

**SEEING THE FOREST FOR THE BRYOPHYTES: THE EFFECTS OF FOREST
FRAGMENTATION ON THE BRYOPHYTE COMMUNITY IN COASTAL
TEMPERATE RAINFORESTS OF BRITISH COLUMBIA**

By

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Abstract

In the coastal temperate rainforests of British Columbia, forest fragmentation from logging has created three different landscape elements that vary in habitat quality for bryophytes: unlogged old-growth remnant forest patches, edge habitats and younger-aged forest stands. Bryophytes are an important component of these forest ecosystems, yet little is known about the impact of habitat fragmentation on bryophyte patterns of richness and abundance. In this thesis I examined the effects of three separate components of fragmentation on patterns of bryophyte species richness, abundance and community composition: (1) effects of proximity to the edge within remaining forest patches, (2) effects of stand age in younger-aged forests adjacent to old-growth patches and (3) effects of remnant patch size. To achieve greater generality in my conclusions, I examine each of these issues through comparative analysis using different sampling scales and both taxonomic and ecological functional groupings of bryophytes.

Edge effects: Edge habitats (sampled from 0-45 m from the patch edge) showed an increase in the richness of clearing-affiliated bryophytes without a loss of old-growth associated bryophytes. In contrast, interior habitats (sampled primarily >100 m from the forest edge) had a greater abundance of old-growth associated bryophyte functional groups (as measured by fine-scale sampling and percent cover estimates). Old-growth associated species exhibited no consistent changes with increasing distance up to 45 m from the edge, implying that the influence of the forest edge on these species extends at least this far into unlogged remnants.

Effect of stand age: Bryophyte species richness peaked in regeneration stands (stand ages 5-30 years), declined to its lowest levels in immature stands (stand ages 25-49 years) and increased in old-growth stands (stand ages >300 years). In comparison with old-growth, both regenerating clear-cuts and immature forests had a greater richness of clearing affiliated bryophytes. There was no loss of old-growth associated species in regeneration plots; however, old-growth associated species in immature plots showed significant declines in richness which

suggests that immature forests represent a propagation bottleneck for bryophytes in harvested landscapes. The pattern of bryophyte species occurrence in younger-aged stands supports an initial floristics model of succession.

Effects of patch size: The richness and abundance of dispersal-limited and microclimate sensitive groups showed significant declines as patch size decreased. In contrast, groups expected to increase in richness or abundance as patch size decreased (colonist and open canopy species) showed little association with patch size indicating that center of small remnant patches had no greater richness of clearing affiliated species than large remnant patches. The absence of clearing affiliated species in the center of small remnant patches may well reflect the lack of available microhabitats.

The results of this thesis imply that the bryophyte community in the study area has been impacted by human disturbance caused by large-scale forest fragmentation. The bryophyte community in disturbed habitats (i.e., edge and younger-aged stands) showed an increase in the number of clearing affiliated species and a decreased abundance of old-growth associated species. This has important management implications. Although variable retention will introduce greater structural heterogeneity into regenerating forests, it will do little to alleviate the effects of fragmentation on bryophytes. The maintenance of bryophyte diversity in coastal temperate rainforests will depend not only on adequate old-growth reserves but also on longer forestry rotations that will help mitigate the adverse environmental effects associated with introduced edges, younger-aged forests and decreasing patch size.

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CHAPTER I. Introduction

The Pacific coast of North America is one of five centers of bryophyte diversity in North America (W.B. Schofield, pers. comm.), with over 700 species found in the coastal temperate rainforests of British Columbia alone (Schofield 1998). With the advent of mechanically-assisted logging in the 20th century, however, temperate rainforests in B.C. have been subject to large-scale timber harvesting, resulting in a dramatic loss in the cover of old-growth forest (Harris 1984, Robbins 1997, MacKinnon and Vold 1998, MacKinnon 2003) and the consequent fragmentation of remaining old-growth forests. In temperate forests, bryophytes make a significant contribution to the overall species diversity, understorey biomass and nutrient cycling (Binkley and Graham 1981, Schofield 1992, Alaback and Pojar 1997, Schofield 1998, Glime 2001), as well as providing habitat for invertebrates (Gerson 1969, Kinchin 1992), cyanobacteria and mycorrhizae (Glime 2001). Despite their importance, we have little understanding of how bryophyte communities have been altered in fragmented landscapes. This dissertation therefore examines the effects of three separate components of fragmentation on patterns of bryophyte species richness, abundance and community composition: (1) effects of proximity to the forest edge within remaining, unlogged forest patches, (2) effects of stand age in younger-aged forests adjacent to old-growth patches and (3) effects of remnant patch size.

Forest fragmentation alters both the overall extent and spatial configuration of the original forest cover (Haila 1999). As the overall extent of forest cover is diminished, the remaining forest patches will decrease in size and increase in isolation (Saunders et al. 1991, Andrén 1994). Furthermore, fragmentation of a forested landscape will increase the proportion of the landscape in “disturbed” habitats such as younger-aged stands and edge habitats. All vegetation is patchy at some scale (Lord and Norton 1990), and fragmentation is expected to have adverse consequences on natural communities only if the fragmentation occurs at a spatial scale that disrupts ecological process (Haila 1999). Natural disturbance regimes provide one set

of standards by which to judge the potential impact of large-scale harvesting on the natural communities in a landscape (Hunter 1993). The coastal temperate rainforests of B.C. consist, in large part, of a mosaic of patches created by small scale-disturbances such as wind, and by heterogeneity in soils and topography (Lertzman et al. 1996). In many parts of this region, fire is an infrequent occurrence with fire-return intervals of 700-3000 years on sites with southerly aspects and 3000-6000 years on sites with northerly aspects (Lertzman et al. 2002). Large-scale timber harvesting has imposed a different disturbance regime varying in both spatial and temporal scale on this landscape (Franklin 1998).

With increasing concern over loss of biological diversity, researchers have investigated the impacts of forest fragmentation on diverse taxa ranging from birds to invertebrates to vascular plants (see review in McGarigal and Cushman 2002); however, the impacts of fragmentation are often species-specific (Haila 1999). Both habitat conditions (i.e., microclimate and substrate) and time (i.e., time for logs to decay, and for dispersal, colonization and growth to occur) may influence the distribution of forest bryophytes (Gustafsson and Hallingbäck 1988, Söderström 1988b, 1988a, Söderström and Jonsson 1989, Rambo and Muir 1998a, 1998b, Rambo 2001). Furthermore, a number of forest bryophyte species have life history characteristics (i.e., limited dispersal ability, low fecundity and sensitivity to altered microclimate) that may predispose them to fragmentation effects (Haila 1999).

Although the total loss of habitat is of great concern to bryologists (Tan and Pócs 2000), the spatial configuration of the remaining habitat patches within a landscape matrix may also be important (Saunders et al. 1991, Haila 1999). Forest fragmentation usually results in a series of differently-sized forest patches surrounded by a matrix of younger vegetation. Unlike agricultural landscapes in which native species are largely restricted to remnant habitat patches, the maintenance of biological diversity in managed forests will depend upon both the continued persistence of species in forest reserves as well as the eventual recovery of species in areas

disturbed by harvesting, such as edge habitats and younger-aged stands (Franklin 1993). From this perspective, remnant patches should be considered as one part of a landscape mosaic which contains elements differing in habitat quality for bryophytes (Wiens 1995, 1997, Jules and Priya 2003).

Based on the commonly observed relationship between area and species richness (Arrhenius 1921, MacArthur and Wilson 1963, 1967, Connor and McCoy 1979), decreasing patch size is often predicted to result in decreasing species richness. Beginning in the 1970's, many ecologists interpreted the smaller number of species found in smaller fragments as evidence of negative impacts of fragmentation; however, criticisms raised by Haila et al. (1993), Haila (1999) and Andrén (1994) pointed out that a relationship (or lack thereof) between total species richness and overall patch size explains little about the effects of fragmentation for two reasons. First, species richness, as an aggregate variable, says nothing about the identity and habitat requirements of individual species (Zimmerman and Bierregaard 1986, Saunders et al. 1991). In small remnant patches, species richness may include species more commonly found in younger forests (Ås 1999). Second, a positive relationship between patch size and species richness may arise from factors other than the effects of fragmentation. The increased number of species found on larger fragments may simply be the result of increased habitat diversity or a result of larger patches "sampling" a greater number of individuals. Sampling differently-sized remnant patches with the same plot size or intensity (Westman 1983, Kelly et al. 1989, Tangney et al. 1990, Ås 1993, Kohn and Walsh 1994, Schieck et al. 1995, Moen and Jonsson 2003) and sampling the same type of habitat or vegetation type (Kelly et al. 1989, Tangney et al. 1990) may help to control for the effect of area and habitat diversity.

Forest fragmentation may, however, adversely affect species diversity through two mechanisms, both of which will be exacerbated as patch size declines. The first effect results from the alteration of the microclimate surrounding and within each remnant patch. Small forest

patches will have a smaller core area which is unaffected by environmental changes associated with forest edges (Saunders et al. 1991), limiting the ability of edge-sensitive species to persist within small patches. The second effect results from the isolation of populations in small patches, which may result in a greater rate of stochastic extinctions (Gilpin and Soule 1986, Soule 1987).

Implicit in the expectation that species richness will decline with decreasing patch size, once patch size and habitat diversity are controlled for, is the assumption that edge habitats and younger-aged forests will not provide viable habitat for the organisms under consideration. However, it is not clear whether younger forest and edge habitats should be viewed as inhospitable barriers or as selective filters (Wiens 1995, Haila 1999, Jules and Priya 2003). Therefore, investigating the impact of stand age and edge effects on bryophyte diversity is important for two reasons: first, younger-aged forests and edge habitat form the majority of the landscape matrix in fragmented forests, and second, documenting changes in bryophyte richness and abundance in younger-aged forests and edge habitats will help decipher the observed patterns of species richness and abundance in differently sized forest remnants.

In the few studies investigating the relationship between patch size and bryophyte species richness (primarily in naturally fragmented habitats, but see Zartman (2003)) no consistent relationship has been found (Tangney et al. 1990, Haig et al. 1999, Kimmerer and Driscoll 2000, Moen and Jonsson 2003). Interestingly, liverwort richness appeared to be affected by proximity to the edge in Scandinavian spruce forests (Moen and Jonsson 2003) but showed little edge effect in tropical forests (Zartman 2003). The conflicting results among these studies highlight the site-specific response of bryophytes to the effects of fragmentation.

Comparisons of younger forest stands with old-growth stands have shown a consistent decline in epixylic (log-dwelling) liverwort richness in second-growth forests (Gustafsson and Hallingbäck 1988, Andersson and Hytteborn 1991, Lesica et al. 1991, Rambo and Muir 1998a,

1998b). The majority of these studies, however, have compared mature or second-growth forests (50 to 80 years old) with old-growth forest; relatively few studies have examined bryophyte diversity within younger forests (0 to 25 years old) (but see Ross-Davis and Frego 2002, Fenton et al. 2003). On the northeastern coast of Vancouver Island, old-growth remnants exist within a matrix of younger stands aged primarily from 0 to 60 years and it is unclear what type of "filter" these forests pose for old-growth associated bryophytes. Furthermore, with the advent of variable retention forestry practices that promote the creation of small, residual forest patches within large harvest blocks that may be strongly influenced by edge effects (Laurance and Yensen 1991), understanding the impacts of artificially-created edges has become even more important.

This study was conducted in two different forest types (one wetter and cooler, one drier and warmer) on the northeastern side of Vancouver Island (Figure 1.1). The forest areas sampled were under tenure by Weyerhaeuser Canada and Canadian Forest Products, Ltd. The fragmentation in this landscape is not the result of a designed field experiment, but rather falls into the "natural experiment" category of Diamond (1986). There are obvious limitations in analyzing patterns resulting from a natural experiment.

First, deforestation is not a random process and thus noise in the data has the potential to mask the effects of fragmentation (Doak and Mills 1994). More importantly, however, the results of a descriptive study such as this one are usually amenable to alternative explanations that cannot be distinguished by investigating the pattern alone (Haila 1999). This is an important limitation in an applied study such as this one, as elucidating the processes underlying ecological patterns is critical to developing predictive capabilities (Levin 1992).

Given these inherent limitations of a descriptive study, my decision to proceed was based on both on the conservation imperative underlying this work as well as the limited availability of possible alternatives. Although forest companies in British Columbia are recognizing that

maintenance of biological diversity is an important consideration (Beese and Zielke 1998, Bunnell et al. 1998), continued harvesting of old-growth forest as well as the use of variable retention logging techniques will increase fragmentation of B.C. temperate rainforests. As alternatives to a descriptive study, either small-scale field experiments or experimental forest fragmentation such as the Biological Dynamics of Forest Fragments Project in the Amazon (Laurance et al. 1998) have the potential to control confounding factors. Results from small scale field experiments, however, while useful at identifying mechanism, can rarely be scaled up to answer landscape-level questions (Murphy 1989, Levin 1992). Furthermore, due to the inherent inertia of plant communities (Davis 1984), the results of controlled harvesting such as the Biological Dynamics of Forest Fragments Project on most plant communities can be best determined in a long-term study (McGarigal and Cushman 2002). Given the ecological imperative to address the effects of fragmentation on bryophytes, I chose to accept the limitations of a descriptive study and work in a landscape that had already experienced a high degree of fragmentation. I also sought through careful sampling design to limit confounding variables and the possible explanations for the observed patterns.

A further motivating question in this thesis was the extent to which bryophyte functional groups (Table 1.1; groups of bryophyte species which would be expected to respond differently to the same environmental perturbation (Gitay and Noble 1997)) could provide evidence about the relative importance of processes underlying the observed patterns. Human-induced disturbances such as habitat fragmentation or climate change are global phenomena; however, efforts to generalize conclusions regarding the impacts of such disturbances are limited by differences in the species pool from one region to another (Pillar and Sosinski 2003). Although the response to fragmentation is likely to be species-specific, detailing the impacts on all species in all regions may be too time-consuming or costly (Gitay and Noble 1997). Classification of plants according to life-history traits has a long tradition in plant ecology (Weiher et al. 1999),

and repeatable patterns in the changes of plant functional traits along gradients are often observed across regions and continents. Functional classifications of plants have been increasingly used to understand large scale environmental perturbations (Diaz and Cabido 1997). Whereas the determination of underlying processes is important for developing predictive capabilities, the distinction between pattern and process may not be as critical for management purposes as it is in ecological research (Haila 1999).

The detection of human impacts on natural communities is a central problem in applied ecology (Haila 1999), yet the scale of analysis can fundamentally modify research conclusions. Changing sampling scales has been shown to alter the interpretation of vegetation classifications (Drewa and Bradfield 2000), community dynamics (Smith and Urban 1988) and the influence of habitat variables on bird communities (Wiens 1984, Naugle et al. 1999). Furthermore, Rahel (1990) has demonstrated that assessments of community persistence depend upon the scale of numerical analysis. There is no “correct” scale to use; however, it is important to understand how the description of a system changes with scale (Levin 1992). In the analyses of the influence of proximity to an edge (Chapter 2) and stand age (Chapter 3) on the bryophyte community, I chose to sample bryophyte richness and abundance at the scale at which bryophytes are likely to interact with their environment (10 cm x 30 cm microplots) and at a larger plot scale (cumulative surveys across five 2 m x 10 m belt transects) integrating conditions within forest stands. Bryophyte richness sampled at the two scales is the result of different ecological processes (Shmida and Wilson 1985); therefore, changes in the bryophyte community at the different scales will have different implications for bryophyte conservation and management.

Bryophyte richness in microplots is primarily the result of species growth, mortality and interspecific interactions, whereas bryophyte richness at the whole plot scale is the consequences of habitat heterogeneity, extirpation (localized loss of species), and mass effects (the migration

of species from optimum habitats) (Shmida and Wilson 1985, Herben 1994a). Obviously, in order for species loss to be measurable at the whole-plot scale, species mortality must occur consistently across all microhabitats. In contrast, loss of species in small microplots reflects a diminished performance (abundance) of bryophytes, rather than a complete loss of species. In temperate forest ecosystems bryophytes may develop extensive mats that influence soil temperature, moisture and nutrient retention (Glime 2001), thus a reduction in overall abundance may affect the role bryophytes play in temperate forests.

Recovery of species loss at the microplot scale could occur through regrowth, while recovery of species at the whole-plot scale requires that bryophyte dispersal from nearby sites and subsequent establishment are successful. Recent research has suggested that in forested landscapes where ground cover is high and dispersing winds relatively weak or absent, establishment via spores may be very limited (Miles and Longton 1992, Økland 1995) and bryophyte dispersal via unspecialized asexual diaspores very localized (McDaniel and Miller 2000, Økland et al. 2003). Loss of bryophyte species at the whole-plot scale likely represents a more severe impoverishment of the bryophyte community that may pose limitations for community assembly in disturbed habitats even after habitat conditions return to pre-disturbance conditions. I used the analysis of different sampling scales and bryophyte functional groups to document the effects of fragmentation on the bryophyte community in the coastal temperate rainforests of northeastern Vancouver Island, British Columbia.

1.1 Tables and Figures

Table 1.1. Bryophyte functional groupings with individual categories based on growth form, substrate-affinity, sampled substrate, life-history strategy and canopy preference as used in Chapters 2, 3 and 4. Growth-form classification for bryophyte species taken from During (1992) after Gimingham and Birse (1957) and Magdefrau (1982). Substrate-affinity classification based on field observations of individual species (if species observed <50 times, then based upon literature reports (Godfrey 1977; Schofield 1976, 1992)). Sampled substrate indicates bryophytes found in microplots restricted to forest floor, downed logs, or tree bases. Life-history strategy classification based on During (1979, 1992). Canopy preference classification denotes shade tolerance and is based on literature reports (Godfrey 1977; Schofield 1976, 1992) and local expertise (W.B. Schofield, pers. comm.). Final column lists the chapter in which each functional group was used.

| Functional Groupings | Categories | Chapters in which grouping used |
|---------------------------|---|---------------------------------|
| 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 (SPH): main shoot >3.0 cm high Cushions (CU): erect main shoots radiating 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-like (TH) and Rough (RM): main shoots 0.5-3.0 cm long Wefts (WE), Pendants (PE) and Dendroids (DE): main shoots >3.0 cm long | 2 |
| Substrate affinity | Epiphytic on treebases Epiphytic (blown down from canopy) Substrate generalists Terricolous on Humus Terricolous on Litter Terricolous on Soil Epixylic (logs) Epilithic (rocks) | 2 |
| Sampled substrate | Forest floor Downed logs Tree bases | 4 |
| Life strategy | Colonists Spore size < 20 μm ; high sporophyte production; life span of few years, vegetative reproduction common; open or short turfs and thalloid mat growth forms Short-lived shuttles 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 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 Spore size < 20 μm ; low sporophyte production; life span of many years; vegetative reproduction common; weft, dendroid, mats and large cushion growth forms | 2,3,4 |
| Canopy preference | Open canopy Shade intolerant Closed canopy Shade tolerant Canopy Shade indifferent generalist | 2,3,4 |

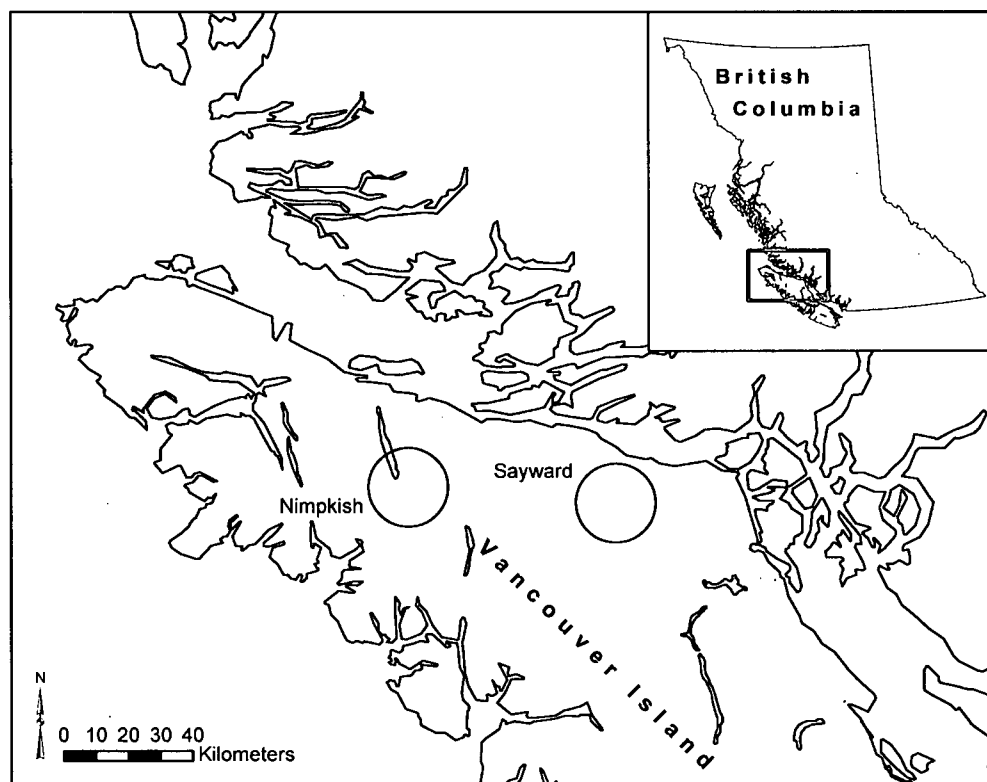


Figure 1.1. Approximate locations of Nimpkish and Sayward study areas on Vancouver Island, British Columbia. Map data are from 1:6,000,000 generalized Provincial planimetry. Source: Surveys and Resources Mapping Branch, Ministry of Sustainable Resource Management, Province of B.C.

CHAPTER II. Edge effects on species richness and composition of bryophyte communities in temperate rainforest fragments of coastal British Columbia, Canada

2.1 Abstract

The species richness and abundance of bryophytes within taxonomic and functional groups, as well as overall species composition, was examined in relation to habitat conditions and distance from the forest edge in nine old-growth forest patches remaining after logging in the Nimpkish River Valley of Vancouver Island, British Columbia. Bryophytes were sampled at a fine scale using 10 cm x 30 cm microplots to estimate species abundance on three substrate-types (forest floor, downed logs and tree bases) and at a coarser scale for species composition within 10 m x 2 m transects located in edge, interior and adjacent clear-cut habitats at each forest patch. Edge habitats, sampled to a depth of 45 m into the forest patches, were characterized by greater disturbance from windthrow along with increases in functional groups of mosses associated with canopy openings and exposed mineral soil. Gamma diversity of bryophytes was higher in edge habitats (70 species) compared to interior habitats (51 species) reflecting invasion of moss species from adjoining clear-cut areas. Patterns of variation in functional group richness and community composition within the edge zone were associated mainly with the locations of windthrown trees creating tip-up mounds for bryophytes to colonize, rather than with distance from the edge *per se*. Interior habitats, primarily sampled >100 m from the forest edge, had a greater abundance of old-growth associated functional groups, as well as a greater abundance of all bryophytes (as measured by bryophyte cover). Furthermore, the patchy distribution of the bryophyte community in edge habitats was associated with significant reductions in the richness of old-growth-associated functional groups at the microplot scale. The results of this study indicate that multiscale sampling combined with recognition of substrate and functional group categories are useful for evaluating the influence of logging-induced edges on forest bryophyte communities.

Keywords: bryophyte communities, depth-of-edge influence, forest edge effects, old-growth temperate rainforests, remnant patches, variable retention logging, functional groups.

2.2 Introduction

Vegetation response to altered environmental conditions found in forest edges has been shown to vary, both by forest strata and by individual species (Murcia 1995). Studies of understorey vegetation within northern temperate forests have found that depth of edge influence varies from 0.5 m to 120 m (see summary table in Euskirchen et al. 2001). Other than Chen et al. (1992), where depth-of-edge influence on woody plants was investigated, little information is available on depth-of-edge influence in coastal forests of the Pacific Northwest. Furthermore, the majority of studies investigating edge effects on plants in other regions have focused on woody species (Sork 1983, MacDougall and Kellman 1992, Esseen 1994, Young and Mitchell 1994, Williams-Linera et al. 1998, Mesquita et al. 1999) and understorey herbs (Matlack 1994b, Fox et al. 1997, Jules and Rathcke 1999, Gehlhausen et al. 2000). Although studies of edge effects on lichens have begun appearing in recent years (Sillet 1995, Sillet et al. 1995, Esseen and Renhorn 1998), previous studies on bryophytes in managed forests have mainly examined old-growth versus second-growth comparisons (Gustafsson and Hallingbäck 1988, Söderström 1988a, Andersson and Hytteborn 1991, Lesica et al. 1991) rather than the specific effects related to forest edges (but see Moen and Jonsson 2003, Zartman 2003).

Bryophytes make a significant contribution to the overall species diversity, understorey biomass and nutrient cycling in temperate rainforests of north-western North America (Binkley and Graham 1981, den Ouden and Alaback 1996, Alaback and Pojar 1997, Schofield 1998). Most bryophyte species are opportunistic in their abilities to colonize a variety of forest habitats via wind, water and animal dispersed spores and vegetative fragments. Some bryophyte species appear to rely on the relatively stable climatic conditions found within mature and old-growth

forests (Gustafsson and Hallingbäck 1988, Söderström 1988a, Lesica et al. 1991, Rambo and Muir 1998a) and may be especially vulnerable to changes along the edges of remnant forest patches after logging. Such “edge habitats” typically suffer greater indirect disturbance through higher light levels, air and soil temperatures, wind velocities and vapour pressure deficits, as well as lower relative humidities and soil and litter moisture levels than forest “interior habitats” (Brothers and Spingarn 1992, Brothers 1993, Young and Mitchell 1994, Chen et al. 1995). Further, edge habitats are often subject to increased direct disturbance from windthrown trees (Chen et al. 1992, Esseen 1994, Young and Mitchell 1994) resulting in greater amounts of coarse woody debris (CWD) and tip-up mounds that may, in turn, favour some bryophyte species over others (Jonsson and Esseen 1990).

Fragmentation of a forest matrix by logging not only diminishes the total forested area but also increases the amount of edge habitat (Laurance and Yensen 1991). With the deliberate creation of small forest patches as part of new forestry practices (often referred to as variable retention logging) to retain old-growth dependent species (Franklin et al. 1997, Beese and Zielke 1998, Spence 2001), studies are needed to determine the degree of edge influence on bryophyte communities and the depth to which that influence extends into the remnant patches. The only study to investigate the influence of variable retention logging on understorey vegetation reported no difference in bryophyte abundance (as measured by crown volume index) in clear-cut areas and variable retention stands (Sullivan et al. 2001).

The temperate rainforests of north-western North America are renowned for their bryophyte species richness and abundance (Alaback and Pojar 1997, Schofield 1998). With over 700 species reported, the taxonomic diversity of bryophytes (including mosses, liverworts and hornworts) found in the coastal forests of British Columbia is the richest in the province (Schofield 1988). Based on growth forms, substrate-types and overstory canopy preferences, forest bryophytes can be categorized into a number of broad, functional groups (Table 1.1) that

are likely to show correlations with environmental factors such as moisture and light as well as disturbance (Gimingham and Birse 1957, Magdefrau 1982, During 1992). For example, cushions and short turfs are characteristic of open disturbed sites, whereas wefts and pendants are intolerant of high illumination and are associated with relatively high humidity (Schofield 1981). Bryophytes have also been classified into life history strategies (During 1979, 1992) similar to the r-K strategies concept (MacArthur and Wilson 1967). Given the taxonomic difficulties of bryophytes in general, categorization by functional groups offers a useful means to assess bryophyte responses to changing conditions within the forest. Understanding the qualitative and quantitative nature of these responses in relation to forest edge effects is a crucial step toward ensuring that biodiversity objectives are being met through forest management.

Ecological communities are influenced by a variety of processes operating over a range of different spatial scales (Wiens 1984, Smith and Urban 1988, Rahel 1990, Levin 1992, Drewa and Bradfield 2000), and it has become increasingly recognized that the influence of disturbance events will vary greatly depending upon the scale of the organism (Levin 1992, Bunnell and Huggard 1999, Haila 1999). Haila (1999) has argued that scale of analysis should be dictated by the size of the organism under analysis. Bryophytes are small plants, often in intimate association with their substrate, and may be strongly influenced by microhabitat conditions (Vitt and Belland 1997, Proctor 2000). Therefore, we chose to sample the bryophyte community on a scale at which bryophytes can be expected to interact with their environment (10 cm x 30 cm microplots). Forest management, however, is unlikely to occur on such small scales (Bunnell and Huggard 1999), and thus we also examined the response of the bryophyte community at the plot-level (cumulative surveys across five 2 m x 10 m belt transects) which integrated conditions across a forest stand. Furthermore, as the ecological processes influencing bryophyte richness and abundance are scale-dependent, changes in the bryophyte community will have different implications for bryophyte conservation and management depending on the scale of assessment.

The primary purpose in this study was to evaluate how overall species composition and abundance of bryophytes, as well as the richness and abundance of bryophytes within functional groups, differed between edge and interior habitats of remnant patches of temperate rainforest following logging in coastal British Columbia. To assess the influence of edge invasion by clearing affiliated species, bryophytes in clear-cut areas were also sampled. Specifically, the data were examined with respect to the following hypotheses. *Altered microclimate hypotheses*: (1) the richness and abundance of old-growth associated bryophytes intolerant of altered microclimatic conditions (liverworts, bryophytes with weft and pendent growth forms and species typically found under closed canopy conditions) will decrease with proximity to the forest edge, and (2) the richness and abundance of clearing affiliated bryophytes (cushion and open turf growth forms, colonists species and species associated with open canopies and clearings) will increase with proximity to the forest edge. *Increased wind disturbance hypothesis*: (3) the richness and abundance of colonists, epilithic (rock-dwelling) and terricolous (soil/humus dwelling) bryophyte species on tip-up mounds created by wind thrown trees will increase with proximity to the forest edge.

2.3 Methods

Study area

This study was conducted in the Nimpkish River valley (50° 10' N 126° 30' W) on the northeast side of Vancouver Island, Canada. Forests in the Nimpkish Valley are primarily in the very dry Coastal Western Hemlock (CWHxm) subzone and consist predominantly of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) and western hemlock (*Tsuga heterophylla*) with minor amounts of western redcedar (*Thuja plicata*) also present (see Pojar et al. 1987, Meidinger and Pojar 1991, Green and Klinka 1994 for descriptions of the biogeoclimatic classification system and details on the CWHxm subzone). Forests in this subzone have warm, dry summers and

moist, mild winters with relatively little snowfall (Green and Klinka 1994). Climate data from Cumberland, British Columbia (49° 37' N 125° 02' W; the closest weather station in CWHxm subzone to the Nimpkish Valley) show that mean annual precipitation is approximately 1638 mm with less than 20% occurring during May-September. Mean monthly temperatures range from a 0.9 °C in January to 16.5 °C in July; weather data for the period 1960-1977 (Environment Canada 2000).

Much of the old-growth forest (i.e., stand age >300 years) in the Nimpkish River valley has been extensively altered through clear-cut logging. Logging began in the late 1800's and accelerated during the second half of the 20th century (unpublished forest history maps). Harvesting operations in this area have occurred primarily along valley bottoms although harvesting is ongoing at higher elevations. Thus, a range of old-growth forest patches differing in size, but representative of the same forest type, are available for comparative study of edge effects on bryophyte communities.

Site selection and bryophyte sampling

Based on recent forest inventories and aerial photographs, nine old-growth (>300 years old) forest patches ranging in size (1.8 ha to >60 ha) and elevation (150 – 460 m a.s.l.) were selected for study. All nine forest patches resulted from logging operations during the last 40 years; however, to control for the confounding influence of edge age, all sampled edges had been created in the last 5-25 years. To minimize the influence of differing aspects, all but one of the sampled forest edges had a south-southeast exposure; the exception was an east facing edge, chosen because the southern edge was inaccessible. In the two smallest forest patches, the interior sampling location was *c.* 75 m from the closest forest edge; for all other patches, the edge-interior distance exceeded 100 m.

