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Epiphyte Habitats in an Old Conifer Forest in Western Washington, U.S.A.

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Abstract. *Old conifer forests in the Pacific Northwest have a wide range of microhabitats induced by canopy structure and substrate characteristics. We used the Wind River Canopy Crane to sample lichens and bryophytes throughout the spectrum of habitats available to epiphytes. Of the 111 species found in 72 sample units, 97 were lichens and 14 were bryophytes. Epiphyte communities showed marked variation with respect to height in the canopy, bark vs. wood, degree of sheltering, and stem diameter. Of these factors, height in the canopy was most strongly related to epiphyte communities. Furthermore, the top two meters of the tallest trees hosted a diverse assemblage of both rare species* (Tholurna dissimilis) *and weedy, nitrophilous species* (Candelaria concolor, Hypogymnia tubulosa, Parmelia sulcata)*, presumably induced by birds delivering lichen propagules and nutrients. Ten species were more frequent on bare wood than bark, including* Ophioparma rubricosa, Letharia vulpina, Placynthiella *spp.*, Ptychographa xylographoides, Trapeliopsis flexuosa, *and* Xylographa parallela. *Species richness was highly variable, even within habitats. The only factor found related to species richness was height in the canopy, the middle and upper layers each having about twice the species per sample unit as lower in the canopy.*

Imagine the structural complexity of a forest from a lichen's point of view. Think of treetop twigs, shady lower trunks, spindly understory trees, leaning trees, and hard, decorticate snags. When an ecologist attempts to understand the resulting variation in epiphyte communities, the vertical gradient—how epiphytes change with height in the canopy—is among the most compelling topics to study. As we shall see, this is rightly so. But is there other important variation in habitat, from an epiphyte's viewpoint?

Vertical gradients in epiphytic lichens and bryophytes have been described in many temperate areas of the world, including rainforests (e.g., Clement & Shaw 1999; Kantvilas & Minchin 1989; McCune 1993; McCune et al. 1997; Pike et al. 1975, 1977; Rosso et al. 2000; Sillett 1995; Sillett & Rambo 2000), boreal forests (e.g., Arseneau et al. 1997; Yarranton 1972), and deciduous forests (e.g., Barkman 1958; Hale 1965; Harris 1971). If there is anything in common among these studies, it is simply the observation that epiphytes change with height in the canopy.

Other habitat variation is present within a canopy, however, besides the gradient with height. Degelius (1964) and Stone (1989) studied changes in

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communities of epiphytes with branch development, combining successional processes with environmental changes. Ryan (1991) studied in detail the factors responsible for the pronounced differences in epiphytes between the upper and lower sides of leaning trunks. Pike et al. (1975, 1977) reported presence of individual species, including crustose lichens and bryophytes, in seven habitats representing different canopy positions, based on a sample of twenty trees in an old-growth conifer forest. Many authors have contrasted epiphytes on various species of trees.

Each of these studies demonstrated some important patterns of variation in epiphytes. Missing are 1) quantification of the relative strength of these various patterns, 2) consideration of dead trees as habitat for epiphytes, and 3) synthesis and reconciliation of seemingly disparate results from various regions. This paper addresses the first two items. Basic research on how species composition of epiphytes varies with structural components of canopies should provide clues about how these species might respond to changes induced by forest management.

How much does bare wood on dead trees and branches contribute to epiphyte diversity? Apparently there are no quantitative studies on this question. We contrasted bare wood substrates throughout the canopy with live, bark-covered substrates. Dead wood is often difficult and dangerous to access by climbing, but lends itself to sampling with a canopy crane.

We also seek to partially redress the notorious avoidance of crustose lichens by American ecologists. In forests of the Pacific Northwest, crustose lichen epiphytes often cover as much or more surface area as macrolichens and bryophytes.

Study Area

We studied the forest of the Wind River Canopy Crane Research Facility in the southern Washington Cascades. The canopy crane is a large construction crane on a fixed platform, providing 3-dimensional access to a 2.3 hectare circular area of old-growth *Pseudotsuga menziesii-Tsuga heterophylla* forest (Franklin & DeBell 1988; nomenclature of vascular plants after Hitchcock & Cronquist 1973; lichens follow Esslinger & Egan 1995 except as indicated; nomenclature for bryophytes is in Table 2). The crane is located in the T. T. Munger Research Natural Area at the Wind River Experimental Forest (45°49′N, 121°57′W) at an elevation of 355 m. Average annual temperature is 8.8°C, with January and July means of 0°C and 18°C respectively (unpublished climatological summary, Wind River Experimental Forest, 1911–1965; Franklin 1972). Average annual precipitation is 250 cm. The oldest trees in the forest are about 400–500 years old. Stratification of the trees was described by Ishii et al. (2000). Parker (1997) described the vertical gradient in light environment. Light is rapidly attenuated between 13 and 37 m high in the canopy, the "light transition zone." Biomass of epiphytic macrolichens at the crane site is about 1.3 metric tons/ha, composed of approximately 42% cyanolichens, 28% alectorioid lichens, and 30% other lichens (McCune et al. 1997).

