






Acknowledgements

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Cover illustrations:

Left column (top to bottom): Hylocomium splendens with Dicranum scoparium and Buckiella undulatum; Rhytidiadelphus loreus; Isothecium myosuroides (all Anthea Farr); Centre two (top to bottom): liverwort sporophyte, bryophyte sporophyte (Biology 321 Blog, University of BC); right column (top to bottom): Rhytidiadelphus triquetrus, Eurhynchium oreganum, Porella navicularis (Biology 321 Blog, University of BC). All found at Brooksdale.

BRYOPHYTE SURVEY IN BROOKSDALE FOREST BIODIVERSITY PLOTS

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Executive Summary

This document describes a summary of a bryophyte survey in the forest biodiversity plots at Brooksdale and findings of that survey. The survey was conducted during the winter and spring of 2014. The objective was to sample bryophytes present on the forest floor in forest biodiversity plots. Survey methods used 1x1 m microplots for each of the three forest macroplots. The target was intended to be 10 microplots for each of the 3 macroplots. To accommodate teaching objectives 34 were sampled.

The report begins with a brief discussion of the role bryophytes play in the forest, followed by a description of study site plus sampling and statistical methods.

Rarefaction analyses demonstrated that the sampling regime was sufficient to acquire a good estimate of the total number of species present (Figure 2). In total 218 samples of 26 species were collected from 34 m^2. Community structure followed the typical dominance-diversity curve (Figure 3). Two species were dominant: variable moss (*Isothecium myosuroides*) and slender beaked-moss (*Eurhynchium praelongum*) comprised 15.7% and 11.5% of all samples, respectively. More than half (15) of the species collected contributed only 5 or fewer specimens to the total, or <2.3% each.

Percent total bryophyte cover on the forest floor varied from 11 to 14%. Liverworts comprised 22% of occurrences, but contributed only 3.4% of the cover (Tables 1 and 2). *Porella navicularis* contributed almost 75% of liverwort cover. Of the 200 samples for which substrate was apparent, most had wood as a substrate (166/200 or 83%). 'Wood' included twiglets, branches and well-rotted logs, but not tree bases; 'forest floor' included humus, soil, other moss and leaf or needle litter; Generally, liverworts and mosses showed no difference in affinity for wood: liverworts 82.3% (28/34) and mosses 83%(166/200). The site can become dry in the summer and logs provide two advantages: 1) sites above competition from rooted plants and 2) a more reliable source of moisture.

Interspecific associations of bryophytes were examined at 3 scales: 20x20 m macroplots, 1x1 m microplots and 'grab samples' of morphospecies. Interspecific associations were most apparent at the 1x1 m scale of microplots. Marked differences in co-occurrences of species within individual microplots primarily indicated mutual avoidance. Positive affinities were generally the result of widespread distribution and largely restricted to the most common species. Reported affinities, both positive and negative, were significant at <0.01.

With two exceptions, differences at the 20x20 m macro-plot level were limited to species recorded 5 times or less. The exceptions, *Orthotrichum lyellii* and *Porella navicularis*, both occurred more than twice as often in macroplot 1 than in the other two macroplots (Table 1). Of all species, they showed the greatest affinity for forest floor (31% and 30% of occurrences, respectively). Macroplot 1 has a much more diverse herbaceous flora, but also much less herb cover than the other two macroplots (Bunnell and Bunnell 2018). Macroplots 2 and 3 are dominated by ferns. The higher abundance of these two species in macroplot 1 may be because the forest floor there is more welcoming there than in macroplots 2 and 3.

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1.0 Mosses in coastal forests

Despite their apparent limitations, mosses accomplish a lot in a forest. Not only are they tiny plants, but they are plants without plumbing. What look like miniature leaves have no veins to move water through them. Water and nutrients must be absorbed through the leaf surface and moved from cell to cell across cell membranes. What look like tiny roots can anchor the plant, but have no conductive tissue (though water and dissolved nutrients can move along them by capillary action). Without plumbing to move water and nutrients they are limited to a few cm in height. Faced with this problem, bryophytes made it an opportunity by exploiting the nooks and crannies among larger plants and the advantages of the boundary layer, where air meets ground, runs into vegetation and other obstacles and slows down.

The boundary layer is a sort of floating greenhouse, draped like a blanket over rocks, soil or logs. This greenhouse is not only warmer and more humid, but the CO_2 concentrations are up to ten times greater than in the air above. Water and CO_2 from moist logs or soil accumulate in the boundary layer where air moves less. On dry, exposed surfaces, such as rock faces, the layer is thin and mosses are shortest. They grow taller on the forest floor, though never more than a few centimeters. Striving upwards after light is not part of bryophytes' game plan; their chlorophyll is finely tuned to the particular wave lengths of light that penetrate forest canopy to the forest floor.

You rarely find single moss plants. They are crowded tighter than blades of grass in a lawn. Holding water against the sun and welcoming back the rain is a communal activity. The intertwined shoots and leaves create a 'sponge' of wee spaces that grab water and hold it. When you look closely, you can see how moss leaves are designed to grab water, guide it and store it.

They may look like soft, cuddly clumps of green waiting for something to happen, but mosses cannot help but change their surroundings. They improve conditions for many species simply by being there. Clumps of moss are nature's second wave of attack in its war against rock. Bryophytes lack lichens' acids for burrowing into rocks, but can be well attached. Sweeping a patio, you may have found that some have a remarkably firm grip. Once in place, all the tiny surfaces and gaps within a moss clump accumulate dust that gradually becomes soil for rooted plants.

Examining bryophytes under a microscope is a romp through a miniature zoo. They provide homes and food for both invertebrates and vertebrates. On the forest floor, a single gram (a muffin-sized clump) of moss holds about 150,000 protozoa, 132,000 tardigrades, 3,000 springtails, 800 rotifers, 500 nematodes, 400 mites, and 200 fly larva. Moss cushions in larger trees of wet forests gradually become perched soil, replete with fungi, arthropods, molluscs, salamanders and even mycorrhizal tree roots growing out of branches. On the ground, on the bole, or as suspended cushions, bryophytes provide food and habitat for a host of invertebrates, including protozoa, nematodes, tardigrades, earthworms, slugs, insects, and spiders. Vertebrates, including songbirds, marbled murrelets and flying squirrels, incorporate moss into their homes. The more you look, the longer the list.

Figure 1. Forest in survey site at Brooksdale. Note moss-covered logs (C. Bunnell) and the Hoh River Valley, Olympic Peninsula, Washington with moss-covered stems (F. Bunnell).

