

## AN ABSTRACT OF THE DISSERTATION OF

Eric B. Peterson for the degree of Doctor of Philosophy in Botany and Plant Pathology  
presented on May 24, 2000. Title: Analysis and Prediction of Patterns in Lichen  
Communities over the Western Oregon Landscape.

Abstract Approved:

*Redacted for Privacy*

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Bruce P. McCune

The diverse lichen flora of the Pacific Northwest is being impacted by population growth and by forest management practices. Accumulating information about our lichen flora will improve our conservation strategies. This dissertation first collects information to improve our understanding of how lichen communities vary among forests of differing structure, and across the western Oregon landscape. It then proposes a method to predict species occurrence in unsampled sites by utilizing the information on forest characters and environmental gradients at sampled sites.

Macrolichen communities sampled in coniferous forests revealed that old-growth stands (> 200 yrs old) harbored communities that differed from those in young forests (50-110 yrs old). Even more atypical communities occurred in macrolichen hotspots, which were primarily in riparian zones. Many macrolichen species were associated with these hotspots, including numerous nitrogen-fixing cyanolichens. Macrolichen species associated with old-growth forested plots included the nitrogen-fixing lichen *Lobaria oregana* and several forage-providing alectorioid lichens. The presence of remnant old trees apparently increased the occurrence of old-growth associates in young stands. The calicioids, a group of microlichens investigated only in the Cascades, had a strong association with old growth forest and remnant trees. Diversity of calicioids may also be increased by legacy structures such as old snags and wolf trees. These structures increase continuity between current and previous stands.

Macrolichen communities varied between the Coast and Cascade Mountain Ranges, following climatic gradients, particularly annual precipitation. Successional patterns in macrolichen communities appeared to differ between the mountain ranges.

The modeling method proposed for using habitat associations to predict occurrence has several advantages over common modeling methods, such as regression. The method is simple, avoids parametric assumptions, provides easy updating of models as additional sites are sampled, and automatically accounts for interactions among predictor variables. It can be linked with GIS data and software to map estimated probability of occurrence across landscapes. The data on calicioids from the Cascades, supplemented with additional stand inventories, were used to test and demonstrate the modeling method.

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Analysis and Prediction of Patterns in Lichen Communities  
over the Western Oregon Landscape

by

Eric B. Peterson

A DISSERTATION

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degree of

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Chair of Department of Botany and Plant Pathology

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Dean of Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Eric B. Peterson, Author

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First and foremost, I thank my wife, Adriane, for her tolerance of my schedule as a graduate student as well as for the many papers she has helped me edit. Perhaps we may soon get to spend an entire weekend having fun together!

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There were many important people on my road to graduate school. My high school biology teacher Ernest Odell cemented my interest in biology. Several professors in the biology department at Humboldt State University further nurtured my interests in botany and mycology, particularly Dr. David Largent, Dr. Michael Mesler, Dr. John Sawyer, and Dr. Denis Walker. Also, two professors in the art department at HSU influenced my eye for patterns and details: Don Anton (photography) and William Anderson (illustration).

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The mycological interests that I first developed under Dr. David Largent at HSU, have been expanded both classes and friendly conversation with Dr. Joseph Spatafora. Dr. George Poinar provided me with a truly intriguing collaboration/side-track: fossilized lichens. Dr. John Tappeiner has helped me to better understand the issues and challenges of forest management. Dr. John Bailey provided a great deal of information on the stands that I sampled for much of the research contained in this dissertation. Dr. David Hibbs has been a very interesting Graduate School Representative to my committee and has frequently assisted me as a regular committee member. Dave has challenged me intellectually, inspiring philosophical contemplation on the nature of science and giving me the chance to say that in my preliminary exams, I actually got one of those questions, "tell me everything about..."

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And of course there are the many students who have helped in innumerable ways, from buying me a beer, to inspiring professionalism. I could easily write another hundred pages here, but should try to be brief. Dylan Keon and I share many computer interests and Dylan has frequently helped me with GIS software. Other members of the McCune/Muir lab have been good friends as well as colleagues: Shanti Berryman, Jennifer Hutchinson, Briana Lindh, Jean Ponzetti, Tom Rambo, Abbey Rosso, Andrea Ruchty, and Steve Sillett. Of course my appreciation extends well beyond our lab. Always willing to help, Dr. Francisco Camacho (Ankie) spent several afternoons last spring guiding my first attempts to extract DNA from the new calicioid listed as 'Species 1' in chapters four and five. Dr. Jamie Platt has been a wonderful collaborator on my side track with fossilized lichens. Diane Greene, Martin Hutten, and Eric T. Peterson helped with another of my side tracks, *Sulcaria badia*. There are also the many students I have chatted with at the Bombs-Away gatherings which have now fizzled out (too bad), various fellow teaching assistants, and many other students that I run into around the halls. However, I'm approaching the end of the page, so perhaps this is a good place to stop.

## **CONTRIBUTION OF AUTHORS**

Dr. Bruce McCune (Oregon State University, Department of Botany and Plant Pathology) assisted with the sampling design, lichen identification, analysis methods, and model development for research contained in this dissertation. Dr. Jouko Rikkinen (University of Helsinki, Department of Plant Biology) contributed a substantial portion of the data for modeling occurrence of calicioids and helped in assessing the calicioid flora of Oregon.

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## **DEDICATION**

This dissertation is dedicated to my father, Richard Peterson, who inspired my love of nature and my determination to get things done; and to my mother, Virginia Peterson, who inspired my creativity and encouraged my intellectual pursuits.

# Analysis and Prediction of Patterns in Lichen Communities over the Western Oregon Landscape

## Chapter 1

### Introduction

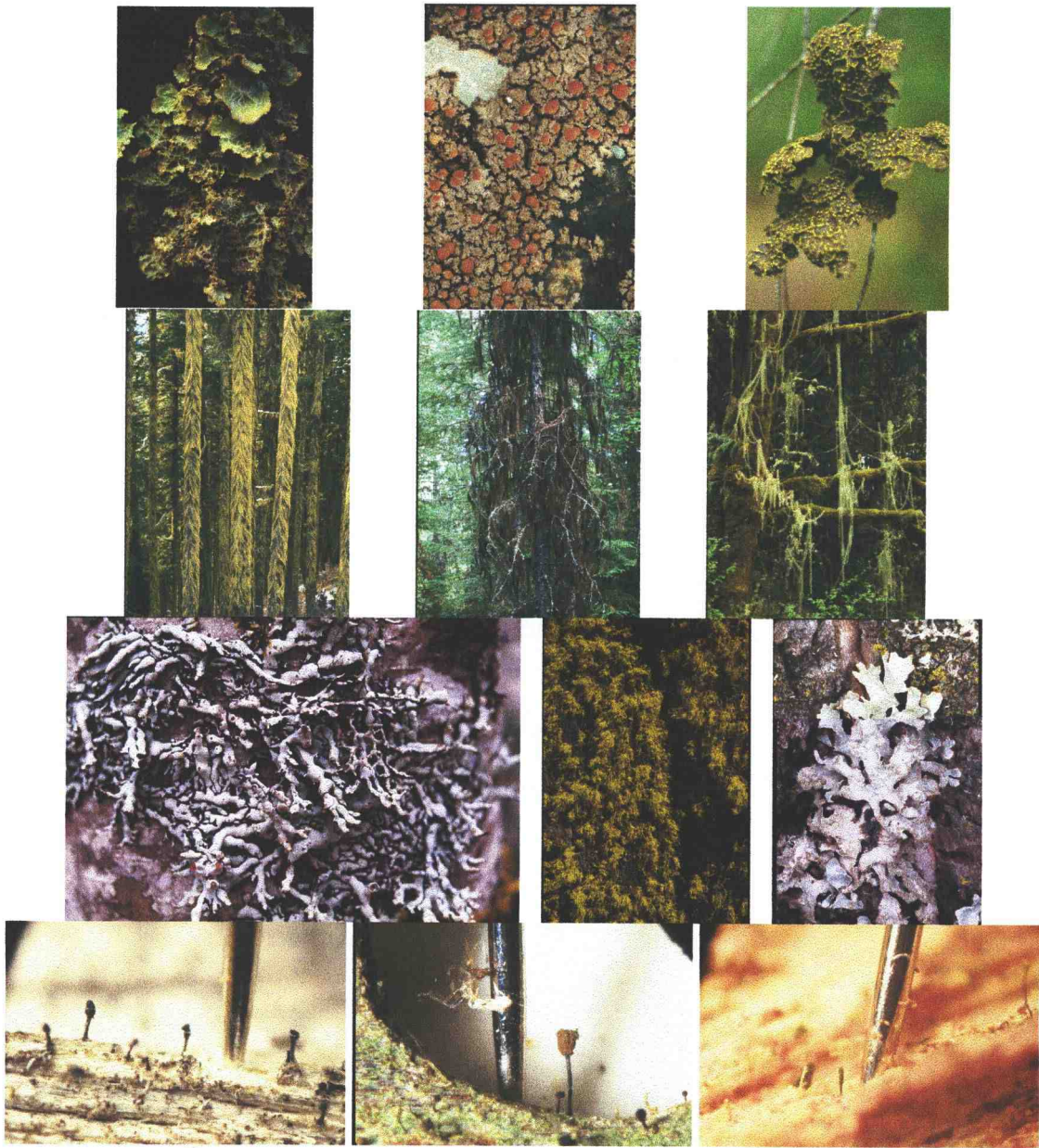
This dissertation has two intents. First it relates variation in lichen communities among stands and across the western Oregon landscape to stand characters and environmental gradients. Then it uses the relevant factors to predict the occurrence of lichens in additional sites.

Understanding the variation in lichen communities, and underlying environmental and historical factors, is important to current issues of forest management (Rosentreter 1995). This understanding can be used to promote lichen diversity and abundance in the landscape.

Prediction of species occurrence from the environmental conditions of a site could be a valuable tool for land managers. Prediction of a species list for a stand prior to a survey can provide surveyors with insight that might improve their ability to detect species within the stand. Managers might compare predictions of species lists for differing hypothetical stands when considering stand prescription options. Maps of species distributions can be drawn by linking the prediction method to GIS data and software. Such maps can be used to identify sites of high conservation value.

This dissertation examines three functional groups of macrolichens (foliose and fruticose lichens) and one ecological group of microlichens (crustose lichens; Figure 1.1). Surveys for, and management of, various lichens from all four groups are required on Federal lands in the USA within the range of the Northern Spotted Owl (USDA and USDI 1994).

The macrolichen functional groups are the nitrogen-fixing cyanolichens, the forage-providing alictorioid lichens, and the matrix lichens. Cyanolichens are important contributors of nitrogen to forests in the Pacific Northwest (Pike et al. 1972; Pike 1978; Rhoades 1983). The long, pendulous alictorioid lichens are known as valuable sources



**Figure 1.1** Examples of the lichens in this dissertation (OSU Lichen Group 1999). (A-C) Cyanolichens (A = *Lobaria oregana*\*\*, B = *Fuscopannaria saubinetii*\*, C = *Pseudocyphellaria crocata*\*\*). (D-F) Alectorioid lichens (D = *Alectoria sarmentosa*\*\*, E = *Bryoria pseudofuscescens*\*\*\*, F = *Usnea longissima*\*\*\*\*). (G-I) Matrix lichens (G = *Hypogymnia enteromorpha*\*\*, H = *Letharia vulpina*\*\*, I = *Parmelia sulcata*\*). (J-L) Calicioids (J = *Calicium glaucellum*\*, K = *Chaenotheca trichialis* parasitized by *Chaenothecopsis viridireagens*\*, L = *Microcalicium ahlneri*\*). Calicioid images include a sewing pin for scale. \* = photographs by E. B. Peterson; \*\* by J. Riley; \*\*\* by B. McCune; and \*\*\*\* by A. Rosso. Species authorities are provided in following chapters.

of food and nest-materials for a variety of animals, including *Glaucomys sabrinus*, the northern flying squirrel (Sharnoff 1994; Rosentreter et al. 1997). Matrix lichens (the remainder of the macrolichens) usually dominate lichen communities in younger stands. They, as well as alectorioid lichens and cyanolichens, provide food sources and a variety of habitats to untold numbers of arthropods. By harboring these arthropods, lichens may form an important link in the food supply of branch-feeding birds (Pettersson et al. 1995).

The microlichens examined in this dissertation are the calicioids. This group includes both lichenized and non-lichenized fungi. Calicioids are linked by habitat requirements, fruiting body morphology, and their historical inclusion in the order Caliciales (Tibell 1997; Wedin and Tibell 1997). Many calicioids associate strongly with old forest structures.

Chapter two begins the examination of patterns in macrolichen communities. The initial focus of this chapter was on differences in lichen communities between old stands, young stands, and young stands that were thinned 10 to 25 yrs earlier to improve tree growth. The stands were broadly distributed over the western Oregon landscape, including both the Coast and Cascade Mountain Ranges. This provided an opportunity to detect landscape-level patterns in macrolichen communities.

Lichen species richness is not uniformly distributed across the landscape. Chapter three compares suspected hotspots of macrolichen diversity with the young and old stands from chapter two. The research identifies environmental conditions associated with high macrolichen diversity. It then examines whether hotspots concentrate a greater number of the common species or contribute to landscape level diversity by harboring species that are underrepresented in typical stands.

Chapter four uses the stands from chapters two and three that were located within the Cascade Mountains to examine patterns in the calicioid communities. This was the first thorough ecological study of calicioid communities in western North America. The research sought to increase our knowledge of the calicioids in western Oregon, and to describe relations between calicioid communities and their environments.

Chapter five proposes a modeling method for predicting the occurrence of species in sites not yet sampled, based on environmental variables that apparently relate to community composition and species occurrence. The goals of the method were to

provide models of species that could be easily updated, without user-intensive rebuilding of the models, and to resolve complicated response patterns of species to environmental gradients. The modeling method is tested and demonstrated with calicioid lichen data from chapter four, plus additional stand inventories. Since we are just beginning to understand calicioids in the Pacific Northwest, and since their occurrence often depends on microhabitat characters that are difficult to summarize for stands, the calicioids provide a challenging test of the modeling method.

Chapter six reviews the major themes and results of chapters two through five. It also summarizes implications for land managers.

## Chapter 2

### Diversity and Succession of Epiphytic Macrolichen Communities in Low-Elevation Managed Conifer Forests in Western Oregon

Eric B. Peterson and Bruce McCune

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## **ABSTRACT**

We examined epiphytic macrolichen communities in Douglas-fir forests across the western Oregon landscape for relationships to environmental gradients, stand age and structure, and commercial thinning. We used a retrospective, blocked design through the Coast and the western Cascade ranges of Oregon. Each of our seventeen blocks consisted of a young, unthinned stand (age 50-110 yrs); an adjacent, thinned stand of equivalent age; and an old-growth stand (age > 200 yrs). We found 110 epiphytic macrolichen taxa in the stands. Forage-providing alectorioid lichens and the nitrogen-fixing cyanolichen *Lobaria oregana* associated strongly with old-growth stands and remnant old trees in younger stands (unthinned + thinned). Relative to unthinned stands, thinned stands had a slightly higher abundance of alectorioid lichens and a greater presence of *Hypogymnia imshaugii*. However, thinned stands hosted a lower landscape-level (gamma) diversity, lacking many species that occurred infrequently in the young stands. Patterns in the lichen community composition correlated strongly with climatic gradients; the greatest variation in composition was between the Coast and Cascade ranges. The difference in communities between mountain ranges was greatest among stands 70-110 yrs old, suggesting a difference in lichen successional dynamics between the ranges.

## **INTRODUCTION**

Loss of biological diversity in landscapes due to human influences is a key issue for ecologists (Grime 1998; Tilman 1999). Our understanding of the importance of biological diversity is still vague and in need of considerable scientific effort (Simberloff 1999). The loss of old forests in the Pacific Northwest of North America has been a focal point for these issues both biologically and politically.

Historically, Pacific Northwest coniferous forests, dominated by *Pseudotsuga*, *Tsuga*, and *Thuja*, were disturbed primarily by fire (Agee 1997). The arrival of Euro-Americans brought fire suppression and the dominant disturbance became logging, a practice which impacts biodiversity (Czech and Krausman 1997). Old forests that once

covered large areas are now fragmented (Spies et al. 1994). Recently, forest management in the Pacific Northwest has begun to change, attempting to accommodate societal concerns over biodiversity in ways that are scientifically credible (Kohm and Franklin 1997).

The lichen component of biodiversity is receiving increasing attention worldwide (Esseen et al. 1996; McCune et al. 1997b; Kuusinen and Siitonen 1998; Pharo et al. 1999) and specifically in the Pacific Northwest (Rosentreter 1995; Neitlich and McCune 1997; Peck and McCune 1997; Rosso 2000b, 2000c). Recognition of ecological functions of lichens is partly responsible for this attention. Macrolichens (non-crustose lichens) are often divided among three functional groups. Cyanolichens are important contributors of nitrogen to forests (Pike et al. 1972; Pike 1978; Rhoades 1983). The long, pendulous alectorioid lichens are known as valuable sources of food and nest-materials for a variety of animals, including *Glaucomys sabrinus*, the northern flying squirrel (Sharnoff 1994; Rosentreter et al. 1997) and are also referred to as forage lichens. Other green-algal lichens, “matrix lichens,” usually dominate lichen communities in younger stands. They, as well as alectorioid lichens and cyanolichens, provide food sources and a variety of habitats to untold numbers of arthropods. By hosting these arthropods, lichens may form an important link in the food supply of branch-feeding birds (Pettersson et al. 1995). Surveys for, and management of, selected macrolichens from all three functional groups are required on Federal lands in the USA within the range of the Northern Spotted Owl (USDA and USDI 1994).

Recent research has enhanced our understanding of how forest management techniques may affect lichen communities. For example, *Lobaria oregana* may reach more than one ton per hectare in old forests, but occurs sparsely (or not at all) in young forests. *Lobaria oregana* barely enters a stand in the first 200 yrs after a major disturbance and may not attain a large biomass until the stand is nearly 400 yrs old (McCune 1993). The reason appears to be that poor dispersal to, and within, the stand slows the establishment of large colonies (Sillett and McCune 1998; Sillett et al. 2000). *Lobaria oregana* is not the only dispersal-limited lichen. Alectorioid lichens gradually build up on branches as the branches age (Esseen et al. 1996), indicating that alectorioids are also slow to establish and grow. Forest managers can promote dispersal-limited

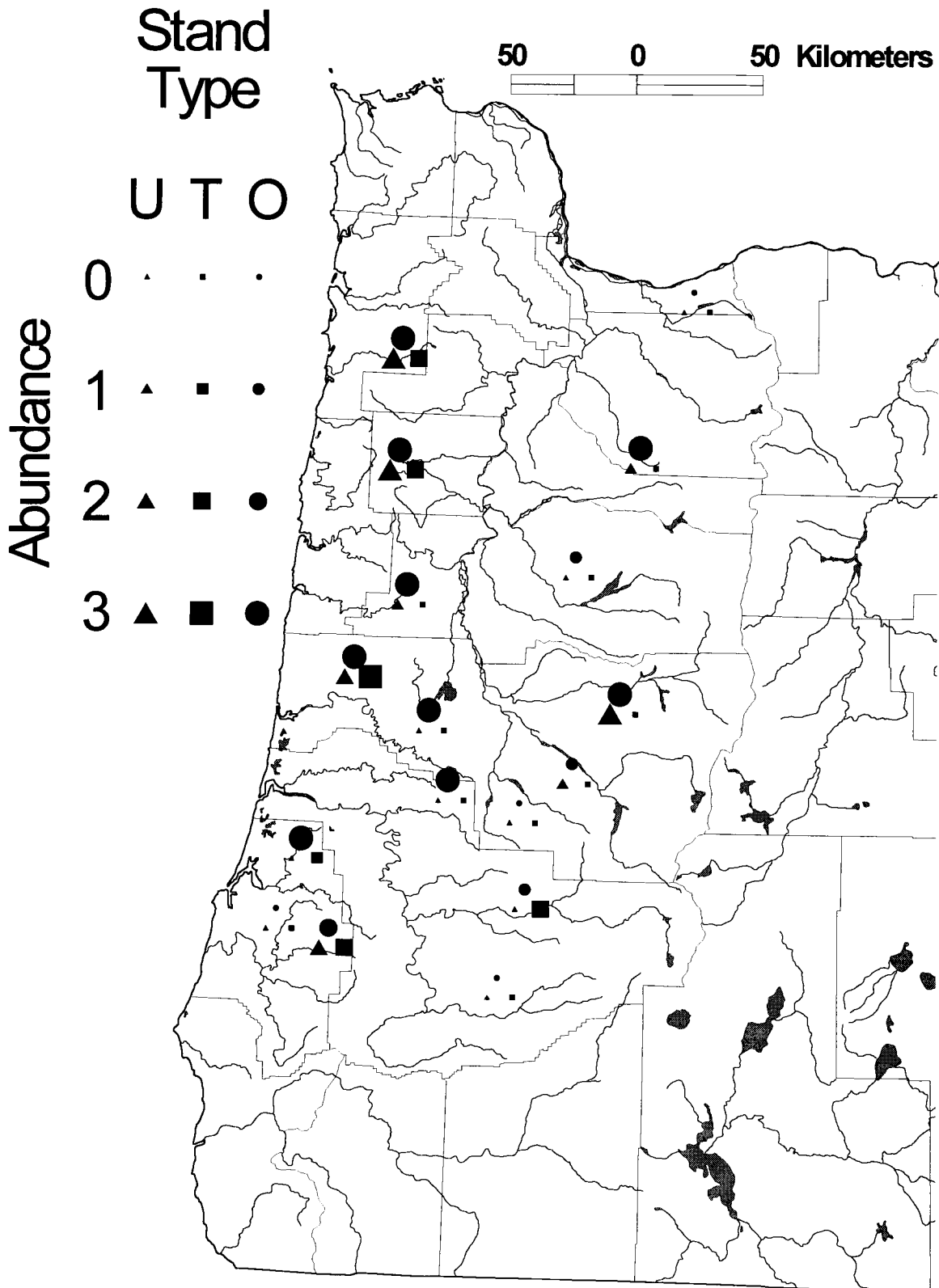
species by retaining some old trees during logging operations; the old trees become refugia and allow the lichens to colonize future stands (Peck and McCune 1997).