Methods

We used stratified random sampling, based on a cross-classification of height class, bark vs. wood (i.e., dead, decorticate stems vs. live stems), and stem class. The word "stem" throughout this paper refers to its anatomical meaning, including trunks, branches, and twigs. Within each cell of the design three quadrats were taken, for a total of 72 quadrats distributed over about 40 trees. The design was nearly balanced although some cells of the design were intentionally empty. For example treetops were only sampled in the highest stratum.

Sample units were taken in haphazard order with respect to the design. No sample units in the same cell of the design were less than 10 m apart in the canopy, dispersing our sampling throughout the cylindric volume accessible by the crane. Otherwise, selection of sample units within cells of the design was arbitrary but without preconceived bias.

Five stem classes were sampled: 1) tree tops (the top two m of the main stem), 2) twigs (< 5 cm diameter), 3) branches > five cm diam, 4) the upper side of leaning trunks, "uplean" for short, and 5) lower side of leaning trunks ("sheltered trunks"). Branches and trunks that were dead but still retained the bark were not included. Stem classes 2, 3, 4, and 5 were sampled in all height classes.

Height classes (canopy strata) were based on the geometry of the dominant trees: a) the upper quarter (vertical) of the dominant tree canopy, a band from 47–64 m, b) a 20% portion including the lower live crowns of the dominant/codominant trees (24–37 m), coinciding with the upper half of the light transition zone, and c) the bottom 10% of the forest (0–6 m). The x, y, and z coordinates of each sample unit were recorded, as well as the host species.

Sampling included all bryophytes and lichens. Vouchers are in OSC and McCune's research herbarium. No epiphytic vascular plants were present. We measured species cover in 20 × 50 cm quadrats with flexible nylon webbing for the 20 cm segments. This quadrat was pinned to the substrate. When the circumference of the substrate was less than 20 cm, the whole circumference of the stem was used. Abundance classes were recorded on a logarithmic scale: < 1%, 1–10%, and 10–100% cover.

The lowest stratum was sampled from the ground. For the remainder we leaned out of a gondola suspended by the crane. Our sampling was constrained somewhat by access with the gondola, because the configuration of branches often prevents the gondola from reaching all parts of the forest. For example, mid-canopy trunks surrounded by a dense array of branches cannot be reached by the gondola.

We sampled in two episodes, March and August, 1996. Species were identified in the field whenever possible. Because destructive sampling is not allowed in the crane area, we sampled unknown species by removing small fragments for later analysis. In almost all cases these were identifiable to species in the laboratory.

The raw data matrix was 72 quadrats × 111 species. Because cover was recorded in coarse classes, no transformation was required. We chose not to relativize the data, thus allowing differences in quadrat totals of abundance of epiphytes to be expressed in the analyses. We

considered totals in epiphyte abundance classes to be informative of some aspects of habitat quality.

Species with fewer than three occurrences were removed from the matrix, resulting in a matrix of 72 quadrats × 61 species. This strengthened the apparent differences among habitats by reducing noise from very infrequent species.

We sought outlier quadrats by examining a frequency distribution of average Sørensen distance between each quadrat and all other quadrats in species space. Only one quadrat had an average distance more than two standard deviations from the mean of this distribution. Because this was only a very weak outlier (average distance 2.08 standard deviations larger than the mean of those averages), we retained it in all analyses. A similar analysis of species in sample space revealed no outlying species.

Groups of quadrats defined by stratum, stem class, tree species, and bark vs. wood were compared with non-metric MRPP (Multi-response Permutation Procedures) and Indicator Species Analysis (McCune & Mefford 1999). MRPP (Mielke 1984) provides a nonparametric multivariate test of differences between groups, while indicator species analysis (Dufrêne & Legendre 1997) describes how well each species differentiates between groups. Non-metric MRPP is the same as MRPP except that the distance matrix is converted to ranks before calculating the test statistic. The A statistic from MRPP describes effect size, the "chance-corrected within-group agreement." When $A = 0$, the groups are no more or less different than expected by chance; when $A = 1$, all sample units are identical within each group. In community ecology $A < 0.1$ is common, even when differences between groups are apparent; $A > 0.3$ is fairly high.

Non-metric multidimensional scaling (NMS; Kruskal 1964; Mather 1976) provided a graphical depiction of community relationships and habitat variables. The "slow-and-thorough" autopilot mode of NMS in PC-ORD (McCune & Mefford 1999) used the best of 40 runs with the real data along with 50 runs with randomized data for a Monte Carlo test of significance. Sørensen distances expressed community resemblances. Habitat variables were superimposed on the resulting ordination using a joint plot, based on the correlations of those variables with the axes of the community ordination. The resulting ordination was rigidly rotated 295 degrees to load the strongest environmental factor on a single axis. Variance explained was expressed by the coefficient of determination between Euclidean distances in the ordination space and the Sørensen distances in the original species space.

We formed groups of species by cluster analysis of the transposed community matrix. First, however, we applied an even more strict criterion for removing rare species, retaining only those species with five or more occurrences, since species with only a few occurrences provide little reliability in assigning them to groups. This 44 species × 72 quadrat matrix was relativized by species sums of squares to de-emphasize clustering based on total abundance alone. Without this step, cluster analysis of species often results in abundant species tending to group together. Instead we sought groupings by habitat preferences. We used Ward's method of clustering (Wishart 1969; also known as the minimum variance method), using a Euclidean distance matrix. Although Sørensen distance is generally preferred for community analysis (Faith et al. 1987), our use of cluster analysis to seek local group structure renders many of the differences between distance measures unimportant. Sørensen distance is incompatible with Ward's method, but the latter is a reliable, effective method of clustering. The resulting dendrogram was scaled by Wishart's objective function converted to a percentage of information remaining (McCune & Mefford 1999).