Bryophytes were sampled along five 10 m x 2 m belt transects located within clear-cut, edge and interior habitats. For the edge and regeneration stands, the belt transects were located

parallel to the remnant edge, defined by the location of the boles of the outermost trees, at distances of 5, 15, 25, 35 and 45 m. Interior transects were located in a 3 x 2 grid pattern (10 m spacing between transects) across the approximate center of each forest patch. To control for microhabitat heterogeneity within the belt transects, bryophytes were sampled using nine 10 cm x 30 cm microplots located on three substrate-types: forest floor, tree bases and fallen logs. Microplot locations were determined as the closest respective substrate-type to three randomly selected points along the centre line of each transect. Following McCune and Antos (1981), microplots were partitioned into six equal size units of 50 cm² and species cover classes recorded to the closest half 50 cm² partition unit. Cover classes were subsequently converted to percentages with one cover class being equal to a mean cover of 16.67%. Assignments of bryophyte species into growth form, substrate-affinity, life-history strategy and canopy preference groups were made according to the criteria in Table 1.1. These assignments were based on either field observations or literature reports (Schofield 1976, Godfrey 1977, Schofield 1992), with uncertainties resolved on the advice of local expertise (W.B. Schofield, pers. comm.). Following the recommendation of McCune and Lesica (1992), full transect searches for bryophyte species not encountered in the microplots also were conducted. In this case, species were recorded by their presence only, and functional group assignments were made in a similar fashion as in the microplot sampling. Specimens obviously blown down from the canopy (lying on but not attached to substrate) were recorded as being epiphytic. After tentative identification in the field, all species identifications were confirmed in the laboratory.

Habitat heterogeneity and stand structure within the belt transects was recorded by visual estimates of percent cover of boulders, litter, humus and exposed mineral soil, as well as by coverage of tree (dbh > 10 cm), sapling (2.5 cm < dbh < 10 cm), shrub and tree seedling (dbh < 2.5 cm) layers. The dbh and status (live tree or snag) of each treebase sampled for bryophytes were noted as a measure of stand tree composition. The diameter and decay class (Maser et al.

1988) of CWD greater than 10 cm diameter intersecting the transect centre line also were recorded. Calculations of CWD volume were made following the method of Howard and Ward (1972). The presence of recent tip-up mounds in each transect was also recorded. Slope and aspect were recorded for each transect and an aspect favorability index was calculated (Beers et al. 1996).

Nomenclature for mosses and liverworts follows Stotler and Crandall-Stotler (1977), Anderson (1990), Anderson et al. (1990) and Flatberg (1993). Voucher specimens are deposited in the University of British Columbia herbarium and in the senior author's herbarium.

Data Analyses

Edge-depth assessment

Depth of edge influence on stand structure, habitat and substrate variables and on the richness and abundance of bryophytes within functional groups was analyzed by comparing transects grouped by the five edge distance intervals (5, 15, 25, 35, 45 m) across the nine study sites. As the data failed to satisfy assumptions of parametric tests, non-parametric methods of comparison were used. Kruskal-Wallis tests were used to determine whether significant differences ($p < 0.05$) occurred in the levels of individual variables with increasing edge distance. We examined two different measures of alpha diversity: 1) mean microplot richness averaged from all microplots within each transect, and 2) whole-transect level inventories, derived from microplots and ocular surveys of transects. Comparisons of species richness among distance intervals were made using taxonomic categories (total bryophytes and mosses and liverworts separately) as well as various functional groups (Table 1.1). Because sampling was conducted at two scales within transects (i.e., microplots on three substrate-types and whole-transect surveys across all substrates), greater refinement in the levels of comparison was possible than if only a single scale of sampling had been used.

In addition to the univariate comparisons described above, the multivariate patterns in overall bryophyte species composition were examined in relation to edge distance and variation in habitat conditions among transects. Two non-parametric multivariate methods were used. First, multi-response permutation procedure (MRPP) was used to test for compositional differences among transects grouped by the five distance intervals sampled. MRPP was performed on a transects-by-species matrix of frequency values and tested the null hypothesis that transects at the different distance intervals supported similar bryophyte communities. Second, non-metric multidimensional scaling (NMS) was used as a method of indirect ordination to characterize the major variation in species frequencies among transects, unconstrained by edge distance. NMS is a dimension reduction technique that escapes many of the distortions of eigenvector techniques (Kenkel and Orlóci 1986, Minchin 1987). To improve interpretability of the results, species occurring in fewer than 5% of transects were omitted, and relativization by species maxima applied. The quantitative version of Sorensen's index was used as the distance measure in both NMS and MRPP. Joint plots were used to depict relationships between individual species and the ordination axes. Pearson correlations (r-values) were used to assess relationships between the NMS ordination axes and stand structure and substrate variables measured within transects. As in the univariate comparisons, MRPP and NMS were performed using bryophyte composition data from the microplot and whole-transect assessment levels to determine whether community relationships are influenced by sampling scale.

The Kruskal-Wallis tests were run using SYSTAT (1995); MRPP and NMS were performed using PC-ORD (McCune and Medford 1999).

Edge comparison with forest interior

The results from edge-depth assessment indicated relatively minor changes in habitat variables and bryophyte communities up to 45 m from the forest edge. Therefore, the five edge

transects at each location were amalgamated into “edge plots” for comparison with the “interior plots” (i.e., amalgamations of the five interior transects). As in the depth of edge analysis, we report two different measures of alpha diversity: 1) mean microplot richness, calculated from all microplots within a plot and 2) cumulative whole-plot species inventories derived from microplots and ocular surveys of all 5 transects. We also report gamma diversity, the combined whole-plot level species inventories, across edge and interior habitats. Whole-plot assessments also were used to examine changes in frequencies of bryophyte functional groups with increasing edge distance. Frequencies were determined as numbers of occurrences in microplots and transect surveys of species representative of particular functional groups. Variation in bryophyte cover found within microplots in edge and interior plots was analyzed separately for the three substrates (forest floor, logs, tree bases). Univariate comparisons of stand structure, habitat and substrate variables (all averaged over transects), species richness of taxonomic and functional groups and bryophyte cover between edge and interior plots were run using Mann-Whitney U Tests (SYSTAT 1995). Multivariate comparisons of species frequencies between edge and interior plots were analysed with MRPP and NMS. Separate comparisons were made using data from microplot and whole-transect assessment levels to determine the influence of sampling scale on the results.

2.4 Results

Edge – depth assessment

Most stand structure and substrate variables showed no significant differences up to 45 m from the forest edge (Table 2.1). Exceptions included significant differences in the cover of canopy trees and exposed mineral soil, and in the volume of CWD in early decay classes. Apart from a generally lower canopy cover near the forest edge, however, none of the variables showed consistent changes with edge distance.

A total of 70 bryophyte species (24 liverworts and 46 mosses) were found in the 45 forest edge transects sampled across the nine forest patches (Appendix A). Based on whole-transect assessments (i.e., combined data from microplots and transect searches), small but significant declines in overall moss species richness, as well as in the richness of colonists, open canopy species, open turf and pendent growth forms (many of the latter occurring as dislodged fragments from overstory canopy), were detected with increasing distance from the forest edge (Table 2.2). None of the functional groups based on substrate affinity showed significant changes in species richness related to edge distance. At the microplot scale, only the richness of open turf and colonist species showed a significant decline with distance from the forest edge (Table 2.2).

The relative uniformity of species richness within the edge zone was supported by the MRPP results which indicated no significant differences in overall species composition among the five distance intervals at both the whole-transect and microplot assessment levels (Table 2.3a). Further evidence for lack of an overall edge-depth gradient in species composition was provided by the NMS ordination results, which showed transects at different distances occupying similar positions in multivariate space (Figure 2.1). The first NMS axis summarized compositional variation among transects related to habitat heterogeneity within the edge zone (i.e., negatively correlated with volume and number of well decayed logs and total bryophyte cover, and positively correlated with cover of boulders and litter; Table 2.4). Species with positive responses along the first NMS axis (i.e., vectors pointing to the right in Figure 2.1) included *Frullania tamarisci* subsp. *nisquallensis*, *Ptilidium californicum* and *Isohetecium myosuroides*. The second NMS axis was positively correlated with the cover of shrubs, total bryophyte cover and the number and volume of well decayed logs. Species responding favourably along this gradient (i.e., upward pointing vectors in Fig.1) included *Calypogeia*

muelleriana, *Blepharostoma trichophyllum* and *Rhytidiadelphus loreus*, whereas *Dicranum scoparium* responded negatively along the same gradient.

Edge – interior comparison

Comparisons of the combined edge transects over the five distance intervals at the nine study sites, with the combined interior transects (i.e., “plot” comparisons) indicated significant ($p < 0.05$) edge – interior differences in a number of forest structural and habitat variables (Table 2.5). Edge plots had significantly higher numbers of transects with tip-up mounds, higher cover of downed logs, higher volume of logs in early decay classes (1-2), higher cover of exposed boulders and higher estimates of annual potential radiation. In contrast, interior plots had higher canopy cover, increased humus cover and greater numbers of standing snags.

A total of 80 bryophyte species, (30 liverworts and 50 mosses) were found in the combined edge and interior transects (Appendix A). Overall species richness was greater in the edge plots (70 species) than in the interior plots (51 species), primarily because of higher numbers of infrequent species that are typically found in open areas (i.e., species with < 10 occurrences in the combined microplot and transect assessments; Figure 2.2). Differences in abundance rankings among species were minor between edge and interior plots (Figure 2.2, log-rank test, $\chi^2 = 1.78$, $df = 1$, $p = 0.183$). It is noteworthy that a high proportion of the edge-restricted species occurred on substrates associated with disturbance (e.g., exposed mineral soil and rocks; Appendix A). Whereas 17 of the 29 edge restricted species (59%) also were recorded from clear-cut transects, only 3 of the 10 interior restricted species (30%) were recorded from clear-cut areas. Six species of moss (*Antitrichia curtipendula*, *Dicranum fuscescens*, *Hylocomium splendens*, *Hypnum circinale*, *Isoetecium myosuroides* and *Rhytidiadelphus loreus*) and four species of liverworts (*Cephalozia lunulifolia*, *Frullania tamarisci* subsp. *nisquallensis*, *Lepidozia*

reptans and *Scapania bolanderi*) were found in all edge and interior plots across the nine study sites.

Differences in bryophyte species richness between edge and interior plots varied depending upon the assessment level (i.e., whole-plot versus microplot) and on the particular taxonomic or functional comparison group (Table 2.6). Whole-plot assessments indicated significantly higher richness in edge plots for total bryophytes (mosses and liverworts combined), total mosses, colonists, open turf and tall turf growth forms, canopy generalist and open canopy species and terricolous species on soil. Total liverwort richness and the Shannon diversity index did not differ significantly between edge and interior plots. In addition to differences in species richness, some functional groups also differed significantly in their frequencies of occurrence between edge and interior plots: open turf and tall turf growth forms, both dominated by mosses, were more frequent in edge plots; conversely, smooth mat and thread growth forms, both dominated by liverworts, were more frequent in interior plots. Likewise, the frequencies of perennial stayers, closed canopy species, as well as epiphytic, epixylic and substrate generalist species were higher in interior plots, whereas only terricolous species on soil had a higher frequency in edge plots (Table 2.6).

With microplot assessment, the richness of several clearing affiliated groups (open turfs, colonists and terricolous species on soil) remained significantly higher in edge plots; however, the richness of old-growth associated functional groups (total bryophytes, liverworts, closed canopy-types, smooth mat and thread growth forms, as well as perennial stayers and epixylic species) was significantly lower in edge plots (Table 2.6). Moreover, total bryophyte cover on tree bases and logs was significantly reduced in edge plots. The reduction in richness and cover at the microplot scale was influenced by the large number of “empty” microplots found in edge habitats, especially on downed logs and tree bases.

The distinction between edge and interior plots was corroborated by the MRPP results which showed significant differences in overall bryophyte species composition at the level of whole-plot assessments, as well as at the level of microplot assessments for each of the three substrate-types (Table 2.3b). A diagram of compositional variation among edge and interior plots derived from NMS ordination (Figure 2.3) shows that the main compositional gradient extended from lower left (edge plots) to upper right (interior plots). Environmental correlates of the edge plots (i.e., stand structure, habitat and substrate variables with negative correlations along the first two NMS axes; Table 2.7) included slope and the cover of boulders, saplings and seedlings, as well as the volume of poorly decayed logs. The main species associated with edge plots included five turf mosses (*Dicranum scoparium*, *Aulacomnium androgynum*, *Pohlia nutans*, *Polytrichastrum alpinum* and *Polytrichum juniperinum*), a moss with a rough mat growth form (*Racomitrium heterostichum*), and a liverwort commonly found in open areas (*Cephaloziella divaricata*). Environmental correlates of the interior plots (i.e., stand structure, habitat and substrate variables with positive correlations along the first two NMS axes; Table 2.7) included the overall cover of canopy trees, shrubs, litter and humus and the volume of well-decayed logs. Four liverwort species (*Cephalozia lunulifolia*, *Lepidozia reptans*, *Frullania tamarisci* subsp. *nisquallensis* and *Blepharostoma trichophyllum*) were strongly associated with the locations of the interior plots (Figure 2.3).

2.5 Discussion

The results of this study indicate that edge and interior habitats differ substantially in terms of bryophyte richness and abundance. The manner in which they differ, however, depends upon the sampling scale used to assess the bryophyte community. Large-scale alpha richness (cumulative plot level species lists derived from whole-transect assessments including microplots) increased in edge plots; in contrast, fine-scale alpha richness (mean microplot

richness) was primarily reduced in edge plots as compared to interior plots. This apparent contradiction is a function of the different sampling resolution of microplots and belt transects and reflects the different biological determinants of richness operating at the two spatial scales (Shmida and Wilson 1985).

Microplots encompass only fine-scale habitat heterogeneity and can be dominated by individual bryophyte colonies, whereas habitat heterogeneity in transects is coarser-grained and transects exceed the size of individual bryophyte colonies. As a result, richness at the microplot scale is determined primarily by species growth, mortality and interspecific interactions, while richness at the plot scale is the consequence of both habitat heterogeneity, extirpation (localized loss of species) and mass effects (the migration of species from optimum habitats) (Shmida and Wilson 1985, Herben 1994a). In addition, the two sampling scales were differentially responsive to both the patchiness of the bryophyte community and the presence of rare or infrequent species. Richness estimates averaged across microplots decreased as patchiness increased within plots (i.e., randomly located microplots contained no bryophytes and lowered the mean richness estimates) and captured relatively few infrequent species as compared to whole-plot sampling.

Edge-depth assessment

The major variation in species richness and composition within the edge zone appeared to be related to habitat heterogeneity unrelated to distance from the edge. There was no evidence to support the hypothesis that the richness of microclimate sensitive bryophytes (i.e., closed canopy species, liverworts and mosses with pendent or weft growth form) would decrease with proximity to the forest edge. We did, however, find that the richness of clearing affiliated bryophytes (colonists, open canopy and open turf mosses) was higher closer to the forest edge when assessed through whole-transect surveys.

In this study, we are unable to state whether the clearing affiliated species found in edge habitats germinated from propagules present in the existing diaspore bank or arrived via dispersal from nearby clear-cut areas. Clearing affiliated species such as *Polytrichum juniperinum* and *Pohlia nutans* dominated diaspore banks in Swedish boreal forests, and are typical of early successional habitats (Jonsson and Esseen 1990, Jonsson and Esseen 1998). Two aspects of the invasion of clearing affiliated species into the edge habitat bear mention. First, the higher richness of clearing affiliated species was much more detectable at the whole-plot scale than at the microplot scale. This is consistent with the prediction that species richness at larger scales is more influenced by mass effects (migration of species from optimum habitats) than richness sampled at smaller scales ($<1.0 \text{ m}^2$) (Shmida and Wilson 1985). In this study, whole-plot sampling not only increased the overall area surveyed for bryophytes, but also included less frequently occurring habitats, such as tip-up mounds from windthrown trees. Second, although our results indicate that clearing affiliated species can invade forest edges, this invasion was largely restricted to transects located closest to the forest edge. Within 45 m from the forest edge, the richness of clearing affiliated species was negatively associated with increasing distance from the edge.

Determination of depth of edge influence is always arbitrary and depends on both the vegetation parameter and the forest system under investigation (Chen et al. 1992, Murcia 1995). Obviously, depth of edge influence and the fragment shape will be primary factors in determining whether forest fragments contain any interior habitat (Laurance and Yensen 1991). For circular forest fragments, depth of edge influences that extend 50 m or more will eliminate any interior habitat in fragments 1.0 ha or less (Laurance and Yensen 1991, Young and Mitchell 1994). Other studies in deciduous temperate forest (Matlack 1994b, Gehlhausen et al. 2000) and tropical forest (Fox et al. 1997, Williams-Linera et al. 1998) have reported that the edge influence is ameliorated within 50 m for forest interior species. We found no variation in either

the richness of old-growth associated species or the bryophyte community as a whole within the edge zone, strongly suggesting that little amelioration of edge effects occurs within the first 45 m.

Comparisons between forest edge and interior

In contrast to the depth-of-edge assessment, we found that old-growth associated and clearing affiliated bryophyte functional groups exhibit distinct patterns of richness and abundance in edge habitats when compared to interior habitats. The use of two sampling scales highlights the complexity of these patterns. The richness and abundance of clearing affiliated functional groups was greater at the whole-plot scale in edge plots. This increase, however, was much less detectable at the microplot scale. In contrast, old-growth associated functional groups (liverworts, closed canopy bryophytes, perennial stayers and epixylic species) were significantly less abundant in edge plots at the whole-plot scale and had lower species richness in edge plots at the microplot scale.

No other study appears to have documented the adverse effect of anthropogenically created edges on either liverwort abundance or richness in temperate forests. However, in a system of naturally occurring forest patches in the northern boreal forest, liverwort cover increased with distance from the edge (Moen and Jonsson 2003). Furthermore, numerous researchers have found that liverwort richness and abundance is higher in old-growth forests than in second-growth forests. In these studies, the observed decrease in liverwort richness has been attributed either to changes in microclimate (Rambo and Muir 1998a), lower levels of CWD in late decay stages (Gustafsson and Hallingbäck 1988), or the relatively young age of second-growth stands which allows only limited time for the gradual accumulation of species (Rambo and Muir 1998a). In our comparison of forest edges and forest interiors, stand age does not differ. Likewise, we found no difference in the levels of CWD in late decay stages, which

implies that of the factors suggested to affect liverwort richness and abundance, altered microclimate may be influencing the observed decrease in liverwort richness and abundance in this study. We originally predicted that bryophytes with growth forms that are more open and diffuse (wefts and pendants) and thus may be more sensitive to desiccation would decline with proximity to the edge. In contrast to the other microclimate sensitive groups (i.e., closed canopy species and liverworts), however, we found no evidence for a decline in either the richness or abundance of these two growth forms in edge plots at either the whole-plot scale or the microplot scale.

The decline in both whole-plot abundance and microplot richness observed for most old-growth associated groups points to the diminished success of these species in edge habitats rather than a complete loss of species. Similar patterns have been exhibited by understorey vascular plants following large scale disturbance in Douglas-fir forests (Halpern 1988, 1989, Halpern and Spies 1995). The persistence of old-growth associated bryophytes in edge habitats appears to result from utilization of optimal microsites. Bryophytes are small plants that occur in close proximity to their substrates and are often strongly affected by local microhabitat conditions (Vitt and Belland 1997). In both edge habitats and adjacent clear-cut areas many species of liverworts were found in moist depressions or shady microhabitats beneath logs or understorey plants (personal observation).

If ecosystem resilience (defined here as the capacity to return to pre-disturbance conditions) is assessed through changes in species composition (Westman and O'Leary 1986, Malanson and Trabaud 1987, Halpern 1988, De Grandpré and Bergeron 1997), the maintenance of old-growth associated bryophyte species in edge habitats indicates the potential for greater ecosystem resilience than if old-growth associated species were completely lost from edge habitats. Recovery could occur if vegetation responses to edge effects are minimized with increasing edge age as is found in temperate deciduous and tropical forests (Matlack 1993,

1994b, Williams-Linera et al. 1998). Amelioration of edge effects in these systems occurs as the dense growth of herbaceous and woody vegetation creates "closed" edges. Evidence suggests that such closed edges may not develop in Douglas-fir forests as stocking densities are actually lower near the forest edge (Chen et al. 1992). Certainly, the greater treefall disturbance observed near the forest edge in our study decreases existing canopy cover and will limit future amelioration of edge effects.

The diminution of the bryophyte community in edge habitats in our study was further substantiated by the significant declines in bryophyte cover detected in microplots on two of the three sampled substrates, downed logs and tree bases. Of the three substrates considered, the forest floor probably receives the greatest amount of shading from understorey vegetation and this shading may have offset altered microclimates typically found in edge habitats. In this study, the bryophyte community in edge habitats was not only reduced in abundance in edge habits but it was also more patchily distributed, as evidenced by the large number of microplots devoid of any bryophytes.

The relationship between diversity and ecosystem stability has been the subject of recent debate (Grime 1997, Tilman 1999, Cameron 2002). However, Levine (2000) and Naeem et al. (2000) have pointed out that loss of species richness at the neighborhood scale (the scale at which species interact (Tilman 1994)), may affect the invasibility of a system. The results of our study support this prediction. Concurrent with the loss of old-growth associated species at the microplot scale in edge plots, the richness of clearing affiliated functional groups, as assessed through whole-transect sampling, increased.

Increases in species richness in forest edges have been hypothesized to result from the influx of clearing or edge-affiliated species that are able to tolerate altered microclimatic conditions (Matlack and Litvaitis 1999). We also suggest that increased bryophyte richness in forest edges may result from a greater number of tip-up mounds being created by wind

disturbance. Uprooting creates microhabitat heterogeneity by exposing numerous substrates such as mineral soil, rocks and tree roots in the tip-up mound (Beatty and Stone 1986, Jonsson and Esseen 1990). Bryophyte richness tends to increase as the number of suitable habitats and habitat heterogeneity increases (Slack 1977, Vitt et al. 1995) and the presence of infrequent habitat types such as rocks and/or exposed mineral soil has been shown to increase bryophyte diversity in coniferous forests (Jonsson and Esseen 1990, Rambo and Muir 1998a, Rambo 2001). In this study, either increased direct disturbance through windthrown trees or indirect disturbance through altered microclimate could be responsible for the observed increase in the richness of pioneer-type bryophytes in edge plots. Many (>50%) of the species that contributed to the increased gamma diversity found in edge habitats were observed on mineral soil or rocks (substrates associated with treefall disturbance) or in adjacent clear-cut areas. Separating the relative importance of these two factors is difficult as many of the species likely to colonize tip-up mounds (e.g., *Polytrichum juniperinum* and *Pohlia nutans*) are also likely to be found in clearings or open canopy forests (Schofield 1976, 1992). However, distinguishing between these two factors may not be critical given that the biological result of both of these factors is to allow an invasion of clearing affiliated species into forest edges.

The invasion of clearing affiliated bryophytes into edge habitats may have been also mediated by the sharp reductions in the cover of old-growth associated bryophytes in edge habitats. Competition in bryophytes appears to occur primarily as a form of interference competition, or more specifically, competition for space (Rydin 1997). Levine (2000) speculated that the cover of resident species may have limited germination of exotic vascular species in a Californian riparian system. Although edge habitats in our study were invaded by "native" bryophyte species, the ecological principles underlying the invasions of exotic species may be very similar to those underlying "natural" invasions (Symstad 2000).

Sampling the bryophyte community at two spatial scales highlighted several important aspects of the invasion of clearing affiliated species invasion into edge habitats. An increase in clearing affiliated functional groups was detectable at the whole-plot scale but not at the microplot scale, at least for most of these groups. This implies that much of the increase in clearing affiliated species is occurring on substrates not sampled with microplots (e.g., tip-up mounds and exposed boulders). Furthermore, although the richness of these clearing affiliated groups is higher in edge habitats, the abundance of these groups did not differ between edge and interior forest habitats, implying that the invasion of clearing affiliated species is limited in its overall impact.

Vegetation responses to edge effects are varied and complex (Murcia 1995) and may result in localized shifts in species composition (Palik and Murphy 1990, Matlack 1994b). This research has documented distinct shifts in the bryophyte community found within forest edge habitats based on both an invasion of clearing affiliated species and a substantial drop in the abundance of old-growth associated species. Furthermore, the extension of edge effects at least 45 m into the forest for bryophytes has important management implications as many forestry companies are beginning to use variable retention practices in British Columbia. A critical mainstay of this forestry program is to leave small forest remnants to act as reservoirs of diversity for surrounding harvested areas (Franklin et al. 1997). While variable retention practices may contribute to the structural diversity of the forest, it is unlikely that bryophyte communities left in remnants less than 1.0 ha in size to will be representative of interior, old-growth forest bryophyte communities. Edge effects that extend 45 m into a 1.0 ha square patch will leave a core of interior habitat that is 10 m x 10 m in size – which we believe will not be large enough to include a representative complement of old-growth associated species or sustain individual populations. For bryophytes, small forest remnants will consist entirely of edge habitat and thus remnants may not contribute to overall biodiversity objectives.

2.6 Tables and Figures

Table 2.1. Comparisons of (a) stand structure variables and (b) substrate variables at increasing distances from the forest edge. Values shown are means (\pm 1 S.E.) for transects at the same distance intervals across the nine forest patches. All comparisons made using Kruskal-Wallis tests. P-values <0.05 are listed in bold.

| | Distance from the forest edge | | | | | P-value |
|--|-------------------------------|--------------|---------------|--------------|--------------|--------------|
| | 5 m Mean | 15 m Mean | 25 m Mean. | 35 m Mean | 45 m Mean | |
| a. Stand structure variables | | | | | | |
| Percent Cover | | | | | | |
| Canopy trees | 22.8±6.8 | 25±5.3 | 38.3±7.5 | 54.4±7.3 | 50.6±6.3 | 0.012 |
| Sapling/seedlings | 16.3±5.8 | 12.4±5.3 | 10±5.3 | 10±4.6 | 7.9±4.1 | 0.611 |
| Shrubs | 15±5.3 | 12.1±5.8 | 10.1±4.6 | 7.2±4.2 | 8±3 | 0.792 |
| Amount of coarse woody debris (CWD) | | | | | | |
| Percent cover of downed logs | 15.3±2.9 | 20.9±3.5 | 16.7±3.7 | 17.2±3.4 | 17.8±4.6 | 0.851 |
| <u>Decay class 1-2 logs</u> | | | | | | |
| Number | 1.6±0.6 | 2.1±0.7 | 0.9±0.5 | 0.9±0.4 | 0.4±0.2 | 0.149 |
| Volume (m³/ha) | 304.9±152.0 | 572.0±205.0 | 169.0±108.2 | 284.1±215.7 | 34.8±27.3 | 0.041 |
| <u>Decay class 3 logs</u> | | | | | | |
| Number | 1.4±0.4 | 1.2±0.5 | 0.8±0.2 | 1.1±0.4 | 1.1±0.3 | 0.830 |
| Volume (m³/ha) | 76.4±38.2 | 116.8±48.7 | 41.6±15.9 | 254.0±78.9 | 184.0±104.8 | 0.420 |
| <u>Decay class 4-5 logs</u> | | | | | | |
| Number | 1.3±0.4 | 1.1±0.5 | 2.4±0.9 | 2.1±0.6 | 2±0.5 | 0.527 |
| Volume (m³/ha) | 221.8±105.7 | 124.9±62.8 | 337.5±120.8 | 221.3±53.0 | 263.6±67.2 | 0.516 |
| b. Substrate variables | | | | | | |
| Mean number of tip-ups | 0.7±0.2 | 0.8±0.1 | 0.6±0.2 | 0.3±0.2 | 0.4±0.2 | 0.355 |
| Exposed mineral soil | 0.7±0.6 | 7.8±2.6 | 5±1.9 | 1.4±1.1 | 1.1±0.7 | 0.048 |
| Boulders | 11.4±5.7 | 9.6±4.6 | 9.7±4.4 | 0.9±0.5 | 1.7±0.8 | 0.111 |
| Litter | 42.4±7.8 | 32.3±7.4 | 31.8±5.3 | 49.3±6.6 | 42.8±7.9 | 0.364 |
| Humus | 12.1±3.0 | 10.9±6.2 | 4.6±1.6 | 7.9±4.1 | 8.3±3.4 | 0.352 |

Table 2.2. Comparisons of (a) Shannon diversity index and (b) species richness within taxonomic and functional groups at increasing distances from the forest edge. Whole-transect assessments are based on cumulative data from microplots and entire transect surveys. Microplot assessments are based on mean richness and cover values within microplots (N=15/transect). Shannon diversity at the whole-transect scale calculated from species frequencies within transects, while Shannon diversity index at the microplot scale based on species percent cover index within microplots. All comparisons made using Kruskal-Wallis tests. P-values less than 0.05 listed in bold.