Thinning young forests may speed development of structural features, causing the stands to resemble more mature stands (Hayes et al. 1997). Goals of commercial thinning include increasing tree growth and crown size (Oliver and Larson 1996; Hayes et al. 1997). However, traditional commercial thinning of stands dominated by Douglas-fir (*Pseudotsuga menziesii*) evens the canopy and eliminates most tree species other than Douglas-fir. Such thinning was widely used in the latter half of the twentieth century and influenced the structure of a large portion of Oregon's managed forests. The present study is part of a multidisciplinary project to examine the effect of traditional thinning on forest structure (Bailey and Tappeiner 1998), non-woody vegetation (Bailey et al. 1998), bats (Humes et al. 1999), shrub epiphyte communities (Rosso et al 2000b; 2000c), birds, insects, and shrub forage quality. The project design compares diversity and abundance of these ecosystem components in thinned, second-growth forests with those in adjacent, equal-aged, unthinned stands and nearby old-growth stands. It defines old-growth stands as those in which a majority of the canopy dominants are 200 years old or more. This paper examines the apparent effects of thinning young stands on lichen communities. We also report on variation in lichen communities over time and across the western Oregon landscape.

## **METHODS**

### **Study Sites**

We used a blocked design, with nine blocks in the Coast Range mountains and eight blocks in the western Cascade mountains of Oregon, USA (Fig. 2.1). Each block consisted of one young unthinned stand, one young thinned stand, and one old-growth stand. The two young stands were adjoining and of identical age. Age of young stands varied between blocks from 50 to 110 yrs; old-growth stands were at least 200 yrs old. Commercial thinning took place 10 to 25 yrs prior to sampling. Old-growth stands were



**Figure 2.1** Location of sampling blocks showing the abundance of *Lobaria oregana* in plots. Symbol size represents abundance codes (0-3). U, T, and O represent unthinned, thinned, and old-growth stands, respectively.

seldom adjacent to the young stands. The distance between young and old-growth stands in a block was typically less than 10 km (maximum = 19 km).

Douglas-fir, or a combination of Douglas-fir and western hemlock (*Tsuga heterophylla*), dominated all stands. Latitudes ranged from 43.03° N to 45.50° N; longitudes ranged from 122.13° W to 124.09° W. Distance from the ocean varied from 20 to 138 km. Elevation ranged from 200 to 900 m. Annual precipitation averages 1.3 to 3.0 m per yr (Daly et al. 1994). Bailey and Tappeiner (1998), and Bailey et al. (1998), used the same stands and provided extensive information on their structure.

## Sampling

Since our study focused on community composition, determining species presence was more important than quantifying the common species. Relative to numerous small plots, the use of a single large plot in each stand emphasized species capture over quantitative accuracy (McCune and Lesica 1992). The plot size and sampling followed the methods developed for the Forest Health Monitoring Program (Tallent-Halsell 1994; McCune et al. 1997b). Plots were circular with a radius of 34.7 m, yielding an area of 0.38 ha. Plot centers were permanently marked with an iron rod hammered into the ground and a white PVC pipe rising above the ground. The first author sampled all plots by ocular survey and recorded all macrolichen species found on: (1) woody vegetation (alive or dead) greater than 0.5 m above ground and accessible without climbing trees, and (2) recent litterfall, which provides a representation of the canopy epiphytes (McCune 1994). The survey time was limited to 2 hrs, with a minimum time of 0.5 hrs. Surveys stopped short of the maximum time only after (1) examining representatives of all microhabitats within the plot and (2) 10 minutes had elapsed without encountering a new species. Each species was assigned an abundance score as follows: 0 = absent; 1 = rare (1-3 individuals in plot), 2 = uncommon (4-10 individuals per plot), 3 = common (> 10 individuals per plot but less than half of appropriate substrates bearing the species), 4 = very abundant (more than half of appropriate substrates bearing the species). Individuals are difficult to distinguish in

strongly colonial lichens such as species of *Cladonia* (DePriest 1993 and 1994). Our study considered a continuous colony to be a single individual. Although we focused on macrolichens, we included *Loxosporopsis corallifera*, a recently described crustose species (Brodo and Henssen 1995), to increase our knowledge of its ecology in the Pacific Northwest.

Nomenclature followed Esslinger and Egan (1995), and McCune and Geiser (1997) except for a few species groups that could not be separated reliably to species. *Cladonia coniocraea* (Flörke) Sprengel was included in “*Cladonia ochrochlora* gr.”. Cup-forming *Cladonia* species fluorescing in short-wave UV were included in “*Cladonia merochlorophaea* gr.” including *C. albonigra* Brodo & Ahti, a recently described species (Brodo and Ahti 1996). Several groups were included for *Usnea*. Aside from the individual species named in Table 2.1, all specimens forming isidioid propagules with their cortex confluent with the branch cortex are grouped as “*U. filipendula* gr.” All specimens forming isidioid propagules that erupt from soredia-like structures are grouped as “*U. subfloridana* gr.” All specimens forming pure soralia without isidioid propagules are grouped as “*U. lapponica* gr.” Most *Usnea* specimens were identified prior to the publication on *Usnea* in British Columbia by Halonen et al. (1998). Specimens decidedly distinct from the species groups were left unnamed until that publication allowed them to be identified as *U. chaetophora* and *U. madeirensis*. Taxonomic groups were considered equivalent to species for our analyses. Additionally, *Cladonia squamosa* var. *squamosa*, *Cladonia squamosa* var. *subsquamosa* were recorded and analyzed as independent species.

In addition to assessing the lichen community in each plot, we recorded the prevailing slope and aspect, topographic position, and distance to nearest source of perennial water. At the plot center and at four equidistant points around the circumference we measured canopy density and basal area for each tree species. In young stands, we recorded the presence of old-growth remnant trees in or near the plots.

Plots were placed within stands arbitrarily but without intentional bias except for two criteria: (1) we attempted to locate the plot within the area of the stand that had been sampled by Bailey and Tappeiner (1998) to maximize the potential for comparing our results to other work in the same stands, and (2) we attempted to match topography of

**Table 2.1** Species list. Table includes abbreviation (Abbr.), functional group (FG), frequency among plots in each mountain range, and a note on young-stand frequency (Note). For functional groups, A = alectorioid lichen, C = cyanolichen, and M = matrix lichen. For young-stand frequency, notes are given only for species occurring in 1-10 young-stand plots; U = occurred in more unthinned than thinned plots, T = occurred in more thinned than unthinned plots, and E = occurred in an equal number of unthinned and thinned plots.

Taxon	Abbr.	FG	Frequency		Note
			Coast Range	Cascade Range	
<i>Alectoria imshaugii</i> Brodo & D. Hawksw.	ALEIMS	A	4	7	U
<i>A. sarmentosa</i> (Ach.) Ach.	ALESAR	A	19	16	
<i>A. vancouverensis</i> (Gyelnik) Gyelnik ex Brodo & D. Hawksw.	ALEVAN	A	13	16	
<i>Bryoria capillaris</i> (Ach.) Brodo & D. Hawksw.	BRYCAP	A	8	19	
<i>B. fremontii</i> (Tuck.) Brodo & D. Hawksw.	BRYFRE	A	0	5	U
<i>B. friabilis</i> Brodo & D. Hawksw.	BRYFRI	A	16	13	
<i>B. fuscescens</i> (Gyelnik) Brodo & D. Hawksw.	BRYFUS	A	15	14	
<i>B. glabra</i> (Mot.) Brodo & D. Hawksw.	BRYGLA	A	1	6	T
<i>B. pseudofuscescens</i> (Gyelnik) Brodo & D. Hawksw.	BRYPSE	A	14	11	
<i>B. trichodes</i> (Michaux) Brodo & D. Hawksw.	BRYTRI	A	1	0	
<i>Candelaria concolor</i> (Dickson) Stein	CANCON	P	1	0	
<i>Cavernularia hultenii</i> Degel.	CAVHUL	P	13	6	E
<i>C. lophyrea</i> (Ach.) Degel.	CAVLOP	P	8	0	T
<i>C. chlorophylla</i> (Willd.) Vainio	CETCHL	P	15	20	
<i>C. orbata</i> (Nyl.) Fink	CETORB	P	24	23	
<i>C. pallidula</i> Tuck. ex Riddle	CETPAL	P	0	4	U
<i>C. platyphylla</i> Tuck.	CETPLA	P	6	10	

**Table 2.1, Continued**

<i>Cetrelia cetrarioides</i> (Duby) Culb. & C. Culb.	CTRCET	P	0	2	T
<i>Cladonia carneola</i> (Fr.) Fr.	CLACAR	P	2	1	U
<i>C. chlorophaea</i> (Flörke ex Sommerf.) Sprengel	CLACHL	P	2	0	U
<i>C. fimbriata</i> (L.) Fr.	CLAFIM	P	11	6	
<i>C. furcata</i> (Hudson) Schrader	CLAFUR	P	1	0	U
<i>C. merochlorophaea</i> Asah. (group)	CLAMER	P	16	7	
<i>C. norvegica</i> Tønsberg & Holien	CLANOR	P	1	1	E
<i>C. ochrochlora</i> Flörke (group)	CLAOCH	P	27	23	
<i>C. squamosa</i> var. <i>squamosa</i> Hoffm.	CLASQU	P	2	2	E
<i>C. squamosa</i> var. <i>subsquamosa</i> (Nyl. ex Leighton) Vainio	CLASSQ	P	19	20	
<i>C. transcendens</i> (Vainio) Vainio	CLATRA	P	10	8	T
<i>Esslingeriana idahoensis</i> (Essl.) Hale & M. J. Lai	ESSIDA	P	2	10	E
<i>Evernia prunastri</i> (L.) Ach.	EVEPRU	P	13	20	
<i>Fuscopannaria leucostictoides</i> (Ohlsson) P. M. Jørg.	PANLEU	C	1	0	U
<i>F. saubinetii</i> (Mont.) P. M. Jørg.	PANSAU	C	2	8	U
<i>Hypocenomyce anthracophila</i> (Nyl.) P. James & Gotth. Schneider	HYCANT	P	2	4	
<i>H. castaneocinerea</i> (Räsänen) Timdal	HYCCAS	P	8	9	
<i>H. friesii</i> (Ach.) P. James & Gotth. Schneider	HYCFRI	P	2	3	U
<i>H. scalaris</i> (Ach.) M. Choisy	HYCSCA	P	0	4	U
<i>Hypogymnia apinnata</i> Goward & McCune	HYPAPI	P	25	22	
<i>H. duplicata</i> (Ach.) Rass.	HYPDUP	P	1	0	
<i>H. enteromorpha</i> (Ach.) Nyl.	HYPENT	P	27	24	

**Table 2.1, Continued**

<i>H. imshaugii</i> Krog	HYPIMS	P	9	20	
<i>H. inactiva</i> (Krog) Ohlsson	HYPINA	P	26	24	
<i>H. metaphysodes</i> (Asah.) Rass.	HYPMET	P	0	2	E
<i>H. occidentalis</i> L. Pike	HYPOCC	P	2	0	E
<i>H. oceanica</i> Goward	HYPOCE	P	1	0	T
<i>H. physodes</i> (L.) Nyl.	HYPPHY	P	22	24	
<i>H. tubulosa</i> (Schaerer) Hav.	HYPTUB	P	19	21	
<i>Hypotrachyna sinuosa</i> (Sm.) Hale	HYPSIN	P	17	10	
<i>Leptogium lichenoides</i> (L.) Zahlbr.	LEPLIC	C	0	1	U
<i>L. polycarpum</i> P. M. Jørg. & Goward	LEPPOL	C	0	7	U
<i>Letharia vulpina</i> (L.) Hue Syn.	LETVUL	P	2	10	U
<i>Lobaria oregana</i> (Tuck.) Müll. Arg.	LOBORE	C	18	9	
<i>L. pulmonaria</i> (L.) Hoffm.	LOBPUL	C	2	14	
<i>L. scrobiculata</i> (Scop.) DC.	LOBSCR	C	0	1	U
<i>Loxosporopsis corallifera</i> Brodo, Henssen & Imshaug	LOXCOR	P	16	0	
<i>Melanelia exasperatula</i> (Nyl.) Essl.	MELEXA	P	8	11	
<i>M. fuliginosa</i> (Fr. ex Duby) Essl.	MELFUL	P	8	12	
<i>M. multispora</i> (A. Schneider) Essl.	MELMUL	P	0	2	U
<i>M. subaurifera</i> (Nyl.) Essl.	MELSUB	P	0	5	T
<i>Menegazzia terebrata</i> (Hoffm.) A. Massal.	MENTER	P	6	2	T
<i>Nephroma bellum</i> (Sprengel) Tuck.	NEPBEL	C	3	4	U
<i>N. helveticum</i> Ach.	NEPHEL	C	3	6	U
<i>N. laevigatum</i> Ach.	NEPLAE	C	1	6	T
<i>N. occultum</i> Wetmore	NEPOCC	C	0	1	
<i>N. resupinatum</i> (L.) Ach.	NEPRES	C	1	3	E
<i>Nodobryoria oregana</i> (Tuck.) Common & Brodo	NODORE	A	14	15	
<i>Parmelia hygrophila</i> Goward & Ahti	PARHYG	P	10	17	

**Table 2.1, Continued**

<i>P. pseudosulcata</i> Gyelnik	PARPSE	P	10	19	
<i>P. saxatilis</i> (L.) Ach.	PARSAX	P	6	13	
<i>P. sulcata</i> Taylor	PARSUL	P	26	24	
<i>Parmeliella parvula</i> P. M. Jørg.	PMLPAR	C	2	0	E
<i>Parmeliopsis ambigua</i> (Wulfen) Nyl.	POPAMB	P	0	2	E
<i>P. hyperopta</i> (Ach.) Arnold	POPHYP	P	12	22	
<i>Parmotrema arnoldii</i> (Du Rietz) Hale	PTRARN	P	2	0	E
<i>P. chinense</i> (Osbeck) Hale & Ahti	PTRCHI	P	3	0	E
<i>Peltigera collina</i> (Ach.) Schrader	PELCOL	C	2	11	U
<i>Physcia adscendens</i> (Fr.) H. Olivier	PHYADS	P	4	4	T
<i>P. aipolia</i> (Ehrh. ex Humb.) Fürnr.	PHYAIP	P	0	7	U
<i>P. stellaris</i> (L.) Nyl.	PHYSTE	P	0	4	U
<i>P. tenella</i> (Scop.) DC.	PHYTEN	P	4	6	T
<i>Platismatia glauca</i> (L.) Culb. & C. Culb.	PLAGLA	P	26	24	
<i>P. herrei</i> (Imshaug) Culb. & C. Culb.	PLAHER	P	22	24	
<i>P. lacunosa</i> (Ach.) Culb. & C. Culb.	PLALAC	P	1	0	
<i>P. norvegica</i> (Lynge) Culb. & C. Culb.	PLANOR	P	3	4	T
<i>P. stenophylla</i> (Tuck.) Culb. & C. Culb.	PLASTE	P	18	23	
<i>Polychidium contortum</i> Henssen	POLCON	C	4	0	E
<i>Pseudocyphellaria anomala</i> Brodo & Ahti	PSEANO	C	3	8	U
<i>P. anthraxis</i> (Ach.) H. Magn.	PSEANT	C	3	6	U
<i>P. crocata</i> (L.) Vainio	PSECRO	C	3	1	E
<i>Ramalina dilacerata</i> (Hoffm.) Hoffm.	RAMDIL	P	0	9	E
<i>R. farinacea</i> (L.) Ach.	RAMFAR	P	14	23	
<i>R. subleptocarpha</i> Rundel & Bowler	RAMSUB	P	2	0	U
<i>R. thrausta</i> (Ach.) Nyl.	RAMTHR	A	3	4	U
<i>Sphaerophorus globosus</i> (Hudson) Vainio	SPHGLO	P	25	23	
<i>Sticta fuliginosa</i> (Hoffm.) Ach.	STIFUL	C	4	2	T
<i>S. limbata</i> (Sm.) Ach.	STILIM	C	3	2	T

**Table 2.1, Continued**

<i>Usnea cavernosa</i> Tuck.	USNCAV	A	2	5	U
<i>U. ceratina</i> Ach.	USNCER	A	1	0	
<i>U. chaetophora</i> Stirton	USNCHA	A	1	0	
<i>U. cornuta</i> Körber	USNCOR	P	9	4	
<i>U. filipendula</i> Stirton (group)	USNFIL	A	27	24	
<i>U. glabrata</i> (Ach.) Vainio	USNGLA	P	15	15	
<i>U. hesperina</i> Mot.	USNHES	A	1	0	
<i>U. hirta</i> (L.) F. H. Wigg.	USNHIR	P	1	0	
<i>U. lapponica</i> Vainio (group)	USNLAP	P	6	7	
<i>U. longissima</i> Ach.	USNLON	A	2	1	
<i>U. madeirensis</i> Mot.	USNMAD	P	2	0	T
<i>U. subfloridana</i> Stirton (group)	USNSUB	P	9	11	
<i>U. wirthii</i> Clerc	USNWIR	P	21	11	
<i>Vulpicida canadensis</i> (Räsänen) J.-E. Mattsson & M. J. Lai	VULCAN	P	0	5	E
<i>Xanthoria polycarpa</i> (Hoffm.) Rieber	XANPOL	P	0	6	U

plots within a block to maximize focus on differences in stand structure. One old-growth plot included a small stream with riparian vegetation.

## Statistical Analysis

We tested differences in species richness and abundance of functional groups between stand types with paired t-tests and blocked ANOVA (SPSS Inc. 1998). Our ANOVA model included blocks (d.f. = 16), stand types (d.f. = 2) and error (d.f. = 32), with no interactions. Blocking allowed comparison between stand types without interference from landscape patterns between sampling blocks. Abundance of functional groups was calculated by summing the abundance scores of member species. We used the Chi-squared test for goodness of fit, to compare the number of infrequent species (occurring in 10 or fewer plots) in unthinned and thinned stands on a landscape level. We tested the difference in species richness between mountain ranges with nested ANOVA (SPSS Inc. 1998) using a model that included blocks within ranges (d.f. = 15), mountain ranges (d.f. = 1), and error (d.f. = 34).

For multivariate analyses, we used PC-ORD (version 3.11, McCune and Mefford 1997; version 4.0 Beta for Blocked MRPP). Blocked MRPP (multi-response permutation procedure; Mielke 1984) was used to test for compositional differences between stand types. We tested association of species with *a priori* groups (e.g. stand type, mountain range) with IndVal, a method for indicator species analysis (Dufrêne and Legendre 1997) combined with randomization tests with 10000 iterations. We used MRPP (Biondini et al. 1985) without blocking to test for a difference in community composition between mountain ranges.

We analyzed interrelationships between taxa and relationships of taxa to stand structure, composition, and environmental features with NMS (non-metric multidimensional scaling; Kruskal 1964; Mather 1976). The NMS ordination was obtained by running the analysis five times with random initial configurations and once each with the initial configuration derived from principal components analysis and Bray-Curtis ordination. The run resulting in the lowest final stress was used for the analyses.

For visual clarity the ordination was then rotated to align longitude with the horizontal axis.

To reduce noise from rare species, those occurring in less than five percent of the plots (less than three plots) were deleted from the data set prior to all multivariate analyses. The quantitative version of Sørensen distance was used for unblocked MRPP and NMS; Euclidean distance was required for blocked MRPP. All community analysis techniques that we used are non-parametric and well suited to data that are non-normal, are on discontinuous scales, and contain a large proportion of zero values.