Bryophytes impact every organism in the area – big or small. They intercept, absorb and evaporate precipitation, thus retaining water in the ecosystem. They are the best there is at collecting moisture and hanging on to it. All life needs water. Nutrients move in the water, so they too are intercepted and retained longer. There is a wee conundrum in a coastal rainforest, home of many of the world's tallest tree species. What came first – the towering stature of the trees or the carpets of moss? The trees would not be nearly so tall without all that moss intercepting and storing water and nutrients to release slowly. The moss would not be nearly so abundant if the trees didn't hoist some of them up to intercept rain and water vapour.

2.0 Site selection and survey methods

2.1 Study area

The study site is the Brooksdale forest biodiversity plots. This study adds to the knowledge of those plots, just as the survey of slime molds and fungi did (Bunnell et al. 2016). The Brooksdale forest biodiversity plots sample older second-growth forest stands. Bunnell and Bunnell (2018) found that rooted vegetation of the stands closely matches the description provided by Nuszdorfer, Klinka & Demarchi (1991) for the Redcedar-Skunk cabbage zonal site association of the Coastal Douglas-fir Biogeoclimatic zone. Macroplots in the stands are described by Bunnell and Bunnell (2018).

2.2 Survey methods

Surveys were similar to those used to sample shrubs and herbs in the Brooksdale forest biodiversity plots (Bunnell and Bunnell 2018). A minimum of 10 1x1 m microplots were selected randomly within each of the three macroplots, for a total of 34 microplots. Number of microplots per macroplot varied with teaching objectives for interns and ranged from 10 to 13. To estimate species richness a variable number of 'grab samples' were collected within each microplot. Within each microplot, a sample clump (grab sample) of every seemingly distinct bryophyte morphospecies observed in the microplot was collected. Identification of species within these samples was used to calculation frequency of occurrence of species. The substrate from which the sample was collected was recorded as soil (including litter) and wood (which included all sizes of wood from fallen twigs to logs).

Total bryophyte cover was estimated as the percent surface of the 1 m^2 area covered by bryophytes, as observed from a position directly above each 1X1m plot. That is, moss cover on the top of a log when looking down was considered cover, but moss cover on the sides of a log and not visible from above was not. This was done to normalize cover estimates across the widely varying surface areas of 3-dimensional plot features. In addition to total bryophyte cover, estimates were also made of the percent cover contributed by each morphospecies while in the field. Morphospecies were simply the clumps of moss present in the microplot that looked different. Under the microscope morphospecies frequently revealed a combination of several species. Once species were identified, contributions of individual species were estimated.

What we term 'bryophyte flora' in this report refers to species collected from the ground or log surface, but often includes fallen twigs. Samples were not collected from tree stems or bases, but may have originated there and fallen to the ground.

2.3 Statistical methods

Most statistical analyses reported were restricted to simple analyses available in Microsoft excel. Derivation of species accumulation curves employed rarefaction techniques available in Estimate S[1] (see Cowell et al. 2004 and 2012). Frequency of occurrence for many species was small, potentially creating misleading chi-squared tests, so tests of association were restricted to species encountered at least 10

[1] http://viceroy.eeb.uconn.edu/estimates/

times and assessed as the proportion of shared occurrences of species pairs across the 34 microplots. Simple regression analyses of the occurrences and co-occurrences of grab samples revealed a strong role of chance, so no further tests of association were employed.

3.0 Results

3.1 Species richness

The initial question was whether the sampling regime implemented was sufficient to capture the richness of bryophytes present. That question is best answered by a species accumulation curve which tallies the total number of species sampled as the number of sample plots increase. The shape of the curve can be significantly influenced by the order in which plots are added or tallied (see Bunnell and Bunnell (2018) for an example of shrubs in these macroplots). Because order of tally influences the shape of the species accumulation curves, researchers have developed probabilistic approaches using repeated sampling of different orders of tally drawn from the actual sample data. That yields expected species richness as a function of number of plots sampled. We used the methodology developed by Colwell et al. (2012) and available in EstimateS. It is illustrated in Figure 2.

A probabilistic approach naturally yields a gradual curve, with the total number of species identified (26) occurring at the total number of sample plots (34). The projected curve indicates the number of species likely to be accrued as sample size increases. The data show that with 50 plots the likely number of species is 26.35; almost 50 more plots than the 34 sampled would be required to yield a single additional species. The curve has reached an asymptote (Figure 2). We conclude that the sampling regime was adequate to survey bryophyte richness.

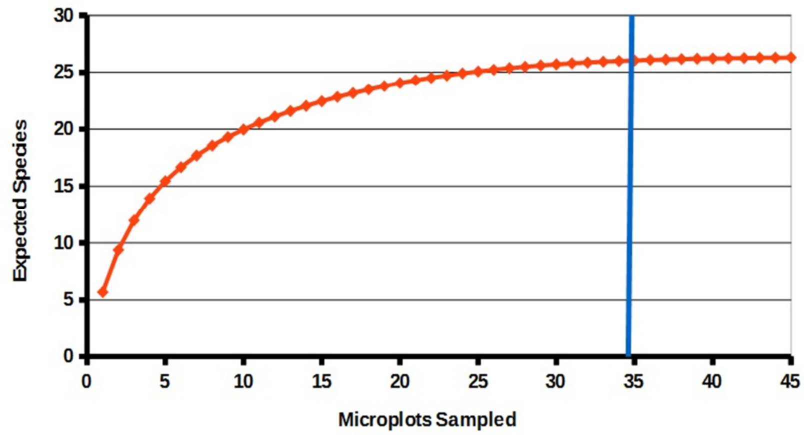


Figure 2. Expected richness of bryophytes based on all sampled micro-plots (n = 34). The blue bar indicates the number of species observed at 34 plots.

3.2 Bryophyte community structure – frequency of occurrence

Nomenclature used here follows e-flora bc - http://www.geog.ubc.ca/biodiversity/eflora/1 – so is not consistent with all relevant sources. For example, many sources now recognize *Plagiothecium undulatum* as *Buckiella undulatum* and *Eurhynchium praelongum* as *Kindbergia praelongum*. Sampling acquired 218 individual bryophyte specimens from 26 species in the 3 macroplots. The three macroplots showed near identical species richness for the bryophyte flora: 19, 19, and 20 per plot.

Two species were clearly dominant: variable moss (*Isothecium myosuroides*) and slender beaked-moss (*Eurhynchium praelongum*) comprised 15.7% and 11.5% of all samples, respectively. More than half (14) of the species collected contributed only 5 specimens to the total, or about 2.3% each. Variable moss may be the most common moss on the coast of British Columbia. It is extremely variable forming hanging curtains from branches, mats on tree trunks, trailing wisps on boulders and sprawling, wispy mats on logs. In some coastal areas it can cover most every tree branch and also boulders and logs, but is much less common on forest litter or humus.

