

Patterns of bryophyte diversity in humid coastal and inland cedar–hemlock forests of British Columbia¹

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Abstract: Mosses and hepatics (bryophytes) are the most diverse and abundant understorey vegetation within the Coastal Western Hemlock (CWH) and Interior Cedar–Hemlock (ICH) zones of British Columbia. This study intensively sampled bryophytes in 287 young- and old-growth stands in the CWH and ICH zones. Two major variables strongly influence the patterning of bryophyte diversity in these zones: stand age and habitat heterogeneity. Canonical correspondence analyses (CCA) identified these as the most important variables explaining stand–environment interactions. Alpha diversity is much greater in old-growth forests and beta diversity is high between young and old forests. Old-growth cedar–hemlock forests have between 60 (ICH) and 100% (CWH) more species than younger forests disturbed by wildfire in the ICH zones or logging in the CWH zones. Furthermore, a stand classification built on species composition partitioned species into stands of different ages and mesohabitat heterogeneity. Beta diversity was also partitioned between stands of different ages and habitat heterogeneity. This indicates that both young and old forests have a unique assemblage of species. Indicator analysis was used to choose a partial lists of species that are indicators of “old growthness”. These old forests support a rich flora of hepatics and rare western North American endemics. High environmental continuity is associated with the most humid watersheds and cedar–hemlock forests within these watersheds have the highest bryophyte diversity. The establishment of rich communities of bryophytes in the moist cedar–hemlock forest has been occurring over the last 2000–7000 years, with the coastal rainforest much older than the inland rainforest. Large-scale disturbance, such as forestry, threatens the existence of these highly diverse communities. A better understanding of the patterning of bryophyte diversity will provide an opportunity to minimize the impact of forest operations on biodiversity. Bryophyte diversity in British Columbia cedar–hemlock forests will be sustained through ecosystem management of old-growth legacies (i.e., landscapes,

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stands, and their components) and preservation of areas of high diversity. Temporal and habitat variables are influential in the patterning of bryophyte diversity. Management plans that consider these variables will be better equipped to manage cedar–hemlock forests for maintaining biodiversity.

Key words: biodiversity, bryophytes, cedar–hemlock, CWH, disturbance, ecosystem management, floristic habitat sampling, forest conservation, ICH, old growth, patterning of diversity, rare species, species richness.

Résumé : Les mousses et les hépatiques (bryophytes) représentent la végétation de sous-étage la plus diversifiée et abondante dans la zone côtière de la pruche de l'Ouest (CWH) et la zone à thuya et à pruche de l'Intérieur (ICH) en Colombie-Britannique. Cette étude a comporté un échantillonnage intensif des bryophytes dans 287 peuplements jeunes et anciens de ces deux zones. Deux variables y exercent une influence majeure sur le patron de répartition de la diversité des bryophytes : l'âge des peuplements et l'hétérogénéité des habitats. Des analyses canoniques des correspondances (ACC) ont indiqué qu'il s'agissait des plus importantes variables pour expliquer les interactions peuplement–environnement. La diversité alpha est beaucoup plus grande dans les forêts anciennes, et la diversité bêta est élevée entre les forêts jeunes et les forêts vieilles. Les forêts anciennes de thuya et de pruche comptent entre 60 % (ICH) et 100 % (CWH) plus d'espèces que les forêts plus jeunes perturbées par un incendie dans la zone ICH ou une récolte dans CWH. De plus, une classification des peuplements reposant sur la composition en espèces a fourni une répartition de la richesse en espèces entre peuplements ayant différentes caractéristiques d'âge et d'hétérogénéité des mesohabitats. La diversité bêta a aussi été répartie entre peuplements ayant différentes caractéristiques. Il ressort que la jeune forêt et la vieille forêt ont toutes deux un assemblage unique d'espèces. Une analyse a été effectuée pour établir une liste partielle d'espèces indicatrices d'« ancienneté ». Les vieilles forêts étudiées abritent une flore riche en hépatiques et en espèces endémiques rares de l'Ouest de l'Amérique du Nord. Une grande continuité de l'environnement est associée aux bassins versants les plus humides, et les forêts de thuya et de pruche de ces bassins renferment la plus forte diversité en bryophytes. L'établissement de riches communautés de bryophytes dans la forêt humide de thuya et de pruche se poursuit depuis des milliers d'années, de 2000 à 7000 ans, la forêt ombrophile côtière étant beaucoup plus âgée que la forêt ombrophile intérieure. Les perturbations de grande échelle, comme l'exploitation forestière, menacent l'existence de ces communautés de grande diversité. Une meilleure compréhension du patron de répartition de la diversité des bryophytes aidera à limiter l'impact des opérations forestières sur la biodiversité. La diversité des bryophytes dans les forêts de thuya et de pruche de la Colombie-Britannique pourra être maintenue en aménageant à l'échelle de l'écosystème les vestiges des forêts anciennes (c.-à-d. paysages, peuplements et leurs composantes) et en préservant des zones à forte diversité. Des variables temporelles et des variables de l'habitat influent sur le patron de répartition de la diversité des bryophytes. Les plans d'aménagement prenant en considération ces variables seront mieux en mesure d'assurer le maintien de la biodiversité des forêts de thuya et de pruche.

Mots clés : aménagement écosystémique, biodiversité, bryophytes, conservation de la forêt, CWH, échantillonnage floristique de l'habitat, espèces rares, forêt ancienne, ICH, patron de répartition de la diversité, perturbation, pruche, richesse en espèces, thuya.

Introduction

Perhaps the least studied area of bryophyte ecology concerns patterning of diversity on the landscape and the effects of large-scale disturbance. Wallace (1878) recognized that regularity in the patterns of diversity suggests they have been produced in conformity with a basic set of principles rather than as accidents of history. Ecological research has investigated some of the factors that influence patterns of bryophyte diversity (Slack 1977; Benzing 1981; Oksanen 1983; Økland et al. 1990; Gignac and Vitt

1994; Belland and Vitt 1995; Vitt and Belland 1995; Vitt et al. 1995). The results of such research indicate the importance of substrates and habitats. Habitats such as streams, fens, and bogs exhibit unique patterns of bryophyte diversity (Slack and Glime 1985; Muotka and Virtanen 1995; Vitt et al. 1995). Vitt and Belland (1997) have shown that patterns of bryophyte diversity are strongly correlated to habitat type and scale of the investigation. Furthermore, they described how the landscape is a hierarchical mosaic of meso-habitats (e.g., streams, cliffs) and microhabitats (e.g., logs, rocks), the patterns of which affect bryophyte diversity patterning. In forest ecosystems, these patterns of diversity may also be affected by large-scale disturbance (e.g., fire, logging). The impacts of catastrophic disturbance on the patterning of bryophyte diversity in forest ecosystems have not been adequately researched (Rose 1992).

In British Columbia, more than 250 000 ha of forest lands are logged each year (Natural Resources Canada 2000). In coastal temperate rain forests, over 60% of the original old growth has been replaced by clearcuts and second-growth plantations (MacKinnon and Eng 1995). These temperate rain forests are found in the Coastal Western Hemlock (CWH) biogeoclimatic zone of British Columbia (Meidinger and Pojar 1991). The effects of logging on bryophyte communities are poorly known and need further scientific investigation (Jonsson and Esseen 1990; Söderström et al. 1992; Herben 1994; Söderström 1995). Bryophyte community dynamics have been linked to substrate and stand age in the northern forest of Ontario (Carleton 1990; Frego and Carleton 1995*a*, 1995*b*), Alberta (Crites and Dale 1995; Johnston and Elliot 1996), Europe (Edwards 1986), and Scandinavia (Söderström 1988*b*, 1993). Furthermore, bryophyte diversity is strongly correlated with habitat heterogeneity in Alberta (Vitt and Belland 1997; Vitt et al. 1995). Clearcutting techniques reduce stand age, number of habitats, and, ultimately, cryptogam diversity (Gustafsson and Hallingbäck 1988; Söderström 1988*b*; Brumelis and Carleton 1989; Andersson and Hytteborn 1991; Lesica et al. 1991). Furthermore, this disturbance creates environmental conditions that are unfavourable for many bryophytes and lichens (Gustafsson et al. 1992; Laaka 1992; Goward 1993, 1994*a*; Johnston and Elliot 1996). Changes to microclimate after logging include humidity, moisture, temperature, and light quality (Bell and Newmaster 2002). In a study of biodiversity in the Ontario boreal mixedwood forest (Newmaster and Bell 2002), bryophyte diversity was dramatically reduced after clearcut logging. Sensitive epixylic hepatics and forest mesophytes disappeared with the less humid microclimate and the reduction in microhabitats and stand age. A small number of fugitives and colonists dominated the site for 8 years after the clearcut. Eventually, forest mesophytes began to recolonize the area from habitat refugia surrounding and within the clearcut. Re-establishment after clearcutting may be difficult if the gap size created is larger than the dispersal capabilities of the species involved (Söderström 1988*b*). Many of the young stands in the CWH have been initiated by clearcut harvesting. In comparison with neighbouring old-growth stands, patterning of diversity in these young stands initiated from logging disturbance is largely unknown (Newmaster 2000).

The coastal rainforests (CWH) are characterized by very infrequent catastrophic disturbances (Arsenault 1995). For example, fire-return intervals often exceed 600 years, and before logging many coastal landscapes were dominated by forests that had not witnessed catastrophic disturbances for 1000 years or more (Arsenault 1995; Gavin et al. 1997). In general terms, inland rainforests (ICHwk1, vk1) have a similar disturbance regime; however, they are more susceptible to fire, insects, and avalanches, resulting in proportionately fewer old-growth forests than their coastal counterparts (Arsenault and Goward 1999). Catastrophic disturbances are considered to occur more frequently in the moist warm variant of the ICH zones (British Columbia Ministry of Forests and British Columbia Environment 1995). Fire is often the most prevalent large-scale natural disturbance in these humid coniferous forests, although outbreaks of western hemlock looper can also have a very dramatic impact on canopy trees in the ICH zones. The effects of these disturbances on bryophyte patterning have not been studied in detail.