TABLE 1. Epiphyte species diversity overall and broken down by groups of sample units. Beta diversity was measured as the total number of species divided by the average number of species.

Group (sample size)	Average species richness (S.D.)	Beta diversity	Total number of species
Overall (72)			
Lichens	8.8 (5.1)	11.0	97
Bryophytes	1.1 (1.3)	12.7	14
Lichens + bryophytes	9.8 (4.5)	11.3	111
Canopy stratum			
Upper (25)	12.5 (2.6)	5.5	69
Middle (21)	12.2 (4.2)	5.2	72
Lower (26)	5.4 (2.6)	4.8	36
Stem class			
tree tops (8)	12.7 (2.9)	3.4	43
small branches (16)	8.6 (4.0)	7.4	64
large branches (23)	10.8 (6.3)	6.4	69
trunks, up-lean (16)	9.3 (2.5)	6.0	56
trunks, sheltered (9)	7.9 (2.8)	4.7	37
Bark vs. Wood			
bark (34)	9.9 (4.6)	8.5	84
wood (38)	9.8 (4.7)	8.3	81

RESULTS

Species diversity.—Species richness was highly variable, with a mean of 10 species per quadrat, but a standard deviation of 4.6 species (Table 1). Most of the epiphytic species were lichens, averaging eight times as many lichen species per quadrat as bryophytes. Overall we found 97 lichen species (including a few species groups) and 14 bryophyte species (Table 2).

Some of this variation in species richness was attributed to measured factors. In particular, over half of the variation in species richness was related to stratum (one-way ANOVA, $F = 39.6$, $p < 0.001$). We found less than half as many species per sample unit in the lowest stratum as in the higher two strata (Table 1). Bryophytes had the opposite pattern, with the highest diversity in the lowest stratum (averaging two species per quadrat) and no bryophytes recorded in the treetops. Again, about half of the variation in number of bryophyte species was attributable to stratum ($F = 29.1$, $p < 0.001$).

Uplean vs. sheltered tree trunks and bark vs. wood made little difference in species richness (Table 1), despite the strong contrasts in species composition (see below). Our sample size was too small

TABLE 2. Species and their average abundance (cover class) and quadrat count. Notes: [1] Usually just a few strands, too small to identify to species. [2] "Mystery olive species" of McCune and Geiser (1997). [3] Spores 1-septate, ca 14 × 3.5 μm; epihymenium blue green; hypothecium orange-brown. [4] Broad sense, including *C. coniocraea* sensu Hammer (1995). [5] Including *Lepraria* and *Leproloma* spp., det. Tor Tønsberg. [6] Sample not collected for chemical verification of *P. icmalea* vs. *P. uliginosa*. [7] Mainly tufted species or ambiguously short individuals of potentially pendulous species. [8] Too small to identify.

Species	Acronym	Abundance	Count
Lichens			
Alectoria sarmentosa	Alesar	1.014	37
Alectoria vancouverensis	Alevan	0.181	7
Bacidia beckhausii	Bacbec	0.014	1
Bacidia lutescens group	Baclut	0.014	1
Biatora nobilis Printzen & Tønsb.	Bianob	0.028	1
Bryoria[1]	Bry	0.264	15
Bryoria friabilis	Bryfri	0.306	14
Bryoris fuscescens	Bryfus	0.111	4
Bryoria olive species[2]	Bryoli	0.014	1
Bryoria pseudofuscescens	Brypse	0.194	7
Buellia erubescens	Bueeru	0.028	1
Buellia muriformis Nordin & Tønsb.	Dptpen	0.056	3
Calicium glaucellum	Clcgla	0.028	2
Candelaria concolor	Cndcon	0.028	2
Catillaria[3]	Ctn	0.014	1
Cetraria chlorophylla (Willd.) Vainio	Cetchl	0.097	6
Cetraria orbata (Nyl.) Fink	Cetorb	0.042	3
Chaenotheca brunneola	Chabru	0.097	4
Chaenothecopsis pusilla	Chppus	0.014	1
Cladonia	Cla	0.222	9
Cladonia carneola	Clacar	0.028	2
Cladonia fimbriata	Clafim	0.139	9
Cladonia macilenta	Clamac	0.069	3
Cladonia ochrochlora[4]	Claoch	0.042	2
Cladonia squamosa var. *squamosa*	Clasqu	0.042	2
Cladonia squamosa var. *subsquamosa*	Classq	0.583	26
Cladonia transcendens	Clatra	0.847	28
Cyphelium inquinans	Cypinq	0.042	2
Esslingeriana idahoensis	Essida	0.069	3
Hypocenomyce friesii	Hcefri	0.042	2
Hypogymnia apinnata	Hypapi	0.042	2
Hypogymnia enteromorpha	Hypent	0.194	7
Hypogymnia imshaugii	Hypims	0.042	2
Hypogymnia inactiva	Hypina	0.056	2
Hypogymnia metaphysodes	Hypmet	0.042	1
Hypogymnia oceanica	Hypoce	0.014	1
Hypogymnia physodes	Hypphy	0.236	14
Hypogymnia tubulosa	Hyptub	0.083	4
Icmadophila ericetorum	Icmeri	0.014	1
Japewia subaurifera	Japsub	0.028	2
Japewia tornoënsis	Japtor	0.361	13
Lecanora circumborealis	Leccir	0.208	6
Lecanora aff. *symmicta*	Lciple	0.014	1
Lecanora varia group	Lecvar	0.028	1
Lecidea sp.	Lci	0.014	1
Lecidea enalla Nyl.	Lciela	0.042	3
Lepraria[5]	Lpr	0.472	20
Letharia vulpina	Letvul	0.153	9
Lobaria oregana	Lobore	0.236	7
Lobaria pulmonaria	Lobpul	0.028	1
Lopadium disciforme	Lopdis	0.167	8
Melanelia elegantula	Melele	0.014	1
Melanelia exasperatula	Melexl	0.028	2
Micarea sp.	Mic	0.014	1
Micarea erratica	Micerr	0.014	1
Micarea melaena	Micmel	0.014	1
Micarea misella	Micmis	0.028	1
Micarea prasina	Micpra	0.181	6
Mycoblastus sanguinarius	Mycsan	0.472	19

