Epiphyte communities on redwood (*Sequoia sempervirens*) in northwestern California

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Abstract. We used rope techniques to access epiphyte communities on nine large and structurally complex redwoods (*Sequoia sempervirens*) occupying old-growth forest reserves of northwestern California. All species of epiphytic lichens, bryophytes and vascular plants were recorded, biomass of dominant vascular epiphytes (*Polypodium scouleri* and *Vaccinium ovatum*) was quantified, and tree crowns were mapped to estimate substrate surface areas. We employed a flexible, plot-based sampling regime defined by available microhabitats within height strata to search for epiphytes. All substrates were examined, including tree surfaces, canopy soils and perennially exposed surfaces of epiphytic vascular plants as well as forest floor vegetation, woody debris and terrestrial soils beneath the redwood crowns. Combined arboreal and terrestrial search efforts revealed 282 species, including 183 lichens, 50 bryophytes and 49 vascular plants. Beta diversities for plots aggregated by floristic group, stratum and substrate type were generally high, indicating a large proportion of infrequent species. Indirect ordination analysis suggested that an environmental gradient from exposed to sheltered habitats was the strongest factor controlling epiphyte community structure. Floristic groups, strata and substrates were highly segregated along the dominant compositional gradient. Chlorolichens, upper crown strata and redwood foliage occupied one end, while vascular plants, forest floor strata and terrestrial woody debris occupied the other end of the gradient. Indicator Species Analyses revealed that many species expressed affinities for particular substrates, including live vs. dead foliage, bark of small vs. large branches and limbs, bark of upper vs. lower surfaces of large limbs, bark of large trunks, bare wood, bryophyte mats, soils, non-redwood stems and terrestrial woody debris. Cluster Analysis identified seven groups of species with similar patterns of distribution across height strata and substrate types. Correlations between tree structure and species distribution suggested that structural complexity promoted epiphyte diversity within height strata. Surface areas of small live trunks, limbs and dead trunks were the best predictors of lichen species richness, *Polypodium scouleri* biomass and *Vaccinium ovatum* biomass, respectively. At least one new species (*Calicium* sp. nov.) was discovered, and two species (*Buxbaumia piperi*, *Icmadophila ericetorum*) normally restricted to terrestrial habitats were found as canopy epiphytes for the first time.

Keywords. *Sequoia sempervirens*, redwood, tree structure, old-growth forest, epiphyte, bryophyte, lichen, community ecology, California.

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Earth's tallest, largest and oldest trees occur in western North America, where temperate forests often exceed 60 m in height. From Alaska to Oregon, the majority of tall coastal forests are dominated by Douglas-fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*) or western hemlock (*Tsuga heterophylla*), living individuals of which grow to 99, 97 and 78 m tall and contain as much as 349, 337 and 141 m^3 of wood, respectively (Van Pelt 2001). In California, coastal forests are mostly dominated by redwood (*Sequoia sempervirens*), the world's tallest and second most massive species. In addition to achieving heights over 115 m and volumes over 1205 m^3 (Sillett unpubl.), redwood possesses more decay- and fire-resistance and, thus, greater longevity than other tree species in these forests (Sawyer et al. 2000). These characteristics of redwood promote higher crown-level structural complexity than is possible in other conifers (Van Pelt 2001), which has important consequences for biodiversity in the forest canopy (Sillett & Antoine 2004; Sillett & Van Pelt 2007).

Trees accumulate structural complexity over time in response to injuries from fire, wind and fungi. Shoots arising from broken main trunks may turn upwards and become new trunks through a process known as reiteration (Hallé et al. 1978). Large, old conifers often have dozens to hundreds of reiterated trunks arising from the main trunk, other reiterated trunks and limbs (Sillett & Van Pelt 2000a, b; Van Pelt 2001). Limbs, defined as branches bearing reiterated trunks (Van Pelt et al. 2004), become the thickest horizontal surfaces in tree crowns because their growth is fueled by foliage on the trunks they support (Sillett & Van Pelt 2007). In old-growth conifer forests, concavities atop broken trunks, crotches between multiple trunks, and the broad, upper surfaces of limbs often accumulate organic litter that develops into soils, which store water and support epiphytic ferns, shrubs and even trees (Enloe et al. 2006; Sillett 1999). These vascular plants provide additional habitats for smaller epiphytes growing on their perennially exposed surfaces (Jarman & Kantvilas 1995). Furthermore, large tree branches are frequently covered by mat-forming mosses that harbor other epiphytes, including cyanolichens, liverworts and the deciduous fern *Polypodium glycyrrhiza* (Ellyson & Sillett 2003; Lovelace 2003; Sillett 1995).

Epiphytes are clearly an important component of coastal forests in western North America, where individual trees can support hundreds of kg of epiphytic material (Ellyson & Sillett 2003; Sillett & Bailey 2003), and individual forest stands can contain over 100 species (McCune et al. 2000; Pike et al. 1975). Epiphyte communities in these forests are structured along environmental gradients in the canopy (Ellyson & Sillett 2003; Lyons et al. 2000; McCune et al. 2000; Pike et al. 1977; Sillett 1995) as well as through time as forests age (McCune 1993). Epiphytes are also affected by substrate qualities, including stability, texture, chemistry and angle of inclination which influences water-holding capacity (Barkman 1958; Carlsen 2000; Ellyson & Sillett 2003; Glime & Hong 2002; Heitz & Heitz-Seifert 1995; Holien 1998; Johansson 1974; Kenkel & Bradfield 1986; Kuusinen 1996; Liu et al. 2000; Malizia 2003; McCune et al. 2000; Pike et al. 1975; Ryan 1991; Sillett et al. 2000a), but the extent to which these factors contribute to community structure within tree crowns is poorly understood.

Given their extreme size, age and structural complexity, large redwood trees provide an ideal setting for an investigation of tree structure and its potential effects on epiphytes. We used rope techniques to explore trees in old-growth redwood forest reserves of northwestern California in order to identify the most important factors affecting epiphytes within their crowns. Our sampling design allowed detection of nearly all species of lichens, bryophytes and vascular plants occurring within the space occupied by individual trees, and our quantification of tree structure allowed us to examine relationships between substrate availability and species richness. We had the following specific objectives in this investigation of epiphytes on redwood: 1) to provide a flora of lichens, bryophytes and vascular plants, 2) to define dominant environmental gradients structuring epiphyte communities and 3) to link microhabitat type and substrate availability to patterns of epiphyte distribution. This study thus provides the first comprehensive, community-level description of epiphytes on redwood.

MATERIALS AND METHODS

Study Areas. Nine large redwood trees were selected for detailed study, three each in Jedediah

Smith Redwoods State Park (JSRSP), Prairie Creek Redwoods State Park (PCRSP) and Humboldt Redwoods State Park (HRSP), California (latitudes 41.8°, 41.4°, and 40.3° N, respectively). All trees occurred between 37 and 103 m elevation on alluvial terraces of major creeks. Annual rainfall in these forests ranged from 1.5 to 2.5 m with over 95% of this occurring from November to May, and air temperatures ranged from −1 to 28°C during the winter and from 7 to 39°C during the summer (www.parks.ca.gov; Sillett unpubl.). Temperatures in HRSP, the driest and farthest inland of the study areas, averaged 10–15°C higher in the summer than in the other parks, which were farther north and closer to the Pacific Ocean.

Redwoods overwhelmingly dominated the vegetation in the study areas, accounting for over 95% of the basal area (Sillett & Van Pelt 2007; Van Pelt & Franklin 2000). In JSRSP and PCRSP, a number of other conifers (i.e., Douglas-fir, Sitka spruce, western hemlock and *Chamaecyparis lawsoniana*) occasionally occurred as canopy trees, and the understory was dominated by angiosperm trees (i.e., *Acer macrophyllum*, *Lithocarpus densiflorus* and *Umbellularia californica*) and shrubs (i.e., *Acer circinatum*, *Gaultheria shallon*, *Rubus spectabilis*, *Vaccinium ovatum* and *Vaccinium parvifolium*) as well as the fern *Polystichum munitum*. In HRSP, redwood was the only upper canopy tree, although some *U. californica*, *L. densiflorus* and *Taxus brevifolia* occurred in the lower canopy, and a sparse understory included *P. munitum*, *Corylus cornuta* and *Sambucus racemosa*.

Tree Selection and Access. Large, structurally complex redwoods supporting well-developed epiphyte communities were favored over small trees with simple structure. To maximize safety, we avoided specimens with declining crowns and emergent, dead spires. Likewise, excessively leaning trees were not considered. All trees selected were named to facilitate their recognition during fieldwork and to provide ties to other research on these trees.

Rope techniques provided access to all portions of study trees. Trees were initially rigged using a compound hunting bow equipped with a spinning reel to launch a fiberglass, rubber-tipped arrow trailing Fireline® over a cluster of robust branches, limbs and/or crotches between trunks. A 3 mm nylon cord followed by a 10 mm static rope was then pulled through the crown. One end of the rope was anchored at ground level, allowing the other end to be climbed via single rope technique (Perry 1978). An 18 m-long, split-tail lanyard (Jepson 2000) constructed of 12 mm arborist rope facilitated movement to outer crown positions and provided access to the treetop above the height of the initial bow shot. Climbing paths were then established along opposite sides of the main trunk from near the treetop all the way to ground level. Nylon cord threaded through a pulley secured near the treetop was used to raise and lower the climbing rope at the beginning and end of a research day.

Tree Structure and Vascular Epiphyte Mapping. Tree structure was mapped by measuring the main trunk and all reiterated trunks greater than 5 cm basal diameter. Main trunk diameters were measured at 5 m intervals, except for their flared bases which required measurements at tighter intervals to capture the rapid and often abrupt changes in diameter. Branches, limbs and structural anomalies (e.g., burls and fusions between stems) often impeded the path of measuring tapes, so we measured both above and below these obstructions to maintain accuracy. For reiterated trunks we measured diameter, height above ground, and distance and azimuth from reference trunk at basal and terminal positions as well as at 5 m intervals along their lengths. As with main trunks, any obstructions and abrupt changes in diameter warranted tighter measurement intervals. For partly or wholly dead trunks, we also recorded the percentage of bare wood at each measurement interval. Thus, measurements delineated all trunks into segments that were each modeled as a regular conic frustum whose dead proportion could be calculated. We also noted whether the top of each trunk was intact versus broken. Since limbs gave rise to reiterated trunks, we included them in the structural mapping as well. Limb heights and basal diameters were measured along with path lengths between trunks, which allowed them to be modeled as regular conic frusta. Reiterated trunks originating from other supporting trunks frequently formed buttresses (i.e., ridge-like swellings of compression wood) that continued down and tapered into their supporting trunks. Buttresses were modeled as inverted cones whose bases were equal in diameter to

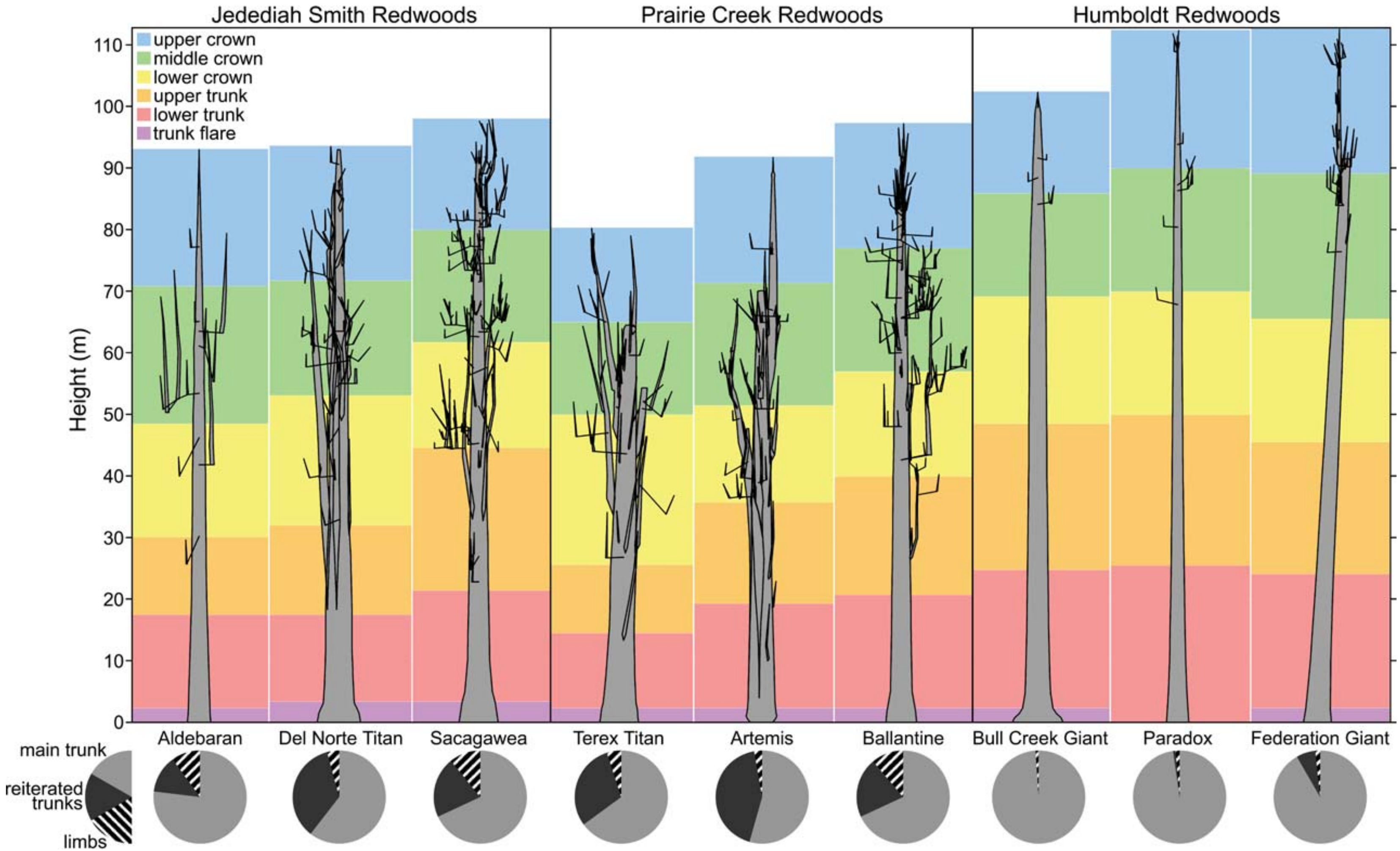


Figure 1. Structure and stratification of nine redwoods sampled in three different redwood state parks, northwestern California, U.S.A. Each diagram displays an undistorted view of a tree's main trunk and all reiterated trunks. Black horizontal lines represent limbs supporting reiterated trunks. Branches are not shown. Colored horizontal bands delineate tree strata. Pie charts display surface area proportions of trunks and limbs.

