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A bryophyte perspective on forest harvest:
The effects of logging on above- and below-ground bryophyte communities in coastal temperate rainforests

by

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Abstract

This thesis examines patterns in bryophyte species richness and composition on the forest floor and in the soil diaspore bank of temperate rainforest stands which varied in time post-harvest. Quantitative data (abundance) was assessed in quadrats (25x25cm) on soil, decaying logs, and tree bases within sites (20x30m). Non-quantitative data (occurrence) was assessed throughout sites. Analyses of variance and ordination analyses were used to examine species richness and composition, respectively.

Above-ground, richness varied significantly with substrate but not stand age. Soils were the most speciose substrates, due to heterogeneity in young stands; logs had higher richness in older stands. Canopy cover significantly affected species composition, with a trend in dominant life strategy from colonists to perennials with canopy closure. Below-ground, richness varied significantly with depth but not with stand age. Diaspore bank richness and composition differed from the above-ground flora; colonists dominated the diaspore bank and perennials thrived above-ground.

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Chapter 1: Introduction

Bryophytes in temperate rainforests

Temperate rainforests comprise only approximately 2.4% of global forested area but can be found scattered worldwide (DellaSala et al. 2011a). Some notable temperate rainforests occur in North America and Japan in the northern hemisphere, and Chile and New Zealand in the southern hemisphere. The Pacific Northwest temperate rainforest, which extends from southeastern Alaska to northern California covers approximately 25,000,000 ha and represents over one third of the world's total temperate rainforest (DellaSala et al. 2011b).

Coastal temperate rainforests are unique among forest ecosystems. Although deciduous tree species make up a significant portion of interior forests, conifers dominate coastal rainforests, as they photosynthesize year-round, taking advantage of moisture and mild temperatures throughout the year (Alaback 1996). Coniferous forest canopies can capture 90% of incoming light, and this constant deep shade limits understory diversity (Alaback and Pojar 1997). These forests are also unique in that stand-replacing disturbances, such as fire, are rare (Arsenault 1995). Instead, the majority of temperate rainforest disturbances affect only a few trees at a time, leaving much of the forest stand intact. Such localized disturbances include windthrow or insect infections (MacKinnon 2003).

The increased structural complexity that results as the forest regenerates from repeated small-scale disturbances is beneficial to overall diversity in general (Connell 1978) and to understory plants in particular (Kimmerer 2005). Bryophytes, consisting of mosses (Bryophyta), liverworts (Marchantiophyta), and hornworts (Anthocerophyta) thrive in this type of heterogeneous environment (Pharo and Lindenmayer 2009). In the coastal western hemlock zone of British Columbia, mosses and liverworts are the most diverse and abundant understory vegetation (Newmaster et al. 2003). Regenerating forest patches provide conditions for a wide variety of bryophyte species to persist. Shade-intolerant species can thrive in forest openings, whereas shade-dependent species exist under closed canopies (Franklin et al. 2002). When a few trees fall in a stand, they

provide new microhabitats including decaying wood and overturned soil, which increases the amount of substrate available for bryophytes to colonize (den Ouden and Alaback 1996; Kimmerer 2005; Turner and Pharo 2005). Additionally, decaying wood provides available substrates above the forest floor, which is beneficial in coastal forests where the forest floor accumulates a thick layer of debris that smothers bryophytes and prevents germination of spores (Richards 1954; Stevens 1997; Fenton and Frego 2005).

Despite their small size, bryophytes are a unique and diverse group of land plants which are fundamentally different from vascular plants. With a dominant gametophytic generation and a lack of true roots and specialized conductive tissue, bryophytes respond to their environments in different ways and are able to fill different niches than vascular plants (Proctor et al. 2007). Therefore, bryophytes are an essential part of forest ecosystems by contributing to overall biomass and nutrient cycling and facilitating the establishment and persistence of other organisms. To be effective in maintaining ecosystem functions, forest management strategies must consider impacts on bryophytes, thus preserving their critical ecological roles.

Forest floor and epiphytic bryophytes contribute substantially to forest biomass, which increases with later successional stages (Binkley and Graham 1981; Nadkarni 1984; Harmon 1989). Although bryophyte biomass in tropical rainforests exceeds that of other forest types, Nadkarni (1984) found that epiphytic bryophyte biomass in temperate rainforest ecosystems can occasionally reach comparable levels, with values of approximately 6800kg/ha. Both forest floor and epiphytic bryophytes help retain moisture and are involved in nutrient cycling throughout the ecosystem (Weber and van Cleve 1984; Coxson 1991; deLucia et al. 2003); in particular, epiphytic bryophytes take up water and slowly release it, thereby increasing the water storage capacity of the forest (Köhler et al. 2007).

Forest floor bryophytes are important in maintaining soil stability and provide substrates for vascular plant seed germination and development (Hart and Shankman 2005). Furthermore, with lichens and microbes, bryophytes are a

component of biological soil crusts, which form at the interface between the soil and the atmosphere. These crusts bind the soil, protecting it from wind and water erosion, and enhancing water retention and infiltration (Eldridge 1998; Delach and Kimmerer 2002; Bowker 2007). Poikilohydry, the ability to withstand desiccation by drying out and rehydrating when moisture returns, is a feature that bryophytes share with fungi and lichens but is absent from most vascular plants (Alpert 2000; Proctor and Tuba 2002; Proctor et al. 2007). Such a trait enables bryophytes to tolerate the harsh conditions that prevail during early succession, and thus, bryophytes, lichens, and fungi are often the first colonists of recently disturbed ground (Rees and Juday 2002; Bowker 2007).

Bryophytes also facilitate the establishment of a diverse community of other organisms. In particular, nutrient-rich leachates from moss gametophytes facilitate the establishment of mycorrhizal fungi, thus promoting mycorrhizal associations with vascular plants (Davey and Currah 2006). Dead mosses also support saprophytic fungi, thus assisting in nutrient cycling in the ecosystem (Davey and Currah 2006). In addition to these ectophytic relationships between mosses and fungi, liverworts also host endophytic fungi, where the fungi typically inhabit rhizoids (Davis et al. 2003). Although the interaction between liverworts and fungi are complex, Carafa et al. (2003) demonstrate that a primitive mycorrhizal fungus inhabiting a liverwort could be an evolutionary precursor to mycorrhizal relationships with vascular plants. Additionally, liverworts and vascular plants potentially serve as alternate hosts for mycorrhizal fungi, thus linking nutrient cycling in the ecosystem (Duckett and Read 1995; Davis et al. 2003). Furthermore, bryophytes provide habitats for cyanobacteria and invertebrates, thus promoting nitrogen fixation by cyanobacteria (During and van Tooren 1990) and facilitating the establishment of invertebrate communities and enhancing nutrient cycling through these communities (Andrew et al. 2003; Korsu 2004; Meyer et al. 2011).

Factors influencing bryophyte diversity and composition

Bryophytes are influenced by local microhabitat characteristics, which vary on a scale of millimetres to centimetres (Vitt and Belland 1997). As a result, bryophyte species composition often varies on a similar scale. Species distribution is determined by the availability of suitable substrates and the ability to disperse among substrate patches (Söderström and During 2005). Because appropriate substrate conditions can be short-lived, bryophyte communities do not generally exist in equilibrium conditions, and therefore, substrate availability is a major factor in shaping these communities (Slack 1990). In contrast, competition, a key component in vascular plant community structure, plays a negligible role in bryophyte communities (Hylander 2009). In addition to the substrate itself, however, microclimate variables also shape bryophyte communities. Hylander et al. (2005) discussed the interaction between substrate and associated microclimate in affecting the persistence of bryophytes following disturbance, demonstrating how closely these characteristics are linked.

a) Substrate

Bryophytes are inextricably linked to substrates, with their occurrence governed to a large extent by substrate characteristics. Bryophytes often establish communities that are substrate-specific, such as forest floor (soil, humus), tree bases, or decaying logs (La Roi and Stringer 1976). However, in humid climates, a species that might be confined to one substrate type in drier conditions may occur on more varied substrates once the moisture limitation has been removed (Turner and Pharo 2005; Tng et al. 2009). This demonstrates the essential role of moisture availability in bryophyte species distribution. Bryophytes depend on water for successful fertilization, as their motile, biflagellate sperm rely on water to reach the egg (Paolillo 1981; Schofield 2001). In addition to moisture, substrates vary in chemical and physical properties that influence bryophyte species composition. Chemical properties include nutrient availability and pH (Vitt 1990; Gustafsson and Eriksson 1995; McGee and Kimmerer 2002). Physical properties of substrates include texture of the substrate, decay class of woody

debris, or substrate vegetation species all play a role in shaping the bryophyte community (Slack 1990; Mills and Macdonald 2005).

b) Microclimate

In addition to the chemical and physical properties of the substrate itself, microclimatic factors also influence bryophyte occurrence. Ambient moisture plays a fundamental role, as bryophytes lack roots and conducting systems (Proctor 2001) and quickly equilibrate to ambient moisture levels (Proctor et al. 2007). This has implications for bryophyte growth, as Vitt (1989) found that bryophyte colony growth is dependent on the amount of time the population remains moist.

Temperature and light are also important factors controlling bryophyte establishment and abundance (Busby et al. 1978; Stewart and Mallik 2006). Both factors affect the vapour pressure deficit of bryophytes (Skre et al. 1983). Excess light can increase leaf temperatures and cause desiccation in bryophytes (Skre et al. 1983). In a study of riparian edge effects in a boreal forest, Stewart and Mallik (2006) found that light, temperature and humidity were highly correlated, and bryophytes had species-specific responses to changes in this set of variables.

Temperate rainforest disturbances and their impacts on bryophytes

Natural disturbances in coastal rainforests facilitate bryophyte diversity and increase structural complexity; however, human-made disturbances have different effects. For nearly two centuries, logging has been a major industry in North America's coastal rainforests (Robbins 1997). British Columbia has the largest forest area of any Canadian province, with more than 50,000,000 ha, and its harvested area represents 20% of the Canadian total (Natural Resources Canada 2011). Currently, clear-cutting is widely used by many forestry companies in British Columbia (Western Red Cedar Export Association 2012). However, companies have recently increased the use of retention strategies to maintain key habitats and representative vegetation (Western Forest Products 2011).

Clear-cutting and salvage logging have substantial negative effects on bryophytes. Newmaster et al. (2003) found lower bryophyte diversity in clear-cut hemlock forests in British Columbia, relative to old-growth forests. In many forest types, clear-cutting reduces the overall stand age and the number of available age-related microhabitats, which consequently lowers cryptogam diversity (Gustafsson and Hallingbäck 1988; Andersson and Hytteborn 1991). When the clear-cut forest begins to regenerate, it is often homogenous and lacks the complexity of an old-growth forest (Kurulok and Macdonald 2007). Open patches and edges of cutblocks are subject to more extreme environmental conditions, such as high light intensity and temperature and increased substrate scouring by wind (Chen et al. 1995). In such areas, weedy colonist species (i.e., *Ceratodon purpureus* (Hedw.) Brid.), which are more desiccation-tolerant and can more easily withstand temperature and light extremes, establish themselves at the expense of endemic species (Bao 2005; Kurulok and Macdonald 2007).

Bryophytes have a variety of regeneration strategies that enable them to establish quickly following a disturbance (Jonsson and Esseen 1998). In particular, bryophytes are predominantly clonal organisms that are capable of regenerating from any vegetative cell (totipotent), enhancing their recolonization potential (Menon and Lal 1977). *In situ* recolonization from persisting individuals or germinating diaspores is a significant source of bryophytes following a disturbance, but many species also recolonize via long distance dispersal (LDD) from *ex situ* populations.

a) Spatial and temporal refugia

When faced with a large-scale disturbance, bryophytes can survive through refugia, either spatial or temporal. Bryophytes can persist through macro-environmental changes due to their close association with microhabitats (Crum 1972). Spatially, biological legacies, such as remnants of fallen trees, stumps, debris, or even concave hollows in the ground, provide shelter, available substrates, and suitable conditions to preserve bryophyte diversity even in a

fragmented landscape (Hylander et al. 2005; Lindenmayer and Noss 2006; Pharo and Lindenmayer 2009; Baldwin and Bradfield 2010).

As a temporal refugium, some bryophytes produce diaspores (i.e. specialized, resistant spores, vegetative propagules, or unspecialized plant fragments) that can exist for prolonged periods in below-ground diaspore banks (During et al. 1987). There is a trade-off between longevity of spores and dispersal potential, so not all species are represented in the diaspore bank. Species that produce numerous small spores favour LDD, whereas those that produce larger spores or specialized asexual propagules favour local population maintenance and tend to appear more frequently in the diaspore bank (During 2001).

In addition to spores, asexual propagules are essential to the life strategies of bryophytes, as many species are only known to reproduce asexually (Imura 1994). Asexual reproduction occurs by specialized propagules (i.e., gemmae, bulbils, tubers, and deciduous leaves) or unspecialized gametophytic or protonemal fragments (Laaka-Lindberg et al. 2003; Frey and Kürschner 2011). All asexual propagules and fragments can give rise to a new individual, and all may be preserved in the long-term diaspore bank (Menon and Lal 1977; Imura 1994; During 2001). Consequently, by preserving both sexual and asexual propagules, the diaspore bank provides a long-term genetic memory of species that previously existed in the area (Hock et al. 2008). Furthermore, a persistent diaspore bank incorporates propagules produced by species inhabiting a changing above-ground environment throughout successional stages (Hock et al. 2008). Thus, the *in situ* diaspore bank community has greater ecological breadth, with propagules poised to rapidly recolonize available microhabitats, once suitable conditions are attained (Jonsson 1993). This is especially advantageous in the earliest stages following a disturbance when rapid recolonization is essential for ecosystem recovery.

b) Dispersal

Bryophytes can also arrive at a newly disturbed site through spore rain from nearby forests (Pohjamo et al. 2006). Bryophyte spores tend to be small, ranging from less than 20μm to 200 μm, and are capable of long-distance transportation via air currents (van Zanten 1976; During 1979). Furthermore, bryophyte spores possess adaptations to promote survival and successful germination following dispersal, such as the ability to survive complete desiccation for long periods of time (van Zanten 1976). Despite the potential for LDD, Hutsemekers et al. (2008) observed the majority of spores dispersing within approximately 6km of the point of origin; however, extreme LDD events (trans-oceanic dispersal) have been reported, demonstrating that the small size of spores and their tolerance to desiccation and freezing contributes to viable spores traveling great distances (hundreds of kilometers) by air or ocean currents (van Zanten 1976). However, the successful germination of these dispersed spores tends to be low, due to competition or sub-optimal conditions (Hutsemekers et al. 2008; Hylander 2009). Furthermore, as forest fragmentation increases, the size of suitable substrate patches decreases with increased distance between them, so species that rely heavily on dispersal may not be able to disperse successfully across greater distances and would consequently have lower persistance (Herben and Söderström 1992).

Unanswered questions

Although bryophytes have key roles in ecosystem recovery and are a highly diverse group, they are often overlooked in forest studies (Pharo et al. 2000). When included, bryophytes are often treated as a unit, even though life strategies and niches can vary significantly among bryophyte species (During 1979; Pharo and Vitt 2000).

Additionally, although diaspore banks have received increasing attention in boreal forest ecosystems (Caners et al. 2009) or grassland ecosystems (During and ter Horst 1983; Bisang 1996; Hock et al. 2008), diaspore banks of temperate and tropical rainforests have received limited attention (but see Bisang et al. 2003;

Maciel-Silva et al. 2012). Hock et al. (2008) found that bryophyte diaspores can persist for several years in grassland ecosystems. Additionally, spores and fragments can remain viable for long periods (13-16 years, with some reports of viable spores up to 50 years) when in dry storage (Meyer 1941; Cleavitt 2002). It is uncertain how temperate rainforest variables, such as soil moisture and microorganisms impact the longevity of viable diaspores. Similarly, in the absence of large-scale natural disturbances, the significance of the diaspore bank in temperate rainforest ecosystems is unclear.

Few bryological studies have focused on coastal temperate rainforests of British Columbia (but see Newmaster 2000; Baldwin 2004), and none have explored the diaspore bank in this region. Through this study, bryophyte richness, diversity, and community composition both above- and below-ground is examined in intact and harvested forest stands of a coastal temperate rainforest. Chapter Two focuses on above-ground richness, diversity, and community composition on a variety of substrates in forest stands of varying ages post-harvesting. Chapter Three explores below-ground richness in the same stands for comparison, thus providing a picture of the species present in the *in situ* diaspore bank following logging disturbance.

Combining investigations of above- and below-ground bryophyte composition in old-growth and regenerating forests provides a thorough description of understory bryophyte richness, diversity and community composition spatially and temporally. A comparison of diversity at the surface and in the soil illucidates the recolonization potential of bryophytes, as this is essential to maintaining post-disturbance diversity. Following a disturbance, bryophytes have a critical role in the recovery of the ecosystem through nutrient and water cycling, soil formation, and facilitating the establishment of communities of fungi, vascular plants, and invertebrates (Glime 2001; Andrew et al. 2003; Hart and Shankman 2005; Davey and Currah 2006). Therefore, incorporating bryophytes into better management practices in the coastal temperate rainforests of British Columbia will enhance the health of these unique forests.

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Chapter 2:
Above-ground patterns in bryophyte species richness and composition among post-harvest forest stands

Introduction

Coastal temperate rainforests of North America are rich in bryophyte species (Table 2-1). As in tropical cloud forests, bryophytes throughout the temperate rainforest region thrive in the cool, moist climate, often surpassing vascular plants as the most abundant understory vegetation (Richards 1954; Frahm 1990; Newmaster et al. 2003).

In coastal temperate rainforests, small-scale disturbances, such as windthrow (single trees felled during windstorm events), prevail over stand-replacing disturbances, promoting bryophyte diversity by increasing forest stand complexity and providing a new suite of diverse substrates for bryophytes to colonize (Slack 1977; MacKinnon 2003). These conditions promote persistence of old-growth, shade- and moisture-dependent bryophytes, but also permit shade-intolerant early successional species to thrive in forest openings, thereby increasing diversity with moderate disturbances (Connell 1978; Franklin et al. 2002). Such a mosaic pattern throughout the forest increases overall diversity.

Human-made disturbances, however, tend to reduce stand complexity and negatively affect bryophyte diversity. In particular, conventional logging practices decrease available substrates for colonization, as standing trees and woody debris in varying stages of decay are removed and soil substrates are overturned and compacted (Gustafsson and Hallingbäck 1988; Andersson and Hytteborn 1991; Jonsson 1993; den Ouden and Alaback 1996). Additionally, logging dramatically changes microclimate conditions as the forest canopy is removed and extensive edges are created, thereby altering bryophyte community composition and species richness (Vitt and Belland 1997; Fenton and Frego 2005; Gabriel and Bates 2005). Light, wind, and moisture extremes that result from logging have profound impacts on community composition (Busby et al. 1978; Proctor 2001). Shade-

loving species, reliant on high moisture, tend to decrease in harvested areas, whereas light- and desiccation-tolerant species flourish (Baldwin and Bradfield 2005).

The capacity for post-harvest recovery differs among forest communities. Biological legacies (organic substrates or living organisms that promote the survival of other species) are essential for recovery (Pharo and Lindenmayer 2009), which variable retention harvesting practices help preserve. For example, standing trees provide some canopy cover for understory species that have corticolous habitats on trunk and branch substrates for epiphytic species (Caners et al. 2010), and woody debris provides substrates for epixylic species and shelter the ground, providing moist, shady microhabitats for terricolous species (Crites and Dale 1995). When debris is removed after harvesting, these biological legacies are lost, limiting the capacity for recovery (Frankin et al. 1997; Lindenmayer and Noss 2006).

In addition to survival facilitated through biological legacies, bryophytes can recolonize a disturbed area by spores dispersed from intact forests (Hutsemekers et al. 2008) and diaspores persisting in the soil (Jonsson 1993). The diaspore bank typically contains a variety of asexual propagules in addition to spores. Given that many species are restricted to clonal reproduction, asexual propagules are essential to maintaining a diverse community of bryophytes (Miles and Longton 1990; Imura 1994). Thus, recolonization spatially and temporally, combined with *in situ* persistence, are critical in maintaining a diverse bryophyte flora during forest regeneration.

In spite of their small size, bryophytes make critical contributions to forest regeneration following disturbance. Bryophytes aid in soil formation and provide physical substrates for vascular plant seeds, facilitating germination, colonization, and establishment (Hart and Shankman 2005). They also facilitate the establishment of mycorrhizal fungi (Davis et al. 2003; Davey and Currah 2006) and provide habitats for cyanobacteria (During and van Tooren 1990) and invertebrates (Andrew et al. 2003). Additionally, they alter a forest's moisture regime and buffer against extreme changes in forest floor temperature, with

implications for other plants and animals (Moul and Buell 1955; Longton and Holdgate 1967; Glime 2001). Therefore, an ecosystem with natural, small-scale disturbances is more capable of maintaining these critical functions, as a high diversity of bryophyte species persist (Pharo and Lindenmayer 2009), whereas in ecosystems with major disturbances, function is reduced, as it takes more time for bryophytes to re-establish and for a diverse community to develop (Fenton and Bergeron 2008)

In many forest studies, bryophytes are often lumped together as a single functioning unit rather than a diverse assemblage of species (Glime 2001). However, boreal forest bryophytes have become the focus of recent ecological studies on logging (Mills and Macdonald 2004; Caners 2010; Newmaster et al. 2007), and coastal temperate rainforest bryophytes have recently gained increasing attention (Newmaster et al. 2003; Baldwin and Bradfield 2005; Baldwin and Bradfield 2010). Furthermore, many bryophyte studies address a single substrate type, and because of different sampling techniques, creating comprehensive understanding of an ecosystem proves difficult (Rambo 2001; Caners et al. 2010). The focus of this study is on the bryophyte component of the species-rich temperate rainforest with an emphasis on a selection of dominant forest floor substrates in forest stands recovering from logging.

The objectives are to compare bryophyte species richness and diversity on three dominant understory substrates: soil patches, fallen logs, and tree bases, among forest stands at varying post-harvest ages to generate a temporal and spatial assessment of bryophyte richness and community composition. It is hypothesized that overall species composition and richness will differ with age, as postulated by the intermediate disturbance hypothesis (Connell 1978). This hypothesis has been widely applied to various ecosystems (Wilkinson 1999) and has been also considered in relation to forest bryophyte communities (Jonsson and Esseen 1990; Baldwin and Bradfield 2005). Forest edges have been found to contain more bryophyte species, due to the occurrence of short-lived disturbance-dependent species (Baldwin and Bradfield 2005). Consequently, species richness is predicted to be highest in young stands due to a greater proportion of colonist

species in fragmented stands due to the increased amount of edge habitats (Connell 1978; Haeussler et al. 2002). Intermediate and old stands will have lower species richness, as stands will be dominated by shade-tolerant perennials. Due to substrate and microhabitat specificity, species on the three substrates will differ from one another, producing distinct communities on each substrate. It is expected that decaying logs will have the greatest species richness (Rambo 2001; Ross-Davis and Frego 2002; Mills and Macdonald 2004).

Methods

Study area

Bryophyte richness and diversity of a temperate rainforest on the west coast of Vancouver Island were examined in the vicinity of Bamfield, British Columbia, at 48˚50' N, 125˚08'W. This region is characterized by the coastal western hemlock (CWH) biogeoclimatic zone (Pojar et al. 1991). The CWH zone is further divided into ten sub-zones based on continentality. The study area is part of the "very wet hypermaritime subzone" (CWHvh; Figure 2-1). The CWHvh zone is characterized by a canopy of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red cedar (*Thuja plicata* Don ex D. Don). The dominant shrubs are *Gaultheria shallon* Pursh and *Vaccinium* L. spp.. This region tends to have a species-poor herb layer with a well-developed bryophyte layer (MacKinnon 2003).

The climate regime for the area indicates the highest rainfall in Canada, with 1400-5000mm mean annual precipitation (MacKinnon 2003). Cool summers and mild winters are typical, with a mean annual temperature of 8˚C. The soils in the region are typically podzols; however, in the wettest regions, folisols are formed (Fox et al. 1987).

Study site

Forest stands were selected to represent various ages in the CWHvh zone. Age classes were defined as young (<20 yrs), intermediate (30-80yrs), and old-

growth (>100yrs), following stages of canopy formation (Arsenault and Bradfield 1995; Yearsley and Parminter 1998). The majority of stand ages were confirmed from vegetation maps provided by Western Forest Products (Sue McDonald, Erin Badesso, personal communications 2011) or from studies of Pacific Rim National Park and the Bamfield-Huu-ay-aht Community Forest (Morgan 2002; Andy MacKinnon, personal communication 2011). A total of 21 stands were chosen to produce equal age classes (7 young, 7 intermediate, and 7 old-growth). All sites were *Tsuga heterophylla/Thuja plicata* dominant, occurred within a 40km^2 area in the vicinity of Bamfield, and were below 150m elevation (National Parks and National Historic Sites of Canada 2005; Figure 2-1; Appendix 2-1).

Sample design and data collection

Sampling design followed a nested format. Three 20x30m sites were randomly located within each of 21 stands. Sites were positioned such that each site was a minimum of 30m from the other two and the site edge nearest the stand perimeter was positioned within 50m of the perimeter (Figure 2-2). In this design, stands are considered the true level of replication; however, sites and substrates were essential for capturing bryophyte richness and diversity.

Within each site, three substrates were sampled: soil patches, decaying logs, and bases of standing trees. Thus, this design followed a nested hierarchy with three age classes, seven stands per age class, three sites per stand, and three distinct substrate types per site. The three substrates were sampled at 10m intervals along a transect that bisected the site lengthwise (30m), yielding four quadrats per site and a total of 252 quadrats sampled per substrate if available across the study area. Soil substrates always fulfilled the total of four quadrats per site (84 quadrats per age class; 252 quadrats overall). However, due to limited occurrences of standing trees and decaying logs in some young sites, fewer tree and log quadrats were sampled. In total, 248 log quadrats were sampled (84 in old, 83 in intermediate, and 81 in young), and 172 tree quadrats were sampled (84 in old, 84 in intermediate, and four in young).

At each 10m interval, the soil patch nearest to the transect, the largest log, and the largest standing tree near the transect were sampled. A 25x25cm rectangular quadrat was positioned on each substrate, and the percent cover of each species was documented (Figure 2A-2). Substrate characteristics including litter depth in each soil quadrat, decay class of fallen logs (using an ordinal scale; Table 2-2), and diameter for standing trees and logs, were also assessed. The species of standing tree and fallen log (where possible) were also recorded.

Bryophytes grow in close association to their substrate, showing patchy distributions on the landscape (Pharo and Lindenmayer 2009). Thus, quantitative sampling of microhabitats (eg. substrates) and mesohabitats (collections of microhabitats; Vitt and Belland 1997) is essential, but will often underestimate diversity when used alone (Newmaster et al. 2005). To compensate for this, a non-quantitative survey was conducted at each site to generate a more comprehensive species inventory. Species presence/absence was taken from all substrates within a site to supplement abundance data from the quadrats. Such substrates included rocks, cliffs, patches of gravel debris, stream banks, and streams, which occurred in multiple sites but were not consistent enough to utilize in the quantitative sampling strategy. Non-quantitative sampling was also done on the dominant substrates (soil, log, tree) outside the quadrats. To ensure consistent survey effort across sites, a zigzag pattern was taken through the site, sampling all unique micro- and meso- habitat types (Doubt and Belland 2000). A maximum of 90 minutes was spent per surveying site.

Environmental variables were measured within each site and stand. Soil moisture and pH were measured at the central point of each site. Moisture and pH measurements for all sites took place between June 20-22, 2011, following two days without precipitation. As well as experiencing no precipitation during this three-day period, the average daily high temperature was 17˚C, with a fairly constant relative humidity between 80-95% (Weaver and Wiebe 2012). Upper and lower canopy cover were measured at 10m intervals along the transect through the middle of each site using a convex spherical densiometer (Forest Densiometers Co., Model A) to generate a percentage of canopy closure. The mean value was

used to establish average site-level measures. Upper canopy measurements were taken from standing height (1.5m). For lower canopy measurements, the densiometer was held directly above the bryophyte layer (0.2m). Slope was estimated visually for each site according to a categorical scale (from 1-7, level to steep), and aspect was obtained by a compass reading. Elevation was obtained from GIS maps of the study area.

Bryophyta (moss) identification follows Lawton (1971), except for the Dicranaceae (Ireland 2007), Ditrichaceae (Seppelt 2007), Bryaceae (Spence 2011) and *Sphagnum* (Vitt and Andrus 1977; McQueen and Andrus 2007). Moss nomenclature follows Crosby et al. (1999). Marchantiophyta (liverwort) identification follows Schuster (1966-1992), Smith (1990), and Schofield (2002). Liverwort nomenclature follows Stotler and Crandall-Stotler (1977). Bryophyte voucher specimens were deposited in the University of Alberta Cryptogamic Herbarium (ALTA).

Bryophyte richness and diversity

Prior to conducting data analyses, rarefaction curves were generated to test whether sampling intensity was sufficient to capture the diversity of species present in the region. Both site-wide survey (non-quantitative) data, as well as the species inventory (quantitative) data for each substrate were tested.

Species richness is based on presence-absence data only (Tuomisto 2010) and can be calculated at a variety of spatial scales, such as within a homogeneous site or across a broader landscape (Moreno and Rodriguez 2010). Species richness is a valuable component in determining species distributions; however, abundance is also essential. Species diversity encompasses both species presence and relative abundance (Moreno and Rodriguez 2011). Whittaker (1972) defined three scales of species diversity, two of which are alpha and gamma. Alpha diversity examines species diversity at a local scale, whereas gamma addresses diversity at the regional scale. Tuomisto (2010) proposed a similar labeling system for species richness, with both alpha and gamma richness.

Although species richness is presented through raw inventory data, species diversity has traditionally been measured using indices, such as the Shannon-Weiner or Simpson indices of diversity. As indices, these numbers have no units and are not readily comparable among studies (Hill 1973). Jost (2006) proposed using true diversities, which convert indices to values of effective number of species, which can be broadly compared to other regions or studies. True diversity tends to underestimate observed species numbers; however, if species are equally abundant, effective number of species will equal actual number of species.

In this study, species richness was used to assess bryophyte patterns using the presence-absence site-wide survey data. Alpha richness was defined as species inventory from each site, and gamma richness was the species inventory from each age class (young, mature, or old), as this was the level of desired comparison. Species diversity was used to examine bryophyte patterns from abundance data obtained from each substrate within a site. Jost's (2006) true diversity based on the Shannon-Weiner index was used to assess diversity (Equation 1).

$$H' = \exp\left(-\Sigma p_i \ln\left(p_i\right)\right) \quad (1)$$

Shannon-Weiner was a suitable index in this study, as it emphasizes differences in rare taxa, rather than differences in abundant taxa (Krebs 1999). This is especially useful in bryophyte sampling, as communities are typically dominated by a large proportion of rare species (>50%), that are controlled by suitable mesohabitat availability (Vitt and Belland 1997; Newmaster et al. 2005). Because the data were log-normally distributed, prior to calculating diversities, all abundance data were natural log (ln) transformed by taking the natural log of each value plus a small constant (in this case, 1). Alpha diversity was defined for each substrate as the true diversity per quadrat, using percent cover.

To compare species richness among age classes, inventory data were analyzed using a single-factor analysis of variance (ANOVA) in SPSS 19 (SPSS

Inc. 2010). To compare the combined effects of age and richness or diversity by substrate, two-factor ANOVA was conducted using SPSS 19 (SPSS Inc. 2010). Limited availability of trees in young stands led to a small sample size compared with other substrate types; therefore, the tree substrate was omitted from subsequent statistical analyses involving young stands. Both substrate type and age class were defined as fixed factors in these analyses. Prior to running the ANOVAs, the assumption of normality in the data sets was tested using the Shapiro-Wilk test. All of the richness data sets, as well as the ln-transformed diversity data sets, met the assumption of normality.

Community composition

Species composition among age classes was analyzed using principal coordinate analyses (PCoA) with PC-ORD version 6 (McCune and Mefford 2011). PCoA was chosen as it permits the user to determine a suitable distance measure, rather than limiting the analysis to Euclidean distance, utilized in principal component analysis (Gotelli and Ellison 2004). PCoA is an improvement over the commonly-used non-metric multi-dimesional scaling, as it gives the same result with each repetition and the ordination axes provide valuable information on the amount of variation explained (Hirst and Jackson 2007). For presence-absence data, Sørensen's distance measure was selected, as it can accommodate zero values. For quantitative abundance data, the Bray-Curtis distance measure was used. Ordinations were accompanied by a multi-response permutation procedure (MRPP) to test the significance of the ordination model. MRPP is a non-parametric analysis that tests for difference between groups in ordination space (McCune and Grace 2002).

Indicator species analyses (ISA) were conducted in PC-ORD (Dufrêne and Legendre 1997) to identify perfect indicator species (those showing high fidelity to one group and absence in all others), and strong indicators(those affiliated with one group over all others; Dufrêne and Legendre 1997; McCune and Grace 2002). ISA was used to detect indicator species for each age class and for each substrate type across age classes. It was conducted using 10,000 Monte Carlo iterations,

and significant indicators had *p*-values <0.05. To complement these analyses, unique species were determined, both by age and by substrate; uniqueness was defined as species restricted to one age class or on one substrate. Local rarity was also assessed. Species were compared with the British Columbia rare species lists (British Columbia Ministry of Environment 2012), and local rarity was defined as having ≤ 5 occurrences within the study area (Vitt and Belland 1997).

