrast to larger streams (Naiman et al. 1993). However recently a 0 - 5 m riparian zone (ecotone) was found around first order high elevation streams by both Hagan et al. (2006) and MacNally et al. (2008) using floristic analyses of vascular plants. Danhey and Kirpes (2000) also detected an ecotone using relative humidity around small streams (1.3 – 5 m) in the dry Ponderosa pine forests. My study has added further support to this current literature by detecting a distinct ecotone around 5 – 10 m in width along the small high elevation stream-upland gradient using poikilohydric bryophytes. Fritz et al. (2009) and Frego (2007) suggest bryophyte assemblages are effective indicators of the hydrology of riparian areas. By detecting a distinct riparian zone around small high elevation streams, more consideration and subsequent protection could be given to protect the rich biodiversity around these headwater streams by forest management.

Furthermore, this study documented that harvesting techniques may have a profound effect on the nature of the bryological gradient extending from the stream to the upland. Two-sided buffers were less effective than one-sided buffers at preventing the decline in both species richness and frequency of forest-associated functional groups (liverworts, perennial stayers, closed canopy species, species found on humus or litter, and epixylics). Although one-sided buffers were more effective at preventing the decline in forest-associated bryophytes, given the current state of harvesting and forestry regulations in BC, one-sided buffer sites are ephemeral and will likely become two-sided buffer sites during future salvage harvesting. It is also important to note that one-sided buffers had intact forest on the northern aspect of the stream side which was not sampled. Future work could be to compare the bryophyte community on the northern aspect of one-sided buffers with two-sided buffers, continuous canopy and clear-cuts to see if there is a difference due to aspect. Hylander (2005) found there was more forest moss growth (*Hylocomium* species) on the northern aspect compared with the southern aspect. This suggests that the type of buffer relative to the stream position maybe important owing likely to changes in microclimate with aspect (edge orientation - sensu Hylander et al. 2005). Other unmeasured environmental variables such as humidity, and either air or soil temperature may have had an overall cooling effect across the stream on the adjacent harvested side (Brosofske et al. 1997). Again future studies could look at the effect of one-sided buffers versus other canopy treatments on these microclimate variables (humidity, air and soil temperature) on the adjacent harvested side.

Forest fire, attack by MPB, and commercial harvesting are the three major sources of disturbance and mortality of mature lodgepole pine in the Interior (Taylor and Carroll 2004, Barclay et al. 2009). Natural disturbance regimes such as wildfire were common in lodgepole pine forests to which the conifer species is well adapted through the use of serotinous cones (Lloyd et al. 1991). However, with fire suppression over the past 85 years the amount of area burned by wildfire in British Columbia has decreased significantly (Taylor and Carroll 2004). As a result 55% of the pine forests became susceptible to mountain pine beetle attack. The cumulative area of BC affected by the mountain pine beetle was estimated at 14.5 million hectares in 2008 (Ministry of Forest and Range 2008). The provincial government (Forest Practices Board 2009) recommended a landscape level approach for maintaining biodiversity during salvage logging for forest managers in the Interior MS region during the MPB attack. The Chief Forester of BC recommended an increase (timber uplift) in allowable annual cut to 80%, as well as a “conservation uplift” (an increase in retention of mature forest structure in harvested areas) at the landscape level (even though it was not be legally binding; Snetsinger 2005). Unfortunately the FPB report found that in post 2005 the salvage logging was not handled at the landscape level but at the stand level. Individual forest action plans driven by various local reasons resultied in large harvested areas (greater than 250 ha ranging up to 1000 ha) with little conservation of mature forests. Thus there are huge tracts of logged forest with little connectivity though reforestation has been done (Ministry of Forest and Range 2008). Disturbance processes such as logging have been shown to drastically alter the bryophyte community particularly around streams by reducing species diversity (Haeussler et al. 1999, Ross-Davis and Frego 2002, Fenton and Frego 2005, Nelson and Halpern 2005, Dynesius and Hylander 2007). Ecologists have suggested that natural disturbances should be used as a guide to manage human-induced disturbances such as logging and grazing as the species would be well adapted to these natural disturbances (Lindenmayer et al. 2008). However, due to the complex nature of natural disturbances it is hard to mimic them. Also both natural and human disturbance regimes will likely exist at the same time in the environment i.e. salvage logging after mountain pine beetle attack. Thus the best approach is to use adaptive management techniques and apply different conservation strategies in different places and monitor the response (Lindenmayer et al. 2008).