Slender beaked-moss does not exploit branches and trunks as variable moss does, but commonly forms irregular mats on logs, humus and tree bases in both lowland and montane wet coastal forests. It generally is more common than its congeneric (*Eurhynchium oregnum*, Oregon beaked-moss). That was true at Brooksdale as well – 25 versus 5 samples (Table 1).

Over all three macroplots, the community showed typical community structure – few dominant species and many more species much less well represented (Figure 3)

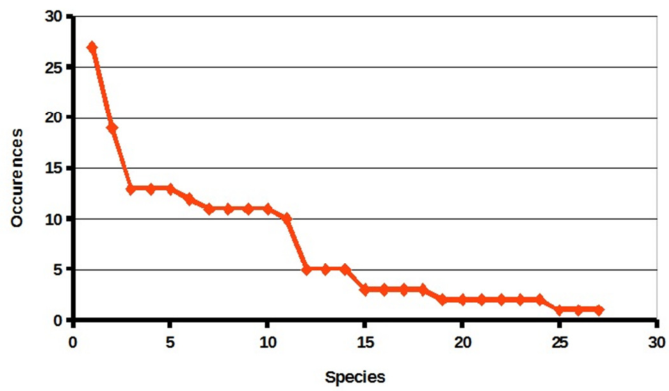


Figure 3. Dominance diversity curve for combined bryophyte samples across the three macroplots. *Isothecium myosuroides* and *Eurhynchium* (*Kindbergia) praelongum* were the most common species.

We neither expected nor found hornworts among the bryophytes at Brooksdale. The proportion of all species that were liverworts was 26.9% (7 of 26 species) or closely comparable to the province-wide average of 24.6% (235 of 955 species). Within the combined samples, 9 of the 26 species occurred in all three macroplots and 6 species occurred in only one of the three macroplots (Table 1). The average number of occurrences per macroplot of species common to all macroplots was 16; the comparable value for species limited to a single macroplot was 2. To a large extent that finding merely quantifies the fact that species that were widespread were encountered frequently. It also shows that species found in only one macroplot were never abundant in that macroplot.

Table 1. Frequency of occurrence of the 26 bryophyte species within the three sample plots and combined. Liverworts are shaded green.

Plot	*Aneura pinguis*	*Calypogeia muelleriana*	*Claopodium crispifolium*	*Dicranum scoparium*	*Eurhynchium oreganum*	*Eurhynchium praelongum*	*Geocalyx graveolens*	*Homalothecium fulgescens*	*Hylocomium splendens*	*Isothecium myosuroides*	*Lepidozia reptans*	*Metaneckera menziesii*	*Neckera douglasii*	*Orthotrichum lyellii*	*Orthotrichum pulchellum*	*Plagiothecium denticulatum*	*Plagiothecium laetum*	*Plagiothecium undulatum*	*Porella navicularis*	*Porella roelli*	*Pseudotaxiphyllum elegans*	*Radula complanata*	*Rhizomnium glabrescens*	*Rhytidiadelphus loreus*	*Rhytidiadelphus triquetrus*	*Tetraphis pellucida*
1	2		1		1	8	3	5	3	10		2	3	10	1	6	3	2	9	6	6		4			
2	1	1			2	7	2			10	2			4		3	4	6	4	4	2	2	5	1	1	2
3			1	2	2	10	6		2	14	1			3		2	4	7	3	1	4	1	4	1	1	1
All	3	1	2	2	5	25	11	5	5	34	3	2	3	17	1	11	11	15	16	11	12	3	13	2	2	3

Appendix 1 summarizes the occurrence of all 218 samples across all macroplots.

3.3 Percent cover – abundance

Percent cover by species was estimated for 10 microplots in macroplots 2 and 3 and 11 microplots in macroplot 3. Average percent cover of all bryophytes in 1x1 m microplots did not differ significantly across macroplots: 11% (plot 1), 13% plot 2) and 14% plot 3. Contributions to cover varied with bryophyte species and across plots. Values of percent cover by species in Table 2 are summations across all microplots within each of the three macroplots. That is, values are the total cover over all microplots in a macroplot; the average cover per macroplot is thus about 1/10th of the value in the Table 2. Note that generally byrophytes contributed relatively little ground cover. For example, the most abundant species (*Isothecium myosuroides*) contributed only 1.8% ground cover over all microplots (Table 2: 55.6% of a total of 3100% available as a sum of 100% in each of 31 plots).

Table 2. Total cover by species summed over all microplots of a macroplot. Liverwort species are shaded green. Major differences between macroplots are shaded gray; species contributing the greatest cover are shaded pink.

Plot	*Aneura pinguis*	*Calypogeia muelleriana*	*Claopodium crispifolium*	*Dicranum scoparium*	*Eurhynchium oreganum*	*Eurhynchium praelongum*	*Geocalyx graveolens*	*Homalothecium fulgescens*	*Hylocomium splendens*	*Isothecium myosuroides*	*Lepidozia reptans*	*Metaneckera menziesii*	*Neckera douglasii*	*Orthotrichum lyellii*	*Orthotrichum pulchellum*	*Plagiothecium denticulatum*	*Plagiothecium laetum*	*Plagiothecium undulatum*	*Porella navicularis*	*Porella roelli*	*Pseudotaxiphyllum elegans*	*Radula complanata*	*Rhizomnium glabrescens*	*Rhytidiadelphus loreus*	*Rhytidiadelphus triquetrus*	*Tetraphis pellucida*
1	0.1				4.1	2.6	0.3	3.1	14.1	22.6		0.1	3.2	8.7	0.1	17.3	1.2		6.6	0.4	4.1		0.3			
2	0.1	0.1			7.1	23.5	0.2			17.6	0.2			0.4		1.2	1.3	16.3	0.4	0.3	0.2	0.2	7.3	0.1	0.1	5.1
3			2.0	1.1	18.1	16.7	0.6		27.0	15.4	0.1			0.3		18.2	5.3	27.1	1.2	0.1	2.2	0.1	8.3	5.0	1.0	1.0
Total	0.2	0.1	2.0	1.1	29.3	42.8	1.1	3.1	41.1	55.6	0.3	0.1	3.2	9.4	0.1	36.7	7.8	43.4	8.2	0.8	6.5	0.3	15.9	5.1	1.1	6.1

Differences in relative abundance were most evident in macroplot 1, suggesting a some difference between it and the other two macroplots. Plot 1 contained much less *Eurhynchium praelongum and Rhizomnium glabrescens* and more *Orthotrichum lyellii* and *Porella navicularis* than the other two plots. *Hylocomium splendens* was absent from macroplot 2, but relatively abundant in the other two macroplots. Macroplot 3 contained markedly more *Eurhynchium oregonum*, *Hylocomium splendens* and *Plagiothecium undulatum* than the other two macroplots.