Large catastrophic fires will affect forest structure and species composition. The result may become a patchy mosaic of highly disturbed and undisturbed forests; the latter are refugia for regenerating future forests (Kershaw 1976, 1985; Larsen 1980). Indirectly, fire maintains forest ecosystem diversity (at the landscape level) because of the randomness, varying intensities, and frequencies of the fires (Connell

and Slayter 1977; Zackrisson 1977; Lindholm and Vasander 1987; Arseneault and Payette 1992; de las Heras et al. 1995). The environmental conditions after a large fire are almost semi-arid, with dry surface soils and high surface temperatures (Auclair 1983; Clément 1990; Garty and Binyamini 1990). Fugitives and early colonizing species such as *Ceratodon purpureus*, *Polytrichum juniperinum*, and *Marchantia polymorpha* are some of the first plant species that dominate burnt areas, probably originating from soil diaspore banks (During and ter Horst 1983, 1987; Heras-Ibáñez et al. 1991; Newmaster et al. 1999; Newmaster and Bell 2002).

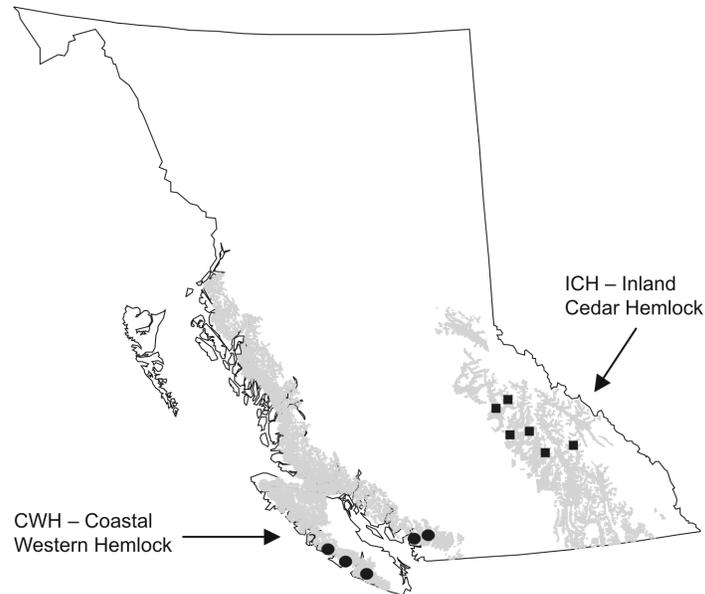
Ecological studies that consider patterns of diversity at different scales on the landscape can offer practical applications for conservation strategies (Whittaker 1960, 1972; Lertzman et al. 1997). Whittaker's (1960, 1977) definition of "inventory diversity" (i.e., epsilon, gamma, alpha, and point) and "differentiation diversity" (i.e., delta, beta, and pattern) can be applied to field research at all scales of diversity, including Vitt and Belland's (1997) mosaic of habitats on the landscape. Biogeographical studies can be modified to investigate patterns of diversity in a quantitative manner at the largest landscape scale (epsilon and gamma inventory diversity; delta differentiation diversity). Although uncommon, bryogeographical studies offer elegant, intuitive conclusions about species diversity, basic floristic concepts, and conservation (Steere 1978; Brassard 1983; Belland and Brassard 1988; Schofield 1988; Vitt 1991; Belland and Schofield 1994; Belland 1995). At the smaller scales, diversity can be investigated at (1) "regional" or MacArthur's (1965) between-stands scale (alpha inventory diversity and beta differentiation diversity) and (2) "local" or MacArthur's (1965) within-stands scale (point inventory diversity and pattern differentiation diversity) (Pielou 1966; Krebs 1985, 1997; Magurran 1988). Different environmental or historical factors may be correlated to patterns of diversity at different scales on the landscape. These correlations could be used to build diversity models and answer questions that are essential for conservation of bryophyte diversity. Conservation strategies often rank diversity as one of the most important criteria for site assessment (Magurran 1988; Slack 1992; Söderström et al. 1992; Fanta 1995; Söderström 1995). Understanding the patterning of diversity in old ecosystems is our best model for future ecosystem conservation and management (Lertzman et al. 1997).

The old-growth forests of the Pacific Northwest of North America have been the focus of considerable public debate in recent years (Harris 1984; Norse 1990; Cadrin et al. 1991; Caufield 1991; Pynn 1999). Forest policy makers and managers are faced with difficult decisions: how much to preserve and how much to dedicate to forestry interest (Goward 1994b; Schoonmaker et al. 1997). Bryophytes are recognized as one of the most abundant components of vegetation in the western red cedar (*Thuja plicata* Donn.) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest ecosystem, which will be referenced as "cedar–hemlock" for the purpose of this paper (Schofield 1988; Alaback and Pojar 1997). This study compares the patterning of bryophyte diversity (at the regional scale) in old-growth forests with that of young forests affected by large-scale disturbances. Specifically, the objectives of this study are to determine (1) if bryophyte diversity changes after logging disturbance in the CWH or fire disturbance in the ICH, (2) if a stand classification built on species composition will adequately partition species richness and if species frequency curves can help interpret the classification, (3) the patterns of bryophyte diversity at a regional scale using relationships between stands, species, and environmental variables within either the ICH or CWH, and (4) beta diversity within young and old stands, as related to sample scores using Hill's scaling in a canonical correspondence analysis (CCA) (ter Braak 1986).

Study area

The research was conducted in British Columbia, Canada, within two distinct biogeoclimatic zones (Meidinger and Pojar 1991): the Coastal Western Hemlock (CWH) and Interior Cedar–Hemlock (ICH) zones (Fig. 1). The CWH is located on the west side of the Coast Mountains and is known as Canada's coastal temperate rainforest. Research in the CWH was confined to the vm1 biogeoclimatic variant. The ICH is located on the westerly, windward slopes of the Columbia Mountains. Research in the ICH was confined to the ICHmw3, ICHwk1, and ICHvk1 biogeoclimatic variants. The wetter portions of

Fig. 1. Research site locations within the Coastal Western Hemlock (CWH) and interior Cedar–Hemlock (ICH) biogeoclimatic zones (● = CWH sites; ◆ = ICH sites).



the ICH (wk1 and vk1 variants) are known as inland rainforests (Goward and Ahti 1992; Arsenault and Goward 1999). Detailed descriptions of glacial history, climate, and floristics can be found in Schofield (1988), Arsenault (1998), Hebda (1995), and Schoonmaker et al. (1997).

Methods

Sampling method

In 1996, 102 cedar–hemlock stands were sampled in the ICH. Sampling in the ICH was confined to the ICHmw3, ICHwk1, and ICHvk1 biogeoclimatic variants. Stands were chosen from the Wells Gray, upper Adams River, and Seymour watersheds. Within these watersheds sampling was evenly distributed between stands that were burned approximately 80–90 years ago (47 stands) and old-growth stands of 250+ years in age (55 stands). In 1997, 185 cedar–hemlock stands were sampled in the CWH. Sampling in the CWH was confined to the vm1 biogeoclimatic variant. Stands were chosen from the Capilano and Seymour watersheds along the mainland coast and in the Sidney, Clayoquot, Tofino, and Walbran watersheds along the western coast of Vancouver Island. Extensive logging activities in the Capilano and Seymour watersheds allowed a balanced sampling between stands that were logged 80 years ago (60 stands) and old-growth stands of 250+ years in age (60 stands). Sampling on Vancouver Island was limited to old-growth forest of 250+ years in age (60 stands) owing to the relatively recent logging activity and lack of fire history in this portion of the CWH.

A stand is generally defined as a standing growth of trees with similar physiognomy (Kimmins 1997). In this study, a stand is similarly defined by the dominant tree species, its age, structure, elevation, slope position, and aspect. Stands vary in size, but most consist of a dominant mesohabitat (the forest) that encloses numerous restricted mesohabitats (e.g., cliffs, streams, seeps). Within each mesohabitat there are a number of microhabitats (i.e., tree base, stumps, acidic rocks) that may be specific to one type of mesohabitat (i.e., wet cliff crevices, submerged rocks in streams) (Newmaster 2000).

Floristic habitat sampling was used to assess patterns in bryophyte community composition over a period of two field seasons (Newmaster 2000). This sampling method stratifies the stand at two

scales: mesohabitats (Vitt and Belland 1997) and microhabitats. At the mesohabitat scale, sampling begins with the estimation of abundance for each mesohabitat within a stand. Species are then recorded by randomly sampling each type of mesohabitat within quadrats of increasing size until maximum richness is achieved (defined by species area curves). At the microhabitat scale, sampling begins with the estimation of abundance for each microhabitat within all types of mesohabitats. Species are then recorded for each type of microhabitat within quadrats of increasing size until maximum richness is achieved (no new species are found). These data were used in the indicator analyses and for identifying the crucial habitats for old-growth bioindicators.

Each species and its abundance was recorded for all mesohabitats (Vitt and Belland 1997) and microhabitats in each stand. Abundance was measured (ocular estimate) on a scale of one to three: 1 = <30% cover; 2 = 30–70% cover; 3 = >70% cover. Total stand abundance was recorded (ocular estimate) within a 20-m diameter circular plot within the stand. Relative mean stand abundance is the percentage of total stand abundance for age groups within either biogeoclimatic zone.

Species nomenclature follows Anderson et al. (1990) for mosses and Stotler and Crandall-Stotler (1977) for hepatics. Voucher specimens collected from each watershed were prepared and deposited at the University of Alberta Cryptogamic Herbarium (ALTA), Kamloops Forest Region Herbarium, and University of British Columbia Herbarium (UBC).

Environmental variables

Twenty-two environmental variables were used for multivariate analyses (Table 1). Stand dynamics, soil variables, and general site variables were collected within a 20-m diameter plot that was located in the stand at least 500 m from any transition zone. Coarse woody debris data were obtained using two 50-m transects, with diameter measurements of logs for each decay class (Bradfield et al. 1998) at each transect intersection. Mesohabitat heterogeneity was measured by the number of different mesohabitats in each stand.