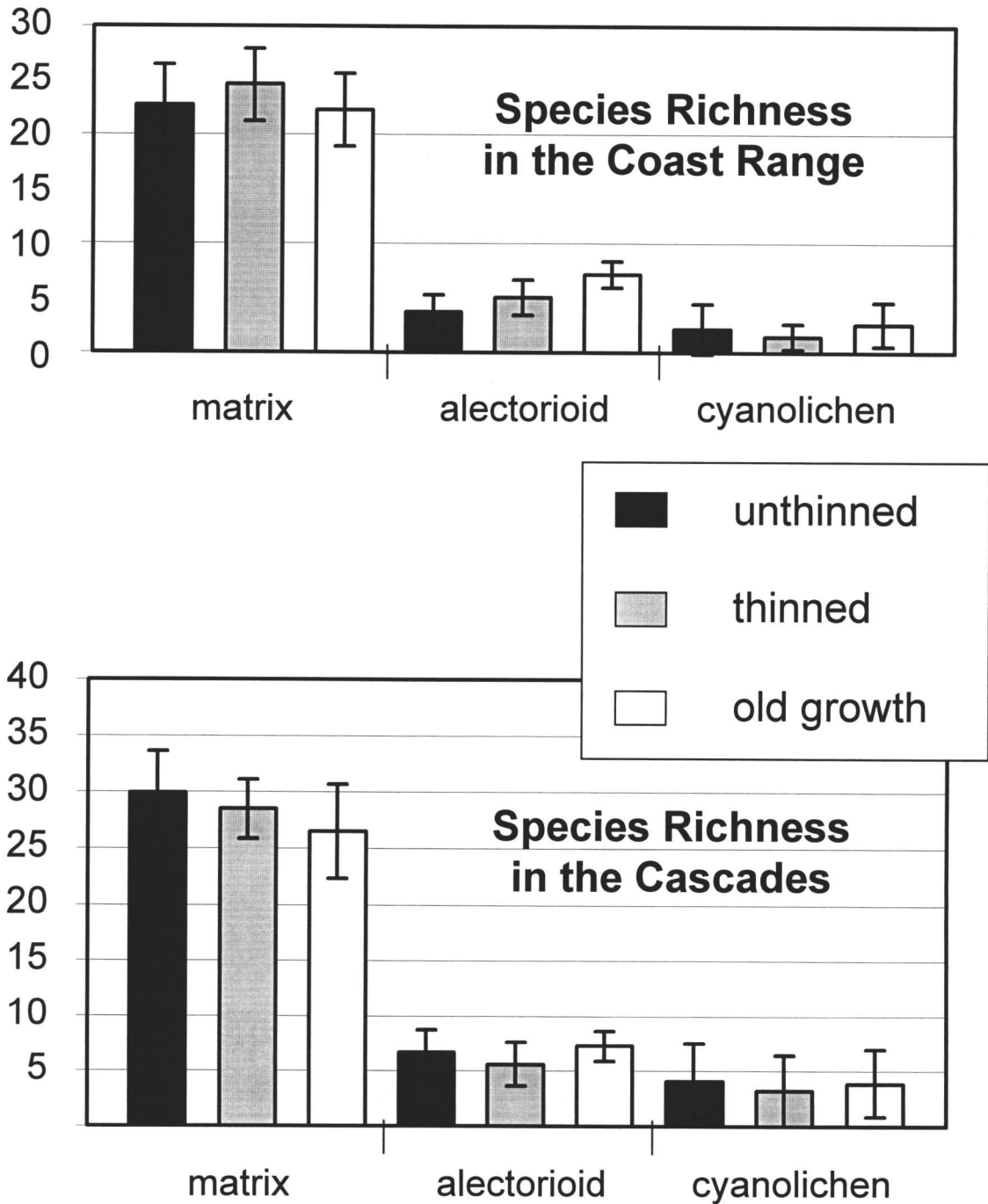
## **RESULTS**

### **Relations of Stand Age and Structure to Lichen Communities**

**Old-growth versus Young Stands.** We found a total of 110 taxa among the 51 plots (Table 2.1). No difference in overall species richness could be detected between old-growth, young unthinned, and young thinned plots (Fig. 2.2; Table 2.2; blocked ANOVA:  $p = 0.965$ ). However, species richness of alectorioid lichens did differ between the plot types (blocked ANOVA:  $p = 0.002$ ) with about two more species on average in old-growth plots (Fig. 2.2). This difference was stronger in the Coast Range than in the Cascades.

Old growth plots differed from the young stand plots in community composition (blocked MRPP:  $p \ll 0.001$  and  $R = 0.04$ ;  $R$  measures within-group agreement). Seven species are associated with old-growth stands (Fig. 2.3; IndVal,  $p \leq 0.05$  each). Of the seven old-growth associates, four are alectorioid lichens, although alectorioid species make up only 16 % of the total species list. Old-growth plots tended to separate from young plots along the vertical ordination axis (Fig. 2.4). The separation was maintained when the data were divided by mountain range and re-ordinated.

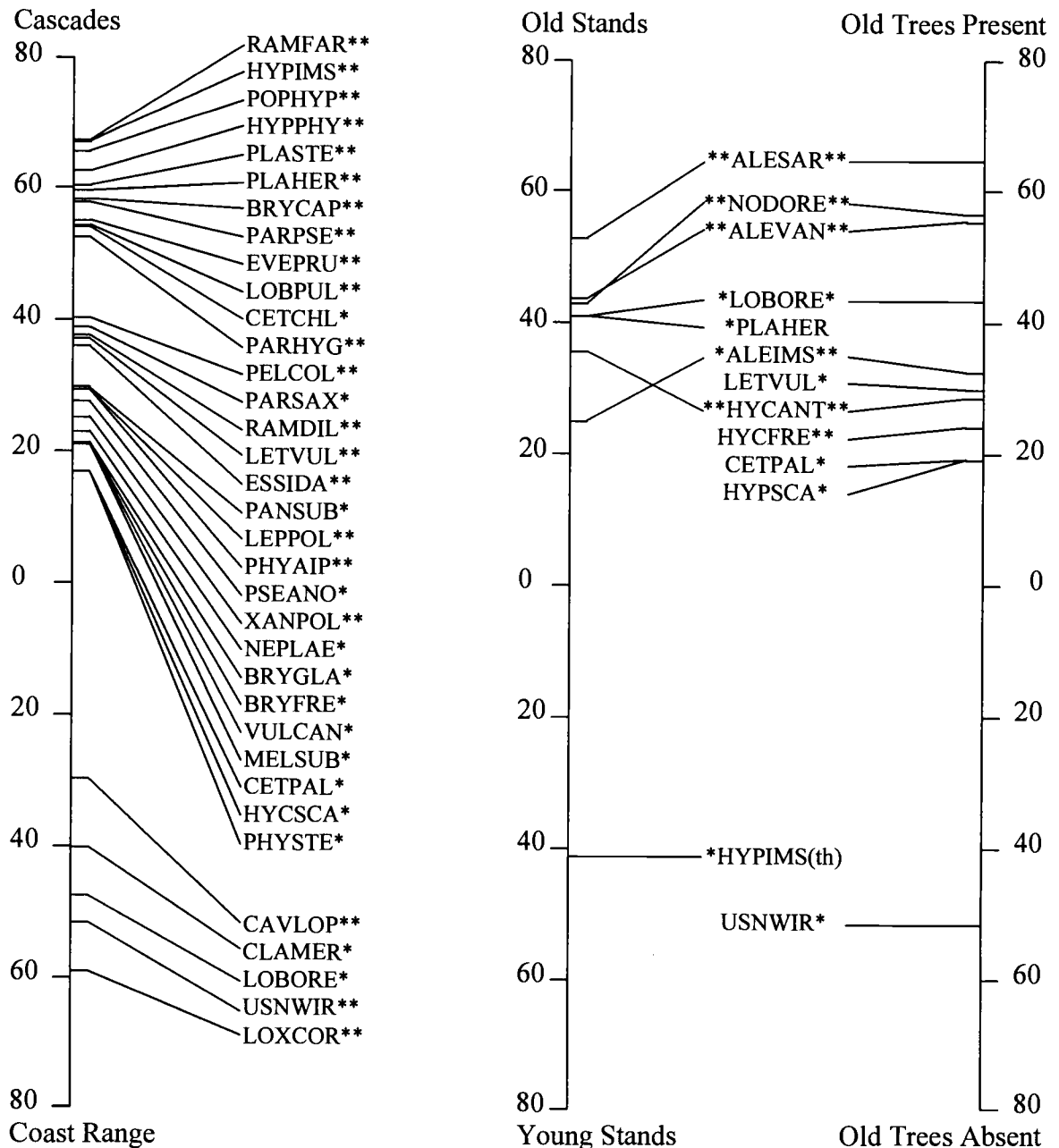
Three old-growth stands were located well within the young stand region of the ordination on the vertical axis (Fig. 2.4). All three plots lacked *Lobaria oregana* and



**Figure 2.2** Mean species richness by stand type, functional group, and mountain range. Error bars enclose 95 % confidence intervals. For the Coast Range,  $n = 9$ ; for the Cascades,  $n = 8$ .

**Table 2.2** Summary statistics for lichen diversity in plot types and mountain ranges (n = number of plots). Beta is calculated as Gamma / Alpha. Average within-group distance (D) is calculated by MRPP (not blocked). Average half-changes =  $\log(1-D) / \log(0.5)$ . Young stand plots are also broken down in to unthinned and thinned stands.

		Alpha Diversity		Beta Diversity			Gamma Diversity
		Species richness	Shannon diversity		Average w/in-group distance	Average half-changes	
		n	(Alpha)	index	Beta		Gamma
Coast Range:							
Young	18	29.8	3.3	2.8	0.43	0.81	83
[ Unthinned	9	28.4	3.2	2.7	0.46	0.90	76
	9	31.1	3.3	2.2	0.41	0.76	67
Old-Growth	9	31.9	3.4	2.5	0.41	0.77	80
Overall	27	30.5	3.3	3.0	0.44	0.83	93
Cascade Range:							
Young	16	39.0	3.6	2.2	0.37	0.66	84
[ Unthinned	8	40.6	3.6	1.9	0.38	0.69	79
	8	37.4	3.5	2.0	0.36	0.65	75
Old-Growth	8	37.6	3.5	1.9	0.41	0.75	73
Overall	24	38.5	3.6	2.3	0.39	0.71	89
Both Ranges:							
Young	34	34.1	3.4	2.9	0.43	0.82	100
[ Unthinned	17	34.2	3.4	2.8	0.46	0.90	96
	17	34.1	3.4	2.6	0.41	0.75	90
Old-Growth	17	34.6	3.4	2.7	0.41	0.79	92
Overall	51	34.3	3.4	3.2	0.44	0.84	110



**Figure 2.3** Indicator values (percent of perfect indication) of species associated with a mountain range, a forest type (young = unthinned and thinned), or the presence of old-growth trees within stands (p-value  $\leq 0.050$ ). Statistical significance (p-value) of individual species is noted as \* = 0.010 to 0.050 and \*\* = 0.000 to 0.009. The indicator value plotted for *Hypogymnia imshaugii* (HYPIMS) is the value specifically for indicating thinned young stands. See Table 2.1 for abbreviations.

**Figure 2.4** NMS ordination, including joint plots, of plots in species space based on the 85 species that occurred in more than 5% of the plots. The horizontal axis accounts for 65.4 % of the variation in the data while the vertical axis accounts for 18.8 %. All correlation vectors have  $r^2 \geq 0.200$ . Length of correlation vectors represents the strength of the correlation. **(A)** Symbols code for plot type (triangle = unthinned, square = thinned, and circle = old growth). **(B)** Joint plot including environmental characters. Age of the stand (Age) was according to stand records from the Bureau of Land Management; longitude (Longitude) was taken from DeLorme Street Atlas 3.0 or from U.S.G.S. 7.5 minute quadrangle maps; distance from the ocean (Ocean) was measured on a U.S.G.S. map of Oregon; average annual precipitation (Precipitation) was according to Daly et al. (1994); the presence of old trees in or near the plot (Remnant) was noted during sampling (coded as: 0 = old trees absent, 1 = old trees nearby, 2 = old trees within the plot). **(C)** Joint plot with alpha diversity (species richness), richness of lichen functional groups, and abundance of selected species. Alpha diversity is abbreviated as ALPHA while the functional groups, alectorioid lichens, cyanolichens, and matrix lichens, are ALECT, CYANO, and MATRIX, respectively. See Table 1 for species abbreviations.

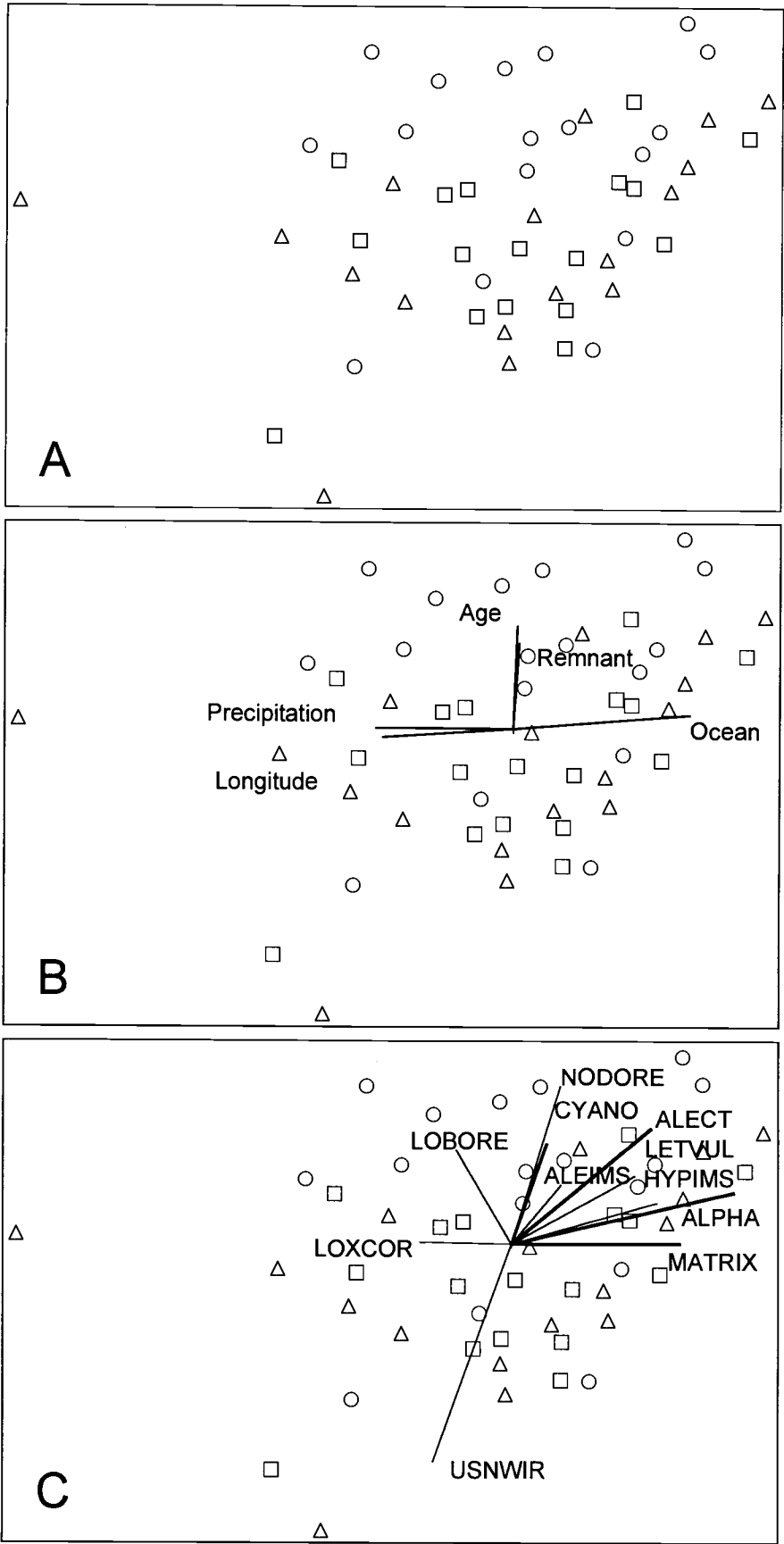


Figure 2.4

harbored few other cyanolichens. Two were located downwind of known pollution sources: the Portland metropolitan area and a pulp mill to the north of Coos Bay.

**Thinned versus unthinned young stands.** Thinned plots did not differ in overall species richness from unthinned plots (blocked ANOVA:  $p = 0.886$ ), nor did they differ noticeably in species richness within functional groups (Fig. 2.2). Overall community composition did not differ between thinned and unthinned plots (blocked MRPP:  $p = 0.217$ ,  $R = 0.004$ ). Summed alectorioid abundance scores averaged about 20 percent more in thinned plots than in unthinned plots (paired t-test, one-tailed  $p = 0.02$ ; Table 2.3). Only one species, *Hypogymnia imshaugii*, was associated with thinned plots (IndVal:  $IV = 41.2$ ,  $p = 0.016$ ; Fig. 2.3).

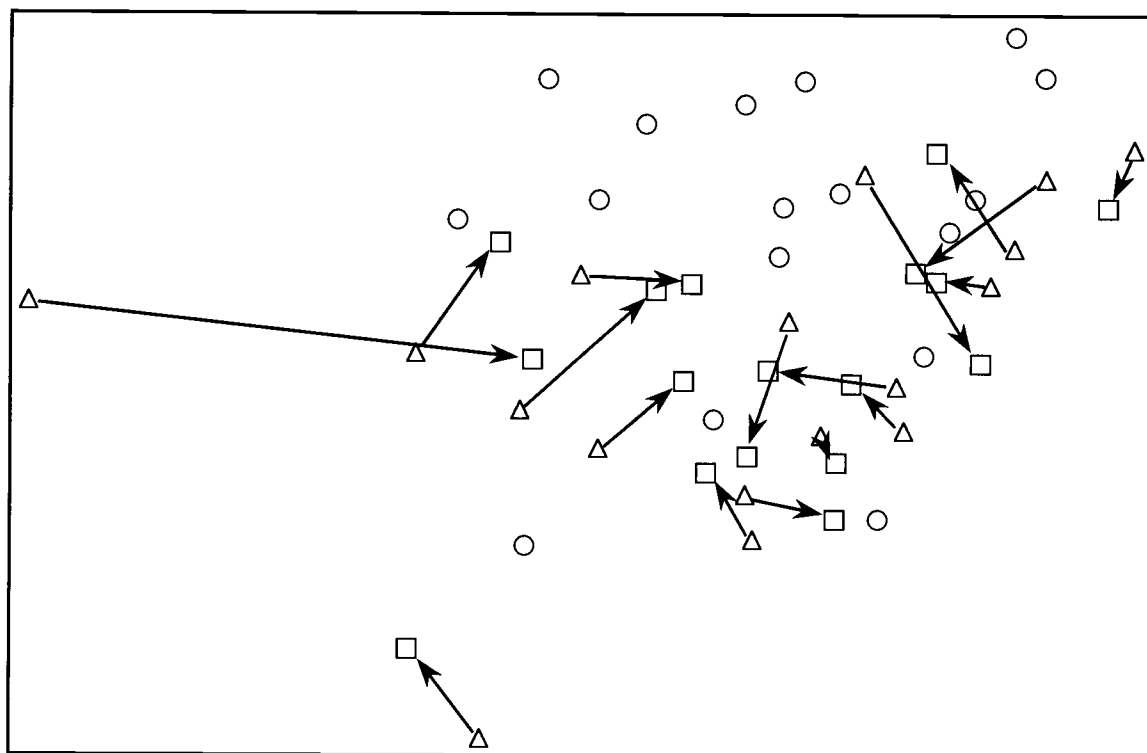
Thinned plots did not show any clear separation from unthinned plots in the ordination (Fig. 2.4). However, vectors drawn from the unthinned plot to the thinned plot within each block reveal a weak pattern: thinned plots are generally placed closer to the center of the horizontal axis than the corresponding unthinned plots (Fig. 2.5). Measures of beta-diversity are greater in unthinned plots than in thinned plots (Table 2.2). The highest species turnover (beta diversity half-changes) between plots is among the unthinned plots. Comparing the total species lists for plot types (gamma diversity) across mountain ranges revealed that unthinned plots hosted six more species than thinned plots. Of the infrequent species (occurred in 10 or fewer young plots), 26 occurred more frequently in unthinned plots, while 14 occurred more in thinned plots and 15 occurred equally in unthinned and thinned plots (Table 2.1). The number of infrequent species occurring in unthinned plots, verses the number in thinned plots, is somewhat greater than could be expected with a random distribution between the plot types (Chi-squared test for goodness of fit, one-tailed  $p = 0.058$ )

## Landscape Patterns in Lichen Communities

**Climate and Stand Gradients.** The horizontal axis of the ordination was strongly climatic as shown by correlations with the distance from the ocean ( $r^2 = 0.47$ ) and estimated mean annual precipitation ( $r^2 = 0.37$ ). The vertical axis correlated with the

**Table 2.3** Sum of abundance classes for allectoroid lichens in unthinned and thinned plots, ranked by age. Total allectoroid abundance in thinned plots was 20 % greater on average (total score 2.1 higher; 95 % confidence interval from 0.1 to 4.0), than in unthinned plots (paired t-test, one tailed  $p = 0.02$ ). \* = stands with remnant old trees in or near our plot.

	Sum of Abundance Scores																	mean
Stand age	50	50	50	60	60	60	60	60	70	70	80	80	90	100	100	100	110	
Unthinned sum	3	4	8	3	6*	10*	11	12*	1	12	5*	23*	17*	8	9	10*	18	9.4
Thinned sum	3	6	10	3	13*	18*	7	9	5	13	10*	23	17*	13	13	18*	14	11.5
Difference (T-U)	0	2	2	0	7	8	-4	-3	4	1	5	0	0	5	4	8	-4	2.1



**Figure 2.5** NMS ordination (as in Figure 2.3) with vectors drawn from the unthinned plot (triangle) to the thinned plot (square) within each block. Thinned plots tend to be closer to the center of the horizontal than the corresponding unthinned plots (the vectors converge).

age of the stand ( $r^2 = 0.28$ ) and the presence of old trees in or near the plot ( $r^2 = 0.20$ ). The climatic and the stand age gradients were independent (Fig. 2.4).

**Species Patterns.** The Cascades had higher average species richness than the Coast Range (Fig. 2.2; Table 2.2; nested ANOVA  $p = 0.019$ ). Species composition differed between the ranges (unblocked MRPP:  $p$ -value  $\ll 0.001$ ,  $R = 0.06$ ). The overall species richness and richness within each functional group correlated with the ordination (Fig. 2.4). Richness of all species, and matrix lichens in particular, increased with distance from the ocean. Richness of cyanolichens increased with stand age. Alectorioid lichen richness increased both with stand age and with distance from the ocean. Numerous species were indicative of either a mountain range or a stand condition (Fig. 2.3).