To encourage old-growth associated biodiversity in younger managed stands and thus recovery from harvesting, we need to improve our understanding of which bryophyte species are associated with old-growth and their habitat requirements (Rambo and Muir 1998). Thus my results have important management implications as they indicate that even small buffers can mitigate forestry impacts on riparian areas adjacent to small, high-elevation streams. Although the remaining canopy cover within 50 m radius strongly affected the bryophytes in the riparian sites, at minimum, forest managers should be encouraged to use narrow (10 -15 m) two-sided buffers to maintain the riparian bryophyte community around small mountain streams, though ideally one-sided buffers maintained higher richness and abundance of forest-associated bryophytes. Ideally the use of a variety of buffer widths and spatial arrangements (one-sided and two-sided) along the length of a single high elevation stream would balance the conflicting management priorities of biodiversity conservation and timber harvest (Dovčiak et al.

2006, Olson et al. 2007). Adaptive management is recommended to allow the preservation of overall species diversity especially as different taxa respond differently which affects overall ecosystem functioning (Gunderson 2000, Lindenmayer et al. 2008, Franklin and Lindenmayer 2009). The use of variable harvesting techniques, with minimal disturbance and a range of buffer widths, maybe more appropriate for preserving bryophytes (Hylander et al. 2002, Fenton and Frego 2005, Rosenvald and Löhmus 2008). This undisturbed buffer canopy may act as refugia especially for liverworts, the most sensitive group (Söderström 1988), and forest mosses (Fenton and Frego 2005). Landscape heterogeneity, habitat quality and substrate features are also important for bryophyte survival (Hylander 2004, Dynesius et al. 2009). Attention should be paid to conserving a variety of decay classes of coarse woody debris as a range of habitats allow for a diversity of forest bryophytes (Rambo and Muir 1998, Rambo 2001, Pharo and Lindenmayer 2009). In particular, soft CWD (decay class 4/5) was important for the survival of certain forest bryophytes (epixylics) such as *Ptilidium pulcherrimum* or *Lophozia species*. Minimizing soil disturbance would also maintain sensitive forest bryophytes particularly around small streams (Fenton and Frego 2005).

Concern exists about how permanent the small narrow riparian buffer strips are due to blowdown (Reid and Hilton 1990, Richardson 2004). Wood recruitment models are used to predict the amount of windthrow at riparian buffers (Liquori 2006). The rate of blowdowns in riparian buffers may not be related to buffer width but to the topography and orientation of the strip to the prevailing wind (Ruel et al. 2001, however see Liquori 2006). Thus narrower buffer widths may not be more prone to blowdown than wider buffer widths. However, Grizzel and Wolff (1998) found on average windthrow affected 33% of the trees around small high elevation streams in northwest Washington. Though I did not look at windthrow per say in my study of riparian buffers around small high elevation streams, I did measure total CWD which is a measure of fallen trees of various decay classes and would indirectly give a sense of wood recruitment. Interestingly the volume of total CWD was not significantly different among the four canopy treatments

(Table 2.4) suggesting there was no more windthrow in riparian buffers strips than continuous riparian forests.

