Hotspots of Epiphytic Lichen Diversity in Two Young Managed Forests

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Abstract: *Understanding within-stand variation in diversity of epiphytes will provide an improved basis for producing timber while conserving biological diversity. Two 80-ha, 50-year-old managed stands of conifers were surveyed to locate 0.4 ha putative "diversity" plots, the areas appearing most diverse in lichen epiphytes. These plots were generally located in areas made heterogeneous by canopy gaps, wolf trees (trees with large-diameter lower branches), and old-growth remnant trees. "Matrix" plots, in contrast, were chosen at random from the remaining, more homogenous forest. Diversity plots hosted from 25% to 40% more epiphytic lichen species than matrix plots in both stands. The strongest within-stand gradients in species composition were correlated with percentage of plot occupied by gaps and wolf trees. Percentage of the plot in gaps was correlated with species richness (r = 0.79). In the more structurally diverse stand, diversity and abundance of nitrogen-fixing "cyanolichens" were correlated with percentage of the plot occupied by gaps (0.5 < r < 0.9), and alectori-oid lichens were correlated with percentage of the plot occupied by old-growth remnant trees (0.5 < r < 0.6). In the stand with more homogenous structure, percentage of the plot under gaps was correlated with regionally common species that were otherwise absent or sparse in the matrix. Protecting gaps, hardwoods, wolf trees, and old-growth remnant trees during thinning or other partial cutting is likely to promote the majority of epi-phytic macrolichens in young conifer forests. Because these features are easily recognized on aerial photos and on the ground by land managers, it is practical to manage for forest structures that would promote li-chen diversity.*

Sitios Críticos de Diversidad de Líquenes Epífitos en Dos Bosques Jóvenes Bajo Manejo

Resumen: *El entendimiento de la variación en la diversidad de epífitas proporcionará una mejor base para producir madera al mismo tiempo que se conserva la diversidad biológica. Dos bosques de coníferas de 80 ha, de 50 años de edad fueron muestreados para localizar parcelas de "diversidad putativa" de 0.4 ha, siendo estas las aparentemente más diversas en líquenes epífitos. Estas parcelas generalmente se localizan en áreas heterogéneas debido a huecos en el dosel de los árboles, árboles lobo (árboles con ramas inferiores de diámetro grande) y árboles viejos. En contraste, se eligieron parcelas "matriz" al azar en el resto del bosque homogéneo. En los dos bosques, las parcelas de diversidad tenían de 25 a 40% más especies de líquenes epífi-tos que las parcelas matriz. Los mayores gradientes de composición de especies fueron correlacionados con el porcentaje de la parcela ocupada por huecos y árboles lobo. Se correlacionó e porcentaje de la parcela con huecos con la riqueza de especies (r = 0.79). En el bosque estructuralmente más diverso se correlacionaron la diversidad y la abundancia de "cianolíquenes" fijadores de nitrógeno con el porcentaje de la parcela ocu-pada por huecos (0.5 < r > 0.9) y los líquenes alectorioides fueron correlacionados con el porcentaje de la parcela ocupada por árboles viejos (0.5 < r > 0.6). En el bosque de estructura más homogénea, el porcentaje de la parcela con huecos fue correlacionado con especies comunes regionalmente que, por lo demás, eran ausentes o escasas en la matriz. La protección de huecos, maderas duras, árboles lobo y árboles viejos al ex-*

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plotar los bosques posiblemente promueva a la mayoría de los macrolíquenes epífitos en bosques jóvnes de coníferas. Debido a que los manejadores de suelos fácilmente reconocen estas características en fotos aéreas y en el suelo, es práctico manejar la estructura del bosque para promover la diversidad de líquenes.

Introduction

If we seek to maintain diversity in a managed landscape, then we must learn more about managing species diversity in our extensive, young, even-aged forests. We hypothesize that species diversity and frequency of late-successional species for many groups of organisms could be enhanced by reintroducing structural diversity into otherwise relatively monotonous young forests.

Forest managers have expressed increased interest in promoting biodiversity by selectively cutting trees or groups of trees in young managed stands. The purpose of this stand manipulation is to promote biodiversity and facilitate rapid recovery of old-growth forest taxa while still harvesting trees. These alterations could be called "thinnings," except that trees would be selected according to different principles than in traditional thinnings. For example, trees might be cut in groups creating gaps in the canopy, rather than thinning to even out canopy density. Hardwoods might be favored in a conifer-dominated system instead of selecting against hardwoods to favor softwood production.

Creative thinning has promise for promoting the diversity and abundance of epiphytes. Managers could avoid cutting in concentrations of epiphyte diversity and improve structural diversity in species-poor, homogeneous areas. Whether this potential is realized depends on the degree to which diversity is concentrated in hotspots and the responsiveness of species diversity to increases in structural diversity.

Lichen diversity and abundance varies with forest age (e.g., Esseen et al. 1992, 1996; Kuusinen 1994*b*; Lesica et al. 1991; McCune 1993; Neitlich 1993), but little is known about variation in lichen diversity among and within young stands or how it differs between manipulated and natural young stands. We had three objectives for this study: (1) to quantify the range of variability of epiphytic lichen diversity in two young, managed stands; (2) to quantify the relationship between epiphytic lichen diversity and rapidly measurable forest characteristics such as presence of canopy gaps and old-growth remnant trees; and (3) to test the idea that hotspots of lichen diversity could be rapidly identified based on stand structure and the presence of a few key lichen species. Related work on structural correlates of diversity has been done over a much broader range of stands (Gustafsson et al. 1992), but we know of no prior work on variation in young, even-aged stands.

