

## Concentration of Rare Epiphytic Lichens Along Large Streams in a Mountainous Watershed in Oregon, U.S.A.

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**Abstract.** *We studied epiphytic macrolichen communities and occurrences of rare species along the transition from upland to riparian forests on a range of stream sizes (intermittent, non-fish-bearing perennial, fish-bearing but less than 5<sup>th</sup> order, and streams larger than 5<sup>th</sup> order), based on 92, 0.38 ha plots in the McKenzie River watershed of the central Cascades of Oregon. The transition from uplands higher in the watershed to riparian areas along large streams is expressed in decreasing elevation and increasing representation of hardwoods. Upland stands were almost 100% conifers, averaging 49 m<sup>2</sup>/ha in stand basal area, decreasing to 48% conifers along fish-bearing streams of fourth order and below, and finally to 30% along large streams. Stand basal areas of hardwoods averaged near zero in uplands, increasing to an average of 11 m<sup>2</sup>/ha along large streams. One NMS ordination axis described this gradient in macrolichen communities, expressing 72% of the variation in community composition. Epiphytic lichens along large streams differed from fish-bearing streams smaller than fifth order; both of these stream classes also differed strongly from each of the other stream classes. Epiphytic lichens in uplands, along intermittent streams, and non-fish-bearing streams overlapped broadly in species composition. Macrolichen species richness was highest along large streams, averaging 38 species per plot, versus about 28 species per plot for uplands and non-fish-bearing streams. This difference is attributable to more species of cyanolichens, matrix lichens, and nitrophilous lichens along the large streams. About half of the individual species differed in abundance among stream classes, based on Indicator Species Analysis. Listed species (considered at risk by a government agency) were 57% more frequent in riparian areas along large streams than in uplands or along small streams. Protecting riparian zones from logging and urbanization and other forms of habitat destruction will, therefore, protect many rare species. Uplands and small streams, however, supported distinctive macrolichen communities, including rare species that were infrequent or absent from the riparian zones of large streams.*

Land managers play a life-or-death game for a large number of species at risk. Two strategies are common. The “fine-filter” strategy tracks individual species (Noss 1987) and decides the fate of specific sites based on the presence of those species, subject to compromises with other management goals (e.g., timber production). The “coarse-filter” approach manages habitats rather than individual species. Decisions about managing a specific site would depend on the value of that habitat for multiple species at risk. The NW Forest Plan (USDA & USDI 1994) combined a coarse-filter approach for most species with a fine-filter approach for species judged to be potentially at risk from the general plan. The large number of poorly known species has frustrated land managers in numerous ways, not least of which is the logistic problems inherent in tracking hundreds of species.

The success of the coarse-filter approach depends on being able to identify key habitats for the perpetuation of species that are currently at risk of de-

clines or extirpation. We need to understand the habitat requirements of these species. This paper contributes to that effort by documenting concentrations of rare lichen species and species diversity along the gradient from uplands to riparian areas along large streams.

Stand age, landscape position, and forest structure are emerging as important determinants of epiphyte communities in moist temperate forests. The importance of old-growth forests as focal points for rare lichens is well studied in the Pacific Northwest (e.g., Lesica et al. 1991; McCune 1993; Peterson & McCune 2001; Price & Hochachka 2001; Rosso et al. 2000; Sillett & Goward 1998; Sillett et al. 2000*a,b*) and elsewhere in the world (e.g., Brown et al. 1994; Holien 1998; Kuusinen & Siitonen 1998; Selva 1994). Other studies have demonstrated the importance of hardwoods as focal points for lichen diversity in a landscape of young coniferous forests (Dettki & Esseen 1998; Esseen et al. 1997; Kuusinen 1996*a*; Neitlich & McCune 1997; Peter-

TABLE 1. Definitions and locations of stream classes.

| Stream class | Abbreviation | Landscape position                             | Source of data                                 |
|--------------|--------------|--|--|
| 1            | Upland       | Upland, < 1,000 m elevation                    | Blue River watershed                           |
| 2            | Interm.      | Intermittent, non-fish bearing                 | Blue River watershed                           |
| 3            | No fish      | Perennial, non-fish bearing                    | Blue River watershed                           |
| 4            | Order < 5    | Perennial, fish bearing, stream order < 5      | Blue River watershed, Marten Creek, Bear Creek |
| 5            | Large        | Perennial, fish bearing, stream order $\geq$ 5 | Deer Creek, Gate Creek, McKenzie River         |

son 2000; Rosso 2000). Despite considerable emphasis on the importance of riparian areas for preserving biodiversity (e.g., Gregory et al. 1991; Naiman et al. 1993, 2000), the value of riparian areas as lichen habitat is poorly known. Although the Northwest Forest Plan (USDA & USDI 1994) recognized numerous lichen species associated with riparian areas, we know of only one study (Ruchty 2000) that explicitly focused on epiphytes in riparian forests.

Ruchty (2000) examined the longitudinal gradient of riparian epiphytes from headwater creeks to major valley streams. She described a "valley gradient" in the central Coast Range of Oregon, with a transition from conifer-dominated forests along narrow steep-walled valleys in the upper reaches down to hardwood dominated corridors through agricultural areas in the broader valleys. Epiphytic bryophytes and lichens changed along this physiographic gradient. In this paper we examine an expanded gradient, including upland forests and intermittent streams, as well as large streams.

#### STUDY AREA

We sampled epiphytic macrolichens in upland and riparian forests in the McKenzie watershed of the Cascade Range, between 44° and 44.5°N and between 122° and 123°W. All plots were within the Central Cascades Adaptive Management Area, managed by the Willamette National Forest and the Bureau of Land Management, Eugene District.

Maps and description of the topography, vegetation, and climate are in Cissel et al. (1999), Berryman (2002), and Hawk and Zobel (1974). The volcanic bedrock is deeply dissected and overlain with thick mantles of soil, colluvium, and alluvium on the lower slopes and valley bottoms. Winters are cool and wet while summers are warm and dry. January and July mean temperatures are about 2° and 22°C, respectively. Annual precipitation averages 240 cm. These conditions result in dominance by conifers in the uplands, mainly *Pseudotsuga*, *Tsuga*, and *Abies*. Hardwoods, especially *Acer macrophyllum*, *Alnus rubra*, and *Populus trichocarpa* are common in the riparian forests. The local lichen communities vary along gradients in forest age and topography (Berryman 2002; McCune 1993). *Alectoria*, *Hypogymnia*, *Lobaria*, *Platismatia*, *Pseudocyphellaria*, and *Sphaerophorus* are among the most prominent epiphytic lichen genera.

#### METHODS

*Plot Selection.*—To describe the gradient from upland mountain forests down to riverine riparian forests, we combined the 62, 0.38 ha plots below 1,000 m sampled by Berryman (2002) with 30 additional plots using the same measurements. Berryman's plots in recent clearcuts were excluded. Berryman sampled throughout the Blue River watershed, a major tributary of the McKenzie River. Hutchinson sampled 30 plots along the McKenzie River and its major tributaries, mostly 5<sup>th</sup> order streams and larger, down to an elevation of 243 m.

