Pacific Northwest Fungi

Epiphytic lichens along gradients in topography and stand structure in western Oregon, USA

Shanti Berryman[1] and Bruce McCune[2]

[1]*Department of Forest Science, Richardson Hall 321, Oregon State University, Corvallis, Oregon 97331;* [2]*Department of Botany and Plant Pathology, Cordley Hall 2082, Oregon State University, Corvallis, Oregon 97331*

Abstract: Epiphytic macrolichen communities were compared among forest stand types in the Blue River watershed of western Oregon. Stand types were defined by stand structure, according to age classes of the younger tree cohort and remnant tree retention. Remnant trees were those in an older cohort that remained following a stand disturbance that initiated tree regeneration, such as a timber harvest or natural forest fire. Stands were located in upland and riparian forests of two vascular plant series (western hemlock and true fir). Presence and abundance of all epiphytic macrolichen species were sampled in a 0.4 ha circular plot in 117 stands. Nonmetric multidimensional scaling (NMS) ordination revealed that the strongest differences in lichen community composition were related to elevation, which was correlated with vascular plant series. Cyanolichens were largely limited to lower elevation forests (470 – 950 m) of the western hemlock series, while matrix lichens and forage lichens with green-algal photobionts dominated high elevation stands (950 – 1470 m) of the true fir series. Lichen communities differed with stand age. In even-aged young stands, lichen communities were species poor and lichen community composition differed from all other stand types. In general, macrolichen species richness varied little among stand types. However, cyanolichen species were most diverse in old-growth and mature stands at lower elevations. Lichen communities in young stands (< 20 yr) with remnants differed from those in even-aged young forests in both

plant series. As a stand develops, the presence of remnant trees may accelerate the development of the lichen community towards those found in older stands. We infer that remnant trees serve as refugia for lichens through a disturbance and provide lichen inoculum to younger trees. Hardwood patches were hotspots for lichen diversity, particularly cyanolichens that are infrequent on conifers. Hardwood patches were most prevalent along perennial streams. To maintain and enhance lichen communities at a landscape level, forest managers must consider the importance of features such as late-successional stands, remnant trees, hardwoods, and riparian areas to lichen communities. These features are especially important to retain in or near regenerating forests to promote colonization by dispersal-limited lichens.

Key words: Cascade Range, cyanolichens, elevation, forage lichens, forest age, stand structure, remnant trees.

Introduction

We studied the importance of various ecological factors, such as stand age, remnant tree retention, and topography to lichen communities across a forested landscape in western Oregon. Others have documented relationships between these factors individually and lichen communities in the Pacific Northwest (PNW; Peck and McCune 1997; Peterson and McCune 2001; Pipp et al. 2001; McCune 1993; Neitlich 1993); however, relationships to combinations of these factors have not been examined at the landscape scale.

Forest fragmentation, clearcutting, and fire suppression have raised concerns regarding the maintenance of biodiversity in forest ecosystems (Harris 1984; Norse 1990). Lichens have become a focus because they represent a responsive component of biodiversity in forests of the Pacific Northwest of North America (Neitlich 1993; Neitlich and McCune 1997; Peterson and McCune 2001; Rosentreter 1995) and in forests throughout the world (Brown et al.1994; Dettki and Esseen 1998; Holien 1998; Kuusinen 1994; Kuusinen and Siitonen 1998; Pharo et al. 1999; Price and Hochachka 2001; Selva 1994). In addition, lichens play important roles in ecosystems. For example, lichens containing cyanobacteria are important contributors of fixed nitrogen in forest ecosystems (Antoine 2001; Pike 1978) and may be particularly important in N-limited old-growth temperate forests of North America (Sollins et al. 1980). Additionally, many epiphytic macrolichens are important in the terrestrial food-webs, providing nutrition for mollusks, small mammals, and large ungulates (summarized in McCune 1993).

Old-growth forests support diverse epiphytic macrolichen communities and provide habitat for many rare lichens in the PNW (Campbell and Fredeen 2004; Keon and Muir 2002; McCune 1993; Neitlich 1993; Peterson and McCune 2001; Rosentreter 1995; Rosso et al. 2000; Sillett and Goward 1998) and in other forests of the world (Brown et al. 1994; Holien 1998; Kuusinen and Siitonen 1998; Selva 1994). In addition, epiphytic macrolichens are abundant in old-growth forest canopies (Berryman 2002; Dettki and Esseen 1998; Esseen 1985; Esseen et al. 1996; McCune 1993; McCune et al. 1997*a*; Neitlich 1993; Pike et al. 1977, 1972; Rhoades 1981). Biomass of old-growth associated lichens develops slowly in the old-growth conifer forests of the PNW (Sillett et al. 2000*a,* 2000*b*; Sillett and McCune 1998), in which cyanolichen biomass can exceed 1 T/ha (Berryman 2002; McCune 1993; Neitlich 1993; Sillett 1995).

In the PNW forests, most of the old growth has been cut. The remaining old growth is largely restricted to federal lands (Harris 1984; Spies et al. 1994). The loss of old-growth forests could result in the decline or local extinction of some old-growth associated lichen species (Goward 1993, 1994; Rosentreter 1995; Rosso et al. 2000; Sillett and Goward 1998), forest continuity and propagules needed for successful dispersal.

Lichen communities in very young forests differ from those in older forests. Lichens may be slow to colonize young forests because the quality of substrate is poor (Esseen et al. 1996) or because of unsuitable habitat due to microclimate conditions or simply because they need time to develop. However, recent transplant and sowing studies have shown that certain old-growth associated lichens grow just as well or better in young stands as compared to old stands (Keon and Muir 2002; Sillett et al. 2000*a*, 2000*b*). Habitat and substrate suitability may be less important than dispersal in limiting certain old-growth-associated lichens (Dettki et al. 2000; Hilmo 2002).

Management strategies can address the lichen dispersal-limitation problem. Maintaining remnant trees in forest stands during timber harvest may promote epiphytic macrolichen diversity and biomass in the landscape. Remnant trees can serve as refugia for lichens during timber harvest, ameliorate the microclimate following harvest and provide lichen inoculum to the regenerating trees (Berryman 2002; Peck and McCune 1997; Sillett and Goslin 1999). In addition, managing to create or maintain structural variability in stands, such as small forest gaps, large snags and wolf trees may also provide important microhabitat for epiphytic lichens, thereby enhancing lichen diversity and biomass in managed forests

(Neitlich and McCune 1997; Peterson and McCune 2001; Pipp et al. 2001). Wolf trees are conifers that are open-grown most of their life history and they have large branches (at least 6 cm diameter) present less than 3 m above the ground (Neitlich and McCune 1997). Maintaining natural diversity "hotspots" in the landscape, such as hardwoods and riparian areas, may also promote lichen diversity at the landscape level (McCune et al. 2002; Neitlich and McCune 1997; Peterson and McCune 2001; Rolstad et al. 2001; Rosso 2000).

In this study we compared epiphytic macrolichen communities among a broad spectrum of forest structural types in the Blue River watershed of the western Cascade Mountains. Forest stands were typed by stand age, degree of remnant tree retention, uplands or riparian areas, and vascular plant series. The relationships between lichen communities and stand structure that were revealed here can be used to predict the likely consequences of alternative forest management strategies for epiphytic lichen presence and biomass in the future landscape (Berryman 2002; McCune et al. 2003).

Materials and Methods

STUDY AREA
The study site is located in the Blue River watershed of the Central Cascades Adaptive Management Area (AMA) in the Willamette National Forest, Oregon (Fig. 1). Stands were sampled between 44.0 and 44.5° N, and 122.0 and 123.0° W. The Blue River watershed consists of 23,900 ha of conifer-dominated forest on steep volcanic terrain of the Cascade Mountain Range, ranging from 317 – 1,639 m in elevation (Cissel et al. 1999). Annual precipitation averages 220 cm (ranging from 55 to 361 cm), deposited as rain or snow in higher elevations, mainly between October and April. The winters are mild and wet with

average temperature of 2°C in January (ranging from -1.5 to 7.3°C), and the summers are warm and dry with average temperature of 19°C in July (ranging from 15 to 22°C). The northern section of the watershed consists of a narrow band of high elevation, *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) and *Abies procera* Rheder (Noble fir) dominated forest (hereafter, "true fir series;" Logan et al. 1987). Most of the watershed is lower elevation forest dominated by *Pseudotsuga menziesii* (Mirb.) Franco. (Douglas fir) and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock; hereafter, "western hemlock series;" Logan et al. 1987).

The Blue River watershed has had decades of fire suppression and timber extraction. Historical fire regimes varied in frequency and severity within the watershed (Weisberg 1998). Forests in true fir series burned infrequently (mean fire interval of 260 yr), but fires were severe with high mortality (> 80%). The fire return interval for the western hemlock series ranged from 100 to 180 yr with less severe burns (40-80% mortality). Consequently, forests in the two plant series will be managed differently in the Blue River watershed, as part of the Landscape Plan (LP) which is an adaptive management approach using historical fire history as reference for management (Cissel et al. 1999).

SAMPLE DESIGN
Lichen communities were sampled in forest stands according to a stratified random design. Forest stands were stratified by four attributes, modified from Cissel et al. (1999; Fig. 2):

(1) two plant series (western hemlock and true fir), plant series were determined based on the key to climax vegetation, Logan et al. 1987;

(2) four age classes (the younger tree cohort; young < 20 yr, pole 21-80 yr, mature 81-200 yr; and old growth > 200 yr);

(3) four classes of remnant retention based on the percent canopy cover of remnant trees that survived from the previous stand, following a disturbance that initiated tree regeneration: 0 = 0 - 7.5%; 15 = 7.5 - 22.5%; 30 = 22.5 - 37.0%; 50 = 37.0 - 62.0%. Remnant trees included the older live trees that remained following the most recent timber harvest or those old trees that survived a natural forest fire. The characteristics of remnant trees (i.e., size, crown structure) varied among stands because remnants from a timber harvest were often smaller and younger than those remnants surviving forest fires. Old-growth stands were not stratified by remnant classes. Only 0% and 15% retention classes were sampled in the true fir series, since future management strategies will prescribe only these retention levels in the true fir series (Cissel et al. 1999);

(4) four topographic classes (upland, and three riparian stream classes: intermittent; perennial non fish-bearing; and perennial fish-bearing). We adopted these stream classes from the LP management strategy to strengthen the link between our results and management activities.

Upland stands were at least two tree-heights (~ 105 m) from perennial streams (hereafter referred to as "perennial fish-bearing") and one tree-height (~ 52 m) from all other streams (USDA and USDI 2001). Riparian stands were defined as having some part of the stream within or immediately bordering the plot boundary. Intermittent streams formed narrow channels and the stream-bank vegetation was similar to that of upland slopes. Perennial streams formed wider channels and vegetation along the stream banks was characteristic of riparian areas, including

hardwood trees and shrubs. We were unable to identify stands along perennial streams with a definite remnant cohort; therefore, these stands were stratified by the age-class of the co-dominant tree cohort, ignoring the remnant stratum (Fig. 2).

The design yielded 34 possible stand types for the western hemlock series and 22 for the true fir series, of which we sought to sample three stands each. However, some stand types were sampled with fewer stands or were not sampled due to their scarcity or absence in the landscape (such as stands with remnant retention ≥ 30%). The 50% remnant retention class was uncommon in the landscape at the time of sampling and was therefore under-represented compared to other retention classes. The 50% retention class will become more prominent in the future landscape as managed under the LP (Cissel et al. 1999). We sampled 27 stand types in the westem hemlock series, 6 of which were sampled with < 3 stands. In the true fir series we sampled 18 stand types, 10 of which were sampled with < 3 stands.