Besides stand age and substrate type that can influence bryophyte richness, diversity, and species composition, environmental variables were also analyzed. Distance-based redundancy analysis (dbRDA) was conducted using CANOCO version 4.5 (ter Braak and Šmilauer 2002). All environmental variables and species were kept in the model. As in PCoA, the Bray-Curtis measure of distance was used, and individual dbRDA analyses were run for each substrate type at the level of the site by assessing mean species richness per substrate type per site.

Results

During the field season (May-June 2011), there was 151.2mm of precipitation in May 2011 and 44mm in June 2011 (Weaver and Wiebe 2012). The average temperatures during the field season were 9.05˚C in May 2011 and 12.32˚C in June 2011.

Species richness

A total of 92 species (65 mosses and 27 liverworts) were found throughout the study area (Table 2-3; Table 2-4). Sampling was determined to be sufficient through rarefaction curves (Appendix 2-3). For both survey and substrate data, cumulative species reached a plateau with increasing samples, indicating adequate sampling.

Species richness and diversity were calculated to determine patterns of bryophyte species composition and distribution across forest stands. Non-quantitative sampling added nineteen species (16 mosses and 3 liverworts) not observed in substrate quadrats, and ten of these 19 species were terricolous. None

of the 92 species belonged to the British Columbia rare species list (British Columbia Ministry of Environment 2012), but 43 species (46.7%) were determined to be locally rare (Table 2-5). One species, *Dicranum brevifolium* (Lindb.) Lindb., represents a new record for Vancouver Island. It had 14 occurrences in this study area, 8 in old-growth stands, 5 in young stands, and a single occurrence in intermediate-aged stands. It primarily grew on soil substrates but had occasional occurrences on tree bases in old-growth stands.

Substrate effects

Across all age classes, soils had the highest richness (58 species), followed by logs (44 species). Trees had the lowest richness (24 species). The trends of total alpha richness (total number of species per stand) and average alpha richness (average number of species per stand) varied significantly among substrates (Figure 2-3). Soil substrates consistently had the highest species richness across age classes (43 species; Table 2-3), including 25 unique species (24 mosses and one liverwort; Table 2-5). This was followed by logs (34 species; Table 2-3), with seven unique species (one moss and six liverworts; Table 2-5). Tree substrates had the lowest richness (19 species; Table 2-3) and the lowest number of unique species (three; two mosses and one liverwort; Table 2-5). ISA showed that log substrates had the most indicator species (12 species, two mosses and ten liverworts) followed by soil (eight species, all mosses), and living trees had the fewest (two species, one moss and one liverwort; Table 2-6).

Age effects

Based on survey data from all substrates in three age classes, age class did not have a significant effect on either total richness ($F_{2,18}$=0.61, p=0.55) or average richness ($F_{2,18}$=2.80, p=0.09) at the stand level (Figure 2-3). However, the age classes differed in environmental characteristics, which in turn influenced bryophyte diversity. In particular, the upper canopy cover of young stands was significantly different from that of older stands (young: 8.68%$\pm$13.18; intermediate: 97.76%$\pm$0.85; old: 91.76%$\pm$5.09; $F_{2,18}$=259.96, p<0.0001). Lower

canopy cover followed the same trend (young: 35.55%±11.40; intermediate: 97.78%±0.73; old: 95.01%±2.91; $F_{2,18}$=186.73, p<0.0001). Soil pH also differed significantly across age classes (young: 5.87+0.38; intermediate: 6.00+0.47; old: 5.43+0.24; $F_{2,18}$=4.43, p=0.03); however, soil moisture was relatively constant (young: 61.47%+14.58; intermediate: 53.13%+20.93; old: 70.14%+11.51; $F_{2,18}$=2.38, p=0.12).

For the survey data, the highest total alpha richness occurred in young stands, with the lowest in intermediate-aged stands (Table 2-3). Out of the regional total of 92 species 84.78% were found in young stands, 52.17% in intermediate stands, and 60.86% in old-growth stands. Thus, young stands had 1.6 times the number of species in intermediate stands, whereas intermediate and old sites were similar, with a difference of only 8 species. The trend differed slightly with average alpha richness, where the highest value occurred in old stands, with similar values for young stands (Figure 2-1).

Thirty species of moss were unique to young stands, with six species (four mosses and two liverworts) restricted to old-growth stands, and intermediate stands lacking any unique taxa (Table 2-5). Young stands had the highest number of significant indicator species, which were mainly mosses (Table 2-7). *Ptychostomum pseudotriquetrum* and *Ceratodon purpureus*, both soil-dwelling species, had indicator values of 100.0 for young stands. Liverwort species were indicators for intermediate and old stands more frequently than for young stands, as liverworts accounted for 50% and 62.5% of all indicator species across all substrates for intermediate and old stands, respectively, compared with 20% in young stands.

Combined effects

For most substrate analyses, substrate type had a significant effect on species richness, whereas age class did not. The interaction term was not statistically significant, indicating that substrate and age factors do not depend on each other when affecting species richness patterns. Because trees were omitted from young stand analyses, a t-test was used to compare richness of soil and logs

in this age class. The results showed a lack of significant difference in total richness across all seven young stands (t=1.983, df=12, p=0.071) and a lack of significant difference in average richness per stand across all seven young stands (t=1.783, df=12, p=0.100) between the two substrate types. However, in subsequent ANOVAs considering intermediate and old stands and all substrates, there was a highly significant substrate effect (Table 2-8). In the analyses involving average species richness on all three substrates in the two older age classes, Tukey's HSD demonstrates that logs were significantly different from soil and trees ($p_{log,soil} < 0.0001$, $p_{logtree} < 0.0001$; Figure 2-3), whereas the latter two were not significantly different ($p_{soil,tree} = 0.371$; Figure 2-3).

When combining substrate and age effects, soil substrates showed different patterns than logs and trees. On soil substrates, young stands had higher average and total richness compared to the two older classes, and intermediate and old stands had equivalent average and total richness (Table 2-3). Average percent cover values for soil substrates were highest in the young age class, with comparable values in the old growth class (Table 2-9). Average percent cover for the intermediate age class was approximately 12% lower. Overall, soil showed less variation in cover among age classes compared with other substrates. At the level of the quadrat, soil alpha diversity showed incremental increases with age classes, reaching its maximum in old-growth stands (Table 2-9). Soil substrates reach maximum values for both richness and diversity at the quadrat level in the old age class.

On both trees and logs, total and average richness and percent cover were lowest in young stands, with intermediate and old stands showing comparable values (Table 2-3; Table 2-9). Across age classes, logs were consistently more species-rich and exhibited greater percent cover than did trees. At the level of the quadrat, both trees and logs exhibited a large increase in alpha diversity between young and intermediate stands and then a slight decline in old stands (Table 2-9). Limited availability of trees in young stands led to a small sample size compared with other substrate types; therefore, the tree substrate was omitted from subsequent statistical analyses involving young stands. The inclusion of these

young age class stands in the analyses led to significant results, driven by the restricted sample size and species richness (see methods).

Analyses of logs were more complex by having variable decay class data. The largest logs were consistently measured at each site, and these logs varied in decay stage within and among sites. In general, intermediate and old age classes had a higher average decay class than did young stands (Figure 2-4). The highest average richness per log quadrat occurred on logs in decay class 5 (5.23±0.37), and the lowest was on decay class 1 (2.31±0.16). The greatest richness (14 species) occurred on a log with a decay class 4 in an old-growth stand. The indicator species of logs were also broken down into those representing different decay classes (Table 2-10). Two species (both mosses) were indicative of recently fallen logs (decay class 1), whereas five species (2 mosses and 3 liverworts) were indicative of decay class 6, where the log is almost completely decayed. Intermediate decay classes had one significant indicator species (one moss) in decay class 4.

In the comparison of richness on logs of different decay classes, age class had a significant effect on average richness of log substrates but decay class did not. The interaction term was not significant, showing that the effects of age and decay class were not interdependent in their effects on species richness (Table 2-11). Tukey's HSD indicated that the significant differences occurred between young and older stands, as intermediate and old age classes were not significantly different ($p_{\text{young,intermediate}} < 0.0001$; $p_{\text{young,old}} < 0.0001$; $p_{\text{intermediate,old}} = 1.000$).

Community composition patterns

Analyses of the species composition of the age classes and substrate data are presented as ordinations. For the PCoAs, the first two axes explained between 29-53% of the variation in the data. The third axis contributed less to the percentage of variation explained, adding between 7.83% and 9.05%. Consequently, only the first two axes were plotted. In the ordinations, site data are used, rather than stand-level data. In the dbRDAs, species-environmental correlations were strong for all substrates, especially on Axis 1, with correlation

values of 0.919 for logs, 0.903 for soil, and 0.650 for trees. All environmental variables were retained in the analyses. In both the PCoA and dbRDAs, rare species with single occurrences were omitted from the analyses.

Overall, across all substrates, as well as in the survey data, sites in the three age classes formed distinct groups in ordination space (Table 2-12; Figure 2-5). Pairwise MRPP comparisons of the three age classes indicated that survey data exhibited highly significant differences among all three age classes, whereas for both soil and logs, young sites were significantly different from older (both intermediate and old-growth) sites (Table 2-12). For trees, the young sites were significantly different from the intermediate, but not the old (Table 2-12). Generally, for all substrates intermediate and old-growth groups also showed significant differences, although these differences were weaker than the comparisons with the young groups.

In the survey data PCoA, species that were associated strongly with the young centroid, based on the coordinates of the species centroids, included colonists *Ptychostomum pseudotriquetrum, Atrichum selwynii,* and *Polytrichum commune*. The species centroids for the perennials *Blepharostoma trichophyllum* and *Calypogeia muelleriana,* and the colonist *Calypogeia suecica,* associated strongly with the intermediate centroid (Figure 2-6a; Appendix 3-3). The species centroids for the perennials *Kurzia pauciflora, Hookeria lucens,* and the long-lived shuttle species *Riccardia latifrons* associated strongly with the old-growth centroid.

The PCoA for soil substrate site data showed numerous species, such as *Dicranum fuscescens* and *Pohlia nutans,* both short-lived shuttle species associating with the young centroid. The perennials *Cephalozia lunulifolia, Eurhynchium oreganum,* and the short-lived shuttle species *Leucolepis acanthoneura* showed strong affiliation with the intermediate centroid. Few species centroids were strongly affiliated with the old-growth centroid; however *Hookeria lucens* and the short-lived shuttle species *Rhizomnium glabrescens* were associated with the old-growth centroid (Figure 2-6b).

In the soil db-RDA, upper and lower canopy covers were the strongest environmental variables (Figure 2-7a). In general, old-growth sites were associated with increasing upper and lower canopy cover and litter depth, whereas many young sites cluster at the opposite end of those environmental variables (Appendix 2-4). Species of *Calypogeia* and *Cephalozia*, as well as *Plagiothecium undulatum* and *Leucolepis acanthoneura* were associated with high canopy cover and litter depth, whereas *Ceratodon purpureus, Pohlia nutans* and *Dicranum montanum* negatively associated with those environmental factors (Figure 2-6a).

The PCoA of log substrates showed that few species (such as *Antitrichia curtipendula*, *Isothecium myosuroides,* and *Dicranum fuscescens*) exhibited strong association with the young centroid (Figure 2-6c). The majority of species clustered around the centroids for intermediate and old-growth age classes. *Rhizomnium glabresens, Calypogeia neesiana*, and *Calypogeia suecica* were strongly affiliated with the intermediate centroid, whereas *Rhytidiadelphus loreus, Riccardia palmata*, and *Hylocomium splendens* showed strong affiliation with the old-growth centroid.

For the log db-RDA, upper canopy, soil moisture, and DBH were the strongest environmental variables. Old-growth sites were affiliated with greater upper canopy cover and decay class, with young sites associating with open canopies and less decayed log substrates (Appendix 2-4). Most liverworts, such as species of *Cephalozia* and *Cephaloziella*, as well as *Bazzania tricrenata* and *Lepidozia reptans*, were found on the negative side of Axis 1, with increasing canopy closure and decay class. *Antitrichia curtipendula, Isothecium myosuroides*, and *Dicranum fuscescens* occurred toward the positive side of this axis. *Sphagnum capillifolium*, a perennial, was found at the extreme negative side of Axis 2, with increasing soil moisture. *Calypogeia neesiana, Rhizomnium glabresens*, and the perennial *Eurhynchium praelongum* occurred to the positive side of Axis 2, with increasing DBH and slope (Figure 2-7b).

Given the variation of log substrates, differences in species composition among decay classes were examined. Decay classes were simplified for the analyses into three categories (1: decay class 1 and 2; 2: decay class 3 and 4; 3:

decay class 5 and 6). In this analysis, there was considerable overlap among the three categories (Figure 2-8a). The liverworts *Cephalozia pleniceps* and *Barbilophozia lycopodioides* and the mosses *Plagiothecium undulatum* and *Rhizomnium glabresens* associated with the centroids for decay categories 2 and 3, and *Antitrichia curtipendula* and *Dicranum fuscescens* associated with the centroid for category 1 (Figure 2-8b; Appendix 2-7). In spite of considerable overlap in the ordination diagram, categories 1 and 2 differed significantly from categories 2 and 3, although categories 1 and 3 were not significantly different from each another (Table 2-12).

In the PCoA of tree substrate data, species centroids did not show a strong relationship with any of the age class centroids (Figure 2-6d). In particular, no species were affiliated with the young age class. *Frullania nisquallensis*, a long-lived shuttle species and *Plagiothecium undulatum* were associated with the intermediate age class, whereas *Rhizomnium glabresens*, *Lepidozia reptans*, and *Scapania bolanderi* were affiliated with the old-growth centroid.

For the tree dbRDA, upper canopy, tree species, and tree DBH were the strongest environmental variables (Figure 2-7c). Sites in the different age classes clustered near the origin, without a distinct separation along any environmental gradient (Appendix 2-4). *Radula complanata*, a short-lived shuttle species and *Isothecium myosuroides* were found with increasing canopy cover and increasing occurrence of cedars over hemlocks (Figure 2-6c). *Mylia taylorii* occurred with very high soil moisture and very large tree DBH. *Pseudotaxiphyllum elegans* and *Eurhynchium oreganum* occurred opposite to *Mylia taylorii*, indicating preference of opposite conditions (Figure 2-7c).

Discussion

It was hypothesized that both substrate and age of forest stand would significantly affect bryophyte species richness and community composition. For CWH rainforests, the results suggest that substrate was highly significant in determining species richness, whereas age class was not, thereby demonstrating

the importance of microhabitat. This data emphasizes the importance of maintaining heterogeneity within stand age in order to maximize bryophyte diversity.

General comments on the flora

Bryophytes make up a considerable component of forest floor communities in forest ecosystems, reaching high diversity in temperate rainforests (Schofield 1988; Newmaster et al. 2003). A total of 92 species were determined in this study, based on quantitative and non-quantitative sampling of three forest stand ages focusing on three dominant substrate types (soil, logs, tree bases). This richness is comparable to other forest floor studies from the area (Rambo 2001; Baldwin 2004). Newmaster et al. (2003) enumerated more species in the CWH region (317 species), due to a sampling strategy that focused on sampling mesohabitat diversity, whereas the present study focused on dominant microhabitats. Similarly, Schofield (1988) described the bryophyte flora of British Columbia's CWH zone as extraordinarily species rich, with an estimated 236 species.

None of the 92 species appear on the British Columbia rare species list (British Columbia Ministry of Environment 2012). However, across all substrates, 46.7% were locally rare. Thus, some species (i.e., *Eurhynchium. praelongum*, *E. oreganum*, *Isothecium myosuroides*, *Dicranum fuscescens*, *Plagiothecium undulatum*, and *Scapania bolanderi*) dominated the flora and were found throughout the study area, in a minimum of 90% of sites, or at least 59 sites out of the 64 sampled. However, a large proportion of species occurred in restricted microhabitats. For example, ten taxa (*Brachythecium starkeii*, *Racomitrium heterostichum*, *Pohlia wahlenbergii*, *Ptychostomum sp. 1*, *Rosulabryum capillare*, *Anisothecium schreberianum*, *Campylopus introflexus*, *Sphagnum angustifolium*, *Metzgeria conjugata*, and *Douinia ovata*) had single occurrences throughout the study area. These rarity values are consistent with bryophyte studies from a broad range of ecosystems, where approximately half of bryophyte species are locally

rare (La Farge-England 1989; Vitt and Belland 1997; Vanderpoorten and Engels 2003; Vitt et al. 2003; Cleavitt 2005).

This study shows a relationship between local rarity and substrate specificity, as the most abundant species (i.e., those found in all sites) occurred on all three dominant substrate types, whereas the rare taxa were generally restricted to a single substrate type. In particular, *Ptychostomum creberrimum* and *Aulacomnium androgynum* were the only rare species observed on both soil and log substrates, whereas all other rare species were observed on only one substrate type. Furthermore, 57.14% (20 out of 35) of taxa that were unique to a particular substrate were also locally rare species, indicating limitations due to substrate specificity. Slack (1990) proposed that locally rare bryophytes exhibit greater substrate specificity, narrower niche breadth, or rare sporophyte production, which is consistent with the patterns observed.

One species, *Dicranum brevifolium* (Lindb.) Lind., was a new record for Vancouver Island. This species is widespread across North America, on rocky soils in mountainous regions (Ireland 2007). It had scattered occurrences within the coastal study area across all age classes and primarily on soil substrates. *Dicranum* is a taxonomically challenging genus, and it is likely that this species existed in the region but was overlooked during sampling due to a patchy distribution or was misidentified as *D. muehlenbeckii*, *D. acutifolium*, or *D. fuscescens*, which are similar taxa and reported from Vancouver Island (Ireland 2007; Beaty Biodiversity Museum 2012). *Dicranum brevifolium* is distinguished based on bulging cell walls between the leaf laminal cells, a prominent costa, and bistratose alar regions (Ireland 2007; Peterson 1979).

The effects of substrate and age on richness, diversity, and species composition

The combined effects of substrate and age had varying effects on bryophyte richness and species composition. Substrate was a significant factor in determining species richness, whereas age class was not. This suggests that microhabitat diversity was essential for preserving bryophyte elements across forest stands and ages. Further illustrating the importance of microhabitats,

Newmaster et al. (2007) found that disrupting microhabitats negatively impacted bryophyte species richness, and Crum (1972) emphasized the role of microniches in facilitating bryophyte persistence.

Across substrates, species richness tended to be highest in young stands, consistent with the predictions of the intermediate disturbance hypothesis, where diversity is expected to decline with increasing time between disturbances (Connell 1978; Wilkinson 1999; Haeussler et al. 2002). However, this differs from previous studies of forest bryophytes where bryophyte richness was highest in old-growth stands, with liverworts in particular showing a strong response to stand age (Gustafsson and Hallingbäck 1988; Newmaster et al. 2003; Botting and Freeden 2006). The high richness observed in young stands in the present study can be discussed in terms of trait-based assembly rules (Wilson 1989; Götzenberger et al. 2012), where the contribution of bryophytes with colonist and perennial life strategies varies in stands of different ages.

Young stands possessed an abundance of species with colonist or short-lived shuttle strategies (46.73% exhibiting either of these strategies). These species occupy temporary niches and have a high reproductive effort, which makes them efficient colonists of open substrates that are abundant following disturbances (During 1979; Baldwin and Bradfield 2010). *Ceratodon purpureus, Pohlia* spp., and members of the Bryaceae have colonist characteristics and were frequent in young stands, although they occurred in exposed microhabitats across age classes. Kurulok and Macdonald (2007) observed a similar pattern with vascular plants, showing that vascular understory richness was higher in young stands following salvage logging, due to an increase of weedy species and heterogeneity within stands.

Closed-canopy associated species, like *Hookeria lucens, Plagiothecium undulatum, Cephalozia lunulifolia,* and *Riccardia* spp., were found more consistently in old growth stands, although they were observed in young stands, where they persisted as remnant populations in moist hollows, under logs, or sheltered by ferns. Thus, substrates serve as biological legacies for bryophytes, preventing the complete destruction of old-growth species and contributing to

greater species richness in young stands. Coarse woody debris and soil hovels preserve species characteristic of intact stands and create moist, shaded microhabitats suitable for old-growth associated species that would otherwise be unable to thrive in exposed sites (Crum 1972; Hylander et al. 2005; Pharo and Lindenmayer 2009; Baldwin and Bradfield 2010).

The lowest species richness was found in intermediate stands (30-80 years), which tended to have closed, single-layer canopies, resulting in a reduction in the amount of light reaching the forest floor. The low richness in intermediate stands was driven by a few common perennials (i.e., *Eurhynchium* spp., *Hylocomium splendens, Plagiothecium undulatum, Rhytidiadelphys loreus* and *Scapania bolanderi)* excluding much of the diversity of weedy colonists. Other studies have found that in older stands, competition favours perennial stayer species, which replace and gradually eliminate colonizers (Jonsson and Esseen 1998; Franklin et al. 2002; Rydgren et al. 2004).

Old-growth richness was greater than that of intermediate stands. Six species, *Warnstorfia exannulata, Plagiomnium insigne, Sphagnum mendocinum, Calliergonella lindbergii, Dounia ovata,* and *Metzgeria conjugata,* were restricted to old-growth stands, indicating sensitivity to moist, protected habitats. Species richness was promoted in old-growth stands due to variable canopy cover and localized disturbances, which affect individual trees or parts of trees (Franklin et al. 2002; MacKinnon 2003). Small-scale disturbances produce gaps in the canopy and disrupt the forest floor, thereby permitting establishment of colonist species to persist in the gaps, with perennial species thriving in intact areas. Old-growth stands had a high degree of upper and lower canopy closure, although the variable cover indicated small scale disturbances affecting patterns within stands.

Although this study and others have reported lower forest floor richness in old-growth forests compared with their younger counterparts (Kurulok and Macdonald 2007; Baldwin and Bradfield 2010), old stands provide a vertical distribution of bryophyte richness, a dimension not surveyed in this study. The epiphytic community develops slowly over time, reaching its greatest diversity

and biomass in old-growth stands (McCune 1993; Sillett 1995; Sillett and Neitlich 1996).

Across age classes, soil had the highest richness, followed by logs. The higher richness found on soil reflects the variation of terricolous microhabitats including soil hovels, undulating terrain, moist stream banks, overturned soil from natural tree fall and from clear-cutting, and stable, intact soils. This variation of habitats, combined with variation in moisture and light intensity, produced heterogeneous conditions that supported a diversity of bryophytes. This was most evident in the young stands, where soils exhibited the greatest richness and cover. In these stands, disturbance-associated colonist bryophytes, such as *Ceratodon purpureus*, as well as members of Polytrichaceae and Bryaceae, co-occurred with species preferring intact forest conditions, (i.e., *Rhizomnium glabrescens*, *Rhytidiadelphus* spp., and *Eurhynchium* spp.). This trend has also been observed in previous studies that found recent disturbances increased soil species richness by providing heterogeneous microhabitats for colonization on a small scale (Jonsson and Esseen 1990; Zechmeister and Moser 2001). Soil substrate richness declined in older stands with increased canopy cover, which enabled perennial stayer species to thrive and replace the colonists.

Despite the impact of disturbance on bryophyte richness, the indicator species for soil substrates were shade-tolerant pleurocarpous species. The strongest indicator species was *Hylocomium splendens*, a wide-spread, dominant forest floor taxon that was especially common in intact coastal forests. *Polytrichum juniperinum* was the only colonist species determined as an indicator of soil substrates. *P. juniperinum* is an early successional species that possesses many characteristics of typical colonist species (Cremer and Mount 1965; During 1979; Baldwin 2004; Caners 2010). Although possessing long-lived rhizomatous stems (Thomas et al. 1988), it preferred bare, exposed terrain, with fewer occurrences in intact forest.

Due to microhabitat heterogeneity, soil substrates had greater richness than logs. This differed from other studies that have found the highest species richness on decaying wood (Rambo 2001; Mills and Macdonald 2004; Cole et al.

2008). Logs are widely recognized as an essential component of forests, contributing to structural complexity and providing a substrate for bryophytes (Andersson and Hytteborn 1991; Rambo 2001; Frego 2007). In this study, logs possessed the highest richness in intermediate and old age classes, but had lower species richness compared to soils in the young age class. This is potentially driven by the humidity on the west coast, enabling soils to maintain moisture, and thereby support a variety of bryophytes over time.

Corticolous species found on fallen logs in early stages of decay, indicated persistent epiphytic species that were replaced by epixylic species as decay progressed. Richness on log substrates increased substantially in older stands, due to the heterogeneity of logs in varying stages of decay. Old-growth stands have the greatest diversity of structure and decay class of woody debris, thus promoting bryophyte species richness (Richards 1954; Crites and Dale 1995; Newmaster et al. 2003). The spongy texture of well-decayed wood, with its ability to retain moisture, makes well-decayed logs an ideal substrate for many bryophytes (Rambo 2001). Furthermore, logs exist above the forest floor carpet in old stands, permitting the persistence of species unable to compete with the dominant forest floor feather mosses (Mills 2001; Fenton and Frego 2005).

The increase in richness on logs in older age classes was driven predominantly by liverworts and shade-dependent species. Well-decayed logs in older forest stands contained a mélange of bryophytes typical of epixylic substrates (i.e., the perennials *Riccardia* spp., *Bazzania tricrenata*, and *Blepharostoma trichophyllum*, and the colonists *Cephalozia* spp. and *Cephaloziella divaricata*), as well as taxa found on early stages of decay (i.e., colonists *Dichodontium pellucidum* and *Dicranum montanum*, short-lived shuttle species *Dicranum fuscescens*, and perennial *Isothecium myosuroides*). The majority of indicator species were liverworts, which are characteristic of higher decay classes and moist, shaded conditions (i.e., *Lepidozia reptans* and *Calypogeia* spp.). One exception was *Dicranum fuscescens*, which was an indicator species of both log substrates and young stands.

Species richness was not significantly different among decay classes. The wet environment in which these logs are situated contributes to a rich liverwort flora across age classes, indicated by similar richness in decay classes 4, 5, and 6, with the highest in decay class 5. These results differ from boreal forest studies, where in these drier forests, species richness increases with decay class, reaching a maximum in decay class 6 (Crites and Dale 1995; Kruys and Jonsson 1999). However, liverwort richness tends to peak in decay classes 4 and 5 (Crites and Dale 1995; Kruys and Jonsson 1999), suggesting that liverworts formed the basis of high diversity in later decay stages (i.e., *Riccardia chamaedryfolia*, *Diplophyllum albicans*, *Cephalozia lunulifolia*, and *Kurzia pauciflora* were found more frequently on well-decayed logs).

Trees had approximately half the richness of the two other substrates. The few trees that were present and sampled (>10cm DBH) in young stands were all remnant rather than regenerating trees; thus, the low richness indicates a loss of epiphytic taxa due to increased light intensity and reduced moisture. Regenerating trees in young stands typically hosted few, if any, bryophyte populations, indicating that epiphytic communities require time to become established. The richness in intermediate and old stands was equivalent, indicating that once trees grow back and the canopy closes, epiphytic richness is relatively stable (Fenton and Frego 2005). The majority of species observed on tree bases (23/26 species) were found on other substrates; in particular, there was overlap between trees and logs in early decay stages. Thus, tree base habitats did not significantly increase the overall region-wide diversity. Similar results were also found by Hylander and Dynesius (2006) in boreal streamside forests.

The effects of microhabitat/microenvironment on species composition

Species showed distinct responses to environmental variables. Many indicating generalist tendencies (i.e., *Eurhynchium* spp. and *Sphagnum* spp. on soils; *Dicranum montanum* and *Plagiochila asplenoides* on logs; and *Herbertus aduncus* and *Calypogeia neesiana* on trees), whereas others exhibited stronger habitat preferences. Some soil-dwelling mosses (i.e., species of the Polytrichaceae

and *Ptychostomum*) tended to associate with open canopies, shallow litter depths, and steeper slopes. Under closed canopies and with greater litter depth and gentle slopes, many liverworts and pleurocarpous mosses (i.e., *Calypogeia muelleriana* and *Hookeria lucens*) were more frequently observed. These species also showed a stronger affiliation with high soil moisture. Other species (i.e., *Sphagnum* spp., *Atrichum selwynii*, *Dicranum scoparium*, *Fontinalis antipyretica*, *Niphotrichum ericoides*, *Bazzania tricrenata*, and *Pellia neesiana*) were more strongly associated with high soil moisture and low soil pH.

Among log inhabitants, most liverworts and perennial pleurocarpous mosses preferred higher decay classes and more canopy cover. The species on logs in open (young) stands tended to be epiphytic mosses, such as *Dicranum fuscescens*, *Isothecium myosuroides*, and *Antitrichia curtipendula*. This illustrates the correlation between open canopies and early stages of decay, as species that associated with open canopies were also those found on logs in early decay stages (Crites and Dale 1995).

Bryophytes on substrates in different age classes are correlated with environmental factors that control species occurrences. Although most bryophytes exhibit some degree of desiccation tolerance, the degree of expression varies (Vitt 1990; Proctor 2000). Some bryophytes exhibit morphological mechanisms, whereas others employ behavioural mechanisms (Gimingham and Birse 1957; Schofield 2001; Proctor and Tuba 2002). The most desiccation-tolerant species can withstand prolonged dry periods and can rapidly recover, thereby tolerating drier environments. Unlike most bryophytes, members of the Polytrichaceae have rudimentary internal water conduction, increasing their resilience (Hébant 1977; Proctor and Tuba 2002). In this study, species of the Polytrichaceae were found in some of the most exposed sites, where it can tolerate water stress associated with high light and lower humidity (Proctor and Tuba 2002; Proctor et al. 2007). Species susceptible to desiccation are confined to moist, sheltered habitats (Busby et al. 1978). Because dependence on water availability and desiccation tolerance are fundamental to bryophyte biology, microhabitat factors that address moisture,

(i.e., canopy cover and ambient moisture) are key in determining bryophyte distribution and in this case the impact of logging on bryophyte distributions.

Conclusions

In west coast cedar-hemlock forests, substrate was a major factor in determining bryophyte species richness and community composition. Species differed in their substrate preferences, although some overlap occurred, particularly between trees and logs in early stages of decay, as well as soil and logs in later decay stages. The close association of bryophytes with substrate and microclimate contributed to patterns of bryophyte richness and species composition varying on a microscale, thereby limiting the role of coarse-scale stand age effects that would have been expected given the intermediate disturbance hypothesis (Connell 1978; Haeussler et al. 2002). However, species composition was affected by stand age, as young stands were more open, with increased light penetration and lower moisture. Consequently, species inhabiting young stands were generally desiccation tolerant, colonist species. Intermediate and old stands exhibited a closed canopy with shaded and moist understory substrates. Species in these stands were characterized as long-lived effective competitors.

Bryophytes are a diverse component of temperate coastal rainforests, and despite their small size they form integral components of forest ecosystems that have essential roles especially during post-harvest recolonization and recovery stages. Consequently, forest management strategies must address the requirements of bryophyte communities to maintain healthy ecosystems (Hylander 2009; Baldwin and Bradfield 2010). Strategies that leave behind standing trees and a variety of woody debris and maintain structural complexity on the forest floor and in the canopy will be beneficial to overall bryodiversity. Although such debris and residual trees help maintain diversity *in situ*, maintaining patches of intact forest will facilitate long-distance dispersal to harvested areas, thus contributing to a more resilient ecosystem overall.

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Table 2-1. Bryophyte species richness from previous studies. Studies describe temperate rainforests and boreal forests of western North America. CWH=coastal western hemlock; IWH=interior western hemlock.

Locality	Number of species	Reference
British Columbia CWH zone	236 (148 mosses, 88 liverworts)	Schofield 1988
Northeast Vancouver Island CWH zone	108 (65 mosses, 43 liverworts)	Baldwin 2004
British Columbia oceanic CWH zone	317	Newmaster et al. 2003
British Columbia IWH zone	300	Newmaster et al. 2003
Southeastern Alaska coastal rainforest	48 (“non-vascular”)	Deal 2007
Southwestern Washington	78 (56 mosses, 22 liverworts)	Evans et al. 2012
Central-Western Oregon	87 (58 mosses, 29 liverworts)	Rambo 2001
Central British Columbia sub-boreal spruce	53 (31 mosses, 22 liverworts)	Botting and Freeden 2006
Northern Alberta boreal	135 (96 mosses, 39 liverworts)	Caners 2010

Table 2-2. Decay classes for logs based on Crites and Dale's (1995) modification of the seven decay classes presented in McCullough (1948).

Decay Class	Description
1	Log whole, bark undecayed, branches and twigs intact
2	Log hard, twigs mostly lacking, less than 50% of bark removed
3	Log soft in places, 50% or more of bark removed
4	Little to no bark remaining, no branches, wood soft with crevices forming
5	Large wood fragments lost, trunk outline slightly deformed, vascular plants beginning to colonize
6	Wood mostly well-decayed, log colonized by herbs and feathermoss
7	Humification nearly 100%, outline indeterminable

Table 2-3. Non-quantitative alpha and gamma species richness of bryophytes throughout study sites. Gamma richness represents the regional total per substrate (soil, log, tree) or the pooled regional total obtained from the survey data. Total and average alpha richness for three substrates (soil, log, tree) and survey data per three age classes (young, intermediate, old) are presented. Average richness was calculated as the average species richness across sites within a stand, with n=7 for all substrates and all age classes. Total richness represents the total number of species enumerated in an age class. Average richness is reported with standard error of the mean.