TABLE 2. Continued.

Species	Acronym	Abundance	Count
Nephroma occultum	Nepocc	0.028	1
Nodobryoria oregana	Nodore	0.417	22
Ochrolechia gowardii	Ochgow	0.014	1
Ochrolechia juvenalis	Ochjuv	0.028	1
Ochrolechia oregonensis	Ochore	0.722	24
Ochrolechia subpallescens	Ochsub	0.028	1
Ophioparma rubricosa	Bacher	0.681	21
Parmelia hygrophila	Parhyg	0.042	2
Parmelia saxatilis	Parsax	0.125	5
Parmelia sulcata	Parsul	0.194	10
Parmeliella parvula P. M. Jørg.	Pllpar	0.056	4
Parmeliopsis hyperopta	Pophyp	0.167	11
Pertusaria borealis	Perbor	0.069	3
Pertusaria ophthalmiza	Peroph	0.139	5
Pertusaria subambigens	Persub	0.111	4
Phlyctis argena	Phlarg	0.056	3
Placynthiella[6]	Plc	0.208	10
Placynthiella icmalea	Plcicm	0.181	8
Placynthiella uliginosa	Plculi	0.069	4
Platismatia glauca	Plagla	1.097	39
Platismatia herrei	Plaher	0.583	26
Platismatia stenophylla	Plaste	0.028	1
Protoparmelia ochrococca	Prooch	0.028	2
Ptychographa xylographoides Nyl.	Ptyxyl	0.125	6
Pyrrhospora cinnabarina	Pyrcin	0.014	1
Rinodina sp.	Rin	0.014	1
Rinodina disjuncta	Riddis	0.042	3
Ropalospora viridis	Ropvir	0.014	1
Sphaerophorus globosus sens. lat.	Sphglo	0.500	23
Tholurna dissimilis	Thodis	0.056	2
Trapeliopsis flexuosa	Trpfle	0.153	8
Trapeliopsis pseudogranulosa	Trppse	0.097	3
Usnea[7]	Usn	0.097	5
Usnea filipendula	Usnfil	0.222	7
Usnea glabrata	Usngla	0.014	1
Usnea scabrata	Usnsca	0.097	5
Xylographa parallela	Xylabi	0.361	13
Xylographa vitiligo	Xylvit	0.042	2
Unknown[8]	unk	0.153	7
Bryophytes			
Antitrichia curtipendula (Hedw.) Brid.	Antcur	0.083	4
Cephalozia lunulifolia (Dum.) Dum.	Ceplun	0.069	3
Cephaloziella	Cll	0.069	3
Dicranum fuscescens Turn.	Dicfus	0.292	10
Dicranum tauricum Sapeh.	Dictau	0.056	4
Frullania tamarisci ssp. *nisquallensis* (Sull.) Hatt.	Frunis	0.139	6
Hypnum circinale Hook.	Hypcir	0.417	14
Isothecium myosuroides Brid.	Isomyo	0.708	19
Neckera douglasii Hook.	Necdou	0.028	2
Porella navicularis (Lehm. & Lindenb.) Lindb.	Pornav	0.083	4
Radula bolanderi Gott.	Radbol	0.014	1
Scapania bolanderi Aust.	Scabol	0.208	5
Scapania umbrosa (Schrad.) Dumort.	Scaumb	0.028	1
Ulota megalospora Vent.	Ulomeg	0.014	1

to allow us to separate host species effects from those of stratum.

Species turnover rates, as measured by beta diversity, were similar for lichens and bryophytes (Table 1). Beta diversity overall was very high, reflecting the wide range of habitats sampled. The large number of infrequent species occurrences (40 species occurred only once or twice in our sample) also contributed to the high beta diversities.