Table 1. Summary of plot types by stratum for an analysis of community composition of old-growth redwood forests. Lower versus upper refers to the overhanging bottom versus upward-facing top surfaces of branches and limbs. Foliage is defined as leaves plus the stem axis to which they are attached. Soil is defined as accumulations of partially decayed, detached organic material less than 1 cm diameter, whereas woody debris is detached organic material greater than 1 cm diameter. Splash zones refer to moist areas beneath deep soil accumulations. Terrestrial redwood plots consist of smaller redwoods growing from soil beneath study trees. Numerical ranges indicate diameter classes (cm). Numbers left of plot types indicate substrate groups used in analyses: 1 = bare wood; 2 = charcoal; 3 = bark, branches & limbs <50; 4 = bark, limbs >50, lower; 5 = bark, limbs >50, upper; 6 = bark, trunks <100; 7 = bark, trunks <100; 8 = foliage, dead; 9 = foliage live; 10 = bryophytes; 11 = soils; 12 = non-redwood leaves; 13 = non-redwood stems; 14 = terrestrial woody debris.

Upper Crown	**Middle Crown**	**Lower Crown**	**Upper Trunk**
Redwood	Redwood	Redwood	Redwood
1 bare wood, branches & limbs, lower	1 bare wood, branches & limbs, lower	1 bare wood, branches & limbs, lower	1 bare wood, branches & limbs, lower
1 bare wood, branches & limbs, upper	1 bare wood, branches & limbs, upper	1 bare wood, branches & limbs, upper	1 bare wood, branches & limbs, upper
2 bare wood, burnt	2 bare wood, burnt	2 bare wood, burnt	2 bare wood, burnt
1 bare wood, knot holes	1 bare wood, knot holes	1 bare wood, knot holes	1 bare wood, knot holes
1 bare wood, trunks	1 bare wood, trunks	1 bare wood, trunks	1 bare wood, trunks
3 bark, branches & limbs <10	3 bark, branches & limbs <10	3 bark, branches & limbs <10	3 bark, branches & limbs <10
3 bark, branches & limbs 10–50, lower	3 bark, branches & limbs 10–50, lower	3 bark, branches & limbs 10–50, lower	3 bark, branches & limbs 10–50, lower
3 bark, branches & limbs 10–50, upper	3 bark, branches & limbs 10–50, upper	3 bark, branches & limbs 10–50, upper	3 bark, branches & limbs 10–50, upper
4 bark, limbs >50, lower	4 bark, limbs >50, lower	4 bark, limbs >50, lower	4 bark, limbs >50, lower
5 bark, limbs >50, upper	5 bark, limbs >50, upper	5 bark, limbs >50, upper	5 bark, limbs >50, upper
2 bark, burnt	7 bark, burl	7 bark, burl	7 bark, burl
6 bark, trunks <10	2 bark, burnt	2 bark, burnt	2 bark, burnt
6 bark, trunks 10–100	7 bark, splash zone	7 bark, splash zone	7 bark, splash zone
7 bark, trunks >100	6 bark, trunks <10	6 bark, trunks <10	6 bark, trunks <10
8 foliage, dead	6 bark, trunks 10–100	6 bark, trunks 10–100	6 bark, trunks 10–100
8 foliage, live	7 bark, trunks >100	7 bark, trunks >100	7 bark, trunks >100
	8 foliage, dead	8 foliage, dead	8 foliage, dead
Epiphytic substrates	8 foliage, live	8 foliage, live	8 foliage, live
10 bryophytes			
11 humus	Epiphytic substrates	Epiphytic substrates	Epiphytic substrates
12 *Gaultheria shallon*, leaves	10 bryophytes	10 bryophytes	10 bryophytes
13 *Gaultheria shallon*, stems	11 humus	11 humus	11 humus
12 *Polypodium scouleri*, leaves	11 humus, splash zone	12 *Lithocarpus densiflorus*, leaves	11 humus, splash zone
12 *Pseudotsuga menziesii*, leaves	12 *Gaultheria shallon*, leaves	13 *Lithocarpus densiflorus*, stems	12 *Polypodium scouleri*, leaves
13 *Pseudotsuga menziesii*, stems	13 *Gaultheria shallon*, stems	12 *Polystichum munitum*, leaves	12 *Vaccinium ovatum*, leaves
12 *Tsuga heterophylla*, leaves	12 *Picea sitchensis*, leaves	12 *Polypodium scouleri*, leaves	13 *Vaccinium ovatum*, stems
13 *Tsuga heterophylla*, stems	13 *Picea sitchensis*, stems	13 *Rhamnus purshiana*, stems	
12 *Vaccinium ovatum*, leaves	12 *Polypodium scouleri*, leaves	13 *Ribes laxiflorum*, stems	
13 *Vaccinium ovatum*, stems	12 *Tsuga heterophylla*, leaves	12 *Tsuga heterophylla*, leaves	
13 *Vaccinium parvifolium*, stems	13 *Tsuga heterophylla*, stems	13 *Tsuga heterophylla*, stems	
	12 *Vaccinium ovatum*, leaves	12 *Vaccinium ovatum*, leaves	
	13 *Vaccinium ovatum*, stems	13 *Vaccinium ovatum*, stems	
	13 *Vaccinium parvifolium*, stems	13 *Vaccinium parvifolium*, stems	

Table 1. Continued.

Lower Trunk	Trunk Flare	Terrestrium	Terrestrium (continued)
Redwood	Redwood	Redwood	Vascular plants
1 bare wood, branches & limbs, lower	2 bare wood, burnt	1 bare wood, branches & limbs, lower	13 *Acer circinatum*, stems
1 bare wood, branches & limbs, upper	1 bare wood, trunks	1 bare wood, branches & limbs, upper	13 *Acer macrophyllum*, stems
2 bare wood, burnt	3 bark, branches & limbs <10	1 bare wood, trunks	12 *Athyrium filix-femina*, leaves
1 bare wood, trunks	7 bark, burl	3 bark, branches & limbs <10	12 *Blechnum spicant*, leaves
3 bark, branches & limbs <10	2 bark, burnt	7 bark, burl	13 *Corylus cornuta*, stems
3 bark, branches & limbs 10–50, lower	7 bark, trunks >100	2 bark, burnt	12 *Dryopteris expansa*, leaves
3 bark, branches & limbs 10–50, upper	8 foliage, dead	6 bark, trunks <10	12 *Gaultheria shallon*, leaves
7 bark, burl	8 foliage, live	6 bark, trunks 10–100	13 *Gaultheria shallon*, stems
2 bark, burnt		7 bark, trunks >100	12 *Selaginella oregana*, leaves
6 bark, trunks <10	Epiphytic substrates	8 foliage, dead	12 *Lithocarpus densiflorus*, leaves
6 bark, trunks 10–100	10 bryophytes	8 foliage, live	13 *Lithocarpus densiflorus*, stems
7 bark, trunks >100	11 humus		12 *Picea sitchensis*, leaves
8 foliage, dead	13 *Acer circinatum*, stems	Course woody debris	13 *Picea sitchensis*, stems
8 foliage, live	12 *Athyrium filix-femina*, leaves	14 hardwood, bare wood, lower	12 *Polystichum munitum*, leaves
	12 *Dryopteris expansa*, leaves	14 hardwood, bare wood, upper	12 *Polypodium scouleri*, leaves
Epiphytic substrates	12 *Gaultheria shallon*, leaves	14 hardwood, bark, lower	12 *Pseudotsuga menziesii*, leaves
10 bryophytes	13 *Gaultheria shallon*, stems	14 hardwood, bark, upper	13 *Pseudotsuga menziesii*, stems
11 humus	12 *Lithocarpus densiflorus*, leaves	14 *Pseudotsuga menziesii*, bare wood, upper	13 *Rhododendron occidentale*, stems
13 *Rhododendron occidentale*, stems	13 *Lithocarpus densiflorus*, stems	14 *Pseudotsuga menziesii*, bark, upper	13 *Rhamnus purshiana*, stems
12 *Vaccinium ovatum*, leaves	12 *Picea sitchensis*, leaves	14 *Sequoia sempervirens*, bare wood, lower	13 *Rosa gymnocarpa*, stems
13 *Vaccinium ovatum*, stems	13 *Picea sitchensis*, stems	14 *Sequoia sempervirens*, bare wood, upper	13 *Rubus leucodermis*, stems
13 *Vaccinium parvifolium*, stems	12 *Polystichum munitum*, leaves	14 *Sequoia sempervirens*, bark, lower	13 *Rubus spectabilis*, stems
	12 *Polypodium scouleri*, leaves	14 *Sequoia sempervirens*, bark, upper	12 *Rubus ursinus*, leaves
	13 *Rhododendron occidentale*, stems	14 *Tsuga heterophylla*, bare wood, lower	13 *Rubus ursinus*, stems
	13 *Ribes laxiflorum*, stems	14 *Tsuga heterophylla*, bare wood, upper	13 *Sambucus racemosa*, stems
	13 *Rubus spectabilis*, stems	14 *Tsuga heterophylla*, bark, lower	13 *Toxicodendron diversilobum*, stems
	12 *Rubus ursinus*, leaves	14 *Tsuga heterophylla*, bark, upper	12 *Tsuga heterophylla*, leaves
	13 *Rubus ursinus*, stems		13 *Tsuga heterophylla*, stems
	13 *Toxicodendron diversilobum*, stems	Bryophytes and soils	12 *Umbellularia californica*, leaves
	12 *Tsuga heterophylla*, leaves	10 bryophytes	13 *Umbellularia californica*, stems
	13 *Tsuga heterophylla*, stems	11 humus and mineral soil	12 *Vaccinium ovatum*, leaves
	12 *Vaccinium ovatum*, leaves		13 *Vaccinium ovatum*, stems
	13 *Vaccinium ovatum*, stems		13 *Vaccinium parvifolium*, stems
	13 *Vaccinium parvifolium*, stems		

their trunks of origin and whose apices were located at their points of disappearance into their supporting trunks. Buttress totals were added to their trunks of origin. In field notebooks, we sketched some portions of crown structure to ease comprehension of elaborately reiterated complexes. Measurements were performed with the aid of clinometers, compasses, measuring tapes and Impulse® laser range finders (Laser Technology, Inc.) that accurately measured horizontal and vertical distances between trunks. Architectural diagrams were generated in Microsoft Excel®, and a macro was used to rotate each diagram 360° so that data could be error-checked (see Sillett & Van Pelt 2007 for details). One view of each tree was chosen for display (**Fig. 1**).

We mapped the locations of all vascular epiphytes by measuring their heights above ground and distances and azimuths from reference trunks. Since *Polypodium scouleri* fern mats and *Vaccinium* shrubs were particularly common, and equations that predicted their dry mass from easily measured variables were available, we collected additional data for these taxa. For each *P. scouleri* mat, we measured length, width, and average soil depth which allowed mat volume to be modeled as an elliptical cylinder. For each fern mat, we also measured the length of the longest frond from its origin at the supporting rhizome to the tip of its terminal pinna. Measurements were accurate to the nearest cm and allowed prediction of total dry mass, including leaves, stems, roots, soil and associated debris for each mat (Sillett & Bailey 2003). For each *Vaccinium* shrub, we measured stem basal diameter to the nearest mm which allowed prediction of total dry mass, including leaves and stems. Predictive equations were available for *V. parvifolium* (Means et al. 1994) but not *V. ovatum*. This problem was bypassed by combining equations for two similar species of *Vaccinium* (i.e., *V. alaskense* and *V. parvifolium*; Sillett & Van Pelt 2007).

Sampling regime. Study trees were stratified into six strata (i.e., upper crown, middle crown, lower crown, upper trunk, lower trunk and trunk flare) on the basis of height and structure (**Fig. 1**). Initially, the length of each tree above the flared base was divided into five equally thick strata. Using this as a guideline, we adjusted the boundaries between strata according to natural gaps between major reiterated complexes and large spaces between foliage. While the foliated lower crown strata of some trees were easily distinguished from their naked trunk strata, other trees supported foliage and reiterated complexes arising from trunk strata. Thus, the actual crowns of some study trees extended into their trunk strata. Trunk flare strata were delineated at the point of transition between the vertical trunk and its expanded base. One tree's trunk flare stratum was buried in floodplain silt and therefore exempted from sampling. On the ground directly below the crown of each study tree, a terrestrial stratum was established by measuring crown radii at cardinal and sub-cardinal directions from the base of the main trunk, thereby outlining an octagonal area within which sampling was conducted. Terrestrial strata extended to 2 m in height but excluded the study trees around which they were established.

Each stratum was further divided into plots, whose boundaries were defined as the microhabitats and substrates available to epiphytes (**Table 1**). Redwood surfaces were sampled separately from non-redwood surfaces. Within a stratum, redwood trunks were partitioned into <10, 10–100, and >100 cm diameter classes for a total of three plots. Branches and limbs were partitioned into <10, 10–50, and >50 cm diameter classes, with the overhanging bottom versus upward-facing top surfaces considered only for the larger two classes. Since horizontal stems >50 cm diameter always gave rise to reiterated trunks, this class was referred to as "limbs >50". Canopy soil (i.e., accumulations of humus and partially decayed organic debris) comprised one non-redwood plot, while the perennially exposed organs of each species of vascular plant constituted many non-redwood plots. Terrestrial strata included redwood plots that consisted of smaller redwoods growing from soil beneath study trees but excluded the study trees themselves. Woody debris was sampled only from terrestrial strata, where the substrate could easily be distinguished from fresh litterfall on the basis of relative water content and decay. This plot system provided a framework for comprehensive sampling that included all redwood and non-redwood surfaces. From three additional large redwoods, we sampled seven plots representing uncommon microhabitats and substrates that potentially supported distinct epiphyte assemblages. These additional plots included upper crown epiphytic western hemlock stems and leaves (two plots), middle crown splash zone bark and canopy soil (four plots), and lower crown splash zone bark (one plot).