### **Successional Patterns**

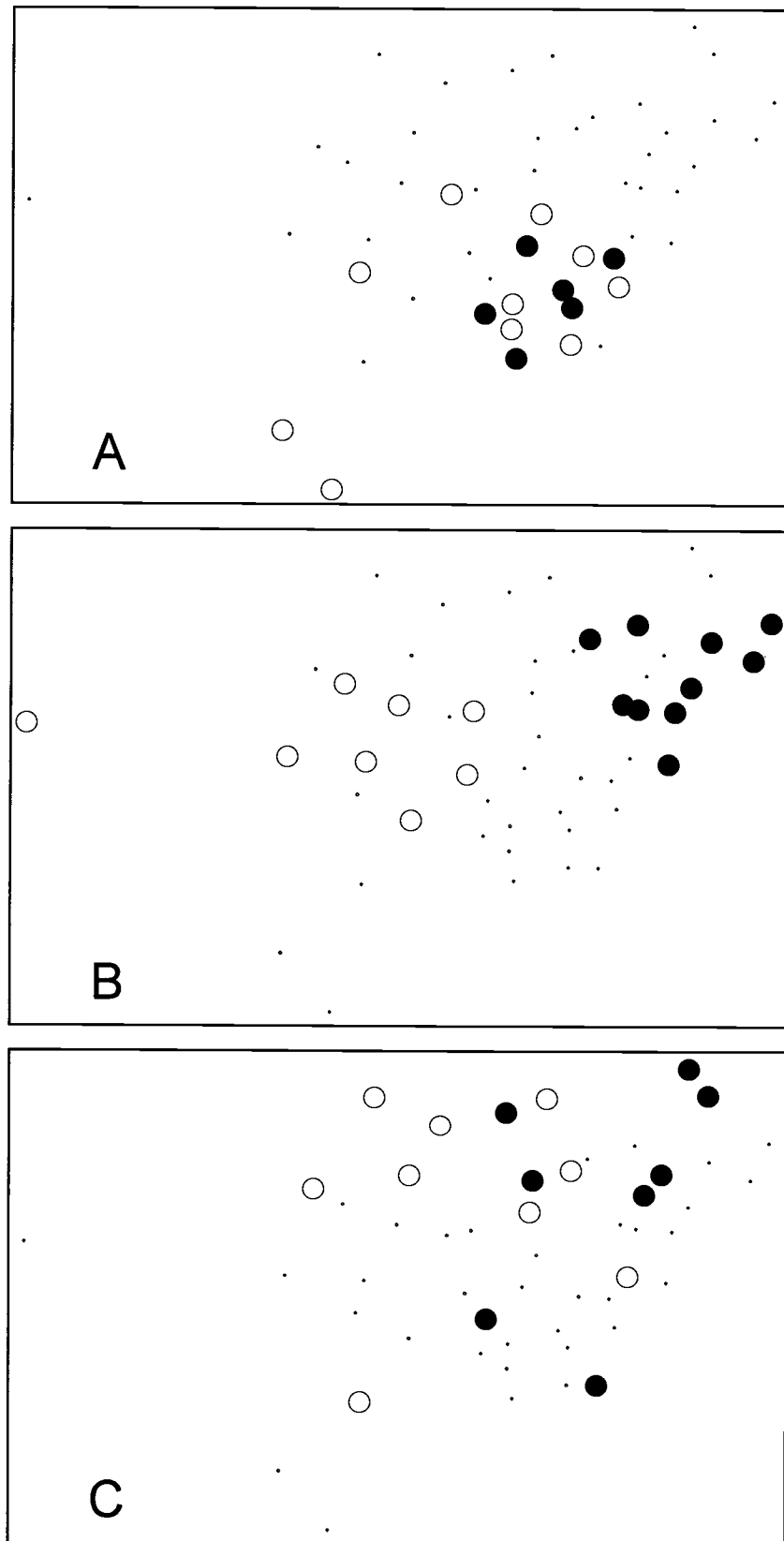
A successional pattern within the young stands emerged when the age of stands was overlaid on the ordination (Fig. 2.6). Plots fit into four groups: plots 50-60 yrs old in both ranges, plots 70-110 yrs old in the Coast Range, plots 70-110 yrs old in the Cascades, and old-growth plots in both ranges. Indicator analysis showed that few species are associated with a single age/range group, although many are unevenly distributed among the four groups. Therefore species were assigned to classes that include one or more of the age/range groups (Fig. 2.7).

## **DISCUSSION**

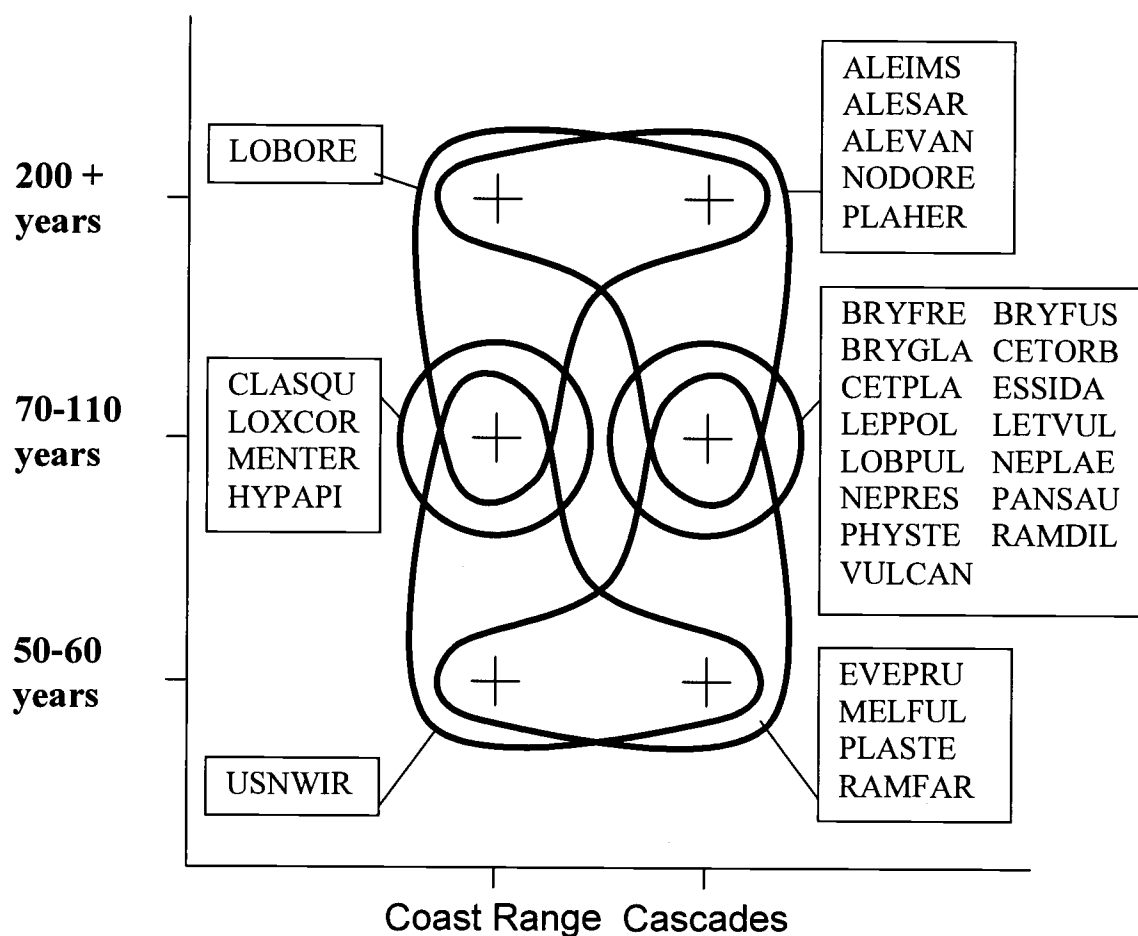
### **Relations of Stand Age and Structure to Lichen Communities**

**Communities in Old-growth Forests.** The association of alectorioid lichens with old-growth stands is well established in the Pacific Northwest (McCune 1993; Peck and McCune 1997) and northern Europe (Esseen et al. 1996). Many alectorioid lichens reproduce primarily by thallus fragmentation, a method that is not conducive to long

**Figure 2.6** Differences between Coast Range and Cascade lichen communities along the stand-age gradient apparent in the ordination (Figure 3). Open circles are Coast Range plots, filled circles are Cascade plots. **(A)** Symbols enlarged for stands 50-60 years of age. **(B)** Symbols enlarged for stands 70-110 years of age. **(C)** Symbols enlarged for stands 200 + years of age.



**Figure 2.6**



**Figure 2.7** Species associated with stand groups defined by mountain range and stand age class. Species abbreviations are given in Table 2.1. Associations are with  $p \leq 0.05$  (IndVal) except *Alectoria imshaugii* and *Nodobryoria oregana*, which were included because of previous detection of value as old-growth indicators. *Platismatia glauca* is not listed; it showed a negative association with 70-110 year old Coast Range stands ( $p \leq 0.05$ ).

distance dispersal. Consequently alectorioid lichens are often thought to require time to colonize a forest and establish large populations, resulting in their association with older forests. Esseen (1985) suggests that dispersal may be more limiting for species of *Alectoria* than of *Bryoria*, which agrees with our finding of association between old-growth stands, or old-growth trees in general, and all three species of *Alectoria*, but only one species of *Bryoria* (*sensu lato*, now in the genus *Nodobryoria*).

The association of *Lobaria oregana* with old-growth stands is even more well established (Pike et al. 1972; McCune 1993; Sillett and Neitlich 1996). Although we found small populations of *L. oregana* in several younger stands, it clearly had a strong association with old growth. *Lobaria oregana* reproduces primarily with relatively large lobules which may cause it to be dispersal-limited (Sillett and McCune 1998; Sillett et al. 2000), much like the alectorioid lichens.

The reasons for associations of *Hypocenomyce* spp. with old-growth forests or remnant trees (Fig. 2.3) are probably different than those for alectorioid lichens or *Lobaria oregana*. *Hypocenomyce* species often prefer charred bark or wood as a substrate (Purvis et al. 1992). Fire suppression and logging, particularly with snag removal, have likely reduced the probability of finding charred substrates that remain in the forest for more than a few years. Trees in old-growth forest, remnant trees, and remnant snags commonly possess old fire scars.

**Remnant Trees.** Old trees remaining in young stands from a previous stand can act as refugia and propagule sources for lichens (Neitlich and McCune 1997; Peck and McCune 1997). The old-growth association of several lichens is statistically strengthened by combining old stands and young stands with old trees present (Fig. 2.3). The presence of old trees in or near our plots is positively correlated with the stand age gradient in the lichen communities (Fig. 2.4); all young stands with old trees plot high on the vertical axis, near the old-growth stands.

Two matrix lichens, *Letharia vulpina* and *Cetraria pallidula*, occurred only in plots containing old-growth trees. These species are not generally considered associates of old growth. They are typically found in continental to suboceanic forests of a variety of ages and are unusual for low elevation forests in western Oregon (McCune and Geiser 1997). Exposure of trunks to sunlight and broader temperature ranges on trees rising well

above the average canopy layer of a young forest, or on trees in gaps within old-growth stands, may be responsible for the occurrence of these species with old growth trees.

**Communities in Thinned Stands.** Alectorioid lichens were slightly more abundant in thinned stands than in unthinned stands, on average. Age of branches has been correlated with the biomass of fruticose lichens (mainly alectorioid species) which they host (Esseen et al. 1996). Thinning opens the canopy, increasing the life span and size of branches. Longer branch life may increase the opportunity for alectorioid lichens to build biomass and continue dispersing within the stand, building their populations. Increased light levels may lead to more rapid growth. Unfortunately, the difference in alectorioid abundance between the unthinned and thinned stands was small and may not be of biological significance for the animals that use them or for adequate dispersal to maintain populations over the landscape.

Indicator species analysis revealed only one species, *Hypogymnia imshaugii*, with an affinity for thinned stands. Much like *Letharia vulpina* and *Cetraria pallidula*, *H. imshaugii* is a matrix lichen that is common in drier forests to the east of the Cascade Crest (McCune and Geiser 1997), so its frequent appearance in our young thinned stands was surprising, especially in the Coast Range. Opening the canopy by thinning may decrease humidity in the stands, making them more suitable for colonization by this dry-forest species.

Traditional commercial thinning can reduce variation in stand structure, which could cause the reduced landscape-level diversity of lichens (gamma diversity) that we found in thinned stands compared to unthinned stands. The traditional commercial thinning operations in our stands were intended to homogenize spacing between trees (Bailey et al. 1998). Although not statistically significant, our data showed fewer tree species in thinned stands relative to unthinned stands, suggesting that species other than Douglas-fir were preferentially removed. Remnant trees were less frequent in the thinned stands than the unthinned stands, also probably due to removal during thinning. Additionally, Rosso et al. (2000b) noted that shrubs were often damaged by thinning operations. Lichen species that occurred more frequently in unthinned plots (Table 2.1) were often collected from the remnant trees (e.g. *Alectoria imshaugii*, *Hypocenomyce friesii*, and *H. scalaris*) or from shrubs (e.g. *Nephroma helveticum*, *Pannaria* spp.,

*Physcia aipolia*, and *Pseudocyphellaria* spp.). The more homogenized stand structure and the corresponding lower lichen gamma diversity in thinned stands (Table 2.2) suggest that diversity of stand structure is important for maintaining landscape-level diversity within young forests. This is compatible with findings in Sweden that many lichen species are less frequent in managed landscapes than in natural landscapes (Dettki and Esseen 1998). The creative thinning ideas discussed by Neitlich and McCune (1997), and careful manipulations to avoid damaging shrubs and unusual structures, could promote a variety of lichens and improve landscape-level lichen diversity.

## Community Patterns across the Landscape

**Environmental Gradients.** The strongest variation in lichen community composition follows a climatic gradient, separating the more oceanic Coast Range from the Cascade Range. Five species are strongly associated with the Coast Range (Fig. 2.3). *Loxosporopsis corallifera* is our strongest indicator of Coast Range sites. *Usnea wirthii* is present in some Cascade sites but more common in the Coast Range, consistent with a positive response to oceanic climates (Halonen et al. 1998). *Cavernularia lophyrea* is also a well known as a coastal species (McCune and Geiser 1997).

The association of *Lobaria oregana* with the Coast Range (Figs. 2.2 and 2.7) is a surprise. Stands with massive biomass of *L. oregana* occur primarily in the Cascades (Pike et al. 1972; McCune 1993; Sillett 1995), so we expected *L. oregana* to also be most frequent in that mountain range. Two factors may allow *L. oregana* to grow more frequently in the Coast Range: (1) the more oceanic climate of the Coast Range may allow the species to establish more quickly in younger stands, or (2) representation of *L. oregana* in our Cascade data may be reduced in the Cascades by pollution from the metropolitan and industrial areas of the Willamette Valley (pollution is further discussed below).

Thirty-one species were associated with the Cascade Mountains. Most of these are species typical of drier areas such as the *Pinus* forests on the east slope of the Cascades (e.g. *Bryoria fremontii*, *Vulpicida canadensis*, *Esslingeriana idahoensis*, and *Hypogymnia imshaugii*). Also included are a number of species common throughout the

Pacific Northwest but identified as Cascade associates by their higher frequency and abundance in the Cascades (e.g. *Lobaria pulmonaria*, isidiate species of *Parmelia*, *Parmeliopsis hyperopta*, *Platismatia herrei*, *P. stenophylla*, and *Pseudocyphellaria anomala*). Some listed as Cascade associates are pollution tolerant and often thought of as lowland and valley species (*Evernia prunastri*, *Hypogymnia physodes*, *Physcia aipolia*, *Physcia stellaris*, *Ramalina farinacea*, and *Xanthoria polycarpa*).

**Air Pollution.** Although we did not design our study to address questions of air pollution, the surprisingly low abundance of the cyanolichen, *Lobaria oregana* (Fig. 2.1), and the high abundance of pollution tolerant, valley species in the Cascade Range warrants discussion. The sensitivity of Cyanolichens is well documented and pollution can even eliminate them on a landscape scale (Hallingbäck 1989). The northernmost block in the Cascades was entirely lacking in cyanolichens and we found the remains of two children's balloons near our plots in this block. Numerous and diverse balloons were also found by Rambo (1998) while working in nearby stands. We believe these to be an indication that air flow, and pollution, frequently comes from Portland directly over these stands. Pollution from various sources in the Willamette Valley could impact lichens through much of our northern Cascade plots.

The Willamette Valley matrix lichens that were associated with the Cascade stands are relatively pollution tolerant. *Hypogymnia physodes* is frequently used for pollution monitoring because of its pollution tolerance (Richardson 1988). *Xanthoria* species are well known nitrophiles that are often abundant in areas of agricultural or industrial pollution (Van Dobben 1993).

## Successional Dynamics

Using the varying ages of our young stands as a chronosequence, the ordination suggests a difference between the Coast Range and Cascades in successional dynamics of lichen communities (Fig. 2.6). The lichen communities are similar between the mountain ranges in the 50-60 yr old stands, differ considerably in stands 70-110 yrs of age, then are similar again in stands over 200 yrs. The pattern is due to many species entering or being lost from forests at different ages in the two ranges (Fig. 2.7). It is likely that the

similarity of 50-60 yr old stands between the ranges is due to the abundance of widespread, early-colonizing lichen species. The divergent then convergent successional patterns in each range after 60 yrs of age are challenging to explain.

Limitations on the occurrence of species in habitats within a forest and in differing forests across a landscape are often based on microclimatic and macroclimatic influences (McCune 1993). The divergence between the Coast and Cascade Range communities that we observed in stands 70-110 yrs old may result from the forests acquiring species that are best adapted to a particular part of the climatic gradient that differs between the mountain ranges. However, recent work suggests that dispersal may be the limiting factor for some late-colonizing species in Oregon (Sillett and McCune 1998; Sillett et al. 2000). Dispersal could cause the observed divergence if the propagule rain for some species differs between the mountain ranges. A species with a higher propagule rain in the Cascades than in the Coast Range will have a greater probability of colonizing a forest in the Cascades. Variation in propagule rain could be caused by climatic influences on populations that provide the propagules, or it could be an historical artifact from disturbance regimes or population migration, or it could be from some unknown factor.

The later convergence of communities between mountain ranges in stands aged 200 yrs or more results from the arrival of the same old-growth associates in both mountain ranges. As a conifer forest in western Oregon ages to 200 yrs and beyond, a pronounced vertical stratification of lichen functional groups forms in the canopy, which is thought to result from a vertical gradient in microclimate (McCune 1993; McCune et al. 1997a). A broadening of the vertical microclimatic gradient would result in diversification of microhabitats in the canopy as a forest ages, which might correspond to an increasingly broad range on the macroclimatic gradient. Old forests juxtapose dry, emergent treetops with perennially shady, humid microhabitats. Colonization of this broad range of microhabitats by species with diverse habitat requirements should lead to rich, regionally similar communities. Alternatively, the convergence may result from gradual accumulation of species with low propagule rain. Differences in dispersal potential that could have led to early divergence in communities may eventually be overcome by the cumulative probability of a species colonizing a forest, also leading to

rich, regionally similar communities. Since we have not observed elevated alpha diversity in old-growth, either our hypotheses are incorrect, our sampling under-represents the upper canopy, or the arrival of old-growth associates is compensated by a loss of some early colonizers.

At present, we have little evidence to help us weigh the relative importance of dispersal limitations and microhabitat diversification in producing the observed divergence, then convergence in communities between the mountain ranges. There may be more explanations we have not considered. Simulation models could help to understand mechanisms for maximized community differences between mountain ranges in the 70-110 yr old stands, but should be presented in a separate paper. Ultimately a combination of dispersal and microhabitat diversification may explain the divergence and later convergence. For example, *Lobaria oregana* can be experimentally established and grown in young forests and even on branches erected in clear-cuts, suggesting that dispersal must be its main limitation to growing in young forests (Sillett and McCune 1998; Sillett et al. 2000). The fragmentation of old-growth forests in much of western Oregon (Spies et al. 1994) should impede dispersal-limited species (With and King 1999). It would follow that *L. oregana* should be most abundant and enter stands at the earliest age in a region where much old-growth is available to supply propagules. This is not so. More old-growth forest remains in the Cascade Range than in the Coast Range of western Oregon, but *L. oregana* is most frequent and enters stands at the earliest age in the Coast Range. Thus, while dispersal limitations may important in causing the old-growth association of *L. oregana*, it is likely that the more oceanic climate of the Coast Range favors early establishment of *L. oregana* in young forests.

## Management Implications

We have known for some time that many lichens are associated with old-growth forests (Pike et al. 1972; McCune 1993) and these lichens are now being considered when designing forest management plans (USDA and USDI 1994). Old-growth associates tend to be forage-providing alectorioid lichens or nitrogen-fixing cyanolichens; loss of old-growth habitat reduces the presence of these functional groups in the

landscape. We found that some old-growth associated lichens may begin to colonize forests between 70 and 110 yrs old. Additionally, these forests provide valuable habitat for many other lichen species. Current forest rotation intervals in Oregon (roughly 50-70 yrs) do not provide much opportunity for these lichens to establish and maintain themselves across the landscape. Increasing rotation intervals could be a simple management technique to provide habitat for a greater variety of lichens. Our observations of young stands with remnant old trees adds to the mounting evidence that retention of some trees during a harvest can help to maintain old-growth associated lichens. However, increasing rotation intervals and harvesting with green tree-retention should not be used as alternatives to reserving old-growth stands, because many of the old-growth species require centuries to build a significant biomass even if they originally colonize a stand at an early age (McCune 1993).