When the data were divided into more homogenous groups (e.g., by stratum) then beta diversity was much lower (Table 1). For a given kind of grouping, beta diversity was consistent across groups with two exceptions: tree tops and sheltered

TABLE 3. Comparison of differences in community composition with non-metric MRPP, based on Sørensen distances; g = number of groups; A = chance-corrected within-group agreement; p = probability of Type I error for H_0: no difference between groups.

Grouping variable	g	A	p	Strong covariation with . . .
Stratum[1]	3	0.320	$<10^{-8}$	stem class, tree species
Stem class[2]	4	0.184	$<10^{-7}$	stratum, tree species
Bark vs. wood	2	0.051	0.001	
Tree species[3]	4	0.251	$<10^{-7}$	stratum, stem class
Uplean vs. sheltered (trunks only)	2	0.095	0.008	

[1] Upper canopy, middle canopy, near ground. [2] Uplean trunks, sheltered trunks, branches, twigs, tree tops. [3] *Pseudotsuga menziesii, Taxus brevifolia, Thuja plicata, Tsuga heterophylla*; excluding the single quadrat on *Abies amabilis*.

trunks were more homogeneous than the other stem classes.

Differences among habitats.—Lichen communities differed strongly among habitats (Table 3; Fig. 1). The importance of canopy stratum is shown by the separation of strata in the ordination of quadrats. The first three axes explained 82% of the community variation (Fig. 1). NMS Autopilot in PC-ORD chose a 3-dimensional representation as providing a substantial and statistically significant reduction in stress, as compared with randomized data (Fig. 2). After rotation, 44% of the variation in communities was explained by the axis aligned with canopy stratum (axis 2 in Fig. 1).

The second most important axis (axis 1), representing 28% of the variation, was related to the size of stem, contrasting trunks with branches. *Isothecium myosuroides* and *Porella navicularis* were most strongly associated with branches, while *Cladonia transcendens* and *Lepraria* spp. showed the strongest association with trunks. Note that the contrast between large stems and small stems (branches) was strongest in the lowest stratum, as indicated by the larger spread of low-stratum points on axis 1 in contrast with the relatively tight clump of high-stratum points on axis 1.

The third axis, representing 10% of the variation, was related solely to the contrast between bark and wood. Samples from bark and wood were strongly segregated on Axis 3.

The relative strengths of substrate and habitat factors from the ordination closely paralleled results from MRPP. In order of decreasing differentiation, lichen communities differed by stratum, tree species, stem class, uplean vs. sheltered, and bark vs. wood (MRPP: $p < 10^{-7}$ for each grouping, except bark vs. wood and lean had $p < 0.008$; $0.05 < A < 0.32$; Table 3).

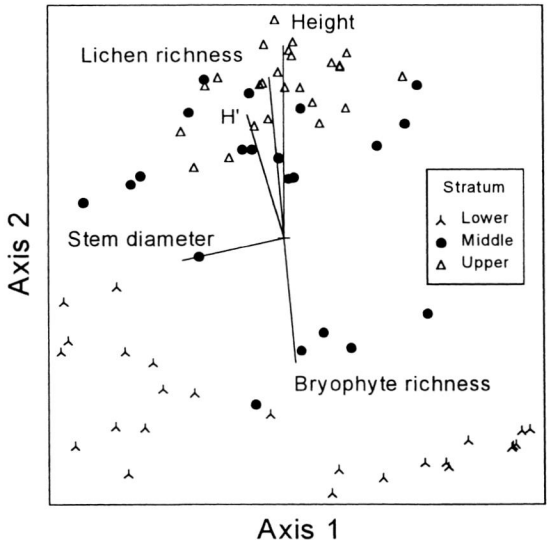

FIGURE 1. Ordination of quadrats in epiphyte species space, with joint plot of substrate and other environmental characteristics. H′ is the Shannon index of diversity (Whittaker 1972). Symbols indicate the stratum where each quadrat was taken. Radiating lines indicate the relative strength and direction of correlation of variables with the ordination.

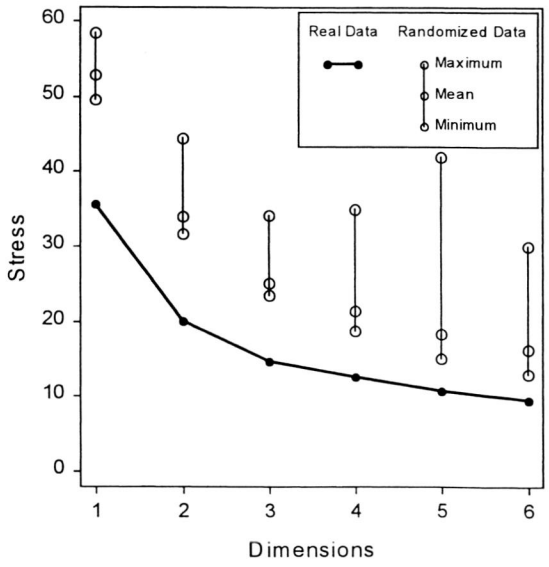

FIGURE 2. NMS scree plot comparing the best run using real data with randomized runs. The scree plot shows the reduction in final stress (improvement in fit) as dimensions in the solution are increased.

TABLE 4. Substrate affinities for epiphytes at the Wind River Canopy Crane site based on Indicator Species Analysis.