There is a large literature on the dynamics of gaps in forests all over the world (see references in "Gaps in Forest Ecology," *Ecology* special feature, **70**[3]) and in the Pacific Northwest (e.g., Lertzman & Krebs 1991; Lertzman 1992; Spies & Franklin 1989; Spies et al. 1990; Stewart 1986, 1988). Responses of some organisms to canopy gaps are known (e.g., Collins & Pickett 1988), but there is a notable lack of corresponding research on the responses of epiphytes to gaps, much less how the epiphytic response may relate to the long-term dynamics of the epiphyte communities of whole stands.

Considerable work has focused on the lichens of mid-elevation forests in the Oregon and Washington Cascades and Olympic Peninsula (Sillett 1995; McCune 1993; Neitlich 1993; Pike et al. 1975; Hoffman & Kazmierski 1969). Therefore, the prevailing ideas on the dynamics and conservation of epiphytes (USDA and USDI 1993, 1994*b*) are centered on the forests dominated by *Lobaria oregana*. Our study at lower elevations reveals important differences in epiphyte communities that should be considered in managing low-elevation conifer forests.

Methods

Study Sites

Epiphytic macrolichens were inventoried in 70 plots (35 per site) of 0.38 ha each at two sites. These sites were selected by the U. S. Bureau of Land Management for studies of creative methods to enhance structural diversity in young forests. Each site consisted of approximately 80 ha of 50 year–old, post-harvest, seemingly uniform, coniferous forest. Soils are deep at both sites and rock outcrops are lacking.

The first site, "Bottom Line," is in the eastern foothills of the Oregon Coast Range near Lorane, Oregon (43°46′N, 123°13′W). Slopes are moderately steep, rising from valleys at about 200 m to ridges at 350 m. Young *Pseudotsuga menziesii* and *Tsuga heterophylla* dominate, with widely scattered clusters of old-growth remnant trees and canopy gaps (≤ 0.3 ha). Gaps host understory hardwood trees and shrubs including *Corylus cornuta*, *Acer macrophyllum*, *A. circinatum*, *Cornus nuttallii*, *Rhamnus purshiana*, *Holodiscus discolor*, and *Gaultheria shallon*. Mean annual rainfall is approximately 120 cm (Taylor 1993).

The second site, "Lookout Point," is just north of the Bull Run watershed in the foothills of the Cascade Range, approximately 40 km east of Portland, Oregon (45°29'N, 122°8'W). Topography is moderate, with elevations ranging from 700 to 800 m. The forest consists principally of young *Tsuga heterophylla* and *Pseudotsuga menziesii* sprinkled with small- to medium-sized gaps 100–1500 m^2), many of these caused by mountain beaver (*Aplodontia rufa*). Gaps host *Acer circinatum*, *A. macrophyllum*, *Prunus virginiana*, and *Gaultheria shallon*. Mean annual rainfall is approximately 250 cm (Taylor 1993).

Field Methods

Each site was divided into four similar units where alternative treatments will be installed. The 35 lichen plots at each site were distributed almost equally among the four units and permanently marked with rebar and PVC pipe.

In each unit four to five areas presumably containing the highest lichen diversity were identified. These presumed hotspots were most rapidly located by examining forest gaps, patchy areas, and old-growth remnant trees. Cyanolichens (lichens containing a nitrogen-fixing cyanobacteria) and alectorioid lichens (pendulous, hair-like lichens in the genera *Alectoria*, *Bryoria*, *Usnea*, and *Ramalina*) were more abundant in these areas and were chosen as potential indicators of high diversity. A "diversity" plot was established in each of the presumed hotspots. Four or five "matrix" plots were then chosen from the remaining area in each unit. These plots were located arbitrarily but without preconceived bias. Riparian areas were excluded from the study. Potential plots were rejected if they fell within 5 m of a road, overlapped with another plot, or fell outside the unit boundary. Thus, the two populations of sample units in this study consisted of the presumed richest plots on the upland landscape ("diversity" plots) and "matrix" plots representing the rest of the upland landscape.

All epiphytic macrolichens occurring more than 0.5 m above the ground, or in litterfall presumed to have originated above this level, were scored from 0–4 according to Forest Health Monitoring protocol (Tallent-Halsell 1994). Scores were assigned as follows: 1 (rare) = 1–3 thalli in plot; 2 (occasional) = 4–10 thalli in plot; 3 (common) = more than 10 thalli present but less than needed for a rating of 4; 4 (abundant) = more than 50% of all available branches and stems in the plot host this species. In the species data approximately 40% of the ratings were 3, 50% were 0 with the remainder distributed among ratings of 1, 2, and 4. Because of the preponderance of 0s and 3s, the dataset tended toward a binary distribution and needed little transformation for effective analysis.