		Young		Intermediate		Old	
	Gamma Richness	Total Richness (per age class)	Average Richness (per site)	Total Richness (per age class)	Average Richness (per site)	Total Richness (per age class)	Average Richness (per site)
Soil	58	43	13.86 $\pm$ 1.01	22	9.43 $\pm$ 0.81	23	9.86 $\pm$ 0.91
Log	44	30	10.29 $\pm$ 1.49	30	17.29 $\pm$ 1.06	34	17.43 $\pm$ 1.00
Tree	24	3	2 $\pm$ 0	19	8.14 $\pm$ 10.06	18	8.57 $\pm$ 0.78
Survey	92	78	21.47 $\pm$ 1.07	48	20.45 $\pm$ 0.77	56	22.83 $\pm$ 0.96

Table 2-4. Species taxonomy and traits for all species enumerated in the study area. Bryophytes are grouped into mosses or liverworts. Life strategy abbreviations are as follows: C=colonist, S=short-lived shuttle species, L=long-lived shuttle species, P=perennial stayer species. Life strategy data taken from During (1979), Baldwin (2004) and Caners (2010). Growth form data taken from Baldwin (2004), Newmaster (2000), and Caners (2010). Specialized asexual propagules indicate known occurrences of such structures in each taxon, compiled from Lawton (1971), Shaw (1980), Imura (1994), Ireland (2007), McQueen and Andrus (2007), Seppelt (2007), Eckel (2010), Miller (2011), and Spence (2011) for mosses, and Schuster (1974), Schuster (1980), Hong (1980), Hong (1989) and Schofield (2002) for liverworts. Data coded as yes, no, unknown for the species from the literature (?), or undetermined due to uncertain taxonomic identity (undet.). Abbreviations include propag.=propagulae, decid.=deciduous, axil.=axillary.
Preferred substrate taken from observations throughout the study area for species observed more than 10 times. For species with fewer than 10 observations, preferred substrate data is taken from the literature (Lawton 1971; Baldwin 2004; Newmaster 2000). Abbrev. refers to species name abbreviations used in the text and ordination analyses.

Abbrev.	Taxon	Family	Life Strategy	Growth Form	Specialized Propagules	Preferred Substrate
Mosses						
Anipal	*Anisothecium palustre* (Dicks.) I. Hagen	Dicranaceae	S	tuft	N	soil
Anisch	*Anisothecium schreberianum* (Hedw.) Dixon	Dicranaceae	S	tuft	N	soil
Antcur	*Antitrichia curtipendula* (Timm ex Hedw.) Brid.	Leucodontaceae	L	weft	N	tree
Atrsel	*Atrichum selwynii* Austin	Polytrichaceae	C	turf	Y:rhizoidal tubers	soil
Auland	*Aulacomnium androgynum* (Hedw.) Schwägr.	Aulacomniaceae	C	turf	Y:apical propag.	soil
Aulpal	*Aulacomnium palustre* (Hedw.) Schwägr.	Aulacomniaceae	C	turf	Y:apical propag.	soil
Brafri	*Brachythecium frigidum* (Müll. Hal.) Besch.	Brachytheciaceae	P	tuft	N	soil
Brasta	*Brachythecium starkii* (Brid.) Schimp. var. *pacificum* (Renauld & Cardon) E. Lawton	Brachytheciaceae	P	mat	N	generalist
Callin	*Calliergonella lindbergii* (Mitt.) Hedenäs	Hypnaceae	P	mat	N	soil
Camint	*Campylopus introflexus* (Hedw.) Brid.	Dicranaceae	C	mat	Y:decid. stem-tip	soil
Cerpur	*Ceratodon purpureus* (Hedw.) Brid.	Ditrichaceae	C	turf	Y:stem filaments	soil
Dicpel	*Dichodontium pellucidum* (Hedw.) Schimp.	Dicranaceae	C	mat	Y:gemmae	soil
Dichet	*Dicranella heteromalla* (Hedw.) Schimp.	Dicranaceae	C	turf	N	soil
Dicbre	*Dicranum brevifolium* (Lindb.) Lindb.	Dicranaceae	C	tuft	N	soil
Dicfus	*Dicranum fuscescens* Turner	Dicranaceae	S	turf	N	log
Dicmon	*Dicranum montanum* Hedw.	Dicranaceae	C	tuft	Y:decid. branchlet	log

Abbrev.	Taxon	Family	Life Strategy	Growth Form	Specialized Propagules	Preferred Substrate
Dicsco	*Dicranum scoparium* Hedw.	Dicranaceae	S	turf	N	soil
Ditamb	*Ditrichum ambiguum* Best	Ditrichaceae	C	tuft	?	soil
Dithet	*Ditrichum heteromallum* (Hedw.) E. Britton	Ditrichaceae	C	turf	Y:rhizoidal tuber	soil
Ditsch	*Ditrichum schimperi* (Lesq.) Kuntze	Ditrichaceae	S	tuft	?	soil
Eurore	*Eurhynchium oreganum* (Sull.) A. Jaeger	Brachytheciaceae	P	weft	N	soil
Eurpra	*Eurhynchium praelongum* (Hedw.) Schimp.	Brachytheciaceae	P	weft	N	soil
Fonant	*Fontinalis antipyretica* Hedw. var. antipyretica	Fontinalaceae	P	mat	N	water
Homful	*Homalothecium fulgescens* (Mitt. Ex. Müll. Hal.) A. Jaeger	Brachytheciaceae	P	mat	N	tree
Hooluc	*Hookeria lucens* (Hedw.) Sm.	Hookeriaceae	P	mat	Y:gemmae	soil
Hylspl	*Hylocomium splendens* (Hedw.) Schimp.	Hylocomiaceae	P	weft	N	soil
Hypcir	*Hypnum circinale* Hook.	Hypnaceae	P	mat	N	tree
Hypdie	*Hypnum dieckei* Renauld & Cardot	Hypnaceae	L	mat	N	soil
Isomyo	*Isothecium myosuroides* Brid.	Brachytheciaceae	P	weft	N	tree
Leuaca	*Leucolepis acanthoneura* (Schwägr.) Lindb.	Mniaceae	S	dendroid	N	soil
Niperi	*Niphotrichum ericoides* (Brid.) Bednarek-Ochyra & Ochyra	Grimmiaceae	P	mat	N	rock
Oliali	*Oligotrichum aligerum* Mitt.	Polytrichaceae	C	turf	N	soil
Phifon	*Philonotis fontana* (Hedw.) Brid. var. *fontana*	Bartramiaceae	S	turf	N	rock
Plains	*Plagiomnium insigne* (Mitt.) T.J. Kop.	Mniaceae	S	turf	N	soil
Plaund	*Plagiothecium undulatum* (Hedw.) Schimp.	Plagiotheciaceae	P	mat	?	soil
Pogcon	*Pogonatum contortum* (Menzies ex Brid.) Lesq.	Polytrichaceae	C	turf	N	soil
Pogurn	*Pogonatum urnigerum* (Hedw.) P. Beauv.	Polytrichaceae	C	turf	N	soil
Pohann	*Pohlia annotina* (Hedw.) Lindb.	Bryaceae	C	turf	Y:gemmae	soil
Pohnut	*Pohlia nutans* (Hedw.) Lindb.	Bryaceae	S	turf	N	soil
Pohwah	*Pohlia wahlenbergii* (F. Weber & D. Mohr) A.L. Andrews	Bryaceae	C	turf	N	soil
Polalp	*Polytrichastrum alpinum* (Hedw.) G.L. Sm. var. *sylvaticum* (Menzies) G.L. Merr.	Polytrichaceae	C	turf	N	soil
Polcom	*Polytrichum commune* Hedw.	Polytrichaceae	C	turf	N	soil
Poljun	*Polytrichum juniperinum* Hedw.	Polytrichaceae	C	turf	N	soil
Polstr	*Polytrichum strictum* Menzies ex Brid.	Polytrichaceae	C	turf	N	soil

Abbrev.	Taxon	Family	Life Strategy	Growth Form	Specialized Propagules	Preferred Substrate
Pseele	*Pseudotaxiphyllum elegans* (Brid.) Z. Iwats.	Hypnaceae	P	mat	Y:axil. filaments	log
Ptycre	*Ptychostomum creberrimum* (Taylor) J.R. Spence & H.P. Ramsay	Bryaceae	C	turf	N	soil
Ptysp1	*Ptychostomum* Hornsch. *sp. 1*	Bryaceae	C	turf	undet.	soil
Ptylon	*Ptychostomum lonchocaulon* (Müll. Hal.) J.R. Spence	Bryaceae	C	turf	N	soil
Ptypse	*Ptychostomum pseudotriquetrum* (Hedw.) J.R. Spence&H.P. Ramsay	Bryaceae	C	turf	Y:gemmae	soil
Rachet	*Racomitrium heterostichum* (Hedw.) Brid.	Grimmiaceae	P	mat	N	rock
Raclan	*Racomitrium lanuginosum* (Hedw.) Brid.	Grimmiaceae	P	tuft	N	rock
Rhigla	*Rhizomnium glabresens* (Kindb.) T.J. Kop.	Mniaceae	S	turf	N	log
Rhylor	*Rhytidiadelphus loreus* (Hedw.) Warnst.	Hylocomiaceae	P	weft	N	soil
Rhytri	*Rhytidiadelphus triquetrus* (Hedw.) Warnst.	Hylocomiaceae	P	weft	N	soil
Roscap	*Rosulabryum capillare* (Hedw.) J.R. Spense	Bryaceae	C	turf	Y:rhizoidal tubers	soil
Rossp1	*Rosulabryum* J.R. Spence *sp. 1*	Bryaceae	C	turf	undet.	soil
Sphang	*Sphagnum angustifolium* (Warnst.) C.E.O. Jensen	Sphagnaceae	P	turf	N	soil
Sphcap	*Sphagnum capillifolium* (Ehrh.) Hedw.	Sphagnaceae	P	turf	N	soil
Sphfal	*Sphagnum fallax* H. Kinggr.	Sphagnaceae	P	turf	N	soil
Sphgir	*Sphagnum girgensohnii* Russow	Sphagnaceae	P	turf	N	soil
Sphmen	*Sphagnum mendocinum* Sull.	Sphagnaceae	P	turf	N	soil
Sphpal	*Sphagnum palustre* L.	Sphagnaceae	P	turf	N	soil
Sphpap	*Sphagnum papillosum* Lindb.	Sphagnaceae	P	turf	N	soil
Tetpel	*Tetraphis pellucida* Hedw.	Tetraphidaceae	C	turf	Y:gemmae, protonemal flaps	log
Warexa	*Warnstorfia exannulata* (Schimp.) Loeske var. *exannulata*	Amblystegiaceae	S	weft	N	water
<u>Liverworts</u>						
Barlyc	*Barbilophozia lycopodioides* (Wallr.) Loeske	Anastrophyllaceae	P	mat	Y:gemmae	soil
Baztri	*Bazzania tricrenata* (Wahlenb.) Trevis.	Lepidoziaceae	P	mat	N	log
Bletri	*Blepharostoma trichophyllum* (L.) Dumort.	Pseudolepicoleaceae	P	thread	Y:gemmae	tree
Calmue	*Calypogeia muelleriana* (Schiffner) K. Müller	Calypogeiaceae	P	mat	Y:gemmae	log

Abbrev.	Taxon	Family	Life Strategy	Growth Form	Specialized Propagules	Preferred Substrate
Calnee	*Calypogeia neesiana* (C. Massal. & Carestia) K. Müller	Calypogeiaceae	L	mat	Y:gemmae	log
Calsue	*Calypogeia suecica* (Arnell & J. Perss.) K. Müller	Calypogeiaceae	C	mat	Y:gemmae	log
Cepbic	*Cephalozia bicuspidata* (L.) Dumort.	Cephaloziaceae	C	thread	Y:gemmae	log
Ceplun	*Cephalozia lunulifolia* (Dumort.) Dumort.	Cephalociaceae	P	thread	Y:gemmae	log
Cepple	*Cephalozia pleniceps* (Austin) Lindb.	Cephaloziaceae	C	thread	Y:gemmae	soil
Cepdiv	*Cephaloziella divaricata* (Sm.) Warnst.	Cephaloziellaceae	C	thread	Y:gemmae	generalist
Dipalb	*Diplophyllum albicans* (L.) Dumort.	Scapaniaceae	P	mat	Y:gemmae	log
Douova	*Douinia ovata* (Dicks.) Buch	Scapaniaceae	P	mat	N	generalist
Frunis	*Frullania nisquallensis* Sull.	Jubulaceae	L	mat	N	tree
Heradu	*Herbertus aduncus* (Dicks.) Gray	Herbertaceae	P	turf	N	tree
Kurpau	*Kurzia pauciflora* (Dicks.) Grolle	Lepidoziaceae	P	turf	N	log
Leprep	*Lepidozia reptans* (L.) Dumort.	Lepidoziaceae	P	mat	N	log
Metcon	*Metzgeria conjugata* Lindb.	Metzgeriaceae	L	mat	N	rock
Mylano	*Mylia anomala* (Hook.) Gray	Myliaceae	L	mat	Y:gemmae	soil
Myltay	*Mylia taylorii* (Hook.) Gray	Myliaceae	L	mat	Y:gemmae	log
Pelnee	*Pellia neesiana* (Gottsche) Limpr.	Pelliaceae	L	mat	N	soil
Plaasp	*Plagiochila asplenoides* (L. emend. Tayl.) Dum.	Plagiochilaceae	P	turf	Y:propagulae	soil
Radcom	*Radula complanata* (L.) Dumort.	Radulaceae	S	mat	Y:gemmae	tree
Riccha	*Riccardia chamedryfolia* (With.) Grolle	Aneuraceae	L	mat	Y:gemmae	log
Riclat	*Riccardia latifrons* (Lindb.) Lindb.	Aneuraceae	L	mat	Y:gemmae	log
Ricmul	*Riccardia multifida* (L.) Gray	Aneuraceae	P	mat	Y:gemmae	log
Ricpal	*Riccardia palmata* (Hedw.) Carruth.	Aneruaceae	P	mat	Y:gemmae	log
Scabol	*Scapania bolanderi* Austin	Scapaniaceae	P	mat	Y:gemmae	log

Table 2-5. Abundance of all species enumerated in the study area. Abundance is measured as the proportion of sites overall and per age class (young, intermediate, old) where each species occurred. Uniqueness by substrate indicates species that occurred on only one substrate (soil (S), log (L), or tree (T)), whereas uniqueness by age indicates species that occurred in only one age class (young (Y), intermediate (I), or old (O)). Taxon abbreviations correspond to those used in the text.

Abbrev.	Taxon	Proportion of Sites Occurring				Unique Species by Substrate			Unique Species by Age		
		Overall	Y	I	O	S	L	T	Y	I	O
Mosses											
Anipal	*Anisothecium palustre* (Dicks.) I. Hagen	0.190	0.429	0.143	0.000						
Anisch	*Anisothecium schreberianum* (Hedw.) Dixon	0.048	0.143	0.000	0.000	*			*		
Antcur	*Antitrichia curtipendula* (Timm ex Hedw.) Brid.	0.286	0.286	0.143	0.429						
Atrsel	*Atrichum selwynii* Austin	0.095	0.286	0.000	0.000	*			*		
Auland	*Aulacomnium androgynum* (Hedw.) Schwägr.	0.048	0.143	0.000	0.000				*		
Aulpal	*Aulacomnium palustre* (Hedw.) Schwägr.	0.095	0.286	0.000	0.000				*		
Brafri	*Brachythecium frigidum* (Müll. Hal.) Besch.	0.095	0.000	0.143	0.143		*				
Brasta	*Brachythecium starkii* (Brid.) Schimp. var. *pacificum* (Renauld & Cardon) E. Lawton	0.048	0.143	0.000	0.000	*			*		
Callin	*Calliergonella lindbergii* (Mitt.) Hedenäs	0.048	0.000	0.000	0.143						*
Camint	*Campylopus introflexus* (Hedw.) Brid.	0.048	0.143	0.000	0.000				*		
Cerpur	*Ceratodon purpureus* (Hedw.) Brid.	0.333	1.000	0.000	0.000				*		
Dicpel	*Dichodontium pellucidum* (Hedw.) Schimp.	0.333	0.714	0.000	0.286						
Dichet	*Dicranella heteromalla* (Hedw.) Schimp.	0.048	0.143	0.000	0.000	*			*		
Dicbre	*Dicranum brevifolium* (Lindb.) Lindb.	0.381	0.429	0.143	0.571						
Dicfus	*Dicranum fuscescens* Turner	1.000	1.000	1.000	1.000						
Dicmon	*Dicranum montanum* Hedw.	0.333	0.714	0.286	0.000						
Dicsco	*Dicranum scoparium* Hedw.	0.048	0.143	0.000	0.000	*			*		
Ditamb	*Ditrichum ambiguum* Best	0.143	0.429	0.000	0.000				*		
Dithet	*Ditrichum heteromallum* (Hedw.) E. Britton	0.095	0.286	0.000	0.000				*		
Ditsch	*Ditrichum schimperi* (Lesq.) Kuntze	0.048	0.143	0.000	0.000				*		
Eurore	*Eurhynchium oreganum* (Sull.) A. Jaeger	1.000	1.000	1.000	1.000						
Eurpra	*Eurhynchium praelongum* (Hedw.) Schimp.	1.000	1.000	1.000	1.000						
Fonant	*Fontinalis antipyretica* Hedw. var. *antipyretica*	0.095	0.286	0.000	0.000	*			*		

Abbrev.	Taxon	Overall	Y	I	O	S	L	T	Y	I	O
Homful	*Homalothecium fulgescens* (Mitt. Ex. Müll. Hal.) A. Jaeger	0.143	0.143	0.143	0.143						
Hooluc	*Hookeria lucens* (Hedw.) Sm.	0.857	0.571	1.000	1.000						
Hylspl	*Hylocomium splendens* (Hedw.) Schimp.	0.952	1.000	0.857	1.000						
Hypcir	*Hypnum circinale* Hook.	0.905	0.857	1.000	0.857						
Hypdie	*Hypnum dieckei* Renauld & Cardot	0.238	0.286	0.000	0.429						
Isomyo	*Isothecium myosuroides* Brid.	1.000	1.000	1.000	1.000						
Leuaca	*Leucolepis acanthoneura* (Schwägr.) Lindb.	0.143	0.000	0.143	0.286	*					
Niperi	*Niphotrichum ericoides* (Brid.) Bednarek-Ochyra & Ochyra	0.381	0.857	0.143	0.143	*					
Oliali	*Oligotrichum aligerum* Mitt.	0.095	0.286	0.000	0.000				*		
Phifon	*Philonotis fontana* (Hedw.) Brid. var. fontana	0.095	0.286	0.000	0.000				*		
Plains	*Plagiomnium insigne* (Mitt.) T.J. Kop.	0.095	0.000	0.000	0.286	*					*
Plaund	*Plagiothecium undulatum* (Hedw.) Schimp.	1.000	1.000	1.000	1.000						
Pogcon	*Pogonatum contortum* (Menzies ex Brid.) Lesq.	0.333	0.571	0.286	0.143						
Pogurn	*Pogonatum urnigerum* (Hedw.) P. Beauv.	0.048	0.143	0.000	0.000	*			*		
Pohann	*Pohlia annotina* (Hedw.) Lindb.	0.048	0.143	0.000	0.000	*			*		
Pohnut	*Pohlia nutans* (Hedw.) Lindb.	0.190	0.571	0.000	0.000	*			*		
Pohwah	*Pohlia wahlenbergii* (F. Weber & D. Mohr) A.L. Andrews	0.048	0.143	0.000	0.000				*		
Polalp	*Polytrichastrum alpinum* (Hedw.) G.L. Sm. var. *sylvaticum* (Menzies) G.L. Merr.	0.190	0.286	0.143	0.143	*					
Polcom	*Polytrichum commune* Hedw.	0.286	0.714	0.000	0.143	*					
Poljun	*Polytrichum juniperinum* Hedw.	0.429	0.857	0.286	0.143	*					
Polstr	*Polytrichum strictum* Menzies ex Brid.	0.095	0.286	0.000	0.000	*			*		
Pseele	*Pseudotaxiphyllum elegans* (Brid.) Z. Iwats.	0.762	0.571	1.000	0.714						
Ptycre	*Ptychostomum creberrimum* (Taylor) J.R. Spence & H.P. Ramsay	0.095	0.286	0.000	0.000				*		
Ptysp1	*Ptychostomum* Hornsch. *sp. 1*	0.048	0.143	0.000	0.000				*		
Ptylon	*Ptychostomum lonchocaulon* (Müll. Hal.) J.R. Spence	0.095	0.286	0.000	0.000	*			*		
Ptypse	*Ptychostomum pseudotriquetrum* (Hedw.) J.R. Spence & H.P. Ramsay	0.333	1.000	0.000	0.000	*			*		
Rachet	*Racomitrium heterostichum* (Hedw.) Brid.	0.048	0.143	0.000	0.000				*		
Raclan	*Racomitrium lanuginosum* (Hedw.) Brid.	0.095	0.143	0.000	0.143						
Rhigla	*Rhizomnium glabresens* (Kindb.) T.J. Kop.	0.952	0.857	1.000	1.000						
Rhylor	*Rhytidiadelphus loreus* (Hedw.) Warnst.	0.952	1.000	1.000	0.857						

Abbrev.	Taxon	Overall	Y	I	O	S	L	T	Y	I	O
Rhytri	*Rhytidiadelphus triquetrus* (Hedw.) Warnst.	0.095	0.143	0.143	0.000			*			
Roscap	*Rosulabryum capillare* (Hedw.) J.R. Spense	0.048	0.143	0.000	0.000				*		
Rossp1	*Rosulabryum* J.R. Spence *sp. 1*	0.048	0.143	0.000	0.000				*		
Sphang	*Sphagnum angustifolium* (Warnst.) C.E.O. Jensen	0.048	0.143	0.000	0.000	*			*		
Sphcap	*Sphagnum capillifolium* (Ehrh.) Hedw.	0.143	0.286	0.000	0.143						
Sphfal	*Sphagnum fallax* H. Kinggr.	0.048	0.143	0.000	0.000	*			*		
Sphgir	*Sphagnum girgensohnii* Russow	0.095	0.143	0.000	0.143	*					
Sphmen	*Sphagnum mendocinum* Sull.	0.048	0.000	0.000	0.143	*					*
Sphpal	*Sphagnum palustre* L.	0.095	0.143	0.000	0.143	*					
Sphpap	*Sphagnum papillosum* Lindb.	0.048	0.143	0.000	0.000	*			*		
Tetpel	*Tetraphis pellucida* Hedw.	0.095	0.000	0.143	0.143			*			
Warexa	*Warnstorfia exannulata* (Schimp.) Loeske var. *exannulata*	0.048	0.000	0.000	0.143						*
<u>Liverworts</u>											
Barlyc	*Barbilophozia lycopodioides* (Wallr.) Loeske	0.286	0.000	0.286	0.571		*				
Baztri	*Bazzania tricrenata* (Wahlenb.) Trevis.	0.667	0.286	0.857	0.857						
Bletri	*Blepharostoma trichophyllum* (L.) Dumort.	0.381	0.286	0.429	0.429						
Calmue	*Calypogeia muelleriana* (Schiffner) K. Müller	0.857	0.857	1.000	0.714						
Calnee	*Calypogeia neesiana* (C. Massal. & Carestia) K. Müller	0.286	0.143	0.571	0.143						
Calsue	*Calypogeia suecica* (Arnell & J. Perss.) K. Müller	0.571	0.000	1.000	0.714						
Cepbic	*Cephalozia bicuspidata* (L.) Dumort.	0.857	0.571	1.000	1.000						
Ceplun	*Cephalozia lunulifolia* (Dumort.) Dumort.	0.762	0.286	1.000	1.000						
Cepple	*Cephalozia pleniceps* (Austin) Lindb.	0.286	0.000	0.143	0.714		*				
Cepdiv	*Cephaloziella divaricata* (Sm.) Warnst.	0.238	0.000	0.429	0.286		*				
Dipalb	*Diplophyllum albicans* (L.) Dumort.	0.857	0.571	1.000	1.000						
Douova	*Douinia ovata* (Dicks.) Buch	0.048	0.000	0.000	0.143						*
Frunis	*Frullania nisquallensis* Sull.	1.000	1.000	1.000	1.000						
Heradu	*Herbertus aduncus* (Dicks.) Gray	0.476	0.714	0.286	0.429						
Kurpau	*Kurzia pauciflora* (Dicks.) Grolle	0.238	0.000	0.143	0.571						
Leprep	*Lepidozia reptans* (L.) Dumort.	0.952	0.857	1.000	1.000						
Metcon	*Metzgeria conjugata* Lindb.	0.048	0.000	0.000	0.143						*
Mylano	*Mylia anomala* (Hook.) Gray	0.238	0.429	0.000	0.286		*				

Abbrev.	Taxon	Overall	Y	I	O	S	L	T	Y	I	O
Myltay	*Mylia taylorii* (Hook.) Gray	0.667	0.571	0.571	0.857						
Pelnee	*Pellia neesiana* (Gottsche) Limpr.	0.333	0.429	0.143	0.429	*					
Plaasp	*Plagiochila asplenoides* (L. emend. Tayl.) Dum.	0.667	0.571	0.571	0.857						
Radcom	*Radula complanata* (L.) Dumort.	0.143	0.143	0.286	0.000			*			
Riccha	*Riccardia chamedryfolia* (With.) Grolle	0.333	0.143	0.429	0.429		*				
Riclat	*Riccardia latifrons* (Lindb.) Lindb.	0.571	0.143	0.857	0.714						
Ricmul	*Riccardia multifida* (L.) Gray	0.095	0.143	0.143	0.000						
Ricpal	*Riccardia palmata* (Hedw.) Carruth.	0.381	0.429	0.429	0.286		*				
Scabol	*Scapania bolanderi* Austin	1.000	1.000	1.000	1.000						

Table 2-6. Substrate indicator species analysis. Output shows indicator species for each of the three substrates (soil, log, tree) across all age classes. Only significant indicator species are included. *=$p<0.01$, **=$p<0.001$. Within each substrate type, taxa are grouped as mosses or liverworts and listed in order of decreasing significance.

	Indicator value	*p*-value
Soil		
Hylocomium splendens	68.8	0.0001**
Rhytidiadelphus loreus	48.5	0.0004**
Eurhynchium oreganum	45.4	0.0005**
Polytrichum juniperinum	33.3	0.0005**
Eurhynchium praelongum	45.1	0.0015*
Hookeria lucens	34.0	0.0020*
Rhizomnium glabresens	41.1	0.0043*
Plagiothecium undulatum	40.6	0.0049*
Log		
Pseudotaxiphyllum elegans	52.6	0.0001**
Dicranum fuscescens	40.6	0.0073*
Cephalozia bicuspidata	53.7	0.0001**
Calypogeia suecica	45.7	0.0001**
Lepidozia reptans	46.1	0.0005**
Cephalozia lunulifolia	43.9	0.0005**
Blepharostoma trichophyllum	19.8	0.0005**
Mylia taylorii	38.7	0.0007**
Riccardia latifrons	33.3	0.0008**
Scapania bolanderi	43.3	0.0219
Diplophyllum albican	39.4	0.0302
Riccardia chamedryfolia	19.0	0.0358
Tree		
Hypnum circinale	38.4	0.0093*
Frullania nisquallensis	64.3	0.0001**

Table 2-7. Age class indicator species analysis. Output shows indicator species for each of the three age classes (young, intermediate, old). Analyses were conducted for survey data and all substrates (soil, log, tree). Only significant indicator species are included. *=p<0.01, **=p<0.001. Within each age class and substrate type, taxa are grouped as mosses or liverworts and listed in order of decreasing significance.

	Indicator Value	*p*-value
Young		
Survey Data		
Ceratodon purpureus	100.0	0.0001**
Ptychostomum pseudotriquetrum	100.0	0.0001**
Niphotrichum ericoides	64.3	0.0088
Polytrichum commune	59.5	0.017
Pohlia nutans	57.1	0.018
Polytrichum juniperinum	57.1	0.026
Dichodontium pellucidum	51.0	0.048
Soil		
Dicranum fuscescens	24.3	0.0001**
Polytrichum juniperinum	15.2	0.0001**
Pogonatum contortum	10.5	0.0001**
Pogonatum urnigerum	8.3	0.0011*
Polytrichum commune	4.8	0.0217
Fontinalis antipyretica var. antipyretica	4.8	0.0241
Sphagnum papillosum	4.8	0.0244
Sphagnum angermanicum	4.8	0.0251
Log		
Dicranum fuscescens	38.7	0.0001**
Antitrichia curtipendula	10.0	0.0003**
Herbertus aduncus	4.5	0.0234
Intermediate		
Survey Data		
Calypogeia suecica	58.3	0.0192

	Indicator Value	*p*-value
Soil		
Eurhynchium oreganum	21.7	0.0021*
Calypogeia suecica	4.6	0.0405
Log		
Rhizomnium glabresens	57.4	0.0001**
Plagiothecium undulatum	39.8	0.0001**
Eurhynchium praelongum	27.1	0.0001**
Pseudotaxiphyllum elegans	23.0	0.0001**
Eurhynchium oreganum	12.8	0.0022*
Calypogeia suecica	24.3	0.0001**
Cephalozia bicuspidata	18.9	0.0006**
Calypogeia muelleriana	8.3	0.0022*
Lepidozia reptans	13.5	0.0058*
Old		
Survey Data		
Cephalozia pleniceps	59.5	0.015
Soil		
Plagiothecium undulatum	28.6	0.0001**
Hylocomium splendens	21.9	0.0003**
Leucolepis acanthoneura	6.0	0.0078*
Scapania bolanderi	9.2	0.0117
Plagiochila asplenoides	6.5	0.0247
Log		
Hylocomium splendens	7.5	0.0076*
Bazzania tricrenata	15.9	0.0001**
Frullania nisquallensis	9.0	0.0106

Table 2-8. Two-factor analyses of variance output for average and total species richness among substrates and age classes, using abundance data at the stand level. All three substrates (soil, log, tree) are included, and only intermediate and old age classes used (young age class excluded). *df*=degrees of freedom. Average richness represents the average number of species across sites within a stand, and total richness represents the total number of species enumerated per stand. *=p<0.01, **=p<0.001, ***=p<0.0001.

	Average Richness			Total Richness		
	df	*F*	*p*-value	*df*	*F*	*p*-value
Age Class (Fixed)	1,36	0.223	0.640	1,36	0.187	0.668
Substrate (Fixed)	2,36	36.476	<0.000***	2,36	53.243	<0.000***
Age Class x Substrate	2,36	1.175	0.321	2,36	0.015	0.985
Error	36	0.654		36	6.230	

Table 2-9. Quadrat level alpha richness, alpha diversity, and average percent cover. Average alpha diversity per quadrat, calculated as effective number of species (exponential of Shannon Diversity Index; Equation 1 in text), averaged per quadrat across age classes, and average alpha richness per quadrat on three substrates across three age classes. Average richness was calculated as the average number of species occurring in a quadrat across age classes. Average percent cover was calculated as an average of cover per quadrat within a stand. Thus, for logs, n_{young}=80, $n_{intermediate}$=84, n_{old}=84; for soil, n=84 for all age classes; for trees, n_{young}=3, n_{int}=84, n_{old}=84. Averages reported with standard errors of the mean.

	Young Quadrats			Intermediate Quadrats			Old Quadrats		
	Diversity	Richness	Average % Cover	Diversity	Richness	Average % Cover	Diversity	Richness	Average % Cover
Soil	2.27 ± 0.11	2.49 ± 0.12	43.19±2.90	2.42 ± 0.11	2.67 ± 0.12	30.46±2.39	3.07 ± 0.15	3.33 ± 0.17	40.13+2.87
Log	1.99 ± 0.10	2.14 ± 0.12	18.00±1.84	4.50 ± 0.16	5.05 ± 0.18	58.76±2.46	4.34 ± 0.22	4.85 ± 0.25	52.79+2.49
Tree	1.58 ± 0.29	1.67 ± 0.33	5.67±1.84	2.30 ± 0.11	2.51 ± 0.12	29.38±2.72	2.21 ± 0.10	2.38 ± 0.11	35.99±2.88

Table 2-10. Decay class indicator species analysis. Output reported for logs of varying decay classes (Classes 1-6) sampled across all age classes. Only significant indicator species are included. *=p<0.01, **=p<0.001. Within each decay class, taxa are grouped as mosses or liverworts and listed in order of decreasing significance.