Berryman's plots were randomly sampled within forest structural classes (Berryman 2002), while Hutchinson's plots were geographically stratified to represent larger streams in approximate proportion to their length within the study area. Additional selection criteria were: presence of some trees > 45 yr old, distance of at least 50 m between plots (normally much farther), and representing a range of habitats and forest structures. Most riparian plots touched or included the average high water mark. Plots straddling small creeks were acceptable. Within these constraints we used the first sites encountered on approaching a target stream.

Plots were assigned to one of five stream classes (Table 1). These are arbitrary divisions of the riparian gradient from uplands to forests along large streams.

Plot centers were permanently marked with a 0.5 m long section of steel reinforcing rod driven flush with the ground, combined with a more visible stake of white plastic pipe. At each plot we recorded site and stand variables, including latitude, longitude, elevation, total basal area (five wedge-prism points per plot), proportion of basal area in hardwoods, the dominant trees and shrubs, and presence of indicator species of vascular plants. Structure of the tree layer was classified by age class and retention class. "Age class" was based on the age of the most recent major cohort of trees, based on increment coring and visual inspection: pole timber (21–80 yr), mature timber (81–200 yr), and old growth (> 200 yr). Retention classes represented the fraction of canopy area composed of trees from an earlier generation (0–7%, 7–22%, and 22–37%, 37–62%, and > 62%; old growth was assigned to the highest retention class; more details in Berryman 2002).

*Lichen Sampling.*—The Forest Health Monitoring (FHM) lichen community plots provide a repeatable method with high species capture rates (McCune et al. 1997a,b). This method has been used for thousands of plots in the Forest Health Monitoring program nationwide (McCune 2000). It is also used by the PNW Forest Service air quality program for about a thousand plots in western Oregon and Washington (L. Geiser, pers. comm., 2000; <http://www.fs.fed.us/r6/air/lichen/>).

The FHM method determines the presence and abundance of macrolichen species on all woody plants in a

0.38 ha plot. The species are recorded in broad abundance classes: 1 = rare, < 3 individuals in plot; 2 = uncommon, 4–10 individuals in plot; 3 = common, > 10 individuals but less than half of the boles and branches have that species present; and 4 = abundant, more than half of trunks and branches in the plot have the subject species present. The population being sampled consists of all macrolichens occurring on woody plants, both living and dead, excluding the 0.5 m basal portions of trees and shrubs. Lichens on fallen branches and other lichen litter are included. Given the large plot area, fallen branches always provide a sample of the canopy lichens. Vouchers specimens were deposited in the Oregon State University herbarium.

Species were assigned a value for listed (1) or not (0). A listed species is defined as a species being present on either the survey-and-manage list from the NW Forest Plan (USDA & USDI 1994) or the Oregon list (ONHP 2001). Species on the survey-and-manage list are considered potentially at risk from logging, while species on the Oregon list are rare in the state.

Many of the species originally listed for survey-and-manage in the original Northwest Forest Plan were removed in the amended Record of Decision (USDA & USDI 2001). Because additions to the list were not considered, the “amended survey & manage species” are a subset of those previously listed.

We assigned all macrolichen species to four functional groups: cyanolichens, forage lichens, matrix lichens, and nitrophilous lichens. Cyanolichens fix nitrogen because they contain cyanobacteria as a primary or secondary photobiont. Forage lichens are pendulous hair-like species commonly used as forage by small and large mammals. Matrix lichens are green-algal foliose and tufted fruticose species, many of which are common throughout the landscape matrix of young forests. Nitrophilous lichens thrive in nutrient-enriched sites and are represented here mainly by the genera *Melanelia*, *Phaeophyscia*, *Physcia*, and *Xanthoria*.

*Data analysis.*—The goals of our analysis were 1) to describe the transition in riparian lichen communities along the gradient from uplands to large streams, 2) contrast the number of rare and listed species between upland and riparian forests, and 3) describe the distribution of rare species along the riparian gradient.

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

Groups of plots defined by stream class were compared with non-metric MRPP and Indicator Species Analysis (McCune & Mefford 1999). MRPP (Mielke 1984) provides a nonparametric multivariate test of differences between groups, while indicator species analysis (Dufrière & Legendre 1997) describes how well each species differentiates between groups. Non-metric MRPP is the same

as MRPP except that the distance matrix is converted to ranks before calculating the test statistic. Group differences are shown with the A statistic, the “chance-corrected within-group agreement” (A = 0 is the expectation under the null model; A = 1 when all members of a group are identical and non-overlapping with other groups; negative values indicate groups more similar than expected by chance). For indicator species analysis we used 1,000 randomizations to test the hypothesis that the largest indicator value for a given species is no larger than that expected by chance.

We expressed the concentration of rare species with a method analogous to making fruit juice from frozen concentrate. If, for example, orange juice is made by adding three cans of water to one can of concentrate, the concentration ratio is 3:1 or simply 3. Similarly, a riparian plot with three times as many rare species as in the average upland plot has a concentration ratio of three.

Do listed species covary? If listed species are distributed at random with respect to each other, then the frequency distribution of the number of listed species observed in a plot should follow a poisson distribution. With the poisson distribution the variance in the number of listed species equals the mean number of listed species. The deviation of the variance-to-mean ratio (V/M) from one informs us whether listed species are more aggregated (V/M > 1) or more evenly distributed than expected (V/M < 1). The more that rare species are aggregated in particular habitats or sites, the more readily they can be managed either with a coarse filter or fine-filter approach to protecting biodiversity of forested ecosystems.

Does protecting different classes of riparian habitats protect different species? Are any species unique to each habitat? We answered these questions by 1) examining overlap in community composition between stream classes, based on a 2-D ordination (NMS) of plots in lichen species space, 2) testing the hypothesis of no difference in community composition among stream classes using a nonparametric multivariate test (nonmetric MRPP), and 3) counting the number of exclusive species per plot in each stream class. “Exclusive” species occurred in only one stream class. The average within-group Sørensen distance (quantitative form) from MRPP described the variability in species composition within each stream class.

## RESULTS

The gradient from uplands higher in the watershed to riparian areas along large streams is one of the strongest ecological structures at the landscape level. This gradient forms a context necessary for understanding the occurrences of rare lichens along streams. We therefore describe the gradient in stand structure and the lichen communities along those gradients, then describe patterns in the occurrences of rare lichens along this gradient.