Traditional commercial thinning appeared to have little effect on epiphytic macrolichens. Although we saw evidence that such thinning may slightly increase abundance of alectorioid species, we also saw evidence that traditional thinning reduces structural diversity and homogenizes lichen communities by reducing their landscape-level diversity. This does not mean that all forms of thinning lack value for lichen communities; thinning methods that strive to maintain or increase variability in forest structure and microhabitats may be beneficial to lichens (Neitlich and McCune 1997).

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### Chapter 3

## The Value of Hotspots, Particularly in Riparian Zones, for Lichen Diversity in the Managed Forests of Western Oregon

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## **ABSTRACT**

We examined lichen community composition in hotspots of lichen diversity, with that in relatively typical young and old-growth stands. A retrospective, blocked design was used with 17 blocks in the Coast Range and the western Cascades of Oregon. Each block consisted of two young matrix stands, one old-growth stand (age > 200 yrs), and one diversity hotspot. Most diversity hotspots were in riparian zones, but some upland hardwood gaps and rock outcrops were included. We found 117 lichen species in the 68 plots. There was no difference in the average species richness between matrix and old-growth plots, but hotspots averaged five more species than those plots (blocked ANOVA  $p = 0.001$ ). Eleven species were associated with old-growth plots, 26 were associated with hotspots, and 28 specifically with hotspots in riparian zones. Most old-growth associates were forage-providing alectorioid lichens while most hotspot and riparian zone associates were nitrogen-fixing cyanolichens. Among the hotspots, riparian zones were the most distinct in community composition from the more typical young and old plots. These locations of high lichen diversity are valuable for conservation of many native lichen species that occur infrequently in typical upland (non-riparian) forests.

## **INTRODUCTION**

Threats to biodiversity of lichens worldwide include loss of natural forest habitats, air pollution, increased fires in areas with historically low fire-frequency, climate change, agriculture, and tourism (Wolseley 1995). Mitigating the effects of these forces, both for lichens and for other organisms, requires habitat protection. This leads to politically troublesome questions concerning which habitats need protection, how much of those habitats, and how strongly to protect them. These questions have no simple answer and must be dealt with to some extent on local scales before a search can be undertaken for global principals.

In the Pacific Northwest of North America, an obvious threat to lichen biodiversity is the loss of old forest habitat due to logging of coniferous forests. After Euro-Americans colonized the region, logging accelerated to become the primary forest

disturbance. Logging often removed forests with an age of 200 yrs or more, and replaced them with plantation forests to be logged on a 50 - 100 yr cycle. In doing so, it removed well-developed lichen communities. Old forests that once covered vast areas are now highly fragmented (Spies et al. 1994). Forest management in the Pacific Northwest is now changing to address concerns for biodiversity in ways that are scientifically credible while maintaining some level of logging (Kohm and Franklin 1997). However, much remains unknown about biodiversity in the region.

Returning to the questions of which habitats need protection, how much of those habitats, and how much protection, we must admit that for many organisms, science is still working on the first question. Recent research on lichens has shown that many species are associated with old forest conditions (McCune 1993), a pattern that is not restricted to the Pacific Northwest (Tibell 1992; Selva 1994; Dettki and Esseen 1998; Kuusinen and Siitonen 1998). Despite a compositional change in lichen communities to include old-growth associated lichens as forests age, the species richness of stands does not appear to increase, suggesting a compensating loss of early colonizers (Peterson and McCune 2000a). However, lichen species richness is not uniformly distributed across the landscape. Localized hotspots of lichen diversity exist within stands and are often associated with unusual stand structure such as pockets of hardwoods (Neitlich and McCune 1997). Remnant old-growth trees in young stands are also valuable for promoting lichen biodiversity by acting as refugia for old-growth associated species (Peck and McCune 1997; Peterson and McCune 2000a).

With the present study, we expand research on hotspots of lichen diversity to the landscape-level and ask several questions. How much greater is species richness in hotspots compared to more typical stands? Do hotspots just concentrate a greater number of common species, or do they contribute to landscape level diversity by harboring species that are underrepresented in typical stands? How do hotspots differ in species composition? What habitats or forest structures are associated with hotspots of lichen diversity?

We examined lichen diversity and community composition both for species and for three functional groups. Cyanolichens are important contributors of nitrogen to forests in the Pacific Northwest (Pike et al. 1972; Pike 1978; Rhoades 1983). The long,

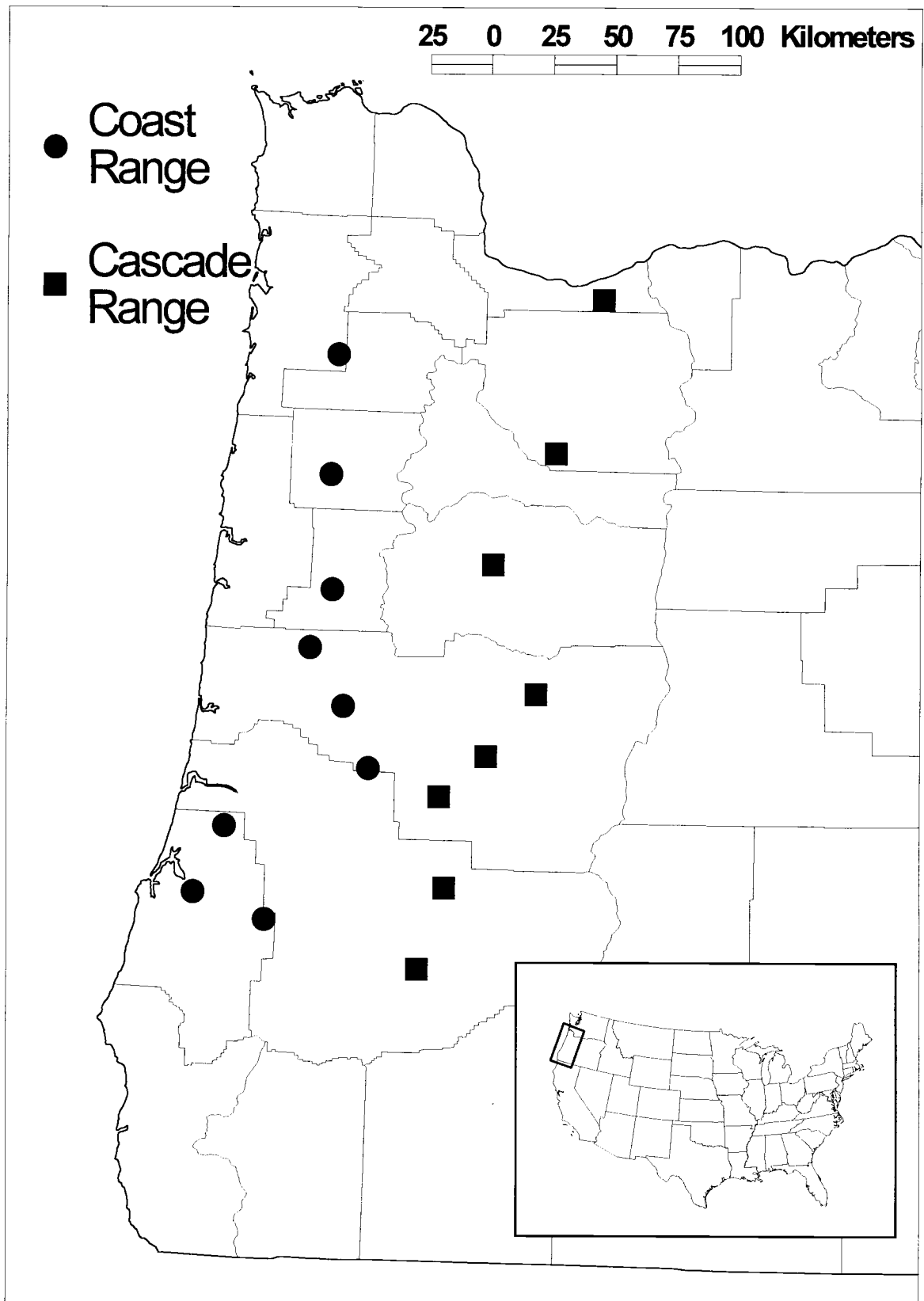
pendulous alectorioid lichens are known as valuable sources of food and nest-materials for a variety of animals, including *Glaucomys sabrinus*, the northern flying squirrel (Sharnoff 1994; Rosentreter et al. 1997). The other green-algal lichens, “matrix” lichens, usually dominate lichen communities in younger stands. They, as well as alectorioid lichens and cyanolichens, provide food sources and a variety of habitats to untold numbers of arthropods. By harboring these arthropods, lichens may form an important link in the food supply of branch-feeding birds (Pettersson et al. 1995). Surveys for, and management of, selected macrolichens from all three functional groups are required on Federal lands in the USA within the range of the Northern Spotted Owl (USDA and USDI 1994).

We examined the importance of lichen hotspots as contributors to diversity across the forested landscape of western Oregon by comparing potential hotspots of lichen diversity or abundance with the stands examined in Peterson and McCune (2000a). The same stands were studied for forest structure (Bailey and Tappeiner 1998), non-woody vegetation (Bailey et al. 1998), bats (Humes et al. 1999), shrub epiphyte communities (Rosso et al 2000b; 2000c), general macrolichen communities (Peterson and McCune 2000a), birds, insects, and shrub forage quality.

## **METHODS**

### **Study Sites**

We supplemented the blocked design of Peterson and McCune (2000a) by adding a hotspot to each of the nine blocks in the Coast Range mountains and eight blocks in the western Cascade mountains of Oregon, USA (Figure 3.1). Each block consisted of two young stands, one old-growth stand, and one macrolichen hotspot. The two young stands were adjoining and of identical age. One of each young stand pair was commercially thinned 10 to 25 yrs prior to sampling. The thinning had no effect on macrolichen diversity within stands, a possible decrease in landscape-level diversity, and only small effects on macrolichen species composition (Peterson and McCune 2000a), so the young



**Figure 3.1** Location of sampling blocks in western Oregon.

stands will be analyzed here as a single stand type. Age of young stands varied between blocks from 50 to 110 yrs. Old-growth stands were defined as having a majority of dominant trees aged 200 yrs or more. We defined macrolichen hotspots as locations that, upon scouting the location, appeared to have high species richness or an unusual species composition of epiphytic macrolichens. Riparian areas were nearly always available as hotspots, but we wanted our hotspots to represent a variety of habitats, so we selected against riparian areas whenever we could find a suitable non-riparian hotspot. Hotspots were found by locating unusual and diverse forest or landscape structures that were visible on maps, on aerial photographs, or by observation from access roads. Although we had no direct measure of the age of hotspot stands, they were either of comparable age to the young stands in the same block, or were clearly over 200 yrs of age based on tree size and structural development.

The old-growth and hotspot stands were seldom adjacent to the young stands. The distance in a block between the young and old-growth was typically less than 10 km (maximum = 19 km) while the distance between the young and hotspot stands was typically less than 4 km (maximum = 6 km).

Douglas-fir (*Pseudotsuga menziesii*), or a combination of Douglas-fir and western hemlock (*Tsuga heterophylla*), dominated all young and old-growth stands, and most hotspot stands. Hardwoods accounted for more than 50 % of the tree basal area in three hotspots. Latitudes ranged from 43.03° N to 45.50° N; longitudes ranged from 122.13° W to 124.09° W. Distance from the ocean varied from 20 to 138 km. Elevation ranged from 200 to 900 m. Annual precipitation averages 1.3 to 3.0 m/yr (Daly et al. 1994). Bailey and Tappeiner (1998), and Bailey et al. (1998), used the same stands and provided extensive information on their structure.

## Sampling

Since our study focused on community composition, determining species presence was more important than quantifying the common species. Relative to numerous small plots, the use of a single large plot in each stand emphasized species

capture over quantitative accuracy (McCune and Lesica 1992). The plot size and sampling followed the methods developed for the Forest Health Monitoring Program (Tallent-Halsell 1994; McCune et al. 1997a). Plots were circular with a radius of 34.7 m, yielding an area of 0.38 ha. Plot centers were permanently marked with an iron rod hammered into the ground and a white PVC pipe rising above the ground. The first author sampled all plots by ocular survey and recorded all macrolichen species found on: (1) woody vegetation (alive or dead) greater than 0.5 m above ground and accessible without climbing trees, and (2) recent litterfall, which provides a representation of the canopy epiphytes (McCune 1994). The survey time was limited to two hrs, with a minimum time of 0.5 hrs. Surveys stopped short of the maximum time only after: (1) examining representatives of all microhabitats within the plot and (2) 10 min had elapsed without encountering a new species. Each species was assigned an abundance score as follows: 0 = absent; 1 = rare (1-3 individuals in plot), 2 = uncommon (4-10 individuals per plot), 3 = common (> 10 individuals per plot but less than half of appropriate substrates bearing the species), 4 = very abundant (more than half of appropriate substrates bearing the species). Individuals are difficult to distinguish in strongly colonial lichens such as species of *Cladonia* (DePriest 1993 and 1994). We considered a continuous colony to be a single individual. Although we focused on macrolichens, we included *Loxosporopsis corallifera*, a recently described crustose species (Brodo and Henssen 1995), to increase our knowledge of its ecology in the Pacific Northwest.

Nomenclature followed Esslinger and Egan (1995), and McCune and Geiser (1997) except for a few species groups that could not be separated reliably to species. *Cladonia coniocraea* (Flörke) Sprengel was included in "*Cladonia ochrochlora* gr." Cup-forming *Cladonia* species fluorescing in short-wave UV were included in "*Cladonia merochlorophaea* gr." including *C. albonigra* Brodo & Ahti, a recently described species (Brodo and Ahti 1996). Several groups were included for *Usnea*. Aside from the individual species named in Table 3.1, all specimens forming isidioid propagules with their cortex confluent with the branch cortex are grouped as "*U. filipendula* gr." All specimens forming isidioid propagules that erupt from soredia-like structures are grouped as "*U. subfloridana* gr." All specimens forming pure soralia without isidioid propagules are grouped as "*U. lapponica* gr." Most *Usnea* specimens were identified prior to the

**Table 3.1** Species list with abbreviations, functional groups, and frequency of occurrence in upland and riparian plots. For functional groups (Func.), A = alectorioid, C = cyanolichen, M = matrix lichen (defined in the introduction).

Species	ABR	Func.	Upland	Riparia
			freq. (%)	n freq. (%)
<i>Alectoria imshaugii</i> Brodo & D. Hawksw.	ALEIMS	A	21	0
<i>A. sarmentosa</i> (Ach.) Ach.	ALESAR	A	66	33
<i>A. vancouverensis</i> (Gyelnik) Gyelnik ex Brodo & D. Hawksw.	ALEVAN	A	55	42
<i>Bryoria capillaris</i> (Ach.) Brodo & D. Hawksw.	BRYCAP	A	54	50
<i>B. fremontii</i> (Tuck.) Brodo & D. Hawksw.	BRYFRE	A	9	8
<i>B. friabilis</i> Brodo & D. Hawksw.	BRYFRI	A	59	8
<i>B. fuscescens</i> (Gyelnik) Brodo & D. Hawksw.	BRYFUS	A	57	25
<i>B. glabra</i> (Mot.) Brodo & D. Hawksw.	BRYGLA	A	13	0
<i>B. pseudofuscescens</i> (Gyelnik) Brodo & D. Hawksw.	BRYPSU	A	50	25
<i>B. trichodes</i> (Michaux) Brodo & D. Hawksw.	BRYTRI	A	2	0
<i>Bryoria</i> (mystery sp.)	BRYMYS	A	2	0
<i>Candelaria concolor</i> (Dickson) Stein	CANCON	M	4	0
<i>Cavernularia hultenii</i> Degel.	CAVHUL	M	36	33
<i>C. lophyrea</i> (Ach.) Degel.	CAVLOP	M	16	25
<i>C. chlorophylla</i> (Willd.) Vainio	CETCHL	M	68	67
<i>C. orbata</i> (Nyl.) Fink	CETORB	M	93	83
<i>C. pallidula</i> Tuck. ex Riddle	CETPAL	M	7	0
<i>C. platyphylla</i> Tuck.	CETPLA	M	32	0
<i>Cetrelia cetrarioides</i> (Duby) Culb. & C. Culb.	CTL CET	M	4	0
<i>Cladonia carneola</i> (Fr.) Fr.	CLACAR	M	5	17
<i>C. chlorophaea</i> (Flörke ex Sommerf.) Sprengel	CLACHL	M	5	17
<i>C. fimbriata</i> (L.) Fr.	CLAFIM	M	34	75
<i>C. furcata</i> (Hudson) Schrader	CLAFUR	M	2	17

Table 3.1, Continued

<i>C. merochlorophaea</i> Asah. (group)	CLAMER	M	43	17
<i>C. norvegica</i> Tønsberg & Holien	CLANOR	M	4	0
<i>C. ochrochlora</i> Flörke (group)	CLAO/C	M	98	100
<i>C. squamosa</i> var. <i>squamosa</i> Hoffm.	CLASQU	M	7	0
<i>C. squamosa</i> var. <i>subsquamosa</i> (Nyl. ex Leighton)	CLASSQ	M	73	83
Vainio				
<i>C. transcendens</i> (Vainio) Vainio	CLATRA	M	38	67
<i>Esslingeriana idahoensis</i> (Essl.) Hale & M. J. Lai	ESSIDA	M	23	0
<i>Evernia prunastri</i> (L.) Ach.	EVEPRU	M	66	75
<i>Fuscopannaria leucostictoides</i> (Ohlsson) P. M. Jørg.	FUSLEU	C	2	25
<i>F. saubinetii</i> (Mont.) P. M. Jørg.	FUSSAU	C	18	17
<i>Hypocenomyce anthracophila</i> (Nyl.) P. James & Gotth. Schneider	HYCANT	M	13	0
<i>H. castaneocinerea</i> (Räsänen) Timdal	HYCCAS	M	34	25
<i>H. friesii</i> (Ach.) P. James & Gotth. Schneider	HYCFRE	M	11	0
<i>H. scalaris</i> (Ach.) M. Choisy	HYCSCA	M	7	0
<i>Hypogymnia apinnata</i> Goward & McCune	HYPAPP	M	93	83
<i>H. duplicata</i> (Ach.) Rass.	HYPDUP	M	2	0
<i>H. enteromorpha</i> (Ach.) Nyl.	HYPENT	M	100	100
<i>H. imshaugii</i> Krog	HYPIMS	M	57	25
<i>H. inactiva</i> (Krog) Ohlsson	HYPINA	M	98	83
<i>H. metaphysodes</i> (Asah.) Rass.	HYPMET	M	4	0
<i>H. occidentalis</i> L. Pike	HYPOCC	M	4	50
<i>H. oceanica</i> Goward	HYPOCE	M	2	0
<i>H. physodes</i> (L.) Nyl.	HYPPHY	M	89	92
<i>H. tubulosa</i> (Schaerer) Hav.	HYPTUB	M	79	67
<i>Hypotrachyna sinuosa</i> (Sm.) Hale	HYTSIN	M	54	92
<i>Leptogium cellulosum</i> P. M. Jørg. & Tønsb.	LEPCEL	C	0	8

**Table 3.1, Continued**

<i>L. corniculatum</i> (Hoffm.) Minks	LEPCOR	C	0	25
<i>L. lichenoides</i> (L.) Zahlbr.	LEPLIC	C	2	0
<i>L. polycarpum</i> P. M. Jørg. & Goward	LEPPOL	C	16	58
<i>Letharia vulpina</i> (L.) Hue Syn.	LETVUL	M	25	0
<i>Lobaria hallii</i> (Tuck.) Zahlbr.	LOBHAL	C	0	8
<i>L. oregana</i> (Tuck.) Müll. Arg.	LOBORE	C	50	67
<i>L. pulmonaria</i> (L.) Hoffm.	LOBPUL	C	36	58
<i>L. scrobiculata</i> (Scop.) DC.	LOBSCR	C	7	33
<i>Loxosporopsis corallifera</i> Brodo, Henssen & Imshaug	LOXOSP	M	30	17
<i>Melanelia exasperatula</i> (Nyl.) Essl.	MELEXA	M	41	17
<i>M. fuliginosa</i> (Fr. ex Duby) Essl.	MELFUL	M	45	42
<i>M. multispora</i> (A. Schneider) Essl.	MELMUL	M	4	0
<i>M. subaurifera</i> (Nyl.) Essl.	MELSUB	M	11	33
<i>Menegazzia terebrata</i> (Hoffm.) A. Massal.	MENTER	M	14	67
<i>Nephroma bellum</i> (Sprengel) Tuck.	NEPBEL	C	14	67
<i>N. helveticum</i> Ach.	NEPHEL	C	20	58
<i>N. laevigatum</i> Ach.	NEPLAE	C	16	58
<i>N. occultum</i> Wetmore	NEPOCC	C	2	0
<i>N. resupinatum</i> (L.) Ach.	NEPRES	C	9	67
<i>Nodobryoria oregana</i> (Tuck.) Common & Brodo	NODORE	A	59	25
<i>Normandina pulchella</i> (Borrer) Nyl.	NORPUL	M	2	33
<i>Parmelia hygrophila</i> Goward & Ahti	PARHYG	M	55	42
<i>P. pseudosulcata</i> Gyelnik	PARPSU	M	55	33
<i>P. saxatilis</i> (L.) Ach.	PARSAX	M	34	25
<i>P. sulcata</i> Taylor	PARSUL	M	98	92
<i>Parmeliella parvula</i> P. M. Jørg.	PANAHL	C	4	0
<i>Parmeliopsis ambigua</i> (Wulfen) Nyl.	POPAMB	M	4	8
<i>P. hyperopta</i> (Ach.) Arnold	POPHYP	M	66	8