Macroclimate data were obtained from the Canadian Climatic Normals and meteorological stations within the local watersheds (Anonymous 1982) and were used as environmental variables in multivariate analyses. Microclimate data were collected only from a subset of 20 stands (divided evenly between young and old forest) within each watershed (20 stands \times 9 watersheds = 180 stands). Within each stand, five replicate sites were randomly chosen to measure temperature and total precipitation. All microclimate stations were set out in May 1997 and measured–removed in October of 1997. Growing season temperature within stands (subset) was calculated using the sucrose inversion (provides integrated or “a datum” temperature data for the length of the growing season) technique as described in Damman (1975).

Diversity analyses

Whittaker’s (1960) terminology and concepts are used to describe diversity at different scales. Species richness (gamma and alpha diversity) was used to compare changes in stand diversity after large-scale disturbance in the ICH and CWH. Inventory diversity is simply species richness, and is defined as either mean stand richness (mean alpha diversity, α) or total richness (gamma diversity, γ) in the following landscape elements: biogeoclimatic zones, biogeoclimatic variants (a finer classification of zones), or watersheds. Mean stand species richness is the mean number of species within stands for the ICH, CWH, or the partition of stands into old-growth forest and young-growth forest disturbed by either fire or logging (Krebs 1985). Species richness within and between stands was compared using ANOVA in SPSS (1999). Abundance was recorded for each species on each type of microhabitat or mesohabitat (see sampling methods above) and averaged for each species within stands.

Multivariate analyses

Patterns of bryophyte diversity were explored using CCA, which ordinated the stands (ICH or CWH exclusively) using environmental variables to constrain the ordination (ter Braak 1986). The multivariate

Table 1. Statistics for variables used in canonical correspondence analysis (CCA) of 103 stands in the ICH and 22 environmental variables.

Environmental variable	Interset correlation		Canonical coefficient		<i>t</i> value	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Site series (SS)	-0.15	-0.07	0.01	-0.03	0.06	-0.29
Elevation (Elv)	-0.38	0.06	-0.08	-0.01	-1.63	-0.11
Slope (SL)	-0.09	-0.19	-0.16*	-0.37*	-2.69	-2.97
Slope position (SP)	-0.11	0.01	0.02	0.18	0.45	1.74
Aspect (As)	0.25	-0.16	0.12	-0.06	1.58	-0.64
Hygrotpe (Hyg)	-0.12	0.25	-0.18*	0.08	-2.74	0.76
Rock cover (RC)	-0.44	0.31	0.09	-0.27*	1.66	-2.53
Rock acidity (RA)	0.49	-0.28	0.19	-0.29*	1.71	-2.74
Soil texture (ST)	-0.01	-0.13	-0.11	-0.27	-1.52	-1.94
Canopy height (CH)	0.39	0.19	-0.03	-0.09	-0.58	0.76
Tree density (DT)	-0.37	-0.26	-0.07	0.15	-1.24	1.15
Tree basal area (BT)	-0.25	-0.40	0.03	0.58	0.53	5.19
Snag density (DS)	0.35	-0.10	0.22*	-0.02	4.55	-0.15
Snag basal area (BS)	-0.01	-0.19	-0.13*	0.06	-2.82	0.58
Log density (DL)	0.03	-0.14	0.03	0.07	0.56	-0.60
Log basal area (BL)	0.29	0.06	-0.12*	0.26*	-2.53	2.46
Shrub cover (SC)	-0.12	0.19	0.10	0.24	1.87	2.08
Herb cover (HC)	0.04	0.19	-0.17*	-0.49*	-3.14	-4.15
Stand age (Age)	-0.78	-0.01	-0.68*	-0.38*	-11.49	-3.12
Rainfall (Rn)	0.01	0.01	0.00	0.00	0.01	0.01
6 month mean temp. (6T)	-0.28	0.08	-0.22*	0.27	-2.16	1.29
Mesohabitats (MsH)	-0.06	-0.59	0.46*	-0.49*	4.43	-9.71

Note: Asterisks indicate significance at $p < 0.05$. Absolute t value > 2.1 is used to indicate important canonical coefficients (ter Braak 1998). Bold values are indicated for variables with significant correlation and canonical coefficients (Hyg. is the only sig. var for axis 3, Int. Cor. = 0.5281 and t value = 6.81; no sig. variables for axis 4).

structure of the data was explored using Canoco™ 4 (ter Braak 1998). The ordination resulted in axis scores for each stand, with the axes correlated to the most important environmental variables in the analysis.

Classification of stands

Cluster analysis (e.g., average linkage sequential agglomerative hierarchical non-overlapping method (SAHN) Euclidean distance measure) was used to classify stands (ICH or CWH) using the CCA stand scores. Five clusters were specified in the ICH and four clusters were specified in the CWH. A K-means cluster analysis provided an independent check for stand membership to the clusters defined in SAHN. The resulting classification was used to partition species richness using ANOVA and identify groups of stands in the CCA ordination. Stands were labeled according to their cluster groups (SAHN) in the ordination diagrams using CanoDraw™ (ter Braak 1998) for both the CWH and ICH. Species richness for each cluster group was related to the ordination. Species frequency curves were prepared for each of the groups defined in the cluster analyses within either the ICH or CWH.

Beta diversity – species turnover

Species turnover was evaluated after large-scale disturbance within the ICH or CWH. Whittaker (1960) used the term “differentiation diversity” as a broad term for species turnover. He further defined differentiation diversity at smaller scales; delta diversity (watersheds), beta diversity (stands), pattern

diversity (microhabitats) (Whittaker 1965). In our study, delta diversity is defined as the change in species composition between biogeoclimatic zones (differences within ICH or CWH gamma diversity) or watersheds (differences in watershed gamma diversity). Beta diversity was the change in species composition between stands. Differentiation diversity within an age class was calculated directly using Whittaker's (1965, 1972, 1977) beta diversity measure (β , eq. [1] below). Species turnover between stand clusters (SAHN) is also considered in our multivariate analysis. Canonical correspondence analysis employing Hill's scaling was used to analyze species turnover between stands. Sample scores from CCA were used to represent the relative position of the stand on a complex gradient and are standardized such that the within-site variance equals 1 (ter Braak 1986). Hill and Gauch (1980) defined the length of the ordination axis to be a range of the site scores, expressed in multiples of the standard deviation (SD). In this scaling, samples or stands that are 2 SD apart can be interpreted as sharing less than one third of the species or have a species turnover of over 60% (Jongman et al. 1987). Samples that are 4 SD would be expected to have no species in common. Beta diversity (changes in species composition) can be calculated between individual groups classified in the cluster analyses, enabling an evaluation of the effects of environmental variables on species richness turnover within a biogeoclimatic zone.

$$[1] \quad \beta_w = (\gamma/\alpha) - 1$$

where γ is the gamma diversity (total species richness per age class) and α is the alpha diversity (mean species richness per stand).

The relative importance of an indicator species within an old-growth forest was estimated using the method of Duf re and Legendre (1997), as implemented in PC-ORD software (McCune and Mefford 1997). The "indicator value" describes the reliability of a species for indicating an old-growth forest and is expressed as a percentage of perfect indication. The indicator value combines, by multiplication, the abundance of a species in each old-growth stand relative to its abundance in all stands, with the frequency of occurrence in the sample units of the designated group of that species (Rambo and Muir 1998a, 1998b). A Monte Carlo analysis (Krebs 1997) assessed statistical significance of indicator values based on the proportion of 1000 randomized trials that equaled or exceeded the maximum indicator value for a species.

Results

Stand diversity

Interior Cedar–Hemlock zone

Diversity was greater in old-growth forests (250+ years) than young forests (80–90 years; disturbed by forest fire) (Table 2). Gamma diversity (γ) is more than 60% higher in old-growth forests than young forests. Mean stand richness (α) is significantly ($p < 0.01$) higher in old-growth forest than young forests (Fig. 2). Furthermore, mean stand abundance is almost twice as high in old-growth forest than in young forest (Fig. 3).

Differences in species richness are apparent among the different ICH biogeoclimatic variants. For younger stands, the driest (ICHmw3) is the richest (Table 3). In old stands, the wet (ICHwk1) but not too wet (ICHvk1) stands are the richest (Table 3). There is no significant difference ($p > 0.05$) in the species richness of the ICHwk1 and ICHvk1 variants. Old stands in the wettest variants have significantly ($p < 0.05$) higher species richness (ICHwk1, 17% higher; ICHvk1, 13% higher) than in the ICHmw3 (Table 3).

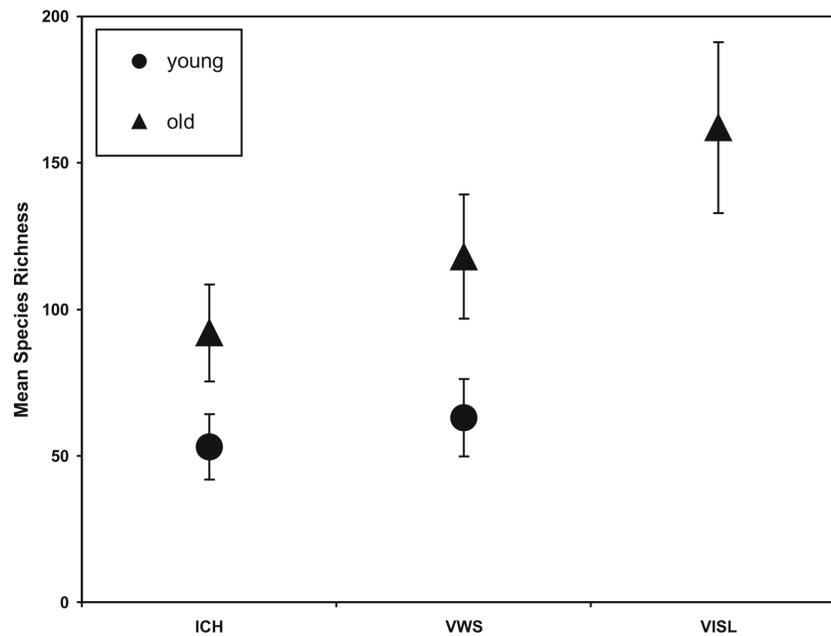
Coastal Western Hemlock zone

Diversity is greater in old-growth forests (250 yrs+) than young forests (80–90 years; disturbed by logging). Gamma diversity (γ) is over 100% higher in old-growth forests than young forests (Table 2).