### THE MCKENZIE RIPARIAN GRADIENT

*Stand structure and environment.*—The riparian gradient is expressed in decreasing elevation and increasing representation of hardwoods (Table 2). Our sample ranged from 243–1,000 m in elevation, with plots along large streams averaging 281 m and plots in uplands averaging 800 m. A 100 m change in elevation appeared to be more important to the

TABLE 2. Means for elevation, stand structure variables, and macrolichen species richness across stream classes. "BA" is stand basal area. "Listed species" are those macrolichen species listed for Survey and Manage under the Northwest Forest Plan. "Sum of abundance" is the sum of abundance classes of all macrolichen species. The one-way univariate ANOVA ( $F$ ,  $p$ ) tests the hypothesis of no difference in species richness across stream classes.

|                                  | Stream class |         |         |           |       | ANOVA   |         |
|----------------------------------|--------------|---------|---------|-----------|-------|---------|---------|
|                                  | Upland       | Interm. | No Fish | Order < 5 | Large | F ratio | $p$     |
| Sample size                      | 30           | 13      | 9       | 16        | 24    |         |         |
| Elevation                        |              |         |         |           |       |         |         |
| Elevation, m                     | 800          | 752     | 804     | 592       | 281   | 52.8    | < 0.001 |
| Log(elevation)                   | 2.90         | 2.87    | 2.90    | 2.73      | 2.45  | 74.2    | < 0.001 |
| Stand structure                  |              |         |         |           |       |         |         |
| BA hardwoods, m <sup>2</sup> /ha | 0.01         | 1.00    | 1.02    | 5.97      | 11.44 | 27.3    | < 0.001 |
| BA conifers, m <sup>2</sup> /ha  | 48.6         | 56.5    | 35.8    | 27.6      | 12.6  | 10.8    | < 0.001 |
| BA total, m <sup>2</sup> /ha     | 48.6         | 57.5    | 36.8    | 33.6      | 24.0  | 6.0     | < 0.001 |
| BA, % conifers                   | 99.9         | 98.5    | 94.2    | 73.0      | 47.7  | 30.1    | < 0.001 |
| Macrolichens                     |              |         |         |           |       |         |         |
| Sum of abundance                 | 75.7         | 77.5    | 69.9    | 74.0      | 94.1  | 4.5     | 0.002   |
| Total richness                   | 27.7         | 28.3    | 28.0    | 30.7      | 37.7  | 11.1    | < 0.001 |
| Cyanolichens                     | 5.9          | 6.8     | 6.9     | 9.7       | 8.5   | 4.1     | 0.004   |
| Forage lichens                   | 4.1          | 3.5     | 3.7     | 3.8       | 3.8   | 0.0     | 0.769   |
| Matrix lichens                   | 18.5         | 18.7    | 18.1    | 17.9      | 23.4  | 8.9     | < 0.001 |
| Nitrophiles                      | 0.1          | 0.3     | 0.2     | 0.2       | 1.9   | 16.1    | < 0.001 |
| Listed species                   | 5.3          | 6.2     | 6.2     | 9.3       | 8.3   | 4.9     | 0.001   |

vegetation at the lower elevations than at higher elevations, so log transforming elevation strengthened the statistical relationships of elevation with stand structure and macrolichen communities.

Total stand basal area and conifer basal area closely covaried (Table 2), because in these forests conifer stands are capable of developing much higher stand basal areas than are hardwood stands. Upland stands were almost 100% conifers, averaging 49 m<sup>2</sup>/ha in stand basal area, decreasing to 48% conifers along fish-bearing streams of fourth order and below, and finally to 30% along large streams (Table 2). Conversely, stand basal areas of hardwoods averaged near zero in uplands, increasing to an average of 11 m<sup>2</sup>/ha along large streams. Other unmeasured structural features of the forest surely covary with the shift from conifers to hardwoods.

*Lichen communities.*—Macrolichen species richness was highest along large streams, averaging 38 species per plot (Table 2), versus about 28 species per plot for uplands and non-fish-bearing streams. This difference is attributable to more species of cyanolichens, matrix lichens, and nitrophilous lichens along the large streams (Table 2). Richness of forage lichens did not differ among stream classes.

A single strong gradient in epiphytic macrolichens parallels the transition from upland forests to intermittent streams, to non-fish-bearing perennial streams, to fish-bearing streams less than 5<sup>th</sup> order, to large streams. This riparian gradient was represented axis one in a 2-D NMS ordination, this first

axis representing 72% of the variation in species composition. The ordination stabilized at a final stress of 17.7, a lower stress than all 50 randomizations, meaning that the observed structure is stronger than expected by chance. An overlay of stream class and the correlation of axis one scores with elevation (especially log of elevation;  $r = 0.92$ ) illustrate the gradient (Fig. 1). The importance of the riparian gradient is underscored by the strong differences in epiphyte communities among stream classes (MRPP,  $A = 0.37$ ,  $p \ll 0.001$ ).

The second NMS axis was much weaker than the first, describing 15.6% of the variation in community composition. The environmental variables most strongly related to the second axis were age class and basal area of conifers (Fig. 1). Cyanolichen richness and number of listed species also increased along the second axis.

Lichen community responses to the age gradient on the second axis were somewhat confounded with the riparian gradient. The vectors angling to the upper right for age class and basal area of conifers (Fig. 1) reflect the greater basal area and proportion of conifers in upland stands (axis one) as well as the tendency for basal area of conifers to increase with stand age (axis 2). The vectors angling to the upper left for numbers of cyanolichens and listed species (Fig. 1) reflect the tendency for cyanolichens to increase with both stand age (axis 2) and proportion of hardwoods (left side of axis one).

Epiphytic lichen communities along large streams differed from communities along fish-bear-