STAND SELECTION AND PLOT INSTALLATION
We located stand types from aerial photos. Most stands were within the Blue River watershed, however some stands were located outside of the watershed, but still on the Willamette National Forest and within the AMA boundaries (Berryman 2002). Stands sampled outside of the Blue River watershed represented stand types that were scarce or absent in the watershed. Stands were sampled in the summers of 1997-1999 using one permanent plot (34.7 m radius, 0.4 ha) per stand following the FHM plot methodology (McCune et al. 1997*b*).

Once the stand was located on the ground, a reference point (RP) was established

along the road to assist in future plot relocation. From the RP (typically a tree) we chose an approximate azimuth into the stand. The RP was labeled with metal tags indicating the azimuth and distance to plot center. This azimuth was followed for 46.0 m (not slope-corrected) plus a two-digit random integer. Plot center was located no less than 46.0 m from: designated reserve areas in timber sales (other than stream buffers); the stand edge; roads; campgrounds; and power lines. Failing this, another random number was chosen and the same azimuth was followed until plot center was located outside of these exclusive areas and at least within 46.0 m of the stand edge. Riparian plots were installed to border the stream edge.

Plot center was marked with steel rebar and PVC pipe to increase the possibility of plot relocation after major disturbances, such as a fire or timber harvest. Three RP trees near plot center were tagged to reference the plot center with an azimuth and distance to facilitate relocation

LICHEN COMMUNITY SURVEY
The Forest Health Monitoring (FHM) lichen method was used to sample lichen communities in each stand. These data will be used as a baseline for long-term monitoring of lichen communities in the managed landscape. In each FHM plot, the surveyor completed a maximum two-hour ocular lichen community survey. The survey method consisted of two parts performed simultaneously (McCune et al. 1997*b*): 1. The field surveyor collected specimens of each species present for identification in the lab. The collection represented the species diversity and composition of epiphytic macrolichens in the plot as fully as possible. The population sampled consisted of all macrolichens occurring on woody plants, excluding the 0.5 m basal portions of trees and shrubs below 0.5 m. Given the large plot area,

lichen litter and fallen branches provided a sample of the canopy lichens. 2. The abundance of each species was estimated using a five-step scale (modified from McCune et al. 1997*b*): 0 = absent; 1 = rare (< 3 individuals per plot); 2 = uncommon (4-10 individuals per plot); 3 = common (>10, but < 40 individuals per plot); 4 = very common (> 40 individuals per plot, but less than half of the available substrate was covered by the species); 5 = abundant (more than half of the available substrate had the species present).

The FHM method has been used to sample lichen communities in over 1,000 plots for the FHM program nationwide (McCune 2000) and has been used by the Pacific Northwest Forest Service Air Quality Biomonitoring Project for nearly 1,000 lichen community plots in Oregon and Washington (L. Geiser, unpublished data). Field methods have been documented for repeatability and quality assurance and are described in McCune et al. (1997*b*).

Lichen nomenclature followed McCune and Geiser (1997), and McCune's key (2002, http://oregonstate.edu/~mccuneb/Usnea.PDF) to the genus *Usnea* in the Pacific Northwest. Representative voucher specimens were deposited in the Oregon State University Herbarium (OSC).

STAND VARIABLES
Latitude and longitude coordinates and topographic features such as slope, aspect, and elevation were recorded at the plot center for each stand. We calculated the heat load index and potential direct incident radiation for each stand. The heat load index represents the amount of heat a site potentially receives and is derived from models based on latitude, slope, and aspect (McCune and Keon 2002). Potential direct incident radiation ($MJ/cm^2/yr$) represents the amount of light a site potentially receives, and is also derived from latitude, slope, and

aspect. Stand basal area (BA, m^2/ha) was measured for all live and dead trees, separating hardwoods and conifers. BA was measured with an angle gauge in five variable-radius subplots within each stand: one at plot center and the other four at 23.0 m in each cardinal direction from plot center. A consistent BA factor was used for all subplots within one stand, though the factor varied across all stands, depending on tree size and density. Diameter at breast height (dbh), crown width, and tree species were measured for the trees recorded in the BA subplots.

The age class of the younger cohort was estimated for the stand, or, if the age class was difficult to determine, we cored representative trees. Old growth was defined as stands > 200 yr with highly variable canopy layers. Total percent canopy cover of remnant trees was used as an estimate of total percent retention of remnants for a stand. We estimated canopy cover of remnants from dbh and crown width. J. Mayo (unpublished data) developed a table for estimating canopy cover of trees from dbh. This table is based on the relationship of dbh to crown width, from which percent canopy cover by each remnant tree was calculated. Remnants were typically *Pseudotsuga menziesii*, and in some cases *Tsuga heterophylla*, *Thuja plicata,* or *Abies procera*. Remnant tree age was not measured, but we documented remnant characteristics (i.e., diameter at breast height, crown width, tree health) and estimated remnant tree age in our field observations.

ANALYSIS: LICHEN COMMUNITY COMPOSITION
We used nonmetric multidimensional scaling to ordinate stands in lichen species space. The ordination was used to assess gradients in lichen community composition and their ecological relationships with topography and stand structure. An

arbitrary cut-off of $R^2 \geq 0.3$ was used when assessing correlations of environmental variables and species richness with the ordination axes. NMS is an iterative technique that can extract non-linear gradients in species space (McCune and Grace 2002). Sørensen distance measure was used with the Slow-and-Thorough autopilot settings in PC-ORD 4.0 (40 runs of 400 iterations; McCune and Mefford 1999). Lichen species present in < 5% of the plots were excluded from the analysis, eliminating 41 rare species to reduce noise in the data ("reduced species matrix").

Multivariate outlier analysis of all 117 stands found nine potential outliers, three of which had average distances to other stands > 3 standard deviations from the grand mean of distances among stands. When the outliers were excluded from the ordination analysis, the patterns of the stands in the ordination did not change appreciably. We concluded that the outliers were non-influential in the ordination and did not disrupt patterns in the other points. Therefore, these stands were included in the subsequent analyses.

NMS was run on the reduced species matrix across vascular plant series. This ordination was rotated to align the elevation gradient with an axis because this was the strongest environmental gradient separating lichen communities in the watershed. The vascular plant series were correlated with the elevation gradient. The species and environmental matrices were then partitioned by vascular plant series to more closely examine the relationship of lichen communities to forest structure and topographic classes. This partitioning diminished the overwhelming influence of elevation on lichen communities. Sampling was limited by the availability of stand types in the watershed and therefore, it was not possible to stratify by elevation within the two plant series.

The ordination of all 117 stands in lichen species space revealed ten high elevation stands classified in the western hemlock series (young *Pseudotsuga menziesii* plantations) that positioned with the true fir stands. These ten stands were thereafter included in the true fir species matrix, because their lichen epiphytes were more similar to those in the true fir series than to those in the western hemlock series. Thus, the final species matrix for the western hemlock series consisted of 67 stands and the true fir series species matrix consisted of 50 stands.

NMS was run separately on the species matrix for each vascular plant series. The western hemlock species matrix had four outliers; one stand was extreme (3.75 standard deviations from the grand mean of distances among stands). The stand was an outlier due to the absence of many common species; however, we chose to retain it in the species matrix since, when excluded, it did not affect the overall patterns of the NMS ordination. Similarly, the true fir matrix had five non-influential outlying stands in the NMS ordination.

We also evaluated differences in lichen communities in the ordinations along a stand structural gradient for each plant series. To achieve this, we developed an age index to integrate the many stand types into a single continuous variable, representing the biological significance of the influence of old trees on lichen communities. The age index combines age "credits" for the age classes and for the remnant trees in each stand and expresses them as a percentage of old growth.

Age credits were assigned according to the median tree age for the age classes of the younger cohort and for old growth (Table 1). The *a priori* median age for old growth was arbitrarily selected as 300 yr based on estimates for old-growth forests we sampled

in the Blue River watershed. The age credits for the younger cohort were the "base age credits." If remnant trees were present in a stand, we added the percent of remnants (15, 30, or 50%) to the "base age credits." This sum was the age index value for the stand (Table 1). Each stand type received a value between 3 and 100, where 100 represented old growth and 3 represented an even-aged young stand. We $\log_{10}$-transformed the age index (hereafter "age index" or "AI") to improve linearity with lichen response variables.

Each 2-D ordination was rotated to maximize the correlation of the age index with one axis, so that the scores on that axis represented the lichen community composition gradient in relation to the age index. We compared ordination scores from the age axis among stand types. This allowed us to assess differences in lichen composition among stages of stand development. We averaged the ordination scores by stand type for all even-aged stands and for young stands (< 20 yr) with 15% remnants and young stands with ≥ 30% remnants (combining the 30 and 50% retention classes) to assess how the presence of remnants following a disturbance is related to lichen community composition in regenerating young stands. When making these calculations for the western hemlock series, we omitted one anomalous young stand with 50% remnant retention (this stand was not an outlier overall). The lichen community in this stand was anomalous compared to those in other stands of the same stand type. In addition, our field observations indicated that the remnants in this stand appeared to be much younger than those present in other stands of the same stand type.

Epiphytic macrolichens were divided into three functional groups (McCune 1993) to analyze patterns in lichen community structure from a functional perspective.

These groups included "cyanolichens," which consist of all N-fixing lichens with cyanobacteria present as either the primary or secondary photobiont; "forage lichens," which consisted of all alectorioid lichens (i.e., fruticose) used as forage by wildlife (Edwards et al. 1960; Rominger & Oldemeyer 1989; Rosentreter et al. 1997), primarily the genera *Alectoria, Bryoria,* and *Usnea*; and "matrix lichens," which included all remaining green-algal macrolichens, primarily foliose lichens. Patterns of lichen composition and diversity for each functional group were assessed in the ordinations with respect to topographic gradients and stand structure.

Multi-Response Permutation Procedures (MRPP; Berry et al. 1983; McCune and Mefford 1999; Mielke 1984) tested for differences in lichen community composition between groups (e.g., between plant series, among topographic classes, and among even-aged stands and stands with remnants), based on Sørensen distances. When comparing lichen communities among topographic classes (i.e., uplands and riparian classes), we used both even-aged stands and stands with remnants. Differences in lichen communities among topographic classes were weak, so we chose to ignore topographic class in our analyses of lichen communities and stand structure.

Within each plant series, MRPP compared differences in lichen composition across all stand types and separately for stands with remnants and even-aged stands without remnants. To further clarify differences in lichen communities with stand types, we made multiple pair-wise comparisons between stand types using MRPP, comparing differences in lichen composition for all macrolichens and for each functional group. A total of 36 multiple pair-wise comparisons were made for the western hemlock series and significant differences in

lichen communities were reported at the 0.05 level. Of these 36 comparisons, we would expect approximately two to be significant by chance at the 0.05 level. Of the fifteen pair-wise comparisons made for the true fir series, we expected approximately one to be significant by chance at the 0.05 level.

Indicator species analysis (ISA; Dufrêne and Legendre 1997; McCune and Mefford 1999) was used to calculate indicator values for lichen species, for the two plant series, for even-aged stands, and for topographic classes. The species indicator value (IV) combines lichen species relative frequency and abundance within given groups of stand types (e.g., between plant series). The indicator value reflects the faithfulness of a species to a particular group. Stand types with fewer than three stands were excluded from the analyses.

