The contributions of forest structure and substrate to bryophyte diversity and abundance in mature coniferous forests of the Pacific Northwest

Shelley A. Evans[2], Charles B. Halpern[1,2], and Donald McKenzie[2,3]

[2] *School of Environmental and Forest Sciences, Box 352100, University of Washington, Seattle, WA 98195-2100, U.S.A.;* [3] *Current address: Pacific Wildland Fire Sciences Lab, USDA Forest Service, 400 N. 34th Street, Seattle, WA 98103, U.S.A.*

Abstract. Many aspects of forest structure are thought to contribute to the presence, abundance, and diversity of forest-floor bryophytes. To what extent easily measured characteristics of local environment (overstory structure or substrate availability) explain patterns of abundance and diversity remains unclear in most forest ecosystems. We explore these relationships in four mature, Douglas-fir dominated forests in southwestern Washington (U.S.A.). At each site, six 13-ha stands were sampled systematically (787 total plots) to capture variation in physical environment, forest overstory and understory vegetation, substrates, and forest-floor bryophytes. We compared bryophyte species composition, richness, and rank abundance among sites. We used multiple linear regression to model local cover and richness as functions of the physical environment, overstory and understory vegetation, and substrate availability. We compared the contributions of substrates to bryophyte abundance and richness and measured the strength and consistency of associations between individual species and particular substrates. Bryophyte composition differed significantly among sites, but patterns of richness and rank abundance were surprisingly similar, despite differences in stand structure and climate. Regression models explained only 18–23% of the variation in bryophyte cover or richness, likely due to weak relationships between vegetation structure and microclimate, disparity in the spatial scales of measurement, and temporal lags in bryophyte responses to structure. Most non-litter substrates (mineral soil, rock, fresh or decayed wood, stumps, shrub and tree bases) contributed minimally to available growing space, but disproportionately to species richness, particularly at the stand scale. Individual species were most often associated with decayed wood, although few species showed strong substrate specificity. In general, however, substrates contributed to ecological redundancy, with most species occupying multiple substrates and most substrates supporting a diversity of species.

Keywords. Forest structure, liverworts, mosses, overstory-understory interactions, substrate associations, Washington Cascades.

---

[1] Corresponding author's email: chalpern@uw.edu

DOI: 10.1639/0007-2745-115.2.278

The Bryologist 115(2), pp. 278–294 0007-2745/12/$1.85/0

◆ ◆ ◆

In forests it is typically assumed that the competitive (shading or below-ground) effects of trees influence the abundance, diversity, and spatial distribution of understory layers. Studies of overstory-understory interactions commonly explore effects on the vascular flora (Both et al. 2011; Gilliam & Roberts 2003; Lindh 2005; McKenzie et al. 2000; Wilson et al. 2009), but less often on bryophytes, despite their prominence in many forest ecosystems. Among studies that have explored relationships between overstory structure and bryophyte community characteristics, few generalizations emerge (Alaback 1982; Baldwin & Bradfield 2005; Márialigeti et al. 2009; Mills & MacDonald 2004; Pharo & Beattie 2002; Rambo & Muir 1998a; Root & McCune 2010; Vellak et al. 2003). Bryophyte abundance and diversity may be correlated with different elements of forest structure to varying degrees, or not correlated at all (e.g., review in Frego 2007). It is not clear to what extent this reflects differences in ecosystems and their component species, the spatial scales of observation, the structural attributes measured, or the methods by which forest structure and bryophytes are sampled.

There is evidence to suggest that the nature of interactions with trees may differ substantially for bryophytes and vascular plants. Bryophytes of closed-canopy forests are typically stress-tolerators, tolerant of deep shade and characterized by long life spans, slow growth rates, and low reproductive output (During 1979, 1992; Grime 1977; Proctor 2000). Lacking roots, they do not compete directly with trees or other vascular plants for soil moisture or nutrients. Moreover, they can colonize growing surfaces (logs, tree boles, or rocks) that are uninhabitable by vascular plants (Schofield 2001; Slack 2011).

Although bryophytes may not compete with vascular plants for soil moisture or nutrients, many aspects of forest structure may contribute directly or indirectly to their presence, abundance, or diversity. Bryophyte presence and abundance may be influenced by light availability which varies with the density, cover, or composition of the overstory (Drever & Lertzman 2003; Heithecker & Halpern 2006; Messier et al. 1998). Effects of canopy shading can also be indirect, mediated through subcanopy strata (understory trees, shrubs, and herbs) that are also responsive to light (McKenzie et al. 2000). In addition to its effects on light transmission, overstory structure can moderate air temperature and humidity, to which bryophytes can be highly sensitive (Proctor et al. 2007). Elements of stand structure that affect light, temperature, or humidity may thus serve as proxies for the abiotic factors that determine the presence and abundance of forest-floor bryophytes. Finally, live and dead trees (snags and logs) can serve as substrates for establishment and growth, thereby enhancing the abundance and diversity of species (Andersson & Hytteborn 1991; Jonsson 1997; Jonsson & Esseen 1990; Rambo 2001; Rambo & Muir 1998a,b). Species with limited dispersal (e.g., Kimmerer 2005) and highly restricted substrate requirements may be extirpated if suitable habitat is lost (due to decay, natural disturbance, or forest management—Bradbury 2006; Söderström 1988a). To what extent easily measured characteristics of the local environment (including overstory structure and substrate availability) explain the abundance and diversity of forest-floor bryophytes remains an important, but unanswered question in many forest ecosystems.

Bryophytes are prominent in the ground flora in west-side (Coast and Cascade Range) forests of the Pacific Northwest (U.S.A.). Previous studies in this region have explored relationships between bryophyte community structure and stand age, overstory characteristics, and substrates, but in a limited set of sites or forest environments (Rambo 2001; Rambo & Muir 1998a,b; Root & McCune 2010). Studies in mature undisturbed forests of this region are rare. It is within these moderately aged forests that coarse woody debris (CWD) typically reaches its minimum, reflecting continuous decay, but little subsequent input, following stand-replacing disturbance (Spies et al. 1988). The amount and quality of CWD—functions of forest age and disturbance history—may be critical determinants of bryophyte abundance and diversity.

Here we explore the contributions of forest structure and forest-floor substrates to the diversity and abundance of bryophytes in mature coniferous forests of western Washington, U.S.A. We use pre-treatment (baseline) data from a large-scale experiment in structural-retention harvests in the Pacific Northwest—the DEMO experiment (Aubry et al. 1999, 2009; Dovčiak et al. 2006). Our measurements comprise a systematic sample of nearly 800 plots from replicate Douglas-fir (*Pseudotsuga menziesii*) dominated stands at four Coast or Cascade Range locations (sites) in southwestern Washington. Sites span low to moderate elevations; an east to west gradient (Puget Trough to just east of the Cascade crest); and forests of varying age, structure, and understory composition. To our knowledge, these represent the most extensive and intensive sample of understory bryophyte communities and associated structural attributes of mature forests in this region. Although the choices of sites and sampling designs were driven by the broader objectives of the experiment (Aubry et al. 1999; Dovčiak et al. 2006; Halpern et al. 2005), the baseline data allow us to explore fundamental aspects of bryophyte community structure. We address the following questions: (1) Does species composition vary among and within mature forests of differing physical environments, ages, or structures? (2) What are the patterns of diversity among and within sites? Specifically, do species-area and dominance-diversity relationships vary? (3) Are local (plot-scale) richness and cover of bryophytes correlated with the overstory or understory characteristics of these forests? (4) How do different substrates (fine litter, fresh and decayed logs, mineral soil, rocks, stumps, and tree and shrub bases) contribute to the abundance and diversity of bryophytes at local and stand scales? (5) With which substrates are individual species associated, and are these associations consistent among sites?

STUDY SITES

The study sites are a subset of those that constitute the Demonstration of Ecosystem Management Options (DEMO) experiment, a regional-scale study of variable-retention harvests in mature, coniferous forests of the Pacific Northwest (Aubry et al. 1999, 2009). Data for the current study were collected during pre-treatment sampling of each of six, 13-ha experimental units (stands) at four locations (sites) in southwestern Washington—three in the Cascade Range (Gifford Pinchot National Forest) and one in the Coast Range (or Black Hills, Capitol State Forest) southwest of Olympia (Aubry et al. 2009). Sites encompass a diversity of physical environments and forest types (**Table 1**). Elevations range from 200 to 1300 m, slopes are gentle to steep, and aspects vary widely. Soils are generally well drained and coarse to medium textured, derived from andesite, breccia, and basalt (Pringle 1990; Wade et al. 1992). The climate of the region is maritime: summers are warm and dry and winters are cool and wet. Most precipitation falls from October to April, resulting in frequent summer drought (Franklin & Dyrness 1988). December mean minimum temperatures range from −5.5 to 0.1°C and August mean maxima from 21.5 to 24.1°C (Thornton et al. 1997). Mean annual precipitation ranges from 1,860 to 2,968 mm.