**Table 3.1, Continued**

<i>Parmotrema arnoldii</i> (Du Rietz) Hale	PTRARN	M	5	8
<i>P. chinense</i> (Osbeck) Hale & Ahti	PTRCHI	M	5	33
<i>Peltigera collina</i> (Ach.) Schrader	PELCOL	C	27	67
<i>P. membranacea</i> (Ach.) Nyl.	PELMEM	C	0	17
<i>P. pacifica</i> Vitik.	PELPAC	C	0	17
<i>Physcia adscendens</i> (Fr.) H. Olivier	PHYADS	M	18	8
<i>P. aipolia</i> (Ehrh. ex Humb.) Fürnr.	PHYAIP	M	13	25
<i>P. stellaris</i> (L.) Nyl.	PHYSTE	M	13	0
<i>P. tenella</i> (Scop.) DC.	PHYTEN	M	21	17
<i>Platismatia glauca</i> (L.) Culb. & C. Culb.	PLAGLA	M	98	83
<i>P. herrei</i> (Imshaug) Culb. & C. Culb.	PLAHER	M	89	67
<i>P. lacunosa</i> (Ach.) Culb. & C. Culb.	PLALAC	M	2	17
<i>P. norvegica</i> (Lynge) Culb. & C. Culb.	PLANOR	M	14	0
<i>P. stenophylla</i> (Tuck.) Culb. & C. Culb.	PLASTE	M	82	25
<i>Polychidium contortum</i> Henssen	LICCAN	C	7	0
<i>Pseudocyphellaria anomala</i> Brodo & Ahti	PCYANO	C	27	67
<i>P. anthraxis</i> (Ach.) H. Magn.	PCYANT	C	21	50
<i>P. crocata</i> (L.) Vainio	PCYCRO	C	14	58
<i>Ramalina dilacerata</i> (Hoffm.) Hoffm.	RAMDIL	M	25	42
<i>R. farinacea</i> (L.) Ach.	RAMFAR	M	73	100
<i>R. subleptocarpa</i> Rundel & Bowler	RAMSUB	M	4	0
<i>R. thrausta</i> (Ach.) Nyl.	RAMTHR	A	11	58
<i>Sphaerophorus globosus</i> (Hudson) Vainio	SPHGLO	M	95	100
<i>Sticta fuliginosa</i> (Hoffm.) Ach.	STIFUL	C	16	67
<i>S. limbata</i> (Sm.) Ach.	STILIM	C	13	42
<i>Usnea cavernosa</i> Tuck.	USNCAV	A	11	17
<i>U. ceratina</i> Ach.	USNCER	A	2	0
<i>U. chaetophora</i> Stirton	USNCHA	A	2	0
<i>U. cornuta</i> Körber	USNCOR	M	25	42

**Table 3.1, Continued**

<i>U. filipendula</i> Stirton (group)	USNFIL	M	100	100
<i>U. glabrata</i> (Ach.) Vainio	USNGLA	M	61	92
<i>U. hesperina</i> Mot.	USNHES	A	2	0
<i>U. hirta</i> (L.) F. H. Wigg.	USNHIR	M	4	0
<i>U. lapponica</i> Vainio (group)	USNLAP	M	27	42
<i>U. longissima</i> Ach.	USNLON	A	5	33
<i>U. madeirensis</i> Mot.	USNMAD	M	4	8
<i>U. subfloridana</i> Stirton (group)	USNSUB	M	39	42
<i>U. wirthii</i> Clerc	USNWIR	M	66	100
<i>Vulpicida canadensis</i> (Räsänen) J.-E. Mattsson & M. J. Lai	VULCAN	M	9	0
<i>Xanthoria polycarpa</i> (Hoffm.) Rieber	XANPOL	M	14	8

publication on *Usnea* in British Columbia by Halonen et al. (1998). Specimens decidedly distinct from the species groups were left unnamed until that publication allowed them to be identified as *U. chaetophora* and *U. madeirensis*. Taxonomic groups were considered equivalent to species for our analyses. Recent work on *Leptogium* (Jørgensen and Tønsberg 1999) allowed us to identify *L. cellulosum*. Additionally, *Cladonia squamosa* var. *squamosa*, *Cladonia squamosa* var. *subsquamosa* and a species of *Bryoria* with unknown taxonomic status (“*Bryoria* mystery species” of McCune and Geiser 1997) were recorded and analyzed as independent species.

In addition to assessing the lichen community in each plot, we recorded the dominant slope and aspect, topographic position, and proximity to perennial water. At the plot center and at four equidistant points around the circumference we measured canopy density and basal area for each tree species. In young stands, we recorded the presence of old-growth remnant trees in or near the plots.

Plots in young and old-growth stands were placed arbitrarily but without intentional bias except for two criteria: (1) we attempted to locate the plot within the area of the stand that had been sampled by Bailey and Tappeiner (1998) to maximize the potential for comparing our results to other work in the same stands, and (2) we attempted to match topography of plots within a block to maximize focus on differences in stand structure. Several young plots were near, or even included, remnant old-growth trees. All young and old-growth stands were upland, except one old-growth stand, which included a small stream with riparian vegetation and was classified as riparian for analyses to detect riparian effects. Plots were placed in hotspot stands to focus on areas of presumed high species richness or unusual composition; no attempt was made to match topography between hotspots and other stands within a block.

## Statistical Analysis

We tested differences in species richness between the three stand types with blocked ANOVA (SPSS Inc. 1998). Our model included blocks (d.f. = 16), stand types (d.f. = 2) and error (d.f. = 49), with no interactions. (For multivariate analyses we used

PC-ORD (version 3.11, McCune and Mefford 1997). MRPP (Multi-Response Permutation Procedure; Biondini et al 1985) was used to test for a difference in community composition between hotspots and other stand types. The tightness of the groups was described with the A statistic, the chance-corrected within-group agreement ( $A = 0$  when random,  $A = 1$  when all items identical within groups). We tested association of species with *a priori* groups (e.g. stand type) with IndVal, a method for indicator species analysis (Dufrêne and Legendre 1997) combined with randomization tests with 10000 iterations. We tested the difference in species richness between mountain ranges with nested ANOVA (SPSS Inc. 1998) using a model with blocks within ranges (d.f. = 15), mountain range (d.f. = 1), and error (d.f. = 51).

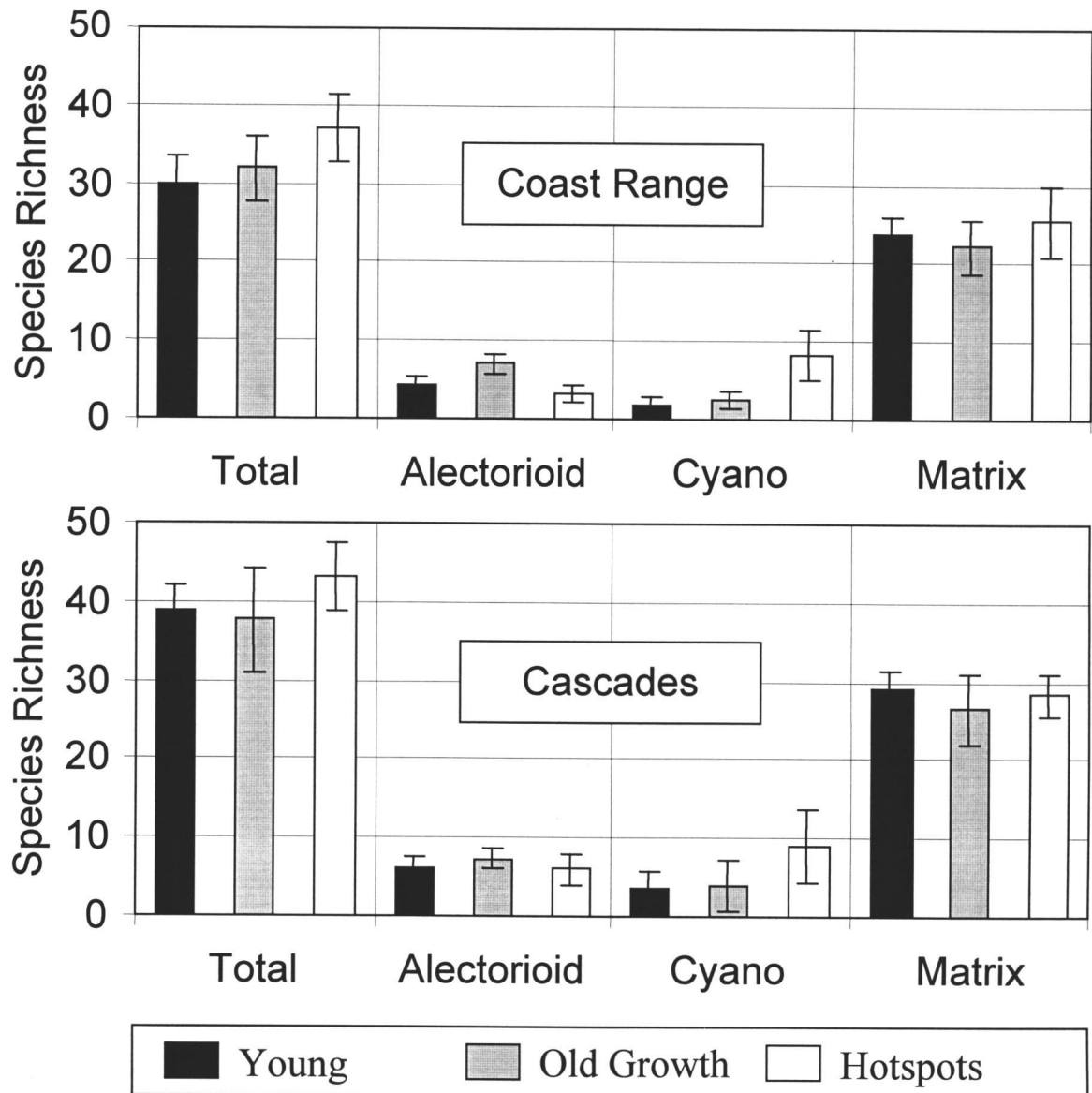
We analyzed interrelationships between taxa and relationships of taxa to stand structure, composition, and environmental features with NMS (Non-metric Multidimensional Scaling; Kruskal 1964; Mather 1976). To prevent error from localized low-stress solutions, the NMS ordination was obtained by running the analysis five times with random initial configurations and once each with the initial configuration derived from Principal Components Analysis and Bray-Curtis ordination. The run resulting in the lowest final stress was used for the analyses. The ordination was then rotated to align longitude with the horizontal axis to improve visual interpretation.

To reduce noise from rare species, those occurring in less than five percent plots ( $< 4$  plots) were deleted from the data set prior to all multivariate analyses. The quantitative version of Sørensen distance was used for NMS and MRPP. All multivariate techniques that we used are non-parametric and well suited to data that are non-normal, are on discontinuous scales, and contain a large proportion of zero values.

## **RESULTS**

### **Lichen Diversity**

A total of 117 species were found in the 68 plots (Table 3.1) with an average of 35.7 species per plot. Species richness of plots was higher in the Cascade Range (39.7)



**Figure 3.2** Species richness, total and separated by functional groups, for stand types. See introduction for functional groups and methods for stand types. Graphs are separated by mountain range due to higher average diversity in the Cascades. Error bars enclose 95% confidence intervals. Coast Range  $n = 9$ , Cascades  $n = 8$ , for each stand type.

than in the Coast Range (32.2; nested ANOVA:  $p = 0.027$ ). While species richness was similar between young and old plots, hotspots averaged five species more than young and old plots (blocked ANOVA:  $p = 0.001$ ). Much of this difference was due to a greater number of cyanolichens in hotspots (Figure 3.2). Old stands had a slightly higher number of alectoroid species than young stands (see Peterson and McCune 2000a).

## Community Composition

Community composition of hotspots differed from young and old plots (MRPP:  $p$ -values  $\ll 0.001$ ,  $A = 0.041$ ). In general, hotspots differed more from old-growth than from young plots (NMS, Figure 3.3a). The horizontal axis captured variation that corresponds to climatic differences between the mountain ranges (see Peterson and McCune 2000a). The vertical axis captured variation related to stand structure and composition. This axis incorporated gradients in conifer-versus-hardwood composition and variation in the canopy cover. Old-growth plots corresponded to a high basal area contributed largely by conifers, young stands were intermediate, and hotspots (no matter the age) corresponded to a low basal area with a large hardwood component and a less even canopy. Non-riparian hotspots harbored communities more similar to the other stand types than were harbored by the riparian hotspots (Figure 3.3b).

Species richness increased along the horizontal (mountain range) axis toward the drier Cascade end. Alectoroid and matrix lichens increased in diversity and abundance along with the overall species richness. Cyanolichens are independent of the others, increasing along the vertical axis toward the hotspots and away from the old growth. Functional group vectors for species richness alone are similar in direction but slightly weaker in the strength of correlation.

Peterson and McCune (2000a) found one species associated with the young stands (specifically the thinned stands), 7 associated with old-growth forests, and 11 associated with old trees in general. Inclusion of hotspots as either young or old plots increased the statistical power of the data set, revealing 11 species as old-growth forest associates (the added four were different from those associated with old trees in general) and three as

**Figure 3.3** NMS ordination of plots in species space based on the 91 species that occur in more than 5 % of the plots. The horizontal axis accounts for 47.6 % of the variation in the data while the second axis accounts for 30.9 % (total = 78.6). For joint plots (insets), length of correlation vectors represents the strength of the correlation; correlation vectors are given only for variables with  $r^2 > 0.200$ . **(A)** Symbols code for plot type: X = young, circles = old growth, and triangles = hotspots. Ordination centroid, the origin for joint plots, is marked with +. **(B)** Symbols code for hotspot type: circles = riparian, squares = upland forest with gaps, triangles = rocky outcrops, and X = non-hotspots. **(Inset, right)** Joint plot of strongly correlated environmental variables: Tot BA = total basal area of trees, % Conifer = percent of basal area contributed by conifers, % Hardwood = percent of basal area contributed by hardwood trees, Hard Rich = species richness of hardwood trees contributing to basal area, SD Canopy = standard deviation of within-plot canopy density, Ocean = distance from the ocean, Precipitation = estimated annual rainfall, and Longitude = longitude in positive numbers. **(Inset, left)** Joint plot vectors for diversity measures: Alpha = species richness,  $\Sigma$  Alect = sum of alectorioid lichen abundances,  $\Sigma$  Matrix = sum of matrix lichen abundances, and  $\Sigma$  Cyano = sum of cyanolichen abundances.

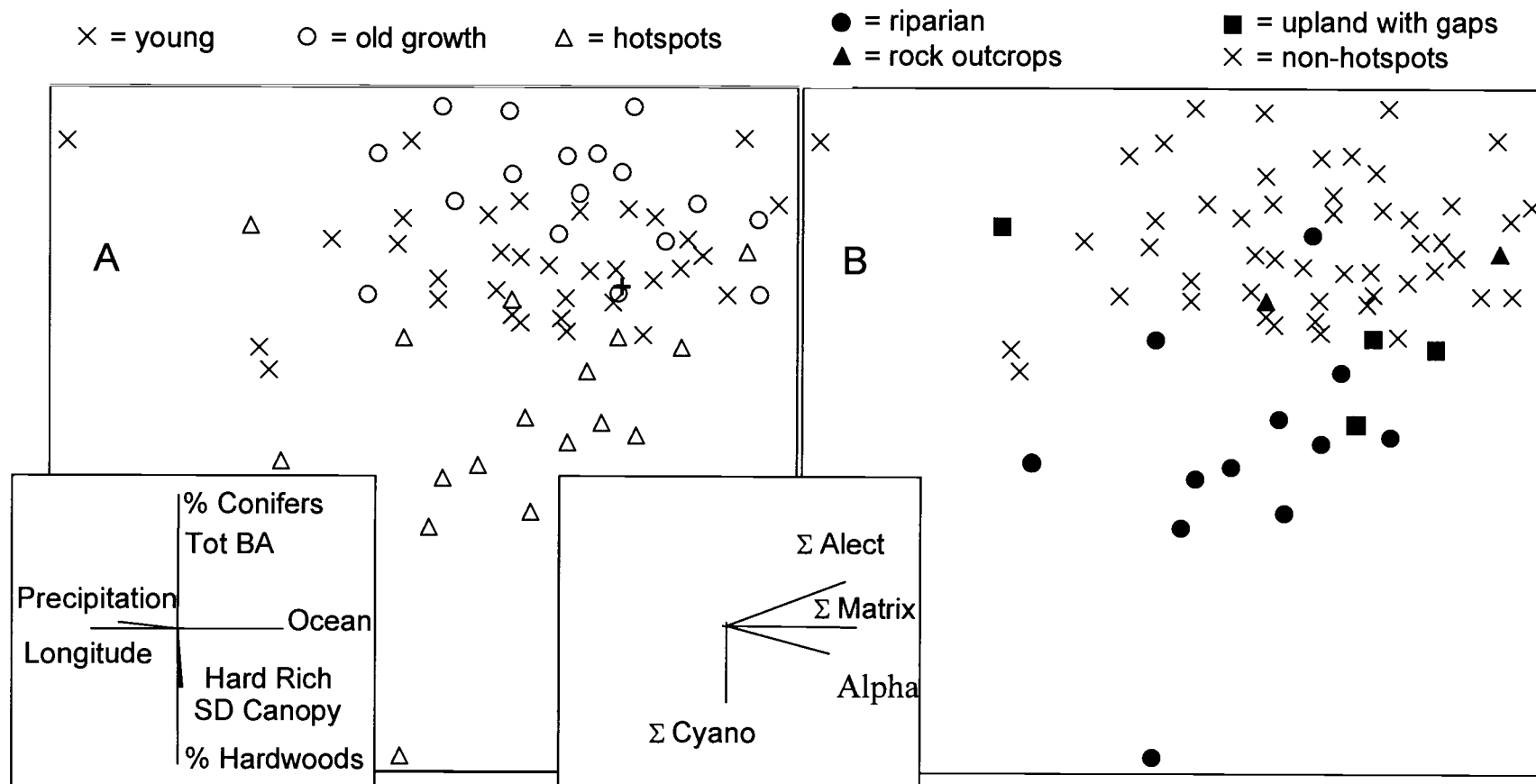


Figure 3.3

**Figure 3.4** Indicator values (percent of perfect indication) for species associated with stand types and the functional-group composition of stand associates. OG = old-growth plots, Yng = young plots plus young hotspots, and the corresponding pie chart is for composition of the old-growth associates. Hot = hotspot plots, non-Hot = non-hotspot plots, and the corresponding pie chart is for the hotspot associates. Rip = riparian plots, Upl = upland plots, and the corresponding pie chart is for the riparian associates. In pie charts, A = alectoroid lichens, C = cyanolichens, M = matrix lichens, and numbers refer to the number of species from each functional group. All species included have IndVal  $p$ -value  $\leq 0.050$ ; for those with an asterisk (\*),  $p < 0.010$ .