Liverworts provided much less cover than did mosses, typically <1% total cover. Across all macroplots, six species dominated contributions to cover, in descending order: *Isothecium myosuroides, Plagiothecium undulatum*, *Eurhynchium praelongum*, *Hylocomium splendens*, *Platiothecium denticulatum* and *Eurhynchium oregonum*. The pattern of relative abundance expressed as percent cover, thus differed from that expressed as frequency of occurrence. Two species (*Isothecium myosuroides* and *Eurhynchium praelongum* dominated observed frequencies (Table 1, Figure 2). More generally, liverworts comprised 22% of occurrences, but contributed only 3.4% of the cover. *Porella navicularis* contributed almost 75% of liverwort cover.

3.4 Species-substrate relations

Two relatively discrete substrates were recognized: forest floor and wood. Forest floor included humus, soil, other moss and leaf or needle litter; wood included twiglets, branches and well-rotted logs, but not tree bases. Twiglets and branches were on the forest floor, not attached to a tree or shrub. In total, 218 samples were identified to species, and 200 could be assigned a substrate (some were labeled 'loose', indicating that they were not 'attached' to any substrate when encountered, and a few samples were not assigned a substrate on collection). Most of the 200 samples had wood as a substrate (166/200 or 83%). 'Wood' ranged from recently dead twigs or well-rotted logs.

The species with the least affinity for wood was the liverwort *Porella navicularis*, with 69% of samples from woody substrates (11/16). Generally, liverworts and mosses showed no difference in affinity for wood: liverworts 82.3% (28/34) and mosses 83.1%(138/166). Appendix 2 summarizes recorded substrate by species.

3.5 Inter-species relationships among bryophytes

Moss are relatively small organisms. The question of interspecific relations can be evaluated at three scales: within 20x20 macroplots, within 1x1 microplots and within the 'grab' sample collected from microplots. At the level of macroplot only 6 species are restricted to a single macroplot (Table 1). Of those 6 species, all contributed less than 5% total cover when summed over all microplots (Table 2). Not only did they occur rarely, but they did not occupy large patches when they did occur. Contributions to total cover by individual species sometimes showed marked differences between macroplots (Table 2). These may reflect differences in vascular flora or other features between the macroplots (see § 3.6)

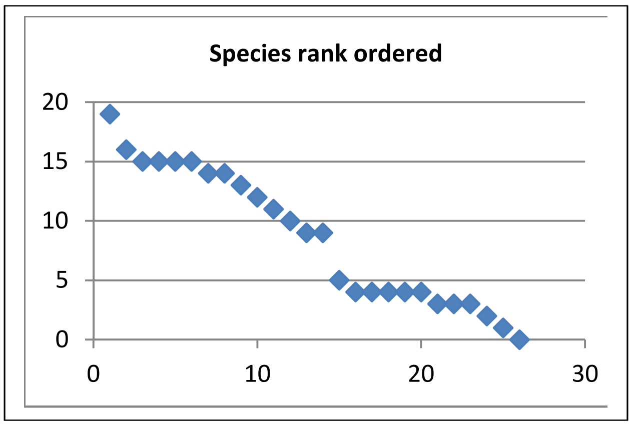
The simplest statistical test for associations among species at the microplot level is a chi square test of association. The numbers collected for some species are small and yield frequencies of 1 or 0 in a 2x2 contingency table. Because the distribution of the χ^2 statistic is highly skewed, some statisticians argue the all frequencies in the contingency table should be >5. We chose a simpler means of showing association by limiting the species examined to those occurring in at least 10 of the 34 microplots, then calculating the portion of those species' occurrences that were present when another species was present. For example, in Table 3, 10 of the 11 occurrences of *Geocalyx graveolus* occurred when *Eurhynchium praelongum* was present (91% of the time). That suggests the two species share some common affinity. Conversely, only 3 of 11 occurrences of *Pseudotaxiplyllum elegans* occurred when *Eurhynchium praelongum* was present or (27% of the time). That suggests those two species have no affinity for each other and seldom share common habitat. The cutoffs for inclusion in Table 3, were 67% to suggest a common affinity and 33% to suggest avoidance. Those cutoff values represent a chi-square probability of independence of <0.006 (assuming values of <5 in the contingency tables did not produce misleading results with n $\geq$20 (at least 10 samples of each species).

Table 3. Percent of shared occurrences by species across the 34 microplots. Green shading suggests a shared affinity; pink shading suggests avoidance.

	Geocalyx graveolens	*Isothecium myosuroides*	*Orthotrichum lyellii*	*Plagiothecium denticulatum*	*Plagiothecium laetum*	*Plagiothecium undulatum*	*Porella navicularis*	*Porella roelli*	*Pseudotaxiphyllum elegans*	*Rhizomnium glabrescens*
Eurhynchium praelongum	91%	–	–	–	–	–	–	–	27%	69%
Geocalyx graveolens		–	30%	22%	–	33%	–	20%	27%	–
Isothecium myosuroides			77%	73%	82%	75%	–	70%	–	77%
Orthotrichum lyellii				27%	–	33%	–	–	27%	–
Plagiothecium denticulatum					27%	33%	–	–	–	–
Plagiothecium laetum						9%	–	20%	27%	23%
Plagiothecium undulatum							–	20%	–	31%
Porella navicularis								–	–	–
Porella roelli									–	30%
Pseudotaxiphyllum elegans										–

Only 10 of the 26 species were recorded from at least 10 of the 34 microplots (3 of the 7 liverworts and 7 of the 19 mosses). In Table 3, most relations meeting the arbitrary cutoff show avoidance at the scale of the microplot. *Eurhynchium praelongum* shows some shared affinity with *Geocalyx graveolus* and *Rhizomnium glabrescens*. *Isothecium myosuroides* shows an apparent affinity for 5 species. To a large extent this is simply a product *Isothecium* occurring in 27 of the 34 microplots. The strong 'avoidance' shared by *Plagiothecium laetum* and *P. undulatum* is striking.

The finest scale at which interspecies relations could be examined was the 'grab samples' or morphospecies. These were samples collected because they appeared different from other samples within the microplot and whose identity would be checked later. Because moss species grow closely together, there frequently was more than one species in a grab sample. In total, 527 co-occurrences of species were documented. Of the 94 grab samples, 33 were of a single species. The pattern of co-occurrences reveals that they were governed largely by chance.