Table 2. Stand diversity in old-growth (250+ yrs.) and young forests (80–90 years) disturbed by fire or logging (n = number of stands sampled; γ = total richness or gamma diversity; α = mean stand richness or mean alpha diversity; β = beta diversity within young or old forest).

Biogeoclimatic zone	Geographic area	Disturbance	n	Species richness		Beta diversity
				γ	α	β
CWH	Oceanic rainforest	Old growth	65	317	162	0.96
	Mainland coastal rainforest	Old growth	60	231	118	0.96
		Logging	60	114	62	0.84
ICH	Inland rainforest	Old growth	55	300	88	2.41
		Wildfire	47	188	54	2.48

Fig. 2. Mean species richness for young- (90 years logging or wildfire) and old-growth rainforests within the ICH or CWH (VWS and VISL). Error bars are shown for one standard deviation on either side of the mean (ICH = Interior Cedar–Hemlock; VWS = Vancouver watershed – CWH; VISL = Vancouver Island – CWH).



Alpha diversity (α) is significantly ($p < 0.01$) higher in old-growth forest than young forests (Fig. 2). Mean stand abundance is almost three times higher in old-growth forest than young forest (Fig. 3).

Old-growth forests along the west coast of Vancouver Island had higher diversity than mainland coastal, old-growth forests from the Vancouver watershed. Gamma diversity and relative abundance were more than 25% higher in oceanic old-growth forests than mainland coastal forests (Fig. 3). Mean species richness (α) was not significantly ($p > 0.05$) higher in oceanic forests (Fig. 2).

Canonical correspondence analysis

Interior Cedar–Hemlock zone

Distinct groups of stands on the ordination are defined by stand age and mesohabitat heterogeneity (Fig. 4). High species–environment correlations (>0.9) indicate that environmental variables for the first

Fig. 3. Relative mean stand abundance for young- (90 years logging or wildfire) and old-growth rainforests within the ICH or CWH (VWS and VISL). Error bars are shown for one standard deviation on either side of the mean. (ICH = Interior Cedar-Hemlock; VWS = Vancouver watershed - CWH; VISL = Vancouver Island - CWH).

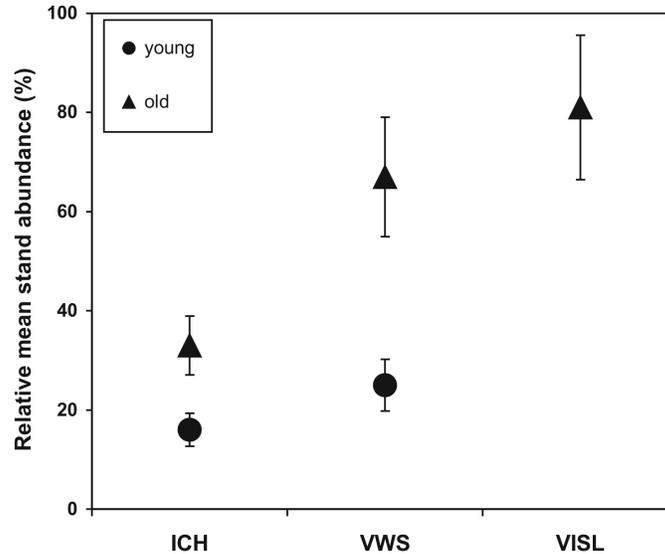


Table 3. Bryophyte diversity within ICH biogeoclimatic variants (n = number of stands sampled; gamma diversity (γ) = species richness within the biogeoclimatic variant).

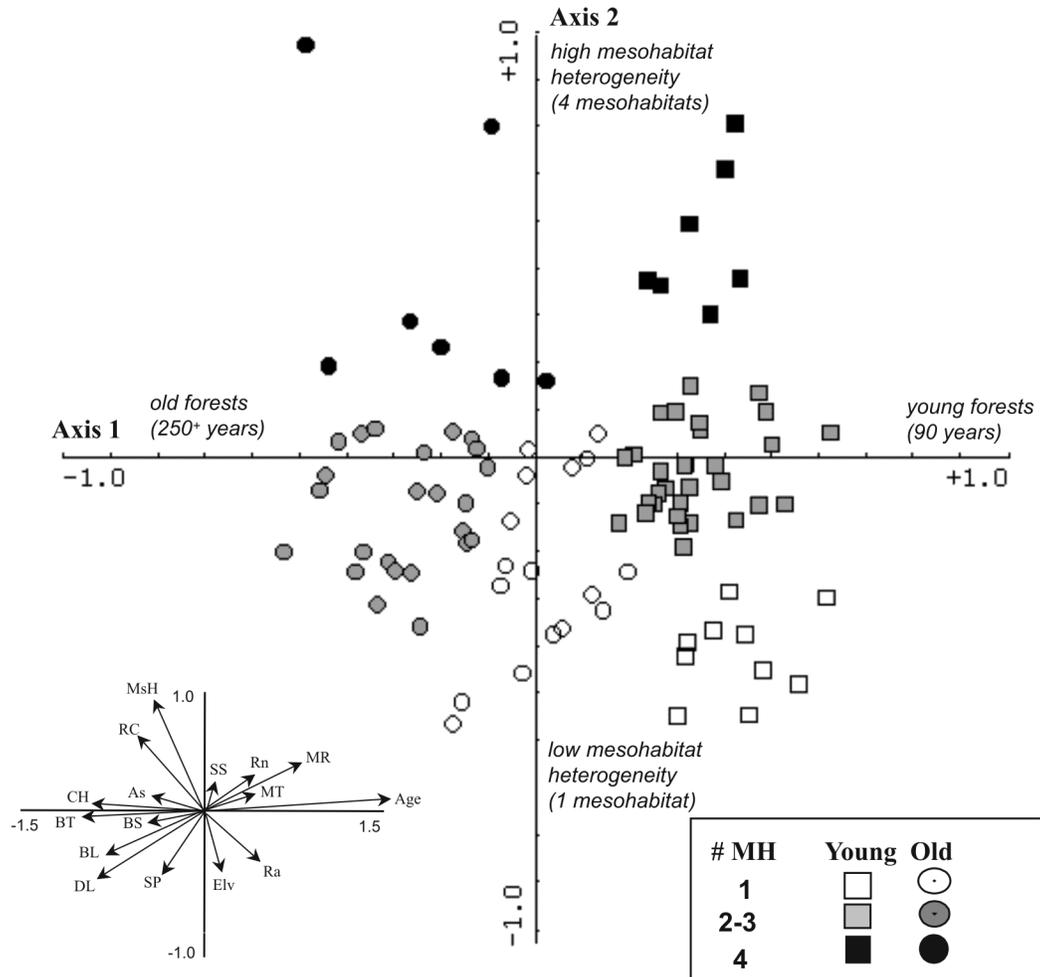
Variants	n	Disturbance	γ
ICHmw3	11	Wildfire	170
	11	Old growth	233
ICHwk1	11	Wildfire	160
	11	Old growth	272
ICHvk1	10	Wildfire	120
	11	Old growth	266

three axes are useful in identifying gradients (Table 4). Interset correlations and significant canonical coefficients were used to identify the environmental variables that best explain the gradients for each axis. The age of the stand is the most important variable defining the first axis (Table 1). Old stands form a distinct group on the left side of the first ordination axis (Fig. 4). Other important variables that correlate to the first axis include forest-structure-related variables such as snag density and log basal area and microclimate (Fig. 4, Table 1). Mesohabitat heterogeneity as measured by the number of different mesohabitats in each stand is most strongly correlated to the second CCA axis (Table 1). Groups of stands with low mesohabitat heterogeneity are found near the bottom of axis 2, and stands with the highest mesohabitat heterogeneity are at the top (Fig. 4). Other variables correlated to the second axis include the abundance and pH of rock habitat (Table 1). On the third axis, stand hygrotape explains an additional 10% of the variance in the species data (sig. t value, $p > 0.05$).

Coastal Western Hemlock zone

Distinct groups of stands on the ordination are defined by stand age and habitat heterogeneity. High species-environment correlations (>0.86) indicate that environmental variables for the first two axes

Fig. 4. CCA ordination of 102 stands in the ICH using 22 environmental variables. The abbreviations for each variable are listed in Table 1 (#MH = no. of different mesohabitats).



are useful in identifying gradients (Table 4). Based on interset correlations and significant canonical coefficients, age of the stands is the most important variable defining the first axis (Table 5). This is reflected in ordinations where old stands form a distinct group on the left side of the first axis (Fig. 5). Snag density is an important stand structure variable correlated to the first axis (Table 5). Mesohabitat heterogeneity is most strongly correlated to the second CCA axis (Table 5). Groups of old stands with low mesohabitat heterogeneity are found near the bottom right side of the ordination and increase with habitat heterogeneity to the top left side of the ordination (Fig. 5). Slope position (i.e., toe, low, mid, etc.) explains an additional 7% of the variance in the species data on axis three (sig. t value, $p > 0.05$).

Stand classification

Interior Cedar–Hemlock zone

Cluster analysis (SAHN) classified all stands into five groups based only on the species in the stands. Differences in species richness among the five groups were significant ($p < 0.05$), but the sums of squares within the groups were low (Tables 6 and 7). Relative species frequency (number of

Table 4. Summary of canonical correspondence analyses (CCA) for 102 ICH stands, and 185 CWH stands with 22 environmental variables (see Table 1).