ANALYSIS: SPECIES DIVERSITY
We calculated several measures of species diversity (Whittaker 1972). Alpha (α) diversity is the average species richness per stand. Gamma (γ) diversity is the total number of species found across all stands in the landscape. Two measures of beta diversity were calculated: Whittaker's beta diversity (γ/α) and average half changes (HC; McCune and Grace 2002) among stands. Whittaker's beta diversity measures compositional heterogeneity across plots, using the ratio of the total number of species, to the average number of species per stand (γ/α). The second measure of beta diversity is the average Sørensen distance among stands, transformed to half changes by: $HC = \log(1-D)/\log(0.5)$, where D is the average distance (one HC equals a 50% change of community composition). All diversity measures were calculated for the full species matrices, which included all rare species.

We evaluated differences in lichen species richness between plant series for all 117 stands, indicating differences for all macrolichens, cyanolichens, forage lichens, and matrix lichens (analyses by SPSS 8.0; Anon. 1998). Differences in macrolichen richness between plant series were tested using an independent sample t-test. Subsequent analyses of lichen species richness were performed on the species matrices partitioned by plant series to reduce the influence of elevation. In each plant series, we assessed differences in epiphytic lichen species richness among stand types and among topographic classes using one-way ANOVA and Tukey's honestly significant difference test (Tukey's HSD) of multiple comparisons between groups. As mentioned above, we ignored topographic class when assessing lichen species richness in relation to stand structure and we combined stand types when assessing lichen species richness in relation to topographic classes. Stand types with fewer than three stands were excluded from the ANOVA.

Results

ELEVATION GRADIENT
Differences in lichen community composition in the Blue River watershed were most strongly related to elevation (Fig. 3; Table 2). The 2-D NMS ordination of 117 stands in species space described 82% of the variance in the community structure (axis 1 = 33% and axis 2 = 49%) and axis 2 was highly correlated with elevation (R^2 = 0.66). Axis 1 was correlated with the age index (R^2 = 0.54) and live tree BA (R^2 = 0.36). Stands in the true fir series generally positioned low on axis 2 (higher elevations, 950 – 1470 m) while stands in the western hemlock series fell higher on axis 2 (lower elevations, 470 –950 m). Lichen communities in stands at intermediate elevations (940 – 1285 m) were similar between the two plant series. The absence

of cyanolichens in the high elevation stands and their abundance at lower elevations was largely responsible for the differences in lichen community composition in stands of the two plant series (MRPP, $p < 0.001$, $A = 0.05$). Other topographic variables such as heat load index, potential direct incident radiation, slope, and aspect were weakly correlated with the ordination axes (maximum $R^2 = 0.05$).

A total of 111 taxa were found across the 117 stands (Table 3). Many lichen species were strongly associated with each plant series (Table 3), of which cyanolichens were more dominant in the western hemlock series at lower elevations (12 cyanolichens). *Lobaria oregana* was present in 90% of the lower elevation stands of the western hemlock series (IV = 77.8, $p = 0.001$). In contrast, *Lobaria* species were found only in four stands in the true fir series at higher elevations and *Pseudocyphellaria anomala*, *P. crocata*, and *Nephroma parile* were present in only a few true fir stands (Table 3). Cyanolichens were always sparse when found in the true fir series.

Several forage lichens were more frequent and in greater abundance at higher elevations, true fir series, including three *Bryoria* spp. and *Nodobryoria oregana* (Table 3). Very little *Bryoria* was found in the lower elevation forests and when present, it was less abundant than in the true fir series. *Alectoria sarmentosa* was present in greatest abundance in the true fir series (IV = 54.8, $p = 0.003$), where it could be found covering > 50% of tree boles and branches in old growth. *Alectoria* and *Bryoria* typically co-occurred in matted clumps on tree boles and branches in the true fir series. Many matrix lichens (e.g., *Hypogymnia* and *Platismatia*) were also dominant species found in the true fir series (Table 3).

Nearly ubiquitous lichens were *Alectoria sarmentosa*, *Hypogymnia inactiva, H. enteromorpha, H. imshaugii, H. physodes, Platismatia glauca, P. herrei, P. stenophylla, Nodobryoria oregana*, *Parmeliopsis hyperopta*, and *Usnea scabrata.* These occurred in most stands regardless of stand structure or plant series. *Alectoria sarmentosa* and *Usnea scabrata* were two of the most common and abundant forage lichens in the watershed, although *A. sarmentosa* was in greatest abundance at higher elevations (Table 3). *Hypogymnia enteromorpha, H. inactiva*, and *Platismatia glauca* were the most frequent matrix lichens throughout the watershed, abundant in most stands (Table 3).

SPECIES DIVERSITY
Cyanolichen diversity differed greatly between the two plant series (Table 4). Cyanolichens were more diverse in the lower elevation western hemlock series than in the true fir series at higher elevations. Gamma diversity was 25% lower in the true fir forests than in the western hemlock series. However, the number of stands sampled in the true fir series (N = 50) was less than in the western hemlock series (N = 67). Consequently, the differences in gamma diversity between the two plant series may be partly a reflection of differences in the area sampled. In addition, average alpha diversity (α) was slightly higher for stands in the western hemlock series as compared to stands in the true fir series (95% CI for the difference in average α between the two plant series = 1.7 to 6.2 species; Table 4). Average forage lichen species richness was slightly higher in stands of the true fir series as compared to stands in the western hemlock series (95% CI for the difference in α of forage lichens = 0.5 to 1.8 species), however, beta diversity and gamma diversity of forage lichens was similar between the two plant series. Average matrix lichen diversity measures were

similar between both plant series. Matrix lichen species richness was higher than that of cyanolichens and forage lichens in both plant series. Lichen diversity did not differ by slope and aspect in this study.

WESTERN HEMLOCK SERIES
We evaluated lichen community composition and lichen diversity in relation to stand structure separately for each plant series to control partially for the influence of elevation. Still, lichen communities varied with elevation (range 469 – 1286 m) within the western hemlock series. The second 2-D ordination described a cumulative variance of 83% in lichen community structure and was rotated to maximize the correlation of the age index with axis 1 (axis 1 = 58% and axis 2 = 25%; Fig. 4A; Table 5). The elevation gradient was orthogonal to age index in the ordination. Cyanolichens were most abundant in low elevation stands with higher age-indices. Total BA of the stand generally increased with stand age and with increased remnant retention (Table 6), but was weakly correlated with lichen communities in the ordination (R^2 = 0.24, with axis 1 and R^2 = 0.08, with axis 2). Other topographic variables such as the heat load index, potential direct incident radiation, slope, and aspect were again unrelated to lichen communities (maximum R^2 = 0.08).

WESTERN HEMLOCK SERIES: LICHEN COMPOSITION AND STAND STRUCTURE
Lichen community composition differed among stand types (MRPP, *A* = 0.08, *p* < 0.001; Table 7). The small *A* statistic from MRPP indicates broad overlap in lichen communities among stand types (Fig. 4A). This variation of lichen communities within stand types may be related in part to the influence of elevation. For example, older stands present at higher elevations in the western hemlock series typically had fewer and less abundant cyanolichens present

than similar aged stands at lower elevations.

Lichen communities differed among all even-aged stand classes and old growth (*A* = 0.09, *p* < 0.001) with the most prominent differences between young (< 20 yr) and old stands (Fig. 4A). Forage and matrix lichen species composition also differed with stand age classes (*A* = 0.03, *p* = 0.05 and *A* = 0.08, *p* < 0.001, respectively). Lichen community composition of even-aged young stands was most different from all other stands, because these stands had few species (Figs. 5 and 6) and those present were in low abundance. Lichen populations in even-aged pole stands were usually more developed than in even-aged young stands, however, the lichen communities still differed from those in old growth and even-aged mature stands (Table 7).

Even-aged mature (81-200 yr) and old-growth (> 200 yr) stands differed somewhat in species composition (*A* = 0.04, *p* = 0.003), primarily due to more cyanolichens in old growth. However, in the ordination, lichen communities of mature and old-growth stands overlapped broadly in composition (Fig. 4A). Many cyanolichens such as *Lobaria oregana*, *L. pulmonaria*, *Nephroma helveticum*, *Pseudocyphellaria anthraspis*, and *P. rainierensis* were abundant in old-growth stands, while cyanolichens were present but less abundant in even-aged mature stands (ISA, Table 3).

Lichen community composition varied considerably within stands with remnant trees. Lichen communities in young stands (< 20 yr) with remnant retention differed from those in even-aged young stands (< 20 yr) and were more similar to those in pole stands with and without remnants (21-80 yr; Fig. 4A). Lichen communities in young stands with 50% retention of remnants were highly variable (Fig. 4A) and differed from

those in old growth (Table 7). Unlike young stands, lichen communities in pole and mature stands with remnants were more similar to those of old-growth stands (Table 7).

WESTERN HEMLOCK SERIES: LICHEN DIVERSITY AND STAND STRUCTURE
Total epiphytic macrolichen species richness differed slightly among stand types (across all topographic classes) in the western hemlock series (ANOVA, F = 2.9, p = 0.01; Fig. 5). Mean species richness of epiphytic macrolichens was highest in old-growth stands (mean = 33.2, s.d. = 6.0) and lowest in even-aged young stands (mean = 22.3, s.d. = 6.1). Lichen diversity was significantly lower in even-aged young stands as compared to even-aged mature stands (Tukey's HSD, 95% CI for the difference = 1.1 to 19.0 species) and old-growth stands (Tukey's HSD, 95% CI for the difference = 1.7 to 20.2 species; Fig. 5). The presence of remnant trees was not related to differences in lichen species richness (Figs. 5 and 6).

Average cyanolichen species richness was highest in old growth, differing significantly from young stands with and without remnants (see Fig. 6 for effect sizes). Average forage lichen species richness was similar among stand types (Fig. 6). Matrix lichens were most diverse in mature stands without remnants, differing significantly from even-aged young stands (Tukey's HSD, 95% CI for the difference = 0.3 to 11.2 species).

TRUE FIR SERIES
No topographic variables were related to patterns in lichen communities of the true fir series (maximum R^2 = 0.07). The NMS ordination of stands in lichen species space for the true fir series resulted in a 2-D solution describing 81% of the community variance, rotated to maximize the correlation of the age index with axis 1 (axis

1 = 50% and axis 2 = 31% after rotation; Fig. 4B).

TRUE FIR SERIES: LICHEN COMPOSITION AND STAND STRUCTURE
The strongest gradient in lichen communities in the true fir forests was correlated with the age index in the ordination (Fig. 4B; Table 5). As in the western hemlock series, BA generally increased with stand age and with increased remnant retention (Table 6). Macrolichen community composition overall differed among even-aged stands (MRPP, A = 0.11, p < 0.001), as did species composition of matrix lichens (A = 0.15, p < 0.001), whereas forage lichen composition did not differ across even-aged stands (A = 0.003, p = 0.41). Cyanolichens were absent from many stands, thus we could not assess compositional differences for this group.

Lichen community composition in even-aged young (< 20 yr) stands differed from that in even-aged pole (21-80 yr) stands (Fig. 4B; Table 7). In addition, lichen communities in even-aged young and pole stands differed from all other stand types (Fig. 4B; Table 7). Lichen communities in young stands with 15% remnants differed in composition from even-aged young stands and were more similar to lichen communities of pole and mature stands (Fig. 4B). Pole stands with remnants were few in the watershed and, therefore, were not included in the analyses. Lichen communities were similar between old-growth and even-aged mature stands (A = 0.001, p = 0.42; Fig. 4B; Table 7) and did not differ from mature stands with 15% remnants (Fig. 4B; Table 7).