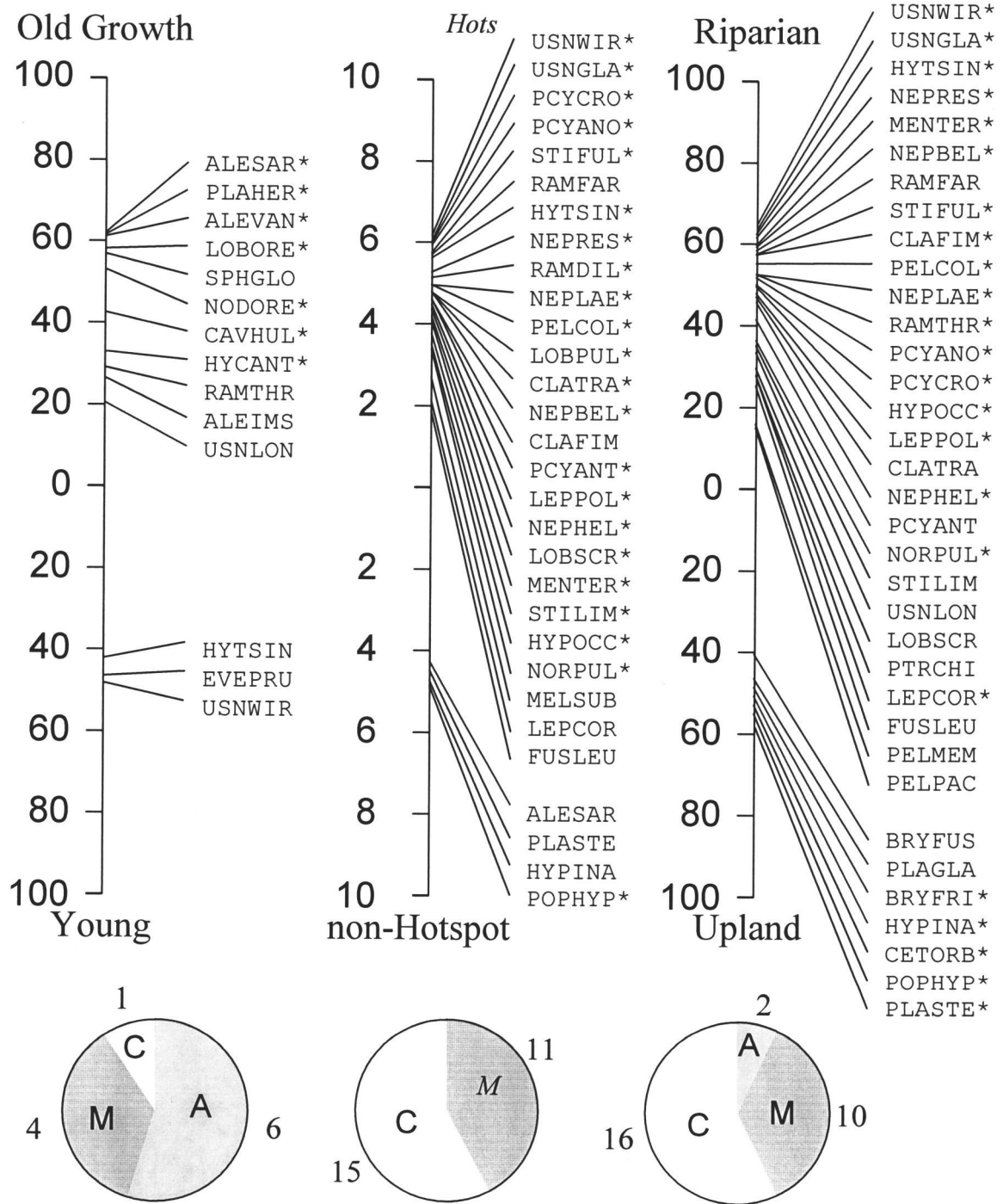
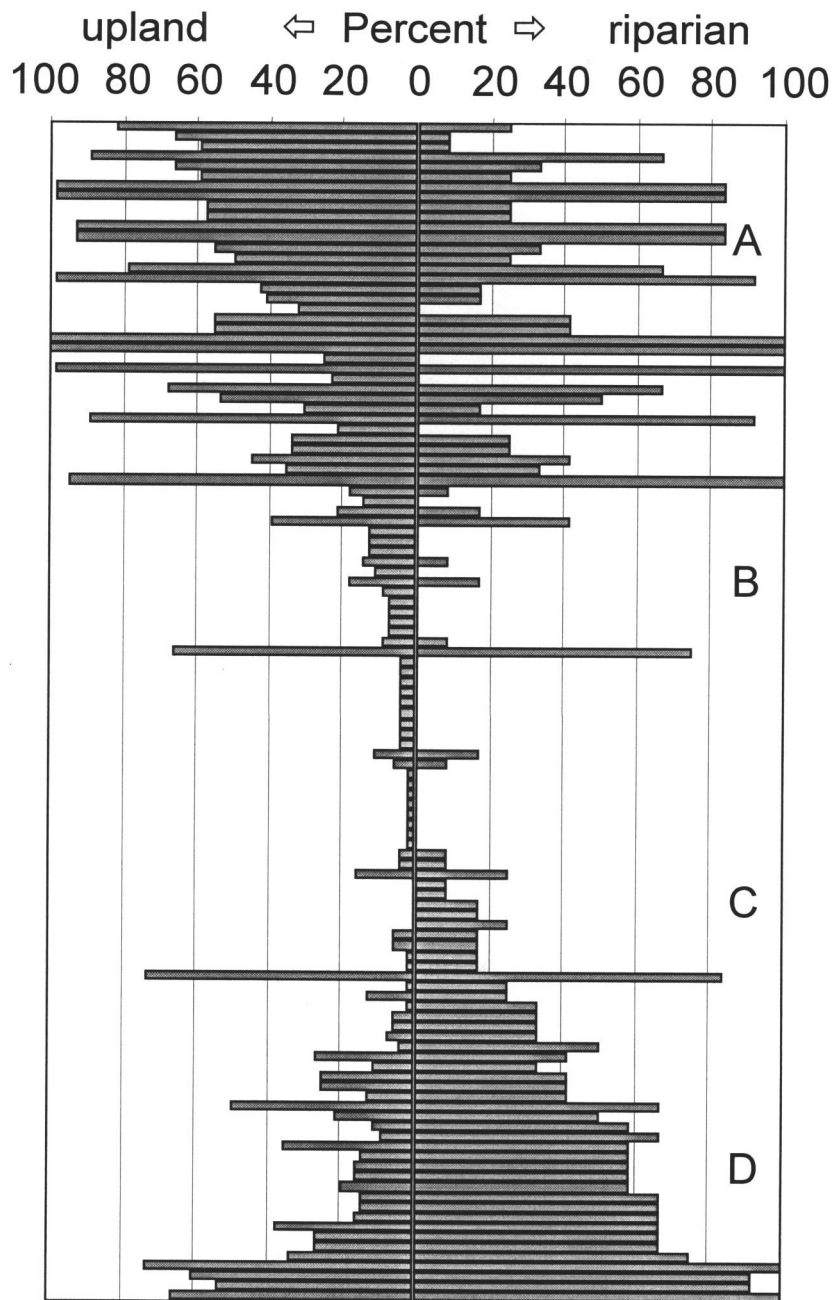


Figure 3.4



**Figure 3.5** Frequencies of occurrence for all 117 species as percent of upland plots ( $n=56$ ) and riparian plots ( $n=12$ ). Species are ranked from top to bottom by the equation  $((a - b) + 0.1) * a$  where  $a$  is the percent of upland plots the species occurs in and  $b$  is the percent of riparian plots the species occurs in (Table 1). The pattern suggests four general zones of species: (A) common-upland, (B) uncommon-upland, (C) uncommon-riparian, (D) common-riparian.

associates of general young stands (Figure 3.4). As in the previous study, the old-growth associates were primarily alectorioid species.

Twenty-six species associated with hotspots (Figure 3.4). Narrowing the focus to riparian hotspots increased the number to 28 and strengthened the association for many species. In both cases, the hotspot associates are primarily cyanolichens. Many of the species we found frequently in riparian hotspots were very infrequent in upland forests (Figure 3.5).

## **DISCUSSION**

### **Hotspots and Lichen Conservation**

Conservation issues for biodiversity of lichens and many other organisms have often focused on old-growth forests and remnant trees (USDA and USDI 1994, Peck and McCune 1997; Peterson and McCune 2000a). This focus is valuable for old-growth associated species, such as the alectorioid lichens, which provide food and nesting material for a variety of wildlife (Rosentreter et al. 1997), and for the cyanolichen *Lobaria oregana*, an ecologically important nitrogen-fixer (Pike 1978; McCune 1993). These lichens provide important ecosystem functions; their reduction in the western Oregon landscape validly raises alarm and warrants conservation of old-growth forests.

We find, however, that diversity hotspots, in both old and young stands, harbor many native lichen species that are poorly represented in typical forests, both young and old. To maintain lichen diversity in the landscape, lichen hotspots should be conserved in addition to old-growth forests. While upland hotspots may have rich epiphytic macrolichen communities, the community composition is not unlike more typical upland stands. However, riparian zones form particularly valuable hotspots with distinctive epiphytic lichen communities rich in nitrogen-fixing species. The Northwest Forest Plan (USDA and USDI 1994) provides some protection for riparian zones in the form of buffers to logging along streams.

In some ecosystems, riparian zones may form conduits for expanding populations of exotic plants (Mullin 1998; Stohlgren et al. 1998). However the benefits of riparian zones may outweigh the problems in most ecosystems. In the Pacific Northwest, riparian zones have vegetation characteristics different from upland areas (Hibbs and Giordano 1996), improve quality of fish habitat (Maser and Sedell 1994) and provide valuable habitat for wildlife (McComb et al. 1993; Hagar 1999). With the addition of lichen habitat to this list, it is clear that continued protection of riparian buffers in the Pacific Northwest will be important for maintaining biodiversity.

Lichen communities in non-riparian hotspots were similar to lichen communities in the young stands, suggesting that their communities are not as atypical as in the riparian hotspots. However, this does not mean they lack conservation value. All non-riparian hotspots had a discontinuous forest canopy. Hardwood shrub branches in these gaps were often densely covered with lichens (Rosso et al. 2000c). Although species composition in these hotspots was similar to more typical young stands, the abundance of lichens in them probably increases availability of propagules for colonizing nearby forests regenerating after logging. Dense lichen cover may also promote epiphytic arthropod communities, which may in turn promote the abundance of branch feeding birds (Pettersson et al. 1995). Our two rock outcrops harbored a variety of rock-dwelling species that are infrequent in the Pacific Northwest. However, our focus on epiphytic lichens excluded most of these species from this research.

### ***Lobaria oregana* versus other Cyanolichens**

Most cyanolichen species were closely associated with riparian hotspots. The vector representing a correlation between the ordination and the sum-of-abundance of cyanolichens was opposite of the old growth stands (Figure 3.3). This was a surprise because cyanolichens have traditionally been considered characteristic of old-growth forests in the Pacific Northwest (Sillett and Neitlich 1996).

Unlike other cyanolichens in our study, *Lobaria oregana* did associate with old growth. It has relatively heavy propagules that may cause its old-growth association by

limiting its dispersal rate (Sillett and McCune 1998; Sillett et al. 2000). The ecological importance of this cyanolichen (Pike et al. 1972; Pike 1978) attracted much attention and may have lead to the mistaken concept that all cyanolichens are old-growth associates. The association of *L. pulmonaria* with old growth in other regions (Rose 1976) may have also contributed; however it is clearly an associate of hotspots, not old growth, in our study. There are at least two other cyanolichens that may be true old-growth associates. *Nephroma occultum* occurred only once in our study, in an old-growth stand, and there is substantial evidence for its association with old growth in our region (Goward 1995; Rosso et al. 2000a). *Pseudocyphellaria rainierensis* Imshaug did not occur at all in our study, and also has substantial evidence for an association with old growth (Sillett 1995; Sillett and Goward 1998).

The association we found between cyanolichens, in general, and riparian hotspots could be due to the high humidity of riparian zones, or the abundance of hardwood trees, or factors we have not measured. Moisture gradients may have major influence of lichen distributions even at small scales (Hale 1952; McCune 1993; Peterson and McCune 2000a). Light may also influence the distribution of cyanolichens in the forest canopies (McCune et al. 1997b). Neitlich and McCune (1997) pointed out that hardwood gaps within young upland forests also provide good habitat for cyanolichens. In hardwood trees, both light and humidity may be modified favorably for lichens growth. Lichens in western Oregon grow primarily during the wet season: fall, winter, and spring (Muir et al. 1997). During much of the wet season, deciduous hardwood trees lack leaves, which may increase lichen photosynthesis and water interception. During the hot dry summers, leaves on the trees may protect lichens from sunburn.

## **Management Implications**

Conservation of old-growth forests is important for preserving diversity but old-growth forests alone will not protect all infrequent species of epiphytic macrolichens. Many infrequent species are closely associated with hotspots, particularly riparian forests with a large component of hardwood trees. Many of the infrequent species that could be

protected by conserving hotspots, particularly riparian hotspots, have ecosystem importance as nitrogen fixers.

Hotspots of macrolichen diversity in the landscape are identifiable from stand and environmental characteristics. Hotspots usually possess one or more of the following characters: a gappy canopy, a large proportion of hardwood versus conifer trees, variable tree sizes, and perennial water bodies. For example, a forest with a beaver pond that forms a large riparian gap, surrounded by old hardwood trees and scattered large, fast-growing conifers would likely be an excellent hotspot.

### **ACKNOWLEDGEMENTS**

Sampled stands were adopted from John Bailey and John Tappeiner, who provided us with information on the stands. Candace Cloud, Andrea Ruchty, Abbey Rosso, and Patricia Muir helped in various ways both in the field and the lab. Funding for this project was provided by the U.S. Geological Survey's Division of Biological Resources and Forest and Rangeland Ecosystem Science Center.

## Chapter 4

### Environmental Relations of Calicioid Lichens and Fungi in a Temperate Landscape

Eric B. Peterson and Bruce McCune

For Submission to *Ecography*.

## **ABSTRACT**

Community ecology of calicioid lichens and fungi (*Caliciales sensu lato*) was studied at low elevation sites in the Western Cascades of Oregon, USA. We examined old-growth forests and young forests, including young forests with wolf trees, large decorticate snags (dead, upright trunks), or remnant old trees. The 32 stands yielded 42 calicioid species. Old-growth forest and young stands with old remnant trees averaged more species than other stands. Ordination (NMS) indicated that calicioid communities vary in relation to average annual precipitation, a gradient in the relative abundance of *Tsuga heterophylla*, and various factors that influence understory exposure including average canopy density, gappiness of the canopy, and heat index (a combination of slope and aspect). Most correlations between communities and environmental gradients were weaker than correlations typically found for macrolichens, probably due to the microhabitat specificity of calicioids, which was poorly represented by macroenvironmental gradients. The highest frequency for most species was among the southern sites with low precipitation, little *Tsuga heterophylla*, and high understory exposure.

## **INTRODUCTION**

Calicioid lichens and allied fungi (*Caliciales sensu lato*, see Tibell 1997; Wedin and Tibell 1997) are tiny organisms that strongly associate with old forest structures. The association of many species with old-growth forest and stand continuity has been demonstrated by researchers in Fennoscandia (Hyvärinen 1992; Tibell 1992; Holien 1996; Kuusinen and Siitonen 1998) and north-eastern North America (Selva 1994).

The association of many calicioids with old forest structures probably results from their substrate specificity. Occurrence of species correlates with the depth of bark texture and with the reduced bark pH of older trees (Hyvärinen 1992). This is unlike many old-growth associated macrolichens, such as *Lobaria oregana* (Tuck.) Müll. Arg., in which the old forest association is probably due to dispersal limitations (Sillett and McCune 1998; Sillett et al. 2000). Biogeography and spore morphology of many species suggest

that calicioids are not appreciably limited by dispersal (Tibell 1994; Kruys and Jonsson 1997).

Boreal regions are known to harbor a high diversity of calicioids (Tibell 1975, 1992, 1999). Studies in Fennoscandia indicate that many calicioids favor sheltered, humid sites (Holien 1996; Kruys and Jonsson 1997). Due to habitat specificity, variety in forest structure may also increase calicioid diversity.

The Pacific Northwest has a relatively large volume of old forest structure and very high diversity of calicioids (Peterson and Rikkinen 1999). Yet surprisingly little attention has been given to calicioids in the region. A taxonomic study with a few ecological notes was conducted in North American boreal forests in the early 1970's (Tibell 1975). That work included areas of British Columbia but did not extend into Washington or Oregon. A floristic survey of the Vancouver region of British Columbia included calicioid taxa (Noble 1982). Keys for many species have recently become available for British Columbia (Goward 1999). Otherwise the only published scientific works are descriptions of a few new species (Tibell 1991, Peterson and Rikkinen 1998) and range extensions for several species (Otto 1970; Otto 1972; Pike 1972; Otto 1983; McCune and Rosentreter 1992; McCune and Rosentreter 1995; Peterson and Rikkinen 1999).

The first ecological work done with calicioids in northwestern North America began in 1995 and was written as a report to the U.S. Bureau of Land Management (Ponzetti 1996). The study identified nine species, most found in old-growth forests. The species capture was low due to lack of experience with calicioids, but the work provided a base for our current, more thorough study.

The present research was undertaken to increase knowledge of calicioids in the Pacific Northwest including their responses to environmental gradients and documenting species occur in our forests and how frequently. For the Pacific Northwest, we hypothesized that (1) calicioid diversity would be greatest in forests with old-growth trees and (2) most calicioids would frequent stands with (a) high humidity (e.g. precipitation) and (b) variable forest structure (tree density or canopy density). We tested these hypotheses by sampling low elevation sites in the Western Cascades of Oregon, USA. The same stands were studied for forest structure (Bailey and Tappeiner 1998), non-

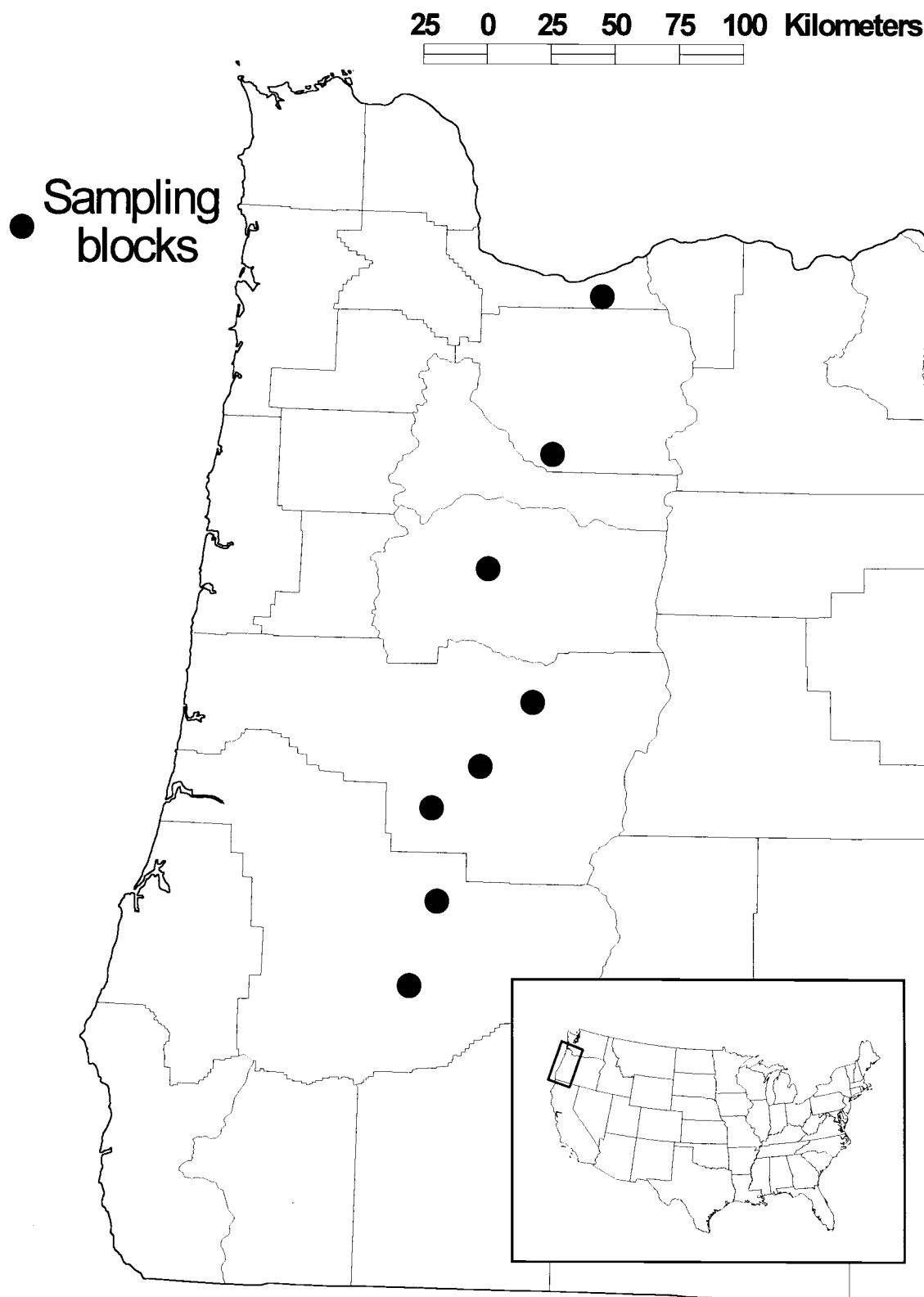
woody vegetation (Bailey et al. 1998), bats (Humes et al. 1999), shrub epiphyte communities (Rosso et al. 2000b; 2000c), general macrolichen communities (Peterson and McCune 2000a; 2000b), birds, insects, and shrub forage quality.

## **METHODS**

### **Study Sites**

We sampled four stand types in each of eight blocks in the western Cascade Mountains of Oregon (Figure 4.1). The stands were sampled using the Cascade plots of Peterson and McCune (2000b). Each block included two young stands, one old-growth stand, and one macrolichen hotspot. The two young stands were adjoining and of identical age, ranging from 60 to 110 yrs. One of each young stand pair was commercially thinned 10 to 25 yrs prior to sampling. The old-growth stands were defined as having a majority of the dominant trees aged 200 years or more. Macrolichen hotspots were defined as locations with high species richness or unusual species composition of epiphytic macrolichens, with no consideration of calicioid species. Riparian areas were nearly always available as hotspots, but the hotspots were intended to represent a variety of habitats, so riparian areas were selected against whenever a suitable non-riparian hotspot was available. Hotspots were found by locating unusual and diverse forest structures that were visible on maps, on aerial photographs, or by observation from access roads. Although we made no direct measure of the age of hotspot stands, they were either of comparable age to the young stands (analyzed as equal age), or were clearly over 200 yrs of age based on tree size and structural development.

Due to the scarcity of old-growth forest in some parts of the Cascade Mountains, the old-growth and hotspot stands were seldom adjacent to the young stands. The distance in a block between the young and old-growth stands was typically less than 10 km (maximum = 14 km) while the distance between the young and hotspot stands was always less than 4 km.



**Figure 4.1** Sampling block locations. Each block contains four plots: 1 young, unthinned; 1 young, thinned; 1 old growth; and 1 macrolichen diversity hotspot.

*Pseudotsuga menziesii* (Douglas-fir), or a combination of *P. menziesii* and *Tsuga heterophylla* (western hemlock), dominated all young and old-growth stands, and most hotspot stands; hardwoods accounted for  $\geq 50$  % of the tree basal area in two hotspots. Latitudes ranged from 43.03° N to 45.50° N; longitudes ranged from 122.13° W to 123.00° W. Elevation ranged from 280 to 890 m. Annual precipitation averaged 1.3 to 2.5 m/yr (Daly et al. 1994). Bailey and Tappeiner (1998), and Bailey et al. (1998), used the same stands and provided extensive information on their structure.