Measurements of forest structure fell into three classes: (1) basal area (m^2/ha) by species and species group, as determined by the wedge prism method (Wenger 1984) using five points per plot; (2) percentage of plot occupied by various structural categories (defined below); and (3) topographic variables. Structural categories were assessed as a percentage of plot area, totalling 100. Wolf trees were defined as conifers that were open-grown throughout most of their life history and had live or dead branches of at least 6 cm in diameter present less than 3 m above the ground. Gaps were defined as areas with no overstory canopy cover (but they usually contained understory hardwood trees and/or shrubs). Old-growth remnant trees were large diameter (usually ≥ 1 m) trees obviously much older (ca. 150–350 years) than the surrounding young forest matrix. Topographic variables included slope and aspect. For analysis aspect was converted to a "heat-load" index using the formula: heat load = 0.5 − (cos (Θ − 45))/2, where Θ is the azimuth in degrees east of north. The heat-load index ranges from zero (at 45° E of N) to 1 (at 225° E of N). Lichen nomenclature follows Egan (1987). Voucher specimens are in the Oregon State University Herbarium (OSC).

Analysis

Alpha diversity (α) was measured as species richness per plot. Gamma diversity (γ) is the number of species in the combined species list from all plots at a site or a within-site group of plots. A second estimate of gamma diversity, γ', is a first-order jackknife estimator of total species richness based on the number of single-occurrence species in the plots (Palmer 1990). Beta diversity (β) is the ratio γ/α (Whittaker 1972; Wilson & Shmida 1984) and is used here to measure the amount of species change across plots.

Community structure was ordinated for each site separately using nonmetric multidimensional scaling (NMS) (Kruskal 1964; McCune & Mefford 1995) on the matrices of plots by species. This is one of the most robust and effective methods for multivariate data reduction, especially with species x sample data and city-block distance measures (Faith et al. 1987; Minchin 1987; McCune 1994). Because NMS is based on ranked distances, it tends to linearize the relation between distance on an environmental gradient and the degree of difference between community samples. The method is an iterative search for placement of entities on a small number of dimensions to maximize the rank correspondence between dissimilarity in the original *n*-dimensional hyperspace and distances in the ordination space. The NMS was performed using the quantitative version of Sørenson's distance measure and two axes. Additional axes provided no more interpretable information. At Bottom

Line 16 of the 82 species occurred in fewer than three plots and were deleted prior to analysis. Deletion of species little improved the ordinations at Lookout, thus all species were retained. One outlier plot with an average compositional dissimilarity greater than 2 standard deviations from the average was deleted from the Lookout Point dataset. Ordinations were then rigidly rotated to align axis 1 with the strongest explanatory variables.

Multi-Response Permutation Procedure (MRPP) (Mielke 1984; McCune & Mefford 1995) was used to examine whether diversity and matrix plots occupied different regions of species space. MRPP is a nonparametric test for multivariate differences between two or more a priori groups.

Results

Rapid Assessment of "Hotspots"

Diversity plots were associated with gaps, patchy areas with wolf trees, and old-growth remnant trees at Bottom Line. Many of these areas were identifiable on aerial photos. At Lookout Point diversity plots were associated exclusively with gaps because remnant trees were absent. Matrix conifer forest plots infrequently contained small gaps and/or old-growth remnants, but not of a size that would have allowed them to be chosen as diversity plots. Choosing "hotspots" by a rapid assessment (ca. 3–5 minutes per 0.4 ha potential plot), looking for groups of indicator species (cyanolichens, alectorioid lichens, and any other unusual taxa), worked well. Approximately 25% of all species were restricted to diversity hotspots. Mean species richness in diversity plots was 38% and 24% higher than in matrix plots at Bottom Line and Lookout Point, respectively (Table 1). The point of this comparison is not to test whether diversity differed be-

tween the two classes of plots, but to evaluate the degree of concentration of species diversity in "hotspots" versus the forest matrix.

Gradient Analysis

Gradient analysis resulted in two-dimensional representations of the strongest compositional gradients (Fig. 1). Diversity and matrix plots occupied opposite regions of species space on axis 1. Diversity and matrix plots also occupied different regions of the unreduced species space (MRPP, $p < 10^{-6}$ and $p < 10^{-2}$ for Bottom Line and Lookout Point, respectively). At each site the structural variables most closely associated with axis 1 were percent gap and percent "matrix conifers." Gaps and matrix forest fostered a different set of species at each of the two sites as described below.

BOTTOM LINE

The NMS ordination (Fig. 1) represented 81% of the variation in the dataset, with 72% loaded on axis 1 and 9% on axis 2. Although many species were nearly ubiquitous in our plots, the differentiating species were abundant only in gap or old-growth remnant diversity plots. Species with the greatest differences in frequency between plot types were strongly correlated with the ordination axes (Table 2). The first ordination axis was related to dominance of cyanolichens, and the second, weaker axis was related to dominance of alectorioid lichens. With the exception of *Lobaria oregana*, which was more closely associated with alectorioid lichens (Table 2), cyanolichens generally exhibited strong correlations with axis 1 and little relationship to axis 2. The alectorioid lichens *Alectoria sarmentosa, A. vancouverensis,* and *Usnea scabrata* had the strongest correlations with axis 2.

These major gradients in lichen species composition were closely related to forest structure (Table 3). Axis 1 showed a strong positive correlation with proportion of plots occupied by gaps, wolf trees, and hardwoods and a strong negative relationship to total basal area in the plot and proportion of the plot occupied by "matrix conifers." Axis 2 was correlated with the abundance of old-growth remnant trees (Fig. 1). Lichen species richness was maximal in plots dominated by gaps and wolf trees, intermediate in plots dominated by old-growth remnant trees, and minimal in dense stands of matrix conifers. These differences in species richness resulted from the addition of a variable and often large numbers of cyanolichens to the more widespread species.