Various studies have shown that both local and landscape level variables acting across multiple scales appear to influence the recovery of disturbed plant communities (Holl and Crone 2004). Local biotic and abiotic factors (overstorey cover, exotic cover, bare ground, elevation, and soil texture) explained much of the variance in riparian vascular plant species richness and abundance, whereas proximity to a source of reproductive propagules (a landscape factor) and dispersal ability were shown to play a small role in the recovery of riparian vascular plant communities (Holl and Crone 2004). Stand age and time since disturbance did not seem to be important for riparian vascular plant recovery. The same findings have been found for the community reassembly of forest bryophytes in *Picea marina* forests where stand age and time since disturbance was shown to be not as important as habitat variables such as percent of mineral soil, shrubs, canopy, total CWD or water table position (Fenton and Bergeron 2008). The relative term old-growth forest depends on the conifer tree species being considered; lodgepole pine-Douglas fir forests in the BC Interior typically reach climax around 50 -75 years. In my study the lodgepole pine-Douglas fir forests examined were young second growth stands with an age range of 0 – > 17 years in order to limit the influence of stand age on the bryophyte response. The average age (time since harvesting disturbance) of the one-sided buffer sites was 10.29 ± 1.38 years, two-sided buffer sites was 9.50 ± 1.45 years, clear-cut sites was 16.86 ± 0.70 years, and continuous sites was approximately > 25 years (last disturbance time unknown). Thus, due to a limited range of disturbance dates per canopy type we did not look at the effect of stand age on bryophyte richness and frequency in our study (Table 2.1). Further work with more sites spanning a wider range of disturbance dates per canopy type is warranted.

The results of this study may result in an increased understanding of the value of riparian buffers around small high elevation streams for protecting various flora and fauna. It also may lead to more flexible guidelines for buffer width in the Interior of BC and can be used to inform management decisions (target-species management – Olson et al. 2007). For example, in certain situations, buffers larger than 10 m may be warranted if land managers are interested in conserving populations of sensitive bird species (Hagg and Dickinson 2000, Staicer et al. 2006), frogs (Olson et al. 2007) and mammals (Cockle and Richardson 2003, Lees and Peres 2008). "We can't manage all species in all places at all times and what benefits one species may not benefit another" (Donnelley and Wedeles 2008). A quantitative review of the riparian buffer width guidelines from Canada and the United States (Lee et al. 2004) outlined a shift away from the "one-size fits all" approach to more "tailor-made" buffers with the more complex guidelines. The use of a variety of buffer widths, patch reserves of different sizes and dispersed tree retention (Aubry et al. 2009) may be a more effective forest management approach to balance conflicting species and timber production priorities (Table 6 in Olson et al. 2007).

Overall, the knowledge that even narrow strip shaped buffers with an average width of 10 – 15 m regardless of position (one-sided versus two-sided) can mitigate the effects of clear-cutting on the riparian bryophyte community around small, high-elevation streams, although there was no effect on community reassembly in the uplands, can be used to support adaptive management decisions made by forestry professionals to enhance conservation.

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Appendix A. Bryophyte species, functional groups, and location. Codes at bottom of last page.