	Indicator Value	p-value
Decay Class 1 (n=26)		
Antitrichia curtipendula	20.4	0.0084*
Isothecium myosuroides	29.2	0.0102
Decay Class 2 (n=64)		
none		
Decay Class 3 (n=78)		
none		
Decay Class 4 (n=44)		
Plagiothecium undulatum	23.8	0.0319
Decay Class 5 (n=31)		
none		
Decay Class 6 (n=5)		
Hylocomium splendens	25.2	0.0143
Sphagnum capillifolium	20.0	0.0185
Cephalozia pleniceps	18.8	0.0127
Mylia taylorii	13.3	0.0302
Kurzia pauciflora	14.5	0.0456

Table 2-11. Two-factor analysis of variance output for average species richness on logs in varying decay classes, using abundance data at the stand level. Decay class is on a scale from 1-6, where 1 is least decayed and 6 is most decayed. All three age classes are included (young, intermediate, old). Both decay class and age class are fixed factors. Average richness was calculated as the average number of species per log quadrat across sites within a stand. *df*=degrees of freedom. See text for model design and sampling methodology. *=p<0.01, **=p<0.001, ***=p<0.0001.

	Average Richness		
	df	*F*	*p*-value
Decay Class (Fixed)	5,58	0.753	0.587
Age Class (Fixed)	2,58	5.375	0.007**
Decay Class x Age Class	7,58	1.060	0.400
Error	58	3.700	

Table 2-12. Multi-response permutation procedures (MRPP) output, using survey data, substrate (soil, log, tree) data, and decay class data. MRPP accompanied each PCoA, and pairwise comparisons among groups defined in the ordination analyses are shown. For survey and substrate data, 1=young, 2=intermediate, and 3=old. For decay class data, 1=decay classes 1 and 2, 2=decay classes 3 and 4, 3=decay classes 5 and 6. T=test statistic for MRPP. A=chance-corrected within-group agreement, a measure of within-group homogeneity. *=p<0.05, **=p<0.01, ***=p<0.001.

	1 vs. 2			1 vs. 3			2 vs. 3		
	T	A	*p*-value	T	A	*p*-value	T	A	*p*-value
Survey	-20.31	0.13	0.000***	-18.07	0.12	0.000***	-5.27	0.034	0.000***
Soil	-14.12	0.106	0.000***	-12.73	0.0806	0.000***	-1.96	0.016	0.047*
Log	-21.86	0.20	0.000***	-16.00	0.12	0.000***	-8.62	0.057	0.000***
Tree	-2.044	0.035	0.036*	-1.44	0.028	0.088	-3.65	0.031	0.0055**
Decay Class	-39.88	0.126	0.000***	-21.15	0.111	0.000***	0.147	-0.0006	0.489

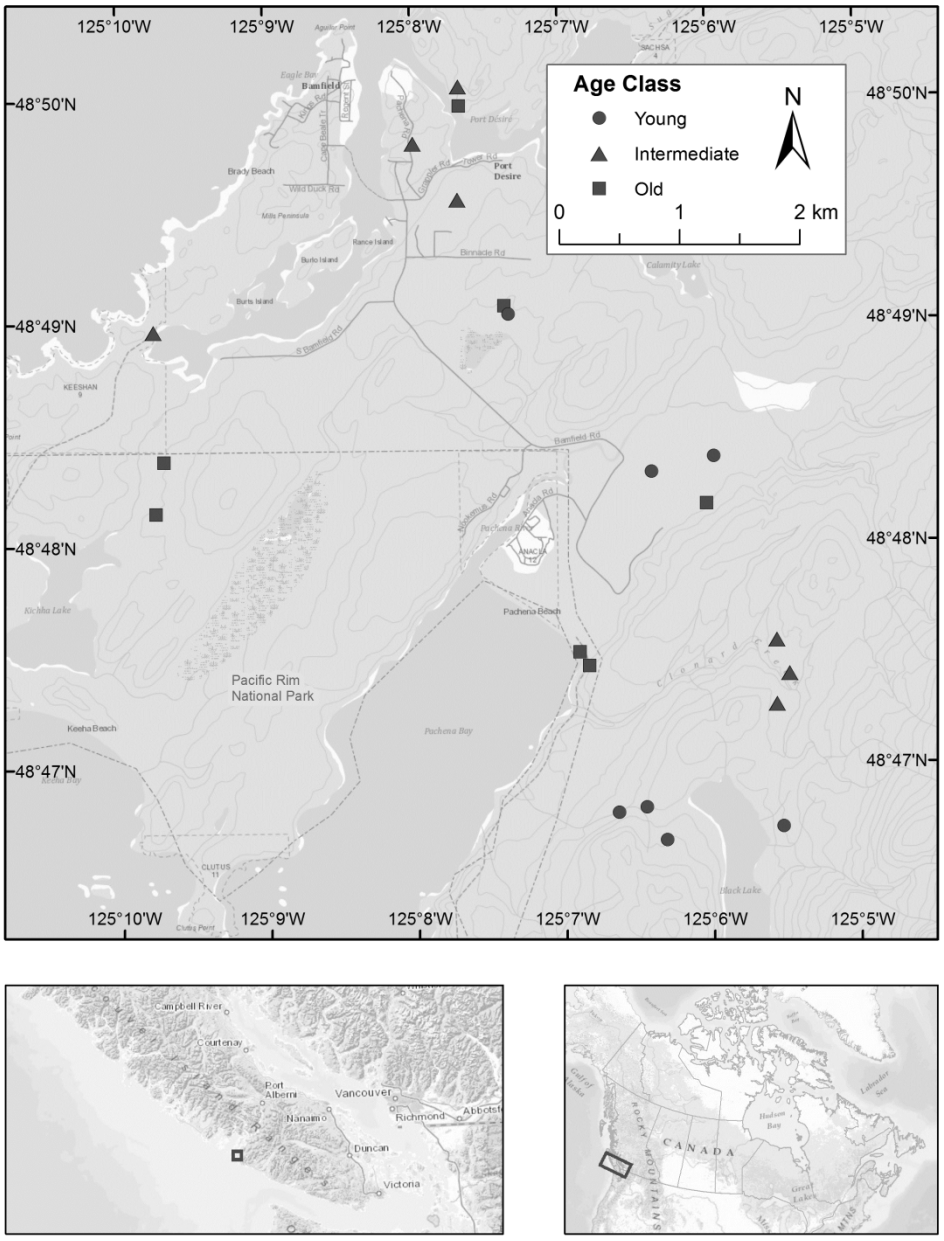


Figure 2-1. Map of the study area, showing stands sampled. Circles indicate young stands (<20 years), triangles indicate intermediate stands (30-80 years), and squares indicate old-growth stands (>100 years). Each stand contained three sampling sites. Inset maps show location of the study area near Bamfield, British Columbia. For stand descriptions, see Appendix 2-1.

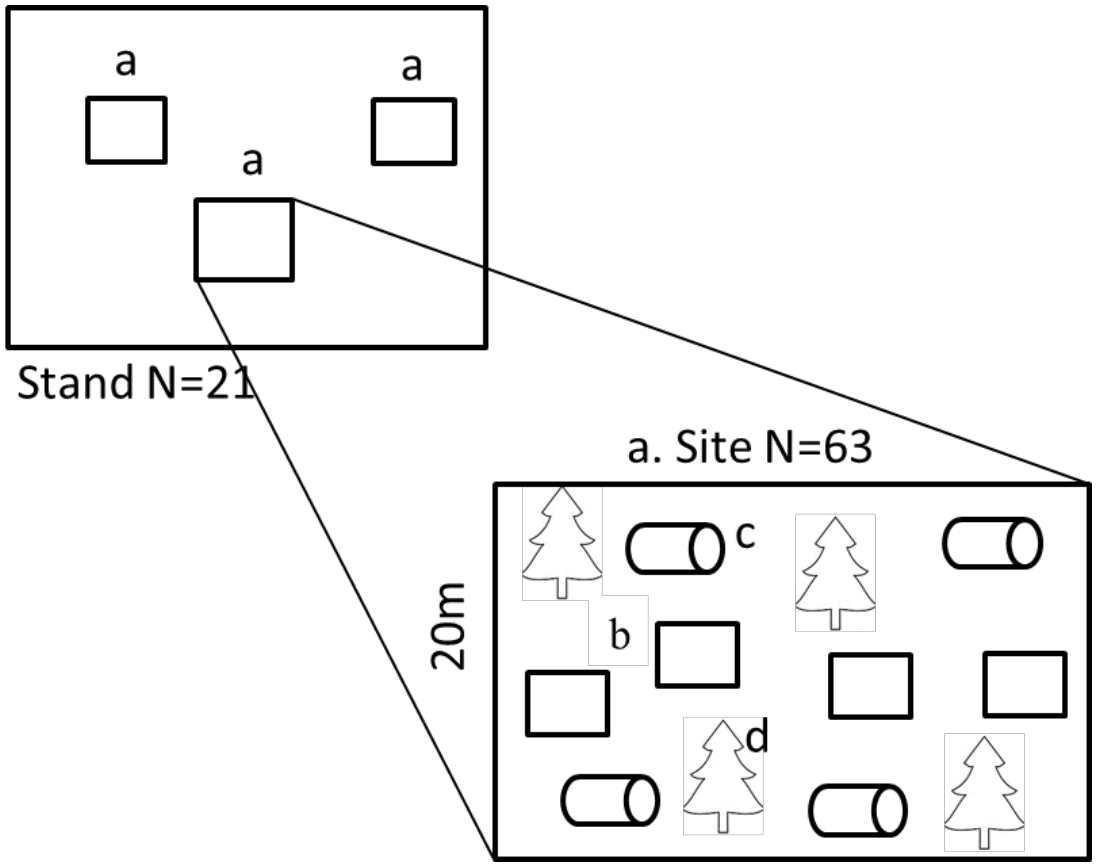


Figure 2-2. Sampling design, showing stands, sites, and substrates. There were three sites per stand, seven stands per age class, and three age classes within the study area, for a total of 21 stands containing 63 sites. There were three substrates per site with four quadrats per substrate, for a total of 12 quadrats per stand and 84 per age class. Each quadrat sampled was 25x25 cm. Given the limitation of substrate availability in some sites, the total number of quadrats sampled was as follows: soil (252), log (248), tree (172) within the study area. a=site (20x30m), b-d=substrate types; b=soil, c=log, d=tree base.

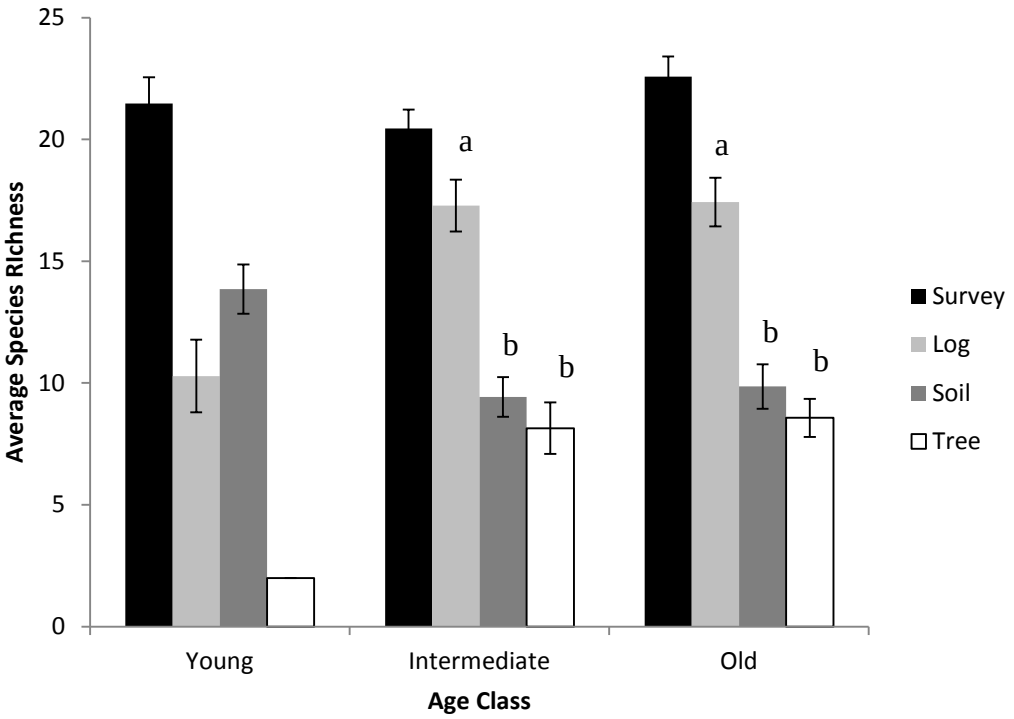


Figure 2-3. Average species richness reported for three dominant substrates based on quantitative data and across all substrates within stands based on survey (non-quantitative) data. For survey data as well as data from each substrate, n=7 per age class. Error bars denote standard error of the mean. Letters (a, b) indicate significant differences among substrates, as calculated by Tukey's HSD for the analysis of variance for average richness on three substrates across intermediate and old age classes.

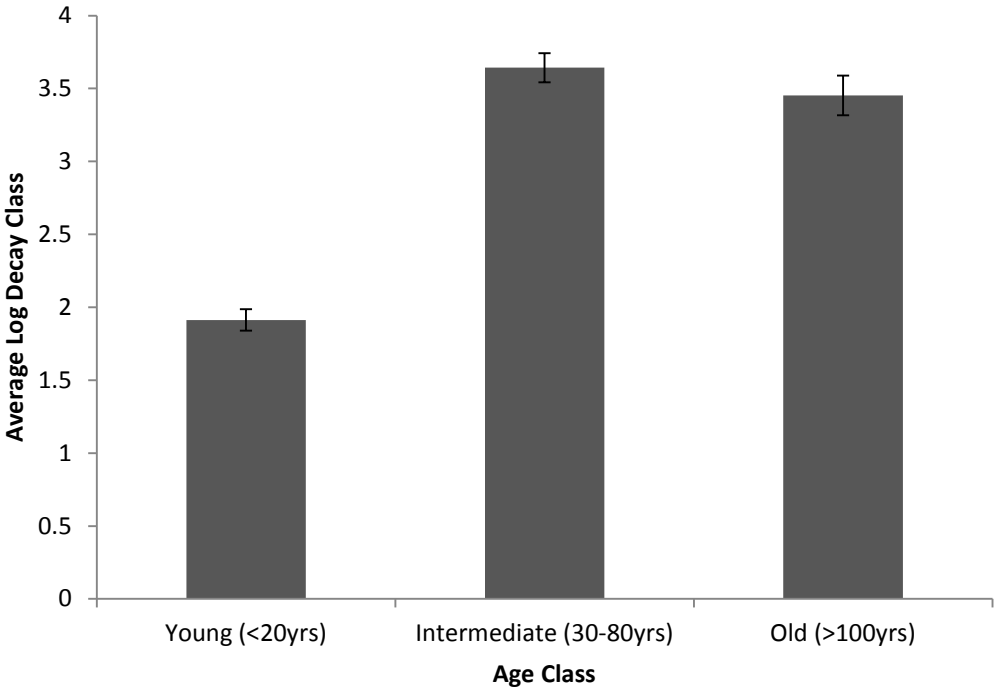


Figure 2-4. Average decay class of fallen logs per age class (young, intermediate, old). In young stands, a total of 80 logs was sampled, and in each of intermediate and old stands, 84 logs were sampled. Averages are shown with standard error.

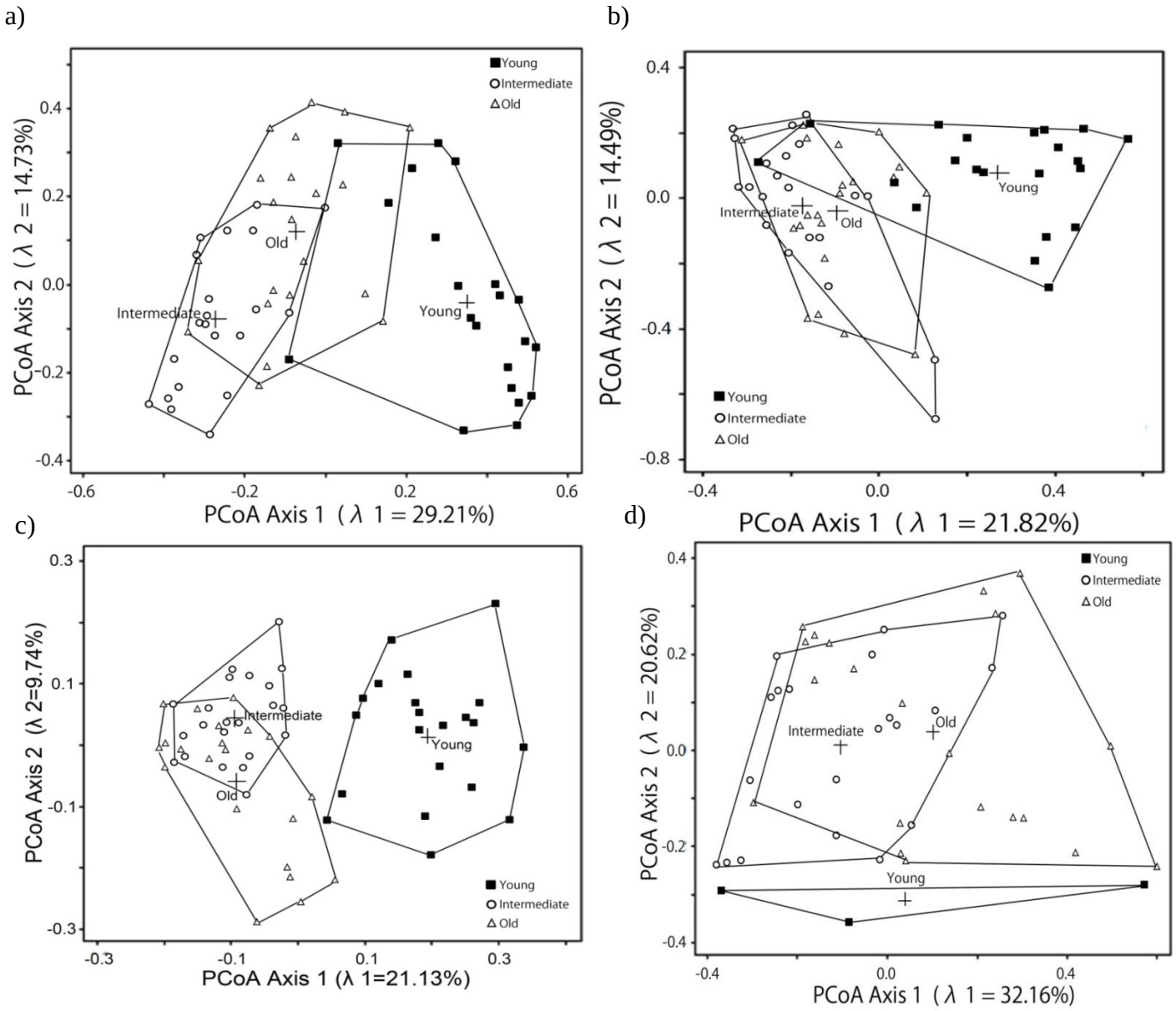

a)
b)
c)
d)
Young
Intermediate
Old
PCoA Axis 2 (λ 2 = 14.73%)
PCoA Axis 1 (λ 1 = 29.21%)
PCoA Axis 2 (λ 2 = 14.49%)
PCoA Axis 1 (λ 1 = 21.82%)
PCoA Axis 2 (λ 2=9.74%)
PCoA Axis 1 (λ 1=21.13%)
PCoA Axis 2 (λ 2 = 20.62%)
PCoA Axis 1 (λ 1 = 32.16%)

Figure 2-5. PCoA output for survey and substrate data, grouped by age classes (young, intermediate, old) and showing sites. Age class centroids and site centroids are shown. Site centroids are coded by age class. a) Survey PCoA was conducted on 82 species and 64 sites, using the Sørensen dissimilarity measure. b) Soil data PCoA on 32 species and 63 sites, using Bray-Curtis dissimilarity measure. c) Log data PCoA on 34 species and 63 sites using Bray Curtis dissimilarity measure. d) Tree data PCoA on on16 species and 45 sites using Bray Curtis dissimilarity measure.

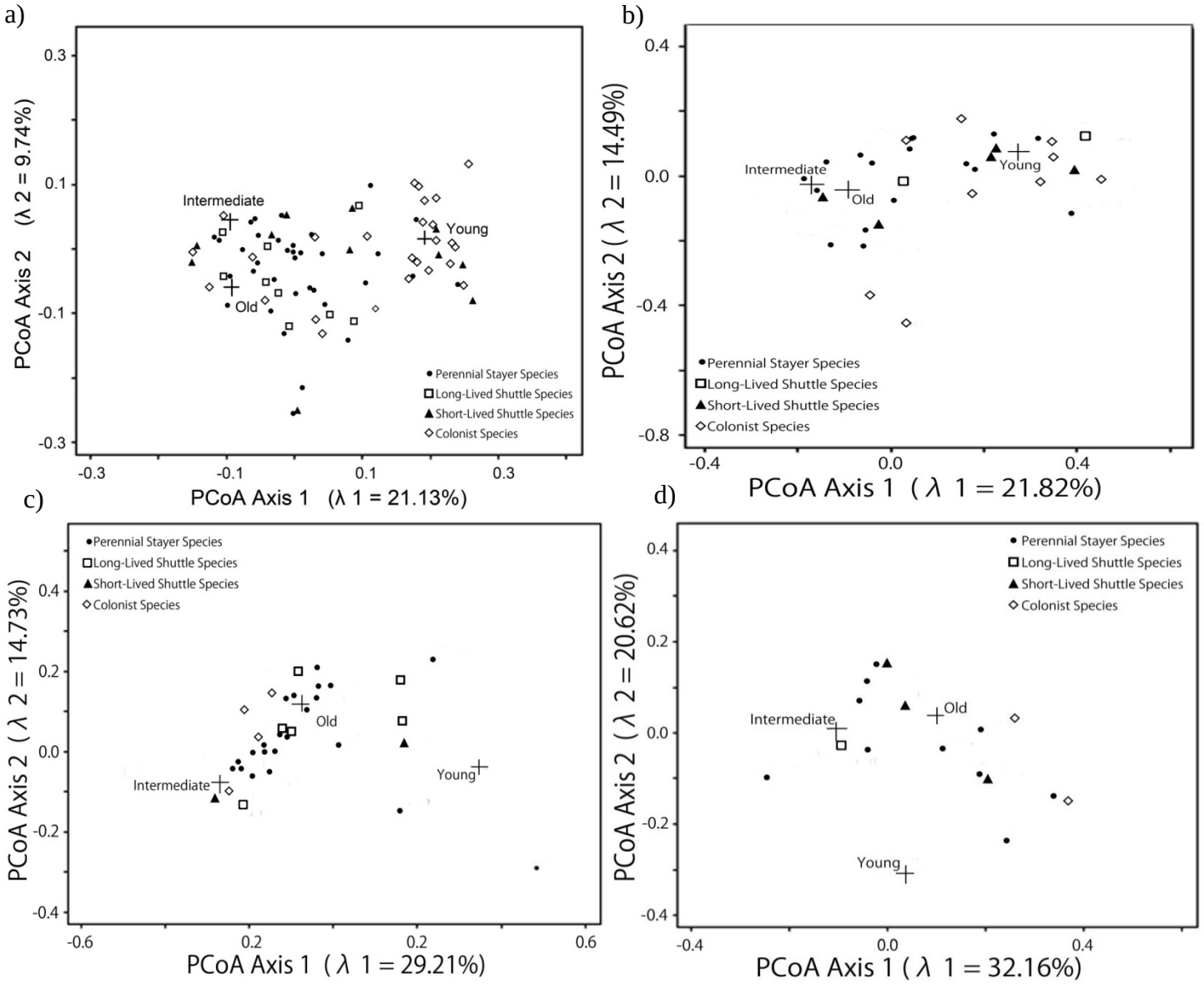

a)
PCoA Axis 2 (λ 2 = 9.74%)
PCoA Axis 1 (λ 1 = 21.13%)
Intermediate
Young
Old
Perennial Stayer Species
Long-Lived Shuttle Species
Short-Lived Shuttle Species
Colonist Species
b)
PCoA Axis 2 (λ 2 = 14.49%)
PCoA Axis 1 (λ 1 = 21.82%)
Intermediate
Young
Old
Perennial Stayer Species
Long-Lived Shuttle Species
Short-Lived Shuttle Species
Colonist Species
c)
PCoA Axis 2 (λ 2 = 14.73%)
PCoA Axis 1 (λ 1 = 29.21%)
Perennial Stayer Species
Long-Lived Shuttle Species
Short-Lived Shuttle Species
Colonist Species
Old
Intermediate
Young
d)
PCoA Axis 2 (λ 2 = 20.62%)
PCoA Axis 1 (λ 1 = 32.16%)
Perennial Stayer Species
Long-Lived Shuttle Species
Short-Lived Shuttle Species
Colonist Species
Intermediate
Old
Young

Figure 2-6. Ordination of survey and substrate data utilizing age classes (young, intermediate, old). PCoA output shows age class centroids and species centroids, with rare species with single occurrences are omitted from the analyses. Species centroids are coded by life strategy; for species labels (first three letters of genus and first three letters of species), see Appendix 3-3 and Table 2-4. a) Survey PCoA was conducted on 82 species and 64 sites, using the Sørensen dissimilarity measure. b) Soil data PCoA on 32 species and 63 sites, using Bray-Curtis dissimilarity measure. c) Log data PCoA on 34 species and 63 sites using Bray Curtis dissimilarity measure. d) Tree data PCoA on on 16 species and 45 sites using Bray Curtis dissimilarity measure.

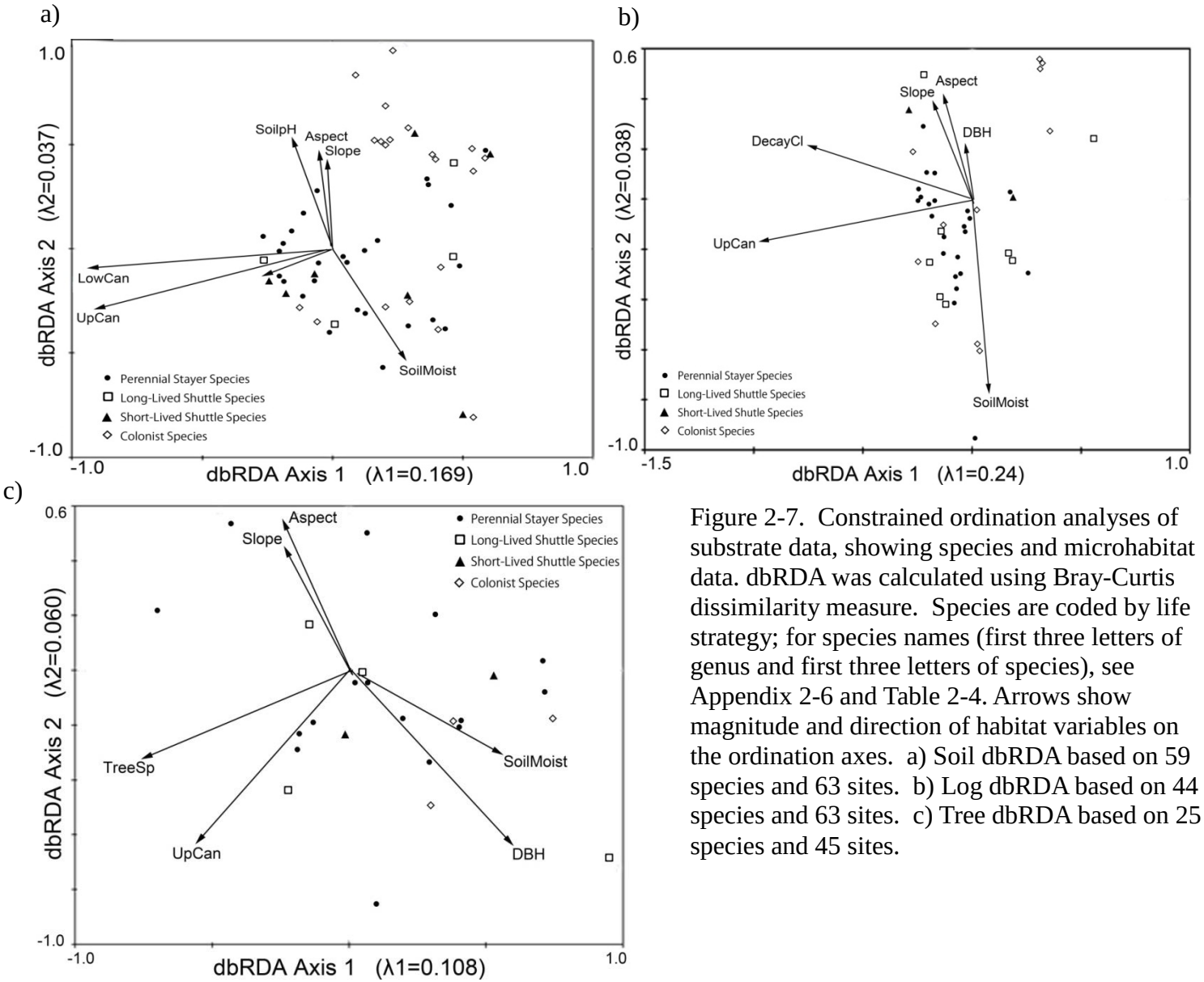


Figure 2-7. Constrained ordination analyses of substrate data, showing species and microhabitat data. dbRDA was calculated using Bray-Curtis dissimilarity measure. Species are coded by life strategy; for species names (first three letters of genus and first three letters of species), see Appendix 2-6 and Table 2-4. Arrows show magnitude and direction of habitat variables on the ordination axes. a) Soil dbRDA based on 59 species and 63 sites. b) Log dbRDA based on 44 species and 63 sites. c) Tree dbRDA based on 25 species and 45 sites.

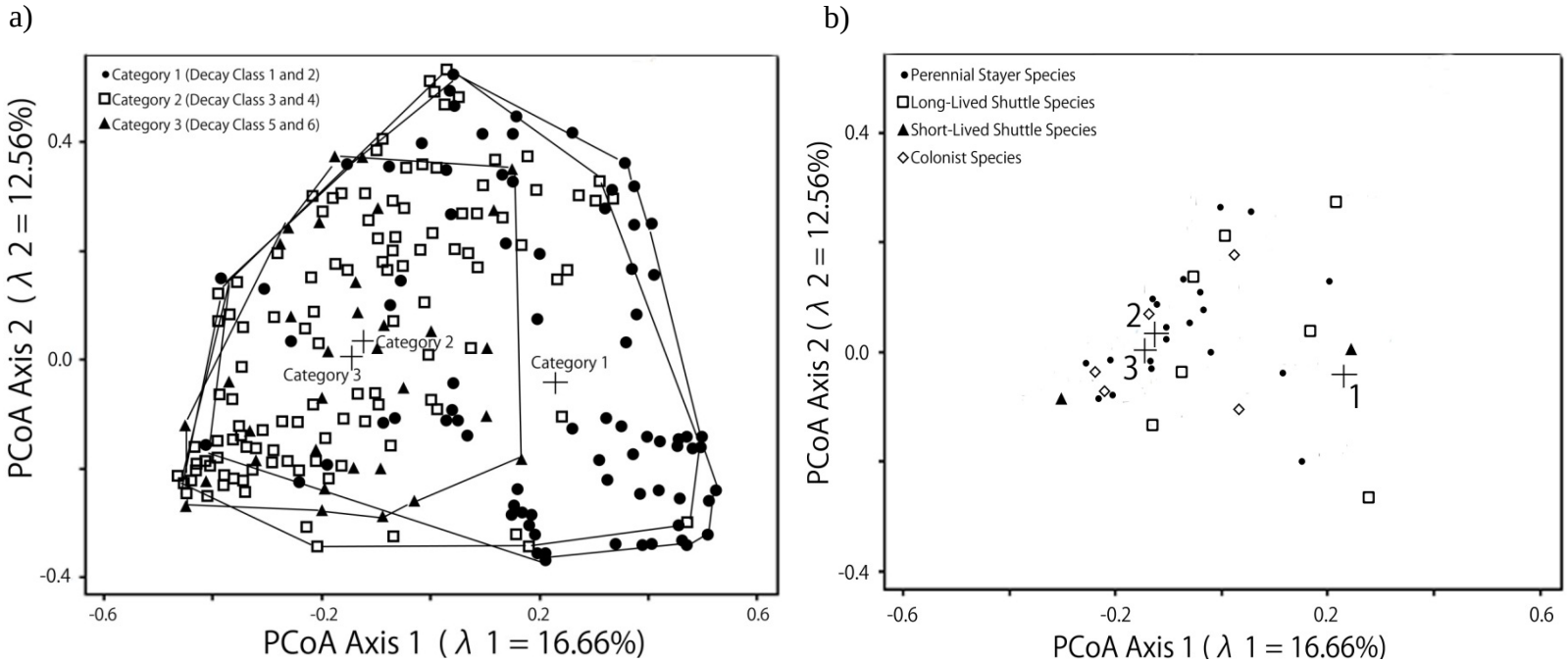


Figure 2-8. PCoA output for log decay class data. Analysis based on 35 species and 248 quadrats using Bray Curtis dissimilarity measure. a) Plot of quadrats coded by decay categories with decay category centroids. To simplify decay classes, they are coded as categories, where category 1= decay class 1 or 2; category 2: decay class 3 or 4; category 3: decay class 5 or 6. b) Plot of species centroids with decay category centroids. For species labels, as coded by life strategy and labeled with first three letters of genus name and three letters of species name, see Table 2-4 and Appendix 2-7.