Plots were examined for presence/absence of lichens, bryophytes and vascular plants. We used an "intuitive meander" approach to capture plot-level richness. Within a given plot, search efforts not only targeted species-rich sites, but also sought to span the maximum possible variety of age, angle, hardness, light, moisture, and textural characteristics available within the confines of the microhabitat and substrate that defined the plot. For example, upper crown branches and limbs <10 cm diameter were always examined at many different locations within the stratum, including inner, middle, and outer crown positions, beneath vascular epiphytes, adjacent to soils, around the periphery of bryophyte mats and knot holes, and at bifurcations, junctions, and other anomalies. All plots were thoroughly examined for richness until additional taxa could not be found. Sampling of individual trees required as much as 40 hours on rope.

Lichen litterfall was sampled beneath each study tree to evaluate the effectiveness of arboreal versus terrestrial search strategies. We examined all available surface area within the boundaries of trunk flare and terrestrial strata for robust macrolichens as well as microlichen fragments. Litterfall was defined as either thalli without an attachment point or thalli attached to a recently fallen substrate. Vagrant alectorioid lichens draped over vascular plants in terrestrial strata always appeared unhealthy and were thus considered litterfall. We sampled litterfall during winter months following storm pulses to capture the maximum possible richness.

Sampling occurred from September 2002 through January 2003. Species were identified in the field when possible. Small pieces of unknown taxa were collected for laboratory identification, and common but morphologically similar species were lumped into species groups, resulting in a taxonomic resolution that was achievable during fieldwork (**Appendix A**). Vouchers were deposited at HSC and the herbarium of Redwood National and State Parks. Nomenclature of liverworts, mosses, lichens, and vascular plants followed Stotler and Crandall-Stotler (1977), Norris and Shevock (2004), Esslinger (2006), and Hickman (1996), respectively.

Data Analyses. The raw binary data matrix consisted of 976 rows (plots) and 235 columns (taxa identifiable in the field, excluding lichen litterfall). Prior to all multivariate analyses, we removed taxa occurring in less than 3% of the plots as well as plots containing less than three taxa. These removals reduced noise from infrequent taxa and plots that provided little community information, whittling the dataset to 643 plots and 63 taxa. Non-metric multidimensional scaling (NMS; Kruskal 1964; Mather 1976), using a random starting configuration and Sørensen distances to express community relationships, was performed on a Beals-smoothed dataset. This transformation strengthened extraction of the dominant compositional gradient by assigning a probability of presence of each taxon in a plot based on patterns of co-occurrence of that taxon with other taxa throughout the dataset (McCune 1994b). PC-ORD's (McCune & Mefford 1999) "slow and thorough" autopilot mode used the best of 40 runs with real data and 50 runs with randomized data for a Monte Carlo test of significance (Dwass 1957). We rigidly rotated the resulting scatterplot +45° to load the strongest environmental gradient onto a single axis. Variables from a secondary matrix, including stratum and number of lichen, bryophyte, and vascular plant taxa, were then overlaid onto the NMS scatterplot to help interpret the dominant compositional gradient.

We performed two separate Indicator Species Analyses (ISA; Dufrêne & Legendre 1997; McCune & Mefford 1999) on groups of plots defined by substrate and park to reveal taxa exhibiting affinities for specific substrates or parks. Formation of substrate groups was a two-stage process. First, original plot types (**Table 1**) were aggregated across strata. Second, several of these aggregated plot types were further grouped on the basis of similar substrate characteristics. Overall, 14 substrate groups were formed. ISA produced indicator values based on the faithfulness of species occurrences within groups of plots and the concentrations of species present in those groups. Indicator values were then tested for statistical significance using a Monte Carlo simulation with 1000 randomizations (Dwass 1957).

Table 2. Summary of tree dimensions and abundance of dominant vascular epiphytes of nine large redwoods surveyed for epiphyte community composition in northwestern California.

	Jedediah Smith Redwoods State Park			**Prairie Creek Redwoods State Park**			**Humboldt Redwoods State Park**		
Structural component	**Aldebaran**	**Del Norte Titan**	**Sacagawea**	**Terex Titan**	**Artemis**	**Ballantine**	**Bull Creek Giant**	**Paradox**	**Federation Giant**
diameter at breast height (cm)	395	723	655	658	531	523	677	381	461
height (m)	93.0	93.5	97.9	80.2	91.7	97.2	102.3	112.3	112.5
main trunk area (m^2)	588.5	946.4	809.7	815.3	738.2	727.2	997.2	620.6	787.0
reiterated trunk area (m^2)	101.2	547.5	250.8	376.6	581.2	223.5	1.9	5.3	58.2
dead trunk area (m^2)	0.0	18.1	4.9	109.4	99.3	23.8	4.0	1.5	18.3
limb area (m^2)	76.0	66.0	128.6	63.2	37.3	118.6	10.3	9.5	13.2
main trunk volume (m^3)	374.4	921.3	676.1	874.1	665.2	554.9	880.2	332.9	570.2
reiterated trunk volume (m^3)	10.5	125.5	21.3	63.2	140.3	19.1	0.1	0.1	5.1
dead trunk volume (m^3)	0.0	3.8	0.6	47.1	38.7	5.0	0.7	0.1	6.8
limb volume (m^3)	16.7	7.8	16.7	9.7	4.0	11.8	1.1	0.6	0.8
Vascular epiphyte (kg dry mass)									
Polypodium scouleri	151.4	172.0	460.1	373.0	503.0	139.5	0.0	0.0	0.0
Vaccinium ovatum	5.5	35.1	20.2	72.2	74.7	10.9	0.0	0.0	5.9
Vaccinium parvifolium	0.0	0.8	0.1	1.4	0.1	0.0	0.0	0.0	0.0

Stepwise multiple regression analysis was used to assess relationships between tree structure and epiphyte distribution. We defined structural variables similarly to the way groups of substrates were defined for ISA, including surface area and volume of live trunks <100 cm, live trunks >100 cm, and live limbs >50 cm diameter as well as surface area and volume of dead trunks for all tree strata. Structural data were further partitioned by stratum ($n = 53$). Since many trunks and limbs passed through the boundaries between strata, we interpolated diameters as well as azimuths and distances from reference trunks at these boundaries and then calculated surface areas and volumes for the new segments. Epiphyte richness was calculated separately for each substrate type whose availability had been quantified during tree mapping (e.g., tree surface areas and dry masses of dominant vascular epiphytes). Some of the correlations were strengthened by improving the linearity of relationships through square-root and cube-root transformations.

A cluster analysis, which employed Ward's method of clustering (Wishart 1969) and a Euclidean distance matrix, of the transposed community matrix was used to identify groups of taxa sharing similar distributions (McCune & Mefford 1999). In order to discourage the clustering of frequent taxa, data were first relativized by species sums of squares. Wishart's objective function converted to a percentage of information remaining scaled the resulting dendrogram.

Results

Habitat Structure. The nine redwoods ranged between 80.2–112.5 m tall, 381–723 cm diameter at breast height, and contained 333.6–1054.6 m^3 of wood (**Table 2**). The trees in HRSP were generally taller and structurally simpler than those in PCRSP and JSRSP, where as many as 137 reiterated trunks were encountered on a single tree (**Fig. 1**). Individual trees supported a tremendous quantity of surface area, including as much as 946 m^2 of main trunks, 581 m^2 of reiterated trunks, 109 m^2 of dead trunks, and 129 m^2 of limbs (**Table 2**). Bare wood was an abundant component of all crown strata, and burnt bark and wood were encountered in every tree. Canopy soil accumulations were common, and 18 species of vascular epiphytes presented perennially exposed surfaces. Terrestrial strata offered abundant woody debris and 25 species of terrestrial vascular plants with perennially exposed surfaces. Thus, these trees provided a diverse array of microhabitats and substrates available to epiphytes. Overall, 976 plots distributed across 69 plot types were surveyed (**Table 1**).

Species Diversity. We encountered 282 taxa, including 183 lichens, 20 liverworts, 30 mosses and 49 vascular plants (**Appendix A**). Lichens were particularly frequent, furnishing 65% of overall species richness as well as 66% of the total species occurrences. However, cyanolichens were scarce, contributing less than 1% of the total species occurrences. Approximately one third of all taxa occurred in less than 3% of the plots, while the most frequent species group was the lichen *Lepraria lobificans*, which occurred in 58% of the plots, and the most frequent species was the moss *Isothecium stoloniferum*, which occurred in 41% of the plots. Epiphytic *Polypodium* ferns and *Vaccinium* shrubs were abundant, especially in JSRSP and PCRSP. One tree (Artemis) held an estimated 503.0 kg dry mass of *Polypodium scouleri* mats and 74.7 kg of *Vaccinium* shrubs (**Table 2**).

Several normally terrestrial species occurred as epiphytes high in the crowns of some redwoods in JSRSP and PCRSP. The microlichen *Icmadophila ericetorum* stained the bark surface of a large trunk in one upper crown stratum. *Buxbaumia piperi*, a saprophytic moss, grew from decaying wood in the middle crown of a complex tree (Terex Titan). Splash zones from middle crown to upper trunk strata supported the moss *Pseudotaxiphyllum elegans*. Soil perched on a large limb in the lower crown of one redwood (Aldebaran) supported a *Polystichum munitum* fern. The conifers *Picea sitchensis*, *Pseudotsuga menziesii*, and *Tsuga heterophylla* occupied soil-filled concavities formed by large broken trunks in several upper and middle crown strata. The angiosperms *Gaultheria shallon*, *Lithocarpus densiflorus*, *Rhamnus purshiana* and *Ribes laxiflorum* exploited soil accumulations in many crown strata. Finally, a single occurrence of the grass *Poa* sp. formed a small vegetative turf in the knot hole of a dead branch at 78 m.

Variability in richness was quite high, averaging 8.4 taxa per plot with a standard deviation of 9.3 taxa (**Table 3**). Beta diversity was also high, especially for both cyanolichens and vascular plants, indicating a large proportion of infrequent species for those groups. Some of this variation was attributed to stratum. Crown strata carried the most richness with upper crowns averaging over 15 epiphyte taxa per plot and supporting a total of 142 taxa. Trunk strata held the least richness with lower trunks holding only 39 taxa and trunk flare strata supporting an average richness of less than four taxa. Terrestrial plots were variably rich, supporting 108 taxa and high beta diversity. Some of the variation in species richness was also attributed to substrate. Dead redwood foliage and bark of small branches and limbs supported many taxa, while live foliage and bark on the bottom of large branches and limbs carried few taxa. Likewise, non-redwood stems were rich with epiphytes, while non-redwood leaves were relatively desolate.

Community Composition. Epiphyte communities changed dramatically along the vertical gradient. NMS ordination on the Beals-smoothed dataset suggested a 2-dimensional configuration that described over 98% of the variation in community structure and represented a substantial reduction in stress compared to randomized data (5 vs. 37). After rotation, 93.3% of the variation was expressed along Axis 1, and plot scores were negatively correlated with stratum height ($r = -0.72$). Lichen richness ($r = -0.74$) was also negatively correlated with plot scores along Axis 1, and lichens as a group had a low average species score on Axis 1 (0.08). Species richness of bryophytes ($r = 0.26$) and vascular plants ($r = 0.34$) were positively correlated with plot scores along Axis 1, and both groups possessed higher average species scores (0.41 and 0.50, respectively) than lichens.

To facilitate interpretation of the compositional gradient, we grouped plots by floristic group, stratum, and substrate and then ranked the groups according to their average plot scores on Axis 1 (**Fig. 2**). Floristic groups included all species belonging to plots for which we had plot scores, thus incorporating most of the species that were removed prior to the NMS analysis and allowing a more detailed portrayal of floristic group positions on Axis 1. Floristic groups were highly organized on this axis; chlorolichens and vascular plants occupied opposite ends while cyanolichens and bryophytes were intermediate. Strata were ordered on Axis 1 along a vertical gradient from upper crown to terrestrial strata. Plots grouped by substrate demonstrated that redwood foliage and bark

Table 3. Average richness and beta diversity for plots aggregated by floristic groups, strata and substrates present in old-growth redwood forests. Substrates represent groups of plot types (see Table 1), five of which include numerical ranges that indicate diameter classes (cm). Beta diversity was calculated as the number of taxa divided by the average species richness. Values are based on the taxonomic resolution exercised during fieldwork. Lichen litterfall data are excluded.

Group	# Plots	Average richness ± S.D.	Beta diversity	# Taxa
Floristic group	976			
all taxa		8.4 ± 9.3	27.8	235
lichens		5.6 ± 8.1	25.5	143
chlorolichens		5.5 ± 7.9	23.0	126
cyanolichens		0.1 ± 0.5	230.4	17
bryophytes		2.5 ± 2.5	17.5	43
liverworts		0.7 ± 1.2	20.2	15
mosses		1.7 ± 1.7	16.4	28
vascular plants		0.4 ± 1.7	110.4	49
Stratum				
upper crown	177	15.6 ± 13.2	9.1	142
middle crown	184	11.5 ± 9.7	10.8	124
lower crown	168	8.0 ± 6.9	13.8	110
upper trunk	102	5.1 ± 4.8	11.6	59
lower trunk	66	4.6 ± 3.6	8.5	39
trunk flare	92	3.7 ± 4.4	16.4	60
terrestrium	187	4.6 ± 5.8	23.3	108
Substrate				
bare wood	127	12.8 ± 10.7	8.9	114
charcoal	20	5.7 ± 5.3	6.5	37
bark, branches, & limbs <50	110	17.3 ± 13.0	6.3	109
bark, limbs >50, lower	21	3.9 ± 2.4	4.4	17
bark, limbs >50, upper	19	8.1 ± 4.1	5.1	41
bark, trunks <100	68	11.6 ± 8.3	7.1	82
bark, trunks >100	117	8.5 ± 3.7	7.8	66
foliage, dead	44	15.2 ± 10.6	5.5	83
foliage, live	44	1.4 ± 1.1	7.3	10
bryophytes	62	5.3 ± 4.1	9.0	48
soils	56	7.2 ± 6.3	10.3	74
non-redwood leaves	119	0.3 ± 0.6	40.8	12
non-redwood stems	118	6.7 ± 9.1	17.9	120
terrestrial woody debris	51	6.2 ± 5.3	6.3	39

of small stems occupied one end of the axis, while soils and terrestrial woody debris occupied the other end. Comparing the relative positions of floristic groups with strata and substrates on Axis 1 (**Fig. 2**) suggested that the compositional gradient was driven by an underlying environmental gradient that extended from habitats exposed to wind and sunlight to habitats sheltered from desiccation. Thus, we interpreted Axis 1 as a gradient from exposed to sheltered habitats. Axis 2 was uninterpretable.