TRUE FIR SERIES: LICHEN DIVERSITY AND STAND STRUCTURE
Matrix lichens were the most abundant and diverse group in the true fir series. Consequently, matrix lichen species

richness was strongly correlated with macrolichen species richness (R^2 = 0.88; Fig. 4B; Table 5). Average species richness for all macrolichens differed among stand types (ANOVA, F = 8.41, p < 0.001). Even-aged young stands (< 20 yr) were the least diverse compared to all other stands (Fig. 5). Lichen species richness for all macrolichens and for matrix lichens increased with total BA and with the age index (Fig. 4B; Table 5). Remnant tree retention was unrelated to lichen species richness in the true fir series (Figs. 5 and 6). Matrix lichen diversity in young stands with and without remnants was similar, but differed from all other stand types (Fig. 6). Forage lichen diversity was consistent across stand types and cyanolichens were nearly absent from true fir stands.

HARDWOODS
The presence of hardwood trees in the stand was recorded in the BA counts. However, many hardwood trees were small in diameter relative to the conifers, resulting in poor representation of hardwoods in the BA measurements (Table 6). Hardwood shrubs were not included in the BA measurements; however, they provide important substrate for lichens (Rosso 2000; Rosso and Rosentreter 1999). Hardwood abundance may have been more effectively represented by a density count, since field observations showed that the presence of even a few hardwoods seemed to enhance lichen diversity. Field observations suggested that common hardwoods such as *Acer circinatum* Pursh*, Acer macrophyllum* Pursh, *Alnus rubra* Bong., *Castanopsis chrysophylla* (Dougl.) A.DC., *Cornus nuttallii* Aud.*, Corylus cornuta* Marsh var. *californica* (A.DC.) Sharp, and *Rhododendron macrophyllum* G. Don provided unique substrates for lichens that were uncommon on the surrounding conifers. Hardwood patches were lichen diversity "hot spots" and were often found in disturbed areas along stream banks or in open rocky areas

of upland forest stands. Lichens commonly found on hardwoods included cyanolichen species in the genera *Nephroma*, *Pseudocyphellaria*, and green-algal lichen genera such as *Melanelia*, *Parmelia*, *Ramalina*, *Evernia,* and *Hypotrachyna.*

UPLAND AND RIPARIAN STANDS
Lichen community composition differed between uplands and riparian stands across all 117 stands (MRPP, A = 0.01, p= 0.01). Lichen community patterns in the upland and riparian classes were evaluated separately for each plant series to account for the influence of elevation on lichen communities.

Lichen communities differed between uplands and stands along perennial fish-bearing streams in the western hemlock series (MRPP, A = 0.02, p = 0.001; Table 8). Lichen communities differed little among the other riparian stream classes or between them and upland sites (Table 8; low A-statistics indicate broad overlap in the lichen communities among topographic classes). Average macrolichen richness was similar between stands in uplands (mean = 27.0) and riparian areas (mean species richness for perennial fish-bearing streams = 30.5, for perennial non-fish bearing = 29.3, and for intermittent streams = 28.4) for the western hemlock series (ANOVA, F = 0.80, p = 0.50). Cyanolichen species richness was, however, higher in stands along perennial fish-bearing streams than in uplands (Tukey's HSD, 95% CI for the difference = 1.3 to 8.5 species). Cyanolichens such as *Fuscopannaria pacifica, Nephroma parile*, and *Sticta weigelii* were most abundant in stands near perennial fish-bearing streams (Table 3). Many of the cyanolichens found in stands along perennial streams were more commonly found on hardwoods and were not typically present on conifers. We were unable to determine if differences in lichen communities along perennial streams was

related to hardwoods, to environmental factors, or to a combination of both.

In the western hemlock series, individual lichen species responded differently with respect to topographic class. Lichen species such as *Hypogymnia oceanica*, *Nephroma occultum*, *N. resupinatum*, *Pseudocyphellaria crocata,* and *P. rainierensis* increased in frequency and abundance from uplands to perennial streams (Fig. 7), but were not strongly associated with any particular topographic position (ISA: all $p > 0.05$). In contrast, species such as *Fuscopannaria pacifica*, *N. parile,* and *Sticta weigelii* were found predominantly in stands near perennial streams and were most strongly associated with stands along perennial fish-bearing streams (ISA: all $p \leq 0.05$; Fig. 7). *Esslingeriana idahoensis*, *Evernia prunastri,* and *Hypogymnia rugosa* were most common and abundant in stands near perennial non fish-bearing streams (Table 3). *Hypogymnia inactiva* was the only lichen that showed a strong association for upland sites in the western hemlock series; this lichen was frequent in all stands in the watershed, but most abundant in uplands.

Upland and riparian stands did not separate in the ordination for the true fir series, nor did lichen communities in upland and riparian classes differ (MRPP; $A = 0.01$, $p = 0.17$). In general, fewer hardwoods were found in the true fir series (Table 6). In the true fir series, 26 of 50 stands were riparian (3 along perennial fish-bearing streams, 10 along perennial non fish-bearing streams, and 13 along intermittent streams). In addition, lichen species richness among stands did not differ between upland and riparian areas in the true fir series (ANOVA, $F = 0.51$, $p = 0.68$). When cyanolichens were found in the true fir series, there was no clear relationship with topographic class

Discussion

Many ecological factors, such as stand age, remnant trees, and topography are important to temperate forest epiphytes (Halpern and Spies 1995; Hazell and Gustafsson 1999; Hyvärinen and Kauppi 1992; Lesica et al. 1991; McCune 1993; Neitlich 1993; Peck and McCune 1997; Peterson and McCune 2001; Pipp et al. 2001; Rolstad et al. 2001; Rose 1976; Sillett and Goslin 1999; Spies 1991). However, the influences of these factors on lichen communities have rarely been studied simultaneously. In this study, we did so to allow an appraisal of the relative strengths of these factors in relationship to epiphytic macrolichens in the Blue River watershed of the Cascade Mountains.

ELEVATION GRADIENT
Lichen communities differed more strongly across the 1,000 m span of elevation than for any other single factor. Lower elevation forests (470 – 950 m) differed in species composition from lichen communities in the true fir forests at higher elevations (950 – 1470 m). We found 16 species that were strongly associated with higher elevation true fir series across all stand types and 17 species most associated with the lower elevation western hemlock series across all stand types.

The elevation differences were mostly due to the abundance and diversity of cyanolichens in low elevation stands and their scarcity in the higher elevation stands. These findings agree with other studies that show cyanolichens to be absent from higher elevation forests in the PNW (1220-1340 m; Peck and McCune 1997) and abundant in old growth at lower elevations (500-1000 m; McCune 1993; Neitlich 1993; Peterson and McCune 2001; Pike et al. 1972,1977; Sillett 1995; Sillett and Neitlich 1996;). Additionally, composition and abundance differences between the two plant series reflected dominance by forage lichens,

primarily Alectoria sarmentosa in old forests of the true fir series. The great abundance of *A. sarmentosa* may limit available substrate for other lichen species to colonize such forests.

Elevation is nearly always an important factor in mountainous landscapes, but in drier climates it can be overshadowed by differences due to slope and aspect. For example, in the drier, suboceanic climate of western Montana, McCune and Antos (1982) concluded "Elevation is poorly correlated with other variables because its effects on microclimate are easily overridden by aspect and other influences of topographic position..." In general, the influence of slope and aspect should diminish in cloudy, high-precipitation climates. We suggest that this explains the relatively low importance of heat load and potential direct incident radiation in our study area, relative to elevation. This difference may be even more pronounced in drier interior forests with more continental climates.

LICHEN COMMUNITIES AND STAND AGE
Epiphytic macrolichen communities clearly change through time in even-aged stands. Differences in lichen community composition with stand age were more apparent than differences in lichen species richness. Lichen community composition in even-aged young stands (< 20 yr) was considerably different from all other even-aged stands. Furthermore, lichen species richness was generally poor in even-aged young stands. Lichen communities in young stands were primarily composed of small numbers of matrix lichens, such as the genera *Platismatia* and *Hypogymnia*. Cyanolichens were absent from young stands, with the exception of a few cases in which cyanolichen propagules appeared to have dispersed from nearby old growth. When selecting even-aged young stands for sampling, we did not consider the proximity

to old growth. Close proximity to old growth may enhance lichen dispersal to young stands. Average total lichen species richness was higher in even-aged pole stands (21-80 yr) than in even-aged young stands in the true fir series, however this was not seen in similar-aged stands of the western hemlock series.

Lichen community composition in even-aged young and pole stands may differ from that in older stands because species may be slow to arrive and establish (Sillett et al. 2000*b*). Even-aged young and pole stands in the PNW forest matrix are predominantly plantations from past clearcuts, many of which were overstocked. These dense plantations result in low light and infrequent wetting/drying cycles; which presumably slows lichen establishment and growth.

Lichen communities in older stands (> 80 yr, with and without remnants) were composed of lichens across all functional groups (with the exception of cyanolichens in the true fir forests). Lichen communities in old-growth and mature stands of the western hemlock series were diverse, providing habitat for many cyanolichens. *Nephroma occultum* and *Pseudocyphellaria rainierensis* are two cyanolichens in the Blue River watershed that were only found in old-growth stands of the western hemlock series and have been documented by others as old-growth associates (Goward 1994, 1995; Rosso et al. 2000; Sillett and Goward 1998). Cyanolichens can also be abundant in hardwood patches and riparian forests along large streams (McCune et al. 2002; Neitlich and McCune 1997; Peterson and McCune 2001; Rosso 2000; Ruchty 2000; Sillett and Neitlich 1996).

Lobaria oregana is a dominant cyanolichen in mid-elevation old growth of the western Cascades (McCune 1993; Neitlich 1993; Pike et al. 1977; Spies 1991). Our results confirm its old growth-association (Peterson

and McCune 2001). However, *L. oregana* can grow well in young stands and may, therefore, be old-growth-associated because of dispersal limitations, rather than a dependence on the environment associated with older forests (Sillett et al. 2000*a*, 2000*b*; Sillett and McCune 1998). Sillett et al. (2000*a*, 2000*b*) suggested that dispersal often limits establishment of old-growth associated lichens in young stands, primarily for lichens that reproduce asexually by coarse propagules or fragments that are not easily dispersed. As a result, the longer a stand persists without disturbance, the more likely it is to be colonized by dispersal-limited lichens. In addition, the close proximity of a propagule source enhances the likelihood of dispersal-limited lichens colonizing younger forests (Dettki 1998).

Dispersal does not limit all old-growth associated lichens. In some cases substrate may be a limiting factor, as demonstrated by Caliciales (pin-lichens) that colonize old bark and old snags (Tibell 1992). Other lichens may be old-growth associates due to specific microsites required for growth. Sillett (1995) suggested that the cyanolichens *Pseudocyphellaria rainierensis* and *Peltigera britannica* as an epiphyte were strongly associated with old growth due to the abundance of moss mats, which they colonize in such forests in the PNW.

LICHEN COMMUNITIES AND REMNANT TREES
The presence of remnant trees makes forest structure resemble older stands and remnant trees may also enhance forest connectivity in a dissected landscape (Franklin et al. 1997). In the Blue River watershed, remnant trees make a striking contribution to lichen communities in young forests, whereas the importance of remnants in older stands was less clear. In both plant series the presence of remnant

trees alters lichen community composition from that in even-aged young stands (Fig. 8). For example, in the western hemlock series, lichen community composition in young stands with remnant retention of 15% or greater was similar to that of even-aged pole forests (21-80 yr). This pattern was also true for young stands with 15% remnant retention in the true fir series. The presence of remnants in young stands following a tree-regenerating disturbance in old growth may accelerate the development of the lichen community towards that of older stands (Fig. 8).