Appendix 2-1. Sampling stand descriptions. Stand name is coded based on land ownership (W=Western Forest Products, H=Huu-ay-aht First Nation, F=Bamfield Huu-ay-aht Community Forest, B=Bamfield village, T=West Coast Trail (Pacific Rim National Park), K=Keeha Beach Trail (Pacific Rim National Park), C=Canopy Trail (Bamfield Marine Sciences Centre)). Age is a minimum estimate provided by these organizations. Average upper canopy cover, soil moisture, and soil pH were calculated from the three sites within each stand. Dominant slope and aspect throughout the stand was assessed based on visual estimates.

Stand Name	Age	Latitude	Longitude	Average upper canopy (%)	Average soil moisture (%)	Average soil pH	Slope	Aspect	Elevation (m asl)
W4a	4 (Y)	48°46'48.30"N	125° 6'26.90"W	0.83	0.68	5.5	slight	N	126
W4b	4 (Y)	48°46'39.40"N	125° 6'18.80"W	0.16	0.58	5.6	moderate	NE	152
H5a	5 (Y)	48°48'22.80"N	125° 5'58.20"W	0.25	0.78	5.4	level	n/a	10
H5b	5 (Y)	48°48'18.80"N	125° 6'23.50"W	0.85	0.52	6.1	level	n/a	13
W12	12 (Y)	48°46'46.97"N	125° 6'38.21"W	26.62	0.73	5.7	moderate	W	109
F16	16 (Y)	48°49'1.60"N	125° 7'21.10"W	29.17	0.67	6.3	slight	E	50
W17	17 (Y)	48°46'42.80"N	125° 5'31.30"W	2.89	0.35	6.4	moderate	NW	151
F35	35 (I)	48°49'32.67"N	125° 7'41.20"W	99.07	0.54	6.3	moderate	W	33
W38	38 (I)	48°47'15.90"N	125° 5'33.50"W	98.05	0.28	6.4	slight	NW	122
W39	39 (I)	48°47'33.20"N	125° 5'33.30"W	96.56	0.45	5.4	slight	SW	118
F40	40 (I)	48°50'3.16"N	125° 7'40.57"W	97.16	0.86	5.4	steep	NE	9
W42	42 (I)	48°47'24.10"N	125° 5'28.20"W	97.66	0.5	6.0	level	n/a	114
F50	50 (I)	48°48'57.70"N	125° 9'45.60"W	97.34	0.68	5.9	steep	E	9
B80	80 (I)	48°49'47.87"N	125° 7'59.15"W	98.46	0.28	6.6	slight	E	31
F120	120 (O)	48°49'3.90"N	125° 7'22.66"W	91.57	0.66	5.7	moderate	SE	48
T300a	>300 (O)	48°47'26.60"N	125° 6'49.60"W	97.94	0.65	5.5	level	n/a	44
T300b	>300 (O)	48°47'30.30"N	125° 6'53.40"W	94.69	0.73	5.1	level	n/a	7
K300a	>300 (O)	48°48'8.60"N	125° 9'45.20"W	89.36	0.95	5.2	level	n/a	23
K300b	>300 (O)	48°48'22.50"N	125° 9'41.80"W	84.69	0.64	5.3	slight	N	23
C300	>300 (O)	48°49'57.90"N	125° 7'40.19"W	97.18	0.66	5.7	slight	NE	17
W300	>300 (O)	48°48'10.10"N	125° 6'1.20"W	86.91	0.62	5.6	slight	NW	118

Appendix 2-2. Non-quantitative (survey) data of species present per sampling site. There was a total of 64 sites within stands (N=21), with three sites per stand and one additional site within stand W39. Stands were further grouped into age classes (young, intermediate, old, 7 stands within each). Sites are coded based on the land ownership of the stand to which they belong (W=Western Forest Products, H=Huu-ay-aht First Nation, F=Bamfield Huu-ay-aht Community Forest, B=Bamfield village, T=West Coast Trail (Pacific Rim National Park), K=Keeha Beach Trail (Pacific Rim National Park), C=Canopy Trail (Bamfield Marine Sciences Centre)). Species are coded by abbreviations used in ordination analyses and shown in Table 2-4. Presence is denoted as "1" if that species had any occurrences within the site, on any substrate type. a) Non-quantitative data for species in young sites; b) non-quantitative data for species in intermediate sites; c) non-quantitative data for species in old-growth cites.

a)

	W4a			**W4b**			**H5a**			**H5b**			**W12**			**F16**			**W17**		
	1	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Mosses																					
Anipal	0	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	1	0	0	0	0
Anisch	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Antcur	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Atrsel	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Auland	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Aulpal	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Brafri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brasta	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Callin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cerpur	0	1	1	0	1	1	1	0	0	0	1	0	0	0	1	0	0	1	0	1	1
Dicbre	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	0	0
Dicfus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dichet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Dicmon	1	1	0	1	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	1	1

	W4a			W4b			H5a			H5b			W12			F16			W17		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Dicpel	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0
Dicsco	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ditamb	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dithet	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ditsch	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Eurore	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
Eurpra	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Fonant	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Homful	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Hooluc	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Hylspl	1	1	1	1	1	1	1	0	1	0	1	1	1	0	0	1	1	1	1	1	1
Hypcir	0	1	0	1	1	1	0	0	0	1	1	0	0	1	1	0	0	1	1	1	1
Hypdie	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Isomyo	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1
Niperi	0	1	1	1	1	1	0	1	0	0	0	1	0	0	0	1	1	1	0	1	0
Oliali	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Plains	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plaund	1	1	1	1	1	1	1	1	0	1	1	0	0	1	1	1	1	0	1	0	1
Pogcon	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0
Pogurn	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Pohann	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pohnut	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Pohwah	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polalp	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0

	W4a			W4b			H5a			H5b			W12			F16			W17		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Polcom	0	1	0	1	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0
Poljun	1	1	0	1	1	1	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1
Polstr	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseele	0	0	0	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0
Ptycre	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
Ptylon	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Ptypse	1	1	0	0	1	0	1	1	0	0	0	1	1	0	0	1	1	0	0	1	1
Ptysp1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rachet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Raclan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Rhigla	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1	0	0	0	1	1	1
Rhylor	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Rhytri	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Roscap	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rossp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Sphang	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sphcap	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sphfal	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphgir	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Sphmen	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphpal	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Sphpap	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tetpel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Warexa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	W4a			W4b			H5a			H5b			W12			F16			W17		
	1	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Liverworts																					
Barlyc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baztri	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Bletri	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Calmue	1	1	0	0	0	1	1	1	0	0	0	0	0	0	1	1	1	0	0	1	0
Calnee	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Calsue	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cepbic	1	1	1	0	0	0	1	1	0	0	0	0	0	1	1	0	1	0	0	0	0
Cepdiv	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceplun	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cepple	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dipalb	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0
Douova	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Frunis	1	1	1	1	0	0	1	1	1	0	1	0	1	1	1	0	1	1	0	1	0
Heradu	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1
Kurpau	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leprep	0	1	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	0
Metcon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mylano	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Myltay	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Pelnee	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Plaasp	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0
Radcom	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Riccha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

	W4a			W4b			H5a			H5b			W12			F16			W17		
	1	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Riclat	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Ricmul	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ricpal	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Scabol	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1

b)

	F35			**W38**			**W39**				**F40**			**W42**			**F50**			**P80**		
	1	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Mosses																						
Anipal	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anisch	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antcur	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Atrsel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Auland	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulpal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brafri	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brasta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Camint	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cerpur	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicbre	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Dicfus	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0
Dichet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicmon	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Dicpel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	F35			W38			W39				F40			W42			F50			P80		
	1	2	3	1	2	3	1	2	3	4	1	2	3	1	2	3	1	2	3	1	2	3
Dicsco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ditamb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dithet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ditsch	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eurore	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Eurpra	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Fonant	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Homful	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hooluc	1	1	1	1	0	1	0	0	1	0	1	0	0	0	1	0	1	1	1	0	0	1
Hylspl	1	1	1	1	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	1	1	1
Hypcir	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
Hypdie	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isomyo	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Niperi	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oliali	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phifon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plains	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plaund	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pogcon	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Pogurn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pohann	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pohnut	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pohwah	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polalp	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	F35			W38			W39				F40			W42			F50			P80		
	1	2	3	1	2	3	1	2	3	4	1	2	3	1	2	3	1	2	3	1	2	3
Polcom	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Poljun	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Polstr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseele	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1
Ptycre	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptylon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptypse	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptysp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rachet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Raclan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhigla	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Rhylor	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Rhytri	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Roscap	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rossp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphang	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphcap	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphfal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphgir	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphmen	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphpal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphpap	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tetpel	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Warexa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	F35			W38			W39				F40			W42			F50			P80		
	1	2	3	1	2	3	1	2	3	4	1	2	3	1	2	3	1	2	3	1	2	3
Liverworts																						
Barlyc	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Baztri	1	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	1
Bletri	1	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Calmue	1	1	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Calnee	0	0	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Calsue	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cepbic	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	1	1	0	1	0
Cepdiv	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ceplun	1	1	1	0	1	0	1	1	1	0	0	1	1	0	1	0	1	0	0	1	0	0
Cepple	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Dipalb	1	1	1	0	1	0	0	1	1	1	1	1	0	0	1	1	1	0	1	0	1	0
Douova	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Frunis	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Heradu	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Kurpau	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leprep	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Metcon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mylano	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myltay	0	1	0	1	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Pelnee	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plaasp	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Radcom	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Riccha	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0	0

	F35			W38			W39				F40			W42			F50			P80		
	1	2	3	1	2	3	1	2	3	4	1	2	3	1	2	3	1	2	3	1	2	3
Riclat	0	0	1	1	1	1	0	1	1	0	1	1	1	0	1	0	1	1	1	0	0	0
Ricmul	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ricpal	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
Scabol	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

c)

	F120			T300a			T300b			R300a			R300b			C300			W300		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Mosses																					
Anipal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anisch	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antcur	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Atrsel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Auland	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulpal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brafri	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Brasta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callin	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Camint	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cerpur	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicbre	1	0	1	0	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0
Dicfus	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dichet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicmon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicpel	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0

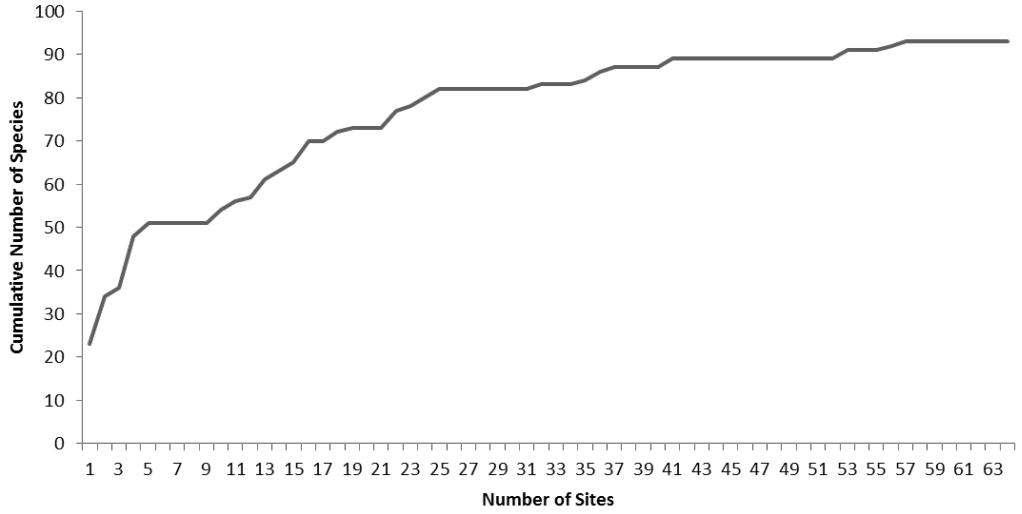
	F120			T300a			T300b			R300a			R300b			C300			W300		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Dicsco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ditamb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dithet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ditsch	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eurore	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Eurpra	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
Fonant	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Homful	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hooluc	1	0	0	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1
Hylspl	1	0	1	1	1	0	1	0	0	1	1	1	1	1	1	1	1	0	0	1	1
Hypcir	0	1	0	0	1	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1
Hypdie	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
Isomyo	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Metcon	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Niperi	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oliali	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phifon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plains	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Plaund	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pogcon	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pogurn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pohann	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pohnut	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pohwah	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	F120			T300a			T300b			R300a			R300b			C300			W300		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Polalp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Polcom	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Poljun	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Polstr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseele	1	1	1	1	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1	1	0
Ptycre	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptylon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptypse	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptysp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rachet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Raclan	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhigla	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Rhylor	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	1	1	1
Rhytri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Roscap	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rossp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphang	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphcap	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
Sphfal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphgir	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphmen	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Sphpal	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Sphpap	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tetpel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

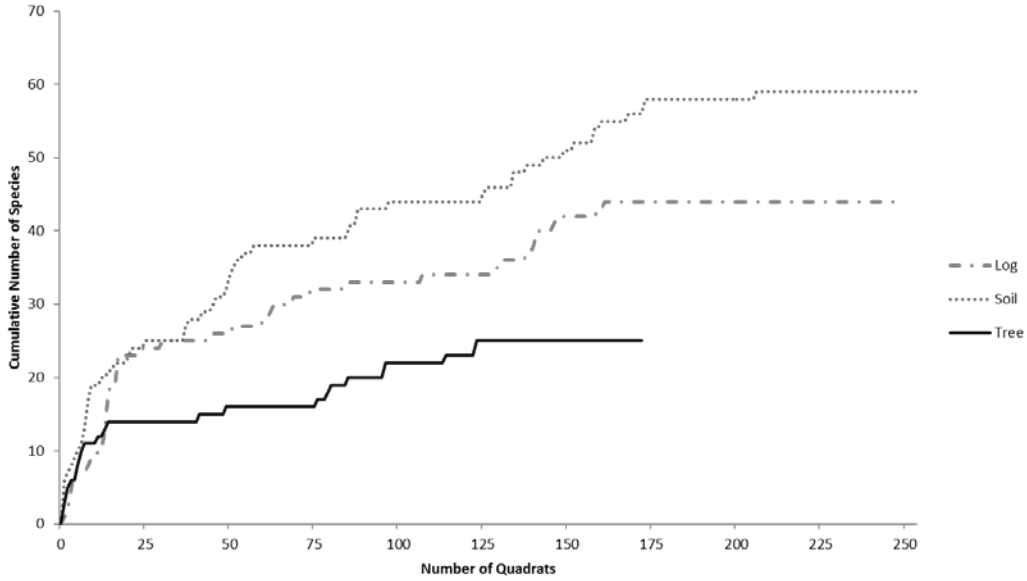
	F120			T300a			T300b			R300a			R300b			C300			W300		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Warexa	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Liverworts																					
Barlyc	1	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0
Baztri	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
Bletri	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Calmue	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	0
Calnee	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calsue	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1
Cepbic	0	1	1	1	1	1	0	1	1	0	1	1	1	1	0	1	0	1	1	1	1
Cepdiv	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceplun	1	0	1	1	1	1	0	1	1	1	1	0	1	0	0	0	1	0	1	1	1
Cepple	0	0	1	1	1	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0
Dipalb	1	1	1	1	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	1	0
Douova	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Frunis	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0
Heradu	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Kurpau	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0	0
Leprep	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1
Metcon	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mylano	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Myltay	1	1	1	0	0	0	0	1	0	1	1	1	1	1	0	1	0	1	0	1	0
Pelnee	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0
Plaasp	1	0	0	1	1	1	0	0	0	1	0	0	1	1	1	1	1	1	0	1	1
Radcom	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	F120			T300a			T300b			R300a			R300b			C300			W300		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Riccha	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0
Riclat	0	0	0	0	1	1	0	0	1	1	0	1	1	1	0	0	0	0	1	0	0
Ricmul	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ricpal	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Scabol	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

a)

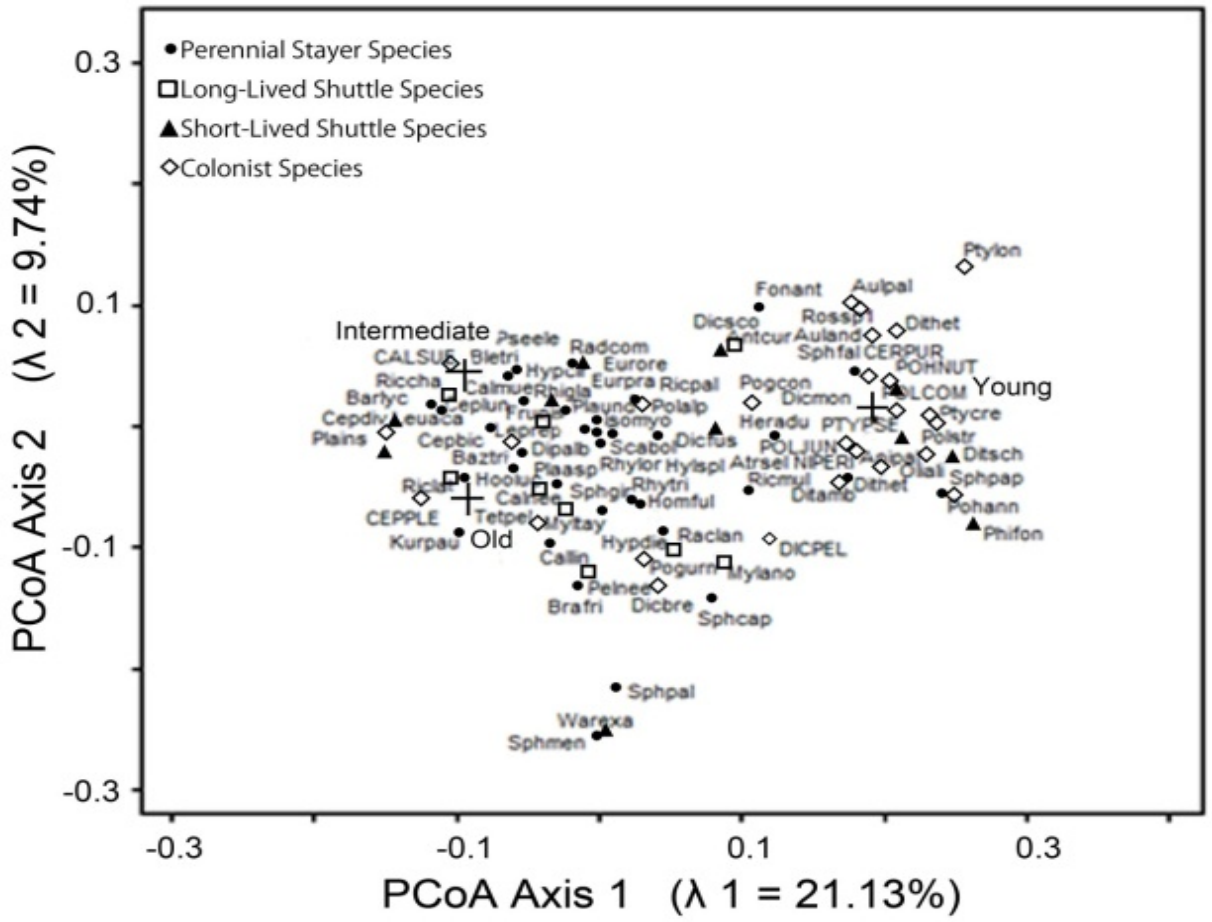


b)

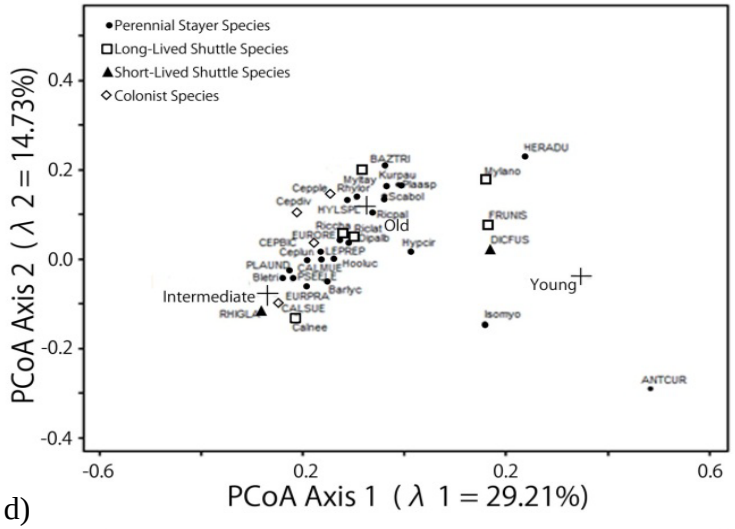


Appendix 2-3. Rarefaction curves, showing cumulative species sampled throughout the study area. a) Rarefaction curve for survey data, using cumulative species richness at the site level. A total of 63 sites were sampled across age classes (21 sites per age class). b) Rarefaction curves for three substrates, using cumulative species richness at the quadrat level (n_{log}=248, n_{soil}=252, n_{tree}=172).

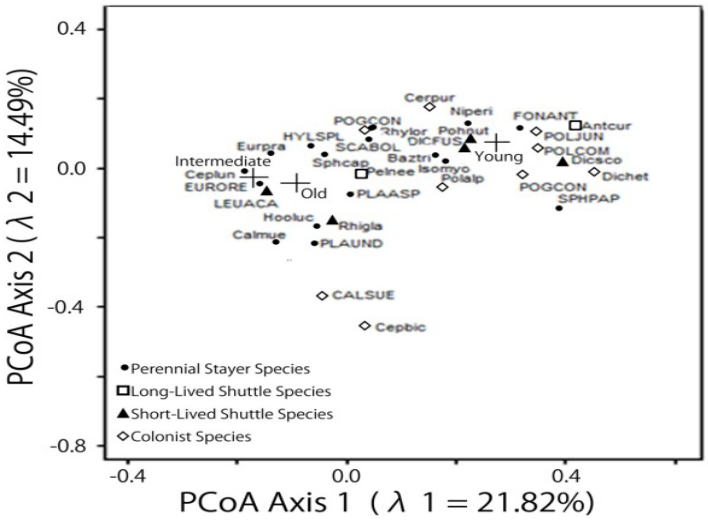
a)


Perennial Stayer Species
Long-Lived Shuttle Species
Short-Lived Shuttle Species
Colonist Species
PCoA Axis 2 (λ 2 = 9.74%)
PCoA Axis 1 (λ 1 = 21.13%)
0.3
0.1
-0.1
-0.3
-0.3
-0.1
0.1
0.3
Intermediate
Young
Old
Ptylon
Fonant
Aulpal
Dicsco
Antcur
Auland
Dithet
Sphfal
CERPUR
POHNUT
Pseele
Radcom
Eurore
Eurpra
Ricpal
Pogcon
Dicmon
Heradu
PTYPSE
Ptycre
Polstr
Ditsch
Sphpap
Pohann
Phifon
Oliali
Ricmul
Ditamb
Dicfus
Scabol
Dipalb
Baztri
Rhylor
Hylspl
Atrsel
Plaasp
Sphgir
Rhytri
Homful
Racian
DICPEL
Mylano
Pelnee
Dicbre
Sphcap
Callin
Brafri
Tetpel
Mytay
Kurpau
CEPPLE
Cepbic
Plains
Sphpal
Warexa
Sphmen

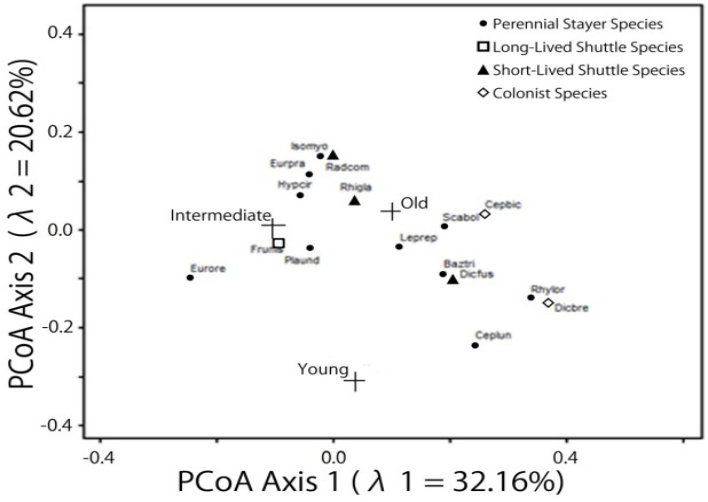
b)



c)

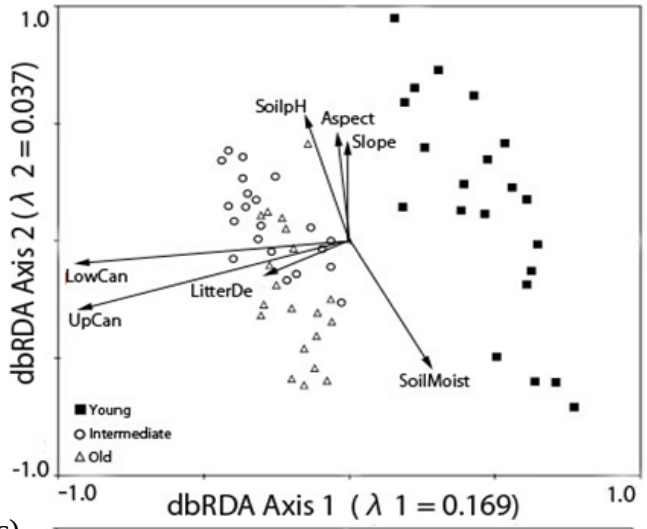


d)

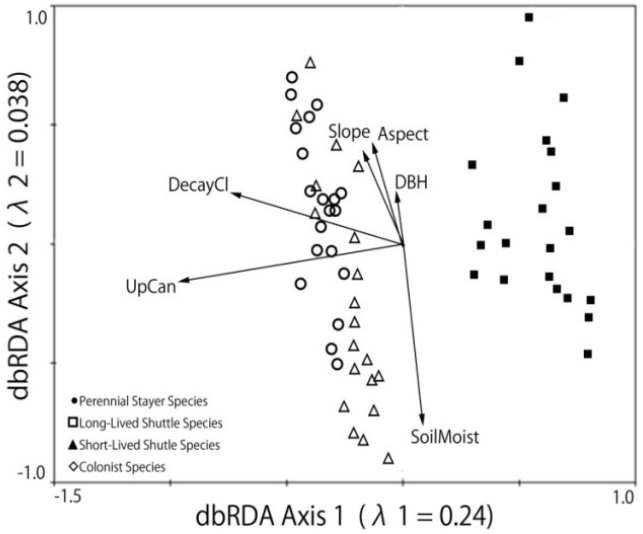


Appendix 2-4. PCoA output for survey and substrate data, grouped by age classes (young, intermediate, old) and showing species. Age class centroids and species centroids are shown. Species centroids are coded by life strategy symbols and are labeled by the first three letters of the genus and first three letters of the species (Table 2-4). In all cases, rare species with single occurrences are omitted from the analyses. a) Survey data PCoA on 82 species and 64 sites using the Sørensen dissimilarity measure. b) Soil data PCoA on 32 species and 63 sites, using Bray-Curtis dissimilarity measure. c) Log data PCoA on 34 species and 63 sites using Bray Curtis dissimilarity measure. d) Tree data PCoA on 16 species and 45 sites using Bray Curtis dissimilarity measure.

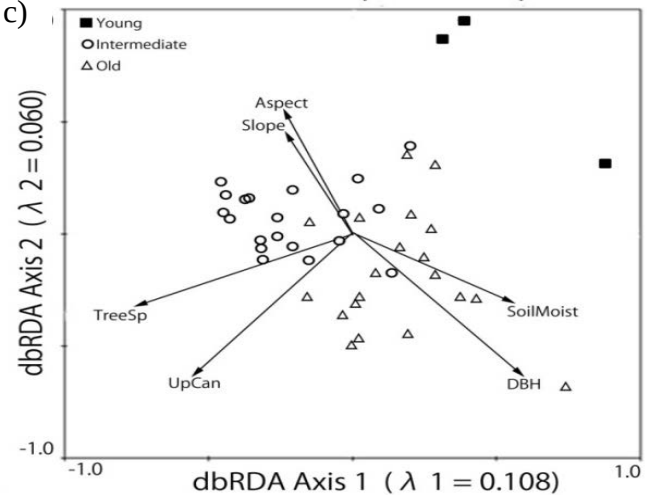
a)



b)

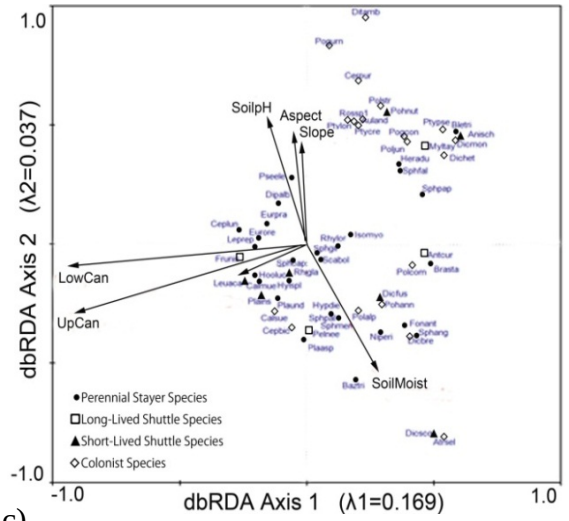


c)

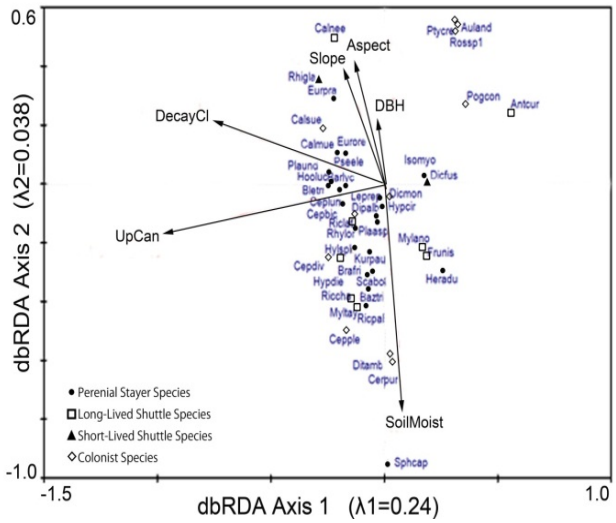


Appendix 2-5. Constrained ordination analyses for substrate data, showing sites and microhabitat data. dbRDA was calculated using Bray-Curtis dissimilarity measure. Sites are coded by age class. Arrows show magnitude and direction of habitat variables on the ordination axes. a) Soil data dbRDA based on 59 species and 63 sites. b) Log dbRDA based on 44 species and 63 sites. c) Tree dbRDA based on 25 species and 45 sites.

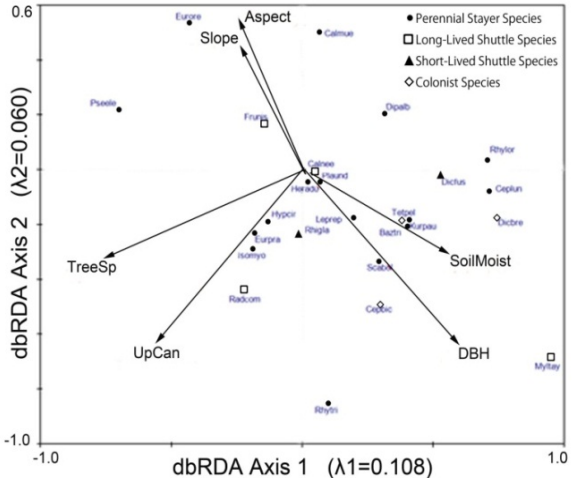
a)



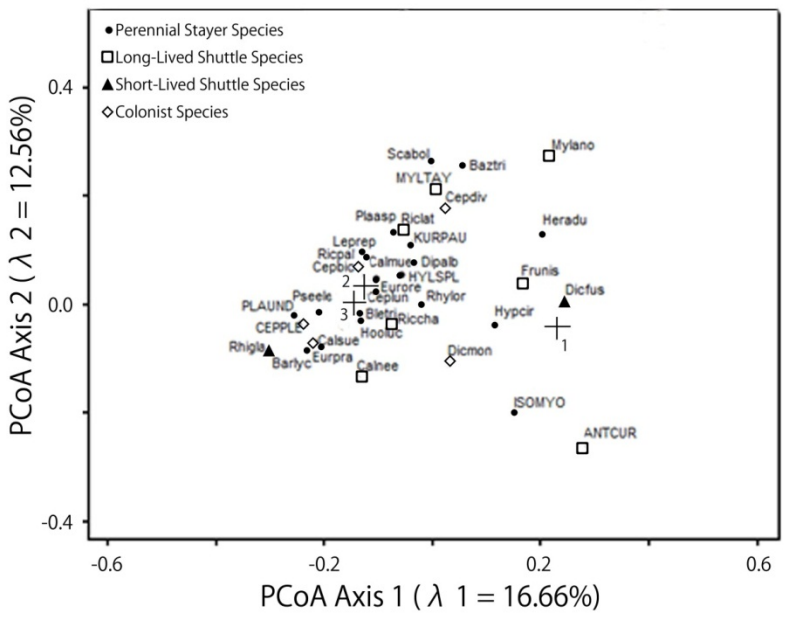
b)



c)



Appendix 2-6. Constrained ordination analyses for substrate data, showing species and microhabitat data. dbRDA calculated using Bray-Curtis dissimilarity measure. Species are coded by life strategy symbols and labeled with the first three letters of genus and first three letters of the species (Table 2-4). Arrows show magnitude and direction of habitat variables on the ordination axes. a) Soil data dbRDA based on 59 species and 63 sites. b) Log dbRDA based on 44 species and 63 sites. c) Tree dbRDA based on 25 species and 45 sites.