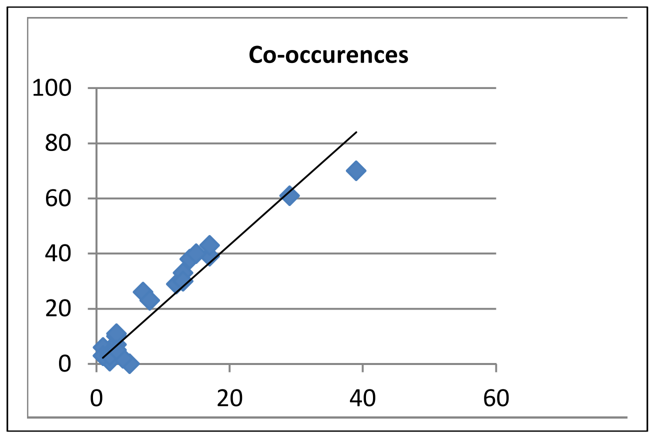


Figure 4. Co-occurrences of species. a) Number of species co-occurring with each of the 26 species sampled. b) Number of co-occurrences of other species as a function of occurrences of species within grab samples (y = 2.154x; R^2 = 0.92).

The '0' value in Figure 4a is for *Hylocomium spelendens* (step moss). Samples of this species were readily identified in the field and not taken back for microscopic scrutiny that may have exposed very small amounts of other species. The rank order of number of other species co-occurring with specific species (Figure 3a) approximates the dominance-diversity curve across the three macroplots (Figure 3). The number of times a species occurred in a grab sample ranged from 1 to 39 (Figure 4b). The number of co-occurrences of other species increased linearly with the increase in number of occurrences of a species (R^2 = 0.92). About 2 further co-occurrences were added for each additional occurrence of a species (Figure 4b). Both findings imply a strong influence of chance on co-occurrences.

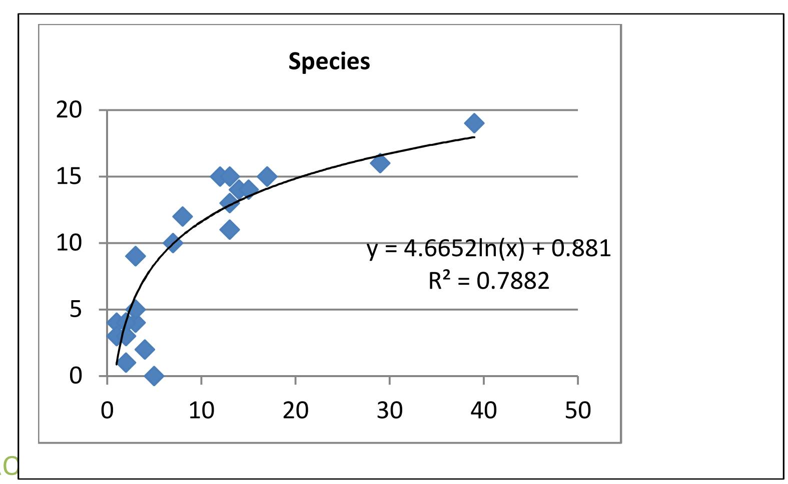


Figure 5. Number of species co-occurring with a species in grab samples as a function of occurrences of a species within grab samples. $y = 4.6652\ln(x) + 0,881$; $R^2 = 0.79$.

Because the frequency of species occurrence followed the classic dominance-diversity curve (Figure 3), the rate at which new co-occurring species were added with an increase in a species occurrence was non-linear (Figure 5). We conclude that the likelihood of association between species in grab samples, was primarily a matter of chance and the relative frequency of individual species. Overall, evaluation of interspecific relations reveals a strong role of chance. Differences among the 20x20 macroplots were largely restricted to species reported from 5 microplots or less (Table 2), indicating a strong role for chance alone. Differences in interspecific affinities were much stronger at the 1x1 microplot level with strong negative and positive affinities both evident (Table 3). We had expected strong affinities at the microscale of grab samples, but chance appears to dominate relations (Figures 4 and 5). That may simply reflect that grab samples were not nearly as repeatable or well-defined as samples at the microplot level.

4.0 Discussion

Species composition of bryophytes on the forest floor (Figure 1) was adequately sampled and assumed a form common among dominance diversity curves (Figure 2). Of the 26 species, two (*Isothecium myosuroides* and *Eurhynchium praelongum)* were clearly dominant while 8 species were encountered only once or twice.

Images of coastal forest of the Pacific Northwest often include a moss-covered forest floor. Those photos are from sites wetter than the plots sampled. Moss cover in the macroplots ranged from 11 to 14%. That apparent disparity is explained by the fact that 166 of 200 estimates of cover (83%) were found on wood, usually rotting logs, and these covered relatively little area of the forest floor. There was no difference between liverworts and bryophytes in their preference for wood. There are two strong reasons for bryophyte affinity for logs. First, logs raise the bryophytes above the competition from vascular plants rooted in the forest floor. Relatively few vascular plants become rooted in rotting logs. Second, rotting wood retains moisture well, and bryophytes lack roots that can extract water from their substrate, though moisture can travel by capillary action.

The advantage of rotting logs as substrate in an environment that becomes dry is persistent. An affinity for particular types of rotten wood also helps to explain why interspecific affinities were most strongly expressed at the scale of 1x1 m plots. That is the scale at which differences in kind and amount of wood are most evident. Differences in bryophyte distribution among macroplots suggests a potential influence of rooted vegetation as well.

With two exceptions, differences at the 20x20 m macro-plot level were limited to species recorded 5 times or less. The exceptions, *Orthotrichum lyellii* and *Porella navicularis*, both occurred more than twice as often in macroplot 1 than in the other two macroplots (Table 1). The two species show no affinity, positive or negative, for each other (Table 3). Of all species, *P. navicularis* and *O. lyellii* shows the greatest affinity for forest floor (31% and 30% of occurrences, respectively); the average across all species is about 17%). Macroplot 1 differs from the other 2 macroplots primarily in its herbaceous vegetation. It has a much more diverse herbaceous flora, but also much less herb cover (Bunnell and Bunnell 2018). Macroplots 2 and 3 are dominated by ferns. The higher abundance of these two species in macroplot 1 may be because the forest floor there is more welcoming there than in macroplots 2 and 3.