Remnant trees may provide refugia from a disturbance, increasing survival of lichen populations. Peck and McCune (1997) suggested that remnants may buffer the microclimate extremes of a stand in the early years following a disturbance. This microclimate buffering may help surviving lichen populations to rebound after the disturbance. Remnants may also serve as a propagule source for lichens in the young regenerating stands following a disturbance (Neitlich and McCune 1997; Peck and McCune 1997; Sillett and Goslin 1999). The influence of remnants on lichen communities will vary, however, depending on the density and quality of remnants, such as remnant age, size, and wind-firmness. Although we did not measure remnant age, we estimated remnant tree age in our field observations. In general, it seemed that large old remnant trees seemed to host more abundant lichens than younger remnant trees, such as those left following a timber harvest. Remnant shrubs may function in the same manner (Rosso 2000).

HARDWOODS AND RIPARIAN AREAS
Riparian and hardwood-dominated areas provide microhabitat for many cyanolichens, old-growth-associates, and other species not commonly found in conifer forests (Keon and Muir 2002; McCune et al. 2002; Neitlich and McCune 1997; Rosso 2000; Ruchty

2000; Sillett and Neitlich 1996). Lichen diversity is often higher in hardwood patches of young and managed stands than in the more homogeneous conifer-dominated portions of these stands (Peterson 2000; Rosso 2000). In our study, lichens typically found on hardwood trees and shrubs included species in the genera *Evernia*, *Hypotrachyna*, *Lobaria*, *Melanelia, Nephroma*, *Parmelia, Pseudocyphellaria, Ramalina,* and *Sticta*. For example, lichen communities in the western hemlock series along perennial fish-bearing streams were cyanolichen rich "hot spots." Many, but not all, of the perennial fish-bearing streams had dominant hardwood shrubs and trees along the stream channels. The increased presence of hardwoods was confounded with the presence of perennial streams and therefore, it was difficult to determine which factors were influencing patterns of lichen communities along perennial streams.

Lack of differences in lichen communities with topographic classes in the true fir series may result in part from the small sample size of stands along perennial streams. Riparian stands, especially those with perennial fish-bearing streams, were scarce in the true fir series since these forests are in the headwaters.

Over the range of stream sizes included in this study, lichen communities differed subtly. Extending the riparian gradient outside of the Blue River watershed to large valley bottom streams in the McKenzie River watershed, however, resulted in much larger differences in lichen communities (McCune et al. 2002). They found that lichen communities in forests along very large streams (5th order streams and larger) were more diverse than upland forests, due to increased abundance of cyanolichens and abundant nitrophilous lichens that are presumably stimulated by air pollution (N-based) in the lower valley bottoms.

FOREST MANAGEMENT IMPLICATIONS

In federal forests of the Cascade Range, maintaining intact old-growth stands in the landscape can provide a viable lichen propagule source, preserve habitat continuity for old-growth-associates (Goward 1995; Rosso et al. 2000), and can help maintain large cyanolichen populations at lower elevations that are important to nutrient cycles in the forest ecosystem (Antoine 2001; Denison 1979; Pike 1978). In addition, mature stands (80-200 yr) are important to maintain in the landscape because they also provide habitat for cyanolichens and for other abundant macrolichens.

The presence of remnants in young stands may enhance lichen communities. Remnants provide temporal continuity of habitat during forest development in managed forests (Hazell and Gustafsson 1999; Peck and McCune 1997; Sillett and Goslin 1999). Remnant retention is especially important for lichens that are dispersal-limited and may prove effective for maintaining long-term old-growth associated lichens in managed forests (Sillett and Goslin 1999). In this study, the remnant trees were old trees that survived from historical wildfires and old trees that remained after timber harvests. Consequently, remnant tree size and age varied greatly. Trees left following harvests were occasionally younger relative to remnant trees from wildfires. More research is needed to determine if the quality of remnant trees is important to lichen communities following timber harvest.

Riparian areas are often buffered during harvest in federal forests of the Cascade Range and are recognized as important habitat for forest and aquatic species. Hardwoods are prevalent along streams and are often "hot spots" for epiphytic macrolichen diversity. Other hardwood gaps located in open areas or rocky areas

and understory shrubs are also important lichen habitat. The loss of hardwood trees and shrubs (especially older individuals) could contribute to the loss of hardwood-associated lichen species in a given area (Peterson 2000; Rosso 2000; Rosso and Rosentreter 1999). Recognizing the importance of hardwood patches and managing for them in the landscape is likely to assist in the maintenance of lichen diversity across the landscape (Neitlich and McCune 1997).

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Table 1. Definition of the age index, where the median age of the stand is calculated as a percentage of the median age of old growth (300 yr assumed for all old growth, see text). Raw age index = ((median age/median age of old growth)*100) + % remnants. AI represents $\log_{10}$(raw age index).

Stand Type	Median age	Raw age index	AI
Young, < 20 yr, no remnants	10	3	0.48
Young, < 20 yr, 15% remnants	10	18	1.26
Young, < 20 yr, 30% remnants	10	33	1.52
Young, < 20 yr, 50% remnants	10	53	1.72
Pole, 21-80 yr, no remnants	50	17	1.23
Pole, 21-80 yr, 15% remnants	50	32	1.51
Pole, 21-80 yr, 30% remnants	50	47	1.67
Pole, 21-80 yr, 50% remnants	50	67	1.83
Mature, 81-200 yr, no remnants	140	47	1.67
Mature, 81-200 yr, 15% remnants	140	62	1.79
Mature, 81-200 yr, 30% remnants	140	77	1.89
Mature, 81-200 yr, 50% remnants	140	97	1.99
Old growth, > 200 yr	300	100	2.00

Table 2. Correlations (R^2) of environmental and lichen community variables with NMS ordination axes (see Fig. 3). Correlations were reported if $R^2 \geq 0.3$ for one axis.

Variables	Axis 1	Axis 2
Elevation	0.004	0.66
Log age index	0.54	0.08
Live tree BA	0.36	0.08
Total lichen richness	0.33	0.17
Cyanolichen richness	0.12	0.65

Table 3. Abundance and indicator values for epiphytic macrolichen species in the 117 stands. AV = average abundance class for each species over all stands; FG = lichen functional group: cyanolichens (C), forage lichens (F), or matrix lichens (M); T = total number of stands in which each species occurred; FR= percent frequency of occurrence. Species are considered to have a strong association with a group (western hemlock (WH) and true fir (TF) plant series, topographic classes, and even-aged stands and old growth) if indicator values were $p \leq 0.05$ for a given group. No indicator values were calculated for stands with remnants. One species can be associated with more than one group.

Lichen species	AV	FG	T	FR	Associations
Alectoria imshaugii	0.5	F	29	25	
Alectoria sarmentosa	3.6	F	114	97	TF
Alectoria vancouverensis	0.1	F	4	3	
Bryoria	0.0	F	2	2	
Bryoria capillaris	1.2	F	53	45	TF
Bryoria fremontii	0.0	F	1	1	
Bryoria friabilis	0.9	F	45	38	
Bryoria fuscescens	0.2	F	12	10	TF
Bryoria glabra	1.0	F	44	38	WH mature
Bryoria mystery olive sp.	0.7	F	35	30	TF
Bryoria pseudofuscescens	0.4	F	17	15	
Bryoria tortuosa	0.0	F	1	1	
Bryoria trichodes	0.1	F	4	3	
Candelaria concolor	0.0	M	1	1	
Cavernularia hultenii	0.6	M	37	32	TF, TF pole, TF with fish
Cetraria canadensis	0.1	M	5	4	
Cetraria chlorophylla	1.4	M	71	61	TF, TF pole
Cetraria merrillii	0.2	M	13	11	
Cetraria orbata	1.1	M	67	57	TF mature, WH mature
Cetraria pallidula	0.3	M	22	19	WH
Cetraria platyphylla	1.2	M	62	53	TF old growth
Cetraria subalpina	0.1	M	2	2	
Cladonia	0.0	M	3	3	
Cladonia albonigra	0.0	M	1	1	
Cladonia carneola	0.0	M	4	3	
Cladonia fimbriata	0.0	M	2	2	
Cladonia norvegica	0.0	M	1	1	
Cladonia ochrochlora	0.2	M	12	10	
Cladonia squamosa	0.1	M	3	3	
Cladonia squamosa v. subsquamosa	0.4	M	19	16	WH
Cladonia transcendens	0.7	M	33	28	TF old growth
Cladonia umbricola	0.1	M	47	40	
Esslingeriana idahoensis	0.9	M	47	40	WH mature, TF mature, WH no fish
Evernia prunastri	0.3	M	24	21	WH no fish

Table 3 Continued.

Fuscopannaria pacifica	0.2	C	12	10	WH, WH with fish
Fuscopannaria leucostictoides	0.0	C	3	3	
Hypogymnia	0.0	M	1	1	
Hypogymnia apinnata	1.4	M	60	51	TF
Hypogymnia enteromorpha	3.2	M	109	93	
Hypogymnia imshaugii	2.6	M	100	85	TF
Hypogymnia inactiva	3.5	M	115	98	WH, WH upland
Hypogymnia metaphysodes	1.0	M	56	48	WH mature, TF mature
Hypogymnia occidentalis	0.5	M	27	23	TF, WH mature
Hypogymnia oceanica	0.4	M	35	30	TF, TF with fish
Hypogymnia physodes	2.3	M	105	90	TF pole
Hypogymnia rugosa	0.5	M	19	16	TF, TF old growth, WH no fish
Hypogymnia tubulosa	1.4	M	79	68	
Hypotrachyna sinuosa	0.2	M	15	13	WH young
Leptogium cyanescens	0.0	C	1	1	
Leptogium polycarpum	0.0	C	2	2	
Letharia columbiana	0.0	M	1	1	
Letharia vulpina	0.3	M	20	17	
Lobaria oregana	1.8	C	63	54	WH, WH old growth
Lobaria pulmonaria	1.1	C	45	38	WH, WH old growth
Lobaria scrobiculata	0.4	C	29	25	WH
Melanelia	0.0	M	4	3	
Melanelia elegantula	0.0	M	1	1	
Melanelia exasperatula	0.2	M	14	12	
Melanelia fuliginosa	0.1	M	3	3	
Melanelia multispora	0.0	M	2	2	
Melanelia subaurifera	0.1	M	8	7	WH young, TF pole
Nephroma	0.0	C	2	2	
Nephroma bellum	0.3	C	19	16	WH
Nephroma helveticum	0.6	C	29	25	WH, WH old growth
Nephroma laevigatum	0.1	C	8	7	
Nephroma occultum	0.1	C	7	6	
Nephroma parile	0.1	C	13	11	WH with fish
Nephroma resupinatum	0.3	C	17	15	WH
Nodobryoria abbreviata	0.0	F	1	1	
Nodobryoria oregana	2.4	F	98	84	TF
Parmelia	0.1	M	5	4	
Parmelia hygrophila	0.9	M	58	50	TF
Parmelia pseudosulcata	0.5	M	25	21	
Parmelia saxatilis	1.1	M	69	59	
Parmelia sulcata	1.2	M	70	60	
Parmeliopsis ambigua	0.3	M	18	15	TF, TF mature

Table 3 Continued.