| | Whole-transect assessment | | | | | | Microplot assessment | | | | | |
|-------------------------------------|-------------------------------|----------|----------|----------|----------|------------------|-------------------------------|-----------|-----------|-----------|-----------|------------------|
| | Distance from forest edge (m) | | | | | | Distance from forest edge (m) | | | | | |
| | 5 | 15 | 25 | 35 | 45 | P-value | 5 | 15 | 25 | 35 | 45 | P-value |
| a. Shannon diversity index | Mean | Mean | Mean | Mean | Mean | | Mean | Mean | Mean | Mean | Mean | |
| | 2.4±0.1 | 2.5±0.1 | 2.3±0.1 | 2.3±0.1 | 2.3±0.1 | 0.540 | 0.98±0.14 | 0.96±0.08 | 0.86±0.08 | 0.84±0.05 | 0.92±0.09 | 0.894 |
| b. Species richness | | | | | | | | | | | | |
| Taxonomic groups | | | | | | | | | | | | |
| Bryophytes | 18.2±1 | 19.7±1.2 | 16.6±1.7 | 15.6±0.9 | 16.2±1.4 | 0.143 | 4.05±0.55 | 3.68±0.23 | 3.58±0.27 | 3.51±0.22 | 3.61±0.3 | 0.906 |
| Liverworts | 7.4±0.8 | 8.6±0.9 | 7.4±1 | 7.4±0.6 | 8.1±0.9 | 0.918 | 2.37±0.29 | 2.23±0.13 | 2.37±0.16 | 2.07±0.14 | 2.17±0.15 | 0.738 |
| Mosses | 10.8±0.6 | 11.1±0.9 | 9.1±0.9 | 8.1±0.4 | 8.1±0.5 | 0.012 | 1.68±0.31 | 1.46±0.18 | 1.21±0.15 | 1.43±0.15 | 1.44±0.26 | 0.804 |
| Growth form groups | | | | | | | | | | | | |
| Cushion | 0.2±0.1 | 0.3±0.2 | 0.1±0.1 | 0.2±0.1 | 0.2±0.1 | 0.869 | 0.01±0.01 | 0.01±0.01 | 0.01±0.01 | 0.02±0.02 | 0.02±0.02 | 0.911 |
| Dendroid | 0 | 0.1±0.1 | 0 | 0 | 0 | 0.406 | 0 | 0.01±0.01 | 0 | 0 | 0 | 0.406 |
| Open turf | 1.3±0.3 | 1.2±0.3 | 0.7±0.5 | 0.3±0.2 | 0.1±0.1 | 0.008 | 0.12±0.05 | 0.01±0.01 | 0.01±0.01 | 0 | 0 | 0.005 |
| Pendent | 1.7±0.2 | 1.7±0.3 | 1.6±0.4 | 0.6±0.2 | 1.0±0.3 | 0.038 | 0.23±0.08 | 0.13±0.04 | 0.12±0.05 | 0.09±0.04 | 0.11±0.03 | 0.718 |
| Rough mat | 1.9±0.3 | 1.4±0.2 | 1.7±0.2 | 1.7±0.3 | 1.9±0.3 | 0.699 | 0.51±0.07 | 0.45±0.05 | 0.46±0.05 | 0.58±0.03 | 0.55±0.05 | 0.202 |
| Smooth mat | 5.1±0.7 | 6.1±0.8 | 5.3±0.7 | 5.3±0.6 | 5.8±0.7 | 0.932 | 1.24±0.2 | 1.31±0.18 | 1.15±0.12 | 1.15±0.15 | 1.13±0.21 | 0.797 |
| Sphagnoid | 0 | 0.1±0.1 | 0 | 0 | 0 | 0.406 | 0 | 0 | 0 | 0 | 0 | |
| Short turf | 2.2±0.3 | 2.7±0.6 | 1.9±0.4 | 1.7±0.3 | 1.9±0.3 | 0.500 | 0.56±0.07 | 0.59±0.07 | 0.58±0.04 | 0.43±0.05 | 0.42±0.05 | 0.125 |
| Thread | 1.6±0.2 | 1.6±0.4 | 1.1±0.4 | 1.3±0.3 | 1.3±0.3 | 0.880 | 0.3±0.09 | 0.22±0.06 | 0.12±0.06 | 0.2±0.04 | 0.22±0.09 | 0.577 |
| Thalloid mat | 0.1±0.1 | 0.1±0.1 | 0.2±0.1 | 0.1±0.1 | 0.2±0.1 | 0.911 | 0 | 0 | 0.01±0.01 | 0 | 0 | 0.406 |
| Tall Turf | 0.7±0.2 | 0.7±0.2 | 0.6±0.2 | 0.2±0.1 | 0.3±0.2 | 0.263 | 0.01±0.01 | 0.03±0.02 | 0.04±0.03 | 0.01±0.01 | 0 | 0.593 |
| Weft | 3.4±0.2 | 3.7±0.2 | 3.4±0.4 | 4.1±0.2 | 3.4±0.3 | 0.395 | 1.06±0.23 | 0.92±0.13 | 1.07±0.12 | 1.02±0.09 | 1.15±0.16 | 0.880 |
| Canopy preference groups | | | | | | | | | | | | |
| Closed canopy | 7.9±1.0 | 9.4±1.1 | 8.4±1.3 | 9.1±0.8 | 9.9±1 | 0.638 | 1.81±0.25 | 1.6±0.17 | 1.49±0.22 | 1.72±0.13 | 1.86±0.16 | 0.629 |
| Canopy generalist | 5.2±0.4 | 5.8±0.3 | 4.9±0.4 | 4.3±0.3 | 4.2±0.4 | 0.062 | 1.55±0.19 | 1.59±0.17 | 1.63±0.12 | 1.41±0.14 | 1.39±0.14 | 0.700 |
| Open canopy | 5.1±0.4 | 4.4±0.4 | 3.6±0.6 | 2.1±0.3 | 2.4±0.5 | <0.001 | 0.69±0.18 | 0.49±0.1 | 0.46±0.08 | 0.38±0.08 | 0.36±0.12 | 0.541 |
| Life-history strategy groups | | | | | | | | | | | | |
| Colonist | 4.8±0.5 | 4.6±0.6 | 3.0±0.7 | 2.1±0.3 | 1.8±0.4 | 0.001 | 0.89±0.17 | 0.77±0.06 | 0.62±0.04 | 0.44±0.05 | 0.39±0.05 | <0.001 |
| Short-lived shuttle | 0.8±0.2 | 1.6±0.3 | 0.8±0.2 | 0.6±0.2 | 0.6±0.2 | 0.065 | 0.04±0.03 | 0.04±0.02 | 0.04±0.02 | 0.02±0.02 | 0.02±0.02 | 0.710 |

| | | | | | | | | | | | | |
|------------------------------------|---------|---------|----------|----------|----------|-------|-----------|-----------|-----------|-----------|-----------|-------|
| Long-lived shuttle | 3.3±0.3 | 3.8±0.5 | 2.7±0.4 | 2.3±0.2 | 3.0±0.5 | 0.115 | 0.75±0.18 | 0.55±0.12 | 0.42±0.12 | 0.49±0.1 | 0.51±0.15 | 0.787 |
| Perennial stayer | 9.2±1.1 | 9.8±0.6 | 10.1±0.9 | 10.6±0.7 | 10.9±0.9 | 0.629 | 2.35±0.30 | 2.33±0.13 | 2.51±0.19 | 2.54±0.18 | 2.69±0.18 | 0.628 |
| Substrate-affinity groups | | | | | | | | | | | | |
| Epiphytic on tree bases | 4.7±0.4 | 5.2±0.5 | 4.7±0.3 | 5±0.4 | 5.7±0.3 | 0.316 | 1.75±0.23 | 1.82±0.15 | 1.74±0.09 | 1.79±0.1 | 1.65±0.14 | 0.836 |
| Epiphytic (blown down from canopy) | 2.8±0.3 | 3±0.4 | 2.3±0.5 | 1.8±0.3 | 2±0.4 | 0.149 | 0.56±0.14 | 0.41±0.09 | 0.37±0.1 | 0.41±0.08 | 0.39±0.12 | 0.879 |
| Epixylic (logs) | 2.0±0.7 | 2.1±0.6 | 2±0.8 | 2±0.4 | 2.3±0.6 | 0.898 | 0.18±0.09 | 0.17±0.06 | 0.15±0.06 | 0.16±0.04 | 0.3±0.1 | 0.788 |
| Epilithic (rocks) | 0.9±0.5 | 0.4±0.2 | 1±0.5 | 0.6±0.2 | 0.4±0.2 | 0.922 | 0 | 0 | 0.04±0.02 | 0.01±0.01 | 0 | 0.058 |
| Generalists | 3.1±0.3 | 3.1±0.2 | 2.7±0.3 | 2.8±0.4 | 2.2±0.3 | 0.214 | 0.82±0.18 | 0.67±0.11 | 0.67±0.07 | 0.58±0.07 | 0.55±0.09 | 0.648 |
| Terricolous on Humus | 0.1±0.1 | 0.2±0.2 | 0.1±0.1 | 0 | 0.1±0.1 | 0.898 | 0.01±0.01 | 0.02±0.02 | 0 | 0 | 0.01±0.01 | 0.718 |
| Terricolous on Litter | 2.0±0.2 | 2.3±0.4 | 2.1±0.4 | 2.4±0.2 | 2.4±0.2 | 0.720 | 0.52±0.15 | 0.51±0.11 | 0.54±0.12 | 0.54±0.07 | 0.71±0.14 | 0.896 |
| Terricolous on Soil | 2.7±0.7 | 3.2±0.7 | 1.7±0.6 | 1±0.4 | 1±0.2 | 0.079 | 0.2±0.11 | 0.08±0.05 | 0.07±0.04 | 0.01±0.01 | 0 | 0.160 |

Table 2.3. Summary of MRPP results comparing bryophyte species composition (a) at five distance intervals from the forest edge and (b) between edge and interior plots. Both comparisons made using data from whole-transect assessments (i.e., combined data from microplots and entire transect surveys) and from microplot assessments by sampling on three different substrate-types. P-values <0.05 listed in bold.

| Test | A* | P-value |
|--|---------|--------------|
| a. Edge – depth comparisons | | |
| Whole-transect assessments | 0.000 | 0.432 |
| Microplot assessments | | |
| All substrates combined | -0.001 | 0.495 |
| Forest floor | -0.0118 | 0.789 |
| Logs | 0.0018 | 0.411 |
| Tree bases | -0.026 | 0.989 |
| b. Edge – interior comparisons | | |
| Whole-plot (based on whole-transect surveys) assessments | 0.067 | 0.004 |
| Microplot assessments | | |
| Forest floor | 0.079 | 0.002 |
| Logs | 0.076 | 0.001 |
| Tree bases | 0.05 | 0.002 |

*A is the chance-corrected within group similarity where $A_{max} = 1$ when all bryophyte communities are identical within groups, $A = 0$ when heterogeneity of communities within groups equals expectation by chance and $A < 0$ when heterogeneity of groups exceeds that expected by chance

Table 2.4. Pearson correlations of stand structure and substrate variables with the first two axes from NMS ordination of bryophyte species frequencies in transects located at five distance intervals from the forest edge (n=45). R^2 values denote variance in species frequency data explained by ordination axes.

| Axis 1 ($R^2 = 0.259$) | | Axis 2 ($R^2 = 0.313$) | |
|---|--------|---|-------|
| Variable | r | Variable | r |
| # of logs in late decay classes (DC 4-5) | -0.469 | % cover of shrubs | 0.439 |
| Vol. of logs in late decay classes (DC 4-5) | -0.456 | % cover of bryophytes | 0.403 |
| % cover of bryophytes | -0.345 | Vol. of logs in late decay classes (DC 4-5) | 0.340 |
| % cover of litter | 0.372 | # of logs in late decay classes (DC 4-5) | 0.303 |
| % cover of exposed boulders | 0.363 | | |

Table 2.5. Comparisons of (a) stand structure variables, (b) habitat variables and (c) substrate variables between forest interior and edge plots. All comparisons made using Mann-Whitney U tests. P-values < 0.05 are listed in bold.

| | Interior Mean± 1 S.E. | Edge Mean±1 S.E. | P-value |
|--|--------------------------|---------------------|--------------|
| a. Stand structure variable | | | |
| Stand density (number of stems sampled on 5 transects in each plot) | | | |
| Amabilis Fir (>10 cm dbh) | 0.4±0.3 | 0.6±0.4 | 1.00 |
| Douglas Fir (>10 cm dbh) | 1.2±0.5 | 1.7±0.6 | 0.711 |
| Western Red Cedar (>10 cm dbh) | 1.3±0.6 | 1.8±0.5 | 0.358 |
| Western Hemlock (>10 cm dbh) | 8.2±0.8 | 9.1±1.0 | 0.415 |
| Total number of stems (>50 cm dbh) | 4.3±0.4 | 5.0±1.0 | 0.721 |
| Snags | 3.7±0.5 | 1.8±0.4 | 0.013 |
| Percent cover | | | |
| Canopy trees | 53.5±3.5 | 35.0±4.0 | 0.022 |
| Saplings/seedlings | 6.7±1.5 | 11.3±3.8 | 0.658 |
| Shrubs | 19.1±8.8 | 10.5±3.8 | 0.860 |
| Presence of coarse woody debris (CWD) | | | |
| Percent cover of downed logs | 11.9±1.6 | 17.4±1.7 | 0.042 |
| <u>Decay class 1-2 logs</u> | | | |
| Mean number of logs/ transect | 0.4±0.1 | 1.2±0.3 | 0.072 |
| Volume (m ³ /ha) | 77.8±31.3 | 273.0±97.7 | 0.038 |
| <u>Decay class 3 logs</u> | | | |
| Mean number of logs/transect | 0.9±0.2 | 1.1±0.2 | 0.685 |
| Volume (m ³ /ha) | 155.3±37.8 | 134.5±28.5 | 0.825 |
| <u>Decay class 4-5 logs</u> | | | |
| Mean number of logs/transect | 1.8±0.3 | 1.3±0.4 | 0.625 |
| Volume (m ³ /ha) | 243.4±32.4 | 233.8±55.2 | 0.270 |
| b. Habitat variables | | | |
| Slope (°) | 13.4±3.6 | 18.9±2.9 | 0.233 |
| Annual Potential Radiation | 161346±7821 | 180344±12223 | 0.047 |
| Aspect favorability | -0.1±0.3 | 0.4±0.2 | 0.171 |
| c. Substrate variables | | | |
| Litter | 54.3±3.9 | 39.7±4.5 | 0.860 |
| Humus | 20.7±2.8 | 8.7±2.1 | 0.007 |
| Boulders | 1.7±0.8 | 6.6±2.0 | 0.027 |
| Exposed mineral soil | 1.4±0.4 | 3.2±0.9 | 0.129 |
| Number of transects with tree tip-ups | 1.0±0.4 | 2.4±0.5 | 0.019 |

Table 2.6. Comparisons of (a) bryophyte cover, (b) Shannon diversity index and (c) species richness within taxonomic and functional groups between edge and interior plots. At the whole-plot scale, Shannon diversity index based on species frequencies within transects, while at the microplot scale Shannon diversity index based on species percent cover values within microplots. Whole-plot assessments of species richness refer to the cumulative species richness from microplots and entire surveys of the five transects comprising a plot; microplot assessments denote mean richness and cover within microplots (N=45/plot). All comparisons made using Mann-Whitney U tests. P-values < 0.05 are listed in bold.

| | Whole-plot assessment | | | Microplot assessment | | |
|---|-----------------------|--------------|------------------|----------------------|---------------|--------------|
| | Interior Mean. | Edge Mean | P-value | Interior Mean | Edge Mean. | P-value |
| a. Bryophyte cover | | | | | | |
| Forest floor | | | | 43.40±6.03 | 42.36±4.69 | 0.514 |
| Logs | | | | 61.31±6.08 | 38.42±4.88 | 0.014 |
| Tree bases | | | | 59.71±3.72 | 46.21±3.44 | 0.020 |
| b. Shannon diversity index | 2.7±0.0 | 2.6±0.0 | 0.887 | 1.06±0.03 | 0.91±0.07 | 0.085 |
| c. Species richness | | | | | | |
| Taxonomic groups | | | | | | |
| Bryophytes | 28.0±1.9 | 33.3±1.2 | 0.019 | 4.53±0.19 | 3.67±0.23 | 0.027 |
| Mosses | 15.2±0.7 | 18.6±1.1 | 0.005 | 2.50±0.18 | 2.23±0.12 | 0.112 |
| Liverworts ^l | 12.8±1.2 | 14.8±0.8 | 0.622 | 2.03±0.13 | 1.44±0.16 | 0.015 |
| Growth form groups | | | | | | |
| Cushion | 0.6±0.2 | 0.6±0.2 | 1.000 | 0.02±0.01 | 0.02±0.01 | 0.592 |
| Dendroid | 0.1 ±0.1 | 0.1 ±0.1 | 1.000 | 0 | 0 | |
| Open turf ^{E*} | 0 | 2.8±0.6 | <0.001 | 0 | 0.03±0.01 | 0.012 |
| Pendent | 1.7±0.3 | 2.2 ±0.3 | 0.135 | 0.15±0.05 | 0.13±0.04 | 0.965 |
| Rough mat | 2.9±0.5 | 3.3 ±0.3 | 0.553 | 0.59±0.04 | 0.51±0.02 | 0.215 |
| Smooth mat ^l | 10.6±0.6 | 10.3 ±0.8 | 0.788 | 1.47±0.06 | 1.19±0.13 | 0.047 |
| Sphagnoid | 0.1 ±0.1 | 0.11±0.11 | 1.000 | 0 | 0 | |
| Short turf | 3.0 ±0.2 | 3.8±0.5 | 0.305 | 0.45±0.04 | 0.52±0.04 | 0.182 |
| Thread ^l | 3.2 ±0.2 | 3.0 ±0.3 | 0.569 | 0.44±0.06 | 0.21±0.04 | 0.010 |
| Thalloid mat | 1.2 ±0.4 | 0.6±0.2 | 0.088 | 0.03±0.02 | 0 | 0.104 |
| Tall Turf ^E | 0.1 ±0.1 | 1.6±0.18 | <0.001 | 0 | 0.02±0.01 | 0.209 |
| Weft | 4.6±0.4 | 5.0 ±0.2 | 0.116 | 1.38±0.17 | 1.04±0.09 | 0.093 |
| Canopy preference groups | | | | | | |
| Closed canopy ^l | 19.1±1.4 | 17.7±1.0 | 0.564 | 2.48±0.18 | 1.69±0.13 | 0.005 |
| Canopy generalist | 5.8±0.4 | 7.7±0.6 | 0.026 | 1.50±0.08 | 1.51±0.13 | 0.965 |
| Open canopy | 3.1±0.2 | 8.0±0.5 | <0.001 | 0.55±0.04 | 0.47±0.08 | 0.401 |
| Life-history strategy groups | | | | | | |
| Colonists | 3.9±0.3 | 8.2±0.5 | <0.001 | 0.43±0.05 | 0.61±0.04 | 0.009 |
| Short-lived shuttles | 2.2±0.3 | 2.6±0.5 | 0.515 | 0.08±0.03 | 0.04±0.01 | 0.086 |
| Long-lived shuttles | 4.7±0.4 | 4.9±0.4 | 0.749 | 0.71±0.06 | 0.54±0.12 | 0.157 |
| Perennial stayers ^l | 17.0±1.2 | 17.60±0.8 | 0.504 | 3.31±0.2 | 2.48±0.13 | 0.007 |
| Substrate-affinity groups | | | | | | |
| Epiphytic on treebases | 7.3 ±0.2 | 6.8±0.32 | 0.200 | 1.83±0.07 | 1.75±0.08 | 0.250 |
| Epiphytic (blown down from canopy) ^l | 3.2 ±0.3 | 3.7±0.3 | 0.332 | 0.63±0.06 | 0.42±0.09 | 0.069 |
| Substrate generalists ^l | 4.1 ±0.2 | 4.2±0.2 | 0.693 | 0.83±0.07 | 0.65±0.07 | 0.085 |
| Terricolous on Humus | 0.6±0.4 | 0.6±0.3 | 0.737 | 0 | 0.01±0.01 | 0.146 |
| Terricolous on Litter | 3.3 ±0.4 | 3.8±0.4 | 0.519 | 0.65±0.12 | 0.57±0.09 | 0.452 |
| Terricolous on Soil ^E | 1.1 ±0.3 | 6.2 ±0.8 | <0.001 | 0 | 0.07±0.03 | 0.005 |

| | | | | | | |
|------------------------------|----------|----------|-------|-----------|-----------|--------------|
| Epixylic (logs) ^I | 6.9±0.2 | 5.7±0.6 | 0.130 | 0.56±0.1 | 0.19±0.04 | 0.003 |
| Epilithic (rocks) | 1.4 ±0.7 | 2.4 ±0.6 | 0.136 | 0.01±0.01 | 0.01±0 | 0.455 |

* Upper case letters denote functional groups showing significantly higher frequency of occurrence in either edge (E) or interior plots (I).

Table 2.7. Pearson correlations of stand structure, habitat and substrate variables with axes from NMS ordination of bryophyte species frequency in edge and interior plots (n=18). R^2 values denote variance in species frequency data explained by ordination axes.

| Axis 1 ($R^2=0.371$) | | Axis 2 ($R^2=0.320$) | |
|---|--------|--|--------|
| Variable | r | Variable | r |
| Slope | -0.489 | % cover of saplings/seedings | -0.505 |
| % cover of boulders | -0.453 | Slope | -0.504 |
| % cover of shrubs | 0.481 | % cover of boulders | -0.437 |
| % cover of humus | 0.325 | Vol. of logs in early decay classes (DC 1-2) | -0.319 |
| Vol. of logs in late decay classes (DC 4-5) | 0.311 | % cover of litter | 0.61 |
| | | % cover of humus | 0.436 |
| | | % canopy cover | 0.35 |

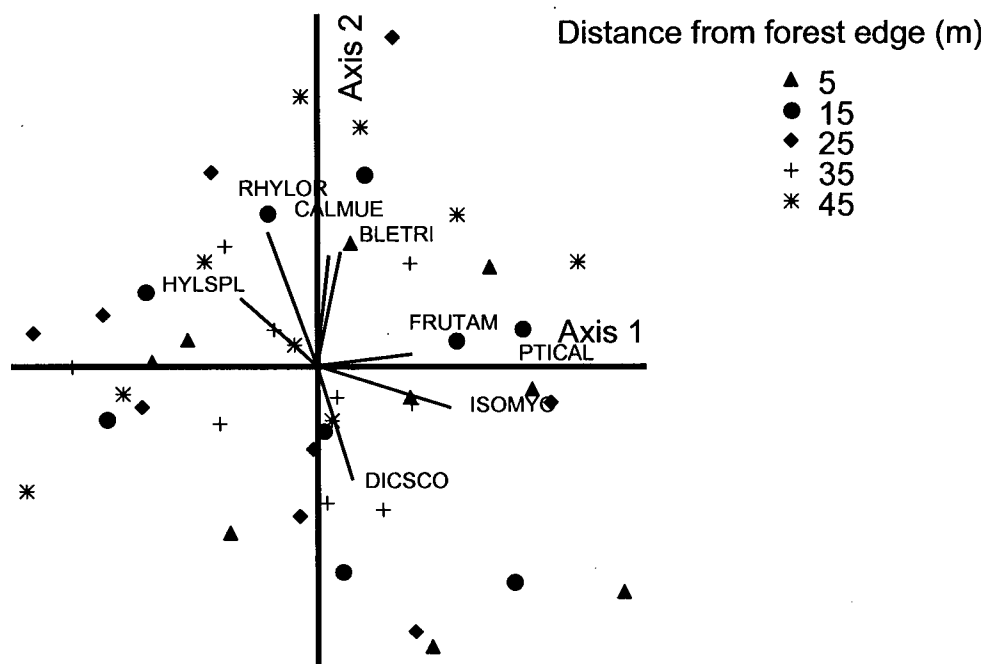


Figure 2.1. Joint plot of NMS ordination of edge zone transects ($n=45$) located at five distances (5, 15, 25, 35, 45 m) from the forest edge overlain by species frequency. Axis 1 accounts for 25.9% of the variation in the data while the second axis accounts for 31.3% (total = 56.2 %). Ordination based on a 3-dimensional solution with a final stress of 17.11. Bryophyte species abbreviations combine the first three letters of the genus and the specific epithet; see Appendix A for species lists.

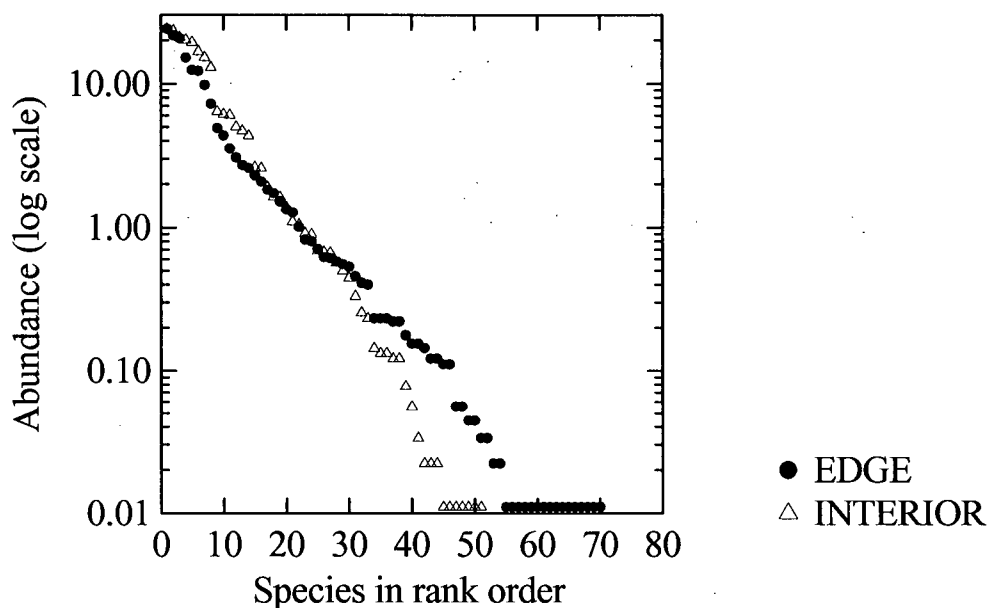


Figure 2.2. Rank-abundance curves for bryophyte abundance (based on species frequency in microplots and transect searches) in interior and edge plots ($n=18$).

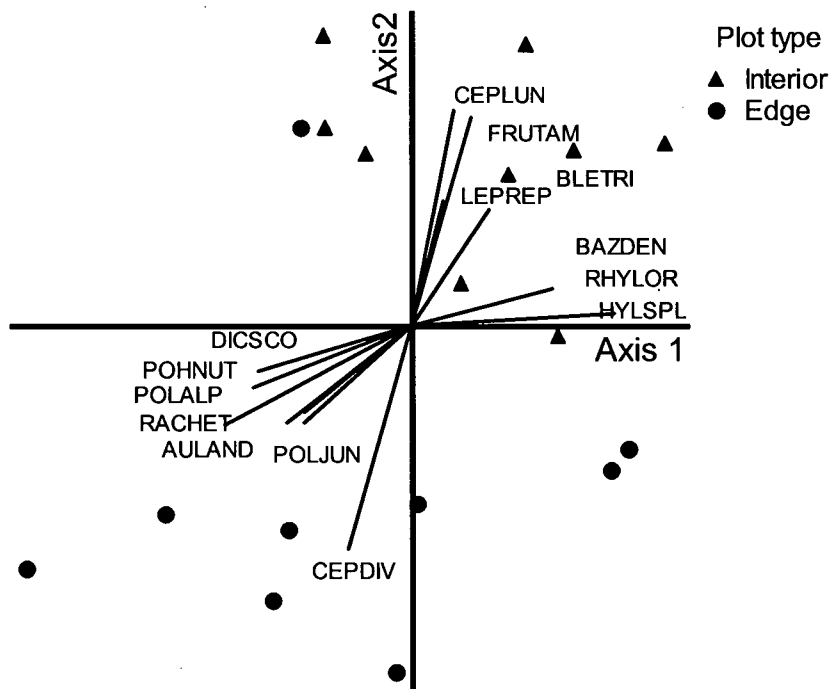


Figure 2.3. Joint plot NMS ordination of edge and interior plot species composition matrix overlain with species frequency. Axis 1 accounts for 37.1% of the variation in the data while the second axis accounts for 32.0% (total = 69.1 %). Ordination based on a 3-dimensional solution with a final stress of 11.14. Bryophyte species abbreviations combine the first three letters of the genus and the specific epithet; see Appendix A for species lists.

CHAPTER III. Effects of stand age on species richness and composition of bryophyte communities in temperate rainforests of coastal British Columbia, Canada

3.1 Abstract

The species richness and abundance of bryophytes within taxonomic and functional groups, as well as overall species composition, was examined in relation to environmental conditions and stand age in two different forest types (warmer, drier vs. cooler, wetter) on Vancouver Island, British Columbia. Bryophytes were sampled at a fine scale using 10 cm x 30 cm microplots to estimate species abundance on three substrate-types (forest floor, downed logs and tree bases), and at a coarser scale for species composition within 10 m x 2 m transects located in naturally regenerating stands (stand ages 7-20 years), immature stands (stand ages 25-49 years) and old-growth forest stands (stand ages >300 years). While wetter forests supported greater alpha and gamma bryophyte diversity than drier forests, bryophyte richness was also strongly related to stand age. Overall bryophyte species richness was highest in regeneration stands, declined to its lowest values in immature stands and increased in old-growth stands. Consideration of bryophyte species richness at different spatial scales introduces greater complexity into the observed pattern of bryophyte richness across stand ages. Large-scale alpha richness was consistent with the above pattern; however, fine-scale alpha richness tended to be lower in both regeneration and immature plots as compared to old-growth plots. Furthermore, bryophyte functional groups showed different patterns of richness and abundance in younger-aged stands when compared to old-growth stands. The richness of clearing affiliated groups was higher in younger-aged forests when sampled at a coarse scale while the richness of old-growth associated species showed few differences at this scale. In contrast, the fine-scale richness of old-growth associated species was significantly reduced in younger aged forests, indicating that while these species are not completely eliminated from young-aged forests, their overall performance is diminished. Furthermore, the cover of all bryophytes was both diminished and

more patchily distributed in younger-aged stands. The pattern of species occurrence where both pioneer and old-growth species are found concurrently in early successional seres supports the initial floristics model of succession. The results of this study indicate that the use of two sampling scales combined with recognition of bryophyte functional group categories are useful for evaluating the influence of stand ages on the forest bryophyte community.

Keywords: bryophyte, stand age, succession, initial floristics, invasion, functional groups, old-growth forest

3.2 Introduction

All forested landscapes consist of a mosaic of forest patches (Pickett and White 1985, Spies and Turner 1999), the size and age of which depend in large part upon the disturbance regime of the landscape (Johnson et al. 1995). In the coastal temperate rainforests of British Columbia, patch size is typically small, driven by underlying soil and topographical heterogeneity and small-scale wind-disturbance, with fire an infrequent occurrence (Arsenault 1995, Lertzman et al. 2002). Large-scale forestry practices in coastal British Columbia have imposed a different disturbance regime on these forests, varying in both spatial and temporal scale. With increased disturbance due to clear-cut logging, average stand age has been reduced (MacKinnon and Vold 1998), resulting in a mosaic of remnant old-growth patches surrounded by a matrix of younger-aged stands. Bryophytes are an important component of these forest ecosystems (Schofield 1976, Binkley and Graham 1981, Alaback and Pojar 1997), yet we have little understanding of the response of the bryophyte community following clear-cut logging. Worldwide, forestry practices have been cited as the greatest contributor to the decline of individual species as well as ecological groups of bryophytes (Christy 1992). The maintenance of species diversity in managed landscapes depends not only on the continual persistence of organisms within remnant old-growth patches but the eventual recovery of communities in

harvested areas (Franklin 1993). An understanding of bryophyte composition and diversity present in younger-aged forests is critical to predicting the eventual outcome of both processes. The primary purpose of this paper, therefore, is to compare the bryophyte community in young and immature forests with that found in old-growth forests.

Conservation theory predicts that species richness in *isolated* forest remnants will decrease over time (MacArthur and Wilson 1967, Doak and Mills 1994). It is not clear, however, to what extent younger-aged forests isolate bryophyte populations found in remnant old-growth patches. Although several studies have compared bryophyte communities in second-growth forests to old-growth forest (Gustafsson and Hallingbäck 1988, Söderström 1988a, Andersson and Hytteborn 1991, Lesica et al. 1991, Rambo and Muir 1998a, 1998b), little work has investigated bryophyte composition and diversity in recently harvested areas (but see Ross-Davis and Frego 2002, Fenton et al. 2003). Obviously, the recovery trajectory of bryophyte communities in harvested areas will be different depending on the bryological legacy found in recently cut areas. The spatial and temporal variation of forest composition is often strongly linked to initial dispersal and establishment (Spies and Turner 1999). Studies investigating bryophyte diversity in managed forests have emphasized the loss of epixylic (log-dwelling) bryophyte species from second-growth (tree age ranging from 50-80 yrs) forests (Gustafsson and Hallingbäck 1988, Söderström 1988a, Andersson and Hytteborn 1991, Lesica et al. 1991, Rambo and Muir 1998a, 1998b). Understanding how early this bottleneck develops in second-growth forest will be critical for forest managers attempting to manage for biological diversity.

The coastal temperate rainforests of British Columbia are renowned for their richness and abundance of bryophyte species (Alaback and Pojar 1997, Schofield 1998). With over 700 species reported, the taxonomic diversity of bryophytes (including mosses, liverworts and hornworts) in these forests is the richest in the province (Schofield 1988, 1998). Based on growth forms, forest bryophytes can be categorized into a number of broad, functional groups

(Table 1.1) that are likely to show correlations with environmental factors such as moisture and light (Gimingham and Birse 1957, Magdefrau 1982, During 1992). For example, cushions and short turfs are characteristic of open sites, whereas wefts and pendants are intolerant of high illumination and are associated with relatively high humidity (Schofield 1981). Bryophytes have also been classified into life strategies (During 1979, 1992) similar to the r-K strategies concept (MacArthur and Wilson 1967, Pianka 1970). Given the taxonomic difficulties of bryophytes in general, categorization by functional groups offers a useful means to assess bryophyte responses to changing conditions within the forest.

As stated in Chapter 2, the effect of spatial scale on research conclusions has become increasingly recognized (Rahel 1990, Levin 1992, Drewa and Bradfield 2000). Haila (1999) has argued that the scale of analysis should be dictated by the size of the organism under investigation (i.e. an "organism-centered" approach). However, forest management is unlikely to occur at very small scales (Bunnell and Huggard 1999), thus we sampled the bryophyte community at two different spatial scales: at the microplot scale (10 cm x 30 cm) that approximated the scale at which individual bryophyte colonies interact with their environment and at the whole-plot scale (cumulative surveys across five 2 m x 10 m belt transects) that are more likely to be integrative across individual stands. The primary purpose of this research was to use the analysis of different sampling scales and bryophyte functional groups to document the effects of stand age on the bryophyte community in the coastal temperate rainforests of northeastern Vancouver Island, British Columbia. Understanding the qualitative and quantitative nature of these responses in relation to forest age is a crucial step toward ensuring that the biodiversity objectives of forest management are being met (British Columbia Ministry of Forests 1995).

3.2 Methods

Study area

Using satellite imagery and aerial photographs of Vancouver Island, Canada, we selected two areas, the Nimpkish River valley (50° 10' N 126° 30' W) and the region near the town of Sayward (50° 10' N 125° 45' W), on northeastern Vancouver Island. The landscape in both of these areas is mountainous with numerous small lakes and rivers and contains numerous remnant patches of old-growth forests. Coastal Western Hemlock is the dominant biogeoclimatic zone in both geographic areas; however, most of the forests in the two geographic regions are in different biogeoclimatic subzones (see Pojar et al. 1987, Meidinger and Pojar 1991, Green and Klinka 1994 for descriptions of the biogeoclimatic classification system and details on the CWH zone and individual subzones).

Forests in the Nimpkish Valley are in the very dry Coastal Western Hemlock (CWHxm) subzone and consist predominantly of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) and western hemlock (*Tsuga heterophylla*) with minor amounts of western redcedar (*Thuja plicata*) also present (Meidinger and Pojar 1991). Forests in this subzone have warm, dry summers and moist, mild winters with relatively little snowfall (Green and Klinka 1994). Climate data from Cumberland, British Columbia (49° 37' N 125° 02' W; the closest weather station in CWHxm subzone to the Nimpkish Valley) show that mean annual precipitation is approximately 1638 mm with less than 20% occurring during May-September (Figure 3.1a). Mean monthly temperatures range from a 0.9°C in January to 16.5°C in July; weather data for the period 1960-1977 (Environment Canada 2000).