5.0 References

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Appendices

Appendix 1. Bryophyte specimens collected in A Rocha forest biodiversity macroplots. Liverwort species are highlighted **green**. The first 3 microplots of macroplot 1 were to introduce interns to sampling. **Red** highlighted values are averages by macroplot. Nomenclature follows e-flora BC; many workers recognize *Plagiothecium undulatum* as *Buckiella undulatum* and *Eurhynchium praelongum* as *Kindbergia praelongum.*

Macro Plot	Micro Plot	% cover by plot	Species	% cover by species	Substrate	Common name
1	1.1b		*Pseudotaxiphyllum elegans*	n/a	Wood	Elegant small flat moss
1	1.1c		*Homalothecium fugescens*	n/a	Wood	Yellow curl moss
1	1.1a		*Plagiothecium undulatum*	n/a	Wood	Flat moss
1	1.2a		*Claopodium crispifolium*	n/a	Ground	Rough moss
1	1.2b		*Pseudotaxiphyllum elegans*	n/a	Wood	Elegant small flat moss
1	1.2c		*Porella navicularis*	n/a	Ground	**Tree ruffle liverwort**
1	1.2d		*Porella roelli*	n/a	Ground	**None**
1	1.2f		*Homalothecium fugescens*	n/a	Ground	Yellow curl moss
1	1.2e		*Metaneckera menziesii*	n/a	Ground	Menzies' neckera
1	1.2g		*Isothecium myosuroides*	n/a	Bark	Variable moss
1	1.2h		*Rhizomnium glabrescens*	n/a	Bark	Large leafy moss
1	1.2i		*Aneura pinguis*	n/a	Bark	**Greasewort**
1	1.3a		*Pseudotaxiphyllum elegans*	n/a	Wood	Elegant small flat moss
1	1.3b		*Plagiothecium denticulatum*	n/a	Wood	Dented silk moss
1	1.3c		*Porella roelli*	n/a	Ground	**None**
1	1.3d		*Homalothecium fulgescens*	n/a	Ground	Yellow curl moss
1	1.3e		*Pseudotaxiphyllum elegans*	n/a	Wood	Elegant small flat moss
1	1.3f		*Plagiothecium undulatum*	n/a	Wood	Flat moss
1	1	20%	*Plagiothecium denticulatum*	15%	Wood	Dented silk moss
1	1		*Pseudotaxiphyllum elegans*	4%	Wood	Elegant small flat moss
1	1		*Isothecium myosuroides*	<1%	Wood	Variable moss
1	1		*Rhizomnium glabrescens*	<1%	Wood	Large leafy moss
1	1		*Eurhynchium oreganum*	<1%	Wood	Oregon beaked-moss
1	2	5%	*Hylocomium splendens*	4%	Ground	Step moss
1	2		*Neckera douglasii*	<1%	Ground	Douglas' neckera
1	2		*Porella navicularis*	<1%	Ground	**Tree ruffle liverwort**
1	2		*Pseudotaxiphyllum elegans*	<1%	Ground	Elegant small flat moss
1	2		*Eurhynchium praelongum*	<1%	Ground	Slender beaked-moss
1	2		*Geocalyx graveolens*	<1%	Bark	**Turpswort**
1	2		*Plagiothecium laetum*	<1%	Ground	Bright silk moss
1	2		*Porella roelli*	<1%	Ground	**None**
1	2		*Plagiothecium denticulatum*	<1%	Bark	Dented silk moss
1	2		*Homalothecium fugescens*	<1%	Wood	Yellow curl-moss
1	2		*Isothecium myosuroides*	<1%	Bark	Variable moss
1	3	15%	*Orthotrichum lyellii*	5%	Bark	Lyell's bristle-moss
1	3		*Orthotrichum lyellii*	<1%	Bark	Lyell's bristle-moss
1	3		*Orthotrichum lyellii*	<1%	Ground	Lyell's bristle-moss
1	3		*Porella navicularis*	5%	Bark	**Tree ruffle liverwort**
1	3		*Porella navicularis*	<1%	Ground	**Tree ruffle liverwort**
1	3		*Porella navicularis*	<1%	Bark	**Tree ruffle liverwort**
1	3		*Neckera douglasii*	2%	Bark	Menzies' neckera
1	3		*Homalothecium fugescens*	3%	Bark	Yellow curl moss
1	3		*Hylocomium splendens*	<1%	Ground	Step moss
1	4	5%	*Orthotrichum lyellii*	2%	Wood	Lyell's bristle-moss
1	4		*Orthotrichum lyellii*	<1%	Loose	Lyell's bristle-moss
1	4		*Porella navicularis*	1%	Wood	**Tree ruffle liverwort**
1	4		*Porella navicularis*	<1%	Loose	**Tree ruffle liverwort**
1	4		*Eurhynchium praelongum*	2%	Wood	Slender beaked-moss
1	4		*Eurhynchium praelongum*	<1%	Loose	Slender beaked-moss
1	4		*Plagiothecium laetum*	<1%	Wood	Flat moss
1	4		*Isothecium myosuroides*	<1%	Wood	Variable moss
1	4		*Geocalyx graveolens*	<1%	Wood	**Turpswort**
1	5	2%	*Isothecium myosuroides*	2%	Wood	Variable moss
1	5		*Isothecium myosuroides*	<1%	Loose	Variable moss
1	5		*Orthotrichum lyellii*	<1%	Wood	Lyell's bristle-moss
1	5		*Orthotrichum lyellii*	<1%	Loose	Lyell's bristle-moss