Among sites, forests vary in age, structure, and understory composition (**Table 1**; Halpern et al. 1999, 2005). The Cascade Range sites were mature (70- to 170-yr-old) undisturbed forests; the Black Hills site was second-growth (65-yr-old) forest that regenerated naturally after clearcut logging in the 1930s. Three forest zones are represented—*Tsuga heterophylla*, *Abies grandis*, and *A. amabilis* (Franklin & Dyrness 1988)—although *Pseudotsuga menziesii* was the dominant canopy species throughout (**Table 1**). Overstory structure (density, basal area, and canopy cover), understory abundance, and abundance of coarse woody debris also varied markedly among and within sites (**Table 1**).

METHODS

Field sampling. Data were collected during summer 1994 and 1995. Within each stand, we established a systematic grid of 63–64 points at 40-m spacing to sample variation in physical environment, forest overstory and understory strata, forest-floor substrates, and bryophytes. A series of nested plots and transects was established at a subset of points (32–37 per stand; 787 plots in total). Slope and aspect were determined at the center of each plot. Overstory

Table 1. Physical environment, vegetation, and forest-floor characteristics in the four study sites. Values are plot means and ranges. Site codes are: BU = Butte, LWS = Little White Salmon, PH = Paradise Hills, and CF = Capitol Forest. Mean aspect is back transformed (see **Table 2**). Precipitation and temperature are estimated from DAYMET (Thornton et al. 1997), a set of 1-km GIS raster coverages generated from meteorological records (1980–1997) and digital elevation data. Tree density and basal area include stems ≥5.0 cm dbh. Cover values are the summed cover of individual species. CWD volume is total CWD (mostly decay classes III–V).

Variable	BU	LWS	PH	CF
Physical environment				
Latitude, longitude (deg)	46.37 N, 121.59 W	45.86 N, 121.69 W	46.01 N, 121.99 W	46.90 N, 123.14 W
Elevation (m)	975–1280	825–975	850–1035	210–275
Slope (%)	45 (11–75)	48 (10–86)	18 (1–94)	38 (3–76)
Aspect (deg)	125 (30–358)	23 (0–359)	95 (3–356)	92 (8–359)
Annual precipitation (mm)	1,860	1,968	2,968	1,973
Dec min. temperature (°C)	−5.5	−4.3	−4.0	−0.1
Aug max. temperature (°C)	21.5	24.0	22.1	24.1
Vegetation and forest-floor characteristics				
Stand age (yr)	70–80	140–170	110–140	65
Overstory tree cover (%)	78 (32–98)	65 (0–93)	83 (35–98)	77 (31–98)
Tree density (trees ha^{-1})	1,151 (250–3,450)	236 (25–1,000)	740 (225–1,725)	362 (75–1,200)
Tree basal area (m^2 ha^{-1})	56.1 (11.9–134.5)	70.7 (0.5–162.1)	72.8 (19.6–121.6)	64.3 (9.9–116.7)
Forest zone	*Tsuga heterophylla*	*Abies grandis*	*Abies amabilis*	*Tsuga heterophylla*
Understory tree cover (%)	8.3 (0–46.9)	10.1 (0–61.6)	5.5 (0–39.3)	1.5 (0–25.0)
Shrub cover (%)	19.9 (0–84.4)	72.4 (9.8–100.0)	12.1 (0–69.2)	39.5 (0–100.0)
Herb cover (%)	29.4 (0–100.8)	54.0 (7.1–115.8)	19.6 (0–65.4)	52.3 (0–118.6)
Total log cover (%)	10.7 (0–44.3)	8.6 (0–33.8)	11.0 (0–33.3)	6.3 (0–33.5)
CWD volume (m^3 ha^{-1})	324 (0–1,651)	146 (0–945)	169 (0–916)	116 (0–1,087)

trees (≥ 5.0 cm dbh) were tallied and measured for diameter in a circular plot of 0.04 ha (11.28 m radius). Cover of tall shrubs and saplings (understory trees ≥10 cm tall and <5.0 cm dbh) was estimated with the line-intercept method along four perpendicular transects (4–10 m from plot center). Saplings were also tallied in four, 1 × 6 m subplots bounded on one side by each transect. Volume of CWD was estimated from the same transects using the methods of Brown (1974); separate estimates were made for fresh (decay classes I–II) and decayed wood (decay classes III–V) (Fogel et al. 1973). Cover of overstory trees was estimated at the end points of each transect (8 per plot) with a moosehorn densiometer.

Bryophytes, herbaceous vegetation, tree seedlings, and forest-floor substrates were sampled in 0.2 × 0.5 m quadrats spaced at 1-m intervals along each transect (24 quadrats per plot). Within each quadrat we recorded: (1) total cover of bryophytes (including epilithic, epixylic, epigeic, but not epiphytic species present as litterfall); (2) presence of each bryophyte taxon; (3) cover of each herbaceous species; (4) number of tree seedlings (<10 cm tall); and (5) cover of each substrate (see **Table 2**). In one of the six stands per site, we also recorded the primary substrate of each bryophyte species in each quadrat. For quadrats that fell on CWD or the bases of shrubs or trees, sampling was limited to a height of 1 m from the forest floor. If a bryophyte could not be identified in the field, a sample was collected for subsequent identification. Species in four genera (*Brachythecium*, *Calypogeia*, *Lophozia*, and *Scapania*) could not be reliably identified and were treated at the generic level. Nomenclature follows Anderson et al. (1990) for mosses and Stotler & Crandall-Stotler (1977) for liverworts.

Analyses. From the overstory data in each plot we computed local stem density, basal area, stand density index, and quadratic mean diameter (**Table 2**). For bryophytes, understory vegetation, and substrate variables (**Table 2**), plot values were

Table 2. Definitions of potential plot-level predictors of bryophyte richness and cover.

Variable	Definition
Physical environment	
Slope	Slope (%)
Aspect	Aspect transformed as $\cos([\pi/180] \cdot \text{azimuth})$; values range from -1 (south) to $+1$ (north)
Overstory vegetation	
Tree basal area	Basal area of overstory trees (≥ 5.0 cm dbh)
Tree density	Density of overstory trees (≥ 5.0 cm dbh)
Stand density index	Composite index of tree basal area and density, computed as $\sqrt{(\text{tree basal area} \cdot \text{tree density})}$
Quadratic mean diam.	Mean tree diameter, computed as $\Sigma\sqrt{(\text{dbh}_i^2/n)}$, where dbh = diameter at breast height and n is number of trees per plot
Understory vegetation	
Sapling density	Density of understory trees (≥ 10 cm tall and <5.0 cm dbh)
Seedling density	Density of tree seedlings (<10 cm tall)
Shrub cover	Summed cover of tall shrub species
Herb cover	Summed cover of herbaceous species including low shrubs and sub-shrubs
Generalist herb cover	Summed cover of herbs present during most stages of forest development and dominant in mature stands (Halpern 1989; McKenzie et al. 2000)
Late-seral herb cover	Summed cover of herbs that reach maximum development in late-seral forests and are sensitive to canopy removal or disturbance (Halpern 1989; Halpern & Spies 1995; McKenzie et al. 2000)
Release herb cover	Summed cover of forest herbs that are typically released by overstory removal (Halpern 1989; McKenzie et al. 2000)
Herb species richness	Total number of herbaceous species per plot
Substrates	
Total CWD volume	Total volume of CWD (all decay classes; Fogel et al. 1973)
Fresh CWD volume	Volume of fresh CWD (decay classes I–II)
Decayed CWD volume	Volume of decayed CWD (decay classes III–V)
Total log cover	Total cover of logs (≥ 5 cm diameter)
Fresh log cover	Cover of fresh logs (≥ 5 cm diameter; decay classes I–II)
Decayed log cover	Cover of decayed logs (≥ 5 cm diameter; decay classes III–V)
Fine litter cover	Cover of leaves, needles, and fine branches (<5 cm diameter)
Mineral soil cover	Cover of mineral soil and small stones (<7 cm width)
Rock cover	Cover of bedrock, exposed boulders, and stones (≥ 7 cm width)
Tree base cover	Cover of live tree bases (including exposed roots) to 1 m height
Shrub base cover	Cover of live shrub bases to 1 m height
Stump cover	Cover of tree stumps (natural and cut [CFOR only]) to 1 m height

computed as means of transect or quadrat values. For individual bryophyte species we computed two measures of abundance at each site: constancy (percentage of plots in which a species was present) and mean frequency of occurrence (mean percentage of quadrats in which a species was present).