	Substrate	
	Bark	Bare wood
Strongly selective	*Bryoria friabilis*	*Ophioparma rubricosa*
	Hypogymnia enteromorpha	*Cladonia subsquamosa*
	Japewia tornoënsis	*Letharia vulpina*
	Lecanora circumborealis	*Placynthiella icmalea*
	Lopadium disciforme	*Placynthiella uliginosa*
	Parmelia sulcata	*Ptychographa xylographoides*
	Sphaerophorus globosus	*Trapeliopsis flexuosa*
	Usnea filipendula	*Xylographa parallela*
Moderately selective	*Cetraria chlorophylla*	*Dicranum tauricum*
	Cetraria orbata	*Micarea prasina*
	Esslingeriana idahoensis	
	Lecidea enalla	
	Parmelia saxatilis	
	Pertusaria ophthalmiza	
	Porella navicularis	
	Scapania bolanderi	

These groupings are interdependent. For example tree species is strongly correlated with stratum, because the canopy dominant, *Pseudotsuga menziesii,* is represented only by trunks (no branches) in the lowest stratum. On the other hand, *Taxus brevifolia* is a short tree (< 10 m) that never reaches our middle stratum. Community differences across host tree species are therefore partly derived from environmental differences dependent on height in the canopy. Table 3 lists other dependencies.

The strongest interactions between grouping variables are among stratum, stem class, and tree species. Uplean vs. sheltered was tested only for trunks, so that interaction with tree species and stratum was reduced. Bark vs. wood was sampled in a balanced design for all strata and stem classes, so it had essentially no confounding with the other grouping variables.

Epiphyte communities on bark differed from those on wood, although this difference was more subtle than the differences among strata or among stem classes (compare *A* statistics in Table 3). Nevertheless, many species differed significantly between bark and wood, based on Indicator Species Analysis (Table 4).

The difference in epiphytes between bare wood and bark is much greater higher in the canopy than on lower trunks. Note how bark-associated species and wood-associated species from Table 4 are mixed in Group 9 below.

Species groups.—The dendrogram from cluster analysis of species was trimmed at nine groups. This level of grouping provided an good compromise between loss of information (about 45% retained) and providing a simple, interpretable summary of ecological affinities among species (Fig. 3). The species groups are described below.

1. Mid to upper canopy, modal species with broad substrate tolerances: *Alectoria sarmentosa, Mycoblastus sanguinarius, Nodobryoria oregana, Platismatia glauca, P. herrei,* and *Ochrolechia oregana.* These species are very frequent in and above the light transition zone. *Alectoria sarmentosa* contributes substantial biomass in the mid to upper canopy.

2. Upper living stems: *Japewia tornoënsis, Hypogymnia enteromorpha,* and *Usnea scabrata.* These species were most common on small to medium diameter living stems (both trunks and branches) in the upper canopy. They were similar to Group 1 in peaking in the upper canopy.

3. Mid to upper canopy bare wood: *Bryoria pseudofuscescens, Letharia vulpina, Ophioparma rubricosa,* and *Trapeliopsis flexuosa* The inclusion of *B. pseudofuscescens* in this group is not representative of more typical habitats that often include living branches. Upper canopy wood is a relatively dry habitat, making this position in the forest the closest approximation to the suboceanic climates of northern Idaho and western Montana in which *B. pseudofuscescens* may dominate.

4. Medium to dry bark microsites, mid to upper canopy: *Alectoria vancouverensis, Cetraria chlorophylla, Parmelia saxatilis, P. sulcata,* and *Usnea filipendula.* Note the subtle tendency for *A. vancouverensis* to occur in drier habitats than *A. sarmentosa.*

5. Dry, upper canopy bark: *Bryoria friabilis, Hypogymnia physodes, Lecanora circumborealis,* and *Usnea* spp (mainly tufted species). The presence of *Lecanora circumborealis* in this group is an excellent example of a species that frequents the lower crowns in drier forests, but is restricted to more exposed sites in this oceanic climate. Similarly, *B.*