1	5		*Neckera menziesii*	<1%	Wood	Menzies' neckera
1	5		*Eurhynchium praelongum*	<1%	Loose	Slender beaked-moss
1	5		*Rhizomnium glabrescens*	<1%	Loose	Large leafy moss
1	5		*Porella navicularis*	<1%	Loose	**Tree ruffle liverwort**
1	6	30%	*Hylocomium splendens*	10%	Wood	Step moss
1	6		*Isothecium myosuroides*	19%	Wood	Variable moss
1	6		*Eurhynchium praelongum*	<1%	Wood	Slender beaked-moss
1	6		*Geocalyx graveolens*	<1%	Wood	**Turpswort**
1	6		*Plagiothecium laetum*	1%	Wood	Bright silk moss
1	7	3%	*Orthotrichum lyellii*	1%	Wood	Lyell's bristle-moss
1	7		*Orthotrichum pulchellum*	<1%	Wood	None
1	7		*Plagiothecium denticulatum*	2%	Wood	Dented silk moss
1	7		*Plagiothecium denticulatum*	<1%	Ground	Dented silk moss
1	7		*Rhizomnium glabrescens*	<1%	Wood	Large leafy moss
1	7		*Eurhynchium praelongum*	<1%	Wood	Slender beaked-moss
1	7		*Porella roellii*	<1%	Wood	**None**
1	8	<1%	*Isothecium myosuroides*	<1%	Wood	Variable moss
1	8		*Porella roellii*	<1%	Wood	**None**
1	8		*Orthotrichum lyellii*	<1%	Wood	Lyell's bristle-moss
1	8		*Metaneckera menziesii*	<1%	Other Moss	Menzies' neckera
1	9	<1%	*Aneura pinguis*	<1%	alder leaf	**Greasewort**
1	9		*Isothecium myosuroides*	<1%	alder leaf	Variable moss
1	9		*Orthotrichum lyellii*	<1%	Loose	Lyell's bristle-moss
1	9		*Porella navicularis*	<1%	alder leaf	**Tree ruffle liverwort**
1	10	6%	*Eurhynchium oreganum*	4%	Wood	Oregon beaked-moss
1	10		*Isothecium myosuroides*	1%	Wood	Variable moss
1	10		*Eurhynchium praelongum*	<1%	Wood	Slender beaked-moss
1	10		*Plagiothecium denticulatum*	<1%	Wood	Dented silk moss
1	10		*Neckera douglasii*	1%	Wood	Douglas' neckera
1	10		*Porella roellii*	<1%	Wood	**None**
		11%				
2	1	21%	*Eurhynchium praelongum*	13%	Wood	Slender beaked-moss
2	1		*Isothecium myosuroides*	2%	Wood	Variable moss
2	1		*Aneura pinguis*	<1%	Wood	**Greasewort**
2	1		*Rhizomnium glabrescens*	5%	Wood	Large leafy moss
2	1		*Plagiothecium laetum*	1%	Wood	Flat moss
2	1		*Tetraphis pellucida*	<1%	Wood	Common four-tooth moss
2	1		*Geocalyx graveolens*	<1%	Wood	**Turpswort**
2	2		*Eurhynchium praelongum*	<1%	Ground	Slender beaked-moss
2	2		*Orthotrichum lyellii*	<1%	loose	Lyell's bristle-moss
2	2		*Plagiothecium laetum*	<1%	loose	Bright silk moss
2	2		*Rhytidiadelphus loreus*	<1%	loose	Lanky moss
2	3	21%	*Plagiothecium undulatum*	13%	Wood	Flat moss
2	3		*Plagiothecium undulatum*	<1%	Bark	Flat moss
2	3		*Tetraphis pellucida*	5%	Wood	Common four-tooth moss
2	3		*Rhizomnium glabrescens*	2%	Ground	Large leafy moss
2	3		*Rhizomnium glabrescens*	<1%	Bark	Large leafy moss
2	3		*Lepidozia reptans*	<1%	Wood	**Little hands liverwort**
2	3		*Calypogeia muelleriana*	<1%	Wood	**Mueller's Pouchwort**
2	3		*Pseudotaxiphyllum elegans*	<1%	Wood	Elegant small flat moss
2	3		*Pseudotaxiphyllum elegans*	<1%	Bark	Elegant small flat moss
2	3		*Isothecium myosuroides*	<1%	Wood	Variable moss
2	3		*Isothecium myosuroides*	<1%	Bark	Variable moss
2	3		*Eurhynchium praelongum*	<1%	Wood	Slender beaked-moss
2	3		*Eurhynchium praelongum*	<1%	Bark	Slender beaked-moss
2	3		*Porella roellii*	<1%	Bark	**None**
2	3		*Orthotrichum lyellii*	<1%	Wood	Lyell's bristle-moss
2	3		*Porella navicularis*	<1%	Wood	**Tree ruffle liverwort**
2	4	<1%	*Plagiothecium laetum*	<1%	Wood	Bright silk moss
2	4		*Isothecium myosuroides*	<1%	Ground	Variable moss
2	5	15%	*Eurhynchium praelongum*	10%	Wood	Slender beaked-moss
2	5		*Isothecium myosuroides*	4%	Wood	Variable moss
2	5		*Plagiothecium denticulatum*	1%	Wood	Dented silk moss
2	5		*Plagiothecium undulatum*	<1%	Wood	Flat moss
2	5		*Rhizomnium glabrescens*	<1%	Wood	Large leafy moss
2	5		*Porella navicularis*	<1%	Wood	**Tree ruffle liverwort**
2	5		*Lepidozia reptans*	<1%	Wood	**Little hands liverwort**

2	5		*Geocalyx graveolens*	<1%	Wood	**Turpswort**
2	6	11%	*Eurhynchium oreganum*	7%	Wood	Oregon beaked-moss
2	6		*Plagiothecium undulatum*	3%	Wood	Flat moss
2	6		*Eurhynchium praelongum*	<1%	Wood	Slender beaked-moss
2	6		*Radula complanata*	<1%	Wood	**Flat-leaved scalewort**
2	6		*Isothecium myosuroides*	<1%	Bark	Variable moss
2	6		*Porella navicularis*	<1%	Bark	**Tree ruffle liverwort**
2	6		*Porella roellii*	<1%	Bark	**None**
2	6		*Plagiothecium denticulatum*	<1%	Bark	Dented silk moss
2	6		*Rhytidiadelphus triquetrus*	<1%	Bark	Electrified cat's-tail moss
2	7	<1%	*Isothecium myosuroides*	<1%	Wood	Variable moss
2	7		*Plagiothecium laetum*	<1%	Wood	Bright silk moss
2	7		*Orthotrichum lyellii*	<1%	Wood	Lyell's bristle-moss
2	7		*Porella roellii*	<1%	Wood	**None**
2	8	10%	*Isothecium myosuroides*	10%	Wood	Variable moss
2	9	1%	*Isothecium myosuroides*	1%	Wood	Variable moss
2	9		*Eurhynchium praelongum*	<1%	Wood	Slender beaked-moss
2	10	<1%	*Isothecium myosuroides*	<1%	Wood	Variable moss
2	10		*Orthotrichum lyellii*	<1%	Wood	Lyell's bristle-moss
2	10		*Rhizomnium glabrescens*	<1%	Wood	Large leafy moss
2	10		*Radula complanata*	<1%	Wood	**Flat-leaved scalewort**
2	10		*Plagiothecium denticulatum*	<1%	Wood	Dented silk moss
2	10		*Plagiothecium undulatum*	<1%	Wood	Flat moss
2	10		*Porella navicularis*	<1%	Wood	**Tree ruffle liverwort**
2	10		*Eurhynchium oreganum*	<1%	Wood	Oregon beaked-moss
		13%				
3	1	4%	*Isothecium myosuroides*	4%	Ground	Variable moss
3	1		*Eurhynchium praelongum*	<1%	Ground	Slender beaked-moss
3	1		*Plagiothecium denticulatum*	<1%	Ground	Dented silk moss
3	2	3%	*Eurhynchium praelongum*	2%	Bark	Slender beaked-moss
3	2		*Eurhynchium praelongum*	<1%	Wood	Slender beaked-moss
3	2		*Isothecium myosuroides*	1%	Wood	Variable moss
3	2		*Geocalyx graveolens*	<1%	Wood	**Turpswort**
3	2		*Porella navicularis*	<1%	Wood	**Tree ruffle liverwort**
3	2		*Plagiothecium laetum*	<1%	Ground	Bright silk moss
3	2		*Rhizomnium glabrescens*	<1%	Wood	Large leafy moss
3	3	8%	*Eurhynchium praelongum*	8%	Wood	Slender beaked-moss
3	3		*Eurhynchium praelongum*	<1%	Bark	Slender beaked-moss
3	3		*Isothecium myosuroides*	<1%	Bark	Variable moss
3	3		*Plagiothecium undulatum*	<1%	Wood	Flat moss
3	3		*Geocalyx graveolens*	<1%	Wood	**Turpswort**
3	4	22%	*Plagiothecium denticulatum*	18%	Wood	Dented silk moss
3	4		*Rhytidiadelphus triquetrus*	1%	Ground	Electrified cat's-tail moss
3	4		*Plagiothecium laetum*	<1%	Wood	Bright silk moss
3	4		*Dicranum scoparium*	1%	Wood	Broom Moss
3	4		*Pseudotaxiphyllum elegans*	1%	Wood	Elegant small flat moss
3	4		*Tetraphis pellucida*	1%	Wood	Common four-tooth moss
3	4		*Radula complanata*	<1%	Wood	**Flat-leaved scalewort**
3	5	8%	*Plagiothecium laetum*	5%	Wood	Bright silk moss
3	5		*Eurhynchium praelongum*	<1%	Wood	Slender beaked-moss
3	5		*Plagiothecium denticulatum*	<1%	Wood	Dented silk moss
3	5		*Geocalyx graveolens*	<1%	Wood	**Turpswort**
3	5		*Porella navicularis*	1%	Wood	**Tree ruffle liverwort**
3	5		*Isothecium myosuroides*	<1%	Wood	Variable moss
3	5		*Isothecium myosuroides*	<1%	Bark	Variable moss
3	5		*Orthotrichum lyellii*	<1%	Bark	Lyell's bristle-moss
3	5		*Rhizomnium glabrescens*	1%	Wood	Large leafy moss
3	5		*Pseudotaxiphyllum elegans*	<1%	Wood	Elegant small flat moss
3	6	3%	*Plagiothecium undulatum*	1%	Wood	Flat moss
3	6		*Isothecium myosuroides*	1%	Wood	Variable moss
3	6		*Plagiothecium laetum*	<1%	Wood	Bright silk moss
3	6		*Porella navicularis*	<1%	Ground	**Tree ruffle liverwort**
3	7	4%	*Plagothecium undulatum*	4%	Wood	Flat moss
3	7		*Pseudotaxiphyllum elegans*	<1%	Wood	Elegant small flat moss
3	7		*Rhizomnium glabrescens*	<1%	Wood	Large leafy moss
3	7		*Lepidozia reptans*	<1%	Wood	**Little hands liverwort**