We used detrended correspondence analysis (DCA; Hill & Gauch 1980) to assess variation in bryophyte species composition among and within sites (question 1). Plots (n = 787) served as samples and species frequency (% presence among quadrats) as the measure of abundance; rare species were down-weighted using default settings in PC-Ord 4.0 (McCune & Mefford 1999). DCA was followed by multiresponse permutation procedures (MRPP, Biondini et al. 1988) to test if bryophyte composition differed among sites, or among stands within sites. MRPP is a non-parametric Monte Carlo method that calculates a weighted mean within-group distance (δ, Sørensen's index), for pre-defined groups of observations (sites or stands within sites). δ is then computed for all possible partitions of the data for groups of the same size. The p-value reported represents the proportion of simulated values less than the observed δ. MRPP was implemented in PC-Ord ver. 4 (McCune & Mefford 1999).

Patterns of bryophyte diversity (question 2) were explored in several ways. Plot-scale richness was used to generate species-accumulation curves for each site, as well as first- and second-order jackknife estimates (predicted richness of sites assuming complete enumeration; Heltsche & Forrester 1983; Palmer 1991). Dominance-diversity (rank-abundance) curves were then used to compare distributions of abundance among species (Magurran 2004). Two measures of abundance were considered: one based on species constancy (proportion of plots), the second on mean frequency of occurrence (proportion of quadrats).

We used multiple linear regression to explore relationships between total bryophyte cover or richness (number of species per plot) and measures of physical environment, overstory structure, understory vegetation, and substrates (question 3). For both models, data were pooled from all sites. Because the number of potential predictors was large, we first computed Pearson correlations among the full sets of predictors and response variables. From these we subjectively chose an initial set of 11 predictors with the highest correlations, excluding predictors that were highly correlated. We then used backward elimination (Neter et al. 1990) to drop predictors whose coefficients were not significantly different from zero at $\alpha = 0.05$. We repeated this procedure with different initial sets of predictors, choosing as our final model that which minimized the mean-squared error of residuals. Standard diagnostics were applied to test for normality and constant variance of residuals, and a Cook's distance plot was used to identify and remove significant outliers. Bryophyte cover was log transformed to meet the assumptions of regression. Analyses were conducted in Splus 2000 (Insightful 2000).

We compared the contributions of eight primary (most abundant) substrates to the total occurrence and richness of bryophytes (question 4). Comparisons were limited to one stand (32 plots) per site. For each quadrat ($n = 768$ per site), we tallied the number of bryophyte taxa supported by each substrate, then summed these values across plots to generate a total occurrence for each substrate. For each plot and stand, we also tallied the number of taxa supported by each substrate to generate a mean richness per substrate per plot and a total richness per substrate per stand. Values for each of these three metrics were qualitatively compared among substrates relative to the cover of each substrate (question 4).

We used indicator species analysis (ISPAN, Dufrêne & Legendre 1997) to measure the strength and consistency of associations between individual bryophyte species and particular substrates (question 5). Analyses were based on proportional occurrence of species among quadrats (frequency) and plots (constancy), with a separate analysis run for each site (32 plots in one stand). Species were considered indicators if they had a significant P value ($P \leq 0.05$) and an $IV_{max} \geq 25$ (Dufrêne & Legendre 1997). Statistical significance of IV_{max} was evaluated using a Monte Carlo randomization method (McCune & Grace 2002). The analysis was implemented in PC-Ord ver. 4 (McCune & Mefford 1999).

RESULTS

Floristics. We observed 78 bryophyte taxa, including 56 mosses and 22 liverworts (**Supplementary Table S1**). Species totals were larger, however, because four taxa (*Brachythecium*, *Calypogeia*, *Lophozia*, and *Scapania*) contained multiple species (**Supplementary Table S1**). Of the full set of taxa, 23 (29%) occurred at all sites, but 22 were unique to individual sites. Within sites, many taxa occurred in most or all stands, but others were limited to fewer than half of the stands (**Supplementary Table S1**).

Community composition. Detrended correspondence analysis (DCA) separated sites distinctly in ordination space (**Fig. 1a**). Plots at Capitol Forest (Coast Range) were completely isolated from plots of the Cascade Range. Among the latter, plots from Butte and Paradise Hills (west of the Cascade crest) exhibited overlap in composition, although plots at Butte were compositionally more variable. Plots from Little White Salmon (slightly east of the Cascade crest) also showed large variation, but had higher scores on DCA2.

The results of MRPP were consistent with DCA. Species composition differed significantly among

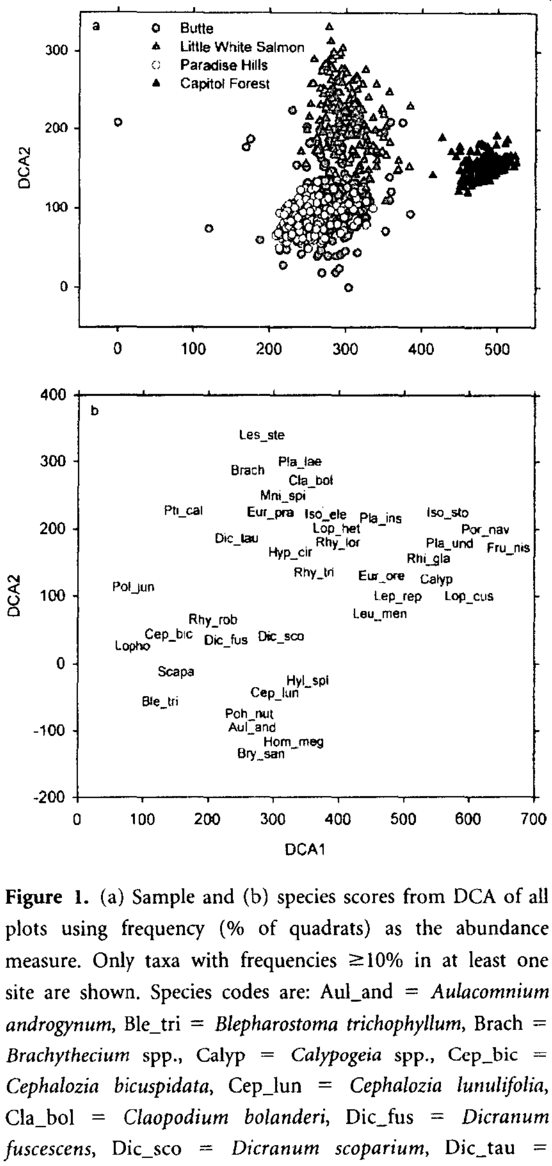

Figure 1. (a) Sample and (b) species scores from DCA of all plots using frequency (% of quadrats) as the abundance measure. Only taxa with frequencies ≥10% in at least one site are shown. Species codes are: Aul_and = *Aulacomnium androgynum*, Ble_tri = *Blepharostoma trichophyllum*, Brach = *Brachythecium* spp., Calyp = *Calypogeia* spp., Cep_bic = *Cephalozia bicuspidata*, Cep_lun = *Cephalozia lunulifolia*, Cla_bol = *Claopodium bolanderi*, Dic_fus = *Dicranum fuscescens*, Dic_sco = *Dicranum scoparium*, Dic_tau = *Dicranum tauricum*, Eur_ore = *Eurhynchium oreganum*, Eur_pra = *Eurhynchium praelongum*, Fru_nis = *Frullania nisquallensis*, Hyl_spl = *Hylocomium splendens*, Hyp_cir = *Hypnum circinale*, Iso_myo = *Isothecium myosuroides*, Lep_rep = *Lepidozia reptans*, Leu_aca = *Leucolepis acanthoneuron*, Lop_cus = *Lophocolea cuspidata*, Lop_het = *Lophocolea heterophylla*, Lopho = *Lophozia* spp., Mni_spi = *Mnium spinulosum*, Pla_ins = *Plagiomnium insigne*, Pla_lae = *Plagiothecium laetum*, Pla_und = *Plagiothecium undulatum*, Poh_nut = *Pohlia nutans*, Pol_jun = *Polytrichum juniperinum*, Por_nav = *Porella navicularis*, Pse_ste = *Pseudoleskea stenophylla*, Pse_ele = *Pseudotaxiphyllum elegans*, Pti_cal = *Ptilidium californicum*, Rhi_gla = *Rhizomnium glabrescens*, Rhy_lor = *Rhytidiadelphus loreus*, Rhy_rob = *Rhytidiopsis robusta*, Rhy_tri = *Rhytidiadelphus triquetrus*, Roe_roe = *Roellia roellii*, Scapa = *Scapania* spp., Tra_meg = *Trachybryum megaptilum*.

sites and among stands within sites, although the magnitude of differences among stands (expressed by the A-statistic, a measure of effect size) was considerably smaller than that among sites (**Table 3**). As evident in the DCA, mean within-group distances were smaller for Paradise Hills and Capitol Forest (0.37) than for Butte or Little White Salmon (>0.53) (**Table 3**).