Appendix 2-7. PCoA output for log decay class data. Analysis based on 35 species and 248 quadrats using Bray Curtis dissimilarity measure. Plot of species centroids with decay category centroids. Species are coded by life strategy and labeled with first three letters of genus name and three letters of species name (Table 2-4).

Chapter 3:
Changes in species richness and composition of the bryophyte diaspore bank with soil depth and forest age in coastal western hemlock forests

Introduction

Bryophytes are an essential and highly diverse component of forest communities with a variety of key roles to play in ecosystem functions (Glime 2001). In particular, bryophytes retain moisture and facilitate nutrient cycling through the ecosystem (Weber and van Cleve 1984; Coxson 1991; deLucia et al. 2003). They help stabilize soils and provide substrates for vascular plant seed establishment, thus contributing to forest succession (Hart and Shankman 2005). However, previous studies of boreal and temperate rainforest disturbances have demonstrated severe impacts on bryophyte species richness and/or composition, as logging removes protective canopies, disturbs the soil, and alters decomposition and nutrient cycles by removal of woody debris (Gustafsson and Hallingbäck 1988; Newmaster et al. 2003; Kurulok and Macdonald 2007; Chapter 2). Whether such disturbances are anthropogenic or part of natural stochasticity, they contribute to rapid changes in available substrates and microhabitat conditions that can have negative effects on bryophytes.

Bryophytes have evolved a number of attributes that promote colonization after disturbance. Spore dispersal, clonal reproduction of existing populations, and germination from the soil diaspore bank facilitate rapid establishment of new populations (Rydgren and Hestmark 1997; Heinken and Zippel 2004; Ross-Davis and Frego 2004). Because bryophytes are often considered to have limited dispersal, *in situ* recolonization is an important process (Hylander 2009). Diaspores, defined as any structure that can potentially produce a new plant, are an essential component of *in situ* recolonization (Rydgren and Hestmark 1997; During 2001). Numerous diaspore types have been found in bryophyte species, including spores, specialized asexual propagules (i.e. gemmae, bulbils, tubers) and plant fragments (Imura 1994; Newton and Mishler 1994). In general, small,

lightweight spores tend to contribute to long distance dispersal of bryophytes, whereas asexual propagules, which tend to be larger and heavier, have limited dispersal distances and are therefore significant contributors to local population maintenance (Kimmerer and Young 1995).

Diaspores accumulated in the soil enable bryophytes to have temporal, as well as spatial, dispersal by remaining dormant until suitable conditions for germination and development occur (Laaka-Lindberg et al. 2003). Soil banks contain diaspores from a broad range of species, including those that occur in ephemeral and long-lived habitats. In particular, above-ground species deposit successive generations of diaspores into the soil, and as above-ground microhabitat conditions change, different successional species develop at the surface and contribute their diaspores (Hock et al. 2008). Thus, a species-rich diaspore bank is created, containing species suitable for inhabiting a variety of microhabitat conditions (During 2001). These diaspore archives extend the longevity of a population through cycles of succession or disturbance at a given microsite (Hock et al. 2008). Thus, the diaspore bank provides a temporal record of species found in the area, preserves diversity through time, and forms a genetic archive of past communities (Caners et al. 2009).

Following disturbances in forest ecosystems, the bryophyte diaspore bank is an essential component of recolonization. Many of the species whose diaspores persist are colonist taxa, which can rapidly recolonize from the *in situ* diaspore bank (Jonsson 1993). Studies have observed a significant discrepancy between above-ground flora and species represented in the diaspore bank, indicating the species that exhibit the greatest longevity in the soil differ from those that dominate above-ground communities (Jonsson 1993; During 2001; Maciel-Silva et al. 2012). The reproductive and life strategies of a species will have a significant impact on its preservation in the diaspore bank. For example, some species produce millions of small spores per capsule, which are effectively dispersed but tend not to survive long periods in the diaspore bank (During 1979; During 2001; Maciel-Silva et al. 2012). Other species produce larger spores or depend primarily on vegetative propagules. Although larger spores and vegetative

propagules have limited spatial dispersal, they tend to survive longer in the diaspore bank. Such strategies describe typical colonist species, whereas above-ground forest communities are typically dominated by perennial-stayer species, which disperse via gametophyte fragments or small spores, neither of which are long-lived in the diaspore bank (Jonsson 1993; Caners et al. 2009).

In addition to the negative impact on above-ground bryophyte flora, the diaspore bank can also be affected. Newmaster et al. (2007) found that the process of mechanical site preparation of a logged site for reforestation can severely disturb the upper soil layers that contain bryophyte diaspores. Such processes could affect the longevity and viability of the diaspore bank. Rydgren et al. (2004) found that species with diaspores at greater depths (i.e., below 5cm) recover better following disturbances, suggesting that shallow diaspores may be more susceptible to damage and disturbance.

Most diaspore bank studies have focused on grassland (During and ter Horst 1983; Bisang 1996; Hock et al. 2008) or boreal forest (Jonsson 1993; Caners et al. 2009) ecosystems. Few have looked at tropical rainforest ecosystems (but see Bisang et al. 2003; Maciel-Silva et al. 2012), and none have focused on temperate rainforests. In particular, temporal comparisons are rarely made between the diaspore bank and above-ground flora. Cool and moist conditions distinguish temperate rainforests from both boreal forests and tropical rainforests; such conditions provide suitable growing conditions for diverse bryophyte assemblages (Newmaster et al. 2003). In laboratory experiments, bryophyte spore longevity is influenced by moisture, with spore survival increased in dry conditions (van Zanten and Pocs 1981). Van Zanten and Pocs (1981) showed that the majority of species could withstand desiccation cycles for up to three years, with the longest drought resistance being 16 years under experimental conditions. Although many bryophytes are highly desiccation tolerant, high soil moisture in temperate rainforests may negatively affect diaspore longevity (Cleavitt 2002; Maciel-Silva et al. 2012).

The objectives of this study were 1) to determine which bryophyte species in the diaspore banks of west coast temperate rainforests of varying ages are

capable of recolonization under clear-cut conditions; 2) to test the effects of soil depth on species richness and composition of the soil diaspore bank; and 3) to compare the diaspore bank and above-ground terricolous taxa to assess the relationship between above- and below-ground floras. Although diaspores from bryophytes growing on other substrates (i.e., rocks, logs, tree bases) could be incorporated into the soil diaspore bank, it was expected that the majority of taxa in the soil diaspore bank would be terricolous species, as diaspore banks have the potential to exist in other substrates (i.e., decaying logs and the bark of trees), which would preferentially host bryophytes inhabiting those substrates (Maciel-Silva et al. 2012).

It was hypothesized that the most species-rich diaspore banks will be from young and intermediate aged stands. In the absence of disturbances, the diaspores of short-lived species in old-growth stands will have either germinated or expired, and due to a few species dominating above-ground, the diaspore bank richness would be consequently reduced (Jonsson 1993). Samples from a given soil core are expected to differ between top and bottom, as richness varies with depth of the sample (Bisang 1996). Finally, it was hypothesized that above and below ground species richness and composition will differ considerably. Above-ground communities are expected to have dominant species with a perennial stayer life strategy, whereas diaspore banks will consist of predominantly colonist and short-lived species, with more resilient propagules.

Methods

Study area

Diaspore bank richness and composition in coastal temperate rainforests of the west coast of Vancouver Island were examined. The study area was located within a 40km^2 area surrounding Bamfield, British Columbia, at 48˚50’ N, 125˚ 08’W, representing the very wet hypermaritime subzone (CWHvh) of the coastal western hemlock (CWH) biogeoclimatic zone, a region of coastal rainforests extending from sea level to approximately 900m asl. (Pojar et al. 1991;

MacKinnon 2003). The CWHvh has a mean annual precipitation of 1400-5000mm and a mean annual temperature in the region of 8˚C (MacKinnon 2003). The soils in the region are typically podzols (MacKinnon 2003); however, in the wettest regions, folisols are formed (Fox et al. 1987).

Study site

The forest stands sampled represented various ages in the CHWvh zone. Age classes were defined as young (<20 yrs), intermediate (30-80yrs), and old-growth (>100yrs), adhering to divisions of canopy formation described in Arsenault and Bradfield (1995) and Yearsley and Parminter (1998). Stand ages were confirmed by vegetation maps and forest studies (Morgan 2002; Andy MacKinnon, personal communication 2011, Sue McDonald, personal communication 2011). A total of 20 stands were studied (7 young, 7 intermediate, 6 old-growth; Figure 3-1). All sites were consistent in dominant above-ground flora and were below 150m elevation (within the CWHvh subzone; National Parks and National Historic Sites Canada 2005).

Sample design and data collection

Sampling design followed a nested format that included three 20x30m sites randomly located within each of 20 stands. Sites were positioned such that each was a minimum of 30m from the other two and the site edge nearest the stand perimeter was positioned within 50m of the perimeter. Above-ground bryoflora was surveyed throughout May and June 2011. Soil samples were taken at each site between June 20-22, 2011, following two days without precipitation. In addition to the lack of precipitation during this three-day period, the average daily high temperature was 17˚C, with a fairly constant relative humidity between 80-95% (Weaver and Wiebe 2012). Three adjacent soil cores were sampled from the central point (approximately 10m from the edge nearest the road and 15m from perpendicular edges) in each of three sites per stand for a total of 180 cores from 20 stands in 3 age classes (7 young, 7 intermediate, and 6 old-growth; Figure 3-2). Cores were taken by scraping all living plant material from the soil surface

and then using a mallet to drive a metal tube (12cm in length, 4cm in diameter) into the soil to a depth of 10 cm. The tube was the pulled out, and soil samples were extruded from the tube, wrapped, and stored at 4˚C until cultured. For an above-ground comparison, four 25x25cm quadrats were placed on soil substrates at 10 m intervals along a transect that bisected the site lengthwise (30m).

Diaspore bank cultures

From each 10cm core, the top 3cm and bottom 3cm were separated. For each site, the three cores were pooled, combining the top sections separately from the bottom. Living vascular plant material, visible, green bryophyte fragments, and large debris (i.e. pebbles and twigs) were removed.

Cultures were established in small sterile polystyrene petri dishes (60x15mm). A thin layer of weed-free potting soil (CIL GRO All-purpose Moisture Mix, containing peat moss, humus, compost, and perlite) was spread on the bottom of the dish to aid in water retention. This layer was covered with approximately 4g of either the top or bottom portion of the field soil core sample. This design yielded a total of 120 experimental dishes, representing the top and bottom soils per site. Control dishes consisted of only potting soil, either autoclaved (five dishes; soil autoclaved at 78˚C for 30 minutes) or unautoclaved (three dishes). Dishes were moistened with sterilized distilled water (autoclaved for 20 minutes at 121˚C) and then were placed in a growth chamber.

The growth chamber temperature was set at 14.9˚C, as cool temperatures during culturing deter the growth of fungal and algal contaminants (During and ter Horst 1983). Furthermore, optimal growing conditions for mosses and hepatics tend to be cool, moist conditions, as seen in the *in situ* growing conditions in the Bamfield study site and demonstrated in additional studies (Schofield 1988; Newmaster et al. 2003). Thus, this temperature mimics those during the growing season in Bamfield, maximizing growth potential. Cultures were grown under a light: dark regime of 16:8hrs, with a light intensity of 74.1μmol s^{-1} m^{-2}, using 215W light bulbs. Dish lids remained closed except when misted with sterile water, once every two or three days. To avoid any positional biases in light

intensity, dishes were repositioned biweekly within the growth chamber. Observations were taken every two weeks.

The first set of cultures was initiated September 5, 2011. To ensure maximum regeneration potential by maintaining substrate nutrient concentrations, the potting soil was unautoclaved for the first set of dishes. For all later dishes, the potting soil was autoclaved. A second set of dishes was initiated November 15, 2011. In the second set, entire soil samples (0-10cm) from sites (3) occurring within the same stand (20) were pooled to ensure adequate material, and samples were not subdivided by depth. Consequently, there was only one dish per stand, for a total of 20 diaspore bank cultures.

A shade treatment was set up on May 18, 2012 to test whether different species develop under conditions of less light. Additional subsamples were taken from the remaining pooled soil core samples and were set up identically to those from November 15, 2011, with one dish per stand, for a total of 20 experimental dishes and one control. These samples were cultivated using material from *in situ* experimental soil samples only, rather than layering experimental soil samples over potting soil. These dishes were placed under a lid that allowed approximately ¼ of full light to penetrate (13.6 μmol s^{-1} m^{-2}).

The full-light experiment was terminated April 30, 2012, after a total of eight months for the first set of dishes and five and a half months for the second set of dishes. The shade experiment was terminated September 27, 2012, for a total of four months of growth.

Identification

Each dish was examined for all germinated bryophyte species. Species determination was constrained by the lack of reproductive structures for some taxa (i.e., *Pohlia*, *Ptychostomum*, *Rosulabryum*, and *Dicranella*). These specimens were identified to genus. For other taxa, sparse material was a limiting factor. In particular, *Sphagnum* is a large and taxonomically challenging genus typically divided into nine sections (McQueen and Andrus 2007); specimens of *Sphagnum* were identified to section due to sparse material and an absence of well-developed

capitula. The pattern of pores and fibrils in stem cells and the shape of chlorophyllous cells in branch leaves were used to assign *Sphagnum* specimens to each section. Presence-absence data for all taxa were tallied per dish. Floras used for bryophyte identification were as follows: Lawton (1971), Ireland (2007), Vitt and Andrus (1977), McQueen and Andrus (2007), and Spence (2011) for mosses (Bryophyta); and Schuster (volumes I-VI 1966-1992), Smith (1990), and Schofield (2002) for liverworts (Marchantiophyta). Species nomenclature follows Crosby et al. (1999) for mosses and Stotler and Crandall-Stotler (1977) for liverworts. Following the growth period, permanent slides of each unique species were made for taxon vouchers and were deposited in the University of Alberta Cryptogamic Herbarium (ALTA).

Bryophyte richness

Species richness and species composition of soil cores taken from the 20 stands within three age classes were assessed. Initially, calculations were made separately for top and bottom segments of the soil cores to determine any variation in species richness. Subsequently, by pooling data from the top and bottom segments and combining these data with the stand-level richness derived from the dishes using stand-wide pooled soil samples, a measure of alpha, or local-scale, richness per stand, was generated (Tuomisto 2010). Although likely underestimating total diaspore bank richness, for the purposes of this study, gamma species richness was defined as the total below-ground number of species across the study area and was calculated by combining all cores within an age class.

To compare patterns of species richness, analyses of variance (ANOVA) were conducted using SPSS 19 (SPSS Inc. 2010). To compare species richness from top and bottom segments of the cores, a two-factor ANOVA was conducted at the stand level, with age class and top/bottom position as fixed factors. A single factor ANOVA was used to compare pooled (stand-level) diaspore bank richness among the age classes.

Species composition

To compare species composition among groups, principal coordinate analyses (PCoA) were conducted using PC-ORD version 6 (McCune and Mefford 2011). PCoA was chosen for the variety of distance measures that can be applied, rather than restricting the analysis to Euclidean distance, as in principal component analysis (Gotelli and Ellison 2004). PCoA gives the same result with each repetition and the ordination axes provide valuable information on the amount of variation in the data explained by each axes, offering an improvement on the widely used non-metric multi-dimensional scaling (Hirst and Jackson 2007). Sørensen's distance measure was used for all analyses, as all data was in presence/absence form. Ordinations were accompanied by a multi-response permutation procedure (MRPP). MRPP is a non-parametric test of the hypothesis of no difference between groups in ordination space, thus determining whether the groups tested in the ordination are significantly different from one another (McCune and Grace 2002). Two PCoAs were run for this study. The first compared species composition between top and bottom portions of the samples, and the second compared species composition among age classes.

Three indicator species analyses (ISA) were conducted (PC-ORD) to determine species indicative of: 1) top or bottom segments of soil cores, 2) the different age classes, and 3) surface samples or diaspore bank samples. A perfect indicator species is described as having a high occurrence in a particular group and absent from all other groups (Dufrêne and Legendre 1997). All indicator species analyses were conducted using 10,000 Monte Carlo iterations. Significant indicator species showed high indicator values and p-values < 0.05. To complement these analyses, unique species lists were created. A unique species occurred only in one group and was absent from all others. Three sets of unique species lists were created, one to complement each ISA. Local rarity (< 5 occurrences throughout all experimental dishes) was also assessed. Species from diaspore bank samples were compared to the British Columbia rare species lists (British Columbia Ministry of Environment 2012).

Results

During the field season (May-June 2011), there was 151.2mm of precipitation in May 2011 and 44mm in June 2011 (Weaver and Wiebe 2012). The mean monthly precipitation for these two months is 144.8mm and 105.5mm, respectively (Environment Canada 2012). The average temperatures during the field season were 9.05˚C in May 2011 and 12.32˚C in June 2011 (Weaver and Wiebe 2012). The average temperatures for those months from 2010-2012 are 10.6˚C and 12.6˚C, respectively (Environment Canada 2012).

Bryophyte germination

Under full light conditions, there was a total of 140 experimental and eight control dishes. The first indication of bryophyte growth was the appearance of protonemata, which are globular clusters of cells (liverworts) or branched, multicellular filaments consisting of chloronemata and caulonemata (mosses; Schofield 2001). Protonemata precede the development of the gametophyte in a moss or liverwort life cycle. Dishes initiated protonemal growth after approximately 10 days in the growth chamber. After three weeks, most plates showed widespread protonemata, with leafy gametophytes appearing after six weeks (Figure 3-3). New growth was minimal after five months, but plates remained in the growth chamber under observation for an eight month period to ensure maximum development for identification. Protonemata developed slowly under shade conditions, with extensive protonemata observed after five weeks and leafy gametophytes appearing after eight weeks.

A total of 28 taxa (22 mosses and 6 liverworts) emerged during the growth period, representing 14 families and 23 genera (Table 3-1). Growth was considerable under full light conditions; however, under shaded conditions, growth was sparse. A total of eight species were cultured across all shade dishes (Table 3-2), all of which were also observed in full light dishes. A total of eight experimental dishes and one control lacked bryophyte growth throughout the shade experimental period.

Seventeen taxa (12 mosses, and 5 liverworts) were identifiable to species. An additional eight taxa, including seven mosses (*Dicranella sp. 1*, *Pohlia* spp. *1* and *2*, *Ptychostomum* spp. *1* and *2*, *Rosulabryum sp. 1*, and *Eurhynchium sp. 1*) and one liverwort (*Cephaloziella sp. 1*), were only identifiable to genus, due to sparse material and lack of sporophytes or asexual reproductive structures. However, these eight taxa represent distinct biological entities that contribute to the overall taxon richness, so they were assigned unique numbers to facilitate their discussion. The final three taxa belonged to the genus *Sphagnum*. The material tended to be small and sparse, with a lack of developed capitula or stem leaves, which are essential for identification. Thus, due to sparse material and because this is a very large genus, taxa were taken to the level of the section within the genus. All determinations belonging to one section were considered the same taxon, as they were unable to be conclusively distinguished as different species. Of the 28 taxa, one taxon (*Ptychostomum sp. 2*) was restricted to a single control dish; because it was not detected in any experimental dishes, it was omitted from subsequent analyses of richness.

The majority of the species preferred soil substrates (75.0%). Log-dwelling species (14.3%) and tree-dwelling species (10.7%) were also represented (Table 3-1). The dominant life strategy represented was the colonist strategy, with 50.0% of taxa fitting the criteria, such as high reproductive effort in both sexual and asexual reproduction and a turf growth form (During 1979). Perennials and short-lived shuttle species also germinated readily (32.1% and 14.3%), whereas long-lived shuttle species and fugitive species were more rare (3.57% for each; Table 3-1).

Species richness

From the soil core cultures, 27 taxa (21 mosses and 6 liverworts) emerged (Table 3-3). None of the taxa are considered rare in British Columbia (British Columbia Ministry of Environment 2012). Five species (four mosses and one liverwort; *Arctoa fulvella*, *Atrichum undulatum*, *Funaria hygrometrica*, *Leptobryum pyriforme*, and *Gyrothyra underwoodiana*) were found exclusively in

the diaspore bank in the study area, with no above-ground occurrences (Table 3-2). This comparison with above-ground occurrences excludes taxa only identified to genus, as these are not conclusively absent above-ground. The depth samples (120 dishes) showed that the top portion of the soil cores produced a total of 23 taxa whereas the bottom portions produced 16.

On above-ground (extant) soil substrates, 59 taxa were enumerated across the study area (Table 3-3). Eleven taxa conclusively overlapped with the diaspore bank. An additional ten diaspore bank taxa represented genera found above-ground, but due to limited material could not be conclusively identified to species. Across all substrates above-ground, a total of 92 species were determined from the study area. Twelve taxa were found in both the diaspore bank and the above-ground flora on all substrates. An additional 11 taxa in the diaspore bank represented genera found above-ground but again could not be identified to species. Of the 92 species found above-ground, 33 species (35.87%) have been reported to produce specialized asexual propagules, even if such propagules were absent from the above-ground samples (Table 2-4). In the diaspore bank soil core samples, 11 out of the total 28 taxa (39.29%) have been reported to produce specialized asexual propagules (Table 3-1).

Effect of diaspore bank depth on richness and species composition

Species richness differed significantly between top and bottom portions of the soil samples, whereas stand age did not have a significant impact on this trend (Table 3-4). Across all age classes, top portions showed consistently higher richness than bottom portions (Table 3-3). The difference was greatest in old-growth samples, where the top portion had 83% more species than the bottom. In young and intermediate classes, top portions had 50.0% and 55.5% more species than the bottom portions, respectively. Both portions had the highest total richness in young stands (18 and 12, respectively), and both exhibited the highest average richness from young and intermediate stands. The average richness from young and intermediate stands were almost identical for top portions (2.71 ± 0.24 and

2.71±0.312, respectively), whereas bottom portions had the highest average richness in samples taken from intermediate stands (1.67±0.19).

In the comparison of top and bottom portions of the soil core, the two groups formed marginally significant groupings in ordination space, in spite of considerable overlap (Table 3-5; Figure 3-4a). Overall, bottom portions of samples tended to be more variable than the top portions. In this analysis, most taxa tend to cluster close to the portion centroids (Figure 3-4b; Appendix 3-2). For example, *Isothecium myosuroides* and *Eurhynchium sp. 1* tended to be strongly affiliated with the top centroid. Two of the three *Sphagnum* taxa also tended to cluster around the top centroid. Conversely, species such as *Polytrichum juniperinum* and *Pohlia sp. 1* were affiliated more strongly with the bottom centroid.

Seven taxa (*Eurhynchium sp. 1*, *Pogonatum urnigerum*, *Polytrichum juniperinum*, *Ptychostomum sp. 1*, *Tetraphis pellucida*, and *Frullania nisquallensis*) were unique to top portions, whereas only *Sphagnum* Sect. *Cuspidata* was unique to bottom portions (Table 3-2). There were no significant indicator species for the comparison of top and bottom portions of the diaspore bank (Table 3-6).

Effect of forest stand age on richness and species composition

When stand age is considered independently, it did not have a significant impact on bryophyte richness (Average richness $F_{2,17} = 1.379$, $p = 0.279$). When top and bottom portions of the soil cores were pooled, species richness was consistent across age classes (Table 3-3). Total richness was highest in young stands (20 species), declining in intermediate stands, with the fewest in old samples (15 species). Average richness in the young and intermediate age classes was almost identical (6.42±1.11 and 6.43±0.78, respectively), whereas average species richness in the old-growth age class was lower (5.00±0.63).

In the comparison among age classes, the groups formed in ordination space were not significantly different from one another (Table 3-5; Appendix 3-3). The greatest separation occurred between young and old sites. Pairwise

comparisons between young/intermediate and intermediate/old groups overlapped considerably (Figure 3-5a).

Three taxa (*Dicranella sp. 1*, *Ptychostomum sp. 1*, *Cephalozia bicuspidata*) were unique to young stands, and three taxa (*Pohlia sp. 1*, *Pohlia sp. 2*, and *Sphagnum* sect. *Cuspidata*) were unique to old-growth stands (Table 3-2). Only two taxa (*Pogonatum urnigerum* and *Frullania nisquallensis*) were unique to intermediate stands (Table 3-2). There were no significant indicator species for the comparison of the diaspore bank among age classes (Table 3-7).

Comparison with above-ground terricolous flora

Numerous significant indicator species were present in the comparison between above-ground and below-ground communities (Table 3-8). In this case, below-ground samples had a total of 6 significant indicator species (5 mosses, 1 liverwort). *Leptobryum pyriforme*, *Arctoa fulvella*, and *Sphagnum* sect. *Acutifolia* were the strongest indicator species. Five species, *Arctoa fulvella*, *Atrichum undulatum*, *Funaria hygrometrica*, *L. pyriforme*, *Gyrothyra underwoodiana*, were unique to the diaspore bank. Above-ground samples had a total of 12 significant indicator species (10 mosses, 2 liverworts). *Eurhynchium praelongum* and *Hylocomium splendens* were the strongest indicator species for above-ground communities.

In vitro cultures

In addition to bryophyte growth, cultures included diaspores of other phyla including algae, fungi, and tracheophytes. Fungi and algae were found in both experimental and control dishes, and growth peaked after approximately eight weeks and before subsiding to a constant, low level. Fern gametophytes also frequently emerged on experimental dishes. Of the seed plants, graminoid seedlings emerged periodically, and broad-leaved seedlings emerged more infrequently. Many studies address fungal contamination of bryophyte growth cultures (During and ter Horst 1983; Bisang 1996; Hock et al. 2008); however, the fungi, algae, and tracheophytes in this study were likely cohabitants of soil

substrates with bryophytes. In particular, fungi, algae, and bryophytes typically form biological soil crusts on bare soil, thus promoting soil stability (Eldridge 1998; Delach and Kimmerer 2002; Bowker 2007); therefore, fungi and algae were expected to appear on the bare soil of the culture dishes.

Out of the total 148 dishes grown in full-light conditions, seven experimental and two control dishes lacked bryophyte growth throughout the growth period. The weedy colonist species *Leptobryum pyriforme*, developed in five control dishes and 119 experimental dishes and was the only bryophyte growth on 52 experimental dishes. As a common greenhouse contaminant, it is possible it originated in the potting soil mixture. Aerial contamination from propagules is unlikely, as the growth chamber was sterilized prior to the study and a concurrent culture experiment did not detect similar levels of contamination. Autoclaving the potting soil reduced the occurrence of *L. pyriforme*, with germination in four out of 21 dishes (19.05%), compared to 120 occurrences out of 129 unautoclaved dishes (93.02%). It was also observed on six out of 20 experimental shade treatment dishes (30.00%), in which only field sample soil was used to establish the dishes. *Leptobryum pyriforme* is reported from the study area (Lawton 1971), although it was not observed above-ground in this study. Because it could not be considered exclusively a contaminant, it was retained for all analyses.

Discussion

It was hypothesized that species richness would be higher in samples from young and intermediate age classes and from top portions of soil cores. It was also expected that the species composition in the diaspore bank would differ from above-ground soil quadrats. This study demonstrated that depth affects species richness, but stand age does not, and species composition above- and below-ground differed. This study demonstrates that diaspore banks are temporal archives of bryophyte diversity, containing propagules from species with a wide array of life strategies and environmental preferences.

Culturing success and life strategies represented in the diaspore bank

A total of 28 bryophyte taxa germinated across all experimental and control dishes. This compares with previous diaspore bank studies of grasslands and both boreal and tropical forests, which ranged from 15 to 56 taxa germinating from culture experiments (During and ter Horst 1983; Bisang 1996; Rydgren and Hestmark 1997; Caners et al. 2009; Maciel-Silva et al. 2012). The majority of the diversity was made up of mosses, as few liverworts germinated. This is in contrast with previous boreal and tropical forest studies, where germinating liverworts were abundant (Jonsson 1993; Rydgren and Hestmark 1997; Bisang et al. 2003; Maciel-Silva et al. 2012). The results of the present study reflect the dominance of soil substrate species. Most of the liverworts in the study area preferred tree or log substrates to soil (Chapter 2), which could contribute to a poor representation in the soil diaspore bank, as diaspores would be preferentially maintained on other substrates (Maciel-Silva et al. 2012). As an alternative to poor representation in the soil diaspore bank, liverwort diaspores may have been present but unable to successfully germinate on soil due to specificity for other substrates.

None of the 28 cultured taxa were considered rare (Environment Canada 2012), indicating that the diaspore bank species consist of common, above-ground taxa in the region. Five species (*Arctoa fulvella*, *Atrichum undulatum*, *Funaria hygrometrica*, *Leptobryum pyriforme*, and *Gyrothyra underwoodiana)* were restricted to the diaspore bank; however, they have been reported previously in the region; Lawton 1971; Schofield 2002). All five preferred open canopies, and they germinated in samples from young, recently disturbed sites. Such findings indicate that the current above-ground conditions in regenerating forests may not be suitable for all diaspores in the diaspore bank, and in particular these five taxa would thrive in different above-ground conditions.

This study demonstrates a species-rich diaspore bank throughout the study area. The life strategies represented in the diaspore bank demonstrate its importance to the patterns trait-based assembly rules, where colonists and perennial guilds utilize the diaspore bank to differing degrees (Wilson 1989; Götzenberger et al. 2012). Anticipated colonist species were well represented in

the diaspore bank, with 15 taxa exhibiting this strategy (Table 3-1). Colonists are generally short-lived, but they invest in both sexual and asexual reproduction (During 1979; During 1992). Above-ground, these species were abundant in recently disturbed stands, where they thrive in short-lived gaps and temporary substrates. A diaspore bank rich in colonists facilitates their rapid colonization (During 1979; Hock et al. 2004; Baldwin and Bradfield 2005).

Perennials (i.e., *Eurhynchium sp. 1*, *Isothecium myosuroides*, *Pseudotaxiphyllum elegans*, *Scapania bolanderi*, and *Cephalozia lunulifolia*, common taxa of the extant flora) also germinated readily, with a total of nine developing in culture. The presence of perennial species germinating from the diaspore bank under full light conditions contrasts with previous studies in which their occurrence in the diaspore bank was rare (Jonsson 1993; During 2001). Although perennial species dominated the above-ground flora in old-growth stands and were sparse in young stands, these findings indicate that perennials are capable of emerging from the diaspore bank immediately following disturbance, as opposed to being restricted to shaded conditions of later successional stages. Similarly, Caners et al. (2009) and Maciel-Silva et al. (2012) found occasional perennial species germinating under full light conditions from boreal mixed-wood and tropical rainforest diaspore bank samples, respectively.

The culture experiment showed that considerably fewer species grew under shaded conditions than under full light. This indicates that many of the taxa present in the diaspore bank prefer growing under full light conditions typical of early stages of succession. These taxa were predominantly colonist and short-lived shuttle species, with the only perennials being *Pseudotaxiphyllum elegans* and *Sphagnum* sect. *Acutifolia* (Table 3A-2). All of the species that grew in the shaded conditions were also observed under full-light conditions, indicating adaptations to a broad range of germination conditions.

Leptobryum pyriforme growth was common on experimental and control dishes. Its occurrence in dishes that did not use potting soil as well as those that did indicates that it likely occurred both in the diaspore bank and the potting soil mix. Although a common greenhouse contaminant, *L. pyriforme* is also a weedy

colonist species in nature, including in the region around Bamfield. It reproduces asexually by bulbils on the protonema and stems and by rhizoidal gemmae (Lawton 1971). *Leptobryum pyriforme* was also the only taxon to produce sporophytes in culture in this study, indicating that it is capable of rapid and prolific reproduction.

Asexual propagation

Bryophytes are predominantly clonal organisms that produce a variety of specialized or unspecialized asexual propagules. Each type may persist for varying lengths of time in the diaspore bank (Miles and Longton 1990; Imura 1994). Many bryophytes produce specialized asexual propagules that employ different germination strategies (Newton and Mishler 1994). In addition to specialized propagules, fragments of leaves, stems, or rhizoids can regenerate whole gametophytes (Laaka-Lindberg et al. 2003). Thus, although unspecialized, fragments are a common and effective means of asexual reproduction for a wide variety of bryophyte species. The taxa observed both above- and below-ground represent a diverse assortment of reproductive strategies, and although asexual propagules were only rarely observed in culture, many of these taxa invest energy in producing such structures.

Of particular interest are the five taxa that were absent from above-ground samples, suggesting long-term survival in or long-distance dispersal to the diaspore bank. Two of the five taxa unique to the diaspore bank, *Arctoa fulvella* and *Funaria hygrometrica*, are not known to produce specialized asexual diaspores. Furthermore, given that these taxa would have dispersed from distant forest stands outside the study area, their appearance in the diaspore bank samples is presumed to be through long-distance dispersal of spores. The remaining taxa produce asexual propagules. As discussed, *Leptobryum pyriforme* reproduces prolifically by both spores and asexual reproduction, as does *Atrichum undulatum*. *Gyrothyra underwoodiana*, the only liverwort unique to the diaspore bank, typically produces gemmae but also invests heavily in spores (Schofield 2002).