Biogeoclimatic zone		Axis	1	2	3	4
ICH	Eigenvalue		0.432	0.192	0.060	0.052
	Species–environment correlation		0.960	0.906	0.902	0.847
	Cumulative % variance of species data explained		18.7	31.6	41.4	48.4
CWH	Eigenvalue		0.450	0.161	0.021	0.012
	Species–environment correlation		0.973	0.862	0.690	0.588
	Cumulative % variance of species data explained		48.8	68.5	75.3	79.3

Table 5. Statistics for variables used in canonical correspondence analysis (CCA) of 185 stands in the CWH, 22 environmental variables.

Environmental variable	Interset correlation		Canonical coefficient		<i>t</i> value	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Site series (SS)	−0.05	0.32	−0.00	0.02	−0.01	0.54
Elevation (Elv)	0.05	−0.31	−0.01	−0.09	−0.27	−1.90
Slope (SL)	−0.00	−0.22	0.07*	0.02	3.32	0.98
Slope position (SP)	0.05	−0.41	−0.01	−0.05	−0.08	−1.81
Aspect (As)	−0.10	−0.14	−0.03	0.01	−1.68	0.75
Hygrotope (Hyg)	0.00	0.33	0.02	−0.05	0.82	0.43
Rock cover (RC)	−0.01	0.01	−0.02	0.02	−1.09	0.81
Rock acidity (RA)	−0.01	0.01	−0.02	0.01	−0.99	0.79
Soil texture (ST)	0.08	−0.07	0.01	−0.01	0.21	−0.69
Canopy height (CH)	−0.49	0.21	0.01	−0.03	0.31	−1.34
Tree density (DT)	0.55	−0.22	0.00	−0.03	0.09	−1.19
Tree basal area (BT)	−0.29	0.13	−0.02	−0.01	−1.06	−0.18
Snag density (DS)	0.31	−0.08	0.05*	0.01	3.07	0.41
Snag basal area (BS)	−0.09	0.04	−0.02	−0.01	−1.09	−0.40
Log density (DL)	−0.23	0.11	0.11	0.03	1.72	0.40
Log basal area (BL)	−0.28	−0.11	−0.02	−0.06	−0.56	−1.75
Shrub cover (SC)	−0.38	0.28	−0.02	0.04	−0.67	1.34
Herb cover (HC)	−0.24	0.41	−0.03	0.03	−1.09	1.25
Stand age (Age)	− 0.73	0.31	−0.31*	0.07	−11.29	2.07
Rainfall (Rn)	0.01	0.01	0.01	0.01	0.01	0.01
6 month mean temp. (6T)	0.01	0.01	0.01	0.01	0.01	0.01
Mesohabitats (MsH)	−0.44	− 0.60	−0.17	−0.09*	−1.68	−10.15

Note: Asterisks indicate significance at $p < 0.05$. Absolute t value > 2.1 is used to indicate important canonical coefficients (ter Braak 1998). Bold values are indicated for variables with significant correlation and canonical coefficients.

stands–species) is not only higher in the first two groups, but the tail of the curve (i.e., the rarer species) is more developed (Fig. 6). There is a drop in the number of hepatics and endemics from group 1 (old stands) through to group 5 (young stands) (Table 7). The shortening of the frequency curves from group 1 through to group 5 indicates that there are fewer rare species in young forest and forest with low habitat heterogeneity (Fig. 6).

Overlaying the clusters (SAHN) onto the CCA ordination of stands showed five distinct groups of stands that are clearly definable based on age and mesohabitat heterogeneity (Fig. 7; Table 1). Old forests

Fig. 5. CCA ordination of 185 stands in the CWH using 22 environmental variables. The abbreviations for each variable are listed in Table 5. (#MH = no. of different mesohabitats).

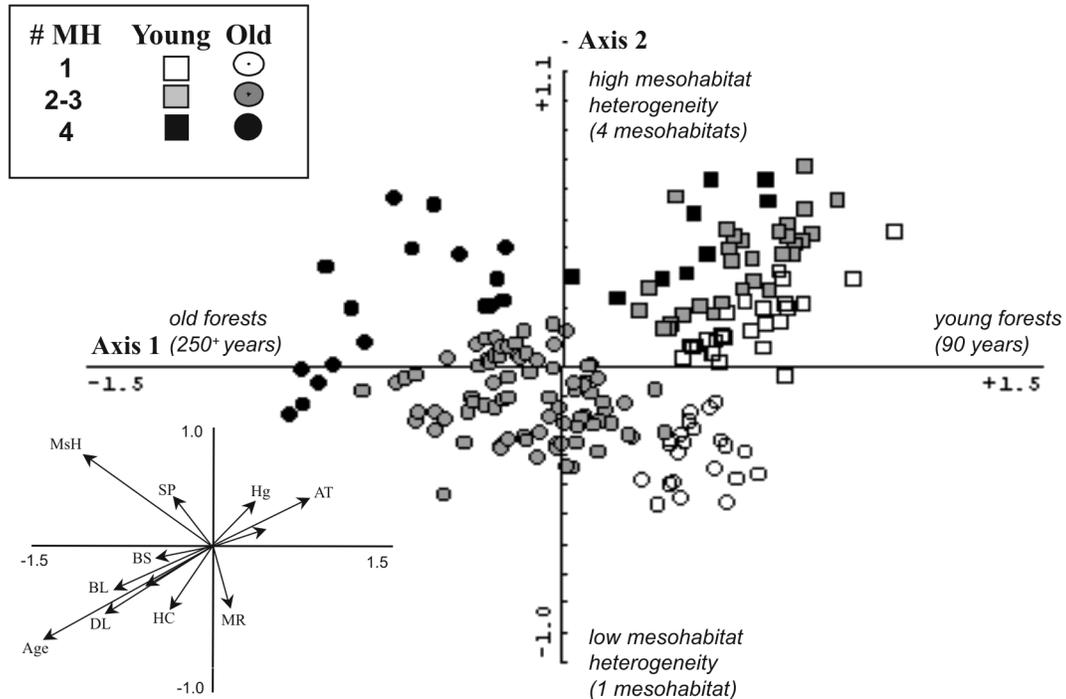


Table 6. Species richness analysis of variance for SAHN cluster groups in the ICH and CWH (Levene Statistic not sig., $p > 0.05$).

Biogeoclimatic zone	ANOVA	Sum of squares	df	Mean Square	F	Sig.
ICH	Between groups	76 559.008	4	19 139.752	162.542	<0.001
	Within groups	11 422.011	97	117.753		
	Total	87 981.020	102			
CWH	Between groups	400 446.773	3	133 482.258	296.645	<0.001
	Within groups	81 445.044	181	449.973		
	Total	481 891.816	185			

with high mesohabitat heterogeneity (group 1) are on the top left side of the ordination (Fig. 7). Young forests with low mesohabitat heterogeneity (group 5) are on the bottom right side of the ordination.

Coastal Western Hemlock zone

Cluster analysis (SAHN) classified all stands into four groups based only on species optimum in stands. Species richness is significantly different ($p < 0.05$) between the groups (Tables 6 and 7). The sums of squares variance for species richness within groups is high when compared with the between groups sums of squares (Table 6). Species frequency in groups 1 and 2 is high, and the tail of these curves is more developed (i.e., more rare species) (Fig. 6). In the CWH, the within-groups partition of variance can be attributed to the high species diversity within stands of old coastal forests (Table 2). Several corresponding patterns are evident from group 1 (old stands) through to 4 (young stands). The number of hepatics and endemics drop from group 1 through to group 4 (Table 7). There are at least

Table 7. Diversity and floristic affinities for K-means species cluster groups within the ICH and CWH.

Biogeoclimatic zone	Cluster group	Dist. age (years)	MH	S γ	\bar{s} α	Number of species with affinities*							
						Hep.	Moss	E	A	M	B	C	T
ICH	1	250+	4	298	126	99	199	20	11	11	190	30	56
	2	250+	2–3	262	91	79	183	11	5	9	179	27	42
	3	†	†	195	78	54	141	9	4	7	131	23	23
	4	90	2–3	157	54	47	110	7	3	7	111	23	20
	5	90	1	91	33	23	68	5	2	4	71	15	12
CWH	1	250+	4	321	220	120	201	36	10	11	152	28	118
	2	250+	2–3	287	147	110	177	33	9	10	137	23	109
	3	250+	1	198	100	68	130	28	7	8	96	18	69
	4	90	1–3	114	60	32	82	16	5	5	58	12	34

Note: MH, = mesohabitat number; S, total species or gamma diversity; \bar{s} , mean species richness or mean alpha diversity; Hep., hepatics; E, western North American endemics; A, arctic; M, montane; B, boreal; C, cosmopolitan; T, temperate.

*Affinities assigned from Belland (1998).

† Includes old-growth stands 250+ years old with one mesohabitat and young stands 90 years old with four mesohabitats.

twice as many hepatics and endemics in old-growth forest than young forests (Table 7). The shorting of the frequency curve from group 1 through to group 4 signifies a loss of many rare species (Fig. 6).