Forests in the watersheds surrounding Sayward are primarily in the very wet maritime Coastal Western Hemlock (CWHvm) subzone and are dominated by western hemlock (*Tsuga heterophylla*), amabilis fir (*Abies amabilis*) and western red-cedar (*Thuja plicata*) (Meidinger and Pojar 1991). This subzone experiences cool summers and moist, mild winters with relatively

little snow (Green and Klinka 1994). Climate data from Sayward, British Columbia (50° 10' N 125° 45' W) indicate that mean annual precipitation is approximately 2030 mm with less than 20% occurring during May-September (Figure 3.1b). Mean monthly temperatures range from -2.6°C in January to 14.9°C in August; weather data for the period 1973-1999 (Environment Canada 2000).

In both areas, extensive deforestation through clear-cut logging has occurred. Logging began primarily in the late 1800's and accelerated during the middle part of the last century so that most second-growth stands in both areas are less than 60 years old (unpublished forest history maps). Logging has been concentrated along valley bottoms, although cutting is continuing at higher elevations. Thus, a range of forest stand ages, including old-growth forest remnants, immature and regenerating clear-cut stands, representative of the two forest types, are available for comparative study of stand age as it relates to bryophyte communities.

Site selection and bryophyte sampling

Based on recent forest inventories and aerial photographs in the two forest types, we identified 17 old-growth stands (8 Sayward stands and 9 Nimpkish stands), 12 immature stands (6 stands in each forest type) and 13 regeneration stands (6 Sayward stands and 7 Nimpkish stands). Old-growth stands had ages >300 years, while immature stands had ages of 25 to 49 years and regeneration stands had ages of 7 to 20 years. The elevation of Sayward stands ranged from 150 m a.s.l. to 670 m a.s.l. and the elevation of Nimpkish stands ranged from 150 m a.s.l. to 425 m a.s.l. Using aerial photographs, we located all old-growth plots at the approximate center of isolated forest patches ranging in size from 1.8 ha to more than 63 ha. Two old-growth plots were located approximately 75 m from the nearest edge, while the distance to the nearest edge exceeded 100 m for all other old-growth plots. As the younger-aged forest plots were originally sampled as part of a pilot study to determine the influence of old-growth remnant patches on harvested areas (Baldwin 2000, Perry et al. 2002), most immature and regeneration plots were

located immediately adjacent to an old-growth forest patch. Due to access problems, five immature plots were located approximately 50 m from the edge of the old-growth forest patch.

Bryophytes were sampled along five 10 m x 2 m belt transects located within each age class at the two study areas. For the immature and regeneration stands, the belt transects were located parallel to the remnant edge, defined by the boles of the outermost trees, 10 m apart from one another. Old-growth belt transects were located in a 3 x 2 grid pattern (each transect 10 m away from another) across the centre of the remnant patch. To account for microhabitat heterogeneity within the belt transects, bryophytes were sampled using nine 10 cm x 30 cm microplots located on three substrate-types: forest floor, tree bases and fallen logs. Microplot locations were determined as the closest respective substrate-type to three randomly selected points along the centre line of each transect. Following McCune and Antos (1981), microplots were partitioned into six equal size units of 50 cm² and species cover classes were recorded to the closest half 50 cm² partition unit. Cover classes were subsequently converted to percentages with one cover class being equal to a mean cover of 16.7%.

Bryophyte species were classified into life history strategies (During 1979, 1992) based primarily on spore size (greater or less than 20 μ m), frequency of sporophyte production (as determined from field observations and literature reports (Schofield 1976, Godfrey 1977)), life span (as estimated from growth form and presence of annual increments) and presence of vegetative reproduction (Table 1.1). Growth form and canopy preference assignments of bryophyte species were made according to the criteria in Table 1.1 and were based on either field observations or literature reports (Schofield 1976, Godfrey 1977, Schofield 1992), with uncertainties resolved on the advice of local expertise (W.B. Schofield, pers. comm.). Following the recommendation of McCune and Lesica (1992), full transect searches for bryophyte species not encountered in the microplots also were conducted. In this case, species were recorded by their presence only. Specimens obviously blown down from the canopy (lying on but not

attached to substrate) were recorded as being epiphytic. After tentative identification in the field, all species identifications were confirmed in the laboratory.

Habitat and stand structure variables within the belt transects were recorded by visual estimates of percent cover of boulders, litter, standing water, humus, exposed mineral soil and CWD greater than 10 cm diameter, as well as by coverage of tree (dbh > 10 cm), sapling (2.5 cm < dbh < 10 cm), shrub and tree seedling (dbh < 2.5 cm) layers. The diameter and decay class (DC 1-5, Maser et al. 1988) of CWD greater than 10 cm diameter intersecting the transect centre line also were recorded. Calculations of CWD volume were made following the method of Howard and Ward (1972). The presence of recent tip-up mounds in each transect was also recorded. Slope and aspect were recorded for each transect and an aspect favorability index was calculated (Beers et al. 1996). The annual potential incident light energy was determined for each transect as a function of latitude, slope and aspect (Buffo et al. 1972).

To assess the effect of substrate heterogeneity within the sampled substrates, the following variables were recorded for each microplot: (1) forest floor microplots—occurrence and cover of substrate-types, (2) downed logs—diameter and decay class of log where sampled and (3) tree bases—dbh and status of the tree base (live tree, stump, or snag). Stump diameter was recorded at the tallest height possible. Based on the dbh of sampled tree bases, the basal area of live trees, stumps and snags was calculated for each plot.

Nomenclature for mosses and liverworts follows Stotler and Crandall-Stotler (1977), Anderson (1990), Anderson et al. (1990) and Flatberg (1993). Voucher specimens are deposited in the University of British Columbia herbarium and in the senior author's herbarium.

Data Analyses

In each sampled stand, stand structure, habitat and substrate variables recorded in the five belt transects were summed or averaged to provide plot-level estimates. Two different measures of alpha diversity were calculated: 1) mean microplot richness, calculated from all microplots in

a plot ($n=45$), and 2) cumulative whole-plot species inventories derived from microplots and ocular surveys of all 5 transects. The Shannon diversity index was compared at both the microplot and whole-plot scale. We also compared gamma diversity, calculated as combined whole-plot level species inventories, across stand ages and forest types. Comparisons of species richness between regeneration, immature and old-growth plots were made using taxonomic categories (total bryophytes and mosses and liverworts separately) as well as using various functional groups (Table 1.1). Because sampling was conducted at two scales within transects (i.e., microplots on three substrate-types and whole-plot surveys across all substrates), greater refinement in the levels of comparison was possible than if only a single scale of sampling had been used.

The influence of stand age on stand structure, habitat and substrate variables and the richness of bryophyte functional groups, as well as on percent cover of bryophytes, was analyzed using generalized linear models, a class of models of which linear regression is a particular case. Generalized linear models allow for a range of relationships to be analyzed between the response and explanatory variables and for the use of other error functions when the normal distribution is not applicable (McCullagh and Nelder 1989). In each model, regeneration and immature plot variables were contrasted with old-growth plot variables using planned comparisons with forest type and stand age entered as categorical variables. For all non-count data (habitat, stand structure and substrate variables), a linear regression model was used (i.e., with a normal error term and an identity link function). In order to better meet the assumptions of the regression model, habitat variables recorded by percent cover estimates were converted to proportions of one and then arcsine-square root transformed. Stand structure variables (CWD volume and the basal area of live trees, snags and stumps) were log transformed.

Following McCullagh and Nelder (1989) an model designed for count data that used a Poisson error term and logarithmic link function was considered the most appropriate for our

species richness data. Overall significance of stand age in the model was assessed by determining whether the drop in deviance residual (the measure of the lack of fit in the model) caused by including the term in the model was significant (Ramsey and Schafer 1997). We encountered difficulties with underdispersion that resulted from the lower than expected variances of the raw data, which were often substantially less than the mean values. As a consequence, we assessed the significance of changes made during model fitting by using scaled changes in deviance (SAS 1999), which are distributed approximately as an F statistic (Ramsey and Schafer 1997). Wald's test (adjusted for underdispersion) was used to determine the significance of the parameters for each level of stand age (i.e., whether regeneration or immature forest species richness differed from old-growth species richness). Because we made planned comparisons of the two younger forest ages with old-growth forests rather than all possible pairwise comparisons, significant contrasts are reported even if the overall effect of stand age was not significant (Ramsey and Schafer 1997).

In addition to the univariate comparisons described above, we also examined the multivariate patterns in overall bryophyte species composition in relation to stand age and variation in habitat conditions among transects. The differences in bryophyte species composition and richness between the two forest types determined that multivariate analyses were performed separately for each forest type. To evaluate the association of individual species with stand age classes at each study area, we used the indicator test of Dufrêne and Legendre (1997). This test compares the relative frequency of occurrence and abundance of species in different groups of plots and identifies species that vary more between groups than would be expected by chance (Dufrêne and Legendre 1997). Indicator value in this analysis range from 0 (no indication) to 100 (perfect indication) where perfect indication means that presence of a species points to a particular group without error (McCune and Mefford 1999).

To test for compositional differences between regeneration and old-growth plots and between immature and old-growth plots, two non-parametric multivariate methods were used. First, multi-response permutation procedure (MRPP) was performed on a matrix of plots by species frequency values, which tested the null hypothesis that plots in stands of different ages supported similar bryophyte communities. Second, non-metric multidimensional scaling (NMS) provided a method of indirect ordination to characterize the major variation in species frequencies among plots, unconstrained by stand age. NMS is a dimension reduction technique that escapes many of the distortions of eigenvector techniques (Kenkel and Orlóci 1986, Minchin 1987). To improve interpretability of the results, species occurring in fewer than 5% of the plot were omitted, and relativization by species maxima applied. The quantitative version of Sorensen's index was used as the distance measure in NMS. Joint plots were used to depict relationships between individual species and the ordination axes. Pearson correlations (r-values) were used to assess relationships between the NMS ordination axes and environmental variables measured within transects. As in the univariate comparisons, MRPP and NMS were performed using bryophyte composition data from both microplot and whole-plot assessment levels to determine whether community relationships are influenced by sampling scale.

The generalized linear models were run using SAS (1999); indicator species analysis, MRPP and NMS were performed using PC-ORD (McCune and Mefford 1999).

3.4 Results

Comparison of forest types

Stand structure, habitat characteristics and substrate availability

After accounting for differences in stand age, few differences in stand structure, habitat or substrate variables were detected between plots sampled in Nimpkish and Sayward forests (Table 3.1). Whereas the number of logs in early decay classes (DC 1-2) was significantly higher (albeit marginally) at Sayward, the corresponding volume estimates were lower at

Sayward than at Nimpkish. The amount of CWD (both volume and number) in later decay classes (DC 3-5) was not significantly different between the two forest types. Other differences included a greater frequency of fine-scale woody debris (FWD, <10 cm diameter) occurring in microplots at Sayward forest plots and higher estimates of annual potential radiation and aspect favorability index at Nimpkish as compared to Sayward.

Bryophyte diversity and composition

A total of 108 bryophyte species (43 liverworts and 65 mosses) were recorded across the age classes at the two study areas (Appendix B). Overall species richness was slightly higher at Sayward (90 species) than at Nimpkish (85 species). After stand age was accounted for, bryophyte species richness, assessed through both cumulative plot-level estimates and mean microplot estimates, was significantly higher at Sayward plots than at Nimpkish (Table 3.2). Most bryophyte species occurred infrequently, with the number of species present within individual plots ranging from 19% to 45% of the total number of species observed in all plots. Over 30% of bryophyte species occurred in only 1 or 2 plots. Only six species—three liverworts (*Lepidozia reptans*, *Frullania tamarisci* subsp. *nisquallensis* and *Scapania bolanderi*) and three mosses, (*Dicranum fuscescens*, *Hypnum circinale* and *Rhytidiadelphus loreus*)—were found in all 42 plots sampled.

Comparison of regeneration plots with old-growth plots

Stand structure, habitat characteristics and substrate availability

After accounting for differences in forest type, significant differences in a number of stand structure and substrate variables were detected between regeneration and old-growth plots (Table 3.3). Regeneration plots had significantly less canopy cover and a greater cover of shrub and seedlings/saplings than did old-growth plots (Table 3.3). Regeneration plots had a greater relative basal area of sampled stumps, whereas old-growth plots had significantly greater relative

basal area of sampled small live trees, large live trees and snags. The mean number of logs in early decay classes (DC 1-2) and medium decay class (DC 3) was significantly greater in regeneration stands than in old-growth stands. In contrast, both the mean number and mean volume of well-decayed logs (DC 4-5) was significantly higher in old-growth plots than in regeneration plots. The number of microplots with litter/humus was significantly higher in old-growth plots, while the number of microplots with exposed soil and rock was significantly higher in regeneration plots (Table 3.3).

Bryophyte diversity and composition

Regeneration plots had higher gamma diversity than old-growth plots in both Nimpkish and Sayward forests. In Sayward forests, 79 species were found in regeneration plots, while only 64 species were found in old-growth plots. In Nimpkish forests, regeneration plots had a gamma diversity of 69 species and old-growth plots had a gamma diversity of 52 species. Differences in bryophyte species richness between regeneration and old-growth plots varied depending the scale of comparison (Table 3.4). When species richness was based on cumulative whole-plot estimates, regeneration plots supported a significantly higher number of bryophytes, driven by an increase in moss richness. In particular, the richness of bryophyte functional groups expected to colonize disturbed habitats (colonists and short-lived shuttles, bryophytes with open canopy preferences or canopy generalists and bryophytes with turf growth forms) was significantly higher in regeneration plots than in old-growth plots. The plot level richness of liverworts, on the other hand, showed no difference between old-growth and regeneration plots when assessed through cumulative whole-plot surveys. Likewise, the mean Shannon diversity indices did not differ between regeneration and old-growth plots (Table 3.4).

In contrast, fine-scale alpha richness in regeneration and old-growth plots displayed very different patterns. The mean microplot richness of mosses did not differ between regeneration and old-growth plots, whereas the mean microplot richness of liverworts was significantly lower

in regeneration plots. Furthermore, although the richness of colonists, open canopy bryophytes and turf mosses at the microplot scale remained significantly higher in regeneration plots, the mean microplot richness of smooth mats, long-lived shuttles and perennial stayers was significantly reduced in regeneration plots. This reduction in richness at the microplot scale was influenced by the significantly higher number of “empty” microplots found in regeneration plots as compared to old-growth plots (Wald’s test, $p < 0.001$). Moreover, the total abundance of bryophytes, as measured by percent cover in microplots, was significantly lower on downed logs and tree bases (Table 3.4). The cover of bryophytes on the forest floor, however, showed no significant differences between old-growth and regeneration plots.

The distinction between regeneration and old-growth plots in Sayward and Nimpkish forests was corroborated by MRPP results which showed significant differences in overall bryophyte species composition with both whole-plot and microplot assessments (Table 3.5). Of the 18 species associated with regeneration plots, 13 species had turf growth forms (Table 3.6), which was significantly higher than expected (Pearson $\chi^2 = 12.54$, $df = 1$, $p < 0.001$). In contrast, species associated with old-growth plots consisted entirely of liverworts, mats (threads, smooth and rough mats), pendants and wefts.

In the NMS ordination of the three stand age classes at Nimpkish, old-growth plots are separated from regeneration plots along the second NMS axis. Environmental correlates of old-growth plots (i.e., habitat and stand structure variables with negative correlations along the second NMS axis) included stand age, relative basal area of sampled large trees and snags, as well as the volume of well-decayed logs (DC 4-5) and percent cover of canopy trees. Environmental correlates of regeneration plots (stand structure and habitat variables with positive correlations along the second NMS axis) included shrub cover and the relative basal area of sampled stumps (Figure 3.2).

The compositional difference in old-growth and regeneration plots at Sayward forests parallels that found at Nimpkish. Old-growth plots are separated from regeneration plots along the second NMS axis (Figure 3.3). Environmental correlates of old-growth plots (i.e., stand structure, habitat and substrate variables with negative correlations on the first axis) included stand age, percent cover of canopy trees, the number of well-decayed logs (DC 4-5) and the relative basal area of sampled large trees. Environmental correlates of regeneration plots included the cover of seedlings and saplings, exposed mineral soil and boulders and the relative basal area of sampled stumps.

Comparison of immature plots with old-growth plots

Stand structure, habitat characteristics and substrate availability

Estimates of canopy, shrub and seedling/sapling cover were not significantly different between immature and old-growth plots (Table 3.3). Immature plots had significantly lower relative basal area of sampled snags and large live trees, and a higher relative basal area of sampled stumps and small live trees. No significant difference was noted between old-growth and immature plots in either the mean volume or number of well-decayed logs. Immature plots, however, showed a significant decrease in the volume of logs in the medium decay class (DC 3). Of the three substrate categories found in forest floor microplots, only FWD showed a significant decrease in immature plots when compared to old-growth stands (Table 3.3). No significant difference in slope, annual potential radiation or aspect favorability index was detected between immature and old-growth plots.

Bryophyte composition and abundance

Old-growth plots had greater gamma diversity than immature plots in both forest types. In Sayward forest, 64 species were documented in old-growth plots while only 59 species were found throughout immature plots. In Nimpkish forests, we found 52 and 50 species in old-growth and immature plots, respectively. Similar to the comparison of old-growth-with

regeneration plots, differences in species richness between immature and old-growth plots varied depending upon the sampling scale. When species richness was based on whole-plot inventories, moss richness was significantly higher in immature plots (Table 3.4). The increase in whole-plot moss richness was driven by an increase in open and tall turf mosses. Other functional groups expected to colonize disturbed areas (colonists and open canopy species) also showed significant increases in immature plots. The only group to show a significant decrease in whole-plot species richness was the pendent growth form (Table 3.4). Whole-plot liverwort richness was lower in immature forests, although only marginally significant ($p=0.06$).

Bryophyte species richness, as determined through microplot sampling, was significantly lower in immature plots than in old-growth plots. Mean microplot richness of total bryophytes, mosses, liverworts, as well as long-lived shuttles, perennial stayers, canopy generalists, closed canopy species, pendants, rough and smooth mats and wefts, was significantly lower in immature plots as compared to old-growth plots (Table 3.4). This reduction in mean microplot richness was influenced by the large number of microplots devoid of bryophytes, which was significantly higher in immature plots than in old-growth plots (Wald's test, $p=0.0003$). Finally, bryophyte cover in forest floor, log and tree base microplots was significantly lower in immature forests (Table 3.4).

Multivariate analysis showed that the separation of immature and old-growth plots in species space differed between the two study areas. With Nimpkish plots, MRRP detected significant differences in overall composition at the whole-plot level, as well as at the level of microplot assessment (Table 3.5b); however, at Sayward, no significant differences in overall bryophyte composition was found. Indicator species analysis revealed only four species that were strongly associated with immature forests at either study area (Table 3.6). In the NMS ordination of Nimpkish plots, immature and old-growth plots are separated along the first axis, which is strongly correlated with relative cover of sampled small trees (Figure 3.2). In

comparison, the ordination of Sayward plots reveals little separation of immature and old-growth plots (Figure 3.3).

3.5 Discussion

Richness patterns by forest type and stand age

The results of this study indicate that, while regional differences in forest type can affect the pool of bryophyte species available, bryophyte richness and composition is strongly affected by forest stand age. In general, this study supports the pattern observed by Franklin (1982) for diversity in different-aged forests in the Pacific Northwest: diversity increases to a peak at some point prior to closure of the tree canopy (approx. < 30 years), declines to its lowest values under canopy closure (approx. 30-100 years) and increases again as canopies of young and mature stands reopen (approx. 100+ years).

Consideration of species richness at different spatial scales, however, introduces greater complexity into the pattern of species richness across stand ages. In this study, large-scale alpha richness (cumulative plot-level species lists derived from whole-transect assessments including microplots) was consistent with Franklin's (1982) model. In contrast, fine-scale alpha richness (mean richness in individual microplots) tended to be lower in both regeneration and immature plots as compared to old-growth plots. This apparent contradiction is a function of the different sampling resolution of microplots and belt transects. In belt transects, habitat heterogeneity is coarse-grained and belt transects far exceed the size of individual bryophyte colonies. In contrast, the habitat heterogeneity encompassed within microplots is much finer scaled and microplots can therefore be dominated by individual bryophyte colonies. Thus species richness at the two spatial scales may be determined by different factors. Based on previous research, richness at the microplot scale (<1.0 m²) is determined primarily by species growth, mortality and interspecific interactions, while richness at the transect scale is likely the consequence of

both habitat heterogeneity, extirpation (localized extinction) and mass effects (the migration of species from optimum habitats) (Shmida and Wilson 1985, Herben 1994a). For bryophytes, this migration may occur spatially as propagules disperse from nearby disturbed habitats or temporally, as propagules germinate from the diaspore bank. Furthermore, richness estimates averaged across microplots will decrease as patchiness increases within transects (i.e., some randomly located microplots will contain no bryophytes and will lower mean richness estimates) and microplot sampling will capture relatively few infrequent species as compared to transect sampling.

The results of this study demonstrate that Sayward stands, which experience a wetter and cooler climate, had consistently higher gamma and alpha diversity, across all age classes, than the drier Nimpkish stands, which are located further inland. Two main factors have been suggested to account for regional differences in bryophyte diversity: climatic differences, specifically increased precipitation and humidity (Fensham and Streiman 1997, Rambo and Muir 1998a) and habitat heterogeneity (Arsenault 1995, Vitt et al. 1995, Rambo and Muir 1998a). Bryophyte richness can increase through the addition of rare species restricted to unique microsites (Vitt and Belland 1997). Although Sayward and Nimpkish forests differed in the amount of CWD present (particularly FWD and downed logs in early decay stages), there was no significant difference in the abundance of soil and rock—two microhabitats that are known to increase bryophyte diversity. Furthermore, the increased richness observed in Sayward stands remained significant even when sampled habitats were restricted to three substrates (forest floor, downed logs and tree bases) common in both forest types, suggesting that climate had a strong influence on the higher alpha diversity found in Sayward stands. It should be noted that not only are Sayward forests typified by lower monthly mean temperatures and greater precipitation than Nimpkish forests, plots sampled in Sayward forests also had lower estimates of annual potential

radiation and lower aspect favorability. The decreased levels of both of these environmental factors may have contributed to the more mesic climate in sampled Sayward stands.

Following the pattern of understorey vascular plants in Douglas-fir forests (Halpern and Spies 1995), bryophyte gamma and alpha diversity (cumulative plot-level estimates) in regeneration stands were higher than in old-growth forests. In contrast, immature plots supported lower gamma diversity and showed little change in plot-level alpha diversity when compared to old-growth plots. Although useful as an index of overall diversity, species richness does not document differences in ecological amplitudes of individual species and may mask important shifts in species composition (Halpern 1988). High species richness in early secondary succession is often predicted to result from reduced dominance of the overstory which allows a variety of pioneering species to flourish (Perry 1994). In this study, the removal of the forest canopy allowed many pioneering bryophyte species (mosses with turf growth forms, species typically found under open canopies, as well as bryophytes with colonist life strategies) to invade regeneration stands; however, we did not observe a concurrent decrease in the richness of species typically associated with old-growth forests.

Richness and abundance of old-growth associated groups by stand age

None of the bryophyte functional groups considered susceptible to the effects of harvesting (liverworts, bryophytes with weft or pendent growth forms, closed canopy species and perennial stayers) showed significant declines in richness in regeneration plots at the whole-plot scale. The lack of a strong decline in overall liverwort richness in regeneration plots is particularly surprising as liverworts are often viewed as the taxonomic group least resistant to changes in microclimate (Sharp 1939, McCullough 1948, Clausen 1964, Söderström 1988a). The persistence of this taxonomic group in regeneration plots results either from greater than expected tolerances of old-growth associated species to changes in habitat conditions or from utilization of optimal microsites. Frank and McNaughton (1991) suggested microsite

heterogeneity promotes community stability in the presence of disturbance. Due to their small size and close proximity to the substrate, bryophytes are often strongly affected by local microhabitat conditions (Vitt and Belland 1997). We suggest that the use of optimum microsites was particularly important for the maintenance of liverworts in regeneration stands as many liverworts were found in moist depressions or shady microhabitats beneath logs or herbaceous plants (personal observation).

Although it is unclear whether old-growth associated species survived *in situ*, regenerated from the diaspore bank, or arrived via dispersal from nearby populations, the richness of old-growth associated bryophytes in regeneration stands in this study reverted relatively quickly to the same levels found in old-growth forests. In comparison, microplot sampling within four years of harvest detected the loss of 11 forest floor species from clear-cuts in New Brunswick (Fenton et al. 2003). If ecosystem resilience (defined here as the capacity to return to a pre-disturbance state) is assessed through changes in species composition (Westman and O'Leary 1986, Malanson and Trabaud 1987, Halpern 1988, De Grandpré and Bergeron 1997), the presence of old-growth associated species in regeneration plots suggests the potential for greater ecosystem resilience than if old-growth associated species were completely lost from harvested areas. Recovery could occur if conditions in immature stands supported the continued existence of old-growth associated species. The results of this study, however, indicate that both coarse and fine-scale richness of old-growth associated species, in particular liverworts, was diminished in immature stands, thereby limiting the potential for ecosystem recovery.

The reduced abundance of old-growth species in immature stands may have resulted from limited availability of either light or woody debris on the forest floor. The majority of immature stands sampled in this study were within the stem exclusion phase (Oliver 1981). Forest stands in this phase often have a dense canopy allowing little light to reach the forest floor which has been correlated with a reduced understorey development (Spies 1997). Low light intensity may

limit bryophyte growth and colony development (Rieley et al. 1979, Furness and Grime 1982, Rincón 1993). Furthermore, although numerous studies in both North America (Lesica et al. 1991, Crites and Dale 1998, Rambo and Muir 1998a) and Scandinavia (Gustafsson and Hallingbäck 1988, Söderström 1988a, Andersson and Hytteborn 1991) have demonstrated large CWD (>10 cm diameter) plays an important role in maintaining the richness of epixylic liverworts, the abundance of fine-scale (<10 cm diameter) woody debris (FWD) may also be important. FWD, which is added to the forest floor from canopy detritus and decomposing logs, adds to the microhabitat heterogeneity of the forest floor. In this study, old-growth plots had a greater abundance of FWD and epixylic liverworts were often found on these small pieces of FWD on the forest floor. In subalpine forests, the presence of woody debris within microplots helped predict the occurrence of several liverwort species (Sadler and Bradfield 2000), and the occurrence of well decayed logs was the best predictor of bryophyte richness in swamp forests in Sweden (Ohlson et al. 1997).

In this study, immature forests appear to pose a bottleneck for the maintenance of old-growth associated species, particularly liverworts and bryophytes with pendent growth forms. This conclusion, however, is based on the assumption that our space-for-time substitution (the chronosequence approach) provides a reasonable description of the successional trajectory of the bryophyte community within naturally regenerating forest stands (Pickett 1989). Although the chronosequence approach has been generally accepted as reasonable method in coastal temperate rainforests (Spies 1991, Arsenault and Bradfield 1995, Halpern and Spies 1995, Rambo and Muir 1998a, 1998b), we cannot eliminate the possibility that species were absent from the pre-harvest forest, rather than lost as regeneration forests moved into the stem-exclusion phase in immature stands. Given this limitation, however, the results of this study are consistent with previous research that has found a loss of liverworts in mature second-growth forests (tree age 50-80 years) (Rambo and Muir 1998a, 1998b).

With the exception of liverworts and pendants in immature forests, old-growth associated species displayed a diminished performance and abundance rather than a complete loss of species in younger-aged stands. Similar patterns have been observed for understorey vascular plants following large scale disturbance in Douglas-fir forests (Franklin 1982, Halpern 1988, 1989, Arsenault and Bradfield 1995, Halpern and Spies 1995). In general, studies in the Pacific Northwest of unmanaged young (stand ages 25-80 years), mature (stand ages 80-200 years), and old-growth (stand ages > 200 years) forests have shown relatively few differences in both plant and animal species richness (Hansen et al. 1991). Coniferous forests in southwestern British Columbia only developed approximately 6000 years BP (Brubaker 1991, Hebda and Whitlock 1997) and thus species in these forests probably do not represent a coevolved complex of species bound together by tightly linked interactions (Brubaker 1991)

The results of this study indicate that with the exception of liverworts and pendants, landscapes composed primarily of younger-aged forests would support similar numbers of old-growth associated bryophyte species. This is not to argue, however, that decreasing stand age is not associated with significant changes in the bryophyte community. The abundance of numerous old-growth associated functional groups was significantly greater in old-growth forests than in regeneration and immature forests. Previous studies have reported similar results (Bingham and Sawyer 1991, Sadler and MacIntosh 1997, Rambo and Muir 1998b). In an examination of vertebrate diversity in differently aged forests, Raphael (1991) argued that loss of forest age classes where vertebrate species reached their maximum abundance could reduce the population viability of these species. In this study the nearly continuous cover of bryophytes seen in old-growth forests is both reduced in overall abundance and more patchily distributed than in younger-aged forest. Decreased bryophyte cover, as well as increased patchiness of the bryophyte mat, may limit the role that bryophytes play in moisture and nutrient retention in

temperate rainforests (Glime 2001) as well as degrading the habitat that moss mats provide for invertebrates (Gonzalez et al. 1998, Gonzalez and Chaneton 2002).

Richness and abundance of clearing affiliated groups across stand ages

Clearing affiliated functional groups (open canopy species, pioneer species and bryophytes with turf growth forms) had a greater richness in younger-aged stands. The invasion of clearing affiliated bryophytes was particularly apparent in regeneration plots. The presence of pioneer species (mosses with turf growth forms, open canopy species and colonists) that are often found on disturbed soils, such as *Pohlia nutans*, *Polytrichum juniperinum* and *Cephaloziella divaricata* (Schofield 1976, Godfrey 1977), was strongly associated with the locations of regeneration plots in the ordinations completed for each forest type. The source for clearing affiliated species found in younger-aged forests may have been the existing diaspore bank in each stand or populations of clearing affiliated species in nearby disturbed habitats. Clearing affiliated species such as *Polytrichum juniperinum* and *Pohlia nutans* dominated diaspore banks in Swedish boreal forests, and are typical of early successional habitats (Schofield 1976, Jonsson and Esseen 1990, Jonsson and Esseen 1998). The establishment of clearing affiliated species in regeneration forests, however, may have been mediated by changes in either abiotic (due to loss of canopy cover and increased soil disturbance) or biotic (reduced bryophyte abundance) conditions.

Harvesting not only reduces canopy cover but also disturbs the forest floor. Regeneration plots had a higher frequency of exposed soil and rock, likely due to mechanical disturbance during harvesting operations. Disturbance of the forest floor through tree tip-ups has been shown to increase overall bryophyte diversity in Swedish forests (Jonsson and Esseen 1990). In this study, alteration of old-growth habitat conditions (through either disturbance of the forest floor or a change in microhabitat conditions) may have facilitated the observed increase in the richness of pioneer-type bryophytes in edge plots. Separating the relative importance of forest

floor disturbance and reduced canopy cover is difficult as many of the species likely to colonize mineral soil or rocks (e.g., *Polytrichum juniperinum* and *Pohlia nutans*) are also likely to be found in clearings or open canopy forests (Schofield 1976, 1992).

The sharp reduction in abundance of old-growth associated bryophytes in regeneration stands may have also contributed to the influx of pioneer bryophytes. Competition in bryophytes appears to occur primarily as a form of interference competition, or more specifically, competition for space (Rydin 1997). Levine (2000) speculated that the cover of resident plant species (which was correlated with the loss of species at a neighborhood scale, the scale at which species interact) may have limited the germination of exotic vascular species in a Californian riparian system. The results of this study support the hypothesis proposed by Naeem et al. (2000) that the loss of species richness at the neighborhood scale may increase the invasibility of a system. Loss of fine-scale alpha diversity of old-growth associated bryophytes occurred concurrently with the increase in large-scale alpha diversity of clearing affiliated bryophytes. It should, however, be noted that while vascular plant succession in the Pacific Northwest Douglas-fir forests includes a few exotic species (Halpern 1989), this was not the case with the bryophyte flora found in regeneration plots in this study. Rather, many of the pioneer species colonizing regeneration stands are species that are found in naturally disturbed forest habitats such as tree tip-up mounds (Schofield 1976, Godfrey 1977).

Bryophyte community patterns across stand ages

Multivariate differences in the bryophyte communities in regeneration and old-growth plots reflected both the introduction of pioneering species as well as the reduction in abundance of old-growth associated species. NMS and MRPP analyses exhibited clear separation of the two stand ages based on overall species composition and these community patterns were strongly related to obvious habitat and stand structure differences between the two stand age classes. Multivariate analyses showed much less separation between immature and old-growth plots,

especially in Sayward forests. This concurs with previous studies of forest succession in coastal British Columbia that have shown that different-aged stands share many vascular species in common (Arsenault and Bradfield 1995). In our analyses, the ordinations emphasize differences in species richness rather than abundance. The clear difference in species richness (especially the introduction of pioneer species) underlies the strong separation between regeneration plots and old-growth plots. In contrast, the pattern of diminished abundance in immature plots as compared to old-growth plots does not strongly separate these two age-classes in the ordination.