Effect of depth within the soil core

Species richness was consistently higher in cultures utilizing the upper soil core diaspore bank (top 3cm) than those using the lower portion (bottom 3cm). This is consistent with previous studies where viable diaspores are unevenly distributed in the soil, resulting in declines of species richness and number of diaspores with increasing depth (Leck and Simpson 1987; Bisang 1996; Rydgren and Hestmark 1997). Top portions are also continuously replenished with diaspores, and due to more viable diaspores occurring in upper portions, germination potential in culture is also greater.

Diaspore survival decreases with time, as those present for longer periods in the diaspore bank are more likely to be subject to degradation, decomposition, and fungal attacks (During 2001; Hock et al. 2008). Only persistent, decay-resistant diaspores can survive diverse taphonomic conditions. As a result, short-lived, less resistant diaspores, such as fragments, are lacking from samples germinated from greater depths. This pattern has been observed in bryophyte diaspore banks (Jonsson 1993; Rydgren and Hestmark 1997; Hock et al. 2008), fern spore banks (Ranal 2003) and seed plants (Sullivan and Ellison 2006).

Across all samples, eight taxa (*Eurhynchium sp. 1*, *Pogonatum urnigerum*, *Pohlia sp. 1*, *Polytrichum juniperinum*, *Ptychostomum sp. 1*, *Frullania nisquallensis*, and *Scapania bolanderi*) were found in the upper soil core samples only, and only one taxon (*Sphagnum* sect. *Cuspidata*) was found exclusively in the bottom soil core samples. Perennial species tended to occur more frequently in top portions of the soil. The diaspores of these taxa were likely vegetative fragments, as sporophytes of these taxa were rarely produced above-ground in the study area, and asexual propagules are not reported for these taxa (Lawton 1971; Imura 1994). Perennial species tend to be under-represented in the diaspore bank and their diaspores tend to be shorter-lived and likely do not persist long enough to migrate to greater depths in the soil (Jonsson 1993; Rydgren and Hestmark 1997; During 2001). This pattern was supported by the indicator species analyses, where *Sphagnum* sect. *Acutifolia*, *Isothecium myosuroides*, and *Eurhynchium sp. 1* were the strongest indicators for top portions.

Soil-dwelling colonist species dominated the bottom portions of the soil samples. *Polytrichum juniperinum* and *Pohlia sp. 1* were strongly associated with bottom portions in the ordination, with *Funaria hygrometrica* and *Dicranella sp. 1* as weak indicator species for bottom portions. These species produce a variety of propagules that are both abundant and viable for long periods in the soil (Miles and Longton 1990; During 2001; Ross-Davis and Frego 2004). *Polytrichum juniperinum*, *Dicranella* spp., and *F. hygrometrica* readily produce spores that can accumulate in the diaspore bank, and *Pohlia* spp. often produce gemmae as well as spores (Lawton 1971). This demonstrates that colonist species, which tend to produce numerous diaspores that remain viable for long periods, may be present throughout the diaspore bank, whereas perennial species tend to be confined to top portions.

Effect of forest stand age

Diaspore bank richness and species composition were consistent across age classes, refuting the hypothesis that diaspore bank richness would decline in older stands due to diaspore mortality and germination outweighing replenishment. This indicates that the taxa represented in the diaspore bank are long-lived and that diaspores are continuously replenished through time (Jonsson 1993; Bisteau and Mahy 2005; Hock et al. 2008).

The species-rich cultures from the diaspore bank in young stands showed that recent logging did not extensively damage or deplete the diaspore bank. This is in contrast to the suggestions of Newmaster et al. (2007) and Rydgren et al. (2004), who proposed that logging practices disrupt the soil, potentially damaging the diaspore bank. In addition to its resilience, the completeness of the diaspore bank in young stands demonstrates the connection between young and old-growth stands. Spores that were deposited under old-growth conditions before deforestation (<20 years ago) remain viable and germinate in young forest samples. In older stands, species tend to be missing from the diaspore bank, due to diaspore mortality and germination over time (During 2001).

The liverwort *Cephaloziella sp. 1* and the mosses *Pohlia nutans*, *Rosulabryum sp. 1*, and *Ptychostomum pseudotriquetrum* were the strongest indicator species for young stands, although not significant. All of these taxa are typically short-lived, soil-dwelling taxa that occurred above-ground in young stands as well, so their diaspores are likely recently deposited in young soil samples. Additionally, because these taxa produce abundant spores or asexual propagules (in the case of *Ptychostomum pseudotriquetrum* and *Cephaloziella sp. 1*), these diaspores are abundant and persistant in the samples, resulting in successful germination.

Perennial species appeared more frequently in the diaspore banks of stands where they occur above-ground, given their short-lived spores and vegetative fragments that require a local source for replenishment (During 2001). During et al. (1987) found a similar pattern, where perennial bryophytes were only found in the diaspore bank in sites where the same species occurred above-ground. This indicates that these taxa rely on vegetative reproduction from fragments, which are short-lived in the diaspore bank. In the present study, it is unclear whether the surface perennial species that likely replenished the diaspore bank survived *in situ* above ground or originated from diaspores dispersed from nearby intact forest. These populations may have been established by long-distance dispersal or expansion of an existing surface population (Rydgren and Hestmark 1997; Heinken and Zippel 2004), rather than from the diaspore bank. Regardless of the main source of these diaspores, the surface populations contribute to the diaspore bank, ensuring the maintenance of these populations.

Comparison with above-ground flora

Although representing different species than the current above-ground community, the diaspore bank flora most closely resembled that of the above-ground soil flora. Community composition differed strongly between above- and below-ground samples, with numerous significant indicator species emerging. Thus, both diaspore bank and above-ground communities are more internally consistent than they are similar to each other. Two species absent from the above-

ground surveys, *Arctoa fulvella* and *Atrichum undulatum*, were significant indicator species for diaspore bank samples. These taxa likely possess propagules that are long-lived in the diaspore bank and they prefer conditions not found in the study site, such as disturbed, rocky soil (Lawton 1971). *Atrichum undulatum* and *Arctoa fulvella* produce abundant spores; Miles and Longton (1990) report thousands of spores per capsule in *Atrichum undulatum*. Furthermore, the asexual propagules (gemmae) of *Atrichum undulatum* further enhance their persistence in the diaspore bank (Lawton 1971; Imura 1994).

Some of the strongest indicator species for above-ground communities included *Dicranum fuscescens*, *Eurhynchium oreganum*, *E. praelongum*, *Hookeria lucens*, *Hylocomium splendens*, *Rhizomnium glabrescens*, and *Rhytidiadelphus loreus*. These species tend not to invest strongly in long-lived diaspores (Rydgren and Hestmark 1997; During 2001). Typically, bryophytes are subjected to a trade-off between adult and diaspore longevity. As a result, long-lived perennial species tend to have short-lived diaspores, limiting their representation in the diaspore bank (During 2001). The discrepancy between diaspore bank and surface demonstrates the importance of preserving the diaspore bank to ensure the survival of species not always found above-ground.

Maciel-Silva et al. (2012) reported that bryophytes can employ diaspore banks in other substrates besides soil, such as in decaying logs or in the bark of trees; thus, bryophytes growing preferentially on such substrates may be found as components of these other diaspore banks, rather than the soil diaspore bank. Therefore, the diaspore banks in substrates other than soil should be examined in the study area to fully understand the full role of bryophytes, including their diverse and persistent diaspores in this ecosystem.

Conclusions

Overall, the diaspore bank flora differed considerably with depth, whereas it was consistent among age classes. Upper portions of the soil cores possessed a greater diversity of bryophyte taxa compared with lower portions. Colonist taxa were abundant in all samples, whereas perennials were more restricted to upper

portions and samples from older age classes. Colonist species relied heavily on the diaspore bank to recolonize after disturbances, having a greater abundance of diaspores surviving for longer periods in the soil. Perennial species invested less in long-lived diaspores, so they tended to be abundant above-ground, but less common in the diaspore bank. The diversity in upper portions of the soil shows that shallow depths were essential for recolonization following disturbances and serving as a genetic memory of the community over time, from which species can germinate when suitable conditions arise.

This study emphasized that the diaspore bank is an important component for bryophyte recolonization following a disturbance. Upper layers of the soil were the most species-rich and thus the most important in maintaining bryodiversity and initiating recolonization. Consequently, forest harvesting techniques that cause minimal disturbances to the soil are ideal to maintain the integrity of the diaspore bank into the future. This study indicates that given the diaspore size, the diaspore bank is relatively resistant to disturbances and species richness of the diaspore bank is not negatively affected by harvesting practices. However, because the diaspore bank contains unique species and represents only a small subset of the above-ground flora, maintaining diversity both above- and below-ground is essential to facilitate regeneration of a species-rich bryoflora following disturbance.

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Table 3-1. Summary table of diaspore bank taxa. Taxa germinated from soil samples in culture under growth-chamber conditions. Abbrev.=species name abbreviations, used in ordination diagrams. Family and taxonomic grouping (moss/liverwort) are also included. Life strategy and growth form compiled from Caners et al. (2009); Baldwin (2004); Schuster (1966-1992); Lawton (1971); and During (1979), where C=colonist, F=fugitive, L=long-lived shuttle, P=perennial, S=short lived shuttle. Preferred substrate determined by comparison with above-ground flora; if absent, preferred substrate determined from Lawton (1971). Specialized asexual propagules indicate known occurrences of such structures in each taxon, compiled from Lawton (1971), Shaw (1980), Imura (1994), McQueen and Andrus (2007), and Spence (2011) for mosses, and Schuster (1974), Schuster (1980), Hong (1980), Hong (1989) and Schofield (2002) for liverworts. For taxa that were identified to genus and represent families where specialized propagules are known to occur, the presence or absence of propagules could not be determined in this study.

Abbrev.	Taxon	Family	Life Strategy	Growth Form	Preferred Substrate	Specialized Asexual Propagules
Mosses						
Arcful	*Arctoa fulvella* (Dicks.) Bruch & Schimp.	Dicranaceae	S	turf	soil	None
Atrund	*Atrichum undulatum* (Hedw.) P. Beauv.	Polytrichaceae	C	turf	soil	Rhizoidal tubers
Dic1	*Dicranella* Schimp. sp. 1	Dicranaceae	C	turf	soil	Undetermined
Eur1	*Eurhynchium* Bruch & Schimp. sp. 1	Brachytheciaceae	P	weft	soil	None
Funhyg	*Funaria hygrometrica* Hedw.	Funariaceae	F	turf	soil	None
Isomyo	*Isothecium myosuroides* Brid.	Brachytheciaceae	P	weft	tree	None
Leppyr	*Leptobryum pyriforme* (Hedw.) Wilson	Bryaceae	C	turf	soil	Rhizoidal tubers
Pogurn	*Pogonatum urnigerum* (Hedw.) P. Beauv.	Polytrichaceae	C	turf	soil	None
Pohann	*Pohlia annotina* (Hedw.) Lindb.	Bryaceae	C	turf	soil	Gemmae (upper leaf axils)
Pohnut	*Pohlia nutans* (Hedw.) Lindb.	Bryaceae	S	turf	soil	None
Poh1	*Pohlia* Hedw. sp. 1	Bryaceae	S	turf	soil	Undetermined
Poh2	*Pohlia* Hedw. sp. 2	Bryaceae	S	turf	soil	Undetermined
Poljun	*Polytrichum juniperinum* Hedw.	Polytrichaceae	C	turf	soil	None
Pseele	*Pseudotaxiphyllum elegans* (Brid.) Z. Iwats.	Hypnaceae	P	mat	soil	Branch-like axillary propagulae
Ptypse	*Ptychostomum pseudotriquetrum* (Hedw.) J.R. Spence & H.P. Ramsay	Bryaceae	C	turf	soil	Gemmae (axillary and rhizoidal)
Pty1	*Ptychostomum* Hornsch. sp. 1	Bryaceae	C	turf	soil	Undetermined
Pty2	*Ptychostomum* Hornsch. sp. 2	Bryaceae	C	turf	soil	Undetermined
Ros1	*Rosulabryum* J.R. Spence sp. 1	Bryaceae	C	turf	soil	Undetermined
Sphacu	*Sphagnum* Sect. Acutifolia (Russow) Schimp.	Sphagnaceae	P	turf	soil	None

Abbrev.	Taxon	Family	Life Strategy	Growth Form	Preferred Substrate	Specialized Asexual Propagules
Sphcus	*Sphagnum* Sect. Cuspidata Lindb.	Sphagnaceae	P	turf	soil	None
SphSqu	*Sphagnum* Sect. Squarrosa (Russow) Schimp.	Sphagnaceae	P	turf	soil	None
Tetpel	*Tetraphis pellucida* Hedw.	Tetraphidaceae	C	turf	log	Gemmae (apical), protonemal flaps
Liverworts						
Cepbic	*Cephalozia bicuspidata* (L.) Dumort.	Cephaloziaceae	C	thread	log	Gemmae (apical)
Ceplun	*Cephalozia lunulifolia* (Dumort.) Dumort.	Cephaloziaceae	P	thread	log	Gemmae (apical)
Cep1	*Cephaloziella* (Spruce) Schiffner sp. 1	Cephaloziellaceae	C	thread	log	Gemmae (apical)
Frunis	*Frullania nisquallensis* Sull.	Frullaniaceae	L	mat	tree	None
Gyrund	*Gyrothyra underwoodiana* M. Howe	Gyrothyraceae	C	mat	soil	Gemmae (apical)
Scabol	*Scapania bolanderi* Austin	Scapaniaceae	P	mat	tree	Gemmae (apical)

Table 3-2. Taxon occurrence in the diaspore banks. Proportion of occurrence is calculated as the number of experimental plates on which each species germinated. Asterisks represent unique species. Unique species by top/bottom shows species found only in top portions or bottom portions. Unique species by age classes show species found in only one age classes. Unique species below-ground shows species found only in soil samples. For above-ground taxa unique to soil substrates, see Chapter 2 Table 2-5.

Abbreviation	Taxon	Proportion of Occurrence		Unique Species by Top/Bottom		Unique Species by Age Class			Unique Species Below-Ground
Mosses		Full Light (N=140)	Shade (N=20)	Top	Bottom	Y	I	O	
Aful	*Arctoa fulvella*	0.136	0						*
Aund	*Atrichum undulatum*	0.129	0						*
Dic1	*Dicranella* sp. 1	0.021	0			*			
Eur1	*Eurhynchium* sp. 1	0.021	0	*					
Fhyg	*Funaria hygrometrica*	0.021	0						*
Imyo	*Isothecium myosuroides*	0.064	0						
Lpyr	*Leptobryum pyriforme*	0.85	0.3						*
Purn	*Pogonatum urnigerum*	0.007	0	*			*		
Pann	*Pohlia annotina*	0.014	0.05						
Pnut	*Pohlia nutans*	0.093	0						
Poh1	*Pohlia* sp. 1	0.007	0	*				*	
Poh2	*Pohlia* sp. 2	0.007	0.15					*	
Pjun	*Polytrichum juniperinum*	0.014	0	*					
Pele	*Pseudotaxiphyllum elegans*	0.05	0.05						
Ppse	*Ptychostomum pseudotriquetrum*	0.029	0.15						
Pty1	*Ptychostomum* sp. 1	0.014	0	*		*			
Pty2	*Ptychostomum* sp. 2	0	0						
Ros1	*Rosulabryum* sp. 1	0.036	0.05						
Sacu	*Sphagnum* Sect. Acutifolia	0.107	0.25						
Scus	*Sphagnum* Sect. Cuspidata	0.007	0		*			*	
SphSqu	*Sphagnum* Sect. Squarrosa	0.043	0						
Tpel	*Tetraphis pellucida* Hedw.	0.014	0	*					
Liverworts									
Cbic	*Cephalozia bicuspidata*	0.021	0.05			*			
Clun	*Cephalozia lunulifolia*	0.029	0						
Cep1	*Cephaloziella* sp. 1	0.043	0						

Abbreviation	Taxon	Full Light (N=140)	Shade (N=20)	Top	Bottom	Y	I	O	Unique Species Below-ground
Fnis	*Frullania nisquallensis*	0.007	0	*			*		
Gund	*Gyrothyra underwoodiana*	0.021	0						*
Sbol	*Scapania bolanderi*	0.021	0	*					

Table 3-3. Gamma richness and total and average alpha richness of soil core portions and overall soil cores shown across three age classes. Gamma species richness represents the total below-ground number of species across the study area. Top denotes the upper 3cm of soil cores, and bottom denotes the bottom 3cm of the cores. Top and bottom averages were taken across all 60 sites in three age classes. Overall denotes richness from entire soil core samples, including top and bottom portions as well as stand-level samples. Average richness is reported with standard errors. There were 60 experimental dishes for each of top and bottom portions. These samples were pooled and combined with 20 stand-level dishes from the second set of dishes that had not been separated into top and bottom segments. A comparison is made with above-ground total and average richness on soil substrates only across 63 sites, within 21 stands across the three age classes.

		Young		*Intermediate*		*Old*	
	Gamma Richness	Total Richness	Average Richness	Total Richness	Average Richness	Total Richness	Average Richness
Top (n=60)	23	18	2.71 $\pm$ 0.24	14	2.71 $\pm$ 0.31	11	2.33 $\pm$ 0.31
Bottom (n=60)	15	12	1.62 $\pm$ 0.19	9	1.67 $\pm$ 0.19	6	1.28 $\pm$ 0.11
Diaspore Overall (n=140)	27	20	6.43 $\pm$ 1.11	19	6.43 $\pm$ 0.78	15	5.00 $\pm$ 0.63
Above-Ground Soil Substrate (n=63)	59	43	13.86 $\pm$ 1.01	22	9.43 $\pm$ 0.81	23	9.86 $\pm$ 0.91

Table 3-4. Analysis of variance output for top and bottom soil core portions. Results from 2-factor analysis of variance for average and total richness in soil core portions among age classes. Age class (3 categories: young, intermediate, old) and position (2 categories: top 3cm, bottom 3cm) are fixed factors. *df*=degrees of freedom, *F*=*F*-statistic (test statistic) generated from ANOVA analysis. Average richness was taken among site samples per age class. Total richness was calculated as the total number of taxa germinated from all dishes per position and age class. *=$p<0.05$, **=$p<0.01$, ***=$p<0.001$.

	Average Richness			*Total Richness*		
	df	*F*	*p*-value	*df*	*F*	*p*-value
Age Class (fixed)	2,34	1.120	0.338	2,34	2.632	0.087
Position (fixed)	1,34	16.314	<0.000***	1,34	22.380	<0.000***
Age Class x Position	2,34	0.170	0.845	2,34	0.058	0.944
Error	34			34		

Table 3-5. Multi-response permutation procedures (MRPP) output for two separate ordination analyses, comparing species composition with depth and among age classes. MRPP accompanied each PCoA, and pairwise comparisons among groups defined in the ordination analyses are shown. Top-bottom addresses PCoA of top and bottom portions of soil cores (24 spp, 118 samples). Age class addresses PCoA of overall soil samples categorized by age class (27 spp, 20 stands). Above-/below-ground represents the PCoA comparing diaspore bank samples to surveys of above-ground soil-dwelling bryophytes (49 taxa, 41 stands). T=test statistic for MRPP, A=chance-corrected within-group agreement (a measure of within-group homogeneity, compared to the random expectation). *=$p<0.05$, **=$p<0.01$, ***=$p<0.001$.

	1 vs 2			1 vs 3			2 vs 3		
	T	A	*p*-value	T	A	*p*-value	T	A	*p*-value
Top-Bottom	-2.40	0.0092	0.031*						
Age Class	-0.73	0.02	0.22	-1.62	0.042	0.07	0.14	-0.0037	0.51

Table 3-6. Soil core portion indicator species analysis. Top denotes upper 3cm and bottom denotes bottom 3cm of the soil cores. All indicator species reported, as no significant indicator species were generated. Within portion, species are divided into mosses and liverworts, and listed in order of decreasing significance.

	Indicator Value	*p*-value
Top		
Sphagnum sect. *Acutifolia*	12.3	0.0571
Isothecium myosuroides	8.6	0.1137
Eurhynchium sp. 1	5.0	0.2410
Rosulabryum sp. 1	5.3	0.3618
Leptobryum pyriforme	50.4	0.3670
Tetraphis pellucida	3.3	0.4835
Pseudotaxiphyllum elegans	3.8	0.6151
Atrichum undulatum	7.6	0.7822
Arctoa fulvella	9.3	0.7927
Pohlia nutans	6.3	1.0000
Sphagnum sect. *Squarrosa*	3.0	1.0000
Pohlia sp. 1	1.7	1.0000
Polytrichum juniperinum	1.7	1.0000
Ptychostomum sp. 1	1.7	1.0000
Scapania bolanderi	5.0	0.2401
Cephalozia lunulifolia	3.8	0.6123
Cephaloziella sp. 1	4.4	0.6812
Cephalozia bicuspidata	2.2	1.0000
Gyrothyra underwoodiana	2.2	1.0000
Frullania nisquallensis	1.7	1.0000
Bottom		
Funaria hygrometrica	2.2	1.0000
Sphagnum sect. *Cuspidata*	1.7	1.0000
Dicranella sp. 1	0.8	1.0000

Table 3-7. Age class indicator species analysis. Three age classes are represented (young, intermediate, old). All indicator species are shown, as no significant indicator species were generated. Within age class, species are divided into mosses and liverworts, and listed in order of decreasing significance.

	Indicator value	*p*-value
Young		
Pohlia nutans	41.1	0.1203
Rosulabryum sp. 1	25.7	0.2793
Ptychostomum pseudotriquetrum	14.3	0.6368
Dicranella sp. 1	14.3	1.0000
Ptychostomum sp. 1	14.3	1.0000
Funaria hygrometrica	7.1	1.0000
Pohlia annotina	7.1	1.0000
Polytrichum juniperinum	7.1	1.0000
Cephaloziella sp. 1	35.7	0.0974
Cephalozia bicuspidata	28.6	0.3084
Scapania bolanderi	19.0	0.5185
Gyrothyra underwoodiana	7.1	1.0000
Intermediate		
Atrichum undulatum	48.6	0.0606
Arctoa fulvella	34.0	0.5106
Pseudotaxiphyllum elegans	23.4	0.5249
Eurhynchium sp. 1	18.0	0.7425
Pogonatum urnigerum	14.3	1.0000
Old		
Pohlia sp. 1	16.7	0.2960
Sphagnum sect. *Cuspidata*	16.7	0.2975
Pohlia sp. 2	16.7	0.3062
Sphagnum sect. *Acutifolia*	28.6	0.4484
Isothecium myosuroides	26.9	0.4528
Sphagnum sect. *Squarrosa*	17.9	0.6540
Tetraphis pellucida	9.0	0.7430
Frullania nisquallensis	16.7	0.3059
Cephalozia lunulifolia	17.9	0.5467

Table 3-8. Above- and below-ground indicator species analysis. Below-ground denotes species that germinated from soil core samples, whereas above-ground denotes terricolous species growing in the study area. Analysis conducted at the level of the stand. Only significant indicator species are shown. Within sampling location, species are divided into mosses and liverworts, and listed in order of decreasing significance.

	Indicator Value	*p*-value
Below-Ground		
Arctoa fulvella	26.7	0.0001
Leptobryum pyriforme	98.3	0.0001
Atrichum undulatum	20.0	0.0005
Sphagnum sect. *Acutifolia*	18.3	0.0007
Pohlia nutans	17.1	0.0063
Cephaloziella sp. 1	10.0	0.0279
Above-Ground		
Eurhynchium praelongum	83.3	0.0001
Hylocomium splendens	61.7	0.0001
Eurhynchium oreganum	60.0	0.0001
Rhytidiadelphus loreus	48.3	0.0001
Rhizomnium glabrescens	58.3	0.0001
Dicranum fuscescens	38.3	0.0001
Hookeria lucens	23.3	0.0001
Plagiothecium undulatum	13.3	0.0072
Polytrichum juniperinum	15.2	0.0085
Pogonatum contortum	11.7	0.0149
Plagiochila asplenoides	13.3	0.0072
Scapania bolanderi	17.6	0.0140

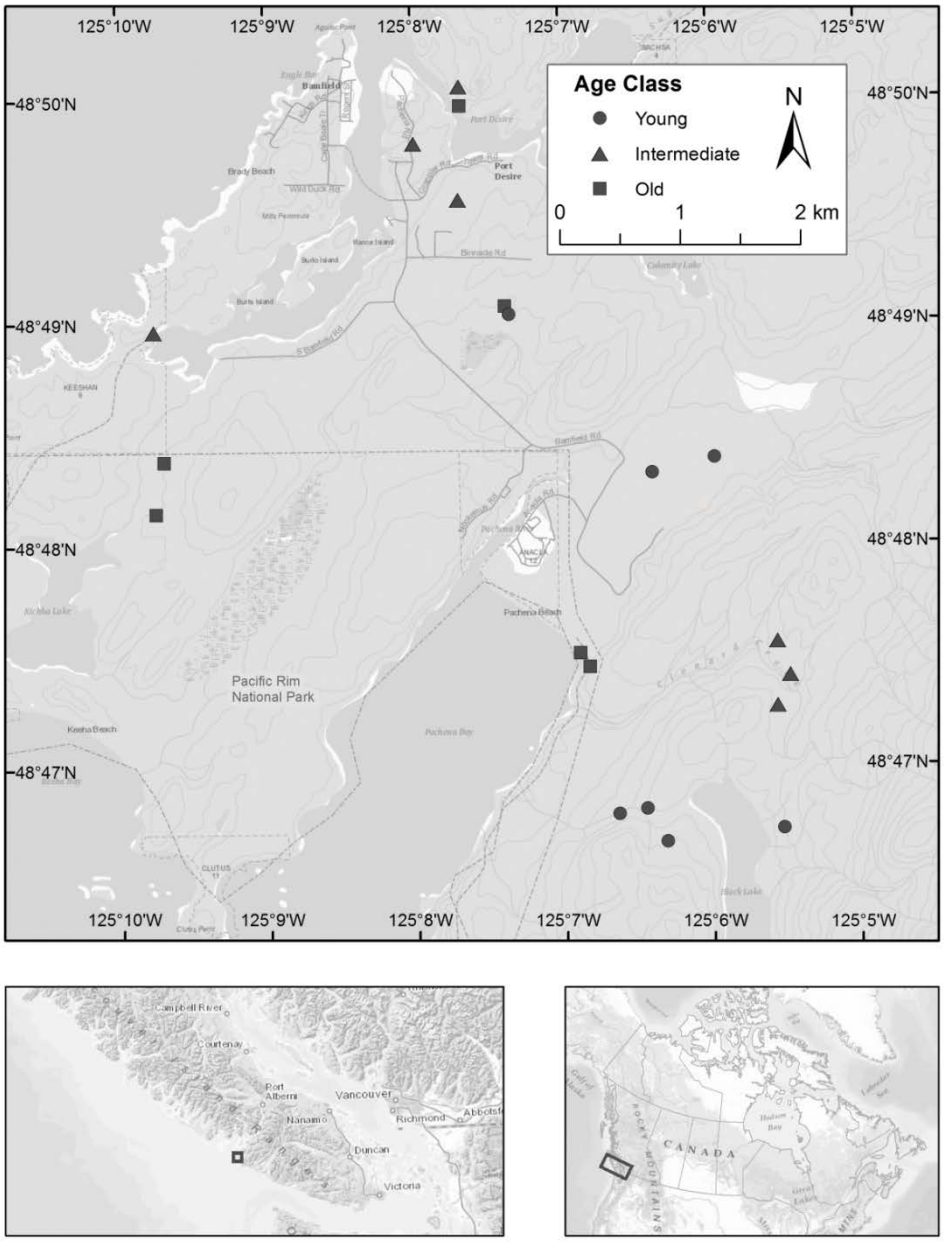


Figure 3-1. Map of the study area, showing stands sampled. Circles indicate young stands (<20 years), triangles indicate intermediate stands (30-80 years), and squares indicate old-growth stands (> 100 years). Each stand contained three sampling sites, from each of which three soil cores were taken. Inset maps show location of the study area near Bamfield, British Columbia. For stand descriptions, see Appendix 3-1.

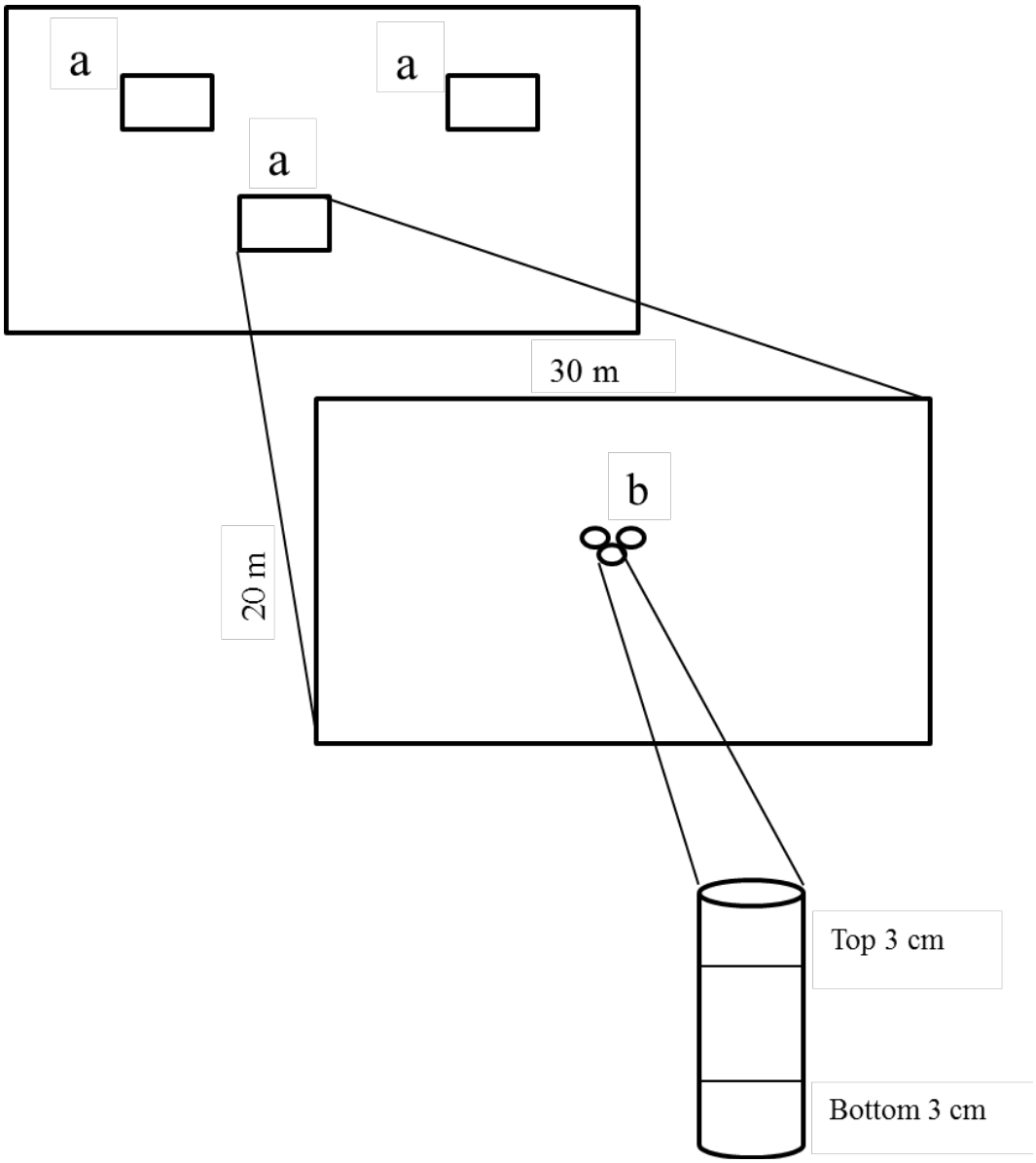


Figure 3-2. Sampling design, showing stands, sites, and soil cores. Three sites were nested within a stand, with seven stands in each of the young and intermediate age classes, and six stands in the old age class, for a total of 60 sites in 20 stands representing the three forest age classes (young, intermediate, old), for a total of 180 cores sampled. Three cores were sampled at the centre of each site. The cores were taken using a metal tube 12 cm long and 4 cm in diameter. The top 3 cm and bottom 3 cm were cultured separately; a third set of dishes used in the middle portion of the core. a=sites (20x30m), b=soil cores.