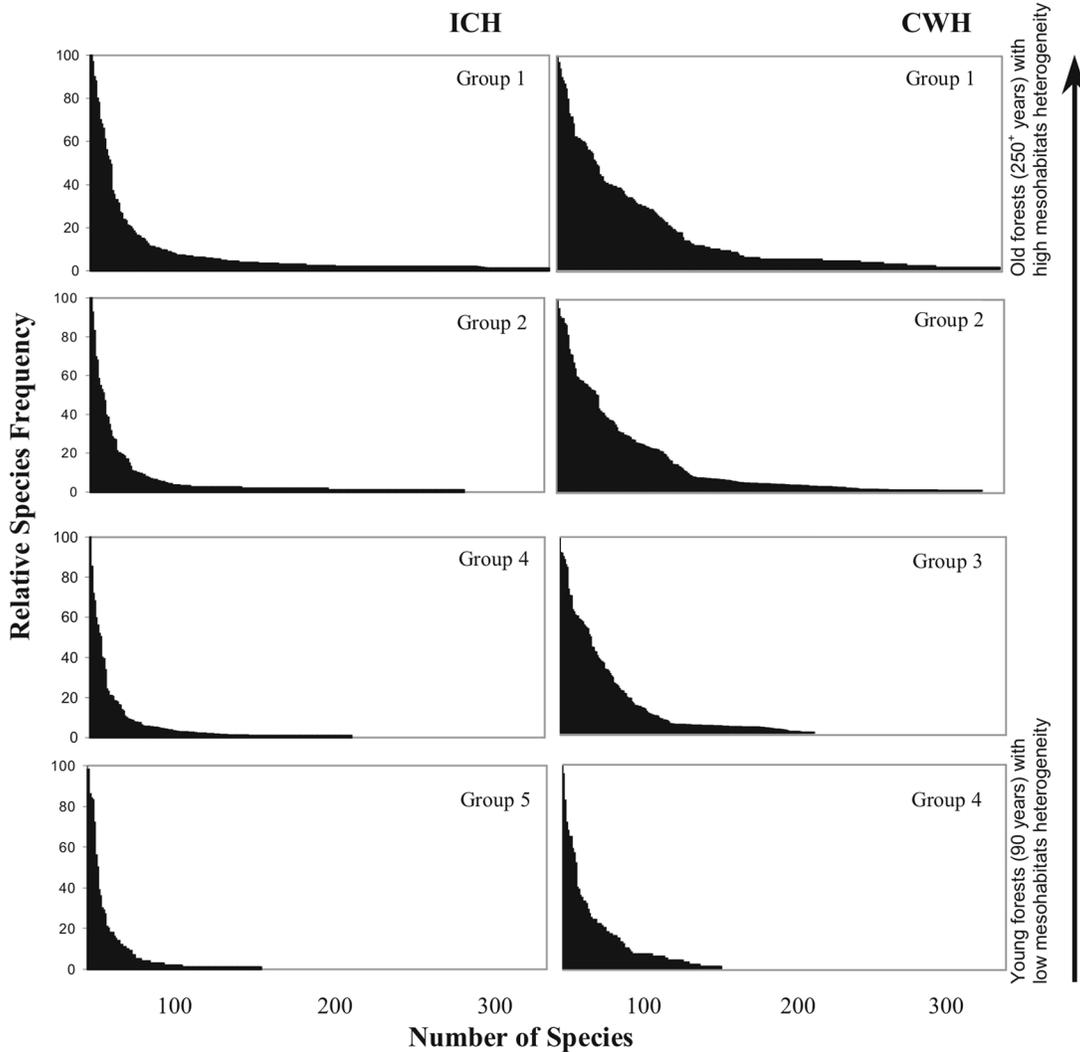
Four distinct groups of stands are apparent when the SAHN clusters are overlaid on the CCA ordination of stands (Fig. 8). The groups are clearly definable based on age and mesohabitat heterogeneity (Table 5). Old-growth forests with high mesohabitat heterogeneity (group 1) are on the top left side of the ordination (Fig. 8). Old-growth forests with low mesohabitat heterogeneity (group 3) are on the bottom right side of the ordination. Young forests (group 4) are clumped on the right side of the ordination.

Beta diversity (species turnover)

Interior Cedar–Hemlock zone

Beta diversity calculated for old stands is almost identical to that calculated for young stands (Table 2). There is considerable species turnover (beta diversity) between cluster group 1 through group 5. Groups 1 through 5 are separated by 2.5 SD of the environmental gradient, suggesting that species turnover between young and old stands is high (Fig. 9). Species turnover between young and old stands is apparent on the ordination when considering the relative sample scores (Fig. 9). Some old stands are 2 SD away from young stands. This suggests that a number of species share only 1/3, and that a number of species are unique to young and old-growth forests. Old forests contain more hepatics and rare western North American endemics than young forests (Table 7). Mesohabitat heterogeneity can account for the 30% (1 SD difference) of species turnover within an age class. The relative importance of an indicator species within an old-growth forest was estimated using an indicator analysis (Dufrêne and Legendre 1997). Many species had indicator values greater than 60 ($p < 0.05$) and are considered indicators of “old growthness” within the ICH. A complete list of these species, including their habitat requirements, is beyond the scope of this report. Table 8 provides a partial list of several bioindicator species for ICH old-growth forests.

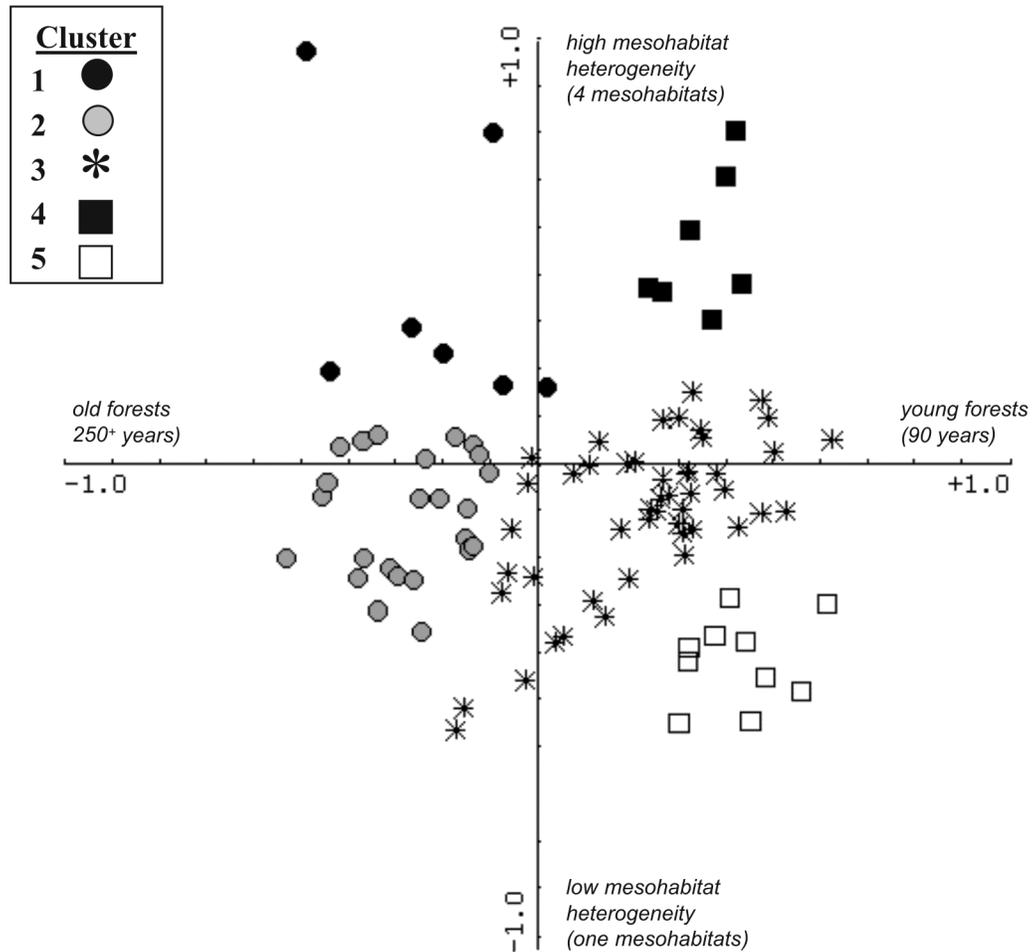
Fig. 6. Relative species frequency curves for stand cluster groups defined by K-means and SAHN within the ICH or CWH (ICH group 3 is excluded).



Coastal Western Hemlock zone

Beta diversity calculated for old-growth stands is only slightly higher than that calculated for young forests (Table 2). The results from the CCA (using Hill's scaling) indicate that there is considerable species turnover between young and old stands. Groups 1 through to 4 are spread over 1.85 SD of the environmental gradient (Fig. 9). Species turnover from young stands to old stands is approximately 30% (1 SD). However, species turnover within old-growth stands themselves is approximately 30%. A unique assemblage of species exists in old CWH forests, which consist of many hepatics and rare western North American endemics (Table 7). Species turnover within old-growth stands increases with mesohabitat heterogeneity (Fig. 9). The increase in sample scores (SD) from groups 1 to 3 corresponds to an increase from one to four mesohabitats per sample (Fig. 9; Table 7). Beta diversity values in the ICH are over twice those of the CWH. This is a result of similar gamma diversity values between the

Fig. 7. Overlay of stand clusters from K-means/SAHN on the CCA ordination of 102 stands in the ICH using 22 environmental variables. The abbreviations for each variable are listed in Table 1.



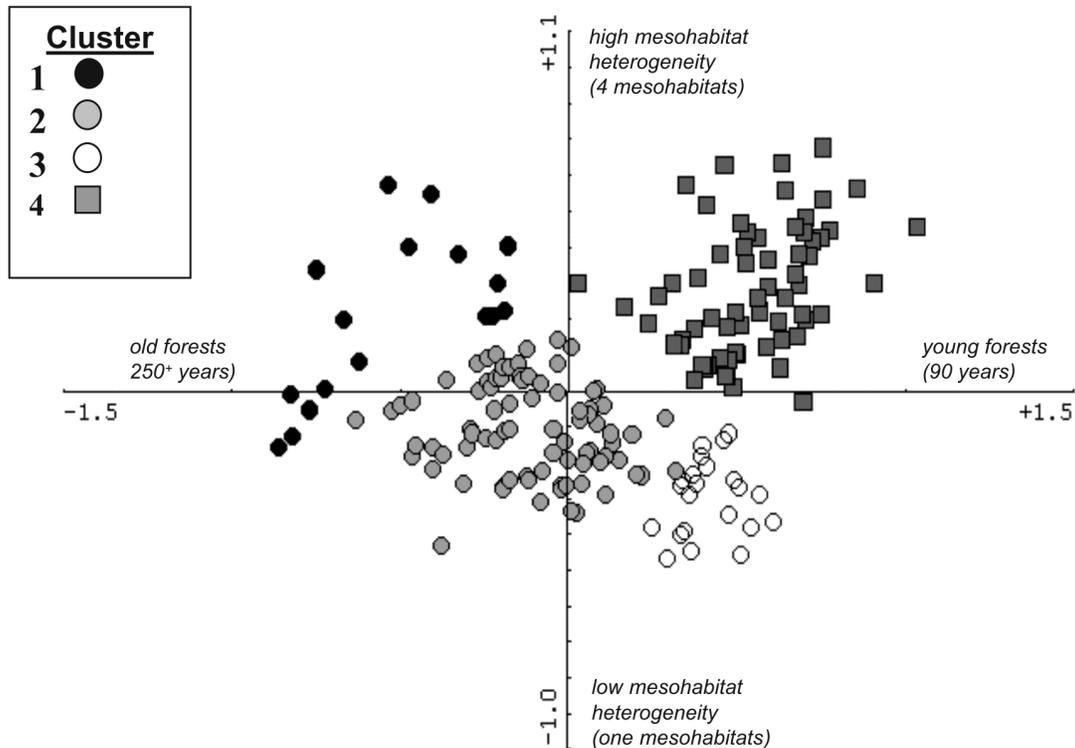
ICH and CWH and higher alpha diversity in the CWH (Table 2). A plethora of species within the CWH had indicator values greater than 60 ($p < 0.05$). A partial list of indicators of “old growthness” within the CWH is provided in Table 8.