In univariate analysis the percentage of plot occupied by gaps was strongly correlated with species richness ($r^2 = 0.63$), whereas the percentage of plot occupied by ma-

Table 1. Average species richness per plot (α) and its standard error (SE), beta (β = γ/α), gamma diversity (γ = total species richness), and γ' (first-order jackknife estimator of total species richness) of lichen study plots.

Location and plot type	N	α (SE)	β	γ	γ'*
Bottom Line					
diversity (gaps, wolf trees and/or old-growth remnant trees)	18	39.6 (1.2)	1.9	76	86
matrix conifer forest	17	28.8 (0.7)	2.1	60	73
total	35	34.3 (1.0)	2.4	82	94
Lookout Point					
diversity (gaps)	17	26.5 (0.9)	2.2	59	69
matrix conifer forest	18	21.3 (0.9)	2.2	47	56
total	35	23.8 (0.8)	2.6	63	73

*The estimate for γ' is based on the number of single-occurrence species in the plots (Palmer 1990).
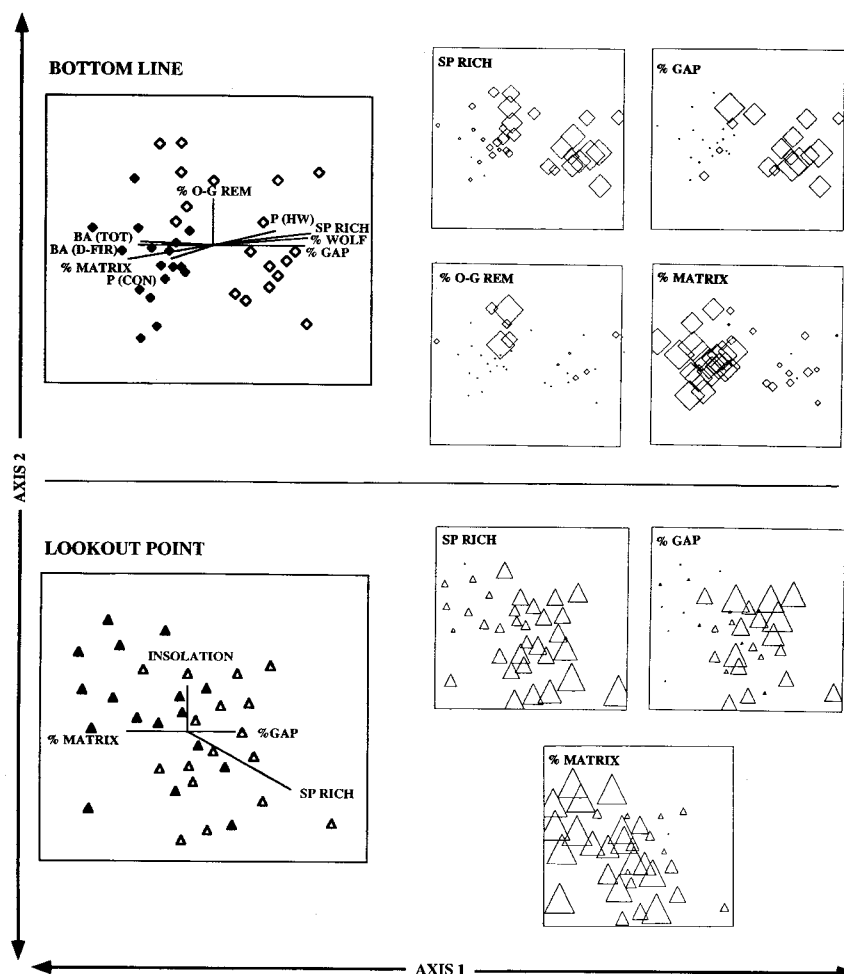
Figure 1. Ordinations (NMS) of 35 plots/site in species space at Bottom Line and Lookout Point, western Oregon (U.S.). In the ordinations on the left, open symbols are diversity plots and solid symbols are matrix plots. Vectors on the ordinations indicate the direction and strength of correlations between axis scores and environmental variables. In the overlays of most important environmental variables at right, the size of the symbol is proportional to the quantity of the variable for each plot. Variables are as follows: BA (TOT), total basal area; BA (D-FIR), basal area of Pseudotsuga; % MATRIX, percentage of plot occupied by gap-free coniferous forest (matrix); P(CON), proportion of basal area in conifers; % GAP, percentage of plot occupied by gaps; % WOLF, percentage of plot occupied by "wolf trees" as defined in text; SP RICH, species richness of lichens; P(HW), proportion of basal area in hardwoods; % O-G REM, percentage of plot occupied by old-growth remnant trees; and INSOLATION, heat load index.

trix conifers was strongly negatively correlated with species richness ($r^2 = 0.63$). Cyanolichens were abundant in plots with gaps and wolf trees and scarce in both matrix plots and plots with abundant old-growth remnant trees.

Plots with old-growth remnant trees but without gaps resembled matrix plots more than they did gap plots, but were readily distinguishable from both by a dominance of alectorioid lichens including *Alectoria*, *Bryoria*, and pendulous *Usnea* species. Plots with numerous old-growth trees are seen clearly in the basic ordination (Fig. 1) as the group of diversity plots clustered near the matrix plots, but slightly higher on axis 2.