Species diversity and cover. The total number of taxa was comparable in three of the sites (45–47), but distinctly higher at Butte (58) which had many locally uncommon taxa (15 with a single occurrence) (**Supplementary Table S1 & Table 4**). However, liverwort richness varied among sites, ranging from 9 taxa (19% of the flora) at Little White Salmon to 16 (36%) at Paradise Hills (**Table 4**).

Species-accumulation curves (**Fig. 2**) and sampled vs. jackknife estimates of site-level richness (**Table 4**) suggest that we observed most common or infrequent species, but missed a number of rarer taxa (particularly at Butte). Dominance-diversity (rank-abundance) relationships, illustrating the distribution of abundance among taxa, were generally similar among sites (**Fig. 3**). Abundance distributions were lognormal, with relatively few dominant or rare taxa and most taxa of intermediate abundance. Butte was an exception, however, with a higher proportion of moderate-abundance taxa and a long tail of "rare" (single-occurrence) taxa (**Fig. 3**).

Total bryophyte cover varied substantially among and within sites (**Table 4**). Mean cover was lowest at Butte (6.8%), the most diverse site, and highest at Paradise Hills (22.5%), the least diverse site.

Models of bryophyte richness and cover. Multiple regression models explained 23% of the variation in bryophyte richness (number of species per plot) and 18% of the variation in bryophyte cover (**Table 5**). Richness was positively correlated with herb species richness, cover of logs (total and decayed), and stand density index. Bryophyte cover was negatively correlated with slope and with cover of "release herbs" (subordinate forest species that respond positively to canopy removal), and positively correlated with cover of "generalist herbs" (forest dominants) and sapling density.

Contributions of substrates to bryophyte occurrence and richness. Fine litter was the most

Table 3. Results of MRPP testing for differences in species composition among sites and among the six stands within each site. The A-statistic (chance-corrected within-group agreement or within-group homogeneity) is a measure of effect size.

	Sample size	Mean within-group distance (Sørensen's index)	A-statistic	*P*
Among sites	787	0.521	0.279	<0.0001
Among stands				
Butte (BU)	197	0.591	0.080	<0.0001
Little White Salmon (LWS)	197	0.535	0.080	<0.0001
Paradise Hills (PH)	196	0.366	0.139	<0.0001
Capitol Forest (CF)	197	0.372	0.127	<0.0001

abundant substrate at all sites (75–92% cover; **Fig. 4**) and generally supported, by an order of magnitude, the greatest number of bryophyte occurrences (**Fig. 4a**). At Paradise Hills, however, bryophytes were considerably more frequent on decayed logs than on fine litter. The remaining substrates were far less abundant and contributed minimally to bryophyte occurrence. In contrast, a greater variety of substrates contributed to bryophyte richness, particularly at the stand scale (**Fig. 4b**). Litter tended to support the greatest diversity of bryophytes, except at Paradise Hills, where decayed logs were richer in taxa. Additional uncommon substrates, including mineral soil, rock, stumps, and the bases of trees and shrubs (mainly *Acer circinatum*), were important for stand-scale diversity at multiple sites (**Fig. 4b**).

Bryophyte associations with substrates. A total of 64 taxa (52 mosses, 12 liverworts; 27–35 taxa per site) were sufficiently common to test for substrate associations using ISPAN. Of 130 tests, 24 (18%) yielded significant associations (12 mosses, 3 liverworts; **Table 6**). Significant associations were most common at Paradise Hills (9) and Butte (7) and on decayed logs (9 species × sites) or tree bases (6 species × sites). Significant associations were rare for fresh logs and shrub bases and absent for stumps and mineral soil. Most associations with a substrate were limited to one or two sites (9 and 5 taxa, respectively); however, for four taxa, substrate affinities differed among sites (typically switching between decayed logs and tree bases). Species fidelity for particular substrates (expressed by the maximum indicator value) ranged from low to moderate (26–56) with a few very high values (>75–92; **Table 6**).

DISCUSSION

Floristics and species composition. Study sites were chosen to represent a diversity of physical environments and mature, coniferous forest types (Aubry et al. 1999; Halpern et al. 2005). Thus, it is not surprising that sites supported very different communities of bryophytes. As many taxa (~30%) were unique to individual sites as were shared in common among sites. The distinct separation of Capitol Forest in DCA space is consistent with its

Table 4. Bryophyte richness and cover at each site. Site codes are: BU = Butte, LWS = Little White Salmon, PH = Paradise Hills, and CF = Capitol Forest.

Community attribute	BU	LWS	PH	CF
Mean no. (range) of bryophyte taxa per plot	9.4 (2–19)	9.2 (2–16)	8.9 (2–19)	7.6 (2–20)
Mean number of bryophyte taxa per stand	35.5	31.2	29.3	30.5
Number of moss taxa per site	46	38	29	32
Number of liverwort taxa per site	12	9	16	13
Number of bryophyte taxa per site	58	47	45	45
1st-order jackknife estimate	72.9	56.0	51.0	51.0
2nd-order jackknife estimate	84.8	61.9	51.0	54.9
Mean (range) of total bryophyte cover (%)	6.8 (0.1–30)	10.5 (0.4–56)	22.5 (0.9–66)	14.5 (1.4–53)

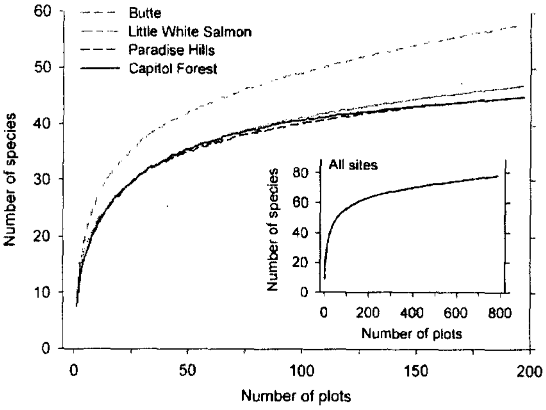

Figure 2. Species-accumulation curves for each site and for all sites combined (inset).

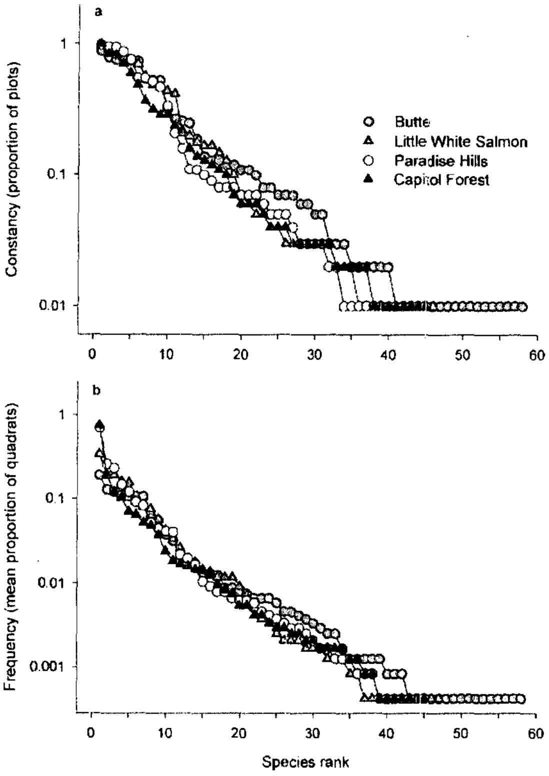

Figure 3. Dominance-diversity curves for each site using (a) constancy and (b) mean frequency as measures of species abundance.

geographic isolation (and lower elevation) in the Coast Range, with sites in the Cascade Range sharing a greater proportion of species. In contrast, stands (which serve as experimental units within sites) were chosen to maximize similarity of topography and vegetation. However, this was difficult to achieve at some sites due to natural landscape features or past management (presence of harvest units or roads). As a consequence, stands within sites still showed detectable differences in species composition.