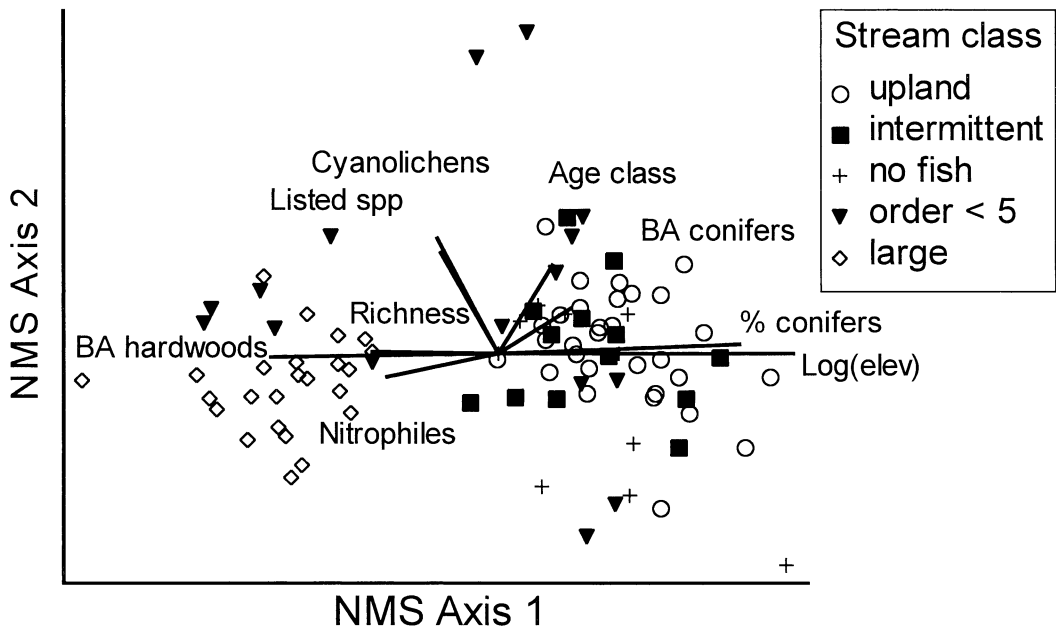


FIGURE 1. Ordination of plots in epiphytic macrolichen species space, the plots arrayed along a gradient from uplands to large streams. Symbols indicate the stream class for each plot. Radiating lines indicate the relative strength and direction of correlation of various parameters with the ordination. "Richness" is total macrolichen species richness.

ing streams smaller than fifth order (Table 4). Both of these stream classes also differed from each of the other stream classes. Epiphytic lichens in uplands, along intermittent streams, and non-fish-bearing streams overlapped broadly in species composition, such that they were nearly indistinguishable by community analysis (Table 4).

About half of the individual species differed in frequency or abundance among stream classes, based on Indicator Species Analysis (Table 3). After excluding six generic categories representing specimens not identifiable to species, 116 species remained. Of those, 46 species had significant indicator value, considerably higher than the six species expected to show significance by chance, based on a significance level of 0.05. Twenty-eight of the indicator species were associated with large streams.

Two of the indicators of large streams are relatively oceanic in distribution: *Bryoria trichodes* and *Menegazzia terebrata* (Table 3). Other indicator species for the large streams are associated with hardwoods (*Evernia prunastri*, *Hypogymnia tubulosa*, *Hypotrachyna sinuosa*, *Leptogium polycarpum*, *Lobaria hallii*, *Nephroma resupinatum*, *Peltigera collina*, *Ramalina dilacerata*, and *R. farinacea*) or nutrient-enriched habitats (*Melanelia fuliginosa*, *Parmelia sulcata*, *Physcia aipolia*, and *Physcia tenella*).

Species associated with uplands to non-fish-bearing streams included *Alectoria imshaugii*, *A. sar-*

*mentosa*, *Cetraria pallidula*, *C. platyphylla*, *Eslingeriana idahoensis*, *Hypogymnia enteromorpha*, *H. imshaugii*, *H. rugosa*, *Nodobryoria oregana*, *Parmeliopsis hyperopta*, and *Platismatia stenophylla*.

Numerous species were found in only one or two habitat classes, but were too infrequent to be useful indicator species. See results on exclusive species under "Concentration of listed lichens . . ." below.

#### CONCENTRATIONS OF LISTED MACROLICHENS IN UPLAND VS. RIPARIAN

Total macrolichen species richness along large streams was about one third higher than in the uplands (Tables 2 and 5). Listed species were more concentrated along streams than were macrolichens overall. We found 24% more listed species per plot along intermittent streams and non-fish-bearing perennial streams than in uplands. Fish-bearing perennial streams smaller than 5<sup>th</sup> order were the richest in listed species with 75% more listed species per plot than the uplands. Riparian habitats along larger streams were also rich in listed species, having 57% more listed species per plot than uplands.

Cyanolichen species were generally more aggregated than other groups of lichens (Table 6). Listed species followed the same pattern because most are cyanolichens. Aggregation of listed species means that if one listed species is found, presence of other listed species is more likely than expected by



TABLE 3. Macrolichen species frequency (N = number of plots), functional groups (c = cyanolichen, f = forage lichen, m = matrix lichen, n = nitrophile), listed species (NW = NW forest plan, OR = Oregon Natural Heritage Program 2001), and indicator values for stream classes (see definitions above). Maximum indicator values that are significantly higher ( $p < 0.05$ ) than other stream classes are in bold. Nomenclature follows Esslinger and Egan (1995); "Bryoria sp." is an apparently undescribed species (see McCune & Geiser 1997, p. 33).