Univariate comparisons were also revealing. *Lobaria*

pulmonaria, for example, behaved typically of cyanolichens as a whole, occurring in 76% of plots containing a gap (with or without remnant trees) but in only 45% of plots with old-growth remnants (with or without a gap). *Lobaria oregana* alone among the cyanolichens retained a high frequency of occurrence in old-growth remnant plots, occurring in 64% of remnant plots and 35% of gap plots. Not even this cyanolichen, however, was abundant in plots with old-growth trees, and showed only low ordination scores on axis 2. *Alectoria sarmentosa*, in contrast, occurred in 35% of plots with gaps and in 64% of plots with remnants and showed high correlation with axis 2.

Table 2. Correlations (r) of epiphytic lichen species with two ordination axes[a] and percent frequency of lichens in two young managed stands in western Oregon.[b]

	Bottom Line				Lookout Point			
	r		frequency (%)[c]		r		frequency (%)[c]	
Species	Axis 1	Axis 2	DIV	MAT	Axis 1	Axis 2	DIV	MAT
Cyanolichens								
Leptogium polycarpum	0.80	−0.25	61	0	0.07	−0.29	6	0
Lobaria oregana	−0.14	0.28	50	29				
L. pulmonaria	0.87	−0.07	72	29				
L. scrobiculata	0.42	−0.28	17	0				
Nephroma bellum	0.46	−0.25	39	0				
N. helveticum	0.81	−0.14	72	6				
N. laevigatum	0.91	0.05	78	6				
N. resupinatum	0.91	−0.10	67	0	0.07	−0.29	6	0
Pannaria saubinetii	0.81	−0.21	61	6				
Peltigera collina	0.86	−0.17	78	18				
P. membranacea					0.07	−0.29	6	0
Pseudocyphellaria anomala	0.71	0.18	61	6				
P. anthraspsis	0.91	−0.10	72	0				
P. crocata	0.59	0.02	33	0	−0.08	−0.11	6	0
Sticta fuliginosa	0.76	0.10	44	0				
S. limbata	0.64	−0.16	33	0				
Alectorioid lichens								
Alectoria sarmentosa	0.16	0.53	50	12	0.45	−0.28	65	33
A. vancouverensis	0.03	0.61	56	24	−0.21	0.09	0	6
Bryoria capillaris	0.15	−0.18	100	100	0.24	−0.26	6	6
B. friabilis	0.19	0.09	78	65				
B. fuscescens	0.28	0.31	39	6				
B. oregana			11	0	0.25	−0.25	6	11
B. pseudofuscescens	0.06	0.38	67	47	0.35	−0.32	12	11
Letharia vulpina	−0.10	0.48	28	0				
Ramalina menziesii			6	0				
R. thrausta	0.07	0.32	28	6				
Usnea spp.	0.00	0.00	100	100	0.36	−0.30	100	94
U. fulvoreagens			6	0				
U. hirta			11	0				
U. lapponica	−0.38	−0.03	6	29	−0.14	0.38	0	11
U. longissima					0.31	−0.21	12	0
U. plicata aggr.	0.00	0.00	100	100	0.42	−0.16	100	94
U. scabrata	0.07	0.50	17	0	0.03	0.01	12	0
U. wirthii	0.04	−0.01	94	94	0.29	−0.14	94	83
Other foliose and fruticose lichens								
Candelaria concolor	−0.15	0.11	22	24				
Cavernularia hultenii	0.02	−0.02	6	12	0.51	−0.29	76	61
Cetraria chlorophylla	0.08	0.04	89	82	0.15	−0.15	24	22
C. orbata	−0.35	−0.26	100	100	0.43	−0.67	76	61
Esslingeriana idahoensis	−0.04	−0.21	6	18	0.20	−0.26	6	11
Evernia prunastri	−0.16	0.02	100	100	0.65	−0.61	94	61
Hypocenomyce castaneocinerea			6	6	0.21	−0.17	6	6
H. friesii					0.43	−0.27	6	0
Hypogymnia apinnata	0.41	0.28	33	0	0.02	−0.48	12	6
H. enteromorpha	0.00	0.00	100	100	0.51	−0.14	100	100
H. imshaugii	−0.25	−0.08	22	35	0.50	−0.16	41	11
H. inactiva	0.00	0.00	100	100	0.00	0.00	100	100
H. metaphysodes					0.00	0.31	12	17
H. occidentalis	0.00	0.00	100	100	0.23	0.22	24	6
H. physodes	0.11	−0.36	100	100	0.00	0.00	100	100
H. tubulosa	−0.03	−0.23	100	100	0.40	0.13	100	100
Hypotrachyna sinuosa	0.13	−0.03	61	71	0.35	−0.05	65	50
Loxosporopsis corallifera					0.32	0.11	12	0
Melanelia sp.					0.22	0.16	12	6