Species List	Taxonomic Group	LHS	Canopy Preference	Growth Form	Main Substrate affinity	Location
Atrichum selwynii	M	Co	open	ST	MS	U
Aulacomnium palustre	M	Ps	open	TT	H	U/R
Barbula convoluta var. eustegia	M	Co	open	ST	MS	R
Barbula (Didymodon) vinealis	M	Co	open	CU	MS	U
Brachythecium species	M	Ps	closed	RM	H	U/R
Bryum caespiticium	M	Co	open	ST	MS	U/R
Bryum capillare	M	Ps	open	ST	G	U/R
Bryum spp.	M	Co	open	ST	MS	U
Bryum weigelii	M	Ss	open	TT	H	U/R
Calliergon stramineum	M	Ps	open	TH	H	U/R
Campylium hispidulum	M	Ps	closed	RM	H	R
Campylium stellatum	M	Ps	open	ST	H	U/R
Ceratodon purpureus	M	Co	open	ST	MS	U/R
Climacium dendroides	M	Ps	open	DE	H	U/R
Cratoneuron filicinum	M	Ps	open	TT	H	R
Dichodontium pellucidum	M	Co	generalist	TT	H	R
Dicranella spp	M	Co	open	ST	L	U/R
Dicranoweisia crispula	M	Ps	open	CU	MS	U/R
Dicranum fuscescens	M	Sl	generalist	ST	G	U/R
Dicranum scoparium	M	Ps	generalist	ST	L	U/R
Dicranum spp	M	Co	generalist	ST	G	U/R
Dicranum tauricum	M	Sl	generalist	ST	LOG	U/R
Encalypta rhaptocarpa	M	Ss	closed	ST	MS	U/R
Eurhynchium pulchellum	M	Ps	open	RM	H	R
Fontinalis antipyretica	M	Sl	closed	WE	R	R
Funaria hygrometrica	M	Co	generalist	OT	MS	U/R
Hygrohypnum ochraceum	M	Ps	closed	WE	MS	R
Hylocomium splendens	M	Ps	closed	WE	H	U/R
Hypnum revolutum	M	Ps	open	SM	L	U/R
Leptobyrum pyriforme	M	Co	open	OT	L	U/R
Mnium ambiguum (lycopodioides)	M	Ss	closed	TT	H	R
Mnium arizonicum	M	Ss	closed	ST	MS	R
Mnium spinulosum	M	Sl	closed	ST	LOG	U/R
Mnium spp	M	Sl	closed	ST	LOG	U/R
Oncophorus wahlenbergii	M	Sl	closed	ST	L	U
Philonotis fontana	M	Ss	open	ST	MS	U/R
Plagiomnium ciliare	M	Ss	closed	TT	H	U/R
Plagiomnium drummondii	M	Ss	closed	TT	H	R
Plagiomnium ellipticum	M	Ps	closed	TT	H	U/R
Plagiomnium insigne	M	Ss	closed	TT	H	U/R
Plagiomnium spp	M	Ss	closed	TT	H	U/R
Plagiothecium denticulatum	M	Sl	closed	SM	LOG	U/R
Plagiothecium cavifolium	M	Ps	closed	SM	H	R
Plagiothecium laetum	M	Sl	closed	SM	H	U/R
Platydictya jungermanioides	M	Ps	closed	SM	H	U/R
Pleurozium schreberi	M	Ps	closed	WE	G	U/R
Pohlia cruda	M	Ss	closed	OT	L	U/R
Pohlia nutans	M	Ss	generalist	OT	L	U/R
Pohlia proligera	M	Co	open	ST	MS	R
Pohlia spp	M	Ss	generalist	ST	L	U/R

Appendix A. continued.