Two separate Indicator Species Analyses performed on groups of taxa defined by substrate and park revealed habitat preferences (**Fig. 3**). The most preferred substrate was dead redwood foliage, which was reliably occupied by four microlichens, three foliose chlorolichens, two alectorioid lichens, and one liverwort, whereas live redwood foliage was preferred by only alectorioid lichens. Redwood bark was preferred by seven lichens and bryophytes, while bare wood was preferred by only one lichen. All four vascular plants included in the analysis showed affinities for soils, and terrestrial woody debris was preferred by six bryophytes. Humboldt Redwoods State Park offered environmental conditions that were

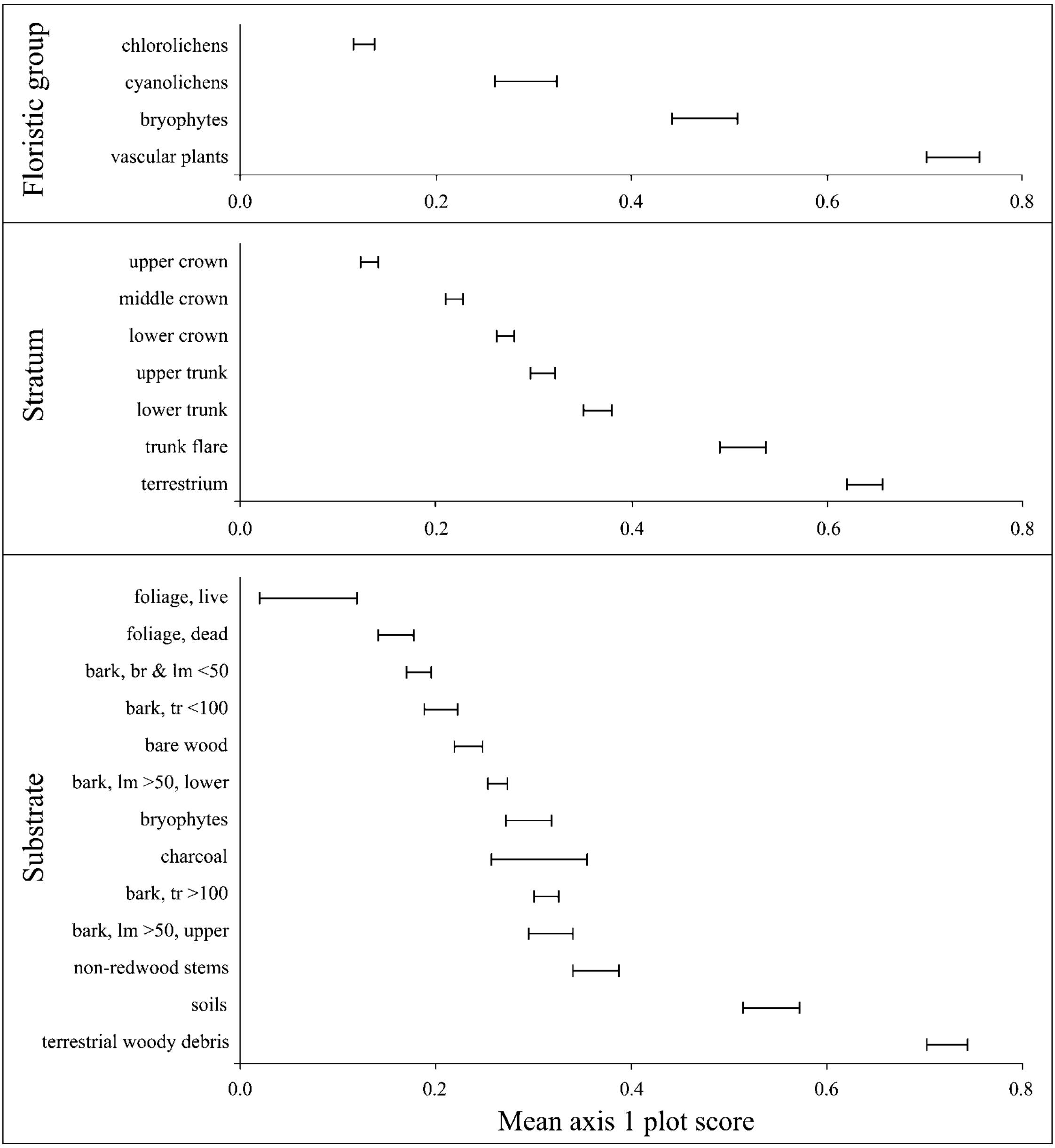
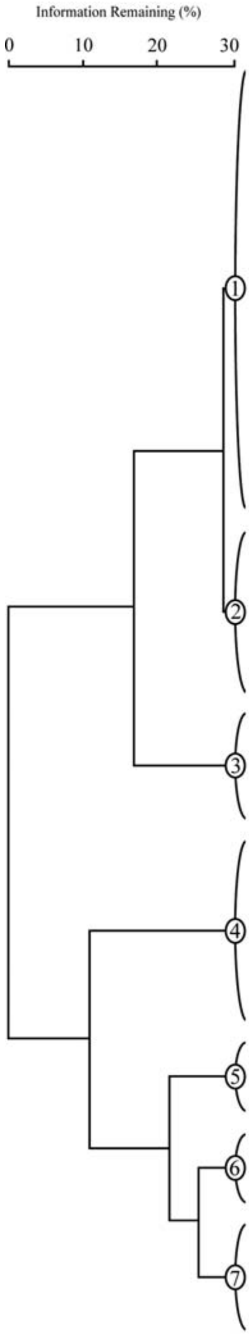


Figure 2. Plots ranked by scores along non-metric multidimensional scaling (NMS) Axis 1 were grouped by floristic group, stratum and substrate to facilitate interpretation of an environmental gradient structuring epiphyte communities in old-growth redwood forests. Substrates represent groups of plot types (see Table 1), five of which include numerical ranges that indicate diameter classes (cm). Plots composing "non-redwood leaves" each contained less than three taxa and were thus excluded from the NMS analysis (see Methods) and this figure. Values are mean plot scores ± one standard error. Lichen litterfall data are excluded. Substrate abbreviations: br = branches, lm = limbs, tr = trunks.

favored by 19 species, while nine and seven species exhibited affinities for PCRSP and JSRSP, respectively.

Stepwise multiple regression analysis elucidated relationships between tree structure and epiphyte distribution. Lichen richness was correlated with square-root transformed surface area of live trunks <100 cm diameter (adjusted $R^2 = 0.52$, $p < 0.0001$). Cube-root-transformed mass of *Polypodium scouleri* mats was predicted by square-root transformed surface area of limbs (adjusted $R^2 = 0.62$, $p < 0.0001$),



			Frequency (%)							ISA (p < 0.01)	
Taxon	Floristic group	NMS axis 1	Upper crown	Middle crown	Lower crown	Upper trunk	Lower trunk	Trunk flare	Terrestrium	Substrate preference	Geographic preference
Parmelia hygrophila	L	0.00	66	28	6	0	0	0	0	bark, br & lm <50	
Usnea longissima	L	0.00	47	27	23	0	0	3	0	foliage, live	JSRSP
Parmelia squarrosa	L	0.01	70	25	4	2	0	0	0	foliage, dead	
Usnea filipendula	L	0.01	46	44	10	0	0	0	0	foliage, live	PCRSP
Alectoria imshaugii	L	0.03	75	22	2	2	0	0	0		
Chrismofulvea dialyta	L	0.03	62	32	5	2	0	0	0		HRSP
Imshaugia aleurites	L	0.03	73	25	2	0	0	0	0		HRSP
Usnea rubicunda	L	0.03	67	22	9	2	0	0	0	foliage, dead	
Alectoria vancouverensis	L	0.04	65	26	8	1	1	0	0	foliage, live	
Hypogymnia enteromorpha	L	0.04	58	26	11	4	0	0	0	foliage, dead	
Platismatia herreii	L	0.04	55	31	10	3	0	0	0		
Usnea ceratina	L	0.04	49	33	15	3	0	0	0	foliage, live	HRSP
Platismatia glauca	L	0.05	55	28	15	1	0	0	0		
Bryoria fuscescens	L	0.06	57	30	13	0	0	0	0		JSRSP
Mycoblastus sanguinarius	L	0.07	56	31	12	2	0	0	0		
Ochrolechia oregonensis	L	0.07	50	29	17	4	1	0	0		
Usnea fragilescens var. *mollis*	L	0.07	45	28	17	7	3	0	0	foliage, dead	PCRSP
Lopadium disciforme	L	0.08	41	34	22	3	1	0	0	bark, br & lm <50	JSRSP
Parmelia saxatilis	L	0.08	45	35	20	0	0	0	0	bark, br & lm <50	
Usnea spp.	L	0.08	48	32	17	2	1	0	0	foliage, dead	
Sphaerophorus globosus	L	0.11	40	34	19	6	1	1	1		
Loxosporopsis corallifera	L	0.13	34	30	19	11	4	1	1	foliage, dead	PCRSP
Cephaloziella rubella	B	0.13	39	39	19	3	0	1	0		HRSP
Douinia ovata	B	0.20	30	43	19	0	0	5	3		JSRSP
Parmelia sulcata	L	0.01	82	14	4	0	0	0	0		HRSP
Buellia muriformis	L	0.02	57	27	12	4	0	0	0	foliage, dead	HRSP
Hypogymnia physodes	L	0.02	64	26	6	3	1	0	0	foliage, dead	
Parmelia pseudosulcata	L	0.03	59	28	10	2	0	0	0	foliage, dead	HRSP
Tuckermannopsis chlorophylla	L	0.03	52	31	14	3	0	0	0		HRSP
Tuckermannopsis orbata	L	0.03	69	23	8	0	0	0	0		
Lecanora expallens	L	0.04	55	25	16	4	0	0	0	foliage, dead	HRSP
Pertusaria amara	L	0.05	44	33	16	6	0	0	0	foliage, dead	
Graphis elegans	L	0.07	37	32	17	11	0	3	1	foliage, dead	
Dicranoweisia cirrata	B	0.03	56	32	10	0	2	0	0		HRSP
Hertelidea botryosa	L	0.03	64	25	11	0	0	0	0		HRSP
Usnea hirta	L	0.04	67	24	6	1	1	0	0		HRSP
Orthodicranum tauricum	B	0.07	50	35	6	5	2	2	0		HRSP
Cyphelium inquinans	L	0.08	54	29	15	2	0	0	0	bare wood	HRSP
Isothecium cristatum	B	0.19	25	28	24	4	3	4	13		HRSP
Chrysothrix candelaris	L	0.15	32	35	22	8	3	0	0		
Calicium lenticulare	L	0.16	31	31	22	11	4	1	0		
Hypocenomyce castaneocinerea	L	0.17	25	36	21	9	8	0	0	bark, tr >100	HRSP
Lepraria lobificans	L	0.22	22	26	22	12	8	5	5	bark, lm >50, lower	
Lecanactis abietina	L	0.23	7	27	41	17	8	0	0		PCRSP
Cladonia macilenta	L	0.24	23	25	21	11	9	6	5	bryophytes	HRSP
Hypnum circinale	B	0.25	25	29	23	12	5	2	5	bark, lm >50, upper	JSRSP
Dicranum fuscescens	B	0.27	24	29	20	9	7	4	7	bark, lm >50, upper	JSRSP
Orthodontium gracile	B	0.28	15	28	25	12	11	9	1	bark, tr >100	HRSP
Chaenotheca ferruginea	L	0.29	11	32	28	14	12	4	0	bark, lm >50 lower	PCRSP
Frullania tamarisci	B	0.20	23	21	17	9	6	5	18	foliage, dead	
Thelotrema lepadinum	L	0.22	15	19	21	13	8	5	19	non-redwood stems	PCRSP
Porella navicularis	B	0.33	18	19	12	7	0	4	40	non-redwood stems	HRSP
Isothecium stoloniferum	B	0.37	11	17	17	10	6	11	29	terrestrial woody debris	PCRSP
Polypodium scouleri	V	0.35	23	35	27	7	0	6	2	soils	
Polypodium glycyrrhiza	V	0.44	10	31	24	3	5	3	24	soils	JSRSP
Vaccinium ovatum	V	0.52	27	17	11	3	5	20	17	soils	PCRSP
Vaccinium parvifolium	V	0.68	13	13	3	0	10	33	27	soils	
Scapania bolanderi	B	0.49	4	17	25	11	9	11	24	terrestrial woody debris	
Lepidozia reptans	B	0.61	1	16	16	11	17	20	20	terrestrial woody debris	PCRSP
Cephalozia lunulifolia	B	0.72	3	8	5	2	8	21	54	terrestrial woody debris	
Kindbergia oregana	B	0.89	0	5	0	0	0	12	83	terrestrial woody debris	
Pseudotaxiphyllum elegans	B	0.89	0	3	3	9	6	25	53	terrestrial woody debris	
Calypogeia fissa	B	1.00	0	0	0	0	0	22	78	terrestrial woody debris	PCRSP

Figure 3. Dendrogram of taxa (left) aligned with table of non-metric multidimensional scaling (NMS) results, frequencies of taxa within strata, and Indicator Species Analyses (ISA) results (right) from multivariate analyses of a data matrix (63 taxa in 643 plots) obtained from intensive sampling of nine large redwood trees. The dendrogram is pruned at 30% information remaining, where branches represent groups of taxa with similar distributions. Substrates represent groups of plot types (see Table 1). Lichen litterfall data are excluded. Abbreviations: B = bryophyte, L = lichen, V = vascular plant, br = branches, lm = limbs, tr = trunks. JSRSP, PCRSP and HRSP refer to Jedediah Smith Redwoods State Park, Prairie Creek Redwoods State Park and Humboldt Redwoods State Park, respectively.

and the best predictor of *Vaccinium ovatum* mass was square-root transformed surface area of dead trunks (adjusted $R^2 = 0.72$, $p < 0.0001$). These correlations suggested microhabitat preferences and also reflected substrate availability for these epiphytes.

Cluster Analysis of the transposed community matrix identified groups of species with similar distributions. We pruned the dendrogram at 30% information remaining and aligned it with NMS and ISA results as well as with the frequencies of taxa within strata to facilitate interpretation of environmental preferences exhibited by these groups (**Fig. 3**). Taxa that clustered together tended to possess similar species scores along Axis 1, exhibit similar frequency distributions across strata, and prefer similar substrates, while separate clusters tended to contrast. We identified seven species clusters that expressed interpretable responses to environmental conditions.