Overall, the pattern of species occurrence in regeneration and immature stands supports the initial floristics theory of secondary succession (Egler 1954). This is characterized by the co-occurrence of clearing affiliated and old-growth associated species in early successional seres, followed by the gradual extinction of pioneer species. Initial floristics has been widely observed in forest ecosystems where residual species and rapidly establishing invaders are major contributors to secondary seres (Trabaud and Lepart 1980, Stickney 1981, Coleman et al. 1982, Abrams and Dickmann 1984, Halpern and Spies 1995, Clark et al. 2003).

The results of this study have important consequences for the management of bryophyte diversity in Pacific Northwest forests. The observed shifts in bryophyte species composition and abundance in younger-aged forests are striking, given that the majority of our younger aged forests were located immediately adjacent to old-growth forests. This proximity, if anything, could have caused us to underestimate differences between old-growth and younger forests as previous studies have shown that understorey plants can migrate from old-growth areas into harvested areas (Matlack 1994a). Most importantly, the overall abundance of bryophytes, as well as the richness of liverworts, is significantly reduced in younger age classes.

Unlike oceanic islands, old-growth forest remnants in coastal British Columbia are not surrounded by a "vacuum," insofar as bryophytes are concerned. Relatively few old-growth associated forest species are completely eliminated from younger forests. However, in order for

younger aged forests to be viewed as adequate habitat (rather than potential “sinks”) allowing for the migration of species between old-growth patches, we must have evidence that old-growth associated bryophytes can not merely survive, but reproduce in these forests. This study demonstrates that old-growth associated bryophytes show substantial declines in abundance in younger aged forests, especially in forests aged 25-50 years. If we take a conservative approach that regeneration will be related in part to the size of individual colonies (Jonsson and Söderström 1988), the reduced abundance of bryophytes in younger forests calls into question the migration (through reproduction and dispersal) of bryophyte species through these habitats. The maintenance of bryological diversity within managed landscapes depends upon both the persistence of species in the remnant patches of old-growth as well as the recovery of species diversity in harvested areas. The reduced bryophyte abundance found in younger forests suggests that remaining old-growth forest patches will be the primary, if not the only, sources for bryophyte colonization.

3.6 Tables and Figures

Table 3.1. Regression analysis summaries of plot scale comparisons between the Nimpkish (n=22) and Sayward (n=20) study areas based on (a) stand structure, (b) habitat and (c) substrate variables. Regressions run using either linear regression model (for non-count variables) or Poisson log-linear models (for count variables) with age class and forest type entered as categorical variables. Percent cover habitat variables were converted to proportions of one, then arcsine-square root transformed. Stand structure variables were log transformed. Regression slopes indicate whether the mean values for the variables at Sayward were greater (+) or smaller (-) than the mean values at Nimpkish after the effect of stand age had been accounted for. P-values <0.05 are shown in bold.

| | F | p-value | slope |
|---|---------|-------------------|-------|
| a. Stand structure variables | | | |
| Basal area | | | |
| Total basal area | <0.0001 | 0.9891 | + |
| Large live tree (relative basal area) | 0.56 | 0.4608 | + |
| Small live tree (relative basal area) | 0.75 | 0.3933 | - |
| Stumps (relative basal area) | 0.41 | 0.5239 | + |
| Snags (relative basal area) | 2.43 | 0.1271 | + |
| Percent cover | | | |
| Canopy cover | 1.32 | 0.257 | - |
| Shrub cover | 2.02 | 0.1631 | - |
| Cover of seedlings/saplings | <0.0001 | 0.932 | - |
| Amount of CWD | | | |
| Percent cover of downed logs | 2.91 | 0.0964 | + |
| <u>Decay class 1-2 logs</u> | | | |
| Mean number of logs/ transect | 3.28 | 0.0483 | + |
| Volume (m ³ /ha) | 10.39 | 0.037 | - |
| <u>Decay class 3 logs</u> | | | |
| Mean number of logs/transect | 0.54 | 0.5866 | + |
| Volume (m ³ /ha) | 3.83 | 0.0578 | + |
| <u>Decay class 4-5 logs</u> | | | |
| Mean number of logs/transect | 0.27 | 0.7616 | - |
| Volume (m ³ /ha) | 0.27 | 0.6093 | + |
| b. Habitat variables | | | |
| Slope (°) | 0.05 | 0.8209 | + |
| Annual Potential Radiation | 6.03 | 0.0187 | - |
| Aspect favorability | 7.48 | 0.0094 | - |
| c. Substrate variables (# of microplots substrate occurred within) | | | |
| Litter/humus | 0.17 | 0.8406 | + |
| FWD (CWD <10 cm diam) | 16.71 | <0.0001 | + |
| Exposed soil and rock | 0.48 | 0.6223 | + |

Table 3.2. Regression analysis summaries of comparisons between Nimpkish (n=22) and Sayward (n=20) study areas based on species richness of taxonomic groups. Regressions run using a Poisson log-linear model with age class and forest type entered as categorical variables. Regression slopes indicate whether the mean variables at Sayward were greater (+) or smaller (-) than the mean values at Nimpkish after the effect of stand age had been accounted for. P-values <0.05 are shown in bold.

| | F | p-value | Slope |
|----------------------------------|-------|---------------|-------|
| Cumulative whole-plot assessment | | | |
| Bryophytes | 8.88 | 0.0006 | + |
| Liverworts | 11.55 | 0.0002 | + |
| Mosses | 3.37 | 0.0448 | + |
| Microplot assessment | | | |
| Bryophytes | 11.71 | 0.0001 | + |
| Liverworts | 11.42 | 0.0001 | + |
| Mosses | 5.57 | 0.0075 | + |

Table 3.3. Regression analysis summaries of plot scale comparisons of regeneration (CC, n=12) and immature (SG, n=13) plots with old-growth (OG, n=17) plots based on (a) stand structure, (b) habitat and (c) substrate variables. Regressions run using either linear regression model (for non-count variables) or Poisson log-linear models (for count variables) with age class and forest type entered as categorical variables. Percent cover habitat variables were converted to proportions of one, then arcsine-square root transformed. Stand structure variables were log transformed. Regression slopes indicate whether the mean values for the variables in younger aged plots were greater (+) or smaller (-) than the mean values in old-growth plots after the effect of stand age had been accounted for. P-values <0.05 are shown in bold.

| | F | p-value | CC-OG comparison | | SG-OG comparison | |
|--|--------|---------|------------------|---------|------------------|---------|
| | | | slope | p-value | slope | p-value |
| a. Stand structure variables | | | | | | |
| Basal area | | | | | | |
| Total basal area | 4.07 | 0.0251 | - | 0.3560 | - | 0.0065 |
| Large live tree (relative basal area) | 101.04 | <0.0001 | - | <0.0001 | - | <0.0001 |
| Small live tree (relative basal area) | 32.62 | <0.0001 | - | <0.0001 | + | <0.0116 |
| Stumps (relative basal area) | 150.88 | <0.0001 | + | <0.0001 | + | <0.0001 |
| Snags (relative basal area) | 64.27 | <0.0001 | - | <0.0001 | - | <0.0001 |
| Percent cover | | | | | | |
| Canopy cover | 123.87 | <0.0001 | - | <0.0001 | + | 0.2587 |
| Shrub cover | 4.27 | 0.0213 | + | 0.011 | + | 0.9488 |
| Cover of seedlings/saplings | 6.46 | 0.0038 | + | 0.002 | + | 0.8729 |
| Amount of CWD | | | | | | |
| Percent cover of downed logs | 0.31 | 0.7319 | - | 0.595 | + | 0.7636 |
| Decay class 1-2 logs | | | | | | |
| Mean number of logs/ transect | 3.98 | 0.0269 | + | 0.0384 | - | 0.4550 |
| Volume (m³/ha) | 3.6 | 0.0371 | + | 0.7852 | - | 0.027 |
| Decay class 3 logs | | | | | | |
| Mean number of logs/transect | 6.81 | 0.0029 | + | 0.0037 | - | 0.5030 |
| Volume (m³/ha)* | 2.6 | 0.0872 | - | 0.5828 | - | 0.0845 |
| Decay class 4-5 logs | | | | | | |
| Mean number of logs/transect | 12.39 | <0.0001 | - | <0.0001 | + | 0.9963 |
| Volume (m³/ha) | 14.85 | <0.0001 | - | <0.0001 | - | 0.4688 |
| b. Habitat variables | | | | | | |
| Slope (°) | 0.59 | 0.5571 | - | 0.7266 | + | 0.437 |
| Annual Potential Radiation | 0.72 | 0.4911 | + | 0.5955 | + | 0.2362 |
| Aspect favorability | 1.39 | 0.2606 | + | 0.2719 | + | 0.1184 |
| c. Substrate variables (# of microplots substrate occurred within) | | | | | | |
| Litter/humus | 5.32 | 0.009 | - | 0.0035 | - | 0.90135 |
| FWD (CWD <10 cm diam) | 4.28 | 0.02 | - | 0.4589 | - | 0.0048 |
| Exposed soil and rock | 3.73 | 0.033 | + | 0.0149 | + | 0.2992 |

Table 3.4. Regression analysis summaries of comparisons of regeneration (CC) and immature (SG) plots with old-growth (OG) plots based on (a) Shannon diversity index, (b) bryophyte species richness in taxonomic and functional groups and (c) bryophyte percent cover. Regressions run using either Poisson log-linear models (for count variables) or linear regression models (for non-count variables) with age class and forest type entered as categorical variables. Percent cover habitat variables were converted to proportions of one, then arcsine-square root transformed. Regression slopes indicate whether the mean values for variables in younger-aged plots were greater (+) or smaller (-) than mean values in old-growth plots, after the effect of stand age had been accounted for. P-values <0.05 are shown in bold.

| | Comparisons (cumulative whole-plot) | | | | | | | | | | Comparisons (mean microplot, n=45) | | | | | |
|-------------------------------------|-------------------------------------|---------|-------|---------|-------|---------|------------------|---------|-------|---------|------------------------------------|---------|------------------|---------|-------|---------|
| | Stand age effect | | CC:OG | | SG:OG | | Stand age effect | | CC:OG | | SG:OG | | Stand age effect | | CC:OG | |
| | F | p-value | slope | p-value | slope | p-value | F | p-value | slope | p-value | slope | p-value | F | p-value | slope | p-value |
| a. Shannon diversity index | 0.84 | 0.4408 | - | 0.3410 | - | 0.2416 | 3.93 | 0.2820 | + | 0.1310 | - | 0.1342 | | | | |
| b. Species richness | | | | | | | | | | | | | | | | |
| Taxonomic groups | | | | | | | | | | | | | | | | |
| Bryophytes | 15.50 | <0.0001 | + | <0.0001 | + | 0.5633 | 7.95 | 0.0013 | - | 0.1205 | - | 0.0001 | | | | |
| Liverworts | 3.56 | 0.0380 | + | 0.4015 | - | 0.0633 | 7.69 | 0.0015 | - | 0.0417 | - | 0.0002 | | | | |
| Mosses | 23.93 | <0.0001 | + | <0.0001 | + | 0.0329 | 3.51 | 0.0400 | - | 0.5898 | - | 0.0095 | | | | |
| Life-history strategy groups | | | | | | | | | | | | | | | | |
| Colonists | 31.23 | <0.0001 | + | <0.0001 | + | 0.0068 | 22.03 | <0.0001 | + | <0.0001 | - | 0.9027 | | | | |
| Short-lived shuttles | 4.68 | 0.0152 | + | 0.0023 | + | 0.1237 | 0.47 | 0.6270 | - | 0.5009 | - | 0.3669 | | | | |
| Long-lived shuttles | 4.23 | 0.0219 | + | 0.0932 | - | 0.1507 | 9.89 | 0.0035 | - | 0.0046 | - | <0.0001 | | | | |
| Perennial stayers | 1.62 | 0.2100 | + | 0.3453 | - | 0.3226 | 6.90 | 0.0028 | - | 0.0187 | - | 0.0005 | | | | |
| Canopy type | | | | | | | | | | | | | | | | |
| Open | 40.68 | <0.0001 | + | <0.0001 | + | 0.0182 | 9.30 | 0.0005 | + | 0.0005 | - | 0.6048 | | | | |
| Canopy generalist | 7.33 | 0.0020 | + | 0.0002 | + | 0.4073 | 6.75 | 0.0030 | - | 0.1409 | - | 0.0003 | | | | |
| Closed | 0.33 | 0.7219 | - | 0.8669 | - | 0.4191 | 3.21 | 0.0514 | - | 0.0969 | - | 0.0174 | | | | |
| Growth form groups | | | | | | | | | | | | | | | | |
| Cushion | 0.13 | 0.8700 | + | 0.7788 | + | 0.8243 | 1.81 | 0.1778 | - | 0.0950 | - | 0.3409 | | | | |
| Dendroid | 0.18 | 0.8345 | - | 0.9888 | - | 0.5871 | 0.01 | 0.9867 | + | 0.9146 | + | 0.9638 | | | | |
| Open turf | 70.84 | <0.0001 | + | <0.0001 | + | 0.0050 | 32.61 | <0.0001 | + | <0.0001 | + | 0.0939 | | | | |
| Pendent | 3.16 | 0.0529 | - | 0.5357 | - | 0.0229 | 8.82 | 0.0007 | - | 0.0840 | - | 0.0030 | | | | |
| Rough mat | 2.36 | 0.1070 | + | 0.0649 | - | 0.8883 | 5.35 | 0.0089 | - | 0.2479 | - | 0.0015 | | | | |
| Smooth mat | 1.32 | 0.2800 | + | 0.1877 | - | 0.7928 | 6.94 | 0.0027 | - | 0.0162 | - | 0.0005 | | | | |
| Short turf | 3.89 | 0.0290 | + | 0.0090 | + | 0.0835 | 7.23 | 0.0020 | + | 0.0308 | - | 0.0567 | | | | |
| Thread | 0.48 | 0.6243 | + | 0.5017 | - | 0.7309 | 0.38 | 0.6836 | - | 0.5370 | - | 0.4138 | | | | |
| Thallose mat | 0.82 | 0.4470 | - | 0.4549 | - | 0.2282 | 0.23 | 0.7917 | - | 0.9788 | - | 0.5313 | | | | |
| Tall Turf | 16.90 | <0.0001 | + | <0.0001 | + | 0.0088 | 11.47 | 0.0002 | + | 0.0004 | + | 0.0096 | | | | |

| | | | | | | | | | | | | |
|-------------------------|------|--------|---|--------|---|--------|-------|---------|---|---------|---|---------|
| Weft | 3.21 | 0.0517 | + | 0.2578 | + | 0.0150 | 2.94 | 0.0648 | - | 0.1134 | - | 0.0234 |
| c. Percent cover | | | | | | | | | | | | |
| All substrates combined | 8.33 | 0.001 | - | 0.0007 | - | 0.0028 | | | | | | |
| Forest floor | | | | | | | 5.04 | 0.0114 | + | 0.7137 | - | 0.0103 |
| Logs | | | | | | | 10.07 | 0.0003 | - | <0.0001 | - | 0.0261 |
| Tree bases | | | | | | | 28.48 | <0.0001 | - | 0.0176 | - | <0.0004 |

Table 3.5. Summary of MRPP results comparing bryophyte species composition between regeneration and old-growth plots (a) and between immature and old-growth plots (b) in both Nimpkish and Sayward study areas. All comparison made using data from whole-plot assessments (i.e., combined data from microplots and entire transect surveys) and from microplot assessments (combined data from microplots on three substrate-types). P-values <0.05 are shown in bold.

| Test | Nimpkish | | Sayward | |
|--|----------|---------------|---------|---------------|
| | A* | P-value | A* | P-value |
| a. Regeneration versus old-growth | | | | |
| Whole-plot assessments | 0.0892 | 0.0008 | 0.0587 | 0.0028 |
| Microplot assessments | 0.0884 | 0.001 | 0.0561 | 0.0056 |
| b. Immature versus old-growth | | | | |
| Whole-plot assessments | 0.0802 | 0.0023 | 0.003 | 0.3568 |
| Microplot assessments | 0.0815 | 0.0026 | 0.0056 | 0.3069 |

*A is the chance-corrected within group similarity where $A_{max} = 1$ when all bryophyte communities are identical within groups, $A=0$ when heterogeneity of communities within groups equals expectation by chance and $A<0$ when heterogeneity of groups exceeds that expected by chance

Table 3.6. Liverwort and moss species significantly associated ($p < 0.05$) with regeneration, immature or old-growth plots at either Nimpkish or Sayward study areas. Shown are indicator values (percent of perfect indication, IV). Functional groups defined as in Table 1.1.

| | Nimpkish IV | Sayward IV | Growth form | Canopy preference | Life-history strategy |
|---|----------------|---------------|----------------|----------------------|--------------------------|
| Regeneration plots | | | | | |
| Liverworts | | | | | |
| <i>Cephaloziella divaricata</i> | 94.9 | 83.3 | TH | open | C |
| <i>Lophozia longifolia</i> | | 87.4 | SM | closed | C |
| <i>Porella navicularis</i> | 63.1 | | PE | open | L |
| Mosses | | | | | |
| <i>Aulacomnium androgynum</i> | | 80.6 | ST | open | C |
| <i>Bryum pseudotriquetrum</i> | | 50 | OT | open | C |
| <i>Ceratodon purpureus</i> | 85.7 | | OT | open | C |
| <i>Cynodontium jenneri</i> | | 50 | OT | open | S |
| <i>Dicranella heteromalla</i> | 57.1 | | OT | open | C |
| <i>Dicranum fuscescens</i> | 43.4 | 50.1 | ST | generalist | C |
| <i>Dicranum scoparium</i> | 51.3 | | ST | open | P |
| <i>Dicranum tauricum</i> | 71.4 | | OT | generalist | C |
| <i>Pogonatum contortum</i> | 42.9 | | TT | open | C |
| <i>Pohlia nutans</i> | 64.1 | 84.8 | OT | open | S |
| <i>Polytrichastrum alpinum</i> | | 76.5 | TT | generalist | C |
| <i>Polytrichum formosum</i> | | 65.8 | TT | closed | C |
| <i>Polytrichum juniperinum</i> | | 66 | TT | open | C |
| <i>Racomitrium canescens</i> | | 50 | RM | open | P |
| <i>Racomitrium heterostichum</i> | | 63.5 | RM | open | P |
| Immature plots | | | | | |
| Liverworts | | | | | |
| <i>Ptilidium californicum</i> | 55.8 | | SM | closed | L |
| Mosses | | | | | |
| <i>Aulacomnium androgynum</i> | 56 | | ST | open | C |
| <i>Eurhynchium praelongum</i> | 59.5 | | WE | generalist | P |
| <i>Plagiothecium laetum</i> | | 62.8 | SM | closed | P |
| Old-growth plots | | | | | |
| Liverworts | | | | | |
| <i>Blepharostoma trichophyllum</i> | 58 | | TH | closed | P |
| <i>Frullania tamarisci</i> subsp. <i>nisquallensis</i> | 53.7 | | SM | generalist | L |
| <i>Porella navicularis</i> | | 80.2 | PE | open | L |
| <i>Scapania bolanderi</i> | 47.4 | | RM | closed | P |
| Mosses | | | | | |
| <i>Antitrichia curtipendula</i> | | 66.3 | PE | generalist | L |

| | | | | |
|-------------------------------|------|----|------------|---|
| <i>Hylocomium splendens</i> | 46.7 | WE | closed | P |
| <i>Hypnum circinale</i> | 42.7 | SM | generalist | P |
| <i>Isothecium myosuroides</i> | 49.3 | WE | generalist | P |
| <i>Rhytidiadelphus loreus</i> | 52.1 | WE | closed | P |

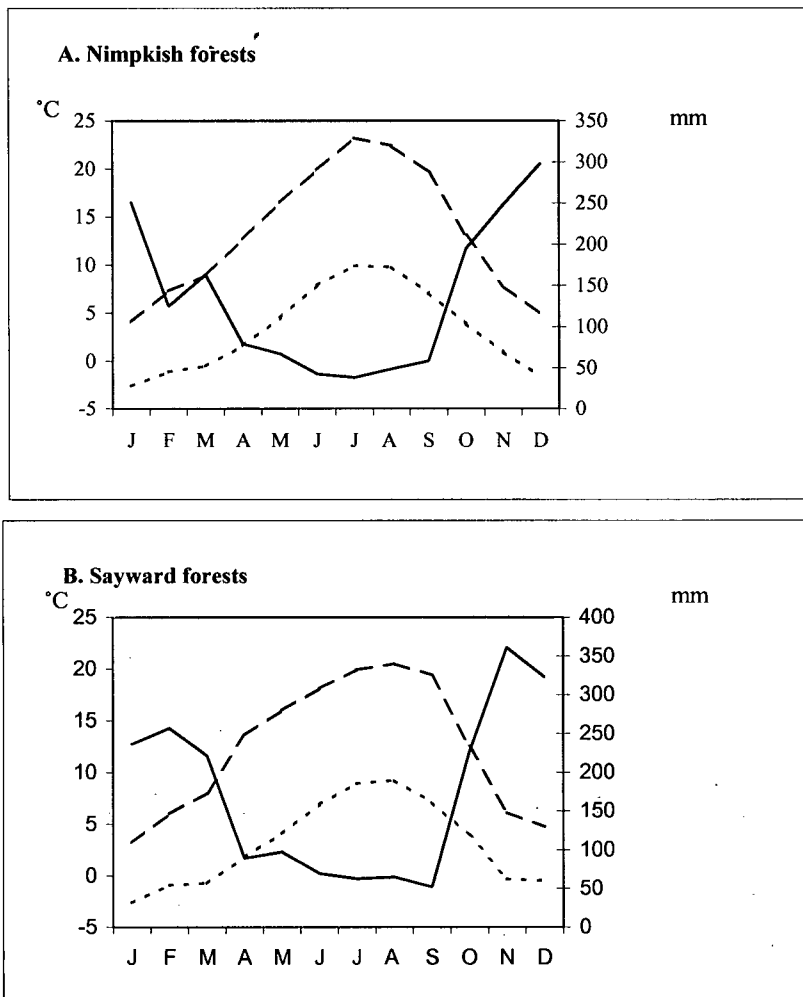


Figure 3.1. Climate diagrams for Nimpkish and Sayward study area forests, showing for each month, mean maximum and minimum temperatures (dashed lines) and total precipitation (solid line). Note the scale change on the axis used for precipitation. Climate data representing Nimpkish forests were collected in Cumberland, B.C., the closest weather station in CWHxm biogeoclimatic subzone to the Nimpkish Valley, for the period 1960-1977. Climate data for Sayward forests were collected in Sayward for the period 1973-1999. Data source: Environment Canada 2000.

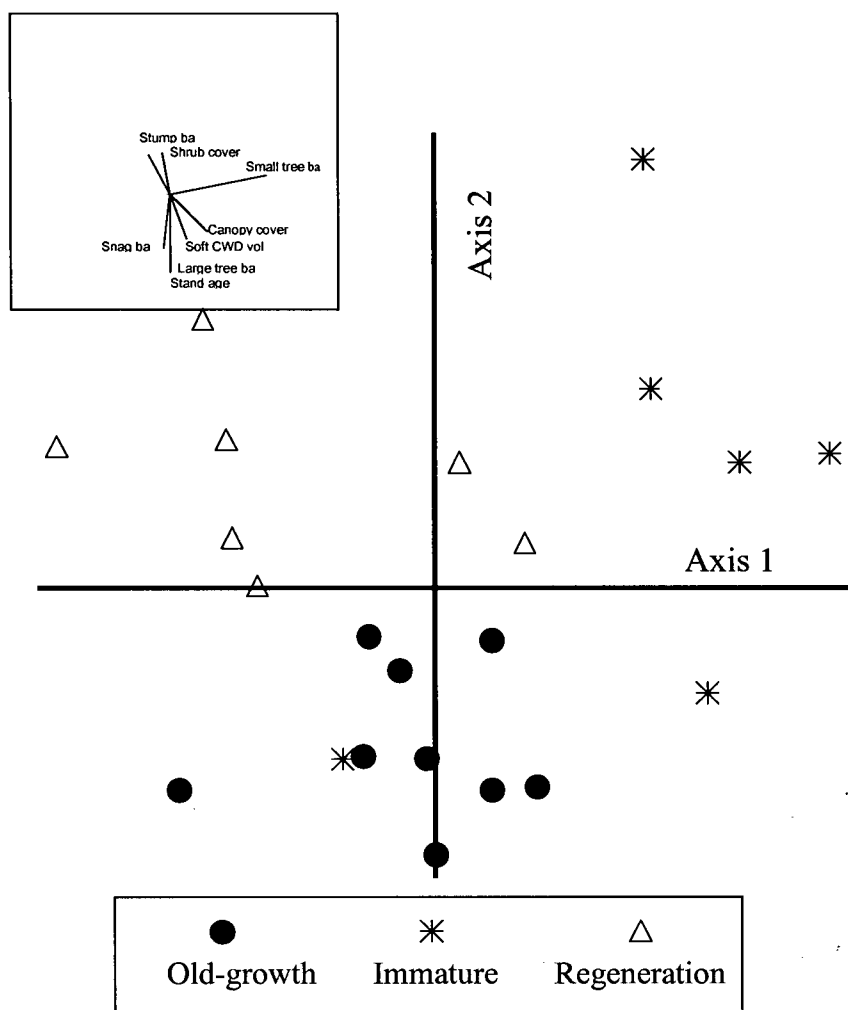


Figure 3.2. NMS ordination of regeneration, immature and old-growth plots in the Nimpkish study area based on bryophyte species frequency data. Axis 1 accounts for 45.7% of the variation in the data while the second axis accounts for 33.4% (total = 79.1%). Ordination based on a 3-dimensional solution with a final stress of 11.25. Inset is joint plot (overlay) of stand structure, habitat and substrate variables with R^2 values > 0.25 . Length of correlation vectors represents the strength of the correlation. Joint plot of strongly correlated variables include: Small tree ba = relative basal area of sampled trees < 50 cm dbh, large tree ba = relative basal area of sampled trees > 50 cm dbh, snag ba = relative basal area of sampled snags, stump ba = relative basal area of sampled stumps, soft CWD vol = volume of well decayed logs (decay classes 4-5), canopy cover = % cover of canopy trees, shrub cover = % cover of shrubs and stand age.

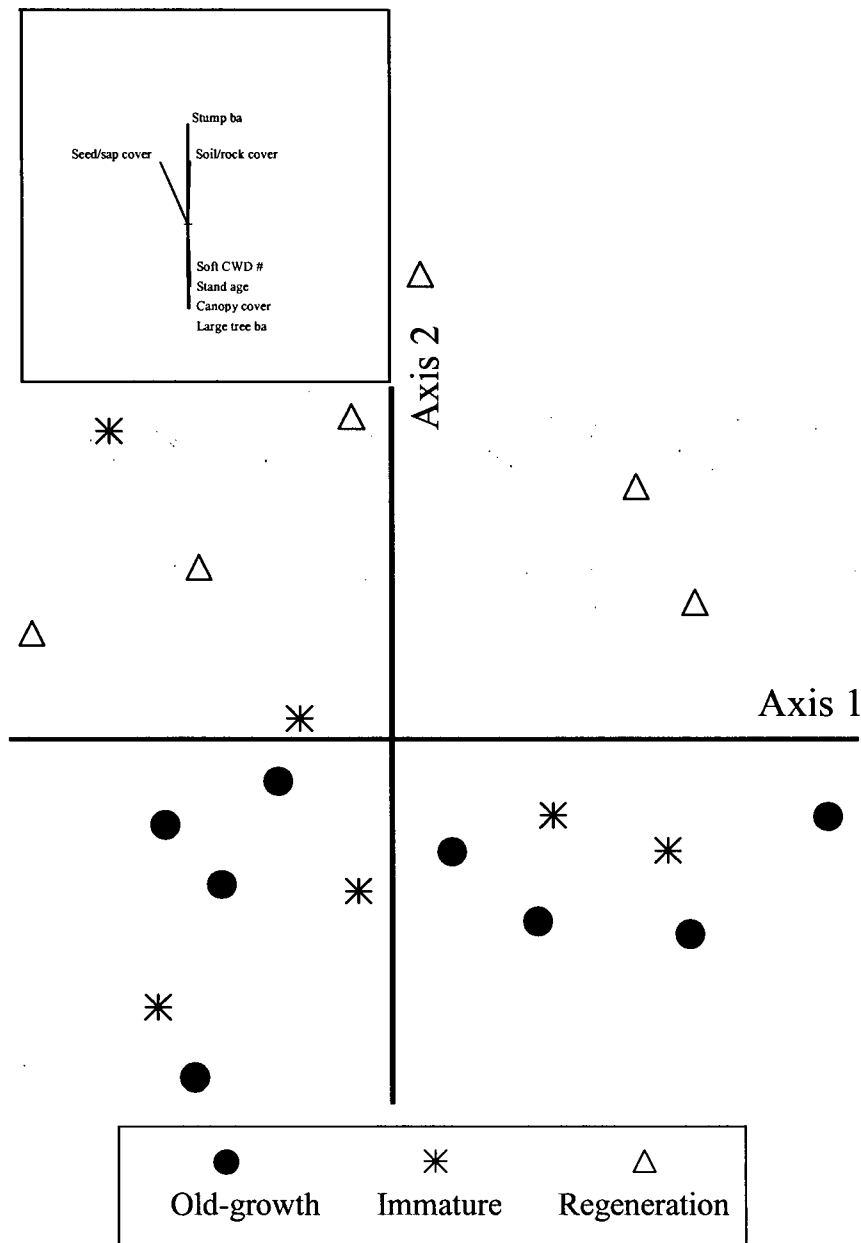


Figure 3.3. NMS ordination of regeneration, immature and old-growth plots in the Sayward study area based on bryophyte species frequency data. Axis 1 accounts for 25.8% of the variation in the data while the second axis accounts for 38.2% (total = 64.0 %). Ordination based on a 3-dimensional solution with a final stress of 11.11. Inset is joint plot (overlay) of stand structure, habitat and substrate variables with R^2 values > 0.25. Length of correlation vectors represents the strength of the correlation. Joint plot of strongly correlated variables include: Large tree ba = relative basal area of sampled trees > 50 cm dbh, stump ba = relative basal area of sampled stumps, canopy cover = % cover of canopy trees, seed/sap cover = % cover of seedlings and saplings, soil/rock cover = % cover of soil and rock, soft CWD # = number of well decayed logs (decay classes 4-5) and stand age.

CHAPTER IV. Effects of remnant patch size on the species richness and composition of bryophyte communities in temperate rainforests of coastal British Columbia, Canada

4.1 Abstract

The species richness and abundance of bryophytes within taxonomic and functional groups was examined in relation to the size of 20 old-growth forest remnant patches remaining after logging in two forest types on Vancouver, Island, British Columbia. To control for the confounding effects of habitat diversity and patch area, bryophytes were sampled in sixty-three 10 cm x 30 cm microplots on three substrate-types (forest floor, downed logs and tree bases). Generalized linear models with a log-link function and a Poisson error distribution demonstrated that decreasing patch size was associated with diminished bryophyte richness and abundance. In particular, the richness and abundance of dispersal-limited groups (perennial stayers) and microclimate sensitive groups (closed canopy species and liverworts) showed significant declines in either richness or abundance as patch size decreased. In contrast, groups expected to increase as patch size decreased (colonists and open canopy species) showed little association (positive or negative) with patch size. The abundance of seven species (all species typically found under closed forest canopies) was significantly related to patch size. The use of bryophyte functional groups illustrates that although overall bryophyte richness was significantly correlated with patch size, this relationship is not true for all groups. Furthermore the lack of relationship between patch size and the richness of clearing affiliated species suggests that although the edges of small patches may be invaded by clearing affiliated species, the invasion is not pervasive enough to be detected through microplot sampling at the center of remnant patches.

Keywords: fragmentation, patch size, bryophyte richness, variable retention logging, functional groups, old-growth temperate rainforests.