Polytrichum juniperinum	M	Co	open	TT	MS	U/R
Polytrichum piliferum	M	Co	open	TT	MS	U/R
Polytrichum strictum	M	Co	open	TT	H	U/R
Polytrichastrum alpinum	M	Co	generalist	TT	MS	U/R
Polytrichium spp	M	Co	open	TT	MS	U/R
Pseudoleska stenophylla	M	Sl	closed	RM	LOG	R
Pseudoleskeella tectorum	M	Sl	closed	RM	L	R
Pterigynandrum filiforme	M	Ps	closed	TH	R	R
Ptillium crista-castrensis	M	Ps	closed	RM	H	R
Rhizomnium magnifolium	M	Ps	generalist	ST	H	U/R
Rhytidiadelphus triquetrus	M	Ps	closed	RM	H	U/R
Rhytidiopsis robusta	M	Ps	closed	WE	H	U/R
Roellia roe	M	Ps	closed	OT	H	U/R
Sanionia uncinata	M	Ps	generalist	WE	H	U/R
Sphagnum warnstorfii	M	Ps	open	TT	H	R
Splachnum sphaericum	M	Ss	closed	TT	SCAT	U/R
Tetraphis pellucida	M	Ss	closed	ST	LOG	U/R
Thuidium recognitum	M	Ps	closed	WE	H	R
Timmia austriaca	M	Ps	closed	TT	H	U/R
Tomentypnum nitens	M	Ps	open	Tsp	H	U/R
Tortula ruralis	M	Sl	open	OT	MS	U/R
Barbilophozia hatcheri	L	Sl	generalist	RM	G	U/R
Barbilophozia lycopodioides	L	Sl	closed	RM	L	U/R
Barbilophozia spp.	L	Sl	closed	RM	G	U/R
Blepharostoma trichophyllum	L	Ps	closed	TH	LOG	U/R
Calypogeia muelleriana	L	Ps	closed	SM	H	U/R
Cephaloziella divaricata	L	Sl	generalist	TH	MS	U/R
Cephalozia lunulifolia	L	Ps	closed	TH	LOG	U/R
Chiloscyphus polyanthos	L	Ps	generalist	SM	H	R
Conocephalum conicum	L	Sl	closed	TM	H	R
Lepidozia reptans	L	Sl	closed	SM	LOG	U/R
Lophocolea heterophylla	L	Co	closed	TH	H	R
Lophocolea minor	L	Co	closed	TH	H	R
Lophozia guadriloba	L	Sl	closed	SM	MS	R
Lophozia heterocolpos	L	Sl	closed	SM	MS	R
Lophozia longidens	L	Sl	generalist	ST	LOG	U/R
Lophozia spp	L	Ps	closed	SM	LOG	U/R
Lophozia ventricosa	L	Sl	closed	ST	LOG	U/R
Marchantia polymorpha	L	Co	generalist	TM	H	U/R
Pellia spp	L	Sl	closed	TM	H	R
Plagiochilla asplenoides	L	Ps	closed	ST	H	U/R
Ptilidium pulcherrimum	L	Sl	closed	SM	LOG	U/R
Ptilidium spp	L	Sl	closed	SM	LOG	U/R
Ptilidium californicum	L	Sl	closed	SM	LOG	U
Scapania mucronata	L	Sl	open	RM	LOG	R
Tritomaria exsectiformis	L	Sl	closed	SM	H	U/R
Tritomaria scitula	L	Sl	closed	SM	L	R
Scapania undulata	L	Ps	open	RM	LOG	U/R

Codes: Co = colonist; Ps = perennial stayer; Sl = long-lived shuttle; Ss = short-lived shuttle; ST = short turf; TT = tall turf; CU= cushion; RM = rough mat; TH - thread mat; TM = thalloid mat; WE = weft; OT = open turf; SM = smooth mat; DE = dendroid; Tsp = sphagnoid; MS= mineral soil; R = rock; H = humus; L = litter; G = general; U = upland; R = riparian.

Appendix B. Regression analysis summaries of the top candidate models based on information-theoretic methods looking at select predictor variables affecting riparian species richness across various functional groups. n= 30 sites.

Functional Groups:

Taxonomic	**Model type**	**AICc**	**K**	**ΔAICc**	**ωi**	**ER**	**logLik**	**D^{2}_{adj}**	**apriori hypotheses**	**Variables**
Bryophyte	top	203.5	5	0.0	0.61	1.00	-95.50	0.44	IE+HQ	50buffcap+mspc+DC4/5+concavity
	top/global	205.3	7	1.8	0.25	2.43	-98.45	**0.25**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Liverwort	top	165.4	4	0.0	0.47	1.01	-77.91	0.33	HQ	mspc+DC4/5+concavity
	top	165.7	5	0.3	0.41	1.15	-76.59	0.35	IE+HQ	50buffcap+mspc+DC4/5+concavity
	global	172.0	7	6.6	0.02	27.41	-76.46	**0.30**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Moss	top	183.0	4	0.0	0.42	1.00	-86.69	0.29	IE+M	50buffcap+*Alnus* spp.percov+slope
	top	184.4	5	1.4	0.20	2.08	-85.96	0.31	IE+HQ	50buffcap+mspc+DC4/5+concavity
	top	185.0	2	2.0	0.15	2.74	-90.27	0.13	IE	50buffcap
	global	186.2	7	3.2	0.08	5.10	-83.57	**0.43**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Life History Strategy										
Colonist	top	145.7	2	0.0	0.35	1.00	-70.62	0.041	HQ	concavity
	top	146.6	2	1.0	0.22	1.61	-71.09	0.014	HQ	mspc
	top	147.3	2	1.6	0.16	2.20	-71.41	-0.004	IE	50buffcap
	global	157.6	7	12.0	0.00	NA	-69.27	-0.08	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Perennial Stayer	top	163.0	2	0.0	0.62	1.00	-79.26	0.35	IE	50buffcap
	global	170.6	7	7.7	0.01	46.51	-75.77	**0.43**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Long lived Shuttle	top	148.3	4	0.0	0.44	1.00	-69.33	0.40	HQ	mspc+DC4/5+concavity
	top	150.0	5	1.7	0.19	2.37	-68.74	0.41	IE+HQ	50buffcap+mspc+DC4/5+concavity
	global	152.2	7	3.9	0.06	7.21	-66.56	**0.46**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Short lived Shuttle	top	129.6	2	0.0	0.36	1.00	-62.57	0.07	M	*Alnus* spp.percov
	top	130.7	2	1.1	0.20	1.77	-63.13	0.01	IE	50buffcap
	top	131.3	2	1.7	0.15	2.41	-63.44	-0.03	M	slope
	global	137.6	7	8.0	0.01	55.05	-59.25	**0.34**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity

Appendix B. continued.

Canopy	**Model type**	**AICc**	**K**	**ΔAICc**	**ωi**	**ER**	**logLik**	**D^2_{adj}.**	**apriori hypotheses**	**Variables**
Closed	top	182.6	5	0.0	0.70	1.00	-85.07	0.52	IE+HQ	50buffcap+mspc+DC4/5+concavity
	global	186.8	7	4.1	0.09	7.85	-83.83	**0.52**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Open	top	158.5	2	0.0	0.51	1.00	-77.02	0.13	HQ	concavity
	top	159.8	4	1.3	0.27	1.92	-75.09	0.17	HQ	mspc+DC4/5+concavity
	global	168.1	7	9.6	0.00	120.00	-74.48	0.09	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Generalist	top	137.3	2	0.0	0.75	1.00	-66.41	0.18	IE	50buffcap
	global	148.9	7	11.6	0.00	337.84	-64.91	**0.18**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Substrate Affinity										
Generalist	top	106.1	2	0.0	0.67	1.00	-50.85	0.00	IE	50buffcap
	global	119.3	7	13.2	0.00	NA	-50.11	-0.11	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Humus	top	168.4	2	0.0	0.40	1.00	-81.97	0.28	IE	50buffcap
	top	169.3	4	0.9	0.25	1.59	-79.86	0.34	IE+M	50buffcap+*Alnus* spp.percov+slope
	top	170.0	5	1.7	0.18	2.28	-78.77	0.38	IE+HQ	50buffcap+mspc+DC4/5+concavity
	global	175.0	7	6.6	0.01	26.76	-77.94	**0.37**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Litter	top	127.5	2	0.0	0.31	1.00	-61.52	0.06	IE	50buffcap
	top	128.4	2	0.9	0.20	1.54	-61.96	0.02	M	*Alnus* spp.percov
	top	129.4	4	1.9	0.12	2.51	-59.88	0.15	IE+M	50buffcap+*Alnus* spp.percov+slope
	global	134.5	7	7.0	0.01	32.19	-57.68	**0.28**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Log	top	137.4	4	0.0	0.39	1.01	-63.92	0.35	HQ	mspc+DC4/5+concavity
	top	137.9	4	0.5	0.31	1.28	-64.15	0.34	IE+M	50buffcap+*Alnus* spp.percov+slope
	global	142.0	7	4.6	0.04	10.00	-61.47	**0.41**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Mineral soil, Rock	top	131.8	2	0.0	0.42	1.01	-63.67	0.11	HQ	concavity
	top	133.2	2	1.4	0.20	2.06	-64.39	0.06	HQ	mspc
	top	133.5	4	1.7	0.18	2.37	-61.95	0.15	HQ	mspc+DC4/5+concavity
	global	142.5	7	10.7	0.00	217.62	-65.24	0.06	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity

Note: Generalized linear models used Poisson error term and logarithmic link function. For each model, AICc (corrected AIC) was used due to small sample size, K = number of estimable parameters including intercept, ΔAICc is the difference between the lowest AICc of all models tested and each model's AICc, ωi is Akaike weight, ER = evidence ratio, logLik is the maximized log-likelihood, D^2_{adj} is the adjusted Deviance squared, global D^2adj, a measure of goodness of fit, is from the most complex (global) model. All other models are nested within global. Only candidate models with a ΔAICc of ≤ 2 from all tested are considered the most likely and are shown. Growth Forms were excluded due to rareness which invalidated many models. IE (immigration & extinction) = 50 m buffer capacity (50buffcap); microclimate (M) = *Alnus* spp. percent cover + slope; HQ (habitat quality) = mineral soil percent cover (mspc) + DC4 & 5 (decay class) + concavity. Bolded > 0.10 global D^2adjusted. A minimum of nine basic models were run for each functional group.NA = not applicable.

Appendix C. Regression analysis summaries of the top candidate models based on information-theoretic methods looking at select predictor variables affecting riparian species frequency across various functional groups. n= 30 sites.

Riparian Species frequency

Functional Groups:

Taxonomic	**Model type**	**qAICc**	**K**	**ΔqAICc**	**ωi**	**ER**	**logLik**	**D^2adj.**	**apriori hypotheses**	**Variables**
Bryophyte	top	55.55	2	0.0	0.65	1.00	-141.95	0.26	HQ	mspc
	top	58.22	4	2.7	0.17	3.79	-136.14	0.26	HQ	mspc+DC4/5+concavity
	global	64.97	7	9.4	0.01	110.73	-166.14	**0.20**	IE+M+HQ	50buffcap+*Alnus spp.* percov+slope+mspc+DC4/5+concavity
Liverwort	top	46.36	2	0.0	0.42	1.00	-162.82	0.15	IE	50buffcap
	top	47.11	2	0.8	0.29	1.46	-165.89	0.13	HQ	mspc
	global	56.18	7	56.2	0.00	136.36	-152.33	0.07	IE+M+HQ	50buffcap+*Alnus spp.* percov+slope+mspc+DC4/5+concavity
Moss	top	56.12	2	0.0	0.66	1.00	-141.02	0.25	HQ	mspc
	global	65.67	7	9.5	0.01	117.86	-132.94	**0.19**	IE+M+HQ	50buffcap+*Alnus spp* percov+slope+mspc+DC45+concavity
Life History Strategy										
Perennial Stayer	top	52.62	2	0.0	0.70	1.00	-159.88	0.41	HQ	mspc
	global	62.67	7	10.0	0.00	151.61	-151.75	0.03	IE+M+HQ	50buffcap+*Alnus spp.* percov+slope+mspc+DC4/5+concavity
Colonist	top/global	69.74	7	0.0	0.50	1.00	-122.79	**0.61**	IE+M+HQ	50buffcap+*Alnus spp.* percov+slope+mspc+DC4/5+concavity
	top	69.76	4	0.0	0.50	1.01	-141.41	0.56	IE+M	50buffcap+*Alnus* spp. percov+slope
Long-lived Shuttle	top	59.69	2	0.0	0.21	1.00	-159.61	0.07	M	slope
	top	59.87	4	0.2	0.20	1.10	-146.12	0.13	IE+M	50buffcap+*Alnus* spp. percov+slope
	top	60.01	2	0.3	0.18	1.18	-160.59	0.06	IE	50buffcap
	top	61.72	3	2.0	0.08	2.77	-158.83	0.04	M	*Alnus* spp. percov+slope
	global	62.18	7	2.5	0.06	3.48	-129.94	**0.20**	IE+M+HQ	50buffcap+*Alnus spp.* percov+slope+mspc+DC4/5+concavity
Short-lived Shuttle	top	54.16	2	0.0	0.23	1.00	-143.90	0.08	M	slope
	top	54.19	2	0.0	0.23	1.00	-143.99	0.08	M	*Alnus* spp.percov
	top	54.51	3	0.3	0.20	1.17	-138.02	0.12	M	*Alnus* spp. percov+slope
	top	55.43	2	1.3	0.12	1.86	-147.72	0.04	HQ	concavity
	global	63.72	7	9.6	0.00	117.35	-135.34	0.01	IE+M+HQ	50buffcap+*Alnus spp.* percov+slope+mspc+DC4/5+concavity

Appendix C. continued.