| Species  | N  | Group | Listed | Stream class |           |           |           |           |
|--|----|-------|--------|--------------|-----------|-----------|-----------|-----------|
|  |    |       |        | Upland       | Interm.   | No Fish   | Order < 5 | Large     |
| <i>Alectoria imshaugii</i>                     | 16 | m     | –      | 7            | 3         | <b>22</b> | 1         | 0         |
| <i>Alectoria sarmentosa</i>                    | 74 | f     | –      | <b>27</b>    | 21        | 22        | 16        | 3         |
| <i>Alectoria vancouverensis</i>                | 13 | f     | –      | 1            | 3         | 0         | 6         | 9         |
| <i>Bryoria capillaris</i>                      | 20 | f     | –      | 6            | 1         | 8         | 9         | 2         |
| <i>Bryoria fremontii</i>                       | 2  | f     | –      | 0            | 0         | 0         | 0         | 8         |
| <i>Bryoria friabilis</i>                       | 25 | f     | –      | 13           | 13        | 5         | 2         | 0         |
| <i>Bryoria fuscescens</i>                      | 6  | f     | –      | 0            | 0         | 2         | 5         | 2         |
| <i>Bryoria glabra</i>                          | 23 | f     | –      | 16           | 3         | <b>25</b> | 1         | 0         |
| <i>Bryoria pseudofuscescens</i>                | 5  | f     | –      | 12           | 0         | 0         | 0         | 1         |
| <i>Bryoria trichodes</i>                       | 4  | f     | –      | 0            | 0         | 0         | 0         | <b>17</b> |
| <i>Bryoria</i> sp.                             | 15 | f     | –      | 11           | 8         | 0         | 3         | 0         |
| <i>Cavernularia hulthenii</i>                  | 17 | m     | –      | 4            | 2         | 7         | 8         | 1         |
| <i>Cetraria chlorophylla</i>                   | 41 | m     | –      | 19           | 11        | 15        | 3         | 3         |
| <i>Cetraria merrillii</i>                      | 9  | m     | –      | 5            | 9         | 2         | 1         | 0         |
| <i>Cetraria orbata</i>                         | 63 | m     | –      | 11           | 11        | <b>24</b> | 2         | 30        |
| <i>Cetraria pallidula</i>                      | 17 | m     | –      | 7            | <b>23</b> | 2         | 1         | 0         |
| <i>Cetraria platyphylla</i>                    | 28 | m     | –      | <b>27</b>    | 19        | 0         | 2         | 0         |
| <i>Cetrelia cetrarioides</i>                   | 1  | m     | NW     | 0            | 0         | 0         | 0         | 4         |
| <i>Cladonia albonigra</i>                      | 5  | m     | –      | 0            | 0         | 0         | 6         | 4         |
| <i>Cladonia carneola</i>                       | 1  | m     | –      | 3            | 0         | 0         | 0         | 0         |
| <i>Cladonia chlorophaea</i>                    | 1  | m     | –      | 0            | 0         | 0         | 6         | 0         |
| <i>Cladonia coniocraea</i>                     | 10 | m     | –      | 1            | 0         | 2         | 6         | 6         |
| <i>Cladonia fimbriata</i>                      | 5  | m     | –      | 0            | 0         | 0         | 1         | 13        |
| <i>Cladonia furcata</i>                        | 2  | m     | –      | 0            | 0         | 0         | 13        | 0         |
| <i>Cladonia norvegica</i>                      | 1  | m     | NW     | 3            | 0         | 0         | 0         | 0         |
| <i>Cladonia ochrochlora</i>                    | 31 | m     | –      | 1            | 0         | 1         | 5         | <b>56</b> |
| <i>Cladonia squamosa</i>                       | 16 | m     | –      | 0            | 1         | 0         | 2         | <b>35</b> |
| <i>Cladonia squamosa</i> v. <i>subsquamosa</i> | 35 | m     | –      | 1            | 10        | 1         | 11        | <b>27</b> |
| <i>Cladonia transcendens</i>                   | 39 | m     | –      | 8            | 13        | 0         | 7         | 18        |
| <i>Cladonia umbricola</i>                      | 7  | m     | –      | 8            | 0         | 0         | 1         | 2         |
| <i>Esslingeriana idahoensis</i>                | 30 | m     | –      | 10           | 8         | <b>30</b> | 4         | 0         |
| <i>Evermia prunastri</i>                       | 38 | m     | –      | 0            | 3         | 3         | 5         | <b>66</b> |
| <i>Hypogymnia apinnata</i>                     | 52 | m     | –      | 11           | 9         | 1         | 11        | <b>26</b> |
| <i>Hypogymnia enteromorpha</i>                 | 90 | m     | –      | <b>21</b>    | <b>21</b> | 16        | 18        | 20        |
| <i>Hypogymnia imshaugii</i>                    | 52 | m     | –      | 24           | 25        | <b>29</b> | 4         | 0         |
| <i>Hypogymnia inactiva</i>                     | 89 | m     | –      | 21           | 21        | 21        | 17        | 17        |
| <i>Hypogymnia metaphysodes</i>                 | 27 | m     | –      | 10           | 21        | 5         | 6         | 0         |
| <i>Hypogymnia occidentalis</i>                 | 32 | m     | –      | 5            | 4         | 0         | 2         | <b>39</b> |
| <i>Hypogymnia oceanica</i>                     | 14 | m     | NW     | 2            | 6         | 6         | 8         | 0         |
| <i>Hypogymnia physodes</i>                     | 86 | m     | –      | 19           | 21        | 23        | 13        | 17        |
| <i>Hypogymnia rugosa</i>                       | 5  | m     | –      | 0            | 1         | <b>26</b> | 0         | 0         |
| <i>Hypogymnia tubulosa</i>                     | 66 | m     | –      | 6            | 7         | 15        | 21        | <b>30</b> |
| <i>Hypotrachyna sinuosa</i>                    | 40 | m     | –      | 1            | 0         | 0         | 18        | <b>60</b> |
| <i>Leptogium corniculatum</i>                  | 7  | c     | –      | 0            | 0         | 0         | 6         | 11        |
| <i>Leptogium cyanescens</i>                    | 1  | c     | NW     | 3            | 0         | 0         | 0         | 0         |
| <i>Leptogium polycarpum</i>                    | 21 | c     | –      | 0            | 0         | 0         | 15        | <b>33</b> |
| <i>Letharia vulpina</i>                        | 6  | m     | –      | 14           | 1         | 0         | 0         | 0         |
| <i>Lobaria hallii</i>                          | 9  | c     | NW     | 0            | 0         | 0         | 1         | <b>30</b> |
| <i>Lobaria oregana</i>                         | 77 | c     | NW     | 23           | 19        | 15        | 23        | 7         |
| <i>Lobaria pulmonaria</i>                      | 72 | c     | NW     | 11           | 14        | 8         | 22        | 25        |
| <i>Lobaria scrobiculata</i>                    | 35 | c     | NW     | 7            | 18        | 4         | 10        | 4         |
| <i>Melanelia exasperatula</i>                  | 6  | m     | –      | 5            | 0         | 0         | 1         | 2         |
| <i>Melanelia fuliginosa</i>                    | 26 | n     | –      | 0            | 1         | 0         | 2         | <b>69</b> |
| <i>Melanelia multisporea</i>                   | 1  | m     | –      | 0            | 0         | 0         | 0         | 4         |
| <i>Melanelia subaurifera</i>                   | 3  | m     | –      | 0            | 0         | 3         | 9         | 0         |
| <i>Menegazzia terebrata</i>                    | 15 | m     | –      | 0            | 0         | 0         | 1         | <b>52</b> |
| <i>Nephroma bellum</i>                         | 20 | c     | NW     | 5            | 8         | 9         | 7         | 0         |
| <i>Nephroma helveticum</i>                     | 47 | c     | NW     | 10           | 4         | 14        | 9         | 17        |
| <i>Nephroma laevigatum</i>                     | 31 | c     | NW     | 0            | 1         | 2         | 11        | <b>42</b> |
| <i>Nephroma occultum</i>                       | 7  | c     | NW, OR | 1            | 6         | 0         | 9         | 0         |

TABLE 3. Continued.