Parmeliopsis hyperopta	2.8	M	103	88	TF, WH mature, TF mature
Peltigera britannica	0.0	C	1	1	
Peltigera collina	0.2	C	11	9	WH
Physcia adscendens	0.0	M	4	3	
Physcia aipolia	0.0	M	2	2	
Physcia tenella	0.0	M	1	1	
Platismatia glauca	3.6	M	116	99	TF,WH mature
Platismatia herrei	2.8	M	102	87	WH mature, TF old growth
Platismatia norvegica	0.1	M	8	7	TF with fish
Platismatia stenophylla	2.7	M	106	91	WH mature
Pseudocyphellaria	0.0	C	1	1	
Pseudocyphellaria anomala	0.9	C	46	39	WH
Pseudocyphellaria anthraspis	o.6	C	27	23	WH, WH old growth
Pseudocyphellaria crocata	0.3	C	25	21	
Pseudocyphellaria rainierensis	0.2	C	10	9	WH, WH old growth
Ramalina dilacerata	0.2	M	10	9	
Ramalina farinacea	0.2	M	12	10	
Sphaerophorus globosus	2.3	M	83	71	WH, WH mature, TF old growth
Sticta fuliginosa	0.2	C	16	14	WH
Sticta limbata	0.1	C	6	5	
Sticta weigelii	0.1	C	8	7	WH with fish
Usnea	0.7	F	35	30	
Usnea chaetophora	0.0	F	3	3	
Usnea cornuta	0.0	F	3	3	
Usnea diplotypus	0.1	F	3	3	
Usnea filipendula	1.0	F	54	46	
Usnea glabrata	0.1	F	7	6	
Usnea glabrescens	0.0	F	1	1	
Usnea scabrata	2.5	F	103	88	WH, WH mature
Usnea substerilis	0.1	F	2	2	
Usnea wirthii	0.2	F	8	7	
Vulpicida canadensis	0.1	M	8	7	
Xanthoria	0.0	M	1	1	
Xanthoria polycarpa	0.0	M	3	3	

Table 4. Diversity of epiphytic macrolichens across all
stands and for stands within the western hemlock and true fir
series (N = number of stands). Alpha diversity (α) is average
species richness, with the standard deviation in parentheses.
Beta diversity is shown as γ/α and as average half changes
(HC), HC were not calculated for cyanolichens because
cyanolichens were absent from some stands. Gamma
diversity (γ) is the total number of species found.

		Diversity Measures		
	α	β		γ
		γ/α	HC	
Overall				
N = 117				
All macrolichens	26.5 (6.4)	4.2	0.9	111
Cyanolichens	3.4 (4.1)	7.1	---	24
Forage lichens	5.8 (1.8)	4.3	0.9	25
Matrix lichens	17.2 (3.8)	3.6	0.7	62
Western hemlock				
N = 67				
All macrolichens	28.2 (6.8)	3.7	0.9	104
Cyanolichens	5.8 (4.0)	4.1	---	24
Forage lichens	5.3 (1.7)	4.5	0.9	24
Matrix lichens	17.1 (3.9)	3.3	0.7	56
True fir				
N = 50				
All macrolichens	24.2 (5.0)	3.2	0.8	78
Cyanolichens	0.3 (0.9)	20.0	---	6
Forage lichens	6.5 (1.8)	3.1	0.8	20
Matrix lichens	17.5 (3.7)	3.0	0.8	52

Table 5. Correlations (R^2) of environmental and lichen community variables with NMS ordination axes (see Fig. 4) for two ordinations: one for each plant series. Correlations were only reported for variables with correlations of $R^2 \geq$ 0.3 for one axis..

	Axis 1	Axis 2
Western Hemlock		
Age index	0.45	0.001
Elevation	0.04	0.38
Total lichen richness	0.50	0.07
Cyanolichen richness	0.47	0.32
True Fir		
Age index	0.66	0.003
Total BA	0.46	0.07
Total lichen richness	0.32	0.01
Matrix lichen richness	0.32	0.21

Table 6. Basal area (BA, m^2/ha) measurements for stand types in each plant series, excluding stand types with < 3 stands. Young = < 20 yr, pole = 21-80 yr, mature = 81-200 yr, and old growth = > 200 yr; percentages refer to percent remnants retained. N = number of stands. Live and dead BA includes remnant trees.

	N	Live BA	Dead BA	% BA Conifers	Remnant BA
Western Hemlock					
Young, 0%	8	12	0	90	0
Young, 15%	10	14	4	100	14
Young, 50%	3	31	2	99	31
Pole, 0%	5	41	4	94	0
Pole, 15%	3	51	4	100	14
Pole, 30%	5	49	8	100	24
Mature, 0%	13	58	3	98	0
Mature, 30%	3	101	10	100	40
Old Growth	11	70	5	98	0
True Fir					
Young, 0%	11	10	0	100	0
Young, 15%	8	11	3	100	11
Pole, 0%	8	35	3	97	0
Mature, 0%	8	54	7	100	0
Mature, 15%	3	71	15	100	21
Old Growth	11	61	13	100	0

Table 7. Pairwise multiple comparisons (from MRPP) among stand types of lichen community composition, broken down by the western hemlock and true fir series. Each cell represents a stand type. One of the cell letters must be the same as another cell to indicate *p*-value > 0.05 for the null hypothesis of no difference in lichen communities between stand types. One asterisk indicates stand types excluded from the analysis, with < 3 stands. Two asterisks indicate stand types not present in the landscape.

Western Hemlock

Age class (yr)	Percent remnant retention			
	0	15	30	50
Young < 20	a	e	*	abce
Pole 21 – 80	b	bcde	bcde	*
Mature 81 – 200	c	**	bcde	*
Old growth > 200	d			

True Fir

Age class (yr)	Percent remnant retention	
	0	15
Young < 20	a	c
Pole 21 – 80	b	*
Mature 81 – 200	d	d
Old growth > 200	d	

Table 8. Chance-corrected within-group agreement (*A*) for comparisons among lichen communities in the four topographic classes (from MRPP). Comparisons were made only for stands in the western hemlock series. Asterisk indicates significant differences ($p \le 0.05$).

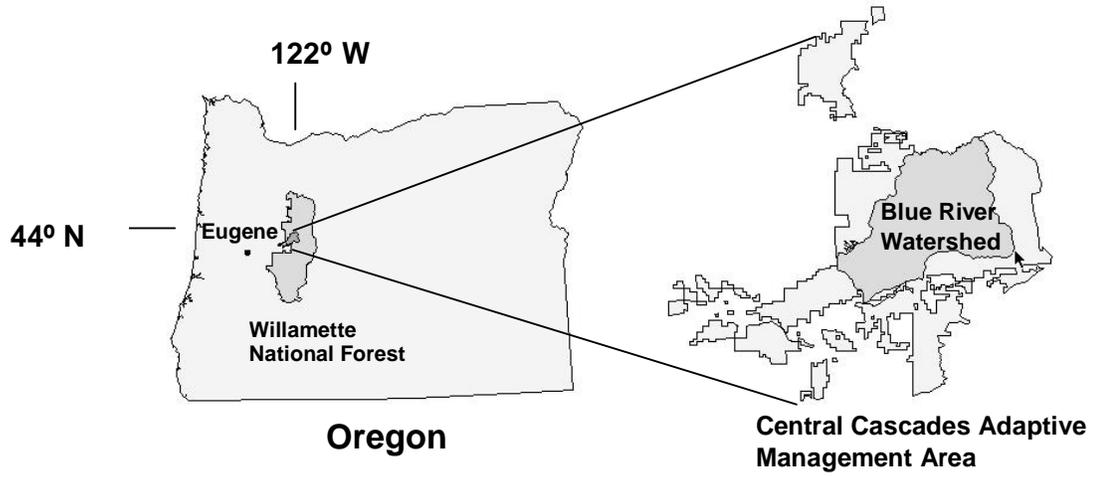|	Upland	Intermittent	Perennial (no fish)
Upland	----		
Intermittent	0.001	----	
Perennial (no fish)	0.007	0.006	----
Perennial (with fish)	0.024[*]	0.008	0.012

Figure 1. Map of the Blue River watershed (gray area on the right) in the Central Cascades Adaptive Management Area of the Willamette National Forest, Oregon, USA
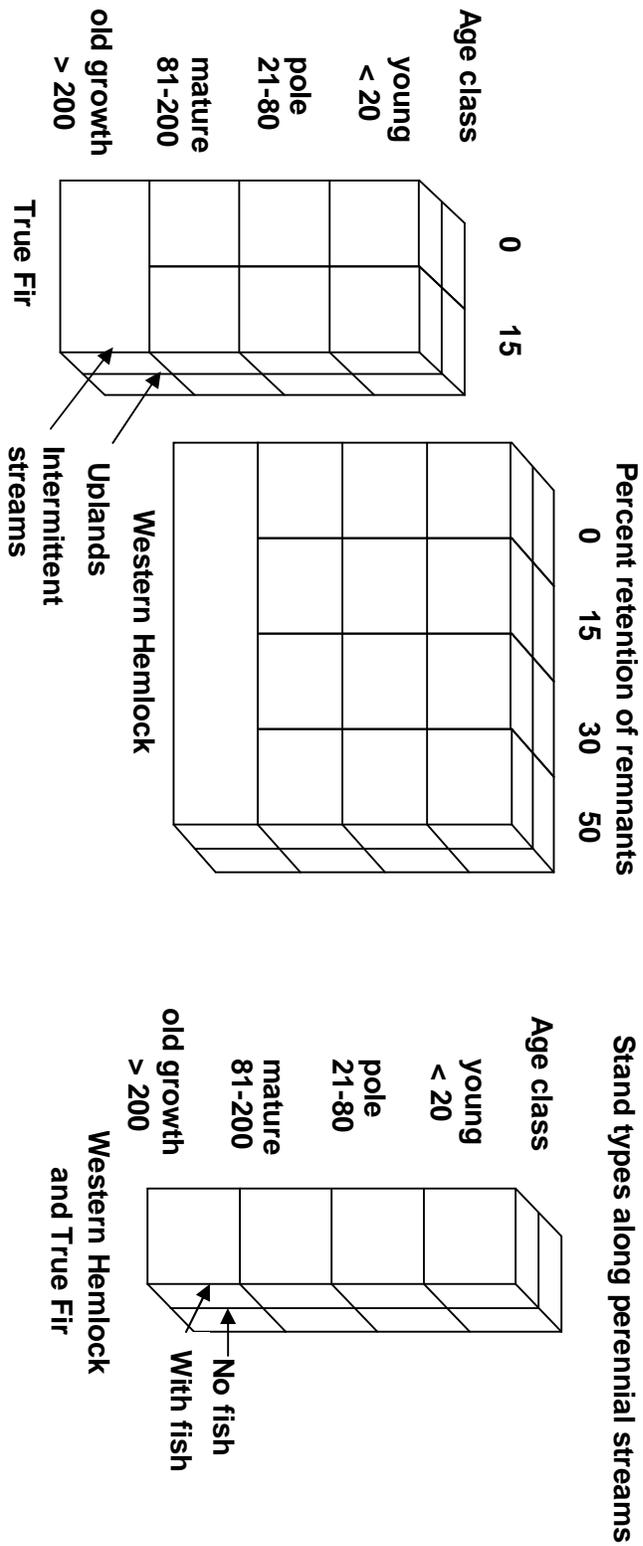
Age class