1. High to moderate exposure tolerance, crown-wide distribution: Species scores along Axis 1 indicated high-moderate exposure tolerances for these 22 chlorolichens and two liverworts. These taxa occurred in crown strata 18 times more frequently than in trunk and terrestrial strata, and collectively they occupied every available substrate type within the tree crowns.

2. High exposure tolerance, dead foliage: These nine chlorolichens preferred the highly exposed habitats of upper crown strata, which held 56% of their occurrences. They were sampled at a higher frequency on dead foliage than on all other substrates. *Graphis elegans* was particularly fond of this substrate, occurring in 55% of all dead foliage plots.

3. Southern and inland geography (HRSP): These three chlorolichens and three mosses were encountered nine times more frequently in HRSP than in JSRSP and PCRSP combined. The mosses *Dicranowesia cirrata* and *Isothecium cristatum* expressed especially high affinities for HRSP, which supported over 85% of their occurrences.

4. Moderate exposure, stable substrates: These seven chlorolichens and three mosses preferred moderately exposed habitats of upper crown through upper trunk strata, and they showed an affinity for old and stable substrates such as large redwood trunks and limbs.

5. Moderate shelter, broad distribution: These four lichens and bryophytes occupied moderately sheltered habitats and were relatively evenly distributed through all strata. Collectively, they colonized every available substrate type within almost every stratum.

6. Moderate shelter, soils: These four vascular plants were commonly epiphytic on canopy soils. Upper crown through lower trunk strata supported 81% of *Polypodium* fern occurrences. Even when present in terrestrial strata, these ferns consistently sat above ground level on substrates such as woody debris, perched soil, epiphytic bryophytes and stems of vascular plants. Fifty-five percent of *Vaccinium* shrub occurrences were epiphytic in upper crown through lower trunk strata. *Vaccinium ovatum* was a particularly common epiphyte component of JSRSP and PCRSP, where it occupied 83% of crown strata.

7. Sheltered, terrestrial woody debris: These four liverworts and two mosses expressed high Axis 1 scores and frequently occupied trunk flare and terrestrial strata, indicating affinities for sheltered habitats. *Calypogeia fissa* occupied the sheltered extreme of the exposure gradient. These bryophytes were found on terrestrial woody debris seven times more frequently than on all other substrates combined.

Terrestrial versus Arboreal Sampling. The two sampling strategies returned very different results, but they complemented each other in capturing total richness (**Fig. 4**). Arboreal sampling detected over 77% of the overall richness, while terrestrial sampling captured only 51%. Arboreal sampling was particularly effective at revealing lichen richness; over 95% of total lichen taxa were found with this strategy. Conversely, terrestrial sampling was more effective for detecting vascular plants. Capture of bryophyte richness did not differ substantially between sampling strategies. Lichen litterfall beneath the crowns of study trees was a poor assessment of epiphytic lichen richness. Only 33% of lichen taxa that occurred above trunk flare strata were recovered as litterfall. Nonetheless, two species were found as litterfall that were not encountered during arboreal sampling. We found *Graphis scripta* on a tiny fragment of redwood bark, and four specimens of *Pseudocyphellaria perpetua* were encountered on litterfall twigs, but the twigs were

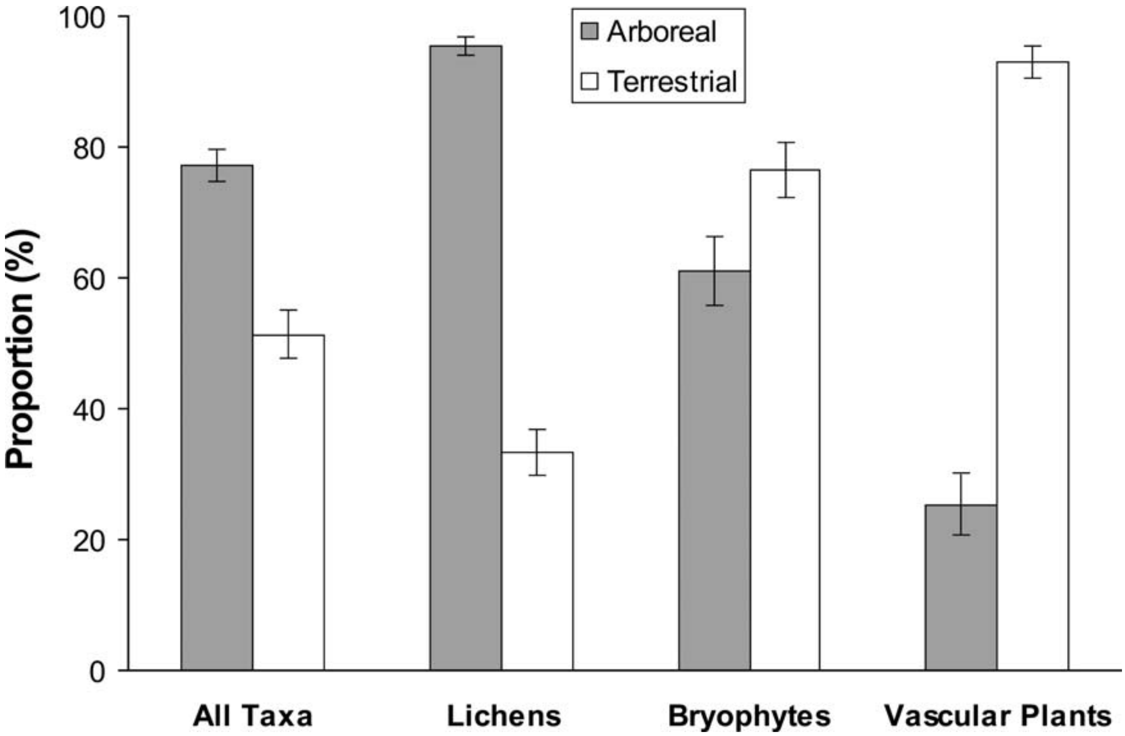


Figure 4. Proportions of floristic groups captured by arboreal versus terrestrial search strategies for species richness in old-growth redwood forests. Values are percentages ± one standard error.

identified as Douglas-fir and Sitka spruce, not redwood.

Discussion

Lichens and Bryophytes on Redwood vs. Douglas-fir and Sitka Spruce. Floristic comparisons between redwood and other tree species were challenging because of differences in sampling methodologies. Nonetheless, comparisons were possible because of the detailed species data provided in a handful of publications, and our sampling design allowed the segregation of epiphytes by substrates as well as the formation of species groups to match the focus and resolution exercised by other authors (**Table 4**). Pike et al. (1975) and McCune et al. (2000) studied the epiphyte floras of 450-year-old, Douglas-fir-dominated forests in the Cascade Range of western Oregon and Washington, respectively. Branch macroepiphyte assemblages were examined on 700-year-old Douglas-fir in the western Oregon Cascades (Sillett 1995), and branch- and foliage-dwelling macroepiphytes were investigated on Sitka spruce growing in an old-growth redwood forest (Ellyson & Sillett 2003).

The lichens *Lepraria* and *Cladonia* were the most widespread on redwood, while *Platismatia glauca*, *Sphaerophorus globusus* and *Usnea* were the most widespread on Douglas-fir and Sitka spruce (Ellyson & Sillett 2003; McCune et al. 2000; Sillett 1995). The cyanolichens *Lobaria oregana* and *L. pulmonaria* were a common component of each flora except for redwood, where they were present but very scant. Some cyanolichens that can be abundant in old Douglas-fir forests were altogether missing from the redwood forest epiphyte flora. We did not encounter the old-growth associated cyanolichens *Nephroma occultum*, *Pseudocyphellaria rainierensis* or *Sticta beauvoisii* that reach a southern limit of distribution in Oregon. *Peltigera britannica*, whose distribution extends well into northwestern California (Brodo et al. 2001), did not occur as an epiphyte in redwood forests (see also Ellyson & Sillett 2003). The mosses *Dicranum fuscescens* and *Isothecium stoloniferum* (broad sense, including *I. myosuroides*; see Norris &

Table 4. Comparison of epiphyte richness between redwood, three different Douglas-fir forests and Sitka spruce growing in a redwood forest. The number of redwood epiphyte taxa (left column of each pair of columns) has been adjusted to match both the sampling focus and taxonomic resolution exercised by the comparing authors (right columns). Abbreviations: br = branches, lm = limbs. Symbols: *microlichens excluded from total, **microlichens not emphasized.

Floristic group	Redwood all strata, all epiphytes	450-year-old Douglas-fir forest (Pike et al. 1975)	Redwood upper crown - lower trunk strata, all epiphytes	450-year-old Douglas-fir forest (McCune et al. 2000)	Redwood live br & lm >10 cm diameter, macroepiphytes	700-year-old Douglas-fir (Sillett 1995)	Redwood br, lm & foliage, macroepiphytes	Sitka spruce (Ellyson & Sillett 2003)
all epiphytes	256	107	215	111	89*	65	112*	76
microlichens	100	25	93	49	49	**	83	**
macrolichens	69	49	77	48	46	45	76	57
cyanolichens	17	21	13	4	9	18	13	11
bryophytes	45	32	27	14	22	19	24	17
liverworts	19	7	9	7	8	6	8	6
mosses	26	25	18	7	14	13	16	11

Shevock 2004) were widespread in each flora, but *D. fuscescens* was much more frequent on redwood than on Sitka spruce (Ellyson & Sillett 2003). *Antitrichia gigantea*, which was the dominant moss on 700-year-old Douglas-fir (cf. *A. curtipendula*, Sillett 1995), was seldom encountered on redwood. *Frullania tamarisci* ssp. *nisquallensis* was the most common liverwort in each flora except for 700-year-old Douglas-fir, where *Douinia ovata* was most common (Sillett 1995).

Compared to Douglas-fir and Sitka spruce, redwood consistently supported more total epiphyte richness, except for cyanolichens (**Table 4**). This richness was likely promoted by structural complexity. Redwood's fire-resistance, longevity and propensity to reiterate encourage the development of unusual substrates (e.g., charcoal, old bark of large trunks and limbs, splash zones and vascular epiphytes) that are simply uncommon or nonexistent on Douglas-fir and Sitka spruce. The microlichens *Hypocenomyce castineocinerea* and *H. oligospora* frequently occupied burnt bark, and *Pycnora xanthococca* was found only on burnt wood. Eleven species of calicioid lichens, including a *Calicium* new to science (L. Tibell pers. comm.) inhabited old and stable substrates. The bryophytes *Cephalozia lunulifolia*, *Lepidozia reptans* and *Pseudotaxifolium elegans* preferred terrestrial woody debris over other substrates, but conditions above trunk flare strata allowed these bryophytes to persist on canopy soils and in splash zones. The stems of epiphytic vascular plants supported the microlichens *Arthonia stellaris*, *Arthothelium norvegicum*, *Bactrospora patellarioides* and *Segestria leptalea* that were not encountered elsewhere in the study. Moreover, the best predictor of total lichen richness was surface area of live trunks <100 cm diameter, demonstrating that presence of reiterated trunks fosters epiphyte richness.

Despite high floristic richness, lichens (particularly cyanolichens) and bryophytes were clearly not abundant on redwood. This paucity was unlikely a result of dispersal limitation as suggested for some lichens in Douglas-fir forests (Sillett et al. 2000a, b), because neighboring Douglas-fir, Sitka spruce and western hemlock trees often supported huge epiphyte loads, especially of cyanolichens (Ellyson & Sillett 2003; pers. observ.). Instead, their low abundance was likely due to a limitation of suitable substrates, as evidenced by Sitka spruce that occasionally grew as epiphytes on redwood. In the middle crown of one study tree (Terex Titan), we encountered several epiphytic Sitka spruce that harbored the moss *Antitrichia gigantea* and the cyanolichen *Pseudocyphellaria anthraspis*, but the two species were never found on the supporting redwood even though it had at least 2300 times more bark surface area. Compared to the rough and stable bark of Sitka spruce, the smooth and flakey bark of young redwood stems appeared to deter establishment by epiphytes, a phenomenon documented in other forests (Carlsen 2000; Heitz & Heitz-Seifert 1995; Malizia 2003). On the other hand, the bark of old redwood stems, which is much more fibrous and stable, also supported a sparse cover of epiphytes. Epiphyte establishment on redwood may be thwarted by the same terpenoid compounds that retard growth of pathogenic fungi (Hall 1985) as well as innocuous endophytic fungi (Espinosa-Garcia et al. 1996), and cyanolichens may be more susceptible to these compounds than chlorolichens or bryophytes. Finally, redwood's shade tolerance (Baker 1949) and resultant production of densely foliated crowns may limit light availability to some epiphytes, especially in lower strata. However, given that many lichens and bryophytes become light-saturated at very low light levels (Demmig-Adams et al. 1990; Green et al. 1997; Zotz et al. 1997) and can attain positive net photosynthesis in deep shade (Green et al. 1991), light limitation seems less likely to account for the low abundance of non-vascular epiphytes on redwood than chemical toxicity.

Climatic Effects. Wind-induced damage from winter storms likely contributed to the higher structural complexity of trees in JSRSP and PCRSP, which were located less than seven km from the Pacific Ocean and without tall intervening ridges, compared to those in HRSP, which were separated from the ocean by over 30 km of mountainous ridges. The resulting differences in crown-level structural complexity clearly promoted vascular epiphytes (Sillett & Bailey 2003; Sillett & Van Pelt 2007). All 30 vascular epiphyte species in this study were encountered on the trees in JSRSP and PCRSP, where they grew mostly from soils perched on large limbs, broken trunks, and in crotches between reiterated trunks. By contrast, the relatively simple structure of trees at HRSP supported only three of these species. Factors other than macroclimate-induced differences in structural complexity, however, must also have affected the distribution of epiphytes among the parks. For example, an extremely complex redwood in Redwood National Park supported five species of vascular epiphytes (Sillett & Van Pelt 2000a), but these were relatively sparse compared to the epiphyte loads on trees in this study, presumably because this tree was separated from the ocean by nine km and a 400–800 m tall, rain-shadowing ridge. Abundant rainfall combined with humid, coastal air infiltrating the canopies in JSRSP and PCRSP probably promoted desiccation-sensitive taxa in these forests compared to those in drier redwood forests. For example, the fern *Polypodium scouleri*, which is intolerant of severe drought and occupies only coastal habitats throughout the Pacific Northwest (Whitmore 1993), was absent from the trees in HRSP. Conversely, desiccation-tolerant epiphytes may prefer drier forests. This could explain why 19 species (six expressing high fidelity) demonstrated preferences for HRSP.