| Species                               | N  | Group | Listed | Stream class |           |           |           |           |
|---------------------------------------|----|-------|--------|--------------|-----------|-----------|-----------|-----------|
|                                       |    |       |        | Upland       | Interm.   | No Fish   | Order < 5 | Large     |
| <i>Nephroma parile</i>                | 13 | c     | NW     | 1            | 5         | 1         | <b>20</b> | 0         |
| <i>Nephroma resupinatum</i>           | 44 | c     | NW     | 1            | 3         | 8         | 19        | <b>36</b> |
| <i>Nodobryoria abbreviata</i>         | 1  | m     | –      | 3            | 0         | 0         | 0         | 0         |
| <i>Nodobryoria oregana</i>            | 44 | f     | –      | <b>26</b>    | 20        | 21        | 3         | 0         |
| <i>Normandina pulchella</i>           | 2  | m     | –      | 0            | 0         | 0         | 3         | 2         |
| <i>Fuscopannaria leucostictoides</i>  | 3  | c     | NW     | 0            | 0         | 5         | 7         | 0         |
| <i>Fuscopannaria pacifica</i>         | 17 | c     | NW     | 4            | 1         | 1         | <b>23</b> | 1         |
| <i>Parmelia hygrophila</i>            | 44 | m     | –      | 7            | 11        | 4         | 5         | 23        |
| <i>Parmelia pseudosulcata</i>         | 19 | m     | –      | 15           | 2         | 10        | 3         | 0         |
| <i>Parmelia saxatilis</i>             | 62 | m     | –      | 13           | 15        | 9         | 9         | 21        |
| <i>Parmelia sulcata</i>               | 73 | m     | –      | 10           | 9         | 10        | 23        | <b>31</b> |
| <i>Parmeliopsis ambigua</i>           | 1  | m     | –      | 3            | 0         | 0         | 0         | 0         |
| <i>Parmeliopsis hyperopta</i>         | 57 | m     | –      | 26           | <b>28</b> | <b>29</b> | 6         | 0         |
| <i>Parmotrema chinense</i>            | 3  | m     | –      | 0            | 0         | 0         | 0         | 13        |
| <i>Peltigera britannica</i>           | 1  | c     | –      | 0            | 8         | 0         | 0         | 0         |
| <i>Peltigera collina</i>              | 35 | c     | NW     | 1            | 3         | 0         | 13        | <b>41</b> |
| <i>Peltigera neopolydactyla</i>       | 4  | c     | –      | 0            | 0         | 0         | 2         | 8         |
| <i>Peltigera pacifica</i>             | 1  | c     | NW     | 0            | 0         | 0         | 0         | 4         |
| <i>Phaeophyscia orbicularis</i>       | 1  | n     | –      | 0            | 0         | 0         | 0         | 4         |
| <i>Physcia adscendens</i>             | 6  | n     | –      | 0            | 2         | 4         | 0         | 5         |
| <i>Physcia aipolia</i>                | 11 | n     | –      | 0            | 1         | 0         | 0         | <b>39</b> |
| <i>Physcia tenella</i>                | 5  | n     | –      | 0            | 0         | 0         | 0         | <b>21</b> |
| <i>Platismatia glauca</i>             | 91 | m     | –      | <b>21</b>    | <b>21</b> | 18        | 19        | 19        |
| <i>Platismatia herrei</i>             | 86 | m     | –      | 22           | 25        | 21        | 19        | 10        |
| <i>Platismatia norvegica</i>          | 5  | m     | –      | 3            | 3         | 3         | 0         | 0         |
| <i>Platismatia stenophylla</i>        | 75 | m     | –      | <b>27</b>    | 25        | 19        | 7         | 9         |
| <i>Pseudocyphellaria anomala</i>      | 60 | c     | NW     | 12           | 22        | 18        | 13        | 7         |
| <i>Pseudocyphellaria anthraspis</i>   | 41 | c     | NW     | 7            | 7         | 14        | 9         | 9         |
| <i>Pseudocyphellaria crocata</i>      | 31 | c     | NW     | 4            | 7         | 8         | 11        | 6         |
| <i>Pseudocyphellaria rainierensis</i> | 10 | c     | NW, OR | 2            | 6         | 2         | 7         | 0         |
| <i>Ramalina dilacerata</i>            | 27 | m     | –      | 0            | 3         | 8         | 0         | <b>46</b> |
| <i>Ramalina farinacea</i>             | 36 | m     | –      | 1            | 2         | 2         | 3         | <b>62</b> |
| <i>Ramalina thrausta</i>              | 10 | f     | NW     | 0            | 0         | 0         | 5         | <b>21</b> |
| <i>Sphaerophorus globosus</i>         | 85 | m     | –      | 22           | 20        | 15        | 17        | 19        |
| <i>Sticta fuliginosa</i>              | 25 | c     | NW     | 3            | 9         | 1         | 10        | 7         |
| <i>Sticta limbata</i>                 | 20 | c     | NW     | 0            | 0         | 9         | 12        | 16        |
| <i>Sticta weigelii</i>                | 9  | c     | NW     | 0            | 1         | 3         | <b>29</b> | 0         |
| <i>Usnea chaetophora</i>              | 2  | f     | –      | 0            | <b>15</b> | 0         | 0         | 0         |
| <i>Usnea cornuta</i>                  | 7  | m     | –      | 0            | 1         | 1         | 1         | 5         |
| <i>Usnea diplotypus</i>               | 3  | m     | –      | 3            | 0         | 0         | 3         | 0         |
| <i>Usnea esperantiana</i>             | 1  | m     | –      | 0            | 0         | 0         | 0         | 4         |
| <i>Usnea filipendula</i>              | 57 | f     | –      | 9            | 3         | 10        | 10        | <b>36</b> |
| <i>Usnea glabrata</i>                 | 24 | m     | –      | 1            | 0         | 0         | 11        | <b>35</b> |
| <i>Usnea glabrescens</i>              | 15 | m     | –      | 0            | 0         | 1         | 1         | <b>46</b> |
| <i>Usnea lapponica</i>                | 1  | m     | –      | 0            | 0         | 0         | 6         | 0         |
| <i>Usnea longissima</i>               | 8  | f     | NW     | 0            | 0         | 0         | 3         | <b>19</b> |
| <i>Usnea pacificana</i>               | 6  | m     | –      | 0            | 0         | 0         | 5         | 10        |
| <i>Usnea scabrata</i>                 | 88 | f     | –      | 22           | 20        | 21        | 18        | 16        |
| <i>Usnea subfloridana</i>             | 13 | m     | –      | 0            | 0         | 0         | 10        | <b>23</b> |
| <i>Usnea substerilis</i>              | 2  | m     | –      | 1            | 0         | 0         | 4         | 0         |
| <i>Usnea wirthii</i>                  | 33 | m     | –      | 0            | 0         | 1         | 9         | <b>65</b> |
| <i>Vulpicida canadensis</i>           | 9  | m     | –      | 8            | 4         | 0         | 2         | 0         |
| <i>Xanthoria candelaria</i>           | 1  | n     | –      | 0            | 0         | 0         | 0         | 4         |
| <i>Xanthoria hasseana</i>             | 6  | n     | –      | 0            | 1         | 2         | 0         | 12        |
| <i>Xanthoria oregana</i>              | 1  | n     | –      | 0            | 0         | 0         | 0         | 4         |

chance. Forage lichens had the most uniform distributions (Table 6).

Listed species were somewhat aggregated in all habitats except along large streams (Fig. 2, Table 6). Note that for large streams, the frequency distribution of numbers of listed species closely fol-

lowed the poisson distribution, implying that listed species were distributed independently of each other ( $V/M \cong 1$ ). In the uplands and along small streams, however, listed species were strongly aggregated: finding one listed species greatly improves the likelihood of finding another.