young < 20

pole 21-80

mature 81-200

old growth > 200

True Fir

0   15

Intermittent streams

Uplands

Western Hemlock

Percent retention of remnants

0   15   30   50

Stand types along perennial streams

Age class

young < 20

pole 21-80

mature 81-200

old growth > 200

Western Hemlock and True Fir

No fish

With fish

Figure 2. Sample design for stand types sampled in the Blue River watershed, modified from the Blue River Landscape Plan. Each cell in the sample design matrix represents a stand type. When possible, three stands were sampled per stand type in both the western hemlock and true fir vascular plant series. Stands in uplands and in areas along intermittent streams were stratified by age class and the percent retention of older remnant trees following the most recent disturbance. Stands located in areas along perennial fish-bearing and perennial non fish-bearing (no fish) streams were stratified by the age class of the co-dominant cohort, ignoring retention class. Old growth was not stratified by retention classes. Stand types in the true fir plant series were sampled only in two remnant retention classes (0 and 15%).
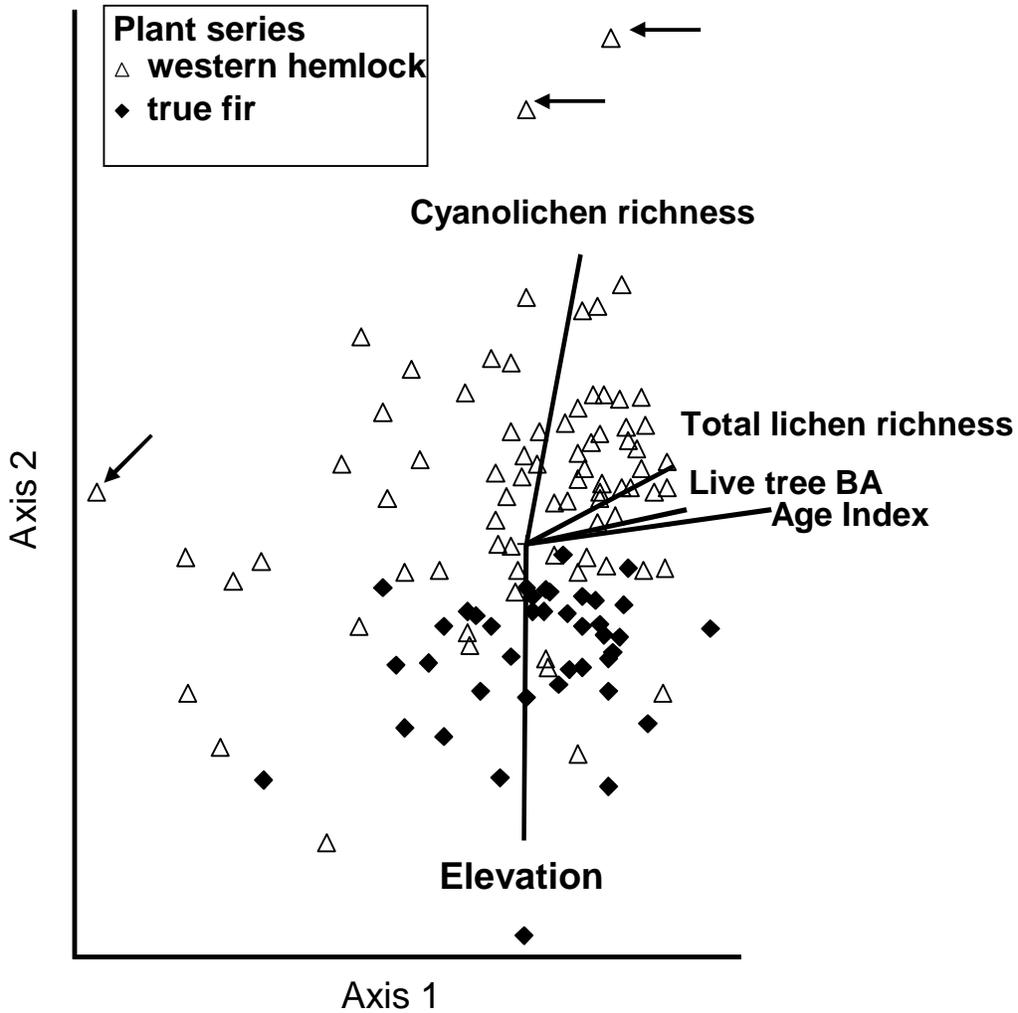
Figure 3. Rotated NMS ordination of stands (N = 117) in lichen species space and joint plot showing correlations of environmental and lichen community variables with each axis (all $R^2 \geq 0.3$ for linear relationships; see Table 2 for correlations of variables with the ordination axes). Vector length corresponds to the strength of the correlation. Arrows indicate non-influential outliers.
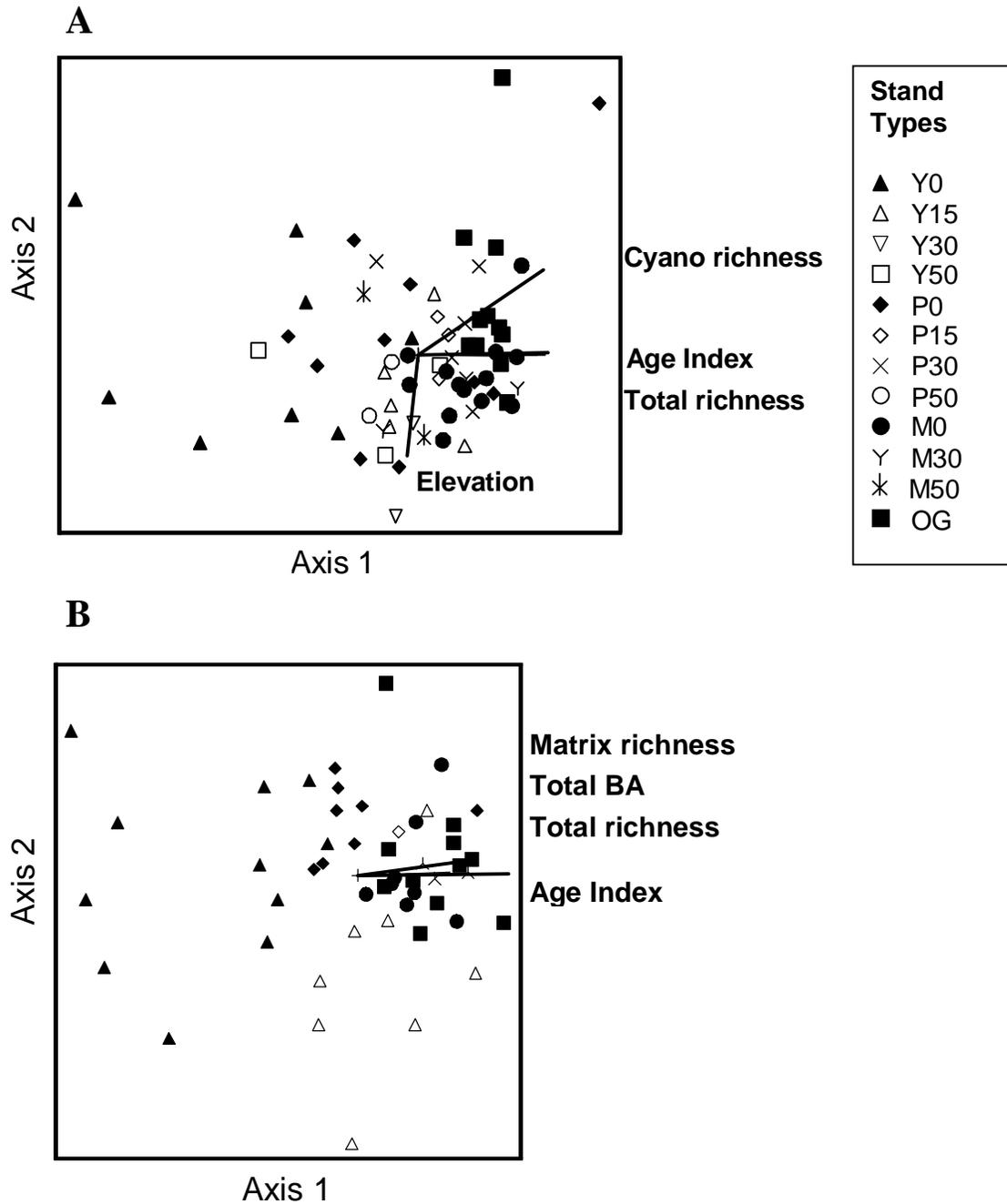
A

B

Figure 4. Rotated NMS ordination of stands in lichen species space for the western hemlock series (A) and the true fir series (B). For the western hemlock series, two axes explained 83% of the variation in lichen community structure: axis 1 = 58% and axis 2 = 25%. For the true fir series, two axes explained 81% of the variation in lichen community structure: axis 1 = 50% and axis 2 = 31%. Joint plots show correlations of environmental and lichen community variables with each axis, showing only those with $\geq R^2 = 0.3$. Vector length corresponds to the strength of the correlation (see Table 5 for correlations). Symbols indicate stand types: Y = young (< 20 yr); P = pole (21-80 yr); M = mature (81-200 yr); OG = old growth (> 200 yr); and 0, 15, 30, and 50 represent the remnant retention classes (see sample design).
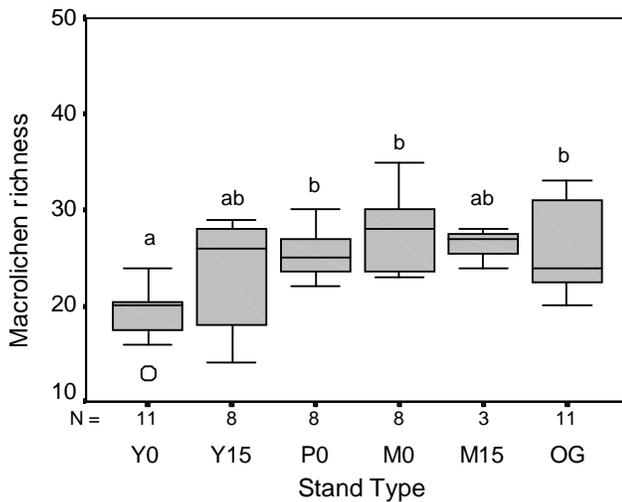
Western Hemlock
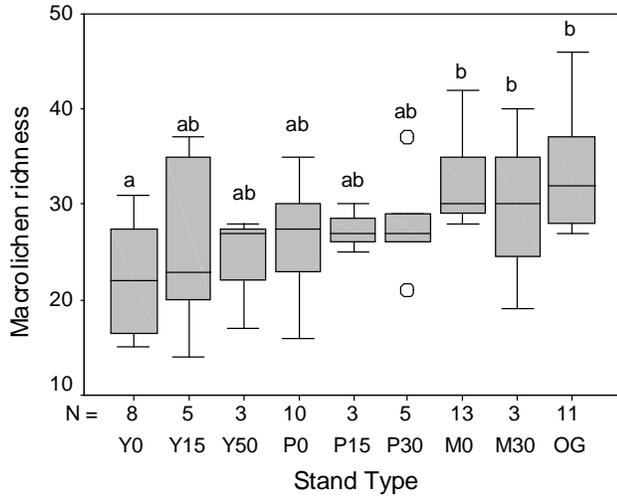
True Fir

Figure 5. Box plots show the distribution of macrolichen species richness in different stand types of the western hemlock and true fir series. Stand types are abbreviated as: Y0 = even-aged young (< 20 yr), Y15 = young with 15% remnants, Y50 = young with 50% remnants, P0 = even-aged pole (21-80 yr), P15 = pole with 15% remnants, P30 = pole with 30% remnants, M0 = even-aged mature (81-200 yr), M15 = mature with 15% remnants, M30 = mature with 30% remnants, OG = old growth (> 200 yr). 50% of the data falls within the interquartile range of the box, with the top of the box representing the 75th percentile and the bottom the 25th percentile. The horizontal line in the box represents the sample median. The whiskers on either end of the box represent the range of values that fall within 1.5 box lengths, showing extreme values that are not considered outliers. Circles indicate moderate outliers (> 3 box lengths from either end). Stand types with N < 3 were are not shown. Letters that differ from each other represent significant differences at p ≤ 0.05 from Tukey's HSD. N = number of stands per stand type.