From the forest floor to emergent treetops, humidity decreases as exposure to desiccating wind and sunlight increases (Campbell & Coxson 2001; Hosokawa et al. 1964; Parker 1995, 1997). Epiphytes respond differentially to these microclimatic conditions and thus segregate by height in tall forests (McCune 1993; McCune et al. 1997; Sillett & Antoine 2004). As in other forests (e.g., Ellyson & Sillett 2003; Sillett 1995), we interpreted the dominant epiphyte compositional gradient in redwood forests to be from exposed to sheltered habitats. Strata were ordered from upper crown to terrestrial strata along the ordination axis. Lichens and vascular plants occupied opposite ends of the gradient, while bryophytes were intermediate. Furthermore, exposed substrates (e.g., redwood foliage and bark of small branches) occupied one end, while sheltered substrates (e.g., soils and terrestrial woody debris) occupied the other end of the gradient. The relative position on this gradient of upper versus lower surfaces of large limbs might seem like a contradiction to this interpretation, especially when considering the potential contribution of stemflow to lower limb surfaces. However, since limbs supported reiterated trunks, foliage on these reiterated trunks likely provided shelter from desiccation, and upper limb surfaces may have experienced prolonged periods of moisture retention compared to lower limb surfaces. The fact that air humidity was significantly lower below than above large limbs of one redwood in PCRSP (Ambrose 2004) supports this assertion. Of the total bryophyte occurrences on large limbs, 74% were on upper surfaces, but only 26% were on lower surfaces. Moreover, bryophytes on upper limb surfaces may amplify differences in water availability by absorbing water and thus reducing stemflow to epiphytes on lower limb surfaces.

Substrate Effects. We found dramatic compositional differences in epiphyte communities on live versus dead redwood foliage. This effect was particularly pronounced on foliage from upper and middle crown strata, where leaves were awl-shaped and nearly appressed against the stem axis (see Koch et al. 2004 for an explanation of variation in leaf structure with height in redwood). The cuticle on live foliage may be too slippery for establishment by most epiphyte propagules; only vagrant alectorioid lichens preferred this substrate. Conversely, a rich assemblage of chlorolichens preferred dead redwood foliage. Leaf mortality seemed to encourage cuticle decay (pers. observ.), allowing leaf axils of dead foliage to serve as pockets for collection of epiphyte propagules and subsequent establishment of juveniles. We observed a slightly different epiphyte community on foliage at the extreme tops of upper crown strata, where the nitrophilous lichens *Candelaria concolor* and *Xanthoria candelaria* were frequently encountered. This treetop phenomenon has been attributed to regular visits by nitrogen-depositing avian fauna (McCune et al. 2000).

Young bark, old bark and bare wood differ greatly in stability and texture. On redwood, action of the vascular cambium of young stems continually exposes fresh, smooth bark as thin and unstable flakes exfoliate. Old bark is by contrast much more fibrous and stable; long strips are shed at a very slow pace. The lichens *Lopadium disciforme*, *Parmelia hygrophila* and *P. saxatilis* preferentially occupied the bark of small branches and limbs, whereas the lichen *Hypocenomyce castaneocinerea* and the moss *Orthodontium gracile* occupied the thick bark of large trunks. *Hypocenomyce* has been documented from stable bark on the lower surfaces of leaning Douglas-fir trunks (Pike et al. 1975), and *O. gracile* has been noted almost exclusively from redwood bark and bare wood in old-growth forests (Christy & Wagner 1996; Lawton 1971; Norris 1987). Compared to bark on live stems, bare wood and terrestrial woody debris lack the rejuvenating action of the vascular cambium, and over time they become either crumbly or spongy depending on the degree of exposure to desiccation or moisture, respectively. For example, exposed xylem on the dead tops of trees was generally hard, crumbly and dry, whereas old woody debris on the forest floor was typically soft, spongy and water-retentive. Bare wood of crown strata was reliably occupied only by the lichen *Cyphelium inquinans*. This result was surprising because bare wood has been documented as a distinctive substrate for epiphytes in other forests (Liu et al. 2000; McCune et al. 2000). Perhaps redwood secondary xylem contains high concentrations of the same terpenoid compounds that are toxic to many fungi (Espinosa-Garcia et al. 1996; Hall 1985). Seven bryophyte taxa expressed affinities for terrestrial woody debris over live bark of adjacent vascular plants in the same stratum. *Calypogeia fissa*, which displayed the strongest affinity for this substrate, is a highly desiccation-sensitive liverwort that probably prefers the water-storage capacity offered by terrestrial woody debris over other substrates.

Water-storage capacity provided by arboreal substrates such as soil, decaying wood and bryophytes appears to be attractive to vascular epiphytes. Abundance of *Vaccinium ovatum* was strongly correlated with availability of dead trunks, supporting previous observations that decaying wood is an important substrate to this shrub (Sillett 1999; Sillett & Van Pelt 2007). *Polypodium scouleri* mat area was best predicted by surface area of limbs, suggesting that large, soil-capturing platforms may promote establishment and development of this evergreen fern, which is the primary soil-former in old-growth redwood forest canopies (Sillett & Bailey 2003; Sillett & Van Pelt 2007). Although *Polypodium glycyrrhiza* may prefer bryophyte mats for establishment and development (Lovelace 2003), this fern was associated with canopy soil rather than bryophytes on redwood. This discrepancy may be explained by the tendency of *P. glycyrrhiza* to capture redwood leaf litter, which over time may smother and suppress underlying bryophytes and subsequently provide an alternative water-storing substrate.

Substrate orientation (i.e., degree of inclination) also influenced epiphyte composition. In previous studies, calicioid and leprose lichens tended to occupy the overhanging, lower surfaces of large branches, limbs and leaning trunks, while bryophytes tended to occupy upper surfaces (Ellyson & Sillett 2003; Kenkel & Bradfield 1986; McCune et al. 2000; Pike et al. 1975). We found the same tendency on large limbs: lower surfaces were preferred by *Chaenotheca ferruginea* and *Lepraria lobificans*, while the bryophytes *Dicranum fuscescens* and *Hypnum circinale* preferred upper surfaces. On large branches, limbs and leaning trunks, the association between stem angle and epiphyte composition is likely the result of differential interception of precipitation rather than stem flow or light (Ryan 1991). The influence of substrate orientation was also evident on expanded tree bases that link the lower trunk to forest floor communities. On redwood, species composition in trunk flare strata was intermediate between lower trunk and terrestrial strata, a trend documented from other conifer forests of the Pacific Northwest (Glime & Hong 2002; Pike et al. 1975). In this transition zone, increased horizontality not only expands interception of precipitation, but also augments catchment of litterfall that leads to both soil development and water-storage capacity, ultimately enticing forest floor communities upwards into epiphytism. We sampled one redwood (Paradox) whose trunk flare was buried in floodplain silt. The transition zone from the nearly vertical lower trunk to the horizontal forest floor was extremely abrupt and supported the fewest forest floor taxa documented near ground level in this study.

Succession. A successional pathway that includes vascular epiphytes is suggested by our results. Foliage was preferentially occupied by alectorioid and other chlorolichens. Bark of small branches was preferred by three lichens, while the upper surface of large limbs was preferred by two bryophytes. Thus, our results support the well-documented succession from lichens (especially alectorioid species) that are the initial colonists of young substrates to bryophytes that eventually dominate older substrates (Lyons et al. 2000; Sillett & Antoine 2004; Stone 1989). On several of the redwood trees, epiphyte succession extended well beyond bryophyte dominance. As structural complexity develops over time, large limbs and crotches accumulate soil that is exploited by a diversity of vascular epiphytes (Sillett 1999; Sillett & Van Pelt 2007) that harbor epiphytes of their own. For example, the liverwort *Porella navicularis* and the microlichen *Thelotrema lepadinum* preferred bark of epiphytic vascular plants over all redwood substrates.

Repeated crown damage followed by reiteration initiates the development of parallel successional pathways that are staggered in time on large redwoods. One of the study trees (Terex Titan) revealed the full spectrum of epiphyte succession, including a climactic stage dominated by woody epiphytes. Thirty-four reiterated trunks to 148 cm diameter emerged from middle and lower crown strata (see Van Pelt 2001). These trunks and their branches harbored lichens and bryophytes in the typical spatial sequence, while the gnarly main section of the tree between 35 and 65 m above the ground consisted of huge, broken trunks and thick, sheared-off limbs that carried abundant soil, decaying wood and eight species of vascular plants. Several of the *P. sitchensis* trees and large *V. ovatum* shrubs in this region of the crown supported distinctive epiphytes rare or absent elsewhere on the redwood tree. Furthermore, old pieces of decaying wood in this portion of the tree were inhabited by typically terrestrial epixylics, including *Buxbaumia piperi*, *Cephalozia lunulifolia* and *Icmadophila ericetorum*.

Arboreal versus Terrestrial Search Strategy. Terrestrial sampling can obviously detect presence or absence of terrestrial organisms, but sampling litterfall may not be dependable for capturing epiphyte richness. Litterfall is both annually and seasonally variable, often dropping in pulses during storms (Coxson & Stevenson 2005; Esseen 1985; Grier 1988). Bryophyte litterfall is often indistinguishable because it aggregates with the terrestrial bryoflora (McCune 1994a). Furthermore, litterfall of different lichen species is consumed by herbivores and decomposes at varying rates (McCune & Daly 1994). Despite these problems with litterfall assessment, the strategy can be an effective tool for estimating epiphytic lichen biomass (McCune 1994a; McCune et al. 1997). But how useful is litterfall sampling for revealing overall presence or absence of lichen taxa? Terrestrial litterfall sampling was only moderately successful at detecting the rare, old-growth-associated cyanolichen *Nephroma occultum*, and a dual approach (ground-based plus tree climbing) was recommended for determining its presence or absence in the canopy (Rosso et al. 2000). From terrestrial and trunk flare strata directly beneath the crowns of study trees, we recovered only 33% of epiphytic lichen richness as litterfall, even when sampling after winter storms. Conversely, the arboreal search strategy captured over 95% of total lichen taxa. It is probable that more litterfall richness would have been recovered with an expanded search area. However, until additional research suggests otherwise, we also recommend combined arboreal and terrestrial surveys to fully capture epiphyte richness in tall forests.

Future Research. We have demonstrated that old-growth redwood forests support rich and well-developed epiphyte assemblages. Quantifying the biomass of lichens and bryophytes on redwood will require a great deal of additional work involving random sampling of a sufficient proportion of total tree surface area (~1%). The enormous sizes of large redwood trees make this impractical. We are certain, however, that the total mass of lichens and bryophytes on individual trees is not only far smaller than the load of vascular epiphytes on these trees (**Table 2**), but also far lower than we have observed on other large trees in both redwood forests (to 200 kg; Ellyson & Sillett 2003) and other temperate rain forests (to 1000 kg; Van Pelt & Williams unpubl.). Determining the mechanisms that cause the relative sparseness of non-vascular epiphytes on redwood will require extraction of potential toxins in the wood, bark and leaves followed by a factorial experiment in which replicate substrates (with and without redwood toxins) are inoculated with epiphyte thalli and propagules (e.g., Sillett et al. 2000b).

Our work contributes to understanding how crown-level structural complexity in redwoods may promote diversity of epiphytes and associated organisms in the forest canopy. Since over 96% of the old-growth redwood forests have been logged (Noss 2000), and nearly all the regenerating redwood forests are younger than rotation age (~50 years), there will be a scarcity of old-growth forests outside the parks for many years to come. Trees in young redwood forests almost always lack reiterated trunks and have dense, conical crowns with small branches. As a consequence of their simple structure, the biological diversity of these forests is extremely low. Vascular epiphytes, canopy soils and many animals associated with old-growth redwood forests are now virtually restricted to the parks (Cooperrider et al. 2000; Sawyer et al. 2000), and it is likely that many of the lichens and bryophytes we observed on the study trees occur as epiphytes only rarely, if ever, outside old-growth forests. A factorial experiment involving arboricultural manipulations that stimulate trunk reiteration and limb formation (see Sillett & Van Pelt 2007) may reveal that accelerating the development of structural complexity in forest trees is feasible. If so, the well-developed epiphyte communities we documented in this study may reclaim tree crowns in regenerating forests protected from further logging.

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Appendix A. Comprehensive flora, species groups and frequencies for taxa encountered during sampling of nine large *Sequoia sempervirens* trees in old-growth redwood forests, northwestern California. Boldface font identifies 63 taxa used in multivariate analyses. Species groups are named for the most frequent species within each group. *Lobaria oregana* and *L. pulmonaria* contained cephalodial cyanobacteria. *Lecanora* spp. lacked the apothecia needed for identification, *Pertusaria* spp. were sterile and mostly too tiny to extract secondary compounds, and *Usnea* spp. were too small to identify. In addition to number of trees and plots, percent frequencies are listed for all taxa identifiable in the field partitioned by stratum (UC = upper crown, MC = middle crown, LC = lower crown, UT = upper trunk, LT = lower trunk, TF = trunk flare, TER = terrestrium, LIT = litterfall) and substrate type (Bark = redwood bark, Wood = exposed redwood xylem, Leaves = all foliar surfaces, Stems = woody stems of vascular plants other than redwood, Bryos = bryophyte mats, Soil = canopy or terrestrial soil) based on 976 plots (+ 9 litterfall plots for lichens only).