4.2 Introduction

The coastal temperate rainforests of British Columbia are renowned for their bryophyte diversity and abundance (Schofield 1992, Alaback and Pojar 1997, Schofield 1998). These forests, however, have also been subject to large-scale forestry operations which have diminished the overall extent of old-growth (MacKinnon and Vold 1998). Many bryophyte species are closely associated with late successional forests (Gustafsson and Hallingbäck 1988, Söderström 1988a, Lesica et al. 1991, Marcot 1997, Rambo and Muir 1998a) and may be especially vulnerable to the effects of forest fragmentation. Large-scale harvesting not only reduces the overall amount of old-growth cover but creates a loss of continuity in the remaining old-growth forest patches. While the overall amount of old-growth forest may affect the landscape level recovery of old-growth associated species (Vellend 2003), the spatial configuration of the remaining old-growth forest may also be important (Saunders et al. 1991, Haila 1999). In particular, decreasing forest patch size may exacerbate the negative effects of forest fragmentation. Small patches may consist entirely of edge habitat and will be unable to support species vulnerable to the environmental changes associated with forest edges (Saunders et al. 1991). Likewise, smaller forest patches will sustain populations that are more vulnerable to stochastic extinction events (Gilpin and Soule 1986, Soule 1987). Bryophytes are an important component of coastal forest ecosystems (Binkley and Graham 1981, den Ouden and Alaback 1996, Alaback and Pojar 1997, Schofield 1998), yet little attention has been paid to the potential adverse effects of decreasing patch size on the diversity of these plants. The intent of this research, therefore, is to document the relationship between decreasing patch size and bryophyte richness and abundance in the coastal temperate rainforests of British Columbia.

New forest management practices, such as variable retention logging, which are meant to maintain biological and structural diversity within harvested areas, will lead to an increasing number of very small forest patches on the landscape. These practices promote retention of

residual patches of live and/or dead trees within clear-cuts that are often less than 1.0 ha in size (Franklin et al. 1997, Beese and Zielke 1998). Since the development of the theory of island of biogeography (MacArthur and Wilson 1963, 1967), the effect of patch size (both natural and anthropogenically-caused patches) on vertebrate and vascular plant diversity has been the subject of numerous studies (see review in McGarigal and Cushman 2002). With the exception of a few studies investigating bryophyte richness in naturally fragmented habitats (Tangney et al. 1990, Haig et al. 1999, Kimmerer and Driscoll 2000, Moen and Jonsson 2003), the impacts of decreasing patch size on non-vascular plants like bryophytes have been largely ignored (but see Zartman 2003).

Demonstrating that species richness decreases with overall patch size, however, does not provide evidence for the adverse effects of fragmentation (Haila et al. 1993, Andr  n 1994). The correlation of species richness with patch size may be one of the most commonly observed trends in ecology (Kelly et al. 1989), and attempts to formalize this relationship date back to the early part of the last century (Arrhenius 1921). When entire remnant patches are sampled, the positive relationship between species richness and area may simply reflect the greater habitat diversity present in larger patches (habitat diversity hypothesis) or may arise from the greater number of individuals found in larger patches (sampling hypothesis)—neither of which are the result of the biogeographic or environmental changes induced by fragmentation. More recently, many habitat/island studies have employed a null model in which differently-sized fragments are sampled with the same size plot or intensity (Westman 1983, Kelly et al. 1989, Tangney et al. 1990,   s 1993, Kohn and Walsh 1994, Schieck et al. 1995, Moen and Jonsson 2003), and habitat diversity is controlled by sampling a constant habitat or vegetation type (Kelly et al. 1989, Tangney et al. 1990).

Furthermore, remnant forest patches created by destruction of surrounding habitat can rarely be considered a random sample of the pre-fragmented forest, and non-random differences

between habitat patches may weaken species-area relationships (Doak and Mills 1994).

Bryophyte richness can be strongly influenced by the presence of rare or infrequent habitats such as cliff faces and or exposed boulders (Slack 1977, Vitt and Belland 1997, Rambo 2001).

Sampling bryophytes on constant habitats (i.e., substrates such as forest floor, downed logs and tree bases that are found in all forest patches) and with constant effort minimizes both the influence of patch area and habitat diversity on bryophyte species richness.

As an aggregate community-level variable, species richness may mask the effects of habitat fragmentation (Robinson et al. 1992), especially as small patches should be more susceptible than large patches to invasion from species commonly found in the surrounding matrix (Murphy 1989, Saunders et al. 1991, Hobbs and Huenneke 1992, Ås 1999). Reviews of population responses to landscape fragmentation (Lord and Norton 1990, Rolstad 1991, Andrén 1994, Fahrig and Merriam 1994) and simulation studies (Hanson et al. 1990, Gardner et al. 1991) have suggested that the persistence of species with low-dispersal capacity will be more influenced by decreasing patch size than species with high dispersal capacity, and that species less capable of withstanding microclimate changes will be more susceptible to edge effects than light-demanding species. Thus, it is reasonable to expect functional groupings of bryophytes that separate species on their dispersal ability and/or the ability to withstand changes in microclimate will show differential responses to decreasing patch size.

Two functional groupings of bryophytes that separate species according to dispersal ability are life strategies and habitat types. During (1979, 1992) classified bryophytes into life-history strategy categories based on spore size, reproductive output, life span and relative investment in asexual reproduction (Table 1.1), similar to the r-K concept (MacArthur and Wilson 1967, Pianka 1970). In During's (1979, 1992) classification, large-spored ($>20\ \mu\text{m}$) species, such as short and long-lived shuttles, are viewed as species which have evolved to exploit relatively short-lived habitats that recur predictably within a community such as tree bark

or downed logs and which rely primarily on local dispersal (During 1979, Longton 1988, During 1992). Small-spored species that produce abundant spores, such as colonists, are viewed as species that can more easily disperse between sites.

Bryophyte species' reliance on dispersal may be also strongly related to the duration, either in time or space, of the habitat type they typically occupy. Herben (1994b) and Söderström and Herben (1997) have illustrated that both trees and logs provide habitat patches that are of smaller size and duration than the forest floor for many temperate and boreal bryophytes. Moreover, Herben (1994b) demonstrated that bryophytes in Britain occupying small (or less contiguous) habitats produce propagules more frequently than bryophytes occupying larger habitats. We hypothesized that the richness of bryophytes sampled on substrates of shorter duration and restricted size (i.e., downed logs and tree bases) would show less relationship with remnant patch size than the richness of bryophytes sampled on habitats of longer duration and unrestricted size (i.e., forest floor).

Overstorey canopy affiliations and taxonomic categories provide two functional groupings that classify bryophytes according to their ability to withstand changes in microclimate. Small remnant patches have a greater portion of their area subject to edge effects than larger remnants. Forest edges typically have increased light, air and soil temperature, wind speed and vapor pressure deficit, as well as lower relative humidity and soil or litter moisture (Brothers and Spingarn 1992, Brothers 1993, Young and Mitchell 1994, Chen et al. 1995), all conditions more similar to those under open canopies. Furthermore, liverworts, particularly leafy liverworts, are often viewed as the taxonomic group least tolerant of changes in microclimate (Sharp 1939, McCullough 1948, Söderström 1988a). We hypothesized that liverworts and closed canopy bryophytes would exhibit a greater association with remnant patch size than would mosses or open canopy bryophytes.

The specific focus of this paper, therefore, is to determine whether the richness and abundance of bryophyte functional groups defined by dispersal and habitat characteristics was significantly associated with patch size in differently-sized forest patches on Vancouver Island, Canada. We also examined the abundances of individual species with respect to fragment size.

4.3 Methods

Study area

Using satellite imagery and aerial photographs of Vancouver Island, Canada, we selected two areas (the Nimpkish River valley (50° 10' N 126° 30' W) and the region near the town of Sayward (50° 10' N 125° 45' W)) on northeastern Vancouver Island with many remnant patches of old-growth forests. The landscape in both of these areas is mountainous with numerous small lakes and rivers. Coastal Western Hemlock is the dominant biogeoclimatic zone in both geographic areas; however the majority of the forests in the two geographic regions are in different biogeoclimatic subzones (see Pojar et al. 1987, Meidinger and Pojar 1991, Green and Klinka 1994 for a description of the biogeoclimatic classification system and details on the CWH zone and individual subzones).

Low-elevation forests in the Nimpkish Valley are primarily in the very dry Coastal Western Hemlock (CWHxm) subzone and consist predominantly of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) and western hemlock (*Tsuga heterophylla*) with minor amounts of western redcedar (*Thuja plicata*) also present (Meidinger and Pojar 1991). Forests in this subzone have warm, dry summers and moist, mild winters with relatively little snowfall (Green and Klinka 1994). Climate data from Cumberland, British Columbia (49° 37' N 125° 02' W, the closest weather station in CWHxm subzone to the Nimpkish Valley) show that mean annual precipitation is approximately 1638 mm with less than 20% occurring during May-September

(Figure 3.1a). Mean monthly temperatures range from a 0.9°C in January to 16.5°C in July; weather data for the period 1960-1977 (Environment Canada 2000).

Low-elevation forests in the watersheds surrounding Sayward are primarily in the very wet maritime Coastal Western Hemlock (CWHvm) subzone and are dominated by western hemlock (*Tsuga heterophylla*), amabilis fir (*Abies amabilis*) and western red-cedar (*Thuja plicata*) (Meidinger and Pojar 1991). This subzone experiences cool summers and moist, mild winters with relatively little snow (Green and Klinka 1994). Climate data from Sayward, British Columbia (50° 10' N 125° 45' W) indicate that mean annual precipitation is approximately 2030 mm with less than 20% occurring during May-September (Figure 3.1b). Mean monthly temperatures range from -2.6°C in January to 14.9°C in August; weather data for the period 1973-1999 (Environment Canada 2000).

During the last 100 years, both areas have been extensively deforested using clear-cut logging. Within both areas, logging has been concentrated along valley bottoms, although cutting is continuing at higher elevations (unpublished forest history maps). Thus, a range of old-growth forest patches differing in size, but representative of the two forest types, is available for comparative study of remnant patch size as it relates to bryophyte communities.

Site selection and bryophyte sampling

Based on recent forest inventories and aerial photographs, we selected 10 old-growth forest patches in both the Nimpkish Valley and the watersheds near the town of Sayward. Sayward patches ranged in size from 0.58 ha to 23.76 ha and had an elevation range of 150 m a.s.l to 670 m a.s.l., while Nimpkish patches ranged from 1.8 ha to 63.6 ha and had an elevation range of 150 m a.s.l. to 400 m a.s.l. With the exception of two remnant patches (located at 60 and 75 m from the nearest old-growth), all of the remnant patches were located more than 250 m from the nearest old-growth patch, with a mean distance to the nearest old-growth of 860 m

(Table 4.1). Remnant patches that had been isolated fewer than 5 years were not included as recently isolated fragments are still early in the "species relaxation track" (Saunders et al. 1991).

Using aerial photographs, we established a 0.1 ha sample plot as near as possible to the center of each forest remnant. Within each sample plot, bryophytes were sampled along six 10 x 2 m belt transects located in a 3 x 3 grid pattern (each transect 10 m apart from one another) across the center of the remnant. To account for microhabitat heterogeneity within the belt transects, bryophytes were sampled using sixty-three 10 cm x 30 cm microplots evenly distributed on three substrate-types: forest floor, tree bases and fallen logs. Microplot locations were determined as the closest respective substrate-type to 21 randomly selected points along the centre line of the belt-transects. Following McCune and Antos (1981), microplots were partitioned into six equal size units of 50 cm² and species cover classes recorded to the closest half 50 cm² partition unit. Cover classes were subsequently converted to percentages with one cover class being equal to a mean cover of 16.7%.

Bryophyte species were classified into life history strategies (During 1979, 1992) based primarily on spore size (greater or less than 20 µm), frequency of sporophyte production (as determined from literature reports and field observations (Schofield 1976, Godfrey 1977)), life span (as estimated from growth form and presence of annual increments) and presence of vegetative reproduction (Table 1.1). Canopy preference assignments of bryophyte species were made according to the criteria in Table 1.1 and were based on either field observations or literature reports (Schofield 1976, Godfrey 1977, Schofield 1992), with uncertainties resolved on the advice of local expertise (W.B. Schofield, personal communication.). Nomenclature for mosses and liverworts follows Stotler and Crandall-Stotler (1977), Anderson (1990), Anderson et al. (1990) and Flatberg (1993). After tentative identification in the field, all species identifications were confirmed in the laboratory. Voucher specimens are deposited in the University of British Columbia herbarium and in the senior author's herbarium.

Data Analysis

The influence of patch size on the richness and abundance of functional groups, as well as the abundance of individual bryophyte species, was analyzed using generalized linear models, a class of models of which linear regression is a particular case. Generalized linear models allow for a range of relationships between the response and explanatory variables, and for the use of other error distributions when the normal distribution is not applicable (McCullagh and Nelder 1989). To evaluate the relationship between patch size and the abundance of bryophyte functional groups, we used normal linear regression with patch size logarithmically transformed and forest type entered as a categorical variable in the model. To better meet the assumptions of the model, we logarithmically transformed all percent cover values.

An error model designed for count data (i.e., using a Poisson error term and logarithmic link function) was the most appropriate for our species richness data. In the model, patch size was logarithmically transformed and forest type was entered as a categorical variable. We assessed the significance of patch size by assessing whether the drop in deviance residual (the measure of the lack of fit in the model) caused by including the term in the model was significant (Ramsey and Schafer 1997). We encountered difficulties with underdispersion caused by the lower than expected variances of the raw data, which were often substantially lower than the mean values. As a consequence, we assessed the significance of changes made during model fitting by using scaled changes in deviance (SAS 1999), which are distributed approximately as for an F statistic (Ramsey and Schafer 1997). In generalized linear models, the residual deviance is equivalent to the sum of squares in linear regression (Cameron and Trivedi 1998). There is no universal definition of the R^2 summary statistic in nonlinear models. We report the pseudo R^2 summary statistic, R^2_{DEV} , devised by Cameron and Windmeijer (1997), which measures the reduction in deviance resulting from the inclusion of regressors. Like the R^2 used in linear regression, R^2_{DEV} lies between 0 and 1, increases as regressors are added, and measures the

proportionate reduction in uncertainty resulting from the inclusion of the regressors (Cameron and Windmeijer 1997). If different categories within a functional grouping (i.e., mosses and liverworts) both showed significant association with patch size, we added a term for the individual categories and an interaction term between patch size and category type into the model which allowed us to determine if one category had a greater association (i.e., slope) with patch size than another.

Two other landscape variables which may affect species richness within forest patches are patch isolation and patch age (Saunders et al. 1991). We estimated patch isolation by determining the distance from each patch to the nearest old-growth forest patch. None of the patches examined in this study had the surrounding forest cut in a single year. We used forest history maps to determine the mean number of years since the surrounding forest had been removed with the age of harvest weighted by the length of edge of that age. We added isolation distance and patch age to the model individually and assessed whether there was a significant drop in deviance. We report the partial F statistics and partial R^2_{DEV} resulting from the inclusion of these landscape variables.

To evaluate the relationship between individual species abundance and patch size, we used a generalized linear model with a logistic link function and a binomial error term. Species abundance in this model was the number of microplots (0-63) that each species occupied in a 0.1 ha plot. Species included in this evaluation were those that occurred in six or more remnant patches. In each model, patch size was logarithmically transformed and forest type was entered as a categorical variable. The drop-in-deviance test was used to assess the significance of each regressor in the model (Ramsey and Schafer 1997). We encountered difficulties with underdispersion caused by the lower than expected variances of the raw data, which were often less than what would be expected from a binomial distribution. As a consequence, we assessed the significance of changes made during model fitting by using scaled changes in deviance (SAS

1999), which are distributed approximately as for an F statistic (Ramsey and Schafer 1997).

Again, we report the R^2_{DEV} (Cameron and Windmeijer 1997).

4.4 Results

Bryophyte species richness and patch size

Fifty-nine bryophyte species (29 liverworts and 30 mosses) were found in at least one remnant forest patch through microplot sampling. Over 40% of the observed species occurred in at least 50% of the remnant patches sampled, while 10 species were found in only one remnant patch. The ten most common bryophyte species included four liverworts (*Scapania bolanderi*, *Frullania tamarisci* subsp. *nisquallensis*, *Cephalozia lunulifolia* and *Calypogeia muelleriana*) and six mosses (*Hypnum circinale*, *Dicranum fuscescens*, *Rhytidiadelphus loreus*, *Isoetecium myosuroides*, *Hylocomium splendens* and *Plagiothecium undulatum*). Of the species observed in microplot sampling, 10 were classified as open canopy species, 12 as canopy generalist species and 37 as closed canopy species, 11 as colonists, 7 as short-lived shuttles, 8 as long-lived shuttles and 32 as perennial stayers (Table 4.2). Seven species that were identified as perennial stayers by virtue of spore size and growth form were either described in the literature or observed in the field as having abundant sporophyte production (identified with asterisks in Table 4.2). Therefore, we created a sub-category of perennial stayers, infertile perennial stayers, which consisted of the 25 perennial stayers that lacked abundant sporophytes.

Species richness in remnant patches varied from a low of 18 species/plot to a high of 36 species/plot with a mean of 26.4 ± 1.1 species/plot. After patch size was accounted for, Sayward remnant patches had a significantly higher richness of bryophytes than Nimpkish patches (Wald's test, $p < 0.0001$).

Relationship between patch size and species richness within microclimate-tolerant functional groups

Both mosses and liverworts showed a positive association between species richness and remnant patch size (Figure 4.1a, b; Table 4.3). However, when measures of landscape fragmentation were added as covariates, neither the richness of mosses or liverworts were related to either the distance to the closest old-growth patch or to the number of years the patch had been isolated (Table 4.3). In order to determine if liverwort species had a stronger relationship with patch size than moss species (i.e., a greater slope), we added both bryophyte “type” and an interaction term between patch size and bryophyte type into the model. In this regression, there was no evidence that the relationship between patch size and species richness differed between moss and liverwort species (Table 4.3).

The richness of closed canopy species showed a significant association with patch size (Figure 4.1c; Table 4.3); whereas the richness of both canopy generalists and open canopy species was only marginally associated with patch size (Figure 4.1d, e; Table 4.3). When measures of landscape fragmentation were added as covariates in the models, only the richness of open canopy species and the distance to the nearest old-growth patch showed a significant association (Table 4.3). In order to determine if any canopy preference category (i.e., open vs. closed canopy) had a greater relationship with patch size than another, we added both canopy preference type and an interaction term between patch size and canopy preference type into the model. In this regression, the interaction term was not significant, indicating that there was no evidence that the association between patch size and species richness differed between closed canopy, canopy generalists, or open canopy species (Table 4.3)

Relationship between patch size and species richness within dispersal ability functional groups

The richness of colonists had no relationship with patch size (Figure 4.1f, Table 4.3), whereas both life-history strategy categories with large spores (i.e., short- and long-lived shuttles) showed a significant association between richness and patch size (Figure 4.1g, h; Table 4.3). The richness of perennial stayers was only marginally positively associated with patch size (Figure 4.1i, Table 4.3), however, when species of perennial stayers that had relatively abundant sporophyte production were removed from this category, the richness of the remaining perennial stayers (infertile perennial stayers) had a significant positive association with patch size (Table 4.3). When measures of landscape fragmentation were included in the models, no life-history strategy category showed a significant association between species richness and the distance to nearest old-growth forest or patch age (Table 4.3). To determine whether any life-history strategy category had a stronger relationship with patch size, we include life-history strategy type and an interaction term between life-history strategy type and patch area into the model. We found no evidence that any life-history strategy category had a stronger association with patch area than another (Table 4.3).

When the richness of bryophytes found on different substrates (forest floor, logs and tree bases) was evaluated, only the richness of bryophytes found on the forest floor had a significant positive association with patch size (Figure 4.1j, Table 4.3). No substrate category showed a significant relationship with richness and either the distance to the nearest old-growth forest or patch age, when measures of landscape fragmentation were included in the regression models.

Relationship between patch size and abundance of functional groups and individual species

The cover of liverworts had a significant association with patch size but the cover of moss species did not (Figure 4.2a, b; Table 4.4). When species were classified by canopy

preference, only the cover of closed canopy species showed a significant positive association with patch size (Figure 4.2c, Table 4.4). Open canopy and canopy generalist species showed no significant association with patch size (Figure 4.2d, e; Table 4.4). Colonists and long-lived shuttles showed no significant association with patch size (Figure 4.2f, h; Table 4.4). In contrast perennial stayers and short-lived shuttles both showed a positive association with patch size (Figure 4.2g, i; Table 4.4). Finally, when we evaluated the percent cover of bryophytes on individual substrates, the cover of bryophytes on the forest floor and downed logs showed a significant association with patch size (Figure 4.2j, k; Table 4.4), while the cover of bryophytes on tree bases did not (Figure 4.2l, Table 4.4).

Of the 26 bryophyte species that were found in six or more remnants, three moss and four liverwort species had significantly positive associations between species abundance and patch size (Table 4.5). No bryophyte species showed a significant negative association with abundance and fragment size (Table 4.5). Of the bryophytes that had a significant relationship between abundance and fragment size, three were classified as perennial stayers, two were classified as colonists, one was classified as a short-lived shuttle and one was classified as a long-lived shuttle. In terms of canopy preferences, all seven of the bryophytes that had significant associations between abundance and patch size were species found typically under closed canopy (Table 4.5).

4.5 Discussion

In this study, bryophyte richness, sampled with constant-sized plots and on constant habitats, was significantly associated with remnant patch size. With the exception of one study in central Amazonia (Zartman 2003), no other study appears to have documented effects of decreasing patch size in anthropogenically fragmented landscapes on bryophyte richness. Furthermore, by examining the richness and abundance of individual bryophyte functional

groups, we have shown that this relationship is not universal for bryophytes. In particular, the richness and abundance of dispersal-limited groups and microclimate sensitive groups showed significant declines in either richness or abundance as patch size decreased. In contrast, groups expected to increase with decreasing patch size (colonists and open canopy species) showed little association (positive or negative) with patch size.

Decline of dispersal-limited and microclimate-tolerant groups

The life-history strategy categories that showed a significant association with patch size also appear to have a high probability of being dispersal-limited (related either to spore size or infrequent sporophyte production). Furthermore, the abundance of two of these categories (perennial stayers and short-lived shuttles) was negatively impacted with decreasing patch size. Is it reasonable to expect that the four bryophyte life strategies in old-growth forest patches would exhibit differing relationships with patch size? Both theory and empirical evidence suggest that differences would occur.

In a simulation study, Herben and Söderström (1992) reported that the distance between habitat localities had the greatest effect on the persistence of bryophyte species occupying patchy habitats. Old-growth forest remnants surrounded by a matrix of clear-cuts and younger forest are by definition isolated from other old-growth forest areas (Saunders et al. 1991). Although bryophyte species are not completely eliminated from younger-aged forests, numerous studies have documented that bryophyte richness, in particular epixylic (dwelling on logs) liverwort richness is reduced in second-growth forests (Gustafsson and Hallingbäck 1988, Söderström 1988a, Andersson and Hytteborn 1991, Lesica et al. 1991, Rambo and Muir 1998a, 1998b). In a separate study of the bryophyte community in both regeneration and immature forests (Chapter 3), we found that the abundance of old-growth associated species, as well as total bryophyte cover, was reduced in younger-aged forests. These studies suggest that distances between

suitable habitat localities in young-aged forests are likely to be greater than what would have been found in continuous old-growth forest.

In Herben and Söderström's (1992) modelling, the magnitude of the effect of distance was related directly to the dispersal ability of the individual species with the same increase in distance between habitat patches having a greater effect on species with restricted dispersal ability. Recent empirical studies have supported the expectations of differential dispersal distance for small and large spores. Spore size can greatly affect the percentage that escape the close confines of the parent colony. Moss species with small spores (8-20 μm in size) deposited only 2.2-12.7% of released spores within 2 m of the source (Miles and Longton 1992), while a liverwort with large spores (25-27 μm in size) deposited 52% of released spores within 2.5 m of the parent colony (Söderström and Jonsson 1989). Colonists and perennial stayers are small-spored species that have the potential to disperse long distances; however, if perennial stayers produce sporophytes infrequently, the dispersal of this group may be limited. We found that the relative production of sporophytes is particularly important, as the relationship between perennial stayers and patch size in this study was only significant when we eliminated fertile perennial stayer species from the analysis. It is also important to note that the successful dispersal via spores may rely not only on the dispersal distance, but also on the probability that a spore lands on a suitable substrate. In Swedish boreal forests, the percentage of all spores produced that landed on suitable substrate for *Ptilidium pulcherrimum*, one of the few species for which rates are known, is only 0.5-0.9% (Söderström and Jonsson 1989)

On the scale of hundreds of meters (between forest remnants) bryophytes disperse via sexual spores and asexual diaspores (vegetative fragments or specially produced propagules such as gemmae or tubers). Of the 59 species observed in this study, 18 species are known to reproduce via asexual diaspores (Godfrey 1977, Schofield 1992). However, unspecialized diaspores such as fragments are likely to be an inefficient means of long-distance dispersal in

forested landscapes where dispersing winds are weak (McDaniel and Miller 2000). Even smaller diaspores such as gemmae may have dispersal distances as short as 10 cm (Kimmerer 1991). Thus, asexual diaspores are likely to contribute primarily to the diaspore bank or within-patch dynamics (Söderström and Herben 1997), rather than dispersal between forest patches.

To our knowledge, no data exists on the bryophyte diaspore bank in coastal temperate rainforests. Theoretically, species persistence in forest patches could be maintained through propagules found in the diaspore bank, just as seed banks form a pool of propagules for vascular plants (Silvertown 1993). However, previous studies of the bryophyte diaspore bank found in diverse habitats in Europe have found that colonist bryophyte species dominate the diaspore bank (During and ter Horst 1983, During et al. 1987, Jonsson 1993). In Swedish boreal forests, the composition of the bryophyte diaspore bank was more similar to bryophyte species composition on tip-up mounds than the bryophyte species composition found on the undisturbed forest floor (Jonsson 1993). Thus, although propagules in the diaspore bank may play an important role in the colonization of disturbed forest floor, it is less likely that they contribute substantially to the maintenance of old-growth associated groups such as perennial stayers and closed canopy species.

Species found on the undisturbed forest floor are most likely to be perennial stayers (During 1979) and have the most limited dispersal abilities, reproducing primarily through either clonal growth or vegetative fragments. Of the 48 species found in forest floor microplots in this study, nearly one-half were perennial stayers. Thus, it is not surprising that when the richness of bryophytes found on different substrate-types (forest floor, downed logs and tree bases) was examined, only the richness of bryophytes found on the forest floor had a significant relationship with remnant patch size. The cover of bryophytes on the forest floor also showed a significant increase with patch size. Similarly, an experimental study of the effect of habitat fragmentation

on vascular plants found that only clonal plants were affected by patch size (Robinson et al. 1992).

Forest patches, by definition, lack continuity with other old-growth forest patches. However, the degree of isolation bryophyte populations in each patch experience will depend upon the characteristics of each bryophyte species, such as dispersal ability, as well as landscape variables, such as the type of matrix surrounding individual forest patches and the distance between patches of remnant old-growth forests. The results of this study indicate that functional groups defined by dispersal ability showed a differential association with decreasing patch size, indicating that isolation effects may be ameliorated by species-specific characteristics. Once patch size was accounted for, however, there was little evidence that landscape-level variables such as patch age (which indirectly describes the age of the forest matrix surrounding each patch) and patch isolation were associated with patch size. This is consistent with previous findings that the degree of isolation played little role in predicting bryophyte richness in naturally fragmented habitats such as granite boulders, limestone cliffs, or islands with a lake (Tangney et al. 1990, Haig et al. 1999, Kimmerer and Driscoll 2000).

While these results suggest that bryophyte species characteristics are more important than landscape level variables in determining the degree of isolation, we caution that our analysis of landscape level variables other than patch size was preliminary by design. We included distance to the nearest old-growth patch and patch age (from forest history maps with age of harvested weighted by the length of edge of that age) as landscape level measures in the regression modeling because they were readily available and provided comparisons with previous studies. However, as a measure of the degree of isolation, the distance to the nearest old-growth patch is confounded by environmental variables such as predominant wind directions. Likewise, although patch age gives a rough estimate of the age of edge surrounding the remnant forest patch, it does not indicate the areal extent of the differently aged forests surrounding each patch.

Thus, we suggest that although our results are interesting, the influence of patch age and patch isolation should be more thoroughly investigated.

In addition to experiencing the effects of lack of forest continuity, species in old-growth forest patches may be subject to edge effects. The bryophyte community in edge habitats may experience direct disturbance through windthrown trees uprooting the forest floor (Esseen 1994, Mitchell et al. 2001) or indirect disturbance through changes in microclimate (Chen et al. 1995). Edge effects have been cited as an important factor determining the richness of bryophytes on “true” islands in Lake Manapouri, New Zealand (Tangney et al. 1990) and the cover of epixylic (on downed logs) liverworts in naturally occurring boreal forest patches (Moen and Jonsson 2003). In this study, we found that decreasing patch size had a negative impact both on the richness and abundance of groups expected to be sensitive to altered microclimate (liverworts and closed canopy bryophytes). This is supported by the results of Chapter 2 that showed that proximity to a forest edge was associated with a reduction in the fine-scale richness of liverworts and closed canopy bryophytes, as well as a decrease in total bryophyte cover.

Along with our initial expectation that the richness of dispersal-limited and microclimate sensitive species would decrease with patch size, we also expected that the richness and/or abundance of clearing affiliated functional groups (i.e., colonists and open canopy species) would increase with decreasing patch size. As small patches have a greater proportion of the patch closer to the forest edge, the center of small patches may be more susceptible to invasion by matrix species than the center of large patches (Saunders et al. 1991, Hobbs and Huenneke 1992, Ås 1999). The relationship between diversity and invasibility has been the subject of recent debate (see review in Levine 1999); however, the effects of reduced diversity on invasibility may be mediated by environmental or biotic factors which covary with diversity (Levine 2000, Naeem et al. 2000). In this study, the observed drop in richness of old-growth associated functional groups (liverworts, closed canopy and perennial stayers) was not

concurrent with an invasion of the clearing affiliated functional groups (moss species, colonists and open canopy species) in smaller patches. In fact, the richness of moss and open canopy species was positively associated with patch size (albeit marginally) while the richness of colonists showed no association (positive or negative) with patch size. This indicates that the smallest forest patches sampled in this study were no more susceptible to the invasion of clearing affiliated species than large forest patches.

Invasion of clearing affiliated species will depend not only on successful dispersal (either spatially from nearby clearcut areas or temporally from the diaspore bank) but on appropriate conditions for establishment in the center of remnant patches. We suggest that the low rate of invasion by clearing affiliated species into small forest patches was a function of limited direct disturbance (i.e., windthrown trees) experienced at the center of the smallest remnant patches as well the sampling method used to estimate species richness in the forest patches. The highest rates of windthrow disturbance in cutblock edges in subalpine forests occurred 5 m from the forest edge (Huggard et al. 1999). In the edge study (Chapter 2) although the number of tip-up mounds did not differ on transects located from 0-45 m from the edge, the cover of exposed mineral soil was negatively associated with distance from the forest edge. These results imply that the center of small patches may have experienced rates of recent direct disturbance equivalent to those found in large forest patches.

Furthermore, the occurrence of colonist species in both the edge study (Chapter 2) and the stand age study (Chapter 3) was highly correlated with the presences of exposed mineral soil. In order to limit the influence of habitat diversity on species richness, we sampled bryophytes in microplots located on the forest floor, downed logs, and tree bases. In the edge and stand age studies (Chapters 2 and 3) microplot sampling detected far fewer clearing affiliated species than whole plot sampling which included infrequently occurring substrates such as exposed tip-up

mounds. Thus it is not surprising that out of the 59 bryophyte species encountered in this study, most were old-growth associated species, either closed canopy species or perennial stayers.

In this study, we used bryophyte functional groupings based on dispersal ability and sensitivity to microclimatic changes to evaluate the primary effects of forest fragmentation on the bryophyte community. It must be recognized that there are liabilities associated with arbitrarily classifying species into discrete categories based on characteristics that exist along a continuum. We view this classification by functional groups as a first hypothesis predicting bryophyte community response to decreasing patch size, even if different responses may occur for species within the same group.

The results of this study suggest that both the lack of forest continuity and edge effects experienced by bryophytes in remnant forest patches influence the overall pattern of bryophyte species richness and abundance. Stating unequivocally that one causal factor was primarily responsible for the observed trends, however, is impossible as a high number of dispersal-limited species were also categorized as closed canopy species (Table 4.2). Discriminating between alternative causes (lack of forest continuity versus edge effects) for observed changes may also be unrealistic as the observed trend may be the result of both factors interacting with one another (Levins and Lewontin 1985).