Patterns of diversity and cover. Despite significant compositional differences among sites, patterns of diversity and the distribution of abundance among species (dominance-diversity curves) were surprisingly similar. Species-area curves and jackknife estimates of richness suggest that we overlooked a number of uncommon taxa, particularly at Butte. However, this is not surprising given that sampling was based on a systematic distribution of plots and quadrats. For studies of vegetation response to experimental treatments, small fixed plots improve the accuracy and repeatability of cover estimates (McCune & Lesica 1992). However, surveys of larger plots (McCune & Lesica 1992) or floristic habitat sampling (Newmaster et al. 2005) are more efficient at species capture. Nevertheless, complete enumeration of the flora was not our objective, nor should the absence of rare taxa influence interpretations of plot-scale patterns.

Dominance-diversity curves, illustrating the ranked distribution of abundance among species conformed to the lognormal series (Preston 1948), with many species of intermediate abundance (constancy or frequency). This pattern is common in mature plant communities in which species abundance is determined by numerous factors whose effects are complex and multiplicative (Whittaker 1975). That patterns of rank abundance were similar among sites with distinctly different floras suggests that similar sets of factors structure the distribution of abundance among forest-floor bryophytes, regardless of location, disturbance history, or other site characteristics. However, diversity patterns at Butte differed in a number of respects. Butte supported a greater proportion of moderately frequent taxa and a larger number of locally rare taxa (25% with a single occurrence). Total bryophyte cover was also lower at Butte (<7% vs. 10–22% elsewhere), thus competitive interactions were likely weaker, allowing for greater evenness in the distribution of abundance. Lower total cover at Butte probably reflects a combination of historical and topographic factors: burial by tephra from the 1980 eruption of Mount St. Helens (which had adverse

Table 5. Significant predictors and total variance explained (R^2) by multiple regression models of bryophyte richness (number of species per plot) and total bryophyte cover. + and – indicate the direction of correlation between response variables and predictors. See **Table 2** for full definitions of predictors.

Bryophyte response variable	Predictors	Full model R^2
Richness (number of species per plot)	Herb species richness (+)	0.23
	Total cover of logs (+)	
	Cover of decayed logs (+)	
	Stand density index (SDI) (+)	
Total cover	Slope (−)	0.18
	Release herb cover (−)	
	Generalist herb cover (+)	
	Sapling density (+)	

effects on forest-floor bryophytes closer to the eruption; Zobel & Antos 1986), and a steep southerly exposure subject to greater solar radiation and heat load—conditions less conducive to most bryophytic growth forms (Hamilton 1953; Hylander 2005). At the same time, tephra deposits may have enhanced site-level richness by facilitating establishment of disturbance-adapted species (e.g., *Polytrichum juniperinum*) that colonize mineral substrates (Baldwin & Bradfield 2010; Jonsson & Esseen 1990; Rambo 2001). It is also possible that lower bryophyte cover at Butte increased detection of rare or smaller-statured taxa.

Although the total richness of species was similar at most sites, the contributions of mosses and liverworts differed. Liverworts made up 19% of the flora at Little White Salmon (in the relatively warm and dry *Abies grandis* zone), but nearly twice that (36%) at Paradise Hills (in the cool, wet, and late-snowlie *Abies amabilis* zone; Franklin & Dyrness 1988). These differences are consistent with patterns observed in other mountain ecosystems, where liverworts show increasing representation with elevation, humidity, and persistence of snow (e.g., Grau et al. 2007; Slack 1977). They are also consistent with the general observation that liverworts are more sensitive than mosses to changes in humidity and temperature (Fenton et al. 2003; Nelson & Halpern 2005; Söderström 1988a; Turner et al. 2006).

Models of bryophyte richness and cover. Our intensive plot-based sampling revealed marked variation (one to two orders of magnitude) in the local richness and cover of bryophytes and in most aspects of forest structure and environment. Nevertheless, in multiple regression models, structural and topographic variables explained only a small portion (18–23%) of the variation in bryophyte richness and cover. Despite limited explanatory power, however, the final set of predictors included reasonable correlates of richness and cover. Richness was positively correlated with the total cover of logs and that of decayed logs. Numerous studies in a diversity of systems have established that the presence of woody substrates in varying stages of decay can enhance the diversity of forest-floor bryophytes (Márialigeti et al. 2009; Mills & MacDonald 2004; Pharo & Beattie 2002; Rambo 2001). Bryophyte richness was also positively correlated with stand density index (SDI, reflecting the combined effects of tree density and basal area). In previous analyses of overstory-understory relationships in these plots, SDI had a strong negative correlation with the cover of tall shrubs (McKenzie et al. 2000). The positive correlation with bryophyte richness may thus represent an indirect effect, mediated by the shrub layer, with greater SDI leading to reduced shrub cover and associated leaf litter. Leaf litter can adversely affect forest-floor bryophytes as a mechanical barrier to establishment or emergence, through allelopathic effects, or by reducing light transmission to the forest floor (Pharo & Beattie 2002; Peintinger & Bergamini 2006; Startsev et al. 2008; Márialigeti et al. 2009). Finally, bryophyte richness was positively correlated with herb richness. Both life forms may respond similarly to the conditions that influence diversity (e.g., cover of shrubs or heterogeneity of ground-surface conditions). Significant correlations between herb

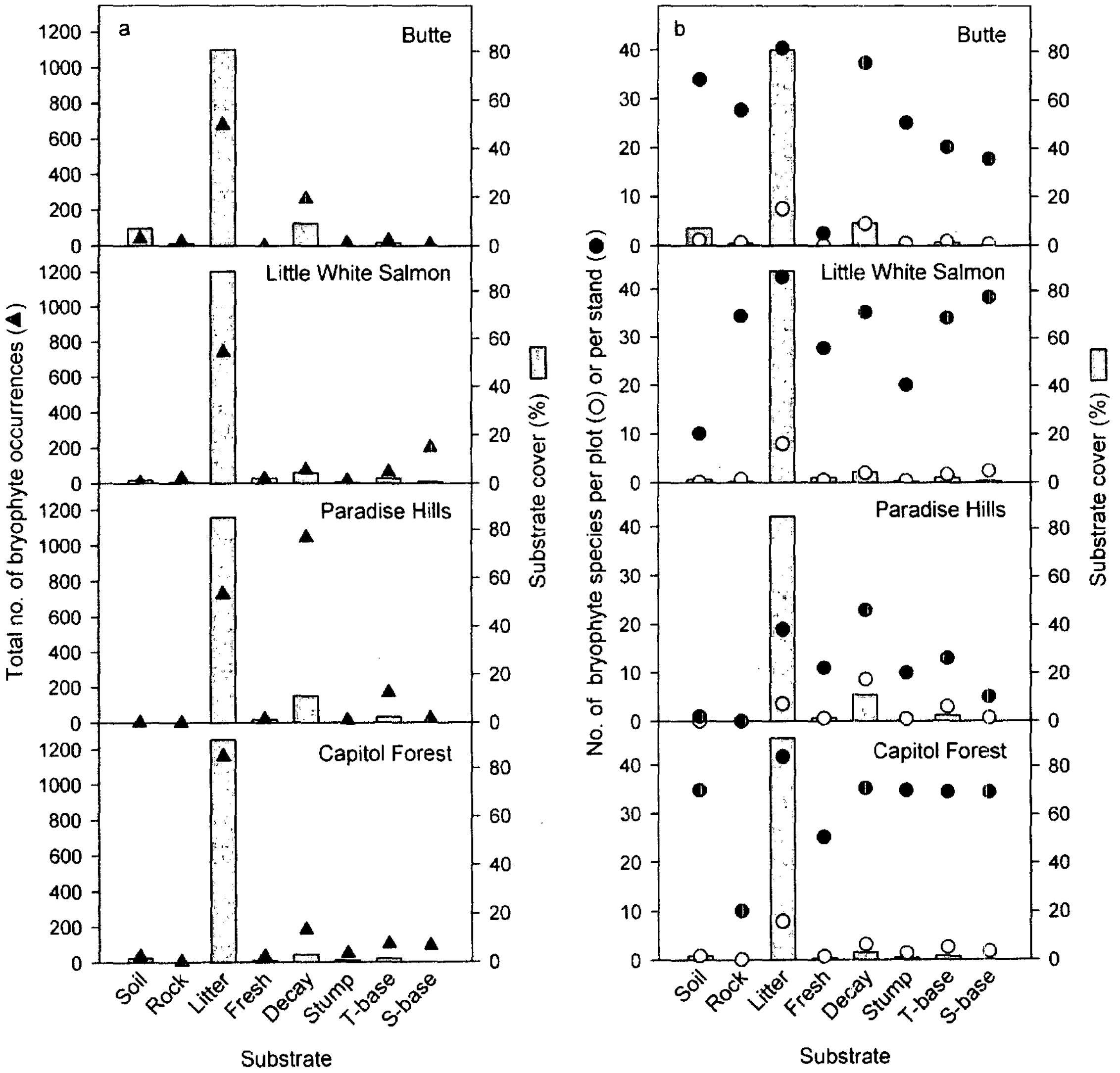

Figure 4. (a) Total bryophyte occurrence (triangles, left axis) and (b) plot- and stand-scale richness (open and closed circles, respectively; left axis) for each of the primary forest-floor substrates. Substrate cover (available space) is shown for comparison (grey bars, right axes). Total occurrence is the summed tally of all bryophyte taxa in all quadrats per site.

and bryophyte diversity have been documented in other systems (Slack 1977; Pharo et al. 1999; Ingerpuu et al. 2001; Márialigeti et al. 2009), although this relationship is not universal (Ewald 2000; Ingerpuu et al. 2003).