TABLE 4. Comparison of species composition among stream classes, based on a nonparametric multivariate method (MRPP). The average within-group distance describes the variability in species composition within each stream class (0.5 = 50% dissimilar). Group differences are shown with the A statistic (A = 0 is the expectation under the null model; A = 1 when all members of a group are identical and non-overlapping with other groups; negative values indicate groups more similar than expected by chance). Bold face indicates a difference greater than expected by chance.

| Stream class  | Average within-group distance | A           |             |             |             |
|---------------|-------------------------------|-------------|-------------|-------------|-------------|
|               |                               | Upland      | Interm.     | No Fish     | Order < 5   |
| Large streams | 0.35                          | <b>0.48</b> | <b>0.39</b> | <b>0.31</b> | <b>0.19</b> |
| Order < 5     | 0.53                          | <b>0.11</b> | <b>0.10</b> | <b>0.09</b> | –           |
| No fish       | 0.44                          | 0.02        | 0.02        | –           | –           |
| Intermittent  | 0.41                          | –0.01       | –           | –           | –           |
| Upland        | 0.39                          | –           | –           | –           | –           |

When only the species on the amended survey-and-manage list (USDA & USDI 2001) were included, the average number of listed species per plot dropped from 7.0 to 1.1. Species on the new list were markedly aggregated in plots along intermittent streams and along fish-bearing streams with stream order < 5 (Table 5). In all other stream classes the level of aggregation was close to the random expectation.

Macrolichen species exclusive to one habitat were most frequent along large streams (Table 6). These exclusive species were well spread among the functional groups, although fewer exclusive cyanolichens were found than expected by chance. Although epiphytic cyanolichens were more frequent along large streams than other stream classes, essentially all of these species were also found along smaller streams or in upland habitats. Matrix lichens found only along the large streams included two relatively rare species, *Cetrelia cetrarioides* and *Parmotrema chinense*. Both of these species are more common in riparian areas in the Coast Range than the Cascades. Many of the weedy nitrophilous species were found only along the large streams. Species found only in the upland plots included two listed species, the matrix lichen *Cladonia norvegica* and the cyanolichen *Leptogium cyanescens*, but both of these occurred in just one plot.

#### DISCUSSION

Epiphytic macrolichen communities change markedly along a gradient from uplands, through riparian areas along small streams, to large streams. Forty percent of the 116 species observed were sufficiently frequent and differentially distributed to show a significant difference among stream classes,

TABLE 5. Concentration of species diversity in four classes of riparian habitats. Concentrations are ratios against upland habitats (1 = no enrichment).

|                                 | Stream class |         |           |       |
|---------------------------------|--------------|---------|-----------|-------|
|                                 | Interm.      | No Fish | Order < 5 | Large |
| All macrolichens                | 1.02         | 1.01    | 1.11      | 1.36  |
| Listed species                  | 1.24         | 1.24    | 1.75      | 1.57  |
| Amended survey & manage species | 1.29         | 1.07    | 2.46      | 0.95  |

using indicator species analysis. Epiphytic macrolichen communities in upland forests were, however, similar to those along intermittent streams and non-fish-bearing perennial streams.

The stream gradient was generally correlated with elevation. Obviously, the largest streams must occur at lower elevations. Both large and small streams occur at low elevations where stream size was the overriding factor.

Listed lichens (mostly on the “Survey-and-manage” list for the BLM and Forest Service) were 57–75% more frequent in riparian areas along fish-bearing streams than in uplands or along small streams. Clearly, riparian areas along large streams are critical contributors to landscape-level diversity of lichens. Protecting riparian zones from logging and urbanization and other forms of habitat destruction will, therefore, protect many rare species. Uplands and small streams, however, held some rare species that were absent from the riparian zones of large streams.

*Coarse-filter vs. single-species management.*—Protecting the biodiversity of our forested ecosystems is a goal of ecosystem management under the Northwest Forest Plan. This plan sought an alternative to tracking every single species at risk, the traditional “fine-filter” approach of the Endangered Species Act of the U.S. (Franklin 1993; Noss 1987). Many managers view the fine-filter approach as impractical for the large numbers of species considered to be at risk from logging. Alternatively, the “coarse filter” approach protects and manages habitats rather than individual species. The debate on protecting biodiversity through habitat management versus individual species management has a very long history (Eisner et al. 1995; Noss & Cooperrider 1994).

The better we understand the habitat needs of our species, the more effectively we can manage them with a coarse-filter approach. Most species are sufficiently common to be protected through tracking and managing habitats. Stochasticity of natural phenomena means, however, that the rarest species will require individual attention—their occurrences are too few to afford any semblance of predictability