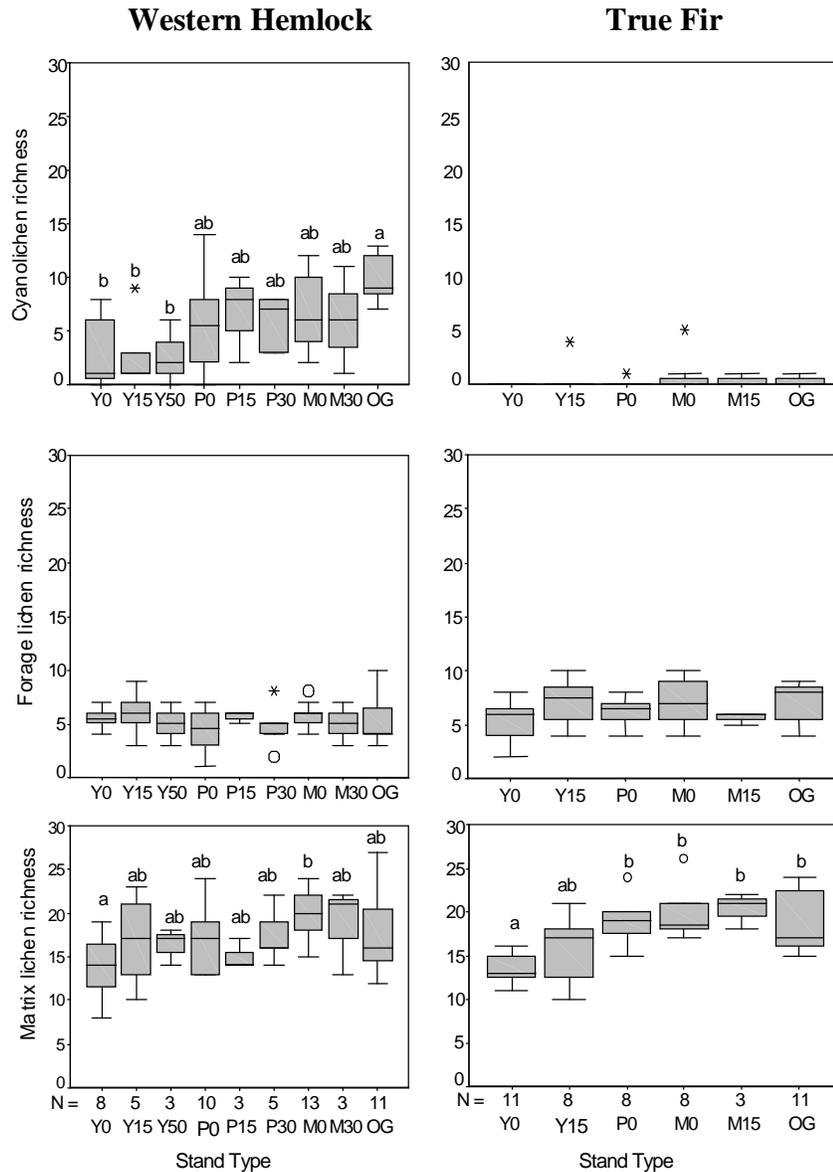**Western Hemlock**   **True Fir**

Figure 6. Box plots show the distribution of epiphytic macrolichen species richness by functional groups in stand types of the western hemlock and true fir series. Stand type abbreviations are described in Figure 5. 50% of the data falls within the interquartile range of the box, with the top of the box representing the 75th percentile and the bottom the 25th percentile. The horizontal line in the box represents the sample median. The whiskers on either end of the box represent the range of values that fall within 1.5 box lengths, showing extreme values that are not considered outliers. Circles indicate moderate outliers (1.5 to 3 box lengths from either end) and asterisks indicate extreme outliers (> 3 box lengths from either end). Stand types with N < 3 were are not shown. Letters that differ from each other represent significant differences at $p \leq 0.05$ from Tukey's HSD. No differences were found for forage lichens. N = number of stands per stand type.
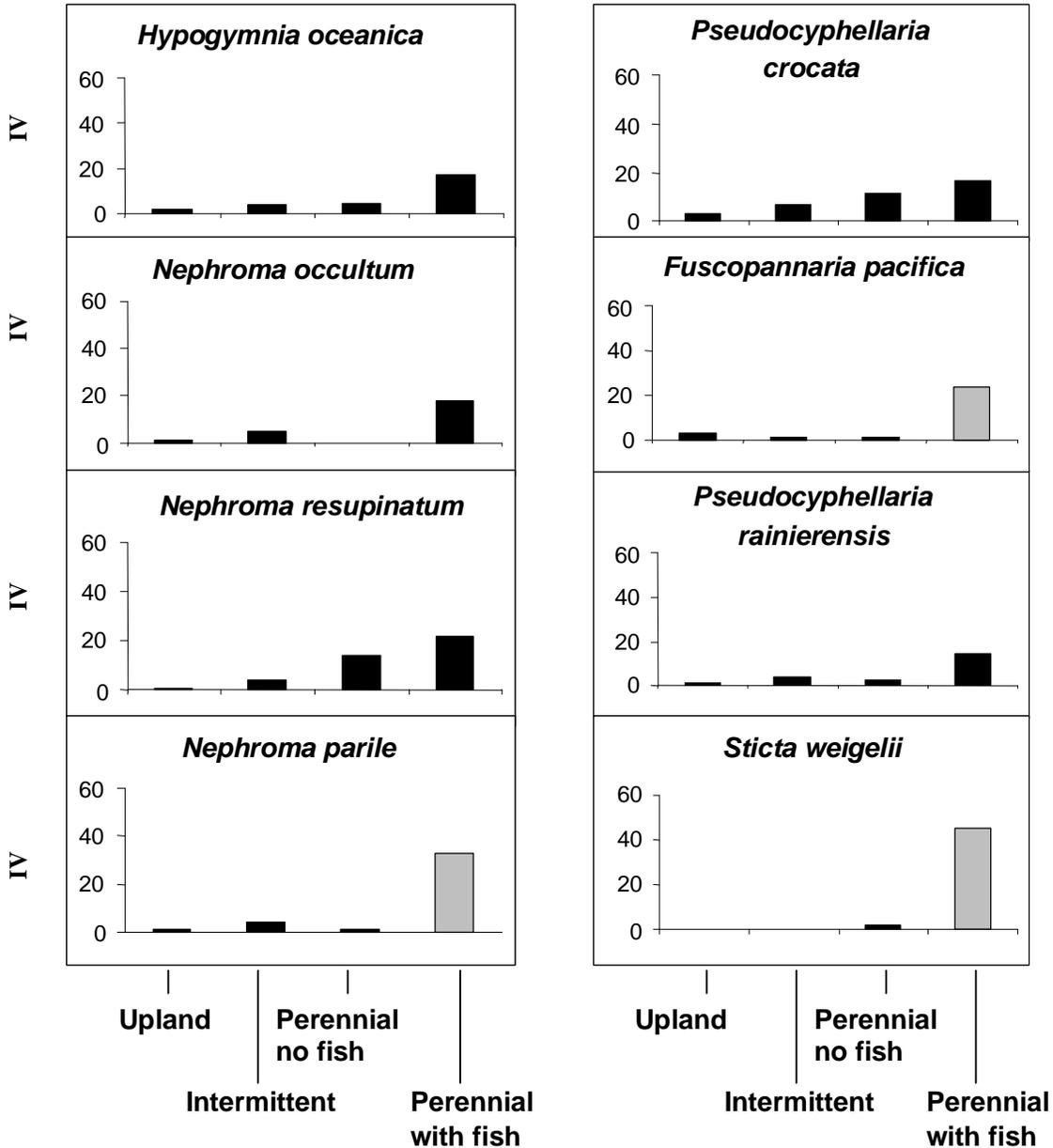
Figure 7. Indicator values (IV) for lichens in the four topographic classes of the western hemlock series, across all stand types. Indicator values represent a combination of species frequency and abundance in the topographic classes. Indicator values for these species were high only in areas along perennial streams. Gray bars indicate significant species indicator values for the topographic class (p ≤ 0.05 from a randomized test from Indicator Species Analysis; see also Table 3).
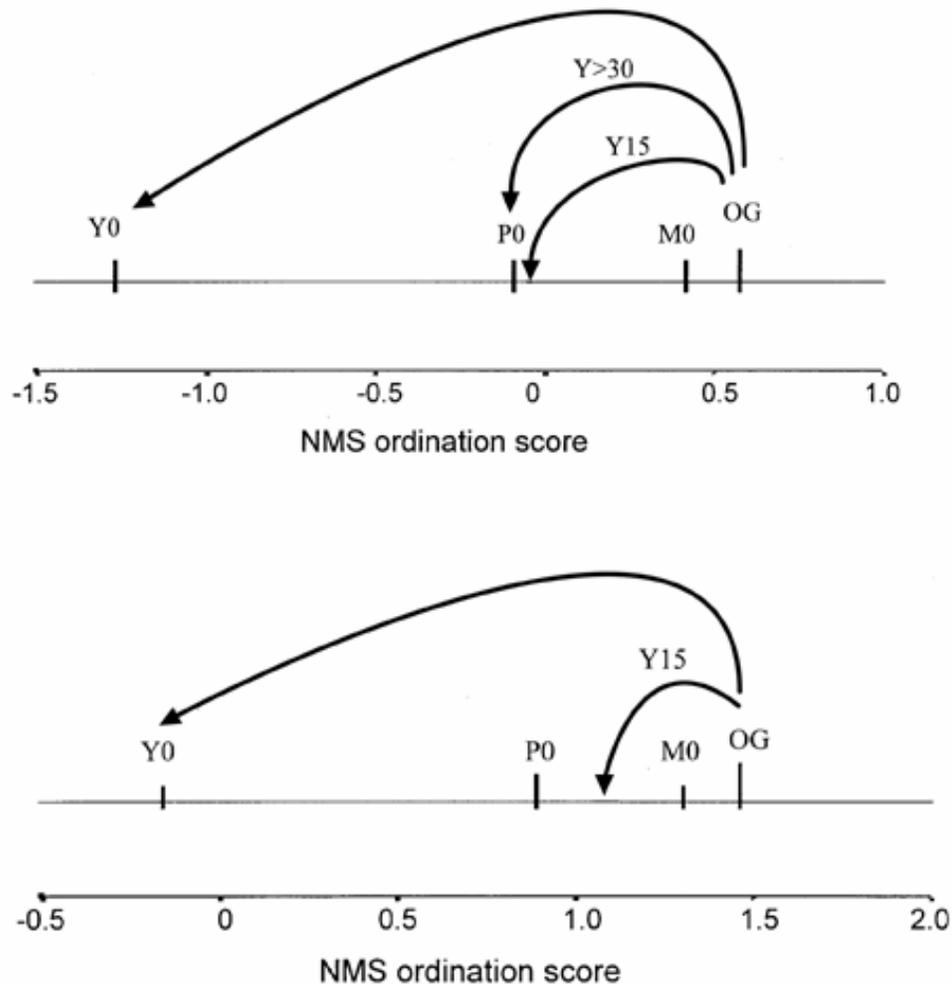
Figure 8. Diagram representing changes in lichen community composition along a gradient in stand structure and stand development within the western hemlock and true fir series (average ordination scores by stand type from axis 1 in each ordination; Figure 4). The lichen community composition gradient was extracted from rotated ordinations for each plant series, for which axis 1 in each ordination was correlated with the age index. The relative distance between stand types represents the relative difference in lichen community composition based on the averaged ordination scores from axis 1 by stand type. Arrows represent a disturbance event occurring in an old-growth stand and some possible scenarios that could occur following the disturbance, such as: total tree mortality, light remnant retention (15%), high remnant retention (> 30%). Y0 = even-aged young stand (< 20 yr), Y15 = young stand with 15% remnant tree retention, Y > 30 = young stand with > 30% remnant tree retention, P0 = even-aged pole stand (21-80 yr), M0 = even-aged mature stand (81-200 yr), OG = old growth (> 200 yr).