Management Implications

Our primary purpose was to assess the relationship between bryophyte species richness and remnant patch size, after accounting for habitat diversity and sample area. Our results show that bryophyte richness as well as their abundance is strongly associated with patch size. Regardless of the causal factors for the observed trend, the results of this study have important implications for forest management. The amount of old-growth forest found at low elevations in British Columbia is projected to decrease in the future (MacKinnon and Vold 1998). Thus, it is

likely that the size distribution of forest remnants will become more and more skewed to smaller, more dispersed forest patches (Andrén 1994). Moreover, the effect of patch size on bryophyte diversity will limit the usefulness of very small remnant patches left behind as a part of variable retention practices. Although proponents of variable retention techniques recognize that retained forest aggregates of less than 1 ha in size are likely to be subject to edge effects, a stated objective of these small forest patches is to provide refugia for elements of biodiversity that might otherwise be lost from the harvested area (Franklin et al. 1997). It is unlikely, however, that remnant patches retained as part of variable retention practices will act as reservoirs of diversity for bryophytes as the overall diversity in small forest patches is likely to have been strongly compromised.

4.6 Tables and Figures

Table 4.1. Characteristics of forest patch remnants sampled at Sayward and Nimpkish study areas.

| | Remnant # | Elevation (m) | Slope (°) | Aspect (°) | Size (ha) | Isolation Distance (m) | Age of fragment |
|-----------------|-----------|------------------|-----------|------------|--------------|---------------------------|--------------------|
| Sayward | 743 | 180 | 0.00 | 0.00 | 5.04 | 570 | 23.30 |
| | 744 | 180 | 2.00 | 28.33 | 14.69 | 1350 | 23.20 |
| | 751 | 150 | 0.00 | 0.00 | 23.76 | 1150 | 25.36 |
| | 753 | 480 | 24.17 | 311.83 | 13.54 | 285 | 11.79 |
| | 754 | 365 | 18.50 | 92.67 | 0.58 | 285 | 18.50 |
| | 756 | 450 | 33.00 | 317.00 | 8.70 | 1000 | 47.20 |
| | 757 | 300 | 35.33 | 230.33 | 0.72 | 950 | 27.20 |
| | 758 | 520 | 0.00 | 0.00 | 4.50 | 1000 | 33.60 |
| | 761 | 670 | 7.50 | 69.67 | 12.70 | 750 | 20.00 |
| | 764 | 300 | 39.00 | 52.00 | 3.46 | 60 | 19.40 |
| Mean ± 1 S.E. | | 359.5±53.8 | 16.0±5.1 | 110.2±40.3 | 8.99±2.2 | 740.0±134.3 | 25.0±3.1 |
| Nimpkish | 822 | 150 | 19.83 | 227.17 | 11.80 | 450 | 25.50 |
| | 826 | 370 | 10.33 | 68.33 | 1.80 | 1800 | 34.90 |
| | 829 | 210 | 6.17 | 82.50 | 10.10 | 750 | 13.20 |
| | 839 | 400 | 16.17 | 238.83 | 34.20 | 900 | 25.13 |
| | 841 | 300 | 0.67 | 12.50 | 38.30 | 1200 | 14.00 |
| | 843 | 425 | 26.33 | 40.67 | 63.60 | 1200 | 10.60 |
| | 849 | 400 | 30.80 | 310.20 | 49.70 | 1500 | 32.70 |
| | 851 | 245 | 5.00 | 156.83 | 6.40 | 1500 | 8.00 |
| | 865 | 180 | 4.17 | 200.83 | 7.20 | 450 | 44.90 |
| | 880 | 180 | 0.00 | 0.00 | 4.68 | 75 | 7.00 |
| Mean ± 1 S.E. | | 286.0±33.5 | 12.0±3.4 | 133.8±34.0 | 22.8±6.9 | 982.5±174.8 | 21.6±4.1 |

Table 4.2. List of species recorded in microplot sampling in plots located at the center of remnant patches. Functional group classification as described in Table 1.1. Abbreviations for functional group categories: OT = open turfs, ST = short turfs, TT = tall turfs, CU = cushions, TM = thaloid mats, SM = smooth mat, TH = thread-like mats, RM = rough mats, WE = wefts, PE = pendants, DE = dendroids, P=perennial stayers, L = long-lived shuttles, S = short-lived shuttles, C = colonist. Sporophyte production (1-3) indicates frequency of sporophyte production given in literature (0=absent, 1=rare/uncommon, 2=infrequent, 3=common/abundant; Godfrey 1977; Schofield 1976)

| | Frequency of occurrence (number of plots) | Growth Form | Life- history strategy | Canopy preference | Sporophyte production | Median spore size |
|---|---|----------------|------------------------------|----------------------|--------------------------|----------------------|
| Liverworts | | | | | | |
| <i>Cephalozia bicuspidata</i> | 3 | TH | C | closed | 3 | 14 |
| <i>Cephaloziella divaricata</i> | 2 | TH | C | open | 1 | 7.5 |
| <i>Jungermannia leiantha</i> | 8 | SM | C | open | 3 | 13.5 |
| <i>Lophocolea bidentata</i> | 10 | TH | C | closed | 3 | 17.5 |
| <i>Lophocolea heterophylla</i> | 7 | TH | C | closed | 3 | 13 |
| <i>Lophozia incisa</i> | 9 | SM | C | closed | 3 | 13 |
| <i>Lophozia longifolia</i> | 6 | SM | C | closed | 3 | 8 |
| <i>Frullania californica</i> | 6 | SM | L | closed | 1 | 47 |
| <i>Frullania tamarisci</i> subsp. <i>nisquallensis</i> | 20 | SM | L | generalist | 1 | 48 |
| <i>Metzgeria conjugata</i> | 1 | TM | L | generalist | 2 | 22 |
| <i>Porella navicularis</i> | 13 | PE | L | open | 1 | 67.5 |
| <i>Ptilidium californicum</i> | 16 | SM | L | closed | 2 | 25.5 |
| <i>Radula bolanderi</i> | 11 | SM | L | generalists | 2 | 35 |
| <i>Riccardia latifrons</i> | 10 | TM | L | closed | 2 | 20 |
| <i>Blepharostoma trichophyllum</i> | 20 | TH | P | closed | 1 | 12 |
| <i>Bazzania denudata</i> | 16 | SM | P | closed | 0 | 13 |
| <i>Calypogeia fissa</i> | 3 | TH | P | closed | 1 | 9.5 |
| <i>Calypogeia muelleriana</i> | 19 | SM | P | closed | 1 | 11 |
| <i>Cephalozia lunulifolia</i> | 20 | TH | P | closed | 1 | 10 |
| <i>Chiloscyphus polyanthos</i> | 2 | SM | P | closed | 1 | 17.5 |
| <i>Diplophyllum albicans</i> | 7 | RM | P | closed | 2 | 13 |
| <i>Douinia ovata</i> | 13 | SM | P | open | 1 | 15 |
| <i>Geocalyx graveolens</i> | 1 | TH | P | closed | 1 | 11 |
| <i>Gyrothyra underwoodiana</i> | 1 | SM | P | open | 1 | 12 |
| <i>Lepidozia reptans</i> | 19 | SM | P | closed | 2 | 13 |
| <i>Plagiochila asplenoides</i> | 13 | ST | P | closed | 2 | 18 |
| <i>Riccardia multifida</i> | 3 | TM | P | closed | 1 | 16.5 |
| <i>Scapania bolanderi</i> | 20 | RM | P | closed | 2 | 11 |
| <i>Scapania umbrosa</i> | 16 | SM | P | open | 2 | 11.5 |
| Mosses | | | | | | |
| <i>Dicranum fuscescens</i> | 20 | ST | C | generalist | 3 | 19 |
| <i>Dicranum scoparium</i> | 2 | ST | C | open | 3 | 19 |
| <i>Pogonatum contortum</i> | 3 | TT | C | open | 3 | 11.5 |
| <i>Polytrichastrum alpinum</i> | 3 | TT | C | generalist | 3 | 17 |
| <i>Antitrichia curtipendula</i> | 18 | PE | L | generalist | 2 | 21.5 |
| <i>Leucolepis acanthoneuron</i> | 2 | DE | S | closed | 3 | 29 |
| <i>Mnium spinulosum</i> | 3 | ST | S | closed | 3 | 20 |
| <i>Neckera douglasii</i> | 3 | PE | S | generalist | 3 | 19.5 |
| <i>Plagiomnium insigne</i> | 2 | TT | S | closed | 3 | 22.5 |
| <i>Pohlia nutans</i> | 1 | OT | S | open | 3 | 19.5 |

| | | | | | | |
|---|----|----|---|------------|---|------|
| <i>Rhizomnium glabrescens</i> | 16 | ST | S | closed | 3 | 37.5 |
| <i>Ulota megalospora</i> | 11 | CU | S | closed | 3 | 44 |
| <i>Claopodium bolanderi</i> | 1 | RM | P | closed | 2 | 13.5 |
| <i>Claopodium crispifolium</i> | 1 | RM | P | closed | 1 | 10.5 |
| <i>Eurhynchium oreganum</i> | 11 | WE | P | generalist | 3 | 14 |
| <i>Eurhynchium praelongum</i> | 7 | WE | P | generalist | 3 | 14.5 |
| <i>Eurhynchium pulchellum</i> var. <i>barnesii</i> | 2 | WE | P | closed | 2 | 13.5 |
| <i>Heterocladium procurrens</i> | 1 | RM | P | closed | 2 | 13 |
| <i>Hookeria lucens</i> | 6 | SM | P | closed | 1 | 13.5 |
| <i>Hylocomium splendens</i> | 19 | WE | P | closed | 2 | 14 |
| <i>Hypnum circinale</i> * | 20 | SM | P | generalist | 3 | 17 |
| <i>Isothecium myosuroides</i> * | 20 | WE | P | generalist | 3 | 18.5 |
| <i>Metaneckera menziesii</i> * | 1 | PE | P | generalist | 3 | 13 |
| <i>Othotricum consimile</i> * | 1 | SM | P | open | 3 | 13 |
| <i>Plagiothecium denticulatum</i> * | 1 | SM | P | closed | 3 | 13 |
| <i>Plagiothecium laetum</i> * | 8 | SM | P | closed | 3 | 13 |
| <i>Plagiothecium undulatum</i> * | 16 | RM | P | closed | 3 | 13 |
| <i>Pseudotaxiphyllum elegans</i> | 8 | SM | P | closed | 2 | 12 |
| <i>Rhytidiadelphus loreus</i> | 20 | WE | P | closed | 2 | 14 |
| <i>Rhytidiopsis robusta</i> | 6 | WE | P | closed | 2 | 11.5 |

* indicates species that were eliminated from infertile perennial stayer grouping due to their high sporophyte production.

Table 4.3. Regression analysis summaries relating bryophyte species richness within taxonomic, functional and substrate categories with remnant forest patch area, distance to nearest old-growth and patch age. Regressions were run using a Poisson log-linear model with patch area logarithmically transformed and effect of forest type (i.e., Nimpkish or Sayward study area) removed (see text for complete description of model). Interaction term indicates whether the slopes of the individual category terms were significantly different from one another. P-values <0.05 are listed in bold. See Fig. 4.1 for graphical display of species richness-patch area relationships.

| Taxonomic | Patch area | | | | Distance to nearest old-growth | | | | Patch age | | | |
|---------------------------------|------------|------------------|------|-------------------------------|--------------------------------|--------------|------|-------------------------------|-----------|---------|------|-------------------------------|
| | F | p-value | df | R ² _{DEV} | F | p-value | df | R ² _{DEV} | F | p-value | df | R ² _{DEV} |
| Mosses | 8.54 | 0.009 | 1,17 | 0.63 | 0.10 | 0.757 | 1,16 | 0.002 | 1.51 | 0.237 | 1,16 | 0.03 |
| Liverworts | 8.37 | 0.006 | 1,17 | 0.46 | 0.62 | 0.441 | 1,16 | 0.04 | 0.19 | 0.670 | 1,16 | 0.01 |
| Interaction term | 0.29 | 0.711 | 1,35 | 0.002 | | | | | | | | |
| Canopy preference | | | | | | | | | | | | |
| Closed canopy | 8.78 | 0.008 | 1,17 | 0.64 | 0.31 | 0.587 | 1,16 | <0.001 | 0.48 | 0.497 | 1,16 | 0.01 |
| Canopy generalists | 4.33 | 0.054 | 1,17 | 0.23 | 0.42 | 0.527 | 1,16 | 0.02 | 0.5 | 0.490 | 1,16 | 0.02 |
| Open canopy | 4.26 | 0.051 | 1,17 | 0.33 | 9.5 | 0.007 | 1,16 | 0.25 | 0.55 | 0.470 | 1,16 | 0.02 |
| Interaction term | 0.55 | 0.580 | 2,53 | 0.001 | | | | | | | | |
| Life-history strategy | | | | | | | | | | | | |
| Colonists | 1.22 | 0.284 | 1,17 | 0.11 | 0.03 | 0.283 | 1,16 | 0.002 | 1.13 | 0.303 | 1,16 | 0.06 |
| Short-lived shuttle | 9.18 | 0.008 | 1,17 | 0.32 | 0.10 | 0.761 | 1,16 | 0.04 | 0.01 | 0.943 | 1,16 | 0.04 |
| Long-lived shuttle | 7.19 | 0.016 | 1,17 | 0.24 | 0.35 | 0.563 | 1,16 | 0.12 | 0.19 | 0.670 | 1,16 | 0.006 |
| Perennial stayers (all species) | 3.8 | 0.068 | 1,17 | 0.11 | 0.05 | 0.818 | 1,16 | 0.003 | 0.39 | 0.541 | 1,16 | 0.01 |
| Infertile perennial stayers | 6.32 | 0.022 | 1,17 | 0.48 | | | | | | | | |
| Interaction term | 1.4 | 0.249 | 3,71 | 0.0043 | | | | | | | | |
| Substrate | | | | | | | | | | | | |
| Forest floor | 16.27 | <0.001 | 1,17 | 0.79 | 0.97 | 0.338 | 1,16 | 0.12 | 2.07 | 0.169 | 1,16 | 0.02 |
| Logs | 4.44 | 0.050 | 1,17 | 0.32 | 0.27 | 0.612 | 1,16 | 0.01 | 0.18 | 0.677 | 1,16 | 0.007 |
| Tree bases | 2.42 | 0.139 | 1,17 | 0.14 | 0.34 | 0.569 | 1,16 | 0.017 | 0.013 | 0.910 | 1,16 | <0.0001 |

Table 4.4. Regression analysis summaries relating bryophyte percent cover within taxonomic, functional and substrate categories with remnant forest patch area. Regressions were run using a linear regression model with bryophyte cover and patch area logarithmically transformed and effect of forest type (i.e., Nimpkish or Sayward study area) removed (see text for complete description of model). P-values <0.05 are listed in bold. See Fig.4.2 for graphical display of cover - patch area relationships.

| | Patch area | | | |
|------------------------------|------------|--------------|------|----------------|
| | F | p-value | df | R ² |
| Taxonomic | | | | |
| Mosses | 2.54 | 0.128 | 1,17 | 0.12 |
| Liverworts | 9.16 | 0.007 | 1,17 | 0.33 |
| Canopy preference | | | | |
| Closed canopy | 6.77 | 0.018 | 1,17 | 0.27 |
| Canopy generalists | 0.131 | 0.722 | 1,17 | 0.15 |
| Open canopy | 3.92 | 0.087 | 1,17 | 0.1 |
| Life-history strategy | | | | |
| Colonists | 3.05 | 0.145 | 1,17 | 0.1 |
| Short-lived shuttle | 8.04 | 0.011 | 1,17 | 0.31 |
| Long-lived shuttle | 0.06 | 0.809 | 1,17 | <0.01 |
| Perennial stayers | 5.42 | 0.033 | 1,17 | 0.24 |
| Infertile perennial stayers | 3.41 | 0.056 | 1,17 | |
| Substrate | | | | |
| Forest floor | 4.8 | 0.042 | 1,17 | 0.21 |
| Logs | 7.43 | 0.014 | 1,17 | 0.29 |
| Tree bases | 2.17 | 0.158 | 1,17 | 0.11 |

Table 4.5. Bryophyte species with a significant relationship between abundance and patch size. Canopy preference classification denotes shade tolerance and is based on literature reports (Godfrey 1977; Schofield 1976, 1992) and local expertise (W.B. Schofield, pers. comm.). Life-history strategy based on During's (1979, 1992) classification: P=perennial stayer, C=colonist, S=short-lived shuttle, L=long-lived shuttle. Slope indicates whether the association with patch size was positive (+) or negative (-). P-values less than 0.05 are listed in bold.

| Species | Frequency (# of patches) | Canopy preference | Life- history strategy | Slope | F | df | p-value |
|-------------------------|-----------------------------|----------------------|------------------------------|-------|-------|------|--------------|
| Liverworts | | | | | | | |
| Calypogeia muelleriana | 19 | closed | P | + | 12.10 | 1,17 | 0.002 |
| Cephalozia lunulifolia | 20 | closed | P | + | 6.83 | 1,17 | 0.018 |
| Lophozia incisa | 9 | closed | C | + | 5.27 | 1,17 | 0.035 |
| Riccardia latifrons | 10 | closed | L | + | 6.35 | 1,17 | 0.020 |
| Mosses | | | | | | | |
| Hookeria lucens | 6 | closed | P | + | 4.82 | 1,17 | 0.040 |
| Plagiothecium undulatum | 16 | closed | C | + | 5.88 | 1,17 | 0.027 |
| Rhizomnium glabrescens | 16 | closed | S | + | 13.96 | 1,17 | 0.000 |

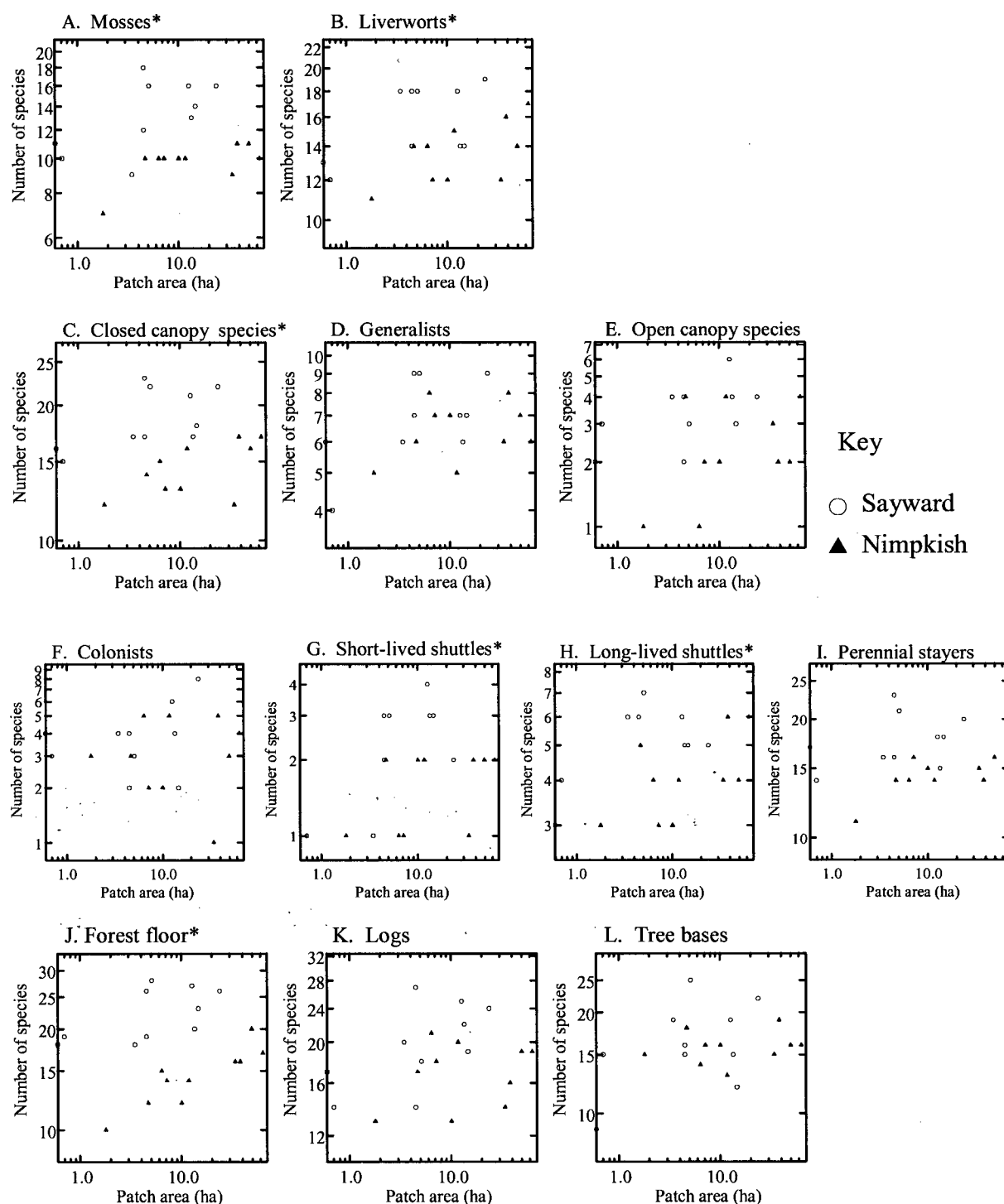


Figure 4.1. Relationship of bryophyte species richness within taxonomic (a,b), functional (c-i) and substrate categories (j-l) to remnant forest patch size in the Sayward (open circles) and Nimpkish (closed triangles) study areas. Asterisks denote significant relationships ($p < 0.05$). See Table 4.3 for regression summaries.

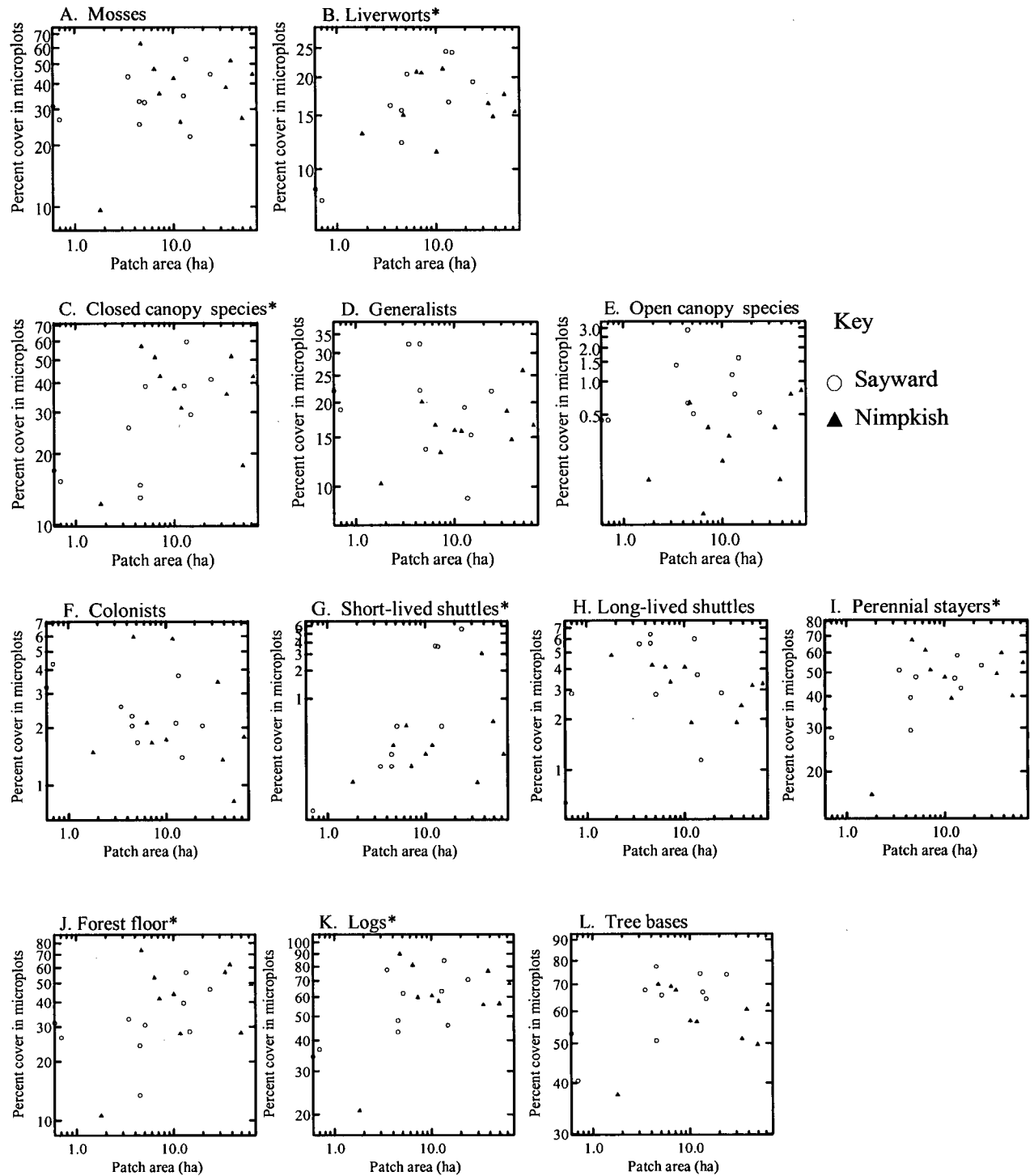


Figure 4.2. Relationships of bryophyte cover within taxonomic (a,b), functional (c-i) and substrate categories (j-l) to remnant forest patch area at the Sayward (open circles) and Nimpkish (closed triangles) study areas. Asterisks denote significant relationships ($p < 0.05$). See Table 4.4 for regression analyses summaries.

CHAPTER V. Conclusion and Synthesis

This thesis has demonstrated that patterns of bryophyte richness and abundance are significantly altered in smaller-sized remnant patches, edge habitats and younger-aged stands as compared to patterns found in the interior of larger old-growth remnant patches. Moreover, bryophyte functional groups (species with similar growth forms, life strategies and microhabitat affinities) exhibited different patterns of response indicating the extent to which different bryophyte species vary in their response to the disturbance imposed by large-scale fragmentation. This dissertation also provides additional support for the argument that fragmentation is best assessed using multiple spatial scales (Haila 2002).

Furthermore, this work fills an important void in fragmentation research. In general, fragmentation research has focused on vertebrates, particularly songbirds, as study organisms (McGarigal and Cushman 2002). Less vagile organisms, such as bryophytes, that respond to the environment at finer scales, may be better suited to fragmentation studies (Haila 1999). Certainly their response to fragmentation cannot be predicted on the basis of previous studies that have focused on larger, more mobile species. The overall effects of forest fragmentation are dependent not only upon the organism under consideration, but also upon the specific system studied (Wiens 1995, Haila 2002)

The three studies making up this doctoral research examined the richness and abundance of the bryophyte community found near or on the forest floor in coastal temperate rainforests on Vancouver Island, B.C. The vast majority of species encountered in this research were either colonists or perennial stayers (*sensu* During 1979, 1992). Important conclusions regarding the influence of stand age, proximity to forest edge, and patch size on the bryophyte community were determined through the analysis of changes in the richness and abundance of clearing-associated bryophytes species (typified by the colonist life strategy) and old-growth associated

species (typified by the perennial stayer life strategy). In light of this, it is instructive to develop a hypothetical model predicting the occurrence of clearing affiliated and old-growth associated species in the pre-harvest forest.

From a bryophyte's perspective, habitat found on the "floor" of coastal temperate rainforests consists of a complex mosaic of decaying logs and humus, litter from the overstorey, the bases of coniferous trees, mixed with infrequent patches of exposed mineral soil and rock created by the uprooting of windthrown trees. Although fire has occurred in some parts of the coastal temperate rainforests, the return-interval of fires is so infrequent (Lertzman et al. 2002) relative to the life-span of most bryophyte species, that such large-scale disturbances are unlikely influence bryophyte community dynamics.

Based on personal observations, the bryophyte community may experience both successional and gap dynamics within the interior of old-growth forest remnants. During field sampling, small gaps in the bryophyte mat presumably caused by animal disturbance (rodent, deer or elk) were observed. Litterfall from the canopy, especially thick clumps of *Antitrichia curtipendula* also appeared to cause localized mortality in the bryophyte mat on the forest floor or on downed logs. Such fine-scale gaps resulted in patches of localized bryophyte mortality but had little effect on underlying organic layers in the forest floor. Based on my research, it is impossible to state whether fine-scale gaps in these forests were invaded by colonists or perennial stayers; however, research in other regions has shown that small gaps in bryophyte mats (especially gaps which do not disturb forest floor and expose mineral soil) are primarily colonized by bryophyte species growing in from the margins of the gap, rather than by an influx of colonists through either spores or vegetative diaspores (Frego 1996, Jonsson and Esseen 1998). This pattern of recolonization via encroachment rather than dispersal was also observed in bryophyte mats on big-leaf maple branches in coastal temperate rainforests (Cobb et al. 2001).

Although the dominance of pleurocarpous, perennial stayer mosses may be achieved through overgrowing established bryophyte colonies, Rydin (1997) has argued that space competition in bryophytes often occurs through pre-emptive competition where an established individual limits the germination or survival of newcomers. It should be noted, however, that even in microplots dominated by perennial stayers (such as *Hylocomium splendens* and *Rhytidiadelphus loreus*), smaller bryophytes such as liverworts were often observed on discrete substrates such as humus or FWD scattered throughout the bryophyte mat.

In contrast to the fine-scale disturbances caused by litterfall or animal disturbance, wind-disturbance in coastal temperate rainforests can create local catastrophic upheavals in which whole trees are uprooted, exposing their root system and underlying mineral soil layers (Lertzman et al. 1996). Previous research has shown that bryophyte community development on the two main types of substrate created by windthrown trees (i.e., tip-up mound and tree boles) is primarily successional (McCullough 1948, Söderström 1988b, Jonsson and Esseen 1990, McAlister 1995, Rambo and Muir 1998a). Due to the changing nature of the substrate, bryophyte community development on downed logs typically includes a successional sequence beginning with epiphytic bryophytes (present before the tree was blown down) passing to epixylic liverworts found on exposed wood xylem and eventually including the overgrowth of the downed log by perennial stayers (Rambo and Muir 1998a). In contrast, the early successional bryophyte community on tip-up mounds is dominated by colonist moss species such as *Polytrichum juniperinum*, *Pohlia nutans*, and *Pogonatum contortum* (Jonsson and Esseen 1990, den Ouden and Alaback 1996). The ability of colonist species to invade young tip-up mounds has been hypothesized to result from either the removal of competitive dominants such as *Hylocomium splendens* and *Rhytidiadelphus loreus*, exposure of new substrates such as exposed mineral soil, stones and boulders, or activation of the diaspore bank that is typically

dominated by colonist propagules (Jonsson and Esseen 1990, Jonsson and Esseen 1998). The length of time these species are present in tip-up mounds varies by forest type: in Swedish boreal forests, colonist species were present on 120-150 year old tip-up mounds whereas in Alaskan rainforests, colonists species were not found on tip-up mounds older than 20 years, except in areas of unstable substrate (den Ouden and Alaback 1996).

If the above model predicting the colonizing ability of perennial stayers and colonists is correct, then the occurrence of colonists in pre-harvest forests may have been primarily determined by the frequency of tip-up mounds. In Clayoquot Sound on the western coast of Vancouver Island, approximately 30% of the forest area is in a canopy gap; however, only 15.6% of the gaps in old-growth forest were created through uprooting (Lertzman et al. 1996), indicating that a relatively small amount of the forest floor may consist of tip-up mounds at any one time. While the disturbance imposed by large-scale harvesting techniques imposes some of the same environmental conditions on the bryophyte community as might be found in gaps created by uprooted trees (i.e., decreased canopy cover and increased soil disturbance), disturbances associated with timber harvesting occurs with greater frequency and over a greater spatial extent. Not only does large-scale harvesting increase disturbance intensity compared to windthrow, it also alters the landscape-level patterns, such as the overall extent of old-growth forest cover and the spatial configuration of remaining old-growth forest patches.

Without reference to unfragmented landscapes, it may be impossible to determine the influence that overall habitat loss has had on the bryophyte community in temperate rainforests. However, the results of the patch size study (Ch. 4) indicate that decreasing patch size was significantly associated with declining bryophyte species richness. Furthermore, species richness within old-growth associated groups hypothesized to be intolerant of edge effects or dispersal-limitations was significantly associated with patch size.

The prediction that the richness of old-growth associated species would decline with decreasing patch size (after accounting for habitat diversity and sample area within differently sized patches) was based on two assumptions about the effects of landscape-level fragmentation on species richness. The first assumption is that at least some old-growth associated bryophyte species would not be able to survive in small forest patches that have little or no core area unaffected by the environmental conditions of the surrounding matrix. The second assumption is that the matrix of younger-aged forest surrounding old-growth forest patches would not act as a source of recolonization for old-growth associated species populations undergoing stochastic extinctions in very small forest patches (Saunders et al. 1991, Haila 1999, 2002).