3	7		*Isothecium myosuroides*	<1%	Wood	Variable moss
3	7		*Orthotrichum lyellii*	<1%	Bark	Lyell's bristle-moss
3	8	25%	*Hylocomium splendens*	7%	Ground	Step moss
3	8		*Rhytidiadelphus loreus*	5%	Wood	Lanky moss
3	8		*Isothecium myosuroides*	6%	Wood	Variable moss
3	8		*Eurhynchium praelongum*	6%	Wood	Slender beaked-moss
3	8		*Eurhynchium praelongum*	<1%	Ground	Slender beaked-moss
3	8		*Plagiothecium undulatum*	1%	Ground	Flat moss
3	9	26%	*Hylocomium splendens*	20%	Wood	Step moss
3	9		*Plagothecium undulatum*	3%	Wood	Flat moss
3	9		*Isothecium myosuroides*	2%	Wood	Variable moss
3	9		*Pseudotaxiphyllum elegans*	1%	Wood	Elegant small flat moss
3	9		*Dicranum scoparium*	<1%	Wood	Broom Moss
3	9		*Geocalyx graveolens*	<1%	Wood	**Turpswort**
3	10	2%	*Isothecium myosuroides*	1%	Wood	Variable moss
3	10		*Eurhynchium praelongum*	<1%	Wood	Slender beaked-moss
3	10		*Porella roelli*	<1%	Wood	**None**
3	10		*Geocalyx graveolens*	<1%	Wood	**Turpswort**
3	10		*Orthotrichum lyellii*	<1%	Wood	Lyell's bristle-moss
3	10		*Rhizomnium glabrescens*	<1%	Wood	Large leafy moss
3	10		*Eurhynchium oreganum*	<1%	Wood	Oregon beaked-moss
3	11	45%	*Plagothecium undulatum*	18%	Wood	Flat moss
3	11		*Rhizomnium glabrescens*	7%	Wood	Large leafy moss
3	11		*Eurhynchium oreganum*	18%	Wood	Oregon beaked-moss
3	11		*Claopodium crispifolium*	2%	Wood	Rough moss
3	11		*Eurhynchium praelongum*	<1%	Wood	Slender beaked-moss
3	11		*Geocalyx graveolens*	<1%	Wood	**Turpswort**
		14%				

Appendix 2. Recorded substrate by species. 'Loose' samples were not affixed to any substrate. Liverwort species are highlighted **green**.

Species	Alder leaf	Other moss	Ground	Forest Floor	Loose	Wood	Bark	All Wood	Total
Aneura pinguis	1					1	1		3
Calypogeia muelleriana						1			1
Claopodium crispifolium			1			1			2
Dicranum scoparium						2			2
Eurhynchium oreganum						6			6
Eurhynchium praelongum			4		2	15	3		24
Geocalyx graveolens						10			10
Homalothecium fugescens			2			2	1		5
Hylocomium splendens			3			2			5
Isothecium myosuroides	1		2		1	20	6		30
Lepidozia reptans						3			3
Metaneckera menziesii		1	1						2
Neckera douglasii			1			1	1		3
Orthotrichum lyellii			1		4	8	4		17
Orthotrichum pulchellum						1			1
Plagiothecium denticulatum			2			8	2		12
Plagiothecium laetum			2		1	8			11
Plagiothecium undulatum			1			11	1		13
Porella navicularis	1		4		2	6	3		16
Porella roellii			3			5	2		10
Pseudotaxiphyllum elegans			1			10	1		12
Radula complanata						3			3
Rhizomnium glabrescens			1		1	10	2		14
Rhytidiadelphus loreus					1	1			2
Rhytidiadelphus triquetrus			1				1		2
Tetraphis pellucida						3			3
Total	**3**	**1**	**30**	**34**	**12**	**138**	**28**	**166**	**212**

Back cover illustration: Most bryophyte samples were obtained from fallen logs rather than the forest floor. The major species on this log is *Rhytidiadelphus loreus* with small contributions of *Rhizomnium glabrescens* and *Dicranum scoparium* (foreground).