Table 2.   Continued

Species	Bottom Line				Lookout Point			
	r		*frequency (%)*[c]		*r*		*frequency (%)*[c]	
	Axis 1	Axis 2	DIV	MAT	Axis 1	Axis 2	DIV	MAT
M. exasperatula	0.08	−0.13	44	35	0.43	−0.31	12	17
M. fuliginosa	−0.14	−0.21	0	24				
M. subaurifera	0.11	−0.33	83	82	0.53	−0.46	65	11
Menegazzia terebrata	0.38	−0.32	17	0				
Parmelia hygrophila	0.03	−0.19	89	82	0.58	−0.47	76	56
P. pseudosulcata	−0.16	0.50	39	47	−0.28	0.19	12	44
P. saxatilis	0.24	−0.20	28	12	0.23	0.06	35	11
P. sulcata	0.00	0.00	100	100	0.19	−0.25	100	100
Parmeliopsis hyperopta	0.24	−0.19	17	6	0.00	−0.07	100	100
Parmotrema arnoldii					0.14	−0.28	0	6
Phaeophyscia rubropulchra					0.19	0.08	6	0
Physcia adscendens	−0.10	0.17	28	24	0.37	−0.48	18	0
P. aipolia					0.30	−0.43	12	0
P. tenella	−0.06	0.19	11	12	0.52	−0.27	18	0
Plastismatia glauca	0.00	0.00	100	100	0.00	0.00	100	100
P. herrei	0.27	0.12	100	100	0.41	−0.02	100	61
P. norvegica			0	6	0.29	−0.07	18	6
P. stenophylla	−0.04	0.04	83	94	0.09	−0.34	88	89
Ramalina dilacerata	0.39	−0.05	28	18	0.23	−0.34	24	0
R. farinacea	−0.21	−0.21	100	100	0.72	−0.37	88	50
Sphaerophorus globosus	0.20	0.34	100	94	0.29	0.04	100	100
Xanthoria candelaria	−0.07	0.05	17	12				
X. polycarpa					0.30	−0.43	12	0
Squamulose lichens								
Cladonia bellidiflora					0.16	0.16	6	0
C. chlorophaea	−0.04	0.24	39	35	0.25	−0.38	47	22
C. cornuta					0.04	0.09	12	6
C. fimbriata	0.53	−0.05	56	12	0.23	−0.10	35	33
C. furcata	0.11	0.13	11	6				
C. ochrochlora	0.22	0.07	89	88	0.10	0.09	100	100
C. subsquamosa	0.09	0.51	78	53	−0.02	−0.57	53	44
C. transcendens	0.08	−0.26	83	82	0.28	0.51	59	50

[a] *Nonmetric multidimensional scaling; Fig. 1.*
[b] *Blanks indicate a species was absent or excluded from the ordination.*
[c] *DIV, diversity plots; and MAT, matrix plots.*

LOOKOUT POINT

The two-dimensional ordination (Fig. 1) represented 68% of the variation in the species matrix, with 41% loaded on Axis 1 and 27% on Axis 2. Major portions of the regional cyanolichen flora were absent from this site (presumably from the combination of air pollution from Portland and extensive historical clearcutting), resulting in fewer differences between diversity (i.e., gap) and matrix plots than at Bottom Line. Only 2 of 35 plots hosted cyanolichens, and the few cyanolichens present received ratings of "rare." The non-structural attribute most strongly correlated with ordination axes was lichen species richness. Percentages of the plot occupied by gaps versus matrix conifers was again the major structural factor associated with Axis 1. The species most strongly correlated with this axis were, however, regionally common. Again, this reflects the low diversity of this system. Species strongly correlated with gap plots at this site included *Ramalina farinacea*, *Evernia pru-*

nastri, *Physcia tenella*, and *Alectoria sarmentosa* (Table 2). Axis 2 was weakly correlated with the heat load index ("insolation" in Fig. 1; r = 0.35). *Cladonia transcendens* and *Usnea lapponica* showed the strongest positive correlations with this axis, whereas *Cetraria orbata*, *C. subsquamosa*, and *Evernia prunastri* showed the strongest negative correlations. The only cyanolichens found at this site occurred in gap plots, but were too rare to show correlations with ordination axes.

Discussion

Importance of Hardwood Gaps in Young Conifer Forests

"Hardwood gaps" are defined as breaks in the coniferous canopy that are filled with hardwood trees and shrubs. Lichen diversity in the two young, managed stands was distinctly higher in hardwood gaps between 0.10 and 0.3 ha and in the associated wolf trees than in

Table 3. Mean and standard error (SE) of selected measurements of stand structure in diversity (DIV) and matrix (MAT) plots, and correlation coefficients (r) of these measurements with NMS ordination axes (axes 1 and 2).

	Bottom Line				Lookout Point			
	r		Mean (SE)		r		Mean (SE)	
Species	Axis 1	Axis 2	DIV n = 18	MAT n = 17	Axis 1	Axis 2	DIV n = 17	MAT n = 18
Basal area (BA, m²/ha)								
Total BA	−.73	.12	32 (2)	43 (2)	−.08	−.30	40 (2)	50 (2)
BA conifers	−.76	.03	29 (2)	42 (2)	−.17	−.25	37 (2)	49 (2)
BA hardwoods	.38	.39	3 (<1)	1 (<1)	.44	−.17	3 (1)	1 (<1)
Percent BA conifers	−.51	−.27	89 (2)	98 (<1)	−.43	.13	92 (2)	98 (<1)
Percent BA hardwoods	.51	.27	11 (2)	2 (<1)	.43	−.13	8 (2)	2 (<1)
BA *Pseudotsuga menziesii*	−.76	.01	28 (2)	42 (2)	.29	−.39	22 (2)	21 (3)
BA *Tsuga heterophylla*	−.13	.21	<1 (<1)	<1 (<1)	−.43	.10	15 (1)	27 (3)
Percent of plot occupied by old-growth remnants	−.07	.53	16 (6)	<1 (<1)	—	—	—	—
Total gaps (excluding recent windfall gaps)	.77	−.01	43 (6)	2 (1)	.63	−.04	51 (4)	6 (2)
Corylus cornuta gaps	.59	−.13	18 (5)	<1 (<1)	—	—	—	—
Acer circinatum gap	—	—	—	—	.29	−.21	21 (5)	2 (1)
Acer macrophyllum gap	.23	.28	5 (3)	<1 (<1)	.31	−.37	2 (2)	<1 (<1)
Alnus rubra gap	—	—	—	—	.27	.19	6 (4)	0
Low shrub – open conifer gap	.40	.07	15 (5)	<1 (<1)	.19	.08	13 (5)	3 (1)
Recent windfall gaps	−.20	−.04	2 (1)	6 (<1)	—	—	—	—
Wolf trees	.82	.01	19 (4)	0	.35	−.15	7 (2)	<1 (<1)
Matrix conifers	−.78	−.25	21 (4)	91 (3)	−.64	.08	43 (4)	93 (2)
Other Factors								
Heat-load index	.47	.16	.64 (.09)	.35 (.08)	−.05	.35	.71 (.09)	.72 (.07)
Slope (°)	−.28	.32	10 (1)	10 (1)	−.23	−.30	5 (1)	5 (<1)
Selected as diversity plot	.75	.32	yes	no	.60	−.22	yes	no
Lichen species richness	.80	.20	40 (1)	29 (<1)	.83	−.66	26 (1)	21 (<1)