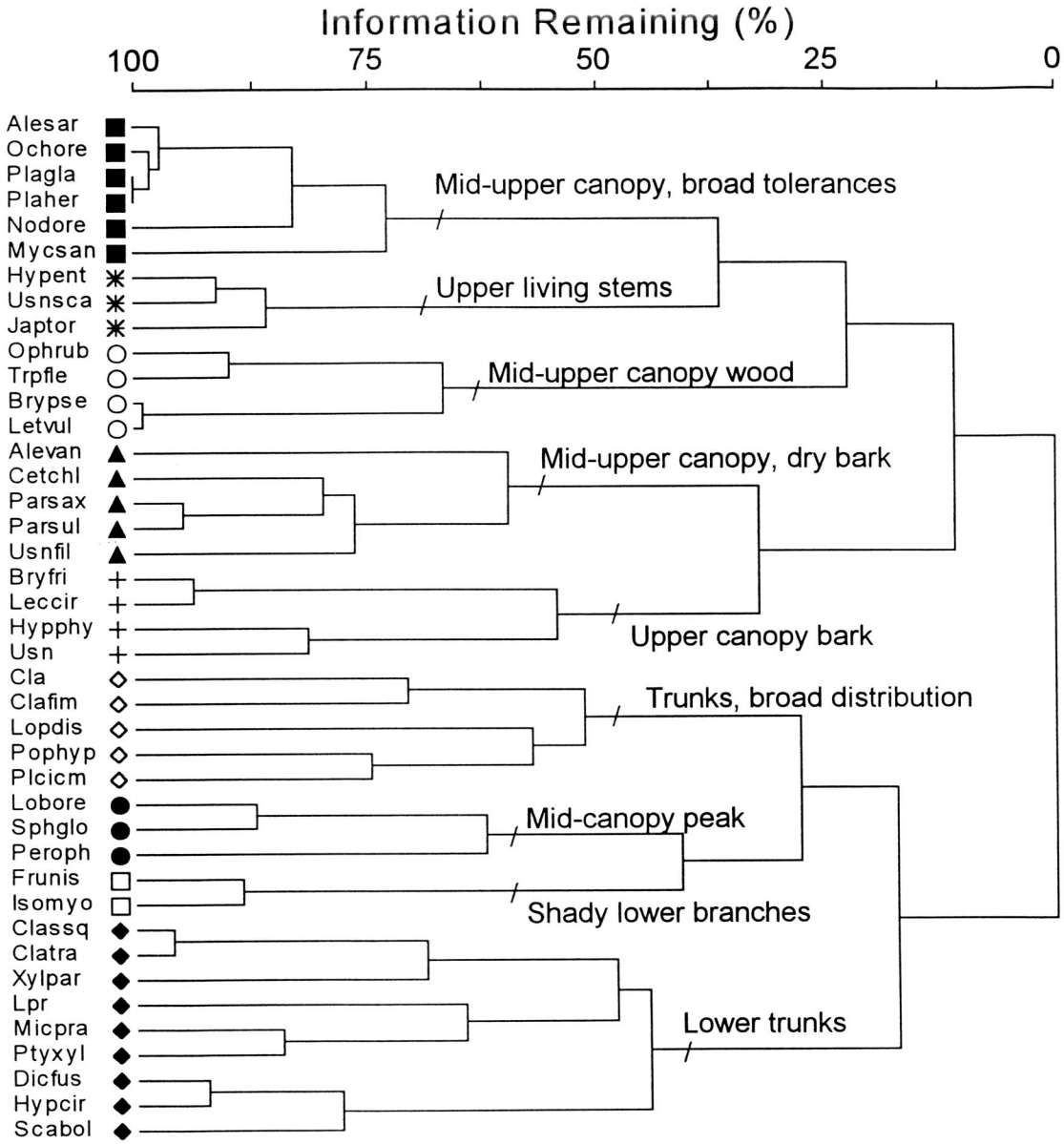

FIGURE 3. Dendrogram of epiphyte species. Symbols indicate species groups.

friabilis may occur in sheltered sites in less oceanic forests (northern Idaho and western Montana), but here occurs primarily in exposed sites. The presence of *Hypogymnia physodes, Lecanora circumborealis,* and tufted *Usnea* species suggests younger branches.

6. Broadly distributed trunks: *Cladonia* squamules, *C. fimbriata, Lopadium disciforme, Parmeliopsis hyperopta,* and *Placynthiella icmalea.* These species were more frequent on trunks, and to a lesser extent on large branches, than on small branches. In contrast to Group nine, however, these species had broad vertical distributions. In drier forests *L. disciforme* and *P. hyperopta* are increasingly restricted to lower trunks.

7. Mid canopy peak: *Lobaria oregana, Pertusaria ophthalmiza,* and *Sphaerophorus globosus.* These species had highest abundance in mid-canopy and were absent or sparse in the upper canopy and near the forest floor. They occur on a wide range of stem diameters, with some tendency to higher frequency on large-diameter branches.

8. Shady lower branches: *Frullania tamarisci* ssp. *nisquallensis* and *Isothecium myosuroides.* Although not included in the cluster analysis, *Antitrichia curtipendula* and *Porella navicularis* also fall

in this group. All of these species commonly occur higher in the canopy in wetter forests (e.g., Sillett 1995).

9. Lower trunks: *Cladonia subsquamosa, C. transcendens, Dicranum fuscescens, Hypnum circinale, Lepraria* spp, *Micarea prasina, Ptychographa xylographoides, Scapania bolanderi,* and *Xylographa parallela.* The tendencies for some of these (*M. prasina, P. xylographoides,* and *X. parallela*) to occur on wood is blurred in the dendrogram because of the relatively low substrate selectivity of some of their associates (such as *Lepraria* and *Cladonia*).

Discussion

Height in canopy.—At Wind River and elsewhere, epiphytes typically change with height in the canopy (e.g., Arseneau et al. 1997; Barkman 1958; Hale 1965; Kantvilas & Minchin 1989; Yarranton 1972). Height in the canopy was easily the strongest of the measured variables in relationship to epiphyte community structure. Attempts of a mechanistic explanation for this stratification in terms of one or two factors have been stymied by the strongly interdependent environmental and successional factors (McCune 1993). We can, however, say that the canopy structure itself creates this vertical gradient, and that it will vary among ecosystems according to canopy structure and climate. For example, species often dominant in less oceanic climates tended to occur high in the canopy at Wind River. In the case of tall forests in a moist environment, such as in this study, epiphytes are strongly stratified with height.