Discussion

Why are old-growth forests rich with bryophytes?

Several studies have shown that bryophyte diversity is higher in old-growth coniferous forests than younger forests (Pike et al. 1975; Edwards 1986; Söderström 1988a; Lesica et al. 1991; Crites and Dale 1995; Rambo and Muir 1998a, 1998b). All these studies have concluded that old stands promote habitat and environmental conditions (i.e., high humidity, low wind, and moderate light) that are favourable for rich bryophyte communities. These old forests have many unique habitats for epiphytic (Pike et al. 1975; Sillett 1995) and epixylic bryophytes. Old forests have a greater diversity of logs in a variety of decay classes and sizes than young forests (Andersson and Hytteborn 1991). Logs provide habitat for many species of bryophytes, and different decay classes and sizes of logs support different communities

Fig. 8. Overlay of stand clusters from K-means/SAHN on the CCA ordination of 185 stands in the CWH using 22 environmental variables. The abbreviations for each variable are listed in Table 5.



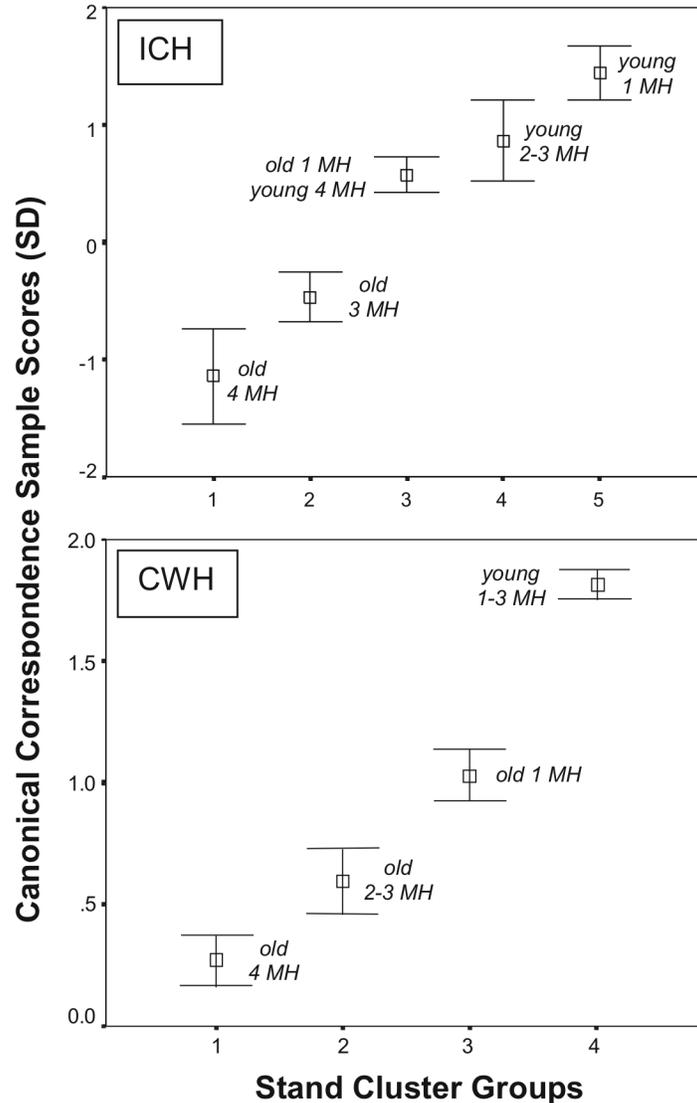
of bryophytes (Gustafsson and Hallingbäck 1988; Söderström 1988a). Disturbing these habitats can reduce bryophyte diversity dramatically (Muotka and Virtanen 1995).

Old-growth cedar–hemlock stands in British Columbia are known to support rich carpets of bryophytes, but surprisingly, there have been no published quantitative data that compare bryophyte diversity in young- and old-growth cedar–hemlock forests. Our research clearly shows that old-growth cedar–hemlock forests have many more species and higher abundance of bryophytes than young forests, regardless of biogeoclimatic zone. Gamma and alpha diversity were approximately twice as high in old-growth cedar–hemlock forests than in young forests. Bryophyte abundance is twice as high in old forest compared with young forest within the ICH and three times higher in the CWH.

Environmental continuity and moisture

High diversity bryofloras may also occur in old-growth forest because of the moist local microclimate (Hallingbäck 1977) and stand continuity (Edwards 1986). Stand continuity has been defined as large stands having the least amount of fragmentation from large-scale disturbance such as fire or logging activities (Krebs 1985). Environmental continuity is directly affected by the size and number of catastrophic disturbances. Edwards (1986) has stated that long environmental continuity favours rare Atlantic bryophyte distributions in Europe. Similarly, Aune (1994) recorded that the floristic composition of the continuous boreal forest in Norway is rich and abundant with rare oceanic and suboceanic bryophytes. Long environmental continuity is associated with high bryophyte diversity in the Pacific Northwest (Rambo and Muir 1998a) and the support of rare and endemic species in ICH and CWH old-growth rainforests.

Fig. 9. Species turnover across stand cluster groups defined by K-means and SAHN within the ICH or CWH. MH = number of mesohabitats (sample scores represent relative position of group along the environmental gradient) (see Table 7 for cluster group definitions).



The high diversity in old-growth cedar-hemlock forests may be partially explained by the fact that these old-growth forests are usually associated with very moist microclimates (Meidinger and Pojar 1991). In cedar-hemlock forests, stand continuity is intimately linked with moist climates, and both these variables (i.e., stand age and moist climates) are associated with higher bryophyte diversity. At the landscape scale, forest fire is still a dominant force. However, fire often leaves some unburned pockets of older forest (Arsenault 1997). These are often quite small (1–2 ha) and are not recognizable on forest fire maps. These small pockets of old growth are often associated with wetter site conditions related to topographic position (i.e., toe positions, depressions, canyons), fine soil texture, and spray zones of waterfalls (Arsenault 1997). The largest stands with the greatest environmental continuity are

Table 8. Preliminary list of bioindicators of “old growthness” within cedar–hemlock forests in British Columbia.

Indicator	Species	Feature
Cedar–hemlock old growth	<i>Neckera douglasii</i>	Epiphytic, also on cliffs and rocks
	<i>Bazzania tricrenata</i>	Epixylic, also on trees, cliffs, and rocks
	<i>Heterocladium macounii</i> [†]	Saxicolous, also on trees and logs
	<i>Claopodium bolanderi</i> [†]	Saxicolous, rarely on tree trunks
	<i>Ptilidium californicum</i>	Epiphytic, also on logs
	<i>Antitrichia curtipendula</i>	Epiphytic, occasionally on cliffs and rocks
	<i>Bazzania denudata</i> [†]	Epixylic, also on tree bases and cliffs
	<i>Metaneckera menziesii</i>	Epiphytic, occasionally on cliffs and rocks
	<i>Thamnobryum neckeroides</i> [†]	-Saxicolous, also on tree bases
	<i>Cephalozia lunulifolia</i>	Epixylic, also on cliffs and humus
CWH old growth	<i>Claopodium crispifolium</i>	Epiphytic, also on cliffs and rocks
	<i>Dicranodontium denudatum</i> [†]	Saxicolous, also on humus and logs
	<i>Douinia ovata</i>	Epiphytic, also on humus and rocks
	<i>Herbertus aduncus</i>	Epixylic, also on trees and humus
	<i>Homalia trichomanoides</i>	Epiphytic, also on humus, cliffs, and rocks
	<i>Hookeria lucens</i>	Epixylic, also on moist soil or rock
	<i>Marsupella emarginata</i>	Saxicolous, occasionally on soil
	<i>Metzgeria conjugata</i>	Saxicolous, also on trees, logs, and humus
	<i>Mylia taylorii</i>	Epixylic, also on trees, humus, and wet soil
	<i>Porella cordaeana</i>	Epiphytic, also on rocks, cliffs, humus, and soil
ICH old growth	<i>Lophocolea minor</i>	Epixylic, also on humus or soil
	<i>Cratoneuron filicinum</i>	Saxicolous (streams), also on wet cliffs
	<i>Heterocladium dimorphum</i>	Saxicolous, also on humus and soil
	<i>Calypogeia suecica</i>	Epixylic, rarely on trees
	<i>Lophozia ascendens</i>	Epixylic, also on humus, rarely rocks and trees
	<i>Leskeella nervosa</i>	Saxicolous (streams), also on trees
	<i>Barbilophozia attenuata</i>	Saxicolous, also on logs
	<i>Blindia acuta</i>	Saxicolous (streams), also wet soil

Note: All species have indicator values >60 estimated using the method of Dufrêne and Legendre (1997) and $p < 0.05$ from a Monte Carlo test of significance.