Canopy Preference	**Model type**	**qAICc**	**K**	**ΔqAICc**	**ωi**	**ER**	**logLik**	**D^2adj.**	**apriori hypotheses**	**Variables**
Closed	top	51.53	2	0.0	0.52	1.00	-190.98	0.33	HQ	mspc
	top	52.82	2	1.3	0.28	1.91	-196.45	0.30	IE	50buffcap
	global	59.27	7	7.7	0.01	47.73	-171.27	**0.32**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
General	top	57.27	2	0.0	0.30	1.00	-169.92	0.05	IE	50buffcap
	top	54.85	2	1.0	0.19	1.64	-173.84	0.02	HQ	mspc
	global	60.65	7	11.3	0.00	290.48	-165.73	-0.10	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Open	top/global	84.92	7	0.0	0.52	1.00	-184.04	**0.51**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
	top	59.60	6	0.6	0.39	1.33	-198.92	0.47	M+HQ	*Alnu*s spp.percov+slope+mspc+DC4/5+concavity
Substrate Affinity										
General	top	44.56	4	0.0	0.54	1.00	-242.28	0.36	IE+M	50buffcap+*Alnus* spp.percov+slope
	global	49.22	7	4.7	0.05	10.23	-220.12	**0.37**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Humus	top	50.95	2	0.0	0.6	1.00	-173.79	0.21	HQ	mspc
	global	61.27	7	10.3	0.00	174.35	-165.70	**0.12**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Litter	top	64.55	2	0.0	0.18	1.00	-117.11	-0.01	HQ	concave
	top	64.80	2	0.2	0.16	1.15	-117.60	-0.02	IE	50buffcap
	top	64.87	2	0.3	0.15	1.20	-117.75	-0.03	HQ	mspc
	top	64.98	2	0.4	0.14	1.26	-117.96	-0.03	HQ	DC4/5
	top	65.06	2	0.5	0.14	1.31	-118.13	-0.03	M	*Alnus* spp.percov
	top	65.09	2	0.5	0.13	1.34	-118.20	-0.03	M	slope
	global	74.16	7	9.6	0.00	124.14	-111.48	-0.11	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Log	top	55.20	2	0.0	0.33	1.00	-125.41	0.25	IE	50buffcap
	top	55.59	2	0.4	0.27	1.20	-126.43	0.24	HQ	mspc
	top	56.82	5	1.6	0.15	2.23	-111.18	0.31	IE+HQ	50buffcap+mspc+DC4/5+concavity
	global	60.42	7	5.2	0.02	13.47	-106.97	**0.14**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity
Mineral Soil/Rock	top/global	69.12	7	0.0	0.87	1.00	-120.52	**0.67**	IE+M+HQ	50buffcap+*Alnus* spp.percov+slope+mspc+DC4/5+concavity

Note: Generalized linear models used quasi-binomial error term. For each model, AICc (corrected AIC) was used due to small sample size, K = number of estimable parameters including intercept, ΔAICc is the difference between the lowest AICc of all models tested and each model's AICc, ωi is Akaike weight, logLik is the maximized log-likelihood, D^2_{adj} is the adjusted Deviance squared, global D2adj, a measure of goodness of fit, is from the most complex model. All other models are nested within global. Only candidate models with a ΔAICc of ≤ 2 from all tested are considered the most likely and are shown. Growth Forms were excluded due to rareness which invalidated many models. IE (immigration & extinction) = 50 m buffer capacity ; M (microclimate) = *Alnus* spp. percent cover + slope ; HQ (habitat quality) = mineral soil percent cover (mspc) + DC 4 & 5 (decay class) + concavity.

ER = evidence ratio. Bolded > 0.10 global D2adjusted. A minimum of nine basic models were run for each functional group.NA = not applicable.