The correlates of bryophyte cover differed from those of richness. Cover was negatively correlated with slope and cover of "release" herbs, but positively correlated with cover of "generalist" herbs and saplings. Lacking roots that serve as anchors, bryophytes may be more susceptible to soil movement or snow creep, or to resulting burial on steeper terrain. The negative correlation of bryophytes and release herbs is consistent with their contrasting responses to light: forest bryophytes benefit from shaded, microclimatically stable environments (Lesica et al. 1991; Rambo & Muir 1998a) and release herbs from greater exposure to light (Halpern 1989; Lindh 2005; Ares et al. 2009). The positive correlation with generalist (dominant) forest herbs and saplings is less clear; both groups may be indicative of microsites that are more stable or successionally advanced (McKenzie et al. 2000). Alternatively, these positive correlations may represent an indirect response to tall shrubs, with saplings, generalist herbs, and

Table 6. Results of indicator species analysis illustrating significant associations with substrates (Substr) at each site. Substrates are: mineral soil (soil), rock, fine litter (litter), fresh logs (fresh), decayed logs (decay), stump, tree base (t-base), and shrub base (s-base). Analyses were conducted separately for plots in one stand in each site. Only significant associations ($IV_{max} \geq 25$, $P \leq 0.05$) are shown (see Table 3 for all taxa). Blank cells indicate non-significant associations; dashes indicate species not tested due to limited abundance or absence. *Calypogeia* includes *C. fissa* and *C. muelleriana*. *Scapania* spp. includes *S. bolanderi* and *S. umbrosa*.

	BU			LWS			PH			CF		
Taxon	Substr	IV_{max}	P	Substr	IV_{max}	P	Substr	IV_{max}	P	Substr	IV_{max}	P
Mosses												
Aulacomnium androgynum	decay	26.1	0.049							—		
Dicranum fuscescens	decay	74.9	0.001				decay	46.0	0.010	t-base	45.1	<0.001
Dicranum scoparium							decay	38.2	0.036			
Dicranum tauricum							t-base	27.6	0.034	—		
Eurhynchium oreganum	litter	51.4	<0.001	rock	40.4	0.012						
Heterocladium procurrens				rock	47.3	<0.001	—			—		
Hypnum circinale	decay	36.9	0.002				t-base	55.7	0.001	t-base	38.9	0.007
Isothecium myosuroides							—			fresh	46.8	0.037
Pseudoleskea stenophylla				s-base	91.7	<0.001	—			—		
Racomitrium heterostichum	rock	27.7	0.013	rock	33.3	0.004	—			—		
Rhytidiopsis robusta	litter	40.6	0.003				litter	87.0	<0.001	—		
Liverworts												
Calypogeia spp.	—			—			decay	38.7	0.003			
Cephalozia lunulifolia				—			decay	46.6	0.003			
Ptilidium californicum							t-base	35.7	0.036			
Scapania spp.	decay	40.1	0.003	—			decay	48.4	<0.001	t-base	37.8	0.001
Number of taxa tested	33			35			27			35		
Number of significant associations	7			4			9			4		
Total number of significant associations: decay = 9, t-base = 6, rock = 4, litter = 3, fresh = 1, s-base = 1, stump = 0, mineral soil = 0												

bryophytes all benefiting from the absence of tall shrubs, although the mechanisms of interaction are likely to differ among life forms (see also Márialigeti et al. 2009).

Attempts to model the diversity or abundance of forest-floor bryophytes from simple measures of forest structure have met with varying success (Rambo & Muir 1998a; Pharo & Vitt 2000; Pharo & Beattie 2002; Mills & MacDonald 2004; Baldwin & Bradfield 2005; Root & McCune 2010). The low explanatory power of our models likely reflects one or more common limitations of this approach. First, an underlying assumption is that simple elements of forest structure can serve as proxies for direct measurements of understory microclimate. Although some microclimatic variables, e.g., light, show predictable relationships with overstory structure (Drever & Lertzman 2003), others do not, e.g., soil or ground-surface temperature or humidity, and may require a more complete elaboration of the vegetation (Aussenac 2000; Prevost & Pothier 2003; Heithecker & Halpern 2006). Second, common measures of forest structure integrate over spatial scales that are much larger than those at which bryophytes are measured or operate physiologically (Proctor 2000; Mills & MacDonald 2004; Frego 2007). Third, bryophytes may show lagged responses to changes in forest structure, reflecting their limited dispersal abilities and generally slow rates of growth (Söderström 1990; Miles & Longton 1992; Ross-Davis & Frego 2004). Static measures of overstory structure cannot account for these temporal lags.

Substrate contributions to species presence, abundance, and diversity. In forest ecosystems, the abundance and diversity of bryophytes are commonly attributed to the abundance, diversity, or quality of suitable substrates (Jonsson & Esseen 1990; Andersson & Hytteborn 1991; Jonsson 1997; Rambo & Muir 1998a, 1998b; Rambo 2001; Mills & MacDonald 2004, 2005). For species of the forest floor, structural features such as logs, tree bases, and boulders may provide an escape from the herb layer (e.g., burial beneath leaf litter; Pharo & Beattie 2002; Márialigeti et al. 2009) or competitively superior bryophytes (Söderström 1988b, Andersson & Hytteborn 1991). Second, woody substrates can provide more favorable microclimate or resource conditions than the forest floor (Gustafsson & Hallingbäck 1988; Söderström 1988b; Pharo & Beattie 2002). Finally, species may have varying substrate requirements related to the chemical or physical properties of these substrates (Söderström 1988b; Bates 1992); greater diversity of substrates or substrate conditions should lead to greater diversity of species.

We considered the contributions of eight substrates to bryophyte abundance and diversity. Fine litter was the principal growing surface at all sites and generally supported the greatest abundance and local richness of species. However, this was not the case at Paradise Hills, where bryophyte abundance and richness were greater on decayed logs. Several factors may contribute to this result: (1) greater abundance of highly decayed wood in a relatively old forest (110–140 yr) providing adequate time for colonization (Edwards 1986); (2) a cooler, wetter setting with reduced summer drought (characteristic of the *Abies amabilis* zone), thus ensuring greater constancy of microclimate and substrate quality; and (3) a relatively large pool of liverworts, including epixylic species, that can readily exploit these conditions (Gustafsson & Hallingbäck 1988; Andersson & Hytteborn 1991; Rambo 2001). The remaining substrates (mineral soil, rock, fresh wood, stumps, and shrub and tree bases) provided minimal growing space at most sites, but supported a disproportionate number of taxa, particularly at the stand scale.

The results of indicator species analyses (ISPAN) suggest that although a number of species exhibited substrate preferences (most often with decayed logs or tree bases), few were highly restricted in their distributions—rarely were maximum indicator values >50. Thus, the contributions of these less common substrates to local- or stand-scale diversity appear to be ecologically redundant, with the vast majority of taxa occurring on multiple substrates (*cf.* Rambo 2001). It is unclear if we can generalize similarly about the lack of specificity for the less common taxa in our sample; species frequencies were too low to assess quantitatively.

Cross-site comparisons of species substrate affinities provide an additional, novel insight. Most significant associations with substrates were limited to one or at most two sites. Moreover, for several species, substrate preferences shifted among sites (most often switching between decayed logs and tree bases). To some degree, the lack of consistency among sites may reflect differences in substrate availability, as suggested by the greater frequency of association with decayed logs where decayed logs were most abundant (Paradise Hills). However, it may also indicate that the mechanisms that underlie these associations (e.g., the physical or chemical properties of bark or wood; Cleavitt 2001; McAlister 1995; Pharo & Beatty 2002) may be altered by factors that operate at broader spatial scales, including climate, community context, or disturbance history (Rajandu et al. 2009). In addition, where a "preferred" substrate may be rare or lacking, the morphological and physiological plasticity of many bryophytes (Shaw & Goffinet 2000) may make it possible to utilize an alternate substrate.