[†]Western North American endemics.

in watersheds that receive heavy annual rainfall. The unique forest structure in these moist, continuous old-growth stands contributes to the diversity of microhabitats for bryophyte colonization. In the CWH, the largest stands with the greatest environmental continuity (Sidney Fjord and Clayoquot and Walbran Watersheds on the west coast of Vancouver Island) had the highest bryophyte diversity.

Old-growth cedar–hemlock forests have a rich flora of oceanic and suboceanic western North American endemics. Fifteen percent of the bryoflora of British Columbia is confined to western North America (Schofield 1988). Preservation of large, old-growth forests will ensure a refugium for many western North American endemics (Schofield 1984). In the ICH, both fire history maps and the relative portion of forests older than 250 years suggest that the wetter biogeoclimatic variants (i.e., ICHwk1 and ICHvk1) have higher environmental continuity because of lower fire frequencies than in the drier ICHmw3 (Arsenault 1997). Old-growth forests in the wetter biogeoclimatic variants had higher species richness than dryer variants. Similar patterning of lichen diversity has been recorded in the ICH (Arsenault and Goward 1999; Goward and Arsenault 2000). However, in young forests (80–90 years), species richness was highest in the drier ICHmw3 variant. This may be because the young forest floor was invaded by many colonizing species in the dry variants, whereas only a few mesophytic species dominated the

forest floor in the wetter variants. Studies on bryophyte succession within the boreal forest have shown that colonizing species are well adapted to the dry conditions and dominate the ground cover after silvicultural disturbances (Newmaster et al. 1999). However, the colonizing species are out competed by forest mesophytes after canopy development and corresponding increases in humidity and lower light intensities (Newmaster and Bell 2002).

Disturbance

Our research does not allow a direct comparison of logging and forest fire disturbance. However, in the CWH, the main disturbance is clearcutting, and the extensive history of clearcutting over the last 100 years allows stands 80 years of age to be compared with the residual old growth. In the ICH, the main disturbance was forest fire, and the extensive logging history is relatively recent. Following either clearcutting or wild fire, microhabitats are disturbed or removed (i.e., logs, stumps, and rocks), temperature extremes and the drying effect of the wind increase, drainage lowers the surface waters, and streams, cliffs, moist logs, and stumps dry out (Hämet-Ahti 1983; Crites and Dale 1995; Newmaster et al. 1999; Laaka 1992). The number of suitable habitats decreases, ultimately decreasing cryptogam diversity (Gustafsson and Hallingbäck 1988; Söderström 1988*a*, 1988*b*; Laaka 1992; McCune 1993; Rambo and Muir 1998*a*; Newmaster and Bell 2002). These disturbances have important consequences for the ecosystem because of the loss of many mesophytic forest species and the invasion of colonizers and fugitives (Newmaster et al. 1999; Bell and Newmaster 2002). The long-term differences in bryophyte diversity in logged and burnt old-growth forests needs to be monitored.

Beta diversity

We used beta diversity to consider species turnover both within and between stands of different age classes. Beta diversity is high when moving on a gradient of young to old stands as expressed in our CCA ordinations and site scores. In either biogeoclimatic zone, stands of the same age had similar beta diversity. This is well known in northern forest in Ontario (Newmaster et al. 1999; Newmaster and Bell 2002), Scandinavia (Söderström 1988*b*), and the Pacific Northwest of the U.S.A. (Rambo and Muir 1988*b*). However, species richness and turnover between old-growth stands can be quite variable. Species turnover is higher among old stands with high mesohabitat heterogeneity than old stands with low mesohabitat heterogeneity.

We have shown that there is significant species turnover along temporal gradients within either the ICH or CWH. This suggests differences in species compositions for both young and old forests. There is a rich flora of hepatics in old-growth ICH and CWH forest. Söderström (1988*b*) demonstrated that hepatics are richer and more abundant in older forest, and unique communities of hepatics and mosses in old-growth forests have been documented in many other research projects (Pike et al. 1975; Lesica et al. 1991; Sillet 1995; Laaka 1992; Rambo and Muir 1998*a*). Rare epixylic hepatics are often associated with an abundance of logs in different decay classes and sizes in old-growth forest (Gustafsson and Hallingbäck 1988; Söderström 1988*a*; Rambo and Muir 1998*a*, 1998*b*). These epixylic specialists have habitat demands that are unique to older forest (Sermander 1936; Schuster 1949; Andersson and Hytteborn 1991). Succession of epixylic communities is continuous because the logs offer only temporary habitat for these rare hepatics; old-growth forest ecosystems provide a continuous supply of logs that maintains rich communities of hepatics. These structural differences support the differences in species richness between young- and old-growth cedar-hemlock forests. Furthermore, there are many more western North American endemics and rare species associated with old-growth CWH and ICH. Bryophytes can be used as bioindicator species for old-growth forests. Some old-growth bioindicators have wide distributions, but other species are restricted to either the CWH or ICH forests. A detailed community analyses of both young and old forests in the ICH and CWH is needed to provide a complete list of indicators of "old growthness", including their habitat requirements.

What are the critical environmental variables?

The gradient analyses

Our multivariate analyses offered insights into the patterning of bryophyte diversity at a regional scale (stands within a biogeoclimatic zone) and the influence of environmental variables. The classification of stands, using only bryophyte species, arranged old stands and young stands in separate groups. Further divisions separated these groups based on habitat heterogeneity. Stands with the greatest mesohabitat heterogeneity had the highest bryophyte diversity. This follows patterning of bryophytes in wetlands (Vitt and Belland 1995; Belland and Vitt 1995). Distinct patterns in bryophyte diversity at a regional scale were apparent using relationships between stands, species, and environmental variables within either the ICH or CWH. The groups on the ordination were complementary to the SAHN stand classification, which used only species abundance. The two most influential correlating environmental variables at the regional scale were stand age and mesohabitat heterogeneity. Forest structure variables that are related to stand age, such as the size of trees and logs, are of importance at finer, local scales (i.e., mesohabitats and microhabitats within stands).

These results have several implications for forest managers concerned with sustainability of bryophyte diversity. Emulating natural disturbance in today's silvicultural prescriptions may not necessarily sustain bryophyte diversity. Old-growth cedar-hemlock forests have been developing for thousands of years and the age of any one stand may exceed 1000 years. Forest rotation cycles do not consider time spans of that length. We must consider preserving old-growth forests that, in turn, will sustain bryophyte diversity.

Bryophyte diversity patterns

Stand age and mesohabitat heterogeneity are very important variables in maintaining high bryophyte diversity. The large number of habitats associated within CWH forests has resulted from geomorphological processes (Montgomery 1997), forest successional processes (Whittaker 1960), and climatic processes (Hebda 1998). Hebda and Whitlock (1997) describe CWH forest as a "biogeochron", which embodies the changes in the living and physical (substrate and climate) components of the landscape. These living and physical components are the basic elements for habitat diversity. Habitat heterogeneity develops over long periods of time (millennia). Cedar-hemlock forest began to disperse and establish starting about 12 000 B.P. Western hemlock expanded in the CWH 5000-7000 B.P., and in the ICH 2000-4000 B.P. (Hebda 1994, 1995, 1997; Brown and Hebda 2002). Infrequent forest fire disturbance (250- to 750-year fire cycles), and successional patterns sustained the cedar-hemlock forests for the last 4000-6000 years (Hebda and Whitlock 1997). In this time, bryophyte species could colonize an undisturbed, moist ecosystem with a highly diverse number of meso- and (or) microhabitats. Bryophytes are dependent on their ability to disperse and establish from local sources of bryophyte diversity. Some areas along the coast escaped glaciation and served as refugia for many of today's western North American endemic bryophytes (Schofield 1988). Dispersal limits are less than 50 m for many bryophytes with spores greater than 25 μm (Söderström 1993). Dispersal and establishment of bryophytes on available habitats can occur only when there is a local source of propagules and sufficient time to develop rich communities. Environmental continuity is an important forest management implication for the maintenance of bryophyte diversity in Canada's rainforest.

Conclusion

A better understanding of the patterning of bryophyte diversity in forested ecosystems will provide an opportunity to minimize the impact of forest operations on biodiversity (Arsenault and Goward 1999). Management plans must consider stand age and mesohabitat heterogeneity as the two most influential environmental variables that influence the patterning of bryophyte diversity in cedar-hemlock forest. The increase in species richness with older, more mesohabitat-rich stands corresponds with an increase

in rare species, endemics, and hepatics. The loss of bryophyte species after logging and forest fire disturbance is well documented and of growing concern (Peet et al. 1983; Laaka 1992; Ehrlich 1990; Andersson 1987; Newmaster et al. 1999; Newmaster and Bell 2002). Recommendations from many analyses of bryophyte diversity promote the protection of old-growth forests and consequently the rare species within them (Gustafsson and Hallingbäck 1988; Söderström 1988*b*; Rambo and Muir 1998*a*; Schofield 1988). Researchers from Norway and other countries have noted the importance of preserving old forest for the conservation of rare bryophytes (Prestø 1996; Weibull and Söderström 1995). Efforts to preserve rare species and areas of high bryophyte diversity have been made throughout Europe (Söderström et al. 1992; Söderström 1995) and North America (Slack 1992; Belland 1998; Rambo and Muir 1998*b*; Newmaster et al. 1999). We suggest that bryophyte diversity in the cedar–hemlock forests of British Columbia will be sustained through ecosystem management of old-growth legacies (i.e., landscapes, stands, and components thereof) and the preservation of areas of high diversity. Our research has identified the importance of old-growth forests and habitat heterogeneity. Further research is needed to identify the unique communities of bryophytes within young and old cedar–hemlock forests, providing a complete list of bioindicators of “old-growthness”. Furthermore, the mesohabitat quality and quantity associated with high bryophyte diversity needs to be quantified and implemented into current management plans within the ICH and CWH.

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