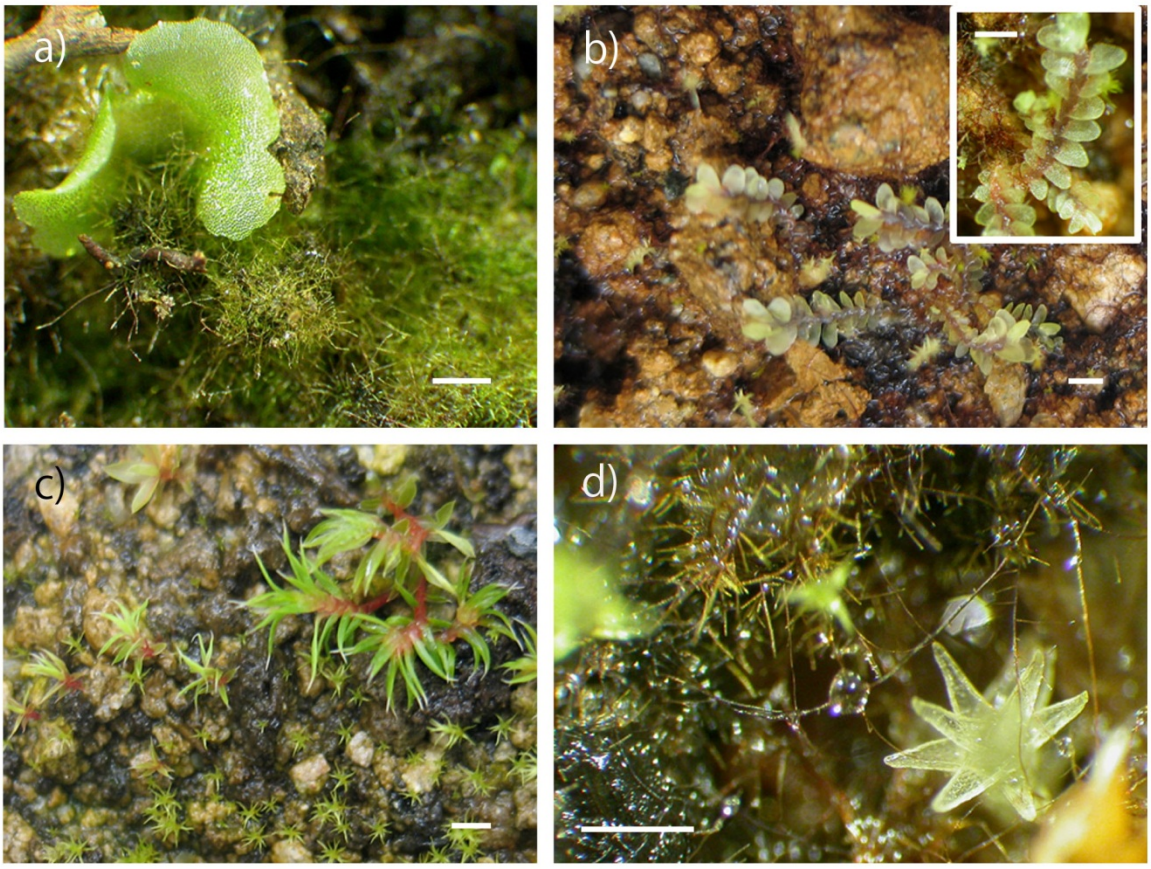


Figure 3-3. A selection of taxa cultivated in the growth chamber experiments. a) Bryophyte protonema, photographed after approximately three months of cultivation. A fern gametophyte is shown in the upper left. b) *Gyrothyra underwoodiana*, a liverwort species unique to the diaspore bank, photographed after approximately four months of cultivation. Moss protonemata are also visible. Inset: close-up of gametophyte stem showing leaf arrangement and rhizoid patches on stem. c) *Polytrichum juniperinum*, a species common between above-ground soil samples and diaspore bank samples, photographed after approximately five months of cultivation, shown in upper right, with *Leptobryum pyriforme* in lower portion. d) *Sphagnum* sect. *Acutifolia*, photographed after approximately four months of cultivation, shown with filamentous protonemata from a different taxon in upper right. Scale bars: a) and d) 1mm; b) and c) 2mm.

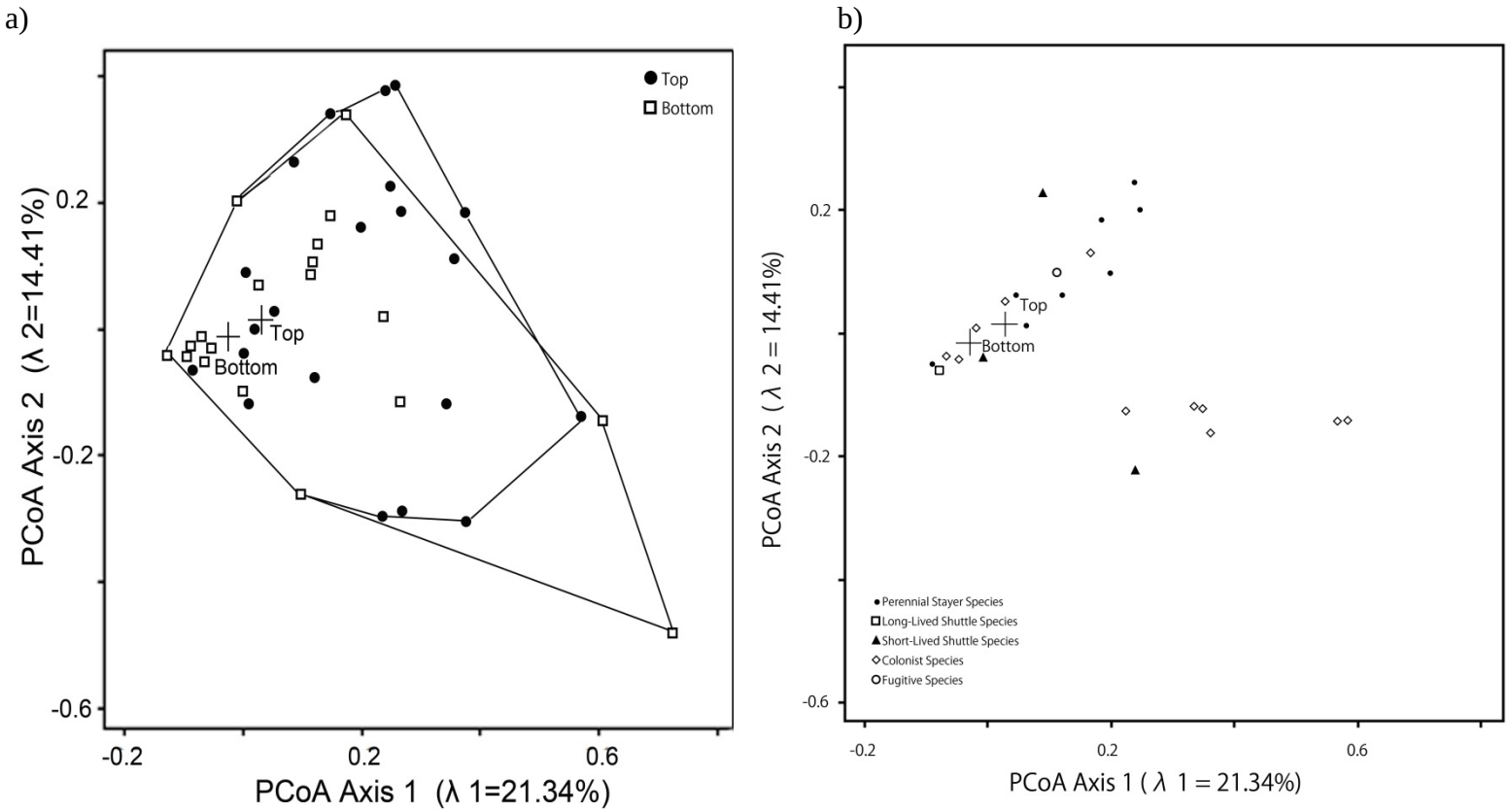


Figure 3-4. PCoA output for diaspore bank samples, showing soil core portions (top, bottom). Samples were taken from top 3cm and bottom 3cm portions of soil cores. Ordination utilizes 24 species and 118 sample portions, using the Sørensen dissimilarity measure. a) Plot of sample portions coded by top/bottom position with position centroids indicated. b) Plot of taxa centroids with core portion centroids. Species coded by life strategy. For taxa names, labeled with the first three letters of the genus name and first three letters of the species name, see Appendix 3-2, and for taxon abbreviations, see Table 3-1.

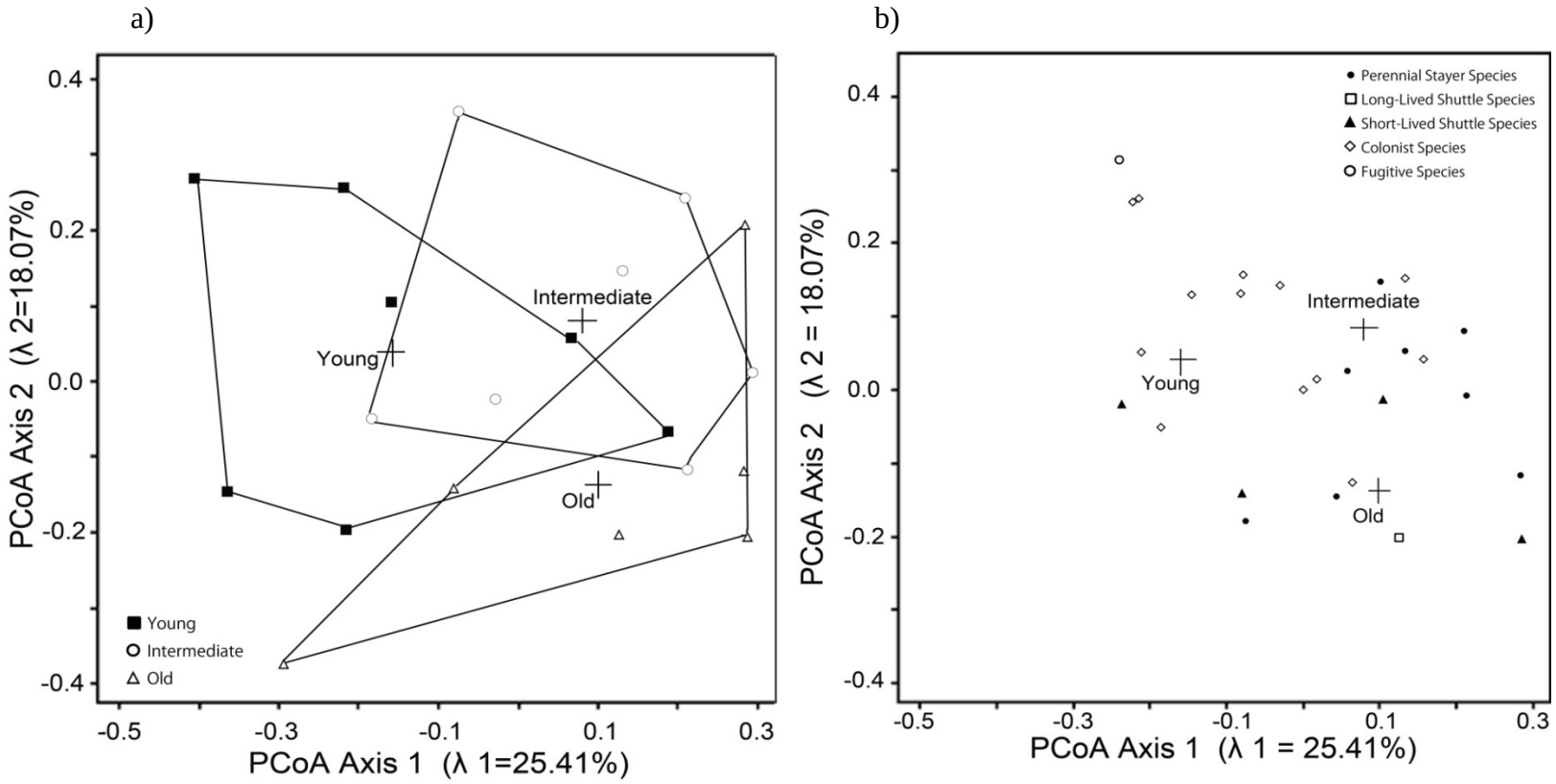
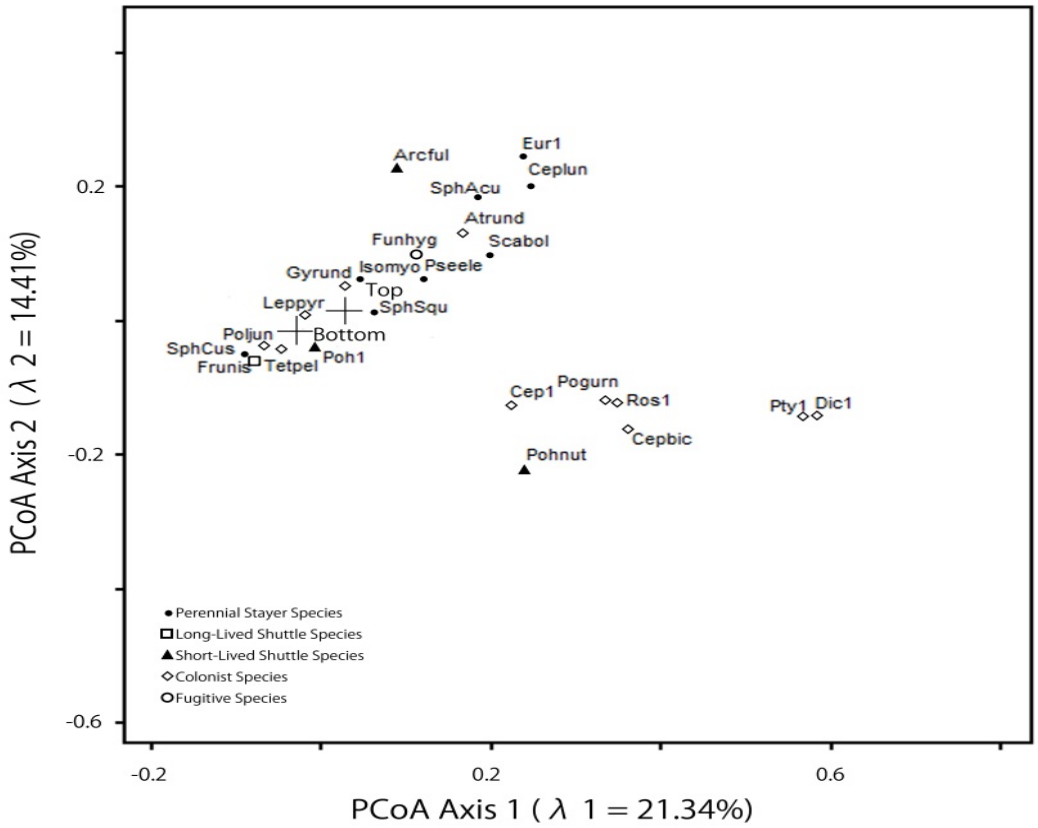


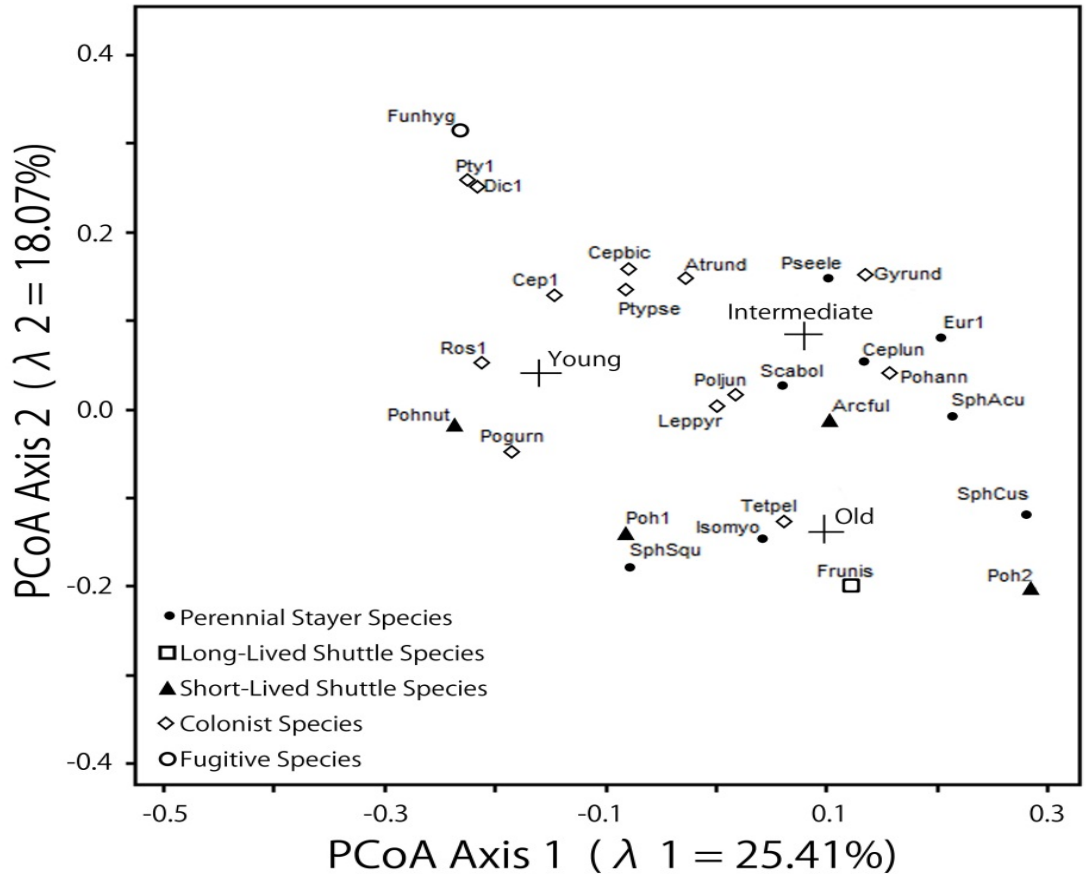
Figure 3-5. PCoA output for diaspore bank samples, grouped by age class (young, intermediate, old). Ordination utilizes 27 species and 20 stands, using the Sørensen dissimilarity measure. a) Plot of samples coded by age class (young, intermediate, and old) with age class centroids. b) Plot of taxa centroids with age class centroids. Species coded by life strategy. For taxa names, labeled with the first three letters of the genus name and first three letters of the species name, see Appendix 3-3, and for taxon abbreviations, see Table 3-1.

Appendix 3-1. Sampling stand descriptions. Stand name is coded based on land ownership (W=Western Forest Products, H=Huu-ay-aht First Nation, F=Bamfield Huu-ay-aht Community Forest, B=Bamfield village, T=West Coast Trail (Pacific Rim National Park), K=Keeha Beach Trail (Pacific Rim National Park), C=Canopy Trail (Bamfield Marine Sciences Centre)). Age is a minimum estimate provided by these organizations. Average upper canopy cover, soil moisture, and soil pH were calculated from the three sites within each stand. Dominant slope and aspect throughout the stand was assessed based on visual estimates.

Stand Name	Age	Latitude	Longitude	Average upper canopy (%)	Average soil moisture (%)	Average soil pH	Slope	Aspect	Elevation (m asl)
W4a	4 (Y)	48°46'48.30"N	125° 6'26.90"W	0.83	0.68	5.5	slight	N	126
W4b	4 (Y)	48°46'39.40"N	125° 6'18.80"W	0.16	0.58	5.6	moderate	NE	152
H5a	5 (Y)	48°48'22.80"N	125° 5'58.20"W	0.25	0.78	5.4	level	n/a	10
H5b	5 (Y)	48°48'18.80"N	125° 6'23.50"W	0.85	0.52	6.1	level	n/a	13
W12	12 (Y)	48°46'46.97"N	125° 6'38.21"W	26.62	0.73	5.7	moderate	W	109
F16	16 (Y)	48°49'1.60"N	125° 7'21.10"W	29.17	0.67	6.3	slight	E	50
W17	17 (Y)	48°46'42.80"N	125° 5'31.30"W	2.89	0.35	6.4	moderate	NW	151
F35	35 (I)	48°49'32.67"N	125° 7'41.20"W	99.07	0.54	6.3	moderate	W	33
W38	38 (I)	48°47'15.90"N	125° 5'33.50"W	98.05	0.28	6.4	slight	NW	122
W39	39 (I)	48°47'33.20"N	125° 5'33.30"W	96.56	0.45	5.4	slight	SW	118
F40	40 (I)	48°50'3.16"N	125° 7'40.57"W	97.16	0.86	5.4	steep	NE	9
W42	42 (I)	48°47'24.10"N	125° 5'28.20"W	97.66	0.5	6.0	level	n/a	114
F50	50 (I)	48°48'57.70"N	125° 9'45.60"W	97.34	0.68	5.9	steep	E	9
B80	80 (I)	48°49'47.87"N	125° 7'59.15"W	98.46	0.28	6.6	slight	E	31
F120	120 (O)	48°49'3.90"N	125° 7'22.66"W	91.57	0.66	5.7	moderate	SE	48
T300a	>300 (O)	48°47'26.60"N	125° 6'49.60"W	97.94	0.65	5.5	level	n/a	44
T300b	>300 (O)	48°47'30.30"N	125° 6'53.40"W	94.69	0.73	5.1	level	n/a	7
K300a	>300 (O)	48°48'8.60"N	125° 9'45.20"W	89.36	0.95	5.2	level	n/a	23
K300b	>300 (O)	48°48'22.50"N	125° 9'41.80"W	84.69	0.64	5.3	slight	N	23
C300	>300 (O)	48°49'57.90"N	125° 7'40.19"W	97.18	0.66	5.7	slight	NE	17



Appendix 3-2. PCoA output for diaspore bank data from top 3cm and bottom 3cm portions of soil cores, showing species. Ordiation utilized 24 species and 118 sample portions, using the Sørensen dissimilarity measure. Sample position centroids shown by crosses. Species centroids are coded by life strategy symbols and are labeled with the first three letters of the genus name and first three letters of species name. Taxa not identified to species are labeled with the first three letters of genus followed by a numerical designation (Table 3-1).



Appendix 3-3. PCoA output for diaspore bank data from soil samples in three age classes (young, intermediate, old), showing species. Ordination utilized 27 species and 20 stands, using the Sørensen dissimilarity measure. Age class centroids shown by crosses. Species centroids are coded by life strategy symbols and are labeled with the first three letters of genus name and first three letters of species name. Taxa not identified to species are labeled with the first three letters of genus followed by a numerical designation (Table 3-1).

Chapter 4: General Discussion

The forests of British Columbia are a key part of Canada's forestry industry (Natural Resources Canada 2011). Although coastal temperate rainforests make up only a small area of British Columbia's total forests, they are diverse ecosystems that are valuable ecologically and economically (Schofield 1988; Alaback and Pojar 1997; Robbins 1997). As concerns for preserving forest structure and maintaining diverse ecosystems increases, forestry companies have begun to adopt new techniques, such as retention harvesting, rather than large-scale clear-cutting (MacKinnon and Eng 1995; Hazell and Gustafsson 1999; Western Forest Products 2011; Western Red Cedar Export Association 2012).

This thesis incorporates a bryophyte's perspective on forest management. In temperate rainforest ecosystems, bryophytes are abundant and highly species rich, often representing the majority of understory plant diversity (MacKinnon 2003; Newmaster et al. 2003). Therefore, truly effective forest management strategies must also consider bryophytes, despite their inconspicuous nature. Chapter Two of this thesis explored the extent to which microhabitat, including substrate and microclimate, as well as forest stand age, affected bryophyte diversity and species composition. Chapter Three examined the composition of the soil diaspore bank and assessed its importance in bryophyte recolonization.

The importance of substrate and forest stand age on bryophyte richness and species composition

Substrate was a significant factor in assessing bryophyte richness and species composition across all classes of stand age, demonstrating clearly that bryophytes are inextricably linked to their substrates, and that this association plays a stronger role in determining species distributions than does forest stand age. Fenton and Bergeron (2008) observed complicated interactions between forest age and habitat that varied among bryophyte species guilds within a black-spruce dominated boreal forest; however, unlike the present study, they ultimately

found that in boreal forests, time since disturbance was the main factor affecting bryophyte species richness.

It was hypothesized in this study that decaying logs would be the most species-rich substrate, due to different stages of decay contributing to a diversity of microniches (Ross-Davis and Frego 2002; Mills and Macdonald 2004). Unexpectedly, soil substrates had the greatest gamma richness. Soils were the most species-rich substrate in young stands, whereas decaying logs were more species-rich in intermediate and old-growth stands. Additionally, soil substrates had the greatest number of unique species, and log substrates had the second highest number. These patterns can be attributed in part to the heterogeneity of these two substrates. Throughout the study area, soil substrates encompassed variation in slopes and aspects and covered a gradient of disturbance, from recently upturned soil to intact soil patches, and such heterogeneity was maximized in young stands. Similarly, Jonsson and Esseen (1990) found that bryophyte diversity increased in patches of disturbed forest floor. In contrast, decaying logs in young stands tended to have low species richness, as most logs in young stands were in uniform, early stages of decay, inhabited by few species. However, in older stands, decaying logs were more heterogeneous, due to many logs representing a variety of different decay classes. Thus, species richness on decaying logs in older age classes surpassed that of soil substrates. Rambo (2001) also emphasized the importance of logs in advanced stages of decay for maintaining bryodiversity.

Variations in life strategies also contribute to the patterns of species richness among the different substrates and age classes. The majority of colonist species (27 out of 31 colonists) preferred soil substrates, whereas the remainder (four out of 31) preferred decaying logs, and no colonist species preferred tree bases. This is supported by the findings of Jonsson and Esseen (1990). Furthermore, competition for space contributes to community structure in equilibrium communities (Slack 1990). In this study, the trend of increasing perennial richness in older stands shows the competitive advantage of perennials

once the canopy begins to close, whereas colonist species had had an advantage under open canopies.

Contrary to the predictions generated by the application of the intermediate disturbance hypothesis to bryophyte communities (Connell 1978; Jonsson and Esseen 1990; Haeussler et al. 2002), forest stand age did not significantly affect species richness. However, stand age did influence species composition due to microhabitat and substrate characteristics of the different age classes. In particular, variables relating to ambient moisture, such as amount of canopy cover, most strongly affected bryophytes. In particular, mosses and liverworts showed different distributions on the three main substrates. This is largely due to differences in desiccation tolerance. In general, mosses tend to be more desiccation tolerant than liverworts, whereas liverworts tend to prefer to moist, shady habitats (Proctor and Tuba 2002; Newmaster et al. 2003; Baldwin and Bradfield 2010). Additionally, mosses tended to show greatest richness on soil, whereas liverworts were more species-rich on decaying logs.

Diaspore bank richness and species composition

Diaspore bank species richness differed significantly with soil depth, where greater species richness occurred at shallower depths. This can be attributed to the slow process of vertical movement of diaspores through the soil, which many spores are not sufficiently long-lived to withstand (Rydgren and Hestmark 1997). In order to be incorporated into the diaspore bank at greater depths, diaspores must be long-lived; therefore, only taxa that produced plentiful diaspores capable of persisting in soil conditions were found at greater depths (Rydgren and Hestmark 1997; Hyalnder 2009). A variety of species with diverse diaspores were represented at shallow soil depths, including both colonists with persistent propagules and perennials and long-lived shuttle species whose vegetative fragments that tend to be shorter-lived. Additionally, upper soil layers had numerous unique species. Conversely, lower soil layers exhibited fewer unique species, and thus, more overlap with shallow depths.

Species richness in the diaspore bank was consistent across stand age classes, indicating that some diaspores were long-lived whereas others were replenished over time. There was a trend towards lower richness in old-growth stands, whereas young stands had the most species-rich diaspore bank samples. The diaspore bank in young stands represented viable diaspores deposited under a variety of previous conditions, including old-growth conditions that occurred within the last 20 years. Thus, the diaspore bank of young stands links the present-day young stands to historical old-growth forests (Hock et al. 2008). In the soils of old-growth stands, many diaspores either germinated or expired over time (Rydgren and Hestmark 1997). Although the above-ground flora contributes new diaspores, the bulk of these new additions are from a few dominant species and thus the below-ground diversity remains low.

Many different species and life strategies were represented, clearly demonstrating that the diaspore bank provides a record of a diverse assortment of taxa. Consequently, the diaspore bank is a key part of the ecosystem, linking past and future communities (Hock et al. 2008). Mosses, particularly colonist species, were well-represented in the diaspore bank. These taxa tend to invest in both sexual and asexual reproduction, and therefore the soil contains a variety of propagules that tend to persist for extended periods of time (During 1979; Laaka-Lindberg et al. 2003). Colonists are essential components of forest succession, as they thrive in exposed sites under open canopies. Although colonists dominated the diaspore bank, perennial stayer species also germinated. These observations demonstrate that perennials are capable of colonizing immediately, even under exposed conditions, rather than germinating only when above-ground conditions have increased moisture and canopy cover.

The flora of the diaspore bank differed significantly from the above-ground, soil-dwelling flora. Above-ground, perennials dominated the forest floor, especially in old-growth stands. Colonist species thrived in young stands or in areas of localized disturbances. Below-ground, however, colonists and other short-lived bryophytes were well-represented relative to perennials. Bryophyte taxa respond to different pressures above- and below-ground; above-ground,

perennials have an advantage in competition for space, whereas below-ground, the ability of colonists to produce numerous durable diaspores is beneficial. This illustrates the trade-off noted by During (2001) between the longevity of the gametophyte and the longevity of the diaspores. The diaspore bank flora showed a greater similarity to the above-ground soil flora rather than the flora of the whole stand, across substrates. This indicates that bryophytes growing on substrates other than soils are less likely to become incorporated in the soil diaspore bank, and thus must rely on other methods to persist through disturbances.

Implications for bryophyte sampling/culturing

This study demonstrates the specificity bryophytes have for their substrates, which results in a patchy distribution on the landscape. Consequently, the survey sampling in this study detected more species than the plot sampling of the most abundant substrates. A similar pattern has been found in other bryological studies, and sampling protocols emphasize the importance of sampling specific microhabitats as they occur in order to capture the associated diversity (Doubt and Belland 2000; Newmaster et al. 2005). This study further recognizes the importance of surveying meso- and microhabitats in order to assess bryophyte diversity at a regional scale, as many taxa with restricted occurrences can be easily overlooked when conducting plot sampling at a large scale.

In this study, numerous bryophyte taxa were represented under full light conditions, and no difference was observed in the species that germinated under full light and shaded conditions. This demonstrates that a diverse assemblage of bryophyte species can be studied under uniform light conditions. Furthermore, closed petri dishes are effective in maintaining moist samples even under high light. Consequently, using potting soil in addition to experimental soil to promote moisture retention is unnecessary and even detrimental, as the potential for contamination increases substantially with the inclusion of potting soil.

Implications for forest management

This study demonstrated that the presence of available substrates was more critical to bryophyte richness and species composition than the overall age of the forest stand. Young stands were found to be different in richness and species composition from older stands, and the overlap between intermediate and old stand age classes indicated that once the forest canopy initially closes (approximately 20 years post-harvest), bryophyte species richness is relatively consistent. Because bryophytes are critical recolonization of harvested landscapes, in order to regenerate and maintain healthy and diverse ecosystems, forest management strategies must address the requirements of bryophyte communities (Hylander 2009; Baldwin and Bradfield 2010). Consequently, strategies that leave behind woody debris and maintain structural complexity will be beneficial to overall bryodiversity, thus enhancing forest integrity throughout succession (Crites and Dale 1995; Rambo 2001; McGee and Kimmerer 2002). In addition to the extant bryophyte community, the diaspore bank is also an important component in bryophyte recolonization. In this study, upper soil layers were the most species-rich, containing a diversity of viable specialized propagules, spores, and fragments. Thus, these layers are most important in maintaining bryodiversity and initiating recolonization. Forest harvesting techniques that cause minimal disturbances to the soil are ideal to maintain the integrity of the diaspore bank. However, this study indicates that the diaspore bank is relatively resistant to soil disturbances, and species richness of the diaspore bank was not found to be negatively affected by harvesting practices.

Future research

Future above-ground studies could further stratify substrate types to provide more precise patterns of bryophyte diversity based on more specific substrate properties within a similar study area. Additionally, the connectivity of forest patches via long distance dispersal mechanisms has been studied for epiphytic bryophytes (Zartman and Nasciento 2006; Löbel et al. 2009), but not for forest floor communities, so a similar study could serve as a test of

metacommunity theory as applied to forest floor bryophytes (Srivastava et al. 2004; Logue et al. 2011). Furthermore, although bryophytes were the major component of the understory of the study forests, assessing species compositions of bryophytes and co-occurring vascular plants would lead to a clearer description of these communities. Such a comparison would be advantageous as bryophytes are difficult and time-consuming to identify compared to vascular plants, so such a study could determine if vascular plant data could be used as a surrogate for bryophytes in the study area. This approach has met with mixed results (Pharo et al. 1999; Pharo et al. 2000; McMullen-Fisher et al. 2010). Finally, Maciel-Silva et al. (2012) recently explored the possibility of bryophyte diaspores persisting in substrates other than soil, such as the bark of trees or within decaying logs. A similar investigation of the regeneration potential of other substrates in the temperate rainforest ecosystem would produce a valuable comparison of the roles and relative importance of different diaspore banks for various species.

Conclusion

Despite their small size, bryophytes are a diverse and integral component of temperate coastal rainforests, which responds to disturbances on a smaller scale than do vascular plants. An awareness of a bryophyte perspective must be incorporated into forest management in order to preserve suitable microhabitats on a similarly small scale. This study emphasizes the importance of microhabitats in maintaining bryophyte diversity and illustrates the role of the soil diaspore bank in recolonization following disturbance. The diaspore bank provides a temporal refuge for bryophytes when suitable conditions do not occur above-ground. Furthermore, the taxa present in the diaspore bank tend to be colonist species which are essential in the recolonization of disturbed stands. The process of incorporating a bryophyte perspective to disturbances involves assessment of above-ground microhabitats and below-ground diversity to determine the ability of a diversity of bryophyte species to persist and thrive in the ecosystem.

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