Forest-floor bryophytes contribute to the biological diversity and ecological functioning of Pacific Northwestern forests. Yet, surprisingly little research has been devoted to the patterns and correlates of their abundance and diversity in undisturbed forests of this region. Our baseline surveys provide an extensive (~800 plot) sample of species presence and of their habitat relationships in Coastal and Cascade Range forests for which similar surveys are lacking. They suggest that some aspects of community structure (species-area and rank-abundance relationships) are highly predictable in forests with distinctly different floras, structures, and disturbance histories. In contrast, at smaller spatial scales (within stands), other community attributes (cover or species richness) are not easily predicted from simple or static measures of the local environment such as overstory structure, vascular plant abundance, substrate availability, or topography. They also indicate that few species have highly restrictive substrate requirements. The ability of most species to occupy multiple substrates, and of most substrates to support a diversity of species, may contribute to the relatively weak relationships between forest structure and the local abundance and diversity of species.

ACKNOWLEDGMENTS

We thank Tammy Stout and numerous field staff for help with data collection, Denise Liguori for assistance with bryophyte identification, and James Saracco for analytical assistance. Melora Halaj, Eric Zenner, and Gody Spycher contributed to data verification and database management. Two anonymous reviewers provided helpful comments on an earlier draft of this paper. This is a product of the Demonstration of Ecosystem Management Options (DEMO) Study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research Station. Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources (http://www.fs.fed.us/pnw/rmp/demo/). Funds were provided by the USDA Forest Service, PNW Research Station (PNW-93-0455, PNW 97-9021-1-CA, and 08-JV-11261993-167).

LITERATURE CITED

Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. Ecology 63: 1932–1948.

Anderson, L. E., H. A. Crum & W. R. Buck. 1990. List of the mosses of North America north of Mexico. The Bryologist 93: 448–499.

Andersson, L. I. & H. Hytteborn. 1991. Bryophytes and decaying wood – a comparison between managed and natural forest. Holarctic Ecology 14: 121–130.

Ares, A., S. D. Berryman & K. J. Puettmann. 2009. Understory vegetation response to thinning disturbance of varying complexity in coniferous stands. Applied Vegetation Science 12: 472–487.

Aubry, K. B., M. P. Amaranthus, C. B. Halpern, J. D. White, B. L. Woodard, C. E. Peterson, C. A. Lagoudakis & A. J. Horton. 1999. Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. Northwest Science (Special Issue) 73: 12–26.

———, C. B. Halpern & C. E. Peterson. 2009. Variable-retention harvests in the Pacific Northwest: a review of short-term findings from the DEMO study. Forest Ecology and Management 258: 398–408.

Aussenac, G. 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. Annals of Forest Science 57: 287–301.

Baldwin, L. K. & G. E. Bradfield. 2005. Bryophyte community differences between edge and interior environments in temperate rain-forest fragments of coastal British Columbia. Canadian Journal of Forest Research 35: 580–592.

——— & ———. 2010. Resilience of bryophyte communities in regenerating matrix forests after logging in temperate rainforests of coastal British Columbia. Botany 88: 297–314.

Bates, J. W. 1992. Influence of chemical and physical factors on *Quercus* and *Fraxinus* epiphytes at Loch Sunart, western Scotland: a multivariate analysis. Journal of Ecology 80: 163–179.

Biondini, M. E., P. W. Mielke Jr. & K. J. Berry. 1988. Data-dependent permutation techniques for the analysis of ecological data. Vegetatio 75: 161–168.

Both, S., T. Fang, M. Böhnke, H. Bruelheide, C. Geißler, P. Kühn, T. Scholten, S. Trogisch & A. Erfmeier. 2011. Lack of tree layer control on herb layer characteristics in a subtropical forest, China. Journal of Vegetation Science 22: 1120–1131.

Bradbury, S. M. 2006. Response of the post-fire bryophyte community to salvage logging in boreal mixedwood forests of northeastern Alberta, Canada. Forest Ecology and Management 234: 313–322.

Brown, J. K. 1974. Handbook for inventorying downed woody material. USDA Forest Service General Technical Report INT-16.

Cleavitt, N. 2001. Disentangling moss species limitations: the role of physiologically based substrate specificity for six species occurring on substrates with varying pH and percent organic matter. The Bryologist 104: 59–68.

Dovčiak, M., C. B. Halpern, J. F. Saracco, S. A. Evans & D. A. Liguori. 2006. Persistence of ground-layer bryophytes in a structural retention experiment: initial effects of level and pattern of overstory retention. Canadian Journal of Forest Research 36: 3039–3052.

Drever, C. R. & K. P. Lertzman. 2003. Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. Canadian Journal of Forest Research 33: 137–146.

Dufrêne, M. & P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366.

During, H. J. 1979. Life strategies of bryophytes: a preliminary review. Lindbergia 5: 2–18.

———. 1992. Ecological classification of bryophytes and lichens. Pages 1–31. In J. W. Bates & A. M. Farmer (eds.), Bryophytes and Lichens in a Changing Environment. Clarenden Press, Oxford, UK.

Edwards, M. E. 1986. Disturbance histories of four Snowdonian woodlands and their relation to Atlantic bryophyte distributions. Biological Conservation 37: 301–320.

Ewald, J. 2000. The influence of coniferous canopies on understorey vegetation and soils in mountain forests of the northern Calcareous Alps. Applied Vegetation Science 3: 123–134.

Fenton, N. J., K. A. Frego & M. R. Sims. 2003. Changes in forest floor bryophyte (moss and liverwort) communities 4 years after forest harvest. Canadian Journal of Botany 81: 714–731.

Fogel, R. M., M. Ogawa & J. M. Trappe. 1973. Terrestrial decomposition: A synopsis. US IBP Coniferous Forest Biome Report 135, College of Forest Resources, University of Washington, Seattle, U.S.A.

Franklin, J. F. & C. T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon, U.S.A.

Frego, K. A. 2007. Bryophytes as potential indicators of forest integrity. Forest Ecology and Management 242: 65–75.

Gilliam, F. S. & M. R. Roberts (eds.). 2003. The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, Inc., New York, New York, U.S.A.

Grau, O., J-A. Grytnes & H. J. B. Birks. 2007. A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. Journal of Biogeography 34: 1907–1915.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111: 1169–1194.

Gustafsson, L. & T. Hallingbäck. 1988. Bryophyte flora and vegetation of managed and virgin coniferous forests in South-West Sweden. Biological Conservation 44: 283–300.

Halpern, C. B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70: 704–720.

———, S. A. Evans, C. R. Nelson, D. McKenzie, D. A. Liguori, D. E. Hibbs & M. G. Halaj. 1999. Response of forest vegetation to varying levels and patterns of green-tree retention: an overview of a long-term experiment. Northwest Science (Special Issue) 73: 27–44.

———, D. McKenzie, S. A. Evans & D. A. Maguire. 2005. Initial responses of forest understories to varying levels and patterns of green-tree retention. Ecological Applications 15: 175–195.

——— & T. A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5: 913–934.

Hamilton, E. S. 1953. Bryophyte life forms on slopes of contrasting exposures in central New Jersey. Bulletin of the Torrey Botanical Club 80: 264–272.

Heithecker, T. D. & C. B. Halpern. 2006. Variation in microclimate associated with dispersed-retention harvests in coniferous forests of western Washington. Forest Ecology and Management 226: 60–71.

Heltsche, J. F. & N. E. Forrester. 1983. Estimating species richness using the jackknife procedure. Biometrics 39: 1–12.

Hill, M. O. & H. G. Gauch Jr. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47–58.

Hylander, K. 2005. Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. Journal of Applied Ecology 42: 518–525.

Ingerpuu, N., K. Vellak, T. Kukk & M. Pärtel. 2001. Bryophyte and vascular plant species richness in boreo-nemoral moist forests and mires. Biodiversity and Conservation 10: 2153–2166.

———, ———, J. Lira & M. Pärtel. 2003. Relationships between species richness patterns in deciduous forests at the north Estonian limestone escarpment. Journal of Vegetation Science 14: 773–780.

Insightful, Inc. 2000. Splus 2000 for Windows. Seattle, Washington, U.S.A.

Jonsson, B. G. 1997. Riparian bryophyte vegetation in the Cascade mountain range, Northwest U.S.A.: patterns at different spatial scales. Canadian Journal of Botany 75: 744–761.

——— & P.-A. Esseen. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. Journal of Ecology 78: 924–936.