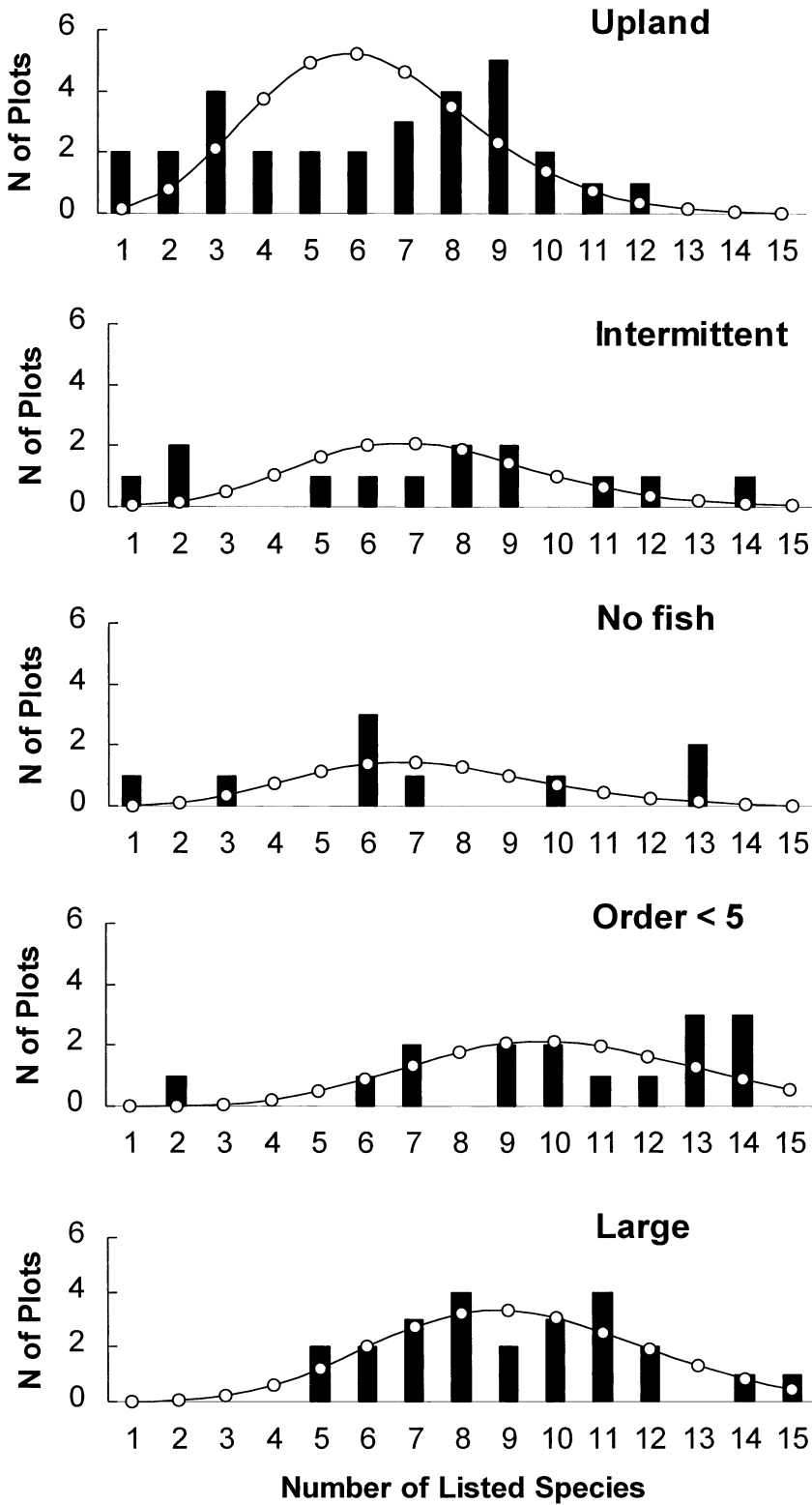


FIGURE 2. Number of plots containing the indicated number of listed species, in each of five stream classes from uplands to large streams. Bars indicate the observed data; lines show the expected values based on the assumption that listed species occur independently of each other (Poisson distribution).

TABLE 6. Aggregation of species diversity in classes of riparian habitats. Aggregation values are the variance/mean ratios (V/M) for number of species (V/M = 1 is random; V/M > 1 is aggregated, shown in **bold** face, V/M < 1 is more even than random). See Figure 2 for the frequency distributions corresponding to V/M for listed species. Exclusive species occurred in only one stream class. "Amended survey & manage" species are defined under "Methods."

|                                 | Stream class |            |            |            |            |
|---------------------------------|--------------|------------|------------|------------|------------|
|                                 | Upland       | Interm.    | No. Fish   | Order < 5  | Large      |
| Aggregation (V/M)               |              |            |            |            |            |
| All macrolichens                | <b>1.3</b>   | <b>1.6</b> | <b>1.8</b> | 1.0        | 0.8        |
| Cyanolichens                    | <b>1.7</b>   | <b>2.6</b> | <b>2.5</b> | <b>1.2</b> | 0.8        |
| Forage lichens                  | 0.5          | 0.3        | 0.6        | 0.6        | 1.1        |
| Matrix lichens                  | 1.0          | 0.7        | 0.5        | 0.8        | 0.3        |
| Nitrophiles                     | 1.0          | <b>4.0</b> | <b>2.0</b> | 0.9        | <b>1.2</b> |
| Listed species                  | <b>1.8</b>   | <b>2.5</b> | <b>2.7</b> | <b>1.3</b> | 1.0        |
| Amended survey & manage species | 1.0          | <b>1.5</b> | 0.7        | <b>1.3</b> | 1.0        |
| Exclusive species/plot          |              |            |            |            |            |
| All macrolichens                | 0.17         | 0.15       | 0.00       | 0.19       | 0.46       |
| Cyanolichens                    | 0.03         | 0.08       | 0.00       | 0.00       | 0.04       |
| Forage lichens                  | 0.00         | 0.08       | 0.00       | 0.00       | 0.08       |
| Matrix lichens                  | 0.13         | 0.00       | 0.00       | 0.19       | 0.13       |
| Nitrophiles                     | 0.00         | 0.00       | 0.00       | 0.00       | 0.21       |
| Listed species                  | 0.07         | 0.00       | 0.00       | 0.00       | 0.00       |
| Amended survey & manage species | 0.07         | 0.00       | 0.00       | 0.00       | 0.00       |
| Number of plots                 | 30           | 13         | 9          | 16         | 24         |

based on habitat alone. A combination of the coarse- and fine-filter approaches is, therefore necessary.

We are rapidly acquiring information on the distribution and abundance of many species that were previously poorly understood. As this information accumulates, we increasingly know which species require individual attention and which species can be managed through their habitats. The concentration of many listed cyanolichens in riparian habitats and their association with hardwoods means that they need not be tracked individually. Protecting riparian habitats from development and logging, while allowing natural disturbance regimes, should protect these species. These measures should also help to perpetuate many of the sporadic occurrences of more oceanic species in the Cascades (e.g., *Bryoria trichodes*, *Cetrelia cetrarioides*, and *Megazozia terebrata*).

Even though listed species were less frequent in uplands, when we found them they were aggregated. Based on analysis of the upland data by Berryman (2002) those aggregations of listed species are most likely in old stands.

Some infrequent species need more study, to better understand their distribution, abundance, and habitat associations. These species include *Cladonia norvegica*, *Leptogium cyanescens*, *Nephroma occultum*, *Pseudocyphellaria rainierensis*, *Ramalina thrausta*, *Sticta weigelii*, *Usnea chaetophora*, and *Usnea longissima*. Nitrophilous species such as *Phaeophyscia orbicularis*, *Physcia tenella*, and *Xanthoria hasseana* should be monitored as indi-

cators of declining air quality and increases in anthropogenic nutrient enrichment in the mountains.

*Riparian or old-growth associated?*—To some extent, old-growth dependency has been confused with habitat characteristics. Many of the species originally listed as old-growth associates in the Northwest Forest Plan (USDA & USDI 1994) turned out to be less strongly associated with old-growth forests per se than with hardwoods and shrubs (Neitlich & McCune 1997) and riparian areas (the present study). Similarly, many lichens considered old-growth associates in Fennoscandia are actually more strongly associated with forested wetlands and riparian areas than with old growth (Kuusinen 1996b; Ohlson et al. 1997; Rolstad et al. 2001).

The confusion is understandable, because some habitat characteristics may favor certain species, at the same time discouraging disturbance by logging or fire. For example, ash (*Fraxinus*) swamps in the Pacific Northwest have slow growing trees with low timber values, occur in areas too wet for most crops, are less prone to fire, and are protected somewhat by state and federal wetland laws. These factors combine to make forested wetlands focal points of stability in an increasingly altered landscape. Furthermore, riparian areas and wetlands have a more humid environment and a frequently broken, irregular canopy that may foster lichen growth and diversity.

Similarly, rock outcrop areas may have brush and stunted trees that discourage logging. The relative stability of these gaps in the forest canopy and

the diversity of woody plants occurring in outcrop areas appear to foster lichen diversity.

Disturbance rates depend on habitat characteristics; presence of old-growth associates depend on both disturbance rates and habitat characteristics. Future research will continue to clarify how disturbances and habitat characteristics interact to influence lichen communities.

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