				Stratum								Substrate					
Taxon	Species group	# Trees	# Plots	UC	MC	LC	UT	LT	TF	TER	LIT	Bark	Wood	Leaves	Stems	Bryos	Soil
CHLOROLICHENS																	
Alectoria imshaugii		9	66	74	21	2	2	0	0	0	2	63	29	8	0	0	0
Alectoria sarmentosa	*Alectoria vancouverensis*																
Alectoria vancouverensis	*Alectoria vancouverensis*	9	135	64	25	7	1	1	0	0	2	48	18	25	6	3	0
Arthonia arthonioides		1	1	0	0	100	0	0	0	0	0	0	0	0	100	0	0
Arthonia ilicina		6	10	50	20	20	10	0	0	0	0	40	0	0	60	0	0
Arthonia leucopellaea		1	1	100	0	0	0	0	0	0	0	0	100	0	0	0	0
Arthonia stellaris		1	1	100	0	0	0	0	0	0	0	0	0	0	100	0	0
Arthothelium norvegicum		1	1	100	0	0	0	0	0	0	0	0	0	0	100	0	0
Bacidia heterochroa		1	1	100	0	0	0	0	0	0	0	0	0	0	100	0	0
Bactrospora patellarioides		1	1	0	100	0	0	0	0	0	0	0	0	0	100	0	0
Biatora efflorescens		8	23	43	43	9	0	0	0	0	4	27	14	45	14	0	0
Biatora globulosa		1	1	0	0	100	0	0	0	0	0	0	100	0	0	0	0
Bryoria fremontii	*Bryoria fuscescens*																
Bryoria furcellata	*Bryoria fuscescens*																
Bryoria fuscescens	*Bryoria fuscescens*	7	68	56	29	13	0	0	0	0	1	55	36	6	3	0	0
Bryoria subcana	*Bryoria fuscescens*																
Bryoria trichodes ssp. *americana*	*Bryoria fuscescens*																
Buellia muriformis		9	89	52	25	11	3	0	0	0	9	48	16	21	15	0	0
Byssoloma marginatum		3	3	0	33	33	0	0	0	33	0	0	0	33	67	0	0
Calicium glaucellum	*Calicium lenticulare*																
Calicium lenticulare	*Calicium lenticulare*	9	231	31	30	22	11	4	1	0	1	70	27	2	0	0	0
Calicium cf. *lutescens*	*Calicium lenticulare*																
Calicium viride	*Calicium lenticulare*																
Calicium sp. nov.	*Calicium lenticulare*																
Caloplaca holocarpa		3	6	83	17	0	0	0	0	0	0	50	0	33	17	0	0
Candelaria concolor		2	4	75	0	25	0	0	0	0	0	25	0	75	0	0	0

Appendix A. Continued.

				Stratum								Substrate					
Taxon	**Species group**	**# Trees**	**# Plots**	**UC**	**MC**	**LC**	**UT**	**LT**	**TF**	**TER**	**LIT**	**Bark**	**Wood**	**Leaves**	**Stems**	**Bryos**	**Soil**
Cavernularia hultenii		4	9	67	22	11	0	0	0	0	0	22	0	22	56	0	0
Cavernularia lophyrea		4	11	82	18	0	0	0	0	0	0	55	0	27	18	0	0
Chaenotheca cf. *australis*	*Chaenotheca ferruginea*																
Chaenotheca brachypoda		2	2	50	0	50	0	0	0	0	0	0	100	0	0	0	0
Chaenotheca brunneola	*Chaenotheca ferruginea*																
Chaenotheca ferruginea	*Chaenotheca ferruginea*	8	57	11	32	28	14	12	4	0	0	68	32	0	0	0	0
Chaenotheca furfuracea		1	1	0	0	0	0	1	0	0	0	100	0	0	0	0	0
Chaenotheca laevigata	*Chaenotheca ferruginea*																
Chaenotheca sphaerocephala	*Chaenotheca ferruginea*																
Chaenotheca trichialis		1	1	0	0	0	0	100	0	0	0	100	0	0	0	0	0
Chaenothecopsis viridireagens		7	23	4	13	30	22	22	9	0	0	91	9	0	0	0	0
Chrismofulvea dialyta		9	61	61	31	5	2	0	0	0	2	68	20	12	0	0	0
Chrysothrix candelaris		9	391	31	34	22	7	3	0	0	2	51	24	10	7	7	1
Cladonia bellidiflora	*Cladonia macilenta*																
Cladonia chlorophaea	*Cladonia macilenta*																
Cladonia coniocraea	*Cladonia macilenta*																
Cladonia macilenta	*Cladonia macilenta*	9	491	22	24	20	11	9	6	5	2	55	23	2	5	11	4
Cladonia cf. *norvegica*	*Cladonia macilenta*																
Cladonia ochrochlora	*Cladonia macilenta*																
Cladonia squamosa var. *subsquamosa*	*Cladonia macilenta*																
Cladonia transcendens	*Cladonia macilenta*																
Cladonia verruculosa	*Cladonia macilenta*																
Cliostomum griffithii		5	10	50	40	10	0	0	0	0	0	10	10	40	40	0	0
cf. *Coccotrema pocillarium*		1	1	0	0	100	0	0	0	0	0	0	100	0	0	0	0
Cyphelium inquinans		9	53	53	28	15	2	0	0	0	2	38	62	0	0	0	0
Evernia prunastri		3	5	80	20	0	0	0	0	0	0	40	0	40	20	0	0
Fellhanera bouteillei		1	1	0	100	0	0	0	0	0	0	0	0	100	0	0	0
Graphis elegans		9	81	35	30	16	10	0	2	1	6	37	5	32	26	0	0
Graphis scripta			1	0	0	0	0	0	0	0	100	0	0	0	0	0	0
Hafellia disciformis		4	7	57	43	0	0	0	0	0	0	14	14	43	29	0	0
Hertelidea botryosa		8	36	64	25	11	0	0	0	0	0	56	39	0	3	0	3

Appendix A. Continued.

Taxon	Species group	# Trees	# Plots	Stratum								Substrate					
				UC	MC	LC	UT	LT	TF	TER	LIT	Bark	Wood	Leaves	Stems	Bryos	Soil
Hypocenomyce castaneocinerea		9	129	25	36	21	9	8	0	0	2	79	21	0	0	0	0
Hypocenomyce oligospora		5	15	27	53	13	0	0	0	0	7	100	0	0	0	0	0
Hypogymnia apinnata	*Hypogymnia enteromorpha*																
Hypogymnia enteromorpha	*Hypogymnia enteromorpha*	9	127	54	24	10	4	0	0	0	7	52	14	18	10	6	0
Hypogymnia heterophylla		2	2	100	0	0	0	0	0	0	0	50	0	0	50	0	0
Hypogymnia imshaugii		3	4	75	0	0	0	0	0	0	25	33	33	33	0	0	0
Hypogymnia inactiva		6	11	73	0	18	0	0	0	0	9	60	0	40	0	0	0
Hypogymnia physodes		9	81	60	25	6	2	1	0	0	5	48	10	22	14	5	0
Hypogymnia tubulosa		4	16	56	38	0	0	0	0	0	6	67	0	27	7	0	0
Icmadophila ericetorum		1	1	100	0	0	0	0	0	0	0	100	0	0	0	0	0
Imshaugia aleurites		8	48	73	25	2	0	0	0	0	0	60	40	0	0	0	0
Japewia tornoënsis		6	27	52	26	19	0	0	0	0	4	54	27	8	12	0	0
Lecanactis abietina		6	76	7	26	41	17	8	0	0	1	71	25	0	4	0	0
Lecania cyrtella		1	1	100	0	0	0	0	0	0	0	100	0	0	0	0	0
Lecanora confusa		5	10	70	20	10	0	0	0	0	0	50	0	40	10	0	0
Lecanora coniferarum		1	1	100	0	0	0	0	0	0	0	0	100	0	0	0	0
Lecanora expallens		9	75	55	25	16	4	0	0	0	0	48	23	21	8	0	0
Lecanora impudens		2	2	50	50	0	0	0	0	0	0	0	0	50	50	0	0
Lecanora cf. *orae-frigidae*		1	1	100	0	0	0	0	0	0	0	0	100	0	0	0	0
Lecanora cf. *pacifica*		1	1	100	0	0	0	0	0	0	0	0	0	0	100	0	0
cf. *Lecanora ramulicola*		1	1	0	100	0	0	0	0	0	0	0	0	100	0	0	0
Lecanora substrobilina		3	4	100	0	0	0	0	0	0	0	50	0	25	25	0	0
Lecanora spp.		2	5	40	60	0	0	0	0	0	0	0	40	40	20	0	0
Lecidea albofuscescens		1	1	0	100	0	0	0	0	0	0	0	0	100	0	0	0
Lepraria diffusa	*Lepraria lobificans*																
Lepraria eburnea	*Lepraria lobificans*																
Lepraria incana	*Lepraria lobificans*																
Lepraria lobificans	*Lepraria lobificans*	9	571	22	26	22	12	8	5	5	1	53	21	7	9	8	2
Lepraria vouauxii	*Lepraria lobificans*																
Letharia vulpina		2	5	100	0	0	0	0	0	0	0	40	60	0	0	0	0
Lichenomphalia umbellifera		3	3	0	0	0	0	0	100	0	0	100	0	0	0	0	0

Appendix A. Continued.

Taxon	Species group	# Trees	# Plots	Stratum								Substrate					
				UC	MC	LC	UT	LT	TF	TER	LIT	Bark	Wood	Leaves	Stems	Bryos	Soil
Lopadium disciforme		9	112	38	32	21	3	1	0	0	5	65	27	5	1	2	0
Loxosporopsis corallifera		6	145	33	29	19	11	4	1	1	3	48	26	14	7	4	1
Megalaria columbiana		2	4	50	0	25	25	0	0	0	0	0	0	50	50	0	0
Melanelixia fuliginosa		1	1	100	0	0	0	0	0	0	0	100	0	0	0	0	0
Melanelixia subaurifera		4	11	73	18	9	0	0	0	0	0	55	0	36	9	0	0
Menegazzia subsimilis		6	34	35	26	21	3	0	0	0	15	34	0	24	41	0	0
Micarea cinerea		1	1	100	0	0	0	0	0	0	0	100	0	0	0	0	0
Micarea hedlundii		1	1	0	0	100	0	0	0	0	0	0	100	0	0	0	0
Micarea prasina		6	10	10	50	10	20	0	0	10	0	40	10	30	10	10	0
Micarea synotheoides		1	1	0	100	0	0	0	0	0	0	0	100	0	0	0	0
Microcalicium disseminatum	*Calicium lenticulare*																
Mycoblastus affinis		8	20	55	30	10	0	0	0	0	5	58	32	0	5	5	0
Mycoblastus caesius		1	1	0	0	100	0	0	0	0	0	100	0	0	0	0	0
Mycoblastus sanguinarius		8	63	52	29	11	2	0	0	0	6	42	51	3	2	2	0
Ochrolechia androgyna	*Ochrolechia oregonensis*																
Ochrolechia arborea	*Ochrolechia oregonensis*																
cf. *Ochrolechia inversa*		2	2	50	0	0	0	0	0	50	0	50	0	0	50	0	0
Ochrolechia juvenalis	*Ochrolechia oregonensis*																
Ochrolechia laevigata	*Ochrolechia oregonensis*																
Ochrolechia oregonensis	*Ochrolechia oregonensis*	9	177	47	28	16	3	1	0	0	5	46	29	13	5	8	0
cf. *Ochrolechia subisidiata*		1	1	100	0	0	0	0	0	0	0	100	0	0	0	0	0
Opegrapha ochrocheila		1	2	0	50	50	0	0	0	0	0	0	0	100	0	0	0
Opegrapha cf. *protuberans*		1	1	0	100	0	0	0	0	0	0	0	100	0	0	0	0
Opegrapha rufescens		6	18	39	39	11	0	0	0	6	6	18	0	12	71	0	0
Ophioparma rubricosa		4	6	100	0	0	0	0	0	0	0	0	100	0	0	0	0
Parmelia hygrophila		9	32	66	28	6	0	0	0	0	0	72	3	0	22	3	0
Parmelia pseudosulcata		9	83	58	28	10	2	0	0	0	2	43	21	21	9	6	0
Parmelia saxatilis		9	66	45	35	20	0	0	0	0	0	71	14	0	0	15	0
Parmelia squarrosa		9	60	67	23	3	2	0	0	0	5	44	16	23	14	4	0
Parmelia sulcata		9	50	80	14	4	0	0	0	0	2	51	20	10	12	6	0
Parmotrema arnoldii	*Parmotrema chinense*																

Appendix A. Continued.

Taxon	Species group	# Trees	# Plots	Stratum								Substrate					
				UC	MC	LC	UT	LT	TF	TER	LIT	Bark	Wood	Leaves	Stems	Bryos	Soil
Parmotrema chinense	*Parmotrema chinense*	7	26	62	27	8	0	0	0	0	4	44	4	20	28	4	0
Parmotrema crinitum		1	1	100	0	0	0	0	0	0	0	100	0	0	0	0	0
Pertusaria amara		9	99	43	32	16	6	0	0	0	2	37	26	20	14	3	0
Pertusaria ophthalmiza		4	8	75	25	0	0	0	0	0	0	13	50	0	38	0	0
Pertusaria spp.		4	6	83	17	0	0	0	0	0	0	83	0	0	17	0	0
Physcia tenella		2	4	25	50	25	0	0	0	0	0	0	0	100	0	0	0
Placynthiella icmalea		5	13	77	23	0	0	0	0	0	0	62	38	0	0	0	0
Platismatia glauca		9	92	51	26	14	1	0	0	0	8	47	27	13	5	8	0
Platismatia herreii		8	61	52	30	10	3	0	0	0	5	53	29	9	7	2	0
Platismatia stenophylla		1	2	50	0	0	50	0	0	0	0	50	50	0	0	0	0
Protoparmelia hypotremella		1	1	100	0	0	0	0	0	0	0	0	100	0	0	0	0
Protoparmelia ochrococca		6	28	57	32	4	0	7	0	0	0	75	25	0	0	0	0
Ptychographa xylographoides		4	10	30	40	20	0	0	0	10	0	30	60	0	10	0	0
Pycnora sorophora		1	1	100	0	0	0	0	0	0	0	0	100	0	0	0	0
Pycnora xanthococca		1	1	100	0	0	0	0	0	0	0	0	100	0	0	0	0
Pyrenula occidentalis		3	4	0	0	0	0	0	0	100	0	0	0	0	100	0	0
Pyrrhospora gowardiana		1	1	100	0	0	0	0	0	0	0	0	0	100	0	0	0
Pyrrhospora quernea		6	8	100	0	0	0	0	0	0	0	13	38	0	50	0	0
Ramalina farinacea		3	9	67	33	0	0	0	0	0	0	33	11	44	11	0	0
Ramalina roesleri		1	3	33	33	33	0	0	0	0	0	0	0	67	33	0	0
Scoliciosporum pruinosum		1	2	100	0	0	0	0	0	0	0	50	0	0	50	0	0
Scoliciosporum sp.		1	1	100	0	0	0	0	0	0	0	100	0	0	0	0	0
Segestria leptalea		1	1	0	0	0	0	0	100	0	0	0	0	0	100	0	0
Sphaerophorus globosus		9	203	38	32	18	5	1	0	1	4	46	29	8	5	11	1
Thelotrema lepadinum		8	106	15	19	21	13	8	5	19	1	28	16	14	42	0	0
Trapelia corticola		1	1	0	0	100	0	0	0	0	0	100	0	0	0	0	0
Trapeliopsis flexuosa		6	10	90	10	0	0	0	0	0	0	50	50	0	0	0	0
Trichothelium aeneum		2	2	50	50	0	0	0	0	0	0	0	100	0	0	0	0
Tuckermannopsis chlorophylla		9	94	51	31	14	3	0	0	0	1	44	26	16	12	2	0
Tuckermannopsis orbata		9	49	67	22	8	0	0	0	0	2	44	23	15	17	2	0
Usnea ceratina		9	100	47	31	14	3	0	0	0	5	49	14	27	5	4	0

Appendix A. Continued.