Despite all of the studies on vertical gradients in epiphytes, the puzzle of its causes is as recalcitrant as ever. Ecophysiological and transplant experiments may help to resolve the factors responsible for stratification with height (Sillett & Rambo 2000). Our transplant studies of *Letharia, Lobaria,* and *Usnea,* at Wind River will be presented in a future paper.

Bark vs. wood.—Bare wood differs from bark not only in physico-chemical attributes but also in the timing of its exposure. Even in a very old forest new bare wood continuously appears. Dying branches or stems eventually lose their bark, initiating a primary succession of epiphytes on the newly exposed wood. This wood appears more stable than bark and it quickly develops a community with complete coverage of the substrate. Typically this is a blend of lichens that are mostly restricted to wood (e.g., *Ophioparma rubricosa, Placynthiella icmalea, Placynthiella uliginosa, Ptychographa xylographoides, Trapeliopsis flexuosa,* and *Xylographa parallela*) along with lichens (especially macrolichens) and bryophytes that are common on bark. Although communities on wood differ statistically from those on bark, in this forest the contrasts are not as great as among strata in the canopy. In shorter, more widely spaced forests, less vertical stratification would be expected and our result could easily reverse, the distinction between bark and wood exceeding the vertical gradient in epiphyte abundance. Bare wood in forests is a critical substrate for the many species largely restricted to wood. Therefore managing for some dead wood in stands will help maintain or increase species diversity of a stand.

Uplean vs. sheltered.—Most large trees have a slight to pronounced lean. We concur with Pike et al. (1975) that in closed forests, position on the trunk relative to the lean has a more pronounced influence on epiphyte communities than the aspect of the position. Ryan (1991), in western British Columbia, found that the lean of trunks influences epiphytes mainly through the interception of precipitation, as opposed to differential stemflow or light. This contrasting environment produces the well-known contrast in lichen communities: the sheltered side with a thin community rich in Caliciales and leprose lichens, with the upper side often heavy with macroepiphytes. At our study site, *Chaenotheca brunneola* and *Lepraria* spp had the strongest association with the lower sheltered side, with a similar but weaker tendency shown by *Hypocenomyce friesii* and *Lopadium disciforme.* Many other species occur in this habitat but were too infrequent to demonstrate their association statistically. Associated with the upper side of leaning trunks were *Cladonia squamosa* var. *subsquamosa, C. transcendens, Ochrolechia oregonensis, Cephalozia lunulifolia, Dicranum fuscescens,* and *Scapania bolanderi.*

Treetops.—More species of epiphytes showed a distinct association with the very tops of trees (within two m of the top) than any other single habitat in the forest. This is particularly noteworthy as we found no mention of this phenomenon in the literature and it is one of the most inaccessible habitats to ground-based or climbing studies. Furthermore, treetops represent a tiny proportion of the total habitat in the forest. Some species were most frequent on dead tree tops while others were more abundant in the living tops. We hypothesize that treetops develop a distinctive epiphyte community because they are so frequently visited by birds (D. Shaw and others, unpubl. data). Birds influence epiphyte communities by bringing propagules on their feet and increasing local nutrient availability through deposition of feces.

We found a remarkable mixture of species at the very tops of the trees, including the rare *Tholurna*

dissimilis; the nitrophilous and weedy *Candelaria concolor, Hypogymnia tubulosa,* and *Parmelia sulcata*; species of exposed habitats such as *Letharia vulpina, Melanelia elegantula, Melanelia exasperatula,* and tufted *Usnea*; numerous alectorioid species, some of which are broadly common in the canopy (*Alectoria sarmentosa* and *Bryoria friabilis*), others more infrequent in the canopy as a whole (*Alectoria vancouverensis, Bryoria* "mystery olive species", *Bryoria pseudofuscescens*); and species broadly distributed in the canopy but with distinct peaks in abundance on the treetops, including *Platismatia glauca* and *P. herrei.*

Some of the treetop associates were more frequent on wood (especially *Alectoria sarmentosa, Bryoria pseudofuscescens,* and *Letharia vulpina*) while others were more frequent on bark on living stems (*Bryoria friabilis, Lecanora circumborealis,* and *Parmelia sulcata*).

Scope.—Which of our results are likely to vary from stand to stand in the Pacific Northwest and which are likely to extend to a broad spectrum of forests? Certainly the particular species found in particular microhabitats, the overall abundance of particular species, and the sharpness of contrasts between various habitat classes will vary among coastal forests of the Pacific Northwest. Climate, succession, geographic variability, disturbance history, landscape context, and variation in stand structure combine to make every stand unique.

The conclusions (in some cases hypotheses) most likely to apply to a broad range of forests in the Pacific Northwest include:

—Height in the canopy, twig vs. branch vs. trunk, position relative to lean, wood vs. bark, and host species are all strongly related to epiphyte communities. Of these, height in the canopy is the strongest factor.

—Old treetops of the dominant conifers have distinctive communities, presumably because frequent bird perching leads to high arrival rates of propagules and elevated nutrient levels in this exposed environment.

—Species diversity is highly variable, even within strata and stem classes. Of the measured factors only height in the canopy showed strong relationships to species richness, the lowest stratum having about half of the species per sample unit as the middle and upper strata.

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