matrix conifer forest, which had depauperate lichen communities (Table 1; no gaps > 0.3 ha were present in this study). Land managers have typically thought of gaps as unproductive areas in which to locate silvicultural access such as logging yards, landings, and roads (P. O'Toole, personal communication). Although there has been increased concern over old-gowth remnants as propagule sources for recovering forests (USDA & USDI 1993; Peck & McCune, unpublished data), gaps have not generally been considered a structural feature worth conserving.

In England Rose (1992) reported that widely-spaced forests with open-grown trees were far richer than plantations in epiphytic lichens. The North American lichenological community has emphasized that most of the more sensitive epiphytes require the conservation of intact blocks of mature to old-growth trees (USDA & USDI 1993), but has not stressed the importance of gaps and hardwoods in younger forests. Of the 20 lichens in this study listed as taxa of concern in the President's Forest Plan (USDA & USDI 1994b), 18 were most associated with gaps and only two were most associated with old-growth remnant trees. Because gaps, wolf trees, and old-growth remnant trees can all be identified easily on

aerial photographs there is great potential to incorporate these features into management planning. Managing for hardwood gaps is likely to significantly increase lichen biodiversity in young conifer forests.

We studied sheltered forest gaps filled mainly with hardwoods and shrubs and no larger than 3000 m². We need to study a broader range in size and contents of gaps. Field observations suggest that very large gaps such as clearcuts do not foster rich lichen communities. Extreme exposure and desiccation are likely to be the causes of relative lichen poverty in and around clearcuts. Data from this study show that the smallest gaps (e.g., 25 m²) have only a slight effect on lichen diversity, whereas hardwood gaps of approximately 1000 m² or greater can dramatically boost lichen diversity. The size at which gaps become optimal for lichen diversity is unknown, as is the size at which lichen diversity per unit area begins to decline. Because lichen diversity apparently responds to light and moisture regimes, the dependency on gap size probably varies by topographic position and aspect.

It is common knowledge among lichenologists that many lichens differ in frequency between hardwoods and conifers (e.g., Barkman 1958). Differences between

conifers and hardwoods are usually viewed as a matter of substrate preference without examining the consequences to the long-term dynamics of epiphytes in forests. In Sweden, Finland, and coastal Alaska, however, old hardwoods in conifer forests are recognized as carriers of exceptional diversity of lichens and other organisms (Esseen et al. 1992; Kuusinen 1994*a*, 1994*b*; Sillett & Neitlich 1996).

After catastrophic disturbance the rate of recovery of epiphytes in conifer forests may depend on the abundance of canopy gaps containing hardwood trees and shrubs. Hardwoods in gaps in young conifer forest host a higher diversity, including some old-growth associated species, than the surrounding forest. We hypothesize that these "hardwood gaps" may be important foci for diversity and entry points for "old-growth species" in young forests. These species appear to colonize both the hardwoods themselves and the sides of the conifer crowns that face the gaps. These foci would be particularly important if colonization of large tracts of early successional forests is delayed by poor dispersal abilities.

Differences in Old-growth Lichens with Elevation

The prevailing ideas on conservation of epiphytes in the Pacific Northwest (e.g., USDA & USDI 1993, 1994*b*) are centered on forests dominated by *Lobaria oregana*. At low elevations, however, we have found important differences in epiphyte communities that should be considered in managing the low-elevation conifer forests.

Cyanolichens are the dominant lichens of old-growth forests at middle-elevations (500–1000 m) (Neitlich 1993; McCune 1993; Sillett 1995) but alectorioid lichens dominate in old-growth forests at other elevations. At Bottom Line cyanolichens other than *Lobaria oregana* occurred primarily in the lower understory (< 4 m above the ground). In middle-elevation, old-growth forests of the central Oregon Cascades, however, good cyanolichen habitat is available throughout the upper two-thirds of the forest's vertical profile (McCune 1993; Sillett 1995). In contrast, in low elevation and drier forests cyanolichen habitat is compressed to the lowest stratum. Well-lit, very moist habitat in these forests may be found only in hardwoods gaps and the associated wolf trees. Cyanolichens were joined by a suite of other lichens that favor hardwoods (e.g., *Ramalina dilacerata, Menegazzia terebrata, Physcia stellaris*), making gaps the focus of diversity in the upland landscape.