Taxon	Species group	# Trees	# Plots	Stratum								Substrate					
				UC	MC	LC	UT	LT	TF	TER	LIT	Bark	Wood	Leaves	Stems	Bryos	Soil
Usnea chaetophora	*Usnea filipendula*																
Usnea cornuta	*Usnea fragilescens* var. *mollis*																
Usnea filipendula	*Usnea filipendula*	9	55	42	40	9	0	0	0	0	9	46	16	32	6	0	0
Usnea flavocardia	*Usnea fragilescens* var. *mollis*																
Usnea fragilescens* var. *mollis	*Usnea fragilescens* var. *mollis*	9	114	42	26	16	7	3	0	0	6	50	19	21	10	0	0
Usnea hirta	*Usnea hirta*	9	87	64	23	6	1	1	0	0	5	51	27	12	11	0	0
Usnea lapponica	*Usnea hirta*																
Usnea longissima		5	31	45	26	23	0	0	3	0	3	47	3	43	7	0	0
Usnea pacificana	*Usnea filipendula*																
Usnea rubicunda		6	47	66	21	9	2	0	0	0	2	37	28	22	13	0	0
Usnea scabrata	*Usnea filipendula*																
***Usnea* spp.**		9	199	48	32	17	2	1	0	0	1	53	25	14	9	0	0
Xanthoria candelaria		2	7	86	0	14	0	0	0	0	0	57	0	43	0	0	0
Xylographa parallela		1	1	100	0	0	0	0	0	0	0	0	100	0	0	0	0
Xylographa vitiligo		4	6	67	33	0	0	0	0	0	0	33	0	67	0	0	0
CYANOLICHENS																	
Fuscopannaria laceratula		1	1	100	0	0	0	0	0	0	0	0	100	0	0	0	0
Fuscopannaria pacifica		4	8	38	13	0	0	0	0	50	0	13	0	13	50	25	0
Leptogium palmatum		2	3	0	0	0	0	0	0	67	33	0	0	0	0	100	0
Leptogium teretiusculum		1	1	0	0	0	0	0	0	100	0	0	0	0	0	100	0
Lobaria oregana		3	14	21	21	7	14	0	0	7	29	40	0	30	10	20	0
Lobaria pulmonaria		3	6	0	17	50	0	0	0	17	17	40	0	40	20	0	0
Lobaria scrobiculata		1	1	0	100	0	0	0	0	0	0	0	0	0	0	100	0
Nephroma bellum		2	3	0	33	33	0	0	0	33	0	0	0	67	33	0	0
Nephroma laevigatum		2	8	25	13	13	13	0	0	13	25	17	0	67	17	0	0
Nephroma resupinatum		3	3	0	0	0	0	0	0	100	0	0	0	0	100	0	0
Parmeliella parvula		1	1	0	0	100	0	0	0	0	0	0	0	0	0	100	0
Peltigera collina		4	7	29	14	0	0	0	0	43	14	0	17	0	33	50	0
Peltigera neopolydactyla		3	8	0	0	0	0	0	0	75	25	0	0	0	50	50	0
Pseudocyphellaria anomala		2	2	50	50	0	0	0	0	0	0	0	50	0	0	50	0
Pseudocyphellaria anthraspis		4	11	9	45	27	0	0	0	9	9	20	10	30	20	20	0

Appendix A. Continued.

				Stratum								Substrate					
Taxon	**Species group**	**# Trees**	**# Plots**	**UC**	**MC**	**LC**	**UT**	**LT**	**TF**	**TER**	**LIT**	**Bark**	**Wood**	**Leaves**	**Stems**	**Bryos**	**Soil**
Pseudocyphellaria perpetua			4	0	0	0	0	0	0	0	100	0	0	0	0	0	0
Sticta fuliginosa		2	5	20	80	0	0	0	0	0	0	40	20	0	20	20	0
Sticta limbata		1	2	0	0	50	0	0	0	50	0	0	0	50	50	0	0
LIVERWORTS																	
Blepharostoma trichophyllum		1	1	0	0	0	0	0	0	100	0	0	0	0	100	0	0
Calypogeja fissa	*Calypogeia fissa*	6	32	0	0	0	0	0	22	78	0	25	41	0	22	0	13
Calypogeja mulleriana	*Calypogeia fissa*																
Calypogeja neesiana	*Calypogeia fissa*																
Cephalozia bicuspidata	*Cephalozia lunulifolia*																
Cephalozia lunulifolia	*Cephalozia lunulifolia*	9	63	3	8	5	2	8	21	54	0	49	29	0	19	3	0
Cephaloziella rubella		8	80	39	39	19	3	0	1	0	0	53	33	0	3	13	0
Douinia ovata		5	37	30	43	19	0	0	5	3	0	51	32	0	3	11	3
Frullania tamarisci* ssp. *nisquallensis		9	179	23	21	17	9	6	5	18	0	28	13	20	32	6	2
Lepidozia reptans		6	76	1	16	16	11	17	20	20	0	58	18	0	7	11	7
Lophocolea cuspidata		1	3	0	0	0	0	0	0	100	0	0	33	0	67	0	0
Lophocolea heterophylla		7	23	0	4	0	0	9	13	74	0	57	26	0	13	4	0
Metzgeria conjugata		3	5	0	0	0	0	0	0	100	0	0	0	0	60	40	0
Plagiochila porelloides		3	9	0	0	0	0	0	0	100	0	11	22	0	67	0	0
Porella navicularis	*Porella navicularis*	9	73	18	19	12	7	0	4	40	0	29	10	7	42	11	1
Porella roellii	*Porella navicularis*																
Radula bolanderi		5	5	0	0	0	0	0	0	100	0	0	0	0	100	0	0
Riccardia latifrons	*Riccardia latifrons*	3	7	0	0	0	0	0	0	100	0	14	57	0	29	0	0
Riccardia multifida	*Riccardia latifrons*																
Scapania bolanderi		9	133	4	17	25	11	9	11	24	0	46	28	0	14	11	2
MOSSES																	
Antitrichia gigantea		4	11	45	27	0	9	0	0	18	0	36	18	9	27	0	9
Aulacomnium androgynum		2	2	0	50	0	0	0	0	50	0	50	50	0	0	0	0
Brachythecium asperrimum		1	1	0	0	0	0	0	0	100	0	0	100	0	0	0	0
Bryum capillare		2	10	50	40	10	0	0	0	0	0	60	20	0	0	0	20
Buckiella undulata		6	27	0	0	0	0	0	7	93	0	19	33	4	33	0	11
Buxbaumia piperi		1	1	0	100	0	0	0	0	0	0	0	100	0	0	0	0

Appendix A. Continued.

				Stratum								Substrate					
Taxon	**Species group**	**# Trees**	**# Plots**	**UC**	**MC**	**LC**	**UT**	**LT**	**TF**	**TER**	**LIT**	**Bark**	**Wood**	**Leaves**	**Stems**	**Bryos**	**Soil**
Buxbaumia viridis		1	1	0	0	0	0	0	0	100	0	0	100	0	0	0	0
Claopodium crispifolium		1	1	0	0	0	0	0	0	100	0	0	0	0	100	0	0
Dicranoweisia cirrata		7	41	56	32	10	0	2	0	0	0	59	32	10	0	0	0
Dicranum fuscescens	*Dicranum fuscescens*	9	353	24	29	20	9	7	4	7	0	62	25	2	6	0	5
Dicranum howellii	*Dicranum fuscescens*																
Fissidens bryoides		2	2	0	0	0	0	0	50	50	0	0	50	0	0	0	50
Homalothecium nuttallii		1	1	0	0	0	0	0	0	100	0	0	0	0	100	0	0
Hookeria lucens		4	6	0	0	0	0	0	0	100	0	33	17	0	33	0	17
Hypnum circinale	*Hypnum circinale*	9	266	25	29	23	12	5	2	5	0	60	30	2	4	0	3
Hypnum subimponens	*Hypnum circinale*																
Isothecium cristatum		6	118	25	28	24	4	3	4	13	0	61	31	3	0	0	6
Isothecium stoloniferum		9	400	11	17	17	10	6	11	29	0	36	22	12	22	0	9
Kindbergia oregana		9	60	0	5	0	0	0	12	83	0	30	15	2	35	0	18
Leucolepis acanthoneura		4	14	0	0	0	0	0	0	100	0	0	14	0	57	0	29
Metaneckera menziesii		1	3	0	0	0	0	0	0	100	0	0	0	0	100	0	0
Neckera douglasii		5	23	9	4	4	9	4	9	61	0	17	9	9	65	0	0
Orthodicranum tauricum		9	62	50	35	6	5	2	2	0	0	56	37	0	6	0	0
Orthodontium gracile		9	137	15	28	25	12	11	9	1	0	81	19	0	0	0	0
Orthotrichum papillosum		5	14	57	29	14	0	0	0	0	0	43	21	29	7	0	0
Plagiomnium medium		1	2	0	0	0	0	0	0	100	0	0	0	0	50	0	50
Porotrichum bigelovii		6	29	0	0	0	0	0	10	90	0	7	14	0	66	0	14
Pseudotaxiphyllum elegans		8	32	0	3	3	9	6	25	53	0	47	31	0	3	0	19
Rhizomnium glabrescens		6	28	0	0	0	0	0	0	100	0	14	29	0	46	0	11
Tetraphis pellucida		5	23	4	0	4	0	0	43	48	0	48	48	0	4	0	0
VASCULAR PLANTS																	
Acer circinatum		3	5	0	0	0	0	0	40	60	0	0	0	0	0	0	100
Acer macrophyllum		2	2	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Actea rubra		1	1	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Adiantum aleuticum		1	1	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Asarum caudatum		1	1	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Athyrium filix-femina		8	12	0	0	0	0	0	25	75	0	0	17	0	8	0	75

Appendix A. Continued.

				Stratum								Substrate					
Taxon	Species group	# Trees	# Plots	UC	MC	LC	UT	LT	TF	TER	LIT	Bark	Wood	Leaves	Stems	Bryos	Soil
Blechnum spicant		4	5	0	0	0	0	0	0	100	0	0	20	0	0	0	80
Cardamine californica		5	6	0	0	0	0	0	17	83	0	0	0	0	0	0	100
Cardamine nuttallii		1	1	0	0	0	0	0	100	0	0	0	0	0	0	0	100
Claytonia siberica		4	6	0	0	0	0	0	33	67	0	0	0	0	0	0	100
Corylus cornuta		3	3	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Dryopteris expansa		3	5	0	0	0	0	0	60	40	0	20	0	0	0	0	80
Galium aperine		5	6	0	0	0	0	0	17	83	0	0	0	0	0	0	100
Gaultheria shallon		4	10	40	20	0	0	0	10	30	0	0	20	0	0	0	80
Glyceria elata		1	2	0	0	0	0	0	50	50	0	0	0	0	0	0	100
Hydrophyllum tenuipes		1	1	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Lithocarpus densiflorus		5	6	0	0	17	0	0	33	50	0	0	0	0	0	0	100
Luzula parviflora		2	3	0	0	0	0	0	33	67	0	0	0	0	0	0	100
Marah fabaceous		3	4	0	0	0	0	0	25	75	0	0	0	0	0	0	100
Oxalis oregana		9	18	0	0	0	0	0	33	67	0	6	11	0	6	0	78
Picea sitchensis		1	4	0	25	0	0	0	25	50	0	25	25	0	0	0	50
Poa sp.		1	1	0	100	0	0	0	0	0	0	0	0	0	0	100	0
Polypodium glycyrrhiza		8	59	10	31	24	3	5	3	24	0	19	10	0	15	27	29
Polypodium scouleri		7	86	23	35	27	7	0	6	2	0	36	24	0	1	10	28
Polystichum munitum		9	15	0	0	7	0	0	33	60	0	0	0	0	0	0	100
Pseudotsuga menziesii		2	2	50	0	0	0	0	0	50	0	0	0	0	0	0	100
Pteridium aquilinum		1	1	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Ranunculus californicus		1	1	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Rhamnus purshiana		3	4	0	0	50	0	0	0	50	0	0	0	0	0	0	100
Rhododendron occidentale		1	3	0	0	0	0	33	33	33	0	0	0	0	0	0	100
Ribes laxiflorum		2	3	0	0	67	0	0	33	0	0	0	0	0	0	0	100
Rosa gymnocarpa		1	1	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Rubus leucodermis		1	1	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Rubus spectabilis		5	6	0	0	0	0	0	33	67	0	0	0	0	0	0	100
Rubus ursinus		3	4	0	0	0	0	0	25	75	0	0	0	0	0	0	100
Sambucus racemosa		3	3	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Selaginella oregana		1	3	0	0	0	0	0	0	100	0	0	0	0	67	33	0

Appendix A. Continued.

				Stratum								Substrate					
Taxon	**Species group**	**# Trees**	**# Plots**	**UC**	**MC**	**LC**	**UT**	**LT**	**TF**	**TER**	**LIT**	**Bark**	**Wood**	**Leaves**	**Stems**	**Bryos**	**Soil**
Sequoia sempervirens		9	9	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Stachys adjugoides		3	3	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Tellima grandiflora		1	1	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Tolmiea menziesii		4	4	0	0	0	0	0	25	75	0	0	0	0	0	0	100
Toxicodendron diversilobum		1	4	0	0	0	0	0	75	25	0	50	0	0	0	0	50
Trillium ovatum		1	1	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Tsuga heterophylla		5	16	6	6	6	0	0	44	38	0	31	25	0	0	0	44
Umbellularia californica		4	4	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Vaccinium ovatum		7	64	27	17	11	3	5	20	17	0	31	33	0	3	0	33
Vaccinium parvifolium		4	30	13	13	3	0	10	33	27	0	33	23	0	3	0	40
Vancouveria hexandra		1	1	0	0	0	0	0	0	100	0	0	0	0	0	0	100
Viola sempervirens		1	1	0	0	0	0	0	0	100	0	0	0	0	0	0	100