In many studies relating habitat patch size and species richness, these two assumptions are held to be true without further investigation (Wiens 1995, Haila 2002). In contrast, I attempted to investigate the adequacy of these two assumptions by sampling in younger-aged forests and edge habitats. I predicted that the loss of old-growth associated species in small forest patches would reflect the loss of old-growth associated species in edge habitats and younger-aged forests. However, the results from the edge study (Chapter 2) and stand age study (Chapter 3) indicate that, with few exceptions, the plot-level richness of old-growth associated groups did not decline in edge habitats and younger-aged forests. At first glance, it is difficult to reconcile the loss of old-growth associated species in small old-growth forest patches with the persistence of these species in edge habitats and younger-aged forests. Several factors combined to present this apparent paradox in the data. First of all, the significant association between species richness and patch size was based on the richness found in microplots, whereas the maintenance of old-growth species in edge habitats and younger-aged forest was based on whole-plot surveys. Species richness from the two sampling methods are not equivalent as

whole-plot sampling included infrequently occurring species and a greater variety of habitats than sampled with microplot sampling.

Furthermore, the overall influence of proximity to the forest edge and stand age on the bryophyte community may have been underestimated in the edge and stand age studies. This underestimation is likely to have resulted from the multiplicity of edge effects that occur when anthropogenic edges are induced into the coastal temperate rainforest (Voller 1998). First of all, in high latitude areas like British Columbia, microclimatic variables have the greatest gradient intensity across southwest-facing edges and the weakest across north-facing edges (Chen et al. 1995). The edges sampled in the edge chapter ranged from south-facing to east-facing edges. The intensity of many microclimatic changes experienced across edges with these orientations is likely to be intermediate from those experienced at either north or southwest facing edges. In contrast, the three smallest remnant patches sampled in the patch size study (Chapter 4) were only 0.58, 0.72, and 1.80 ha in size. If the indirect influence of the edge (i.e., altered microclimate) is assumed to extend at least 45 m into the forest patch, even the center of the smallest forest patches sampled in the patch size study would have been susceptible to the altered microclimate found at all sides of the patch, including the south-western edge. Thus it is not unreasonable to expect that species loss in the center of very small patches would be greater than that experienced in the edge of larger remnant patches. Furthermore, the loss of species in the edge habitats sampled may have been mitigated by the dispersal of old-growth species from the adjacent interior old-growth stands (Matlack 1994a). Again due to the size, the three smallest patches examined in the patch size study were unlikely to contain a substantial core interior that could act as a source of old-growth associated species.

The creation of an induced edge in coastal temperate forests not only exposes the edge of old-growth remnant forest to environmental conditions found in the clearing (Chen et al. 1995),

but conditions in the clearing adjacent to the old-growth forest are modified by proximity to the old-growth forest (Murcia 1995). As the younger-aged forest plots were originally sampled as part of a pilot study to determine the influence of old-growth remnant patches on harvested areas (Baldwin 2000, Perry et al. 2002), most immature and regeneration plots were located immediately adjacent to an old-growth forest patch. Microclimatic conditions in this “harvest area edge” may have been less severe than those experienced further out into the harvested area and species loss mitigated. Moreover, the physical proximity of the younger-aged forest plots to an old-growth forest patch may have also allowed old-growth associated species to migrate into the younger-aged forest plots. In fact, preliminary analysis from the pilot study (not presented in this dissertation) indicated that overall bryophyte species richness in immature forests was higher immediately adjacent to the old-growth patch edge than further out into the clearcut (Baldwin 2000, Perry et al. 2002).

Based on the abundance of clearing affiliated species in both edge habitats and younger-aged forests, I originally expected that the richness of these species would increase with decreasing patch size. This prediction was not supported by the patch size study, which found no association (positive or negative) between clearing affiliated groups and patch size. However, if the presence of clearing affiliated groups, especially colonists, is dictated by wind disturbance that creates tip-up mounds and exposed mineral soil (Jonsson and Esseen 1990, den Ouden and Alaback 1996), the results of the edge study and previous research of windthrow across forest edges (Huggard et al. 1999) indicate that this “direct” disturbance might not have penetrated to the center of even the smallest forest patches. Moreover, clearing-affiliated species were encountered much more frequently in whole-plot sampling which not only increased the total area surveyed for bryophytes but also included infrequently occurring substrates such as tip-up mounds.

Therefore, the apparently contradictory results of increased clearing affiliated species richness in younger-aged forest and edge habitats without a concurrent invasion of clearing affiliated species into small forest patches may have resulted from the sampling methods used to sample small forest patches. First, bryophytes were sampled at the center of the forest patches where increased wind disturbance was less likely to occur and second, bryophytes were sampled using microplots placed on discrete substrates (forest floor, downed logs, and tree bases)—a method less likely to detect the presence of clearing affiliated species than whole-plot sampling.

The similarity of the bryophyte community response in edge and younger-aged forests represents an important synthesis from this thesis. Conclusions derived from observational studies are strengthened when associations are consistent over many sites or across populations expected to respond in a similar fashion (Diamond 1986). The response of old-growth associated bryophytes was the same (i.e., diminished performance) in edge habitats and younger-aged forests, while clearing affiliated bryophytes displayed the same response (i.e., increased richness) in both types of disturbed habitats. It is important to note, however, that there is often a time lag in organisms' response to environmental perturbations (Davis 1984, Wiens 1984), and it is unclear whether the decreased performance of old-growth associated bryophytes in disturbed habitats is the extent of the response or merely an intermediate stage before species loss.

Scale has become an increasingly important issue in fragmentation research. Not only may different processes be invoked to account for bryophyte patterns at different scales (Haila 1990, Lord and Norton 1990), but the perceived persistence or stability of a community is often dependent upon the scale of analysis (Fiedler et al. 1997). Rahel (1990) argued that most published studies fail to examine persistence across several scales and "thus make implicit or explicit claims about assemblage stability that may be appropriate at only certain analytical scales." If community stability is assessed through the maintenance of old-growth associated

species (referred to as resistance by Halpern (1988)), then the bryophyte community in both edge and younger-aged forests sampled at a coarse scale (i.e., whole-plot estimates) appears relatively stable (i.e., few species were lost). It is important to note that even at the coarse scale, the richness of liverworts is depressed in immature forests and self-thinning forests may represent a bottleneck for the maintenance of liverworts in managed landscapes.

With fine-scale sampling, old-growth associated species displayed a lower abundance in both edge habitats and younger-aged forests. As stated in the stand age study (Chapter 3), the loss of forest age classes where species achieve their maximum abundance could reduce the population viability of these species (Raphael 1991). Furthermore, decreased bryophyte cover, as well as the increased patchiness in the bryophyte mat, in edge habitats and younger-aged forests may limit the role that bryophytes play in moisture and nutrient retention (Glime 2001).

Large-scale clear-cutting is a disturbance that differs in spatial extent and intensity from the historical disturbances of the coastal temperate rainforests of British Columbia (Lertzman et al. 1996, Lertzman et al. 2002). Such an altered disturbance regime not only impacts harvested areas but also has secondary impacts on remaining old-growth patches through the introduction of artificial edges and the isolation of old-growth remnants. Haila (2002) has cogently argued that fragmentation is a landscape-level perturbation that is best viewed as overall habitat degradation rather than as an opportunity to apply the tenets of island biogeographical theory. The results of this study have demonstrated that bryophyte abundance is reduced in matrix habitats surrounding old-growth remnants (edge habitats and younger-age forests) and that the richness of old-growth associated bryophytes decreases with remnant patch size. Further questions, however, remain to be addressed. The decline in bryophyte abundance in matrix habitats raises the question of bryophyte reproductive viability in these habitats. With the exception of a few weedy mosses, little is known about population biology of most bryophyte

species (Söderström and Herben 1997). Several studies have shown that bryophytes can grow and survive in habitats where they cannot sexually reproduce (McQueen 1985, Söderström 1993). It is, therefore, unclear whether old-growth associated species in edge habitats and younger-aged forests will act as source or sink populations (*sensu* Pulliam 1988).

The effective management of bryophyte diversity is unlikely to occur at a patch scale—rather, whole landscapes should be the focus of management. A critical question is what percentage of habitat loss results in diminished bryophyte richness. Recent studies (Vellend 2003) have shown that the amount of original habitat remaining on the landscape can strongly influence the recovery of herbaceous plant diversity in post-agricultural forests. McGarigal and Cushman (2002) argue that the effects of fragmentation can be best understood through analyses of demographic responses across different landscapes that vary in terms of both original habitat remaining and the amount of fragmentation (division) of that habitat. The northeast side of Vancouver Island with its highly fragmented forests may provide an ideal landscape in which to explore these questions.

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Appendix A

Bryophyte species encountered during sampling listed by frequency of occurrence in edge and interior plots at the nine forest sites sampled (numbers of site occurrences shown for each species within each sampling zone: interior and edge, max=9; clearcut, max = 8). Abbreviations denote taxonomic and functional groups: M = moss, L = liverwort, TT = tall turf, ST = short turf, OT = open turf, RM = rough mat, SM = smooth mat, PE = pendent, SPH = sphagnoid, TH = thread, TM = thallose mat, WE = weft, P = perennial stayer, L = long-lived shuttle, S = short-lived shuttle, C = colonist. Functional group classification as in Table 1.1.

| | Taxonomic group | Sampling zone (No. sites) | | | Growth Form | Substrate Type | Canopy preference | Life-history strategy |
|--|-----------------|------------------------------|------|----------|-------------|----------------|-------------------|-----------------------|
| | | Interior | Edge | Clearcut | | | | |
| Edge and interior species | | | | | | | | |
| <i>Antitrichia curtipendula</i> | M | 9 | 9 | 6 | PE | epiphytic | generalist | L |
| <i>Bazzania denudata</i> | L | 8 | 5 | 5 | SM | bark | closed | P |
| <i>Blepharostoma trichophyllum</i> | L | 9 | 7 | 5 | TH | bark | closed | P |
| <i>Calypogeia muelleriana</i> | L | 9 | 7 | 6 | SM | log | closed | P |
| <i>Cephalozia lunulifolia</i> | L | 9 | 9 | 7 | TH | log | closed | P |
| <i>Cephaloziella divaricata</i> | L | 1 | 8 | 7 | TH | generalist | closed | C |
| <i>Chiloscyphus polyanthos</i> | L | 2 | 1 | 0 | SM | log | closed | P |
| <i>Claopodium bolanderi</i> | M | 2 | 3 | 1 | RM | rock | closed | P |
| <i>Dicranum fuscescens</i> | M | 9 | 9 | 7 | ST | bark | generalist | C |
| <i>Diplophyllum albicans</i> | L | 5 | 6 | 3 | RM | rock | closed | P |
| <i>Douinia ovata</i> | L | 6 | 7 | 5 | SM | generalist | open | P |
| <i>Eurhynchium oreganum</i> | M | 7 | 8 | 6 | WE | litter | generalist | P |
| <i>Eurhynchium praelongum</i> | M | 3 | 4 | 5 | WE | litter | generalist | P |
| <i>Frullania tamarisci</i> subsp. <i>nisquallensis</i> | L | 9 | 9 | 7 | SM | epiphytic | open | L |
| <i>Heterocladium macounii</i> | M | 1 | 1 | 0 | RM | rock | closed | P |
| <i>Hookeria lucens</i> | M | 2 | 1 | 0 | SM | humus | closed | P |
| <i>Hylocomium splendens</i> | M | 9 | 9 | 7 | WE | litter | closed | P |
| <i>Hypnum circinale</i> | M | 9 | 9 | 7 | SM | bark | generalist | P |
| <i>Isoetecium myosuroides</i> | M | 9 | 9 | 7 | WE | generalist | generalist | P |
| <i>Lepidozia reptans</i> | L | 9 | 9 | 7 | SM | bark | closed | P |
| <i>Leucolepis acanthoneuron</i> | M | 1 | 1 | 1 | DE | humus | closed | S |
| <i>Lophocolea heterophylla</i> | L | 2 | 2 | 4 | TH | log | closed | C |
| <i>Lophozia longifolia</i> | L | 4 | 7 | 5 | SM | log | closed | C |
| <i>Lophozia incisa</i> | L | 8 | 5 | 4 | SM | log | closed | C |
| <i>Mnium spinulosum</i> | M | 3 | 3 | 0 | ST | soil | closed | S |
| <i>Neckera douglasii</i> | M | 1 | 3 | 2 | PE | epiphytic | generalist | S |
| <i>Plagiochila asplenoides</i> | L | 6 | 5 | 2 | ST | generalist | closed | P |
| <i>Plagiothecium undulatum</i> | M | 7 | 5 | 6 | RM | litter | closed | P |
| <i>Porella navicularis</i> | L | 4 | 7 | 7 | PE | epiphytic | open | L |
| <i>Porotrichum bigelovii</i> | M | 1 | 1 | 0 | PE | rock | closed | P |
| <i>Pseudotaxiphyllum elegans</i> | M | 7 | 5 | 4 | SM | soil | closed | P |
| <i>Ptilidium californicum</i> | L | 7 | 9 | 6 | SM | bark | closed | S |
| <i>Radula bolanderi</i> | L | 3 | 4 | 6 | SM | bark | generalist | L |
| <i>Rhizomnium glabrescens</i> | M | 9 | 5 | 7 | ST | log | closed | S |
| <i>Rhytidiadelphus loreus</i> | M | 9 | 9 | 7 | WE | generalist | closed | P |
| <i>Rhytidiopsis robusta</i> | M | 3 | 5 | 2 | WE | litter | closed | P |

| | | | | | | | | |
|---|---|---|---|---|-----|------------|------------|---|
| <i>Riccardia latifrons</i> | L | 8 | 4 | 5 | TM | log | closed | L |
| <i>Scapania bolanderi</i> | L | 9 | 9 | 7 | RM | bark | closed | P |
| <i>Scapania umbrosa</i> | L | 6 | 7 | 3 | SM | log | open | P |
| <i>Sphagnum rubiginosum</i> | M | 1 | 1 | 1 | SPH | litter | open | L |
| <i>Ulota megalospora</i> | M | 5 | 5 | 3 | CU | epiphytic | closed | S |
| <u>Interior species</u> | | | | | | | | |
| <i>Apometzgeria pubescens</i> | L | 1 | 0 | 0 | TM | rock | open | C |
| <i>Cephalozia bicuspidata</i> | L | 2 | 0 | 0 | TH | log | closed | C |
| <i>Eurhynchium pulchellum</i> var. <i>barnesii</i> | M | 1 | 0 | 0 | WE | epiphytic | closed | P |
| <i>Heterocladium procurrens</i> | M | 2 | 0 | 0 | RM | rock | closed | P |
| <i>Jungermannia leiantha</i> | L | 1 | 0 | 0 | SM | log | open | C |
| <i>Lophocolea bidentata</i> | L | 6 | 0 | 2 | TH | generalist | closed | C |
| <i>Metzgeria conjugata</i> | L | 1 | 0 | 0 | TM | rock | generalist | L |
| <i>Pellia neesiana</i> | L | 1 | 0 | 0 | TM | humus | closed | L |
| <i>Plagiomnium insigne</i> | M | 1 | 0 | 2 | TT | humus | closed | S |
| <i>Plagiothecium laetum</i> | M | 3 | 0 | 3 | SM | bark | closed | P |
| <u>Edge species</u> | | | | | | | | |
| <i>Atrichum selwynii</i> | M | 0 | 1 | 1 | ST | soil | open | C |
| <i>Aulacomnium androgynum</i> | M | 0 | 7 | 2 | ST | soil | open | C |
| <i>Bryum capillare</i> | M | 0 | 1 | 2 | OT | rock | open | C |
| <i>Buxbaumia piperi</i> | M | 0 | 1 | 1 | SM | log | closed | P |
| <i>Calypogeia fissa</i> | L | 0 | 1 | 1 | TH | litter | closed | P |
| <i>Ceratodon purpureus</i> | M | 0 | 4 | 6 | OT | soil | open | C |
| <i>Dicranella heteromalla</i> | M | 0 | 2 | 4 | OT | soil | open | C |
| <i>Dicranoweisia crispula</i> | M | 0 | 3 | 0 | OT | soil | open | C |
| <i>Dicranum scoparium</i> | M | 0 | 3 | 4 | ST | soil | generalist | C |
| <i>Dicranum tauricum</i> | M | 0 | 2 | 5 | OT | log | generalist | C |
| <i>Didymodon vinealis</i> | M | 0 | 1 | 0 | OT | rock | open | C |
| <i>Diplophyllum obtusifolium</i> | L | 0 | 3 | 2 | SM | soil | open | C |
| <i>Ditrichum heteromallum</i> | M | 0 | 1 | 0 | OT | soil | open | C |
| <i>Ditrichum montanum</i> | M | 0 | 1 | 0 | OT | soil | generalist | C |
| <i>Fissidens bryoides</i> | M | 0 | 2 | 0 | OT | soil | generalist | C |
| <i>Homalothecium megaptilum</i> | M | 0 | 1 | 0 | WE | litter | closed | P |
| <i>Hypnum subimponens</i> | M | 0 | 1 | 0 | SM | rock | open | P |
| <i>Mnium thomsonii</i> | M | 0 | 1 | 0 | OT | rock | closed | L |
| <i>Philonotis fontana</i> | M | 0 | 1 | 1 | ST | rock | open | S |
| <i>Plagiothecium cavifolium</i> | M | 0 | 3 | 1 | SM | humus | closed | P |
| <i>Pogonatum contortum</i> | M | 0 | 3 | 3 | TT | soil | open | C |
| <i>Pohlia nutans</i> | M | 0 | 5 | 7 | OT | soil | generalist | S |
| <i>Polytrichastrum alpinum</i> | M | 0 | 3 | 0 | TT | soil | closed | C |
| <i>Polytrichum juniperinum</i> | M | 0 | 8 | 7 | TT | soil | open | C |
| <i>Racomitrium heterostichum</i> | M | 0 | 4 | 2 | RM | rock | open | P |
| <i>Riccardia multifida</i> | L | 0 | 1 | 0 | TM | log | closed | P |
| <i>Scapania americana</i> | L | 0 | 1 | 0 | RM | rock | closed | P |
| <i>Schistidium trichodon</i> | M | 0 | 1 | 1 | RM | rock | open | P |
| <i>Trichostomum cylindricum</i> | M | 0 | 1 | 0 | OT | soil | closed | C |

Appendix B

Liverwort and moss species encountered during sampling in stand age study listed by occurrence in stand age and forest type. Numbers of site occurrences shown for each species in Sayward (S; old-growth max=8, immature max=6, regeneration max=6) and Nimpkish (N; old-growth max=9, immature max=6, regeneration max=7) forests by stand age. Abbreviations denote functional groups: TT = tall turf, ST= short turf, OT = open turf, RM = rough mat, SM = smooth mat, PE = pendent, SPH = sphagnoid, TH = thread, TM = thallose mat, WE = weft, C=colonist, L=long-lived shuttle, S=short-lived shuttle and P=perennial stayer. Functional group classification as in Table 1.1.

| Species | Stand Age | | | | | | Canopy preference | Growth form | Life-history strategy |
|---|------------|---|----------|---|--------------|---|-------------------|-------------|-----------------------|
| | Old-growth | | Immature | | Regeneration | | | | |
| | S | N | S | N | S | N | | | |
| Liverworts | | | | | | | | | |
| <i>Apometzgeria pubescens</i> | 1 | 1 | 0 | 0 | 0 | 0 | open | TM | C |
| <i>Bazzania denudata</i> | 7 | 8 | 6 | 1 | 6 | 5 | closed | SM | P |
| <i>Bazzania tricrenata</i> | 0 | 0 | 0 | 0 | 1 | 0 | closed | SM | P |
| <i>Blepharostoma trichophyllum</i> | 8 | 9 | 5 | 4 | 5 | 5 | closed | TH | P |
| <i>Calypogeia fissa</i> | 4 | 0 | 1 | 0 | 0 | 1 | closed | TH | P |
| <i>Calypogeia muelleriana</i> | 8 | 9 | 6 | 6 | 6 | 6 | closed | SM | P |
| <i>Cephalozia bicuspidata</i> | 2 | 2 | 1 | 0 | 2 | 0 | closed | TH | C |
| <i>Cephalozia lunulifolia</i> | 8 | 9 | 6 | 6 | 6 | 7 | closed | TH | P |
| <i>Cephaloziella divaricata</i> | 0 | 1 | 0 | 2 | 5 | 7 | closed | TH | C |
| <i>Cephaloziella spp.</i> | 0 | 0 | 0 | 0 | 1 | 0 | open | TH | C |
| <i>Chiloscyphus polyanthos</i> | 2 | 2 | 2 | 1 | 1 | 0 | closed | SM | P |
| <i>Conocephalum conicum</i> | 1 | 0 | 0 | 0 | 1 | 0 | closed | TM | L |
| <i>Diplophyllum albicans</i> | 6 | 5 | 4 | 2 | 5 | 3 | closed | RM | P |
| <i>Diplophyllum obtusifolium</i> | 0 | 0 | 0 | 1 | 0 | 2 | open | SM | C |
| <i>Douinia ovata</i> | 5 | 6 | 3 | 4 | 3 | 5 | open | SM | P |
| <i>Frullania californica</i> | 4 | 0 | 2 | 0 | 3 | 0 | closed | SM | L |
| <i>Frullania franciscana</i> | 0 | 0 | 1 | 0 | 0 | 0 | generalist | SM | L |
| <i>Frullania tamarisci subsp. nisquallensis</i> | 8 | 9 | 6 | 6 | 6 | 7 | open | SM | L |
| <i>Geocalyx graveolens</i> | 1 | 0 | 0 | 0 | 0 | 0 | closed | TH | P |
| <i>Gyrothyra underwoodiana</i> | 0 | 0 | 0 | 0 | 0 | 2 | open | SM | P |
| <i>Jungermannia confertissima</i> | 0 | 0 | 1 | 0 | 0 | 0 | open | SM | P |
| <i>Jungermannia leiantha</i> | 6 | 1 | 4 | 0 | 2 | 0 | open | SM | C |
| <i>Lepidozia reptans</i> | 8 | 9 | 6 | 6 | 5 | 7 | closed | SM | P |
| <i>Lophocolea bidentata</i> | 3 | 6 | 4 | 4 | 2 | 2 | closed | TH | C |
| <i>Lophocolea heterophylla</i> | 5 | 2 | 5 | 3 | 2 | 4 | closed | TH | C |
| <i>Lophozia longiflora</i> | 1 | 4 | 2 | 4 | 6 | 5 | closed | SM | C |
| <i>Lophozia incisa</i> | 6 | 8 | 4 | 2 | 6 | 4 | closed | SM | C |
| <i>Marsupella emarginata</i> | 0 | 0 | 0 | 0 | 2 | 0 | generalist | SM | P |
| <i>Metzgeria conjugata</i> | 2 | 1 | 0 | 0 | 0 | 0 | generalist | TM | L |
| <i>Pellia neesiana</i> | 0 | 1 | 1 | 0 | 2 | 0 | closed | TM | L |
| <i>Plagiochila asplenioides</i> | 7 | 6 | 5 | 1 | 4 | 2 | closed | ST | P |
| <i>Porella navicularis</i> | 7 | 4 | 1 | 3 | 2 | 7 | open | PE | L |
| <i>Ptilidium californicum</i> | 6 | 7 | 5 | 6 | 5 | 6 | closed | SM | L |
| <i>Ptilidium pulcherrimum</i> | 0 | 0 | 0 | 1 | 0 | 1 | closed | SM | L |

| | | | | | | | | | |
|---|---|---|---|---|---|---|------------|----|---|
| <i>Radula bolanderi</i> | 6 | 3 | 4 | 4 | 4 | 6 | indis | SM | L |
| <i>Riccardia latifrons</i> | 6 | 8 | 4 | 6 | 4 | 5 | closed | TM | L |
| <i>Riccardia multifida</i> | 2 | 0 | 0 | 0 | 1 | 0 | closed | TM | P |
| <i>Riccardia palmata</i> | 0 | 0 | 0 | 0 | 1 | 0 | closed | TM | P |
| <i>Scapania americana</i> | 0 | 0 | 0 | 0 | 2 | 0 | closed | RM | P |
| <i>Scapania bolanderi</i> | 8 | 9 | 6 | 6 | 6 | 7 | closed | RM | P |
| <i>Scapania scandica</i> | 1 | 0 | 0 | 0 | 2 | 0 | indis | RM | P |
| <i>Scapania umbrosa</i> | 7 | 7 | 5 | 3 | 6 | 3 | open | SM | P |
| <i>Scapania undulata</i> | 0 | 0 | 0 | 0 | 1 | 0 | open | RM | P |
| Mosses | | | | | | | | | |
| <i>Antitrichia curtipendula</i> | 7 | 9 | 3 | 2 | 4 | 6 | generalist | PE | L |
| <i>Atrichum selwynii</i> | 0 | 0 | 0 | 0 | 0 | 1 | open | ST | C |
| <i>Atrichum undulatum</i> | 0 | 0 | 0 | 0 | 0 | 1 | open | ST | C |
| <i>Aulacomnium androgynum</i> | 0 | 0 | 2 | 4 | 5 | 2 | open | ST | C |
| <i>Bartramia pomiformis</i> | 0 | 0 | 0 | 0 | 1 | 0 | closed | ST | L |
| <i>Bryum capillare</i> | 0 | 0 | 0 | 0 | 0 | 2 | open | OT | C |
| <i>Bryum creberrimum</i> | 0 | 0 | 0 | 0 | 0 | 1 | open | OT | C |
| <i>Bryum miniatum</i> | 0 | 0 | 0 | 0 | 0 | 1 | open | ST | P |
| <i>Bryum pseudotriquetrum</i> | 0 | 0 | 0 | 0 | 3 | 0 | open | OT | C |
| <i>Buxbaumia piperi</i> | 0 | 1 | 0 | 0 | 1 | 1 | closed | SM | P |
| <i>Ceratodon purpureus</i> | 0 | 0 | 0 | 0 | 1 | 6 | open | OT | C |
| <i>Claopodium bolanderi</i> | 2 | 2 | 2 | 0 | 1 | 1 | closed | RM | P |
| <i>Claopodium crispifolium</i> | 1 | 0 | 0 | 0 | 0 | 1 | closed | RM | P |
| <i>Cynodontium jenneri</i> | 0 | 0 | 0 | 0 | 3 | 1 | open | OT | S |
| <i>Dicranella heteromalla</i> | 0 | 0 | 1 | 0 | 3 | 4 | open | OT | C |
| <i>Dicranum fuscescens</i> | 8 | 9 | 6 | 6 | 6 | 7 | generalist | ST | C |
| <i>Dicranum scoparium</i> | 1 | 0 | 2 | 1 | 3 | 4 | generalist | ST | P |
| <i>Dicranum tauricum</i> | 0 | 0 | 0 | 0 | 0 | 5 | generalist | OT | C |
| <i>Ditrichum montanum</i> | 0 | 0 | 0 | 1 | 2 | 0 | generalist | OT | C |
| <i>Dryptodon patens</i> | 0 | 0 | 0 | 1 | 0 | 0 | open | RM | P |
| <i>Eurhynchium oreganum</i> | 4 | 7 | 6 | 6 | 5 | 6 | generalist | WE | P |
| <i>Eurhynchium praelongum</i> | 3 | 3 | 4 | 5 | 5 | 5 | generalist | WE | P |
| <i>Eurhynchium pulchellum</i> var. <i>barnesii</i> | 2 | 1 | 1 | 0 | 0 | 0 | closed | WE | P |
| <i>Heterocladium macounii</i> | 1 | 1 | 1 | 0 | 2 | 0 | closed | RM | P |
| <i>Heterocladium procurrens</i> | 1 | 2 | 0 | 1 | 1 | 0 | closed | RM | P |
| <i>Homalothecium fulgescens</i> | 0 | 0 | 0 | 0 | 1 | 0 | generalist | RM | P |
| <i>Homalothecium nuttallii</i> | 0 | 0 | 0 | 0 | 0 | 1 | generalist | RM | P |
| <i>Hookeria lucens</i> | 6 | 2 | 2 | 0 | 2 | 0 | closed | SM | P |
| <i>Hylocomium splendens</i> | 7 | 9 | 6 | 6 | 6 | 7 | closed | WE | P |
| <i>Hypnum circinale</i> | 8 | 9 | 6 | 6 | 6 | 7 | generalist | SM | P |
| <i>Hypnum dieckii</i> | 0 | 0 | 0 | 0 | 2 | 0 | closed | SM | L |
| <i>Hypnum subimponens</i> | 0 | 0 | 0 | 0 | 1 | 0 | open | SM | P |
| <i>Isothecium myosuroides</i> | 8 | 9 | 6 | 6 | 5 | 7 | indis | WE | P |
| <i>Leucolepis acanthoneuron</i> | 2 | 1 | 2 | 0 | 2 | 1 | closed | DE | S |
| <i>Metaneckera menziesii</i> | 1 | 0 | 0 | 0 | 0 | 0 | generalist | PE | L |
| <i>Mnium spinulosum</i> | 4 | 3 | 5 | 3 | 2 | 0 | closed | ST | S |
| <i>Neckera douglasii</i> | 2 | 1 | 1 | 1 | 0 | 2 | generalist | PE | S |
| <i>Oligotrichum aligerum</i> | 0 | 0 | 0 | 0 | 0 | 1 | open | ST | C |
| <i>Orthotrichum lyellii</i> | 0 | 0 | 0 | 0 | 0 | 1 | generalist | RM | S |

| | | | | | | | | | |
|-----------------------------------|---|---|---|---|---|---|------------|-----|---|
| <i>Othotricum consimile</i> | 1 | 0 | 0 | 0 | 2 | 0 | open | SM | P |
| <i>Philonotis fontana</i> | 0 | 0 | 0 | 0 | 0 | 1 | open | ST | S |
| <i>Plagiomnium insigne</i> | 2 | 1 | 3 | 1 | 1 | 2 | closed | TT | S |
| <i>Plagiothecium cavifolium</i> | 0 | 0 | 3 | 0 | 1 | 1 | closed | SM | P |
| <i>Plagiothecium denticulatum</i> | 0 | 0 | 1 | 0 | 1 | 0 | closed | SM | P |
| <i>Plagiothecium laetum</i> | 6 | 3 | 6 | 3 | 3 | 3 | closed | SM | P |
| <i>Plagiothecium undulatum</i> | 7 | 7 | 6 | 5 | 6 | 6 | closed | RM | P |
| <i>Pogonatum contortum</i> | 4 | 0 | 2 | 0 | 4 | 3 | open | TT | C |
| <i>Pohlia nutans</i> | 1 | 0 | 2 | 3 | 6 | 7 | generalist | OT | S |
| <i>Polytrichastrum alpinum</i> | 1 | 0 | 3 | 0 | 6 | 0 | closed | TT | C |
| <i>Polytrichum formosum</i> | 1 | 0 | 0 | 0 | 4 | 2 | closed | TT | C |
| <i>Polytrichum juniperinum</i> | 0 | 0 | 2 | 6 | 5 | 7 | open | TT | C |
| <i>Porotrichum bigelovii</i> | 0 | 1 | 0 | 0 | 0 | 0 | closed | PE | P |
| <i>Pseudotaxiphyllum elegans</i> | 7 | 7 | 4 | 5 | 6 | 4 | closed | SM | P |
| <i>Racomitrium aquaticum</i> | 2 | 0 | 1 | 0 | 1 | 0 | closed | RM | P |
| <i>Racomitrium canescens</i> | 0 | 0 | 0 | 1 | 3 | 0 | open | RM | P |
| <i>Racomitrium heterostichum</i> | 1 | 0 | 0 | 3 | 4 | 2 | open | RM | P |
| <i>Rhizomnium glabrescens</i> | 7 | 9 | 5 | 6 | 6 | 7 | closed | ST | S |
| <i>Rhytidiadelphus loreus</i> | 8 | 9 | 6 | 6 | 6 | 7 | closed | WE | P |
| <i>Rhytidiopsis robusta</i> | 3 | 3 | 2 | 4 | 2 | 2 | closed | WE | P |
| <i>Schistidium trichodon</i> | 0 | 0 | 0 | 0 | 0 | 1 | open | RM | P |
| <i>Sphagnum rubiginosum</i> | 0 | 1 | 0 | 0 | 2 | 1 | open | SPH | L |
| <i>Tetraplodon mnioides</i> | 0 | 0 | 0 | 0 | 0 | 1 | indis | TT | C |
| <i>Thamnobryum neckeroides</i> | 1 | 0 | 0 | 0 | 0 | 1 | closed | DE | P |
| <i>Tortella tortuosa</i> | 0 | 0 | 0 | 1 | 0 | 0 | closed | OT | C |
| <i>Ulota megalospora</i> | 3 | 5 | 1 | 3 | 4 | 3 | closed | CU | S |