## Sampling

Since this study focused on community composition, determining species presence was more important than quantifying the species. We used a single large plot in each stand to emphasize species capture (McCune and Lesica 1992) and measured only presence or absence of calicioid species. Rationale for locating the plots and stand characters are described in Peterson and McCune (2000b) and Rosso et al. (2000c). The plot size matches those used for off-frame macrolichen plots under the Forest Health Monitoring Program (Tallent-Halsell 1994; McCune et al. 1997): circular with a radius of 34.7 m, yielding an area of 0.38 ha. Plot centers were permanently marked with an iron rod hammered into the ground and a white PVC pipe rising above the ground. We examined the plots by ocular survey, sampling all sexually reproductive calicioid fungi accessible without climbing trees. Anamorphs were excluded from the study even though anamorphs of *Chaenothecopsis viridireagens* (Tibell 1993) were found parasitizing other calicioids. Anamorphs are extremely difficult to sample in the field due to their size (often  $< 0.1$  mm). The survey time was at least 0.5 hrs with no maximum limit, but it generally did not surpass 2 hrs. Surveys were stopped only after (1) examining representatives of all microhabitats within the plot and (2) 10 min had elapsed without encountering a new species as best determinable with a 20X hand lens under field conditions.

Since no identification guides exist for calicioids in Oregon, species identification involved numerous taxonomic works for outside regions (Tibell 1975, 1977, 1980; Noble

1982; Tibell 1982, 1984; Middelborg and Mattsson 1987; Tibell 1987, 1991; Titov and Tibell 1993; Tibell and Ryman 1995; Tibell 1996a, 1996b). Several undescribed taxa are included in the discussion.

In addition to assessing the calicioid community in each plot, we recorded the dominant slope and aspect. A heat index equation (Beers et al. 1966) was modified to simultaneously represent both slope and aspect:

$$heatindex = \left( \left( \frac{1 - \cos(A - 45)}{2} \right) - 0.5 \right) \left( \frac{1 - \cos(4S)}{2} \right) + 0.5$$

where  $A$  = aspect in degrees east of true north and  $S$  = slope in degrees. Values range from zero (north-east facing, 45° slope) to one (south-west facing, 45° slope). The equation is invalid with slopes greater than 45 degrees, however our maximum slope was 42 degrees. At the plot center and at four equidistant points around the circumference we measured basal area for each tree species and canopy density. Standard deviations across these five measurement points were used to represent variation in basal area (SDBA) and canopy density (gappiness; SDCanopy). Due to the infrequency of plots with low average canopy density, the variable was cube-transformed for analyses ( $X_{canopy}^3$ ). In young stands we recorded the presence of old-growth remnant trees, wolf trees, and old snags. Wolf trees are defined by having exceptionally large trunks for an apparently young tree and remains of large branches low on the trunk. These characters evidence a period of open growth, probably as small trees left behind from the previous stand. Small trees in the previous stand (advance regeneration) could be deceptively old (Oliver and Larsen 1996) so the true age of these trees can be difficult to estimate visually. Old snags are defined by a weathered appearance suggesting that they have remained as snags for more than 10 yrs. These snags typically had a diameter of more than 1 m.

Plots in young and old-growth stands were placed arbitrarily but without intentional bias except for two criteria: (1) we attempted to locate the plot within the area of the stand that had been sampled by Bailey and Tappeiner (1998) to maximize the potential for comparing results to other work in the same stands, and (2) we attempted to match topography of plots within a block to maximize focus on differences in stand structure. No attempt was made to match topography between hotspots and other stands within a block. Plots were placed in hotspot stands to focus on areas of presumed high

macrolichen richness or unusual composition, with no consideration of calicioids. Since the original grouping of stand types did not represent old-growth structures as they might relate to calicioids (e.g. old snags, wolf trees, and remnant old trees), the stands are also examined with four groups defined more clearly by old-growth structures. The structural groups were: young stands lacking older or larger structures (young), young stands possessing wolf trees or large decorticate snags (legacy), young stands possessing remnant trees (remnant), and old-growth forested stands (old growth). The legacy and remnant stands may be considered as having retained some continuity with the stands that preceded them.

### **Statistical Analysis**

We tested differences in species richness between stand types with blocked ANOVA (SPSS Inc. 1998). For multivariate analyses we used PC-ORD (version 4.08, McCune and Mefford 1999). We used MRPP (multi-response permutation procedure; Biondini et al. 1985) to test for differences in community composition between stand types. Association of taxa with plot types was tested with a method for indicator species analysis (IndVal; Dufrêne and Legendre 1997) combined with a randomization procedure with 10000 iterations. We analyzed interrelationships between taxa and relationships of taxa to stand structure, composition, and environmental features with NMS (Non-metric multidimensional scaling; Kruskal 1964; Mather 1976). NMS ordinations were obtained by running the analysis in slow and thorough autopilot mode, and limiting results to ordinations with two or three axes. For visual clarity, ordinations of subsets of the data were rotated to match the whole-data set ordination.

To reduce noise from rare species, those occurring in less than five percent of the plots (less than three plots for the whole data set, less than two plots for subsets) were deleted from the data sets prior to multivariate analyses. The quantitative version of Sørensen (city-block) distance was used for both MRPP and NMS. Since the species data were presence/absence, Beals Smoothing (Beals 1984; McCune 1994) was considered but did not noticeably improve the ordinations. All multivariate techniques

used are non-parametric and well suited to data that are non-normal, are on discontinuous scales, and contain a large proportion of zero values.

## **RESULTS**

### **Diversity of Calicioid Species**

Forty-two species of calicioid fungi were found including 20 lichenized species (Table 4.1). Species richness differed among the four original plot types with old-growth plots having the highest average richness (blocked ANOVA,  $p = 0.017$ ; Figure 4.2A; note that species richness was not normally distributed within these plot types, so the  $p$ -value should be interpreted with caution). Revising the stand type groups to structural categories clarified that old-growth forest plots did harbor greater calicioid diversity than young plots lacking older structures, and that plots with legacy structures and remnant old trees may also harbor increased calicioid diversity (Figure 4.2B). The remnant category had a very large confidence interval due to inclusion of only three plots, each differing greatly in diversity from the others. Despite that variability, there was a strong difference in species richness between plots with and without old growth trees, confirming our first hypothesis. Further, the three legacy plots with highest species richness were also the three with neighboring remnant old trees.

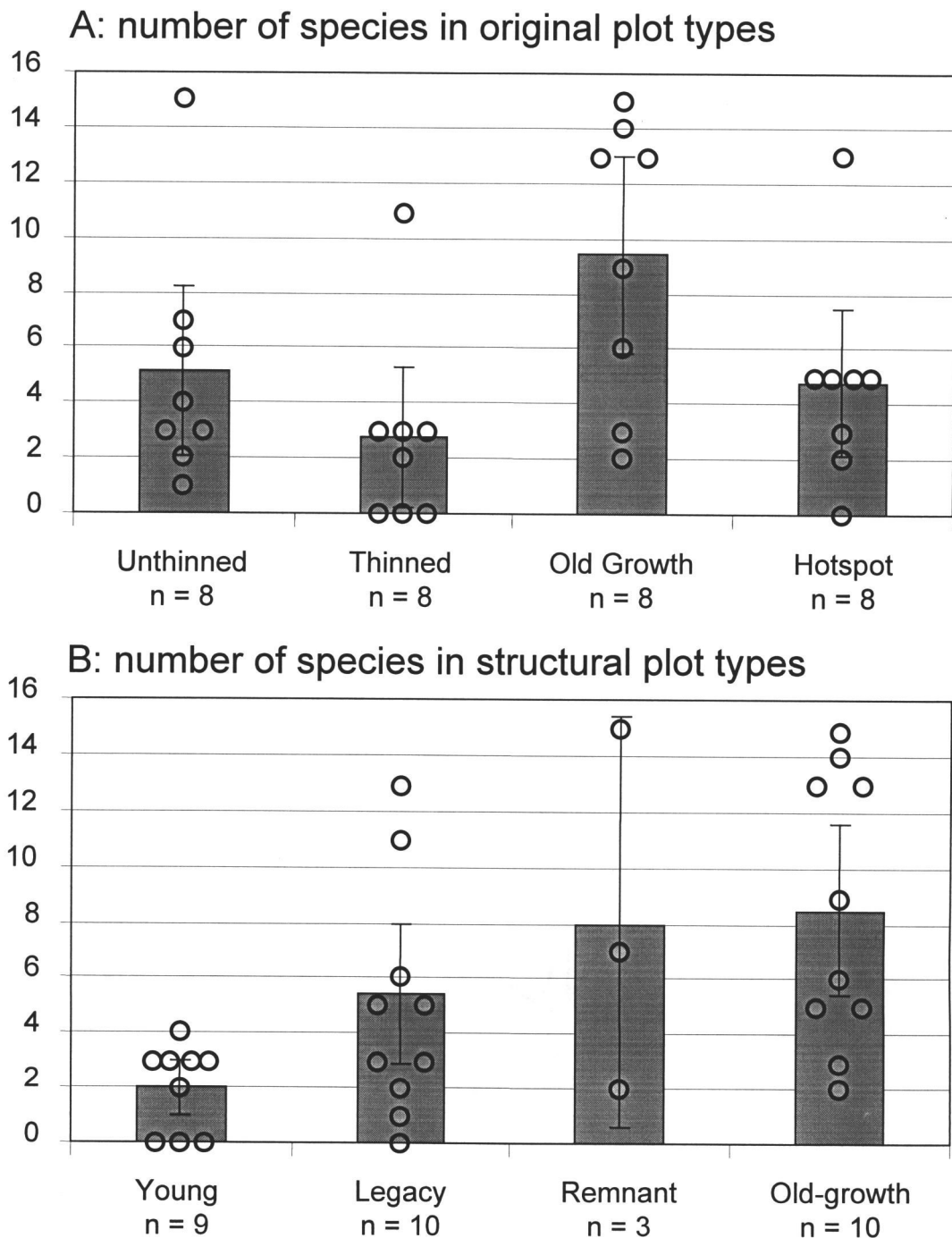
Only a few species were clearly associated with plots that contained old-growth trees according to IndVal (Table 4.1). However, the analysis had low statistical power because of the small number of plots in each stand type and the infrequency of most species. Many species occurred only in plots with old trees, but were simply too infrequent to be detected as indicators of old-growth.

**Table 4.1** Species list. Table includes acronyms used elsewhere, frequency of occurrence in three kinds of plots (**young** = young forest lacking old remnant trees, wolf trees, and large snags; **legacy** = young forest lacking old remnant trees but having wolf trees or large snags; and **old-trees** = old-growth forest plus young forest with old remnant trees), and a note indicating if the species is lichenized (**L**). The remnant and old-growth forest categories were combined because most calicioids found in both categories were on bark of old-growth trees and because there were few remnant stands. Statistical significance (IndVal) of association with structural categories is noted with \* for  $0.05 < p\text{-value} < 0.10$ , and \*\* for  $p\text{-value} < 0.05$ .

Species	Acronym	# in	# in	# in	L
		young	legacy	old-trees	
		n = 9	n = 10	n = 13	
<i>Calicium adaequatum</i> Nyl.		1	1	0	Y
<i>C. adpersum</i> Pers.		0	0	1	Y
<i>C. glaucellum</i> Ach.	Ca_gla	2	5	4	Y
<i>C. lenticulare</i> Ach.	Ca_len	0	0	3	Y
<i>C. parvum</i> Tibell	Ca_par	0	0	4*	Y
<i>C. salicinum</i> Pers.		0	0	1	Y
<i>C. viride</i> Pers	Ca_vir	0	3	4	Y
<i>Chaenotheca brachypoda</i> (Ach.) Tibell		0	1	0	Y
<i>C. brunneola</i> (Ach.) Müll. Arg.	Ch_bru	3	7	9	Y
<i>C. chrysocephala</i> (Turner ex Ach.) Th. Fr.	Ch_chr	5	6	10	Y
<i>C. cinerea</i> (Pers.) Tibell		0	0	1	Y
<i>C. ferruginea</i> (Turner & Borrer) Mig.	Ch_fer	0	1	5*	Y
<i>C. furfuracea</i> (L.) Tibell	Ch_fur	1	3	3	Y
<i>C. gracillima</i> (Vainio) Tibell		0	1	0	Y
<i>C. hygrophila</i> Tibell	Ch_hyg	1	0	2	Y
<i>C. laevigata</i> Nádv.		0	0	2	Y
<i>C. phaeocephala</i> (Turner) Th. Fr.	Ch_pha	0	1	2	Y
<i>C. stemonea</i> (Ach.) Müll. Arg.		0	0	1	Y
<i>C. consociata</i> (Nádv.) A. F. W. Schmidt	Chp_co	1	1	1	N
<i>C. trichialis</i> (Ach.) Th. Fr.	Ch_tri	0	1	8**	Y
<i>C. debilis</i> (Turner & Borrer ex Sm.) Tibell		0	0	2	N

**Table 4.1, Continued**

<i>C. nana</i> Tibell	Chp_na	0	2	7**	N
<i>C. pusilla</i> (Ach.) A. F. W. Schmidt	Chp_pu	0	2	4	N
<i>C. rubina</i> Tibell		0	0	2	N
<i>C. nigra</i> Tibell (cf.)		0	0	1	N
<i>C. savonica</i> (Räsänen) Tibell		1	1	0	N
<i>C. tasmanica</i> Tibell		0	0	2	N
<i>C. ussuriensis</i> Titov.		0	0	2	N
<i>C. species 1</i>	Chp_1	0	0	3*	N
<i>C. species 2</i>		0	0	1	N
<i>C. species 3</i>	Chp_3	0	1	3	N
<i>C. viridireagens</i> (Nádv.) A. F. W. Schmidt		0	1	0	N
<i>Cyphelium inquinans</i> (Sm.) Trevisan	Cy_inq	1	3	7*	Y
<i>Microcalicium ahlneri</i> Tibell	Mi_ahl	0	0	4**	N
<i>M. arenarium</i> (Hampe ex A. Massal.) Tibell		0	0	1	N
<i>M. disseminatum</i> (Ach.) Vainio	Mi_dis	0	1	2	N
<i>Mycocalicium subtile</i> (Pers.) Szat.		0	0	2	N
<i>Phaeocalicium species 1</i>		0	1	0	N
<i>Species 1</i>	Genus1	0	0	3*	N
<i>Stenocybe clavata</i> Tibell	St_cla	2	3	3	N
<i>S. fragmenta</i> E. B. Peterson & Rikkinen		0	1	0	N
<i>S. major</i> (Nyl.) Körber		0	1	0	N



**Figure 4.2** Species richness in (A) the four original plot types and (B) the four structural categories (young = young plots without old remnant trees, wolf trees, or large snags; legacy = young plots with wolf trees or large snags, but no remnant old trees; remnant = young stands with remnant old trees; and old-growth = old-growth forest). Richness of individual plots is represented by circles. Error bars enclose 95% confidence intervals.

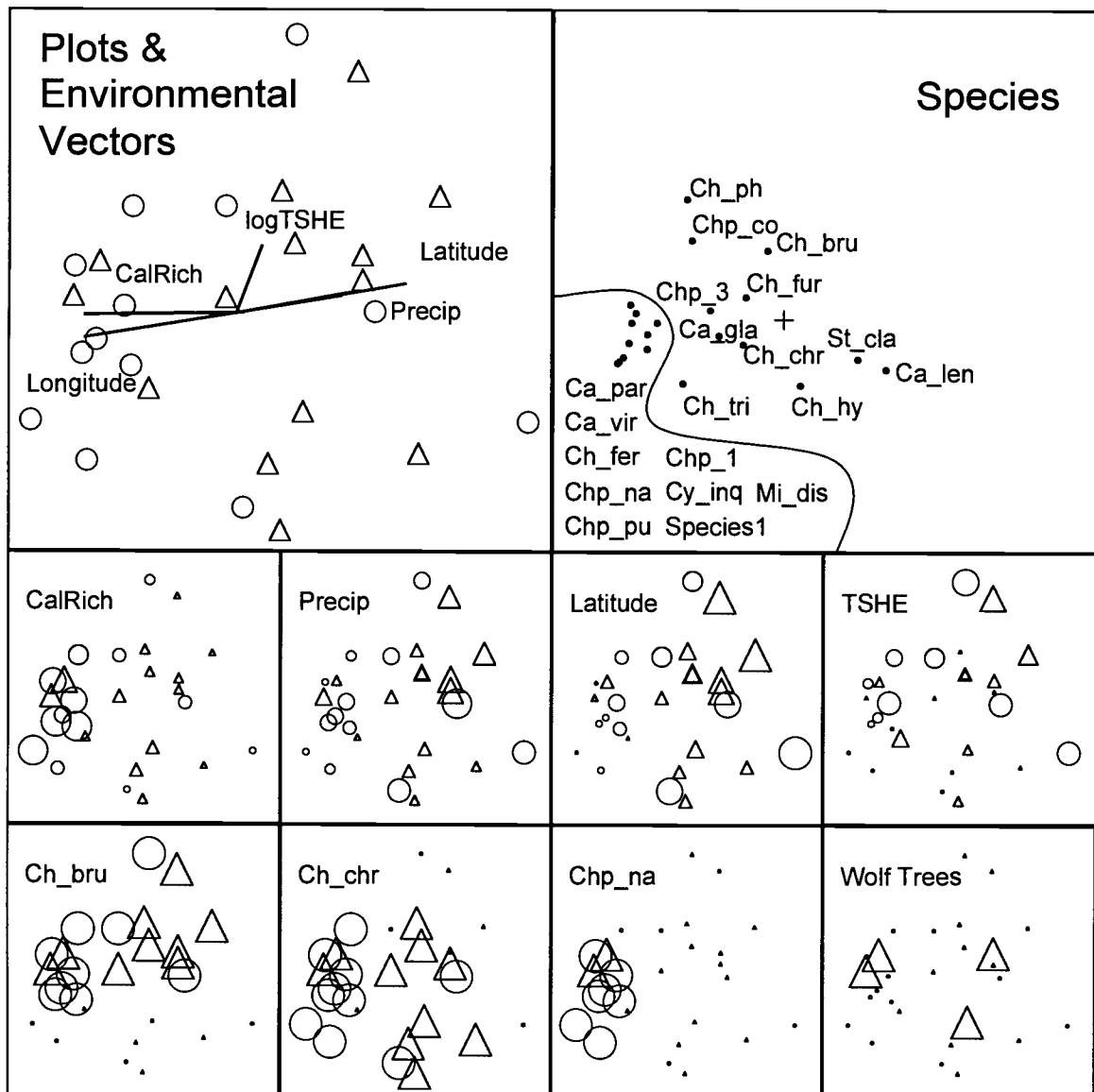
## Community Gradients

Calicioid communities did not differ statistically between the original stand types (MRPP;  $p = 0.271$ ,  $A = 0.013$ ). Differences between the four structural categories (MRPP;  $p = 0.083$ ,  $A = 0.037$ ) were less clear, than the difference between plots with old-growth trees and plots without (MRPP;  $p = 0.008$ ,  $A = 0.0426$ ).

NMS ordination of the plots in species space yielded a three axis solution (Figure 4.3). Plots with and without old-growth trees were rather intermixed, though there was some tendency for those with old-growth trees to ordinate low on the X axis. This axis was correlated positively with latitude and precipitation, and negatively with calicioid species richness. Latitude and precipitation were confounded due to increasing precipitation northward in the Cascade Mountains. High richness of calicioids was correlated with the more southern, lower precipitation plots.

A gradient in forest composition from pure *Pseudotsuga menziesii* to increasing relative abundance of *Tsuga heterophylla* correlated positively with the Y axis, while canopy gappiness correlated positively with the Z axis. The *Tsuga* gradient may influence lower trunk habitats in multiple ways. *Tsuga heterophylla* is very shade tolerant, often filling the lower canopy of a forest, reducing light penetration and increasing humidity. Previous researchers have related both light (Rikkinen 1995) and humidity (Holien 1996; Kruys and Jonsson 1997) to diverse calicioid communities. Also, *Tsuga* can succeed *Pseudotsuga* in this region, so a large component of *T. heterophylla* may indicate exceptionally old *P. menziesii*. In two of the old-growth forests that were high in *T. heterophylla* the bark of many old *P. menziesii* trees had begun to rot and shed. This bark harbored very few epiphytes.

While most species were concentrated in the higher diversity plots, *Chaenotheca brunneola* and *C. chrysocephala* spread widely across the ordination. These two species were partly segregated on the Y axis, with *C. brunneola* being more frequent among sites with more *Tsuga*. Occurrences of *Chaenothecopsis nana* were concentrated among southern sites with old trees. *C. nana* did occur in two young plots lacking old remnant trees (Table 1), but both plots included wolf trees and were adjacent to old-growth forests.



**Figure 4.3** Ordination of plots in species space (species with less than three occurrences removed). The ordination has three dimensions accounting for 29.6, 21.9, and 25.3 percent of the variation in the data ( $\Sigma = 76.9\%$ ); only the first two axes are shown. **Plots and Environmental Vectors:** ordination with overlay showing presence (circles) or absence (triangles) of old-growth trees; correlation vectors for dominant environmental variables radiate from the ordination centroid. **Species:** plot of species scores on the ordination; species abbreviations are placed close to their plotted point except for the large group of species on the left. **Small plots:** overlays of variables and species on the ordination. Symbols code for presence (circles) or absence (triangles) of old-growth trees. Size of symbols corresponds to the variable or species value. Calicioid richness (CalRich) is the number of species in each plot. Estimated annual precipitation (Precip) is from Daly et al. (1994). Log abundance of *Tsuga heterophylla* (logTSHE) is from our basal area measures. Species and abbreviations are explained in Table 1.