Kimmerer, R. W. 2005. Patterns of dispersal and establishment of bryophytes colonizing natural and experimental treefall mounds in northern hardwood forests. The Bryologist 108: 391–401.

Lesica, P., B. McCune, S. V. Cooper & W. S. Hong. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. Canadian Journal of Botany 69: 1745–1755.

Lindh, B. C. 2005. Effects of conifer basal area on understory herb presence, abundance and flowering in a second-growth Douglas-fir forest. Canadian Journal of Forest Research 35: 938–948.

Magurran, A. E. 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford, UK.

Márialigeti, S., B. Németh, F. Tinya & P. Ódor. 2009. The effects of stand structure on ground-floor bryophyte assemblages in temperate mixed forests. Biodiversity and Conservation 18: 2223–2241.

McAlister, S. 1995. Species interactions and substrate specificity among log-inhabiting bryophyte species. Ecology 76: 2184–2195.

McCune, B. & J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software, Glenden Beach, Oregon, USA.

——— & P. Lesica. 1992. The trade-off between species capture and quantitative accuracy in ecological inventory of lichens and bryophytes in forests in Montana. The Bryologist 95: 296–304.

——— & M. J. Mefford. 1999. PC-Ord Multivariate Analysis of Ecological Data (ver. 4). MjM Software Design, Gleneden Beach, Oregon, U.S.A.

McKenzie, D., C. B. Halpern & C. R. Nelson. 2000. Overstory influences on herb and shrub communities in mature forests of Western Washington, U.S.A. Canadian Journal of Forest Research 30: 1655–1666.

Messier, C., S. Parent & Y. Bergeron. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. Journal of Vegetation Science 9: 511–520.

Miles, C. J. & R. E. Longton. 1992. Deposition of moss spores in relation to distance from parent gametophytes. Journal of Bryology 17: 355–368.

Mills, S. E. & S. E. Macdonald. 2004. Predictors of moss and liverwort species diversity of microsites in conifer-dominated boreal forest. Journal of Vegetation Science 15: 189–198.

——— & ———. 2005. Factors influencing bryophyte assemblage at different scales in the western Canadian boreal forest. The Bryologist 108: 86–100.

Nelson, C. R. & C. B. Halpern. 2005. Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. Canadian Journal of Botany 83: 610–620.

Neter, J., W. Wasserman & M. H. Kutner. 1990. Applied Linear Statistical Models. Irwin Press, Homewood, Illinois, U.S.A.

Newmaster, S. G., R. J. Belland, A. Arsenault, D. H. Vitt & T. R. Stephens. 2005. The ones we left behind: Comparing plot sampling and floristic habitat sampling for estimating bryophyte diversity. Diversity and Distributions 11: 57–72.

Palmer, M. W. 1991. Estimating species richness: the second-order jackknife reconsidered. Ecology 72: 1512–1513.

Peintinger, M. & A. Bergamini. 2006. Community structure and diversity of bryophytes and vascular plants in abandoned fen meadows. Plant Ecology 185: 1–17.

Pharo, E. J. & A. J. Beattie. 2002. The association between substrate variability and bryophyte and lichen diversity in eastern Australian forest. The Bryologist 105: 11–26.

———, ——— & D. Binns. 1999. Vascular plant diversity as a surrogate for bryophyte and lichen diversity. Conservation Biology 13: 282–292.

——— & D. H. Vitt. 2000. Local variation in bryophyte and macro-lichen cover and diversity in montane forests of western Canada. The Bryologist 103: 455–466.

Preston, F. W. 1948. The commonness, and rarity, of species. Ecology 29: 254–283.

Prévost, M. & D. Pothier. 2003. Partial cuts in a trembling aspen–conifer stand: effects on microenvironmental conditions and regeneration dynamics. Canadian Journal of Forest Research 33: 1–15.

Pringle, R. F. 1990. Soil Survey of Thurston County, Washington. USDA Soil Conservation. Service in cooperation with Washington State Department of Natural Resources and Washington State University Agricultural Research Center. Government Printing Office, Washington, D.C., U.S.A.

Proctor, M. C. F. 2000. Physiological ecology. Pages 225–247. In A. J. Shaw & B. Goffinet (eds.), Bryophyte Biology. Cambridge University Press, Cambridge, UK.

———, M. J. Oliver, A. J. Wood, P. Alpert, L. R. Stark, N. L. Cleavitt & B. D. Mishler. 2007. Desiccation tolerance in bryophytes: a review. The Bryologist 110: 595–621.

Rajandu, E., K. Kikas & J. Paal. 2009. Bryophytes and decaying wood in *Hepatica* site-type boreo-nemoral *Pinus sylvestris* forests in southern Estonia. Forest Ecology and Management 257: 994–1003.

Rambo, T. R. 2001. Decaying logs and habitat heterogeneity: implications for bryophyte diversity in western Oregon forests. Northwest Science 75: 270–277.

——— & P. S. Muir. 1998a. Forest floor bryophytes of *Pseudotsuga menziesii–Tsuga heterophylla* stands in Oregon: influences of substrate and overstory. The Bryologist 101: 116–130.

——— & ———. 1998b. Bryophyte species associations with coarse woody debris and stand ages in Oregon. The Bryologist 101: 366–376.

Root, H. T. & B. McCune. 2010. Forest floor lichen and bryophyte communities in thinned *Pseudotsuga menziesii – Tsuga heterophylla* forests. The Bryologist 113: 619–630.

Ross-Davis, A. L. & K. A. Frego. 2004. Propagule sources of forest floor bryophytes: spatiotemporal compositional patterns. The Bryologist 107: 88–97.

Schofield, W. B. 2001. Introduction to Bryology. The Blackburn Press. Caldwell, New Jersey, U.S.A.

Shaw, A. J. & B. Goffinet (eds.). 2000. Bryophyte Biology. Cambridge University Press, Cambridge, UK.

Slack, N. G. 1977. Species Diversity and Community Structure in Bryophytes: New York State Studies. New York State Museum Bulletin Number 428. University of the State of New York, Albany, New York, U.S.A.

———. 2011. The ecological value of bryophytes as indicators of climate change. Pages 3–12. In Z. Tuba, N. G. Slack & L. R. Stark (eds.), Bryophyte Ecology and Climate Change. Cambridge University Press, Cambridge, UK.

Söderström, L. 1988a. The occurrence of epixylic bryophyte and lichen species in an old natural and a managed forest stand in Northeast Sweden. Biological Conservation 45: 169–178.

———. 1988b. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. Nordic Journal of Botany 8: 89–97.

———. 1990. Dispersal and distribution patterns in patchy, temporal habitats. Pages 103–113. In S. F. Krahulec, A. D. Q. Agnew, S. Agnew & J. H. Willems (eds.), Spatial Processes in Plant Communities. SPB Academic Publishing, The Hague, The Netherlands.

Spies, T. A., J. F. Franklin & T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69: 1689–1702.

Startsev, N., V. J. Lieffers & S. M. Landhausser. 2008. Effects of leaf litter on the growth of boreal feather mosses: implication for forest floor development. Journal of Vegetation Science 19: 253–260.

Stotler, R. & B. Crandall-Stotler. 1977. A checklist of the liverworts and hornworts of North America. The Bryologist 80: 405–428.

Thornton, P. E., S. W. Running & M. A. White. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. Journal of Hydrology 190: 214–251.

Turner, P. A. M., J. B. Kirkpatrick & E. J. Pharo. 2006. Bryophyte relationships with environmental and structural variables in Tasmanian old-growth mixed eucalypt forest. Australian Journal of Botany 54: 239–247.

Vellak, K., J. Paal & J. Liira. 2003. Diversity and distribution pattern of bryophytes and vascular plants in a boreal spruce forest. Silva Fennica 37: 3–13.

Wade, J., L. Herman, T. High & D. Couche. 1992. Soil Resource Inventory, Gifford Pinchot National Forest. USDA Forest Service, Pacific Northwest Region, Portland, Oregon, U.S.A.

Whittaker, R. H. 1975. Communities and Ecosystems (2nd ed.). Macmillan, New York, New York, U.S.A.

Wilson, D. S., P. D. Anderson & K. J. Puettmann. 2009. Evaluating the consistency of understorey vegetation response to forest thinning through synthetic analysis of operational-scale experiments. Forestry 82: 583–596.

Zobel, D. B. & J. A. Antos. 1986. Survival of prolonged burial by subalpine forest understory plants. American Midland Naturalist 115: 282–287.

ms received March 28, 2012; accepted May 2, 2012.

Supplementary online Table S1. Species abundance expressed as the percentage of stands and plots in which a species was observed.