In contrast, low-elevation, old-growth remnant trees harbored sizable loads of alectorioid lichens. These lichens supply important winter forage for many rodents and ungulates (Richardson & Young 1977; Stevenson 1978). Most of the alectorioid species that we found are well represented at various other places on the landscape, usually in old growth. One notable exception was

Ramalina thrausta, which is regionally unusual, but is absent from mid- to high-elevation old growth.

Lobaria oregana is the dominant cyanolichen of mid-elevation old-growth forests. At lower elevations (Bottom Line) it showed a fairly faithful association with the old-growth remnants, but was seldom abundant. We know of no low-elevation, old-growth stands in which *Lobaria oregana* is the dominant epiphyte.

Old Growth Is Not the Only Reservoir of Lichen Diversity

In recent forest plans (USDA & USDI 1993, 1994*a*, 1994*b*), old-growth forests are held as a key reservoir of species in the Pacific Northwest. Cyanolichens are depicted as old-growth-dependent species. Although these assertions are true, it is important to remember that protecting old growth is not synonymous with preserving biodiversity. Hardwood gaps, even in young forests, are an important habitat for cyanolichens. Furthermore, low-elevation, old-growth forests are more clearly distinguished from young forests by their alectorioid lichens than by cyanolichens.

The challenge of recreating lichen communities associated with old-growth forests should be supplemented by the challenge of identifying the different structural features of forests that are likely to host high biodiversity and rare taxa over a variety of landscape positions.

Management of Stand Density and Hardwoods

One of the driving questions behind this study was whether "density management" could enhance the recovery of old-growth-related species. We speculate that a traditional, uniform thinning of already dense forests may have comparatively little effect, but that creation of gaps might make significant contributions to lichen diversity 20 to 50 years from now. Dense forests rarely have well-developed lower branches (see Esseen et al. 1996). Even heavy thinning would do little to create new habitat at the bottom of the vertical profile. In contrast, gap creation or early successional thinning to create patchy forests rich in wolf trees would probably help significantly. In northern Idaho Rominger et al. (1994) found that live *Abies lasiocarpa* branches supported approximately 60% greater lichen biomass than dead branches. Wolf trees and gap-edge conifers retain larger proportions of live branches than does surrounding forest. In addition, they maintain the oldest conifer branches in a young forest, giving them the greatest time to accumulate lichen propagules. Because of the large quantity of low, old, live conifer branches and abundant hardwood trees and shrubs, it appears reasonable that gaps should generally host the greatest lichen biomass and diversity in a young stand. It is likely that a structurally heterogeneous young forest that includes gaps and remnant

trees may host greater lichen diversity than even a dense old-growth stand.

The importance of hardwoods as focal points of diversity in conifer-dominated systems seems to be in conflict with the traditional attitude of land managers toward hardwoods, "...within the forestry community there has been a persistent image of hardwoods as an overabundant resource, and foresters have viewed hardwoods as economically undesirable competitors of the preferred and better recognized softwoods species. Along with the image of overabundance in the woods has come the image of low-valued manufactured products and underuse of available raw materials by the hardwood industry" (Raettig et al. 1995). This view resulted in widespread use of herbicides and other measures to control hardwoods in the Pacific Northwest. Yet Raettig et al. point out that, "Immediate and long-run hardwood supply prospects...are in doubt." From both conservative and consumptive viewpoints it is important to manage for hardwoods.

Evaluation of Sampling Method

Use of the Forest Health Monitoring lichen protocol (Tallent-Halsell 1994) revealed clear community differences even on a small scale with low β diversity. Although this strategy of visual assessment in large plots has relatively low precision, "species capture" is high (McCune & Lesica 1992). Although the method does not allow comparisons of large differences in biomass (i.e., both 1 and 100 kg/ha of a species would probably receive a rating of 3), it does allow for rapid assessment of major community gradients. Moreover, the data do not usually require relativizations or other transformations to produce an interpretable result.

For this study we examined only two sites in western Oregon. This necessarily limits the scope of the conclusions. Field work for other studies in progress, however, suggests that the within-site structural variation at these two sites is fairly typical of young, even-aged conifer stands at low to middle elevations. We do not, however, believe the results should be extrapolated to forests on the east side of the Cascades. There, the frequency of cyanolichens is much lower, the climate is drier, and canopies are often less dense.

Conclusions

Protecting gaps, wolf trees, and old-growth remnant trees is likely to promote the majority of epiphytic macrolichens, especially those sparsely distributed on the landscape or requiring specialized habitats. Because these features are easily recognized on aerial photos and on the ground by non-lichenologists, it is practical to manage for forest structures that would promote lichen diversity. Such management is likely to yield more frequent occurrence of cyanolichens and alectorioid lichens in our landscape of abundant young forests. Although this biodiversity is valuable in its own right, the functional roles of these groups as nitrogen-fixers and forage lichens are also likely to be enhanced.

Enhancing habitat for one group of species often detracts from habitat for another group of species because diversity of different groups responds to different factors (Berg et al. 1994; McCune & Antos 1981*a, b*). In this case, however, we hypothesize that the important structural features identified here could have a positive effect on many groups of organisms (e.g., Pettersson et al. 1995) by reintroducing structural diversity into otherwise relatively monotonous young forests.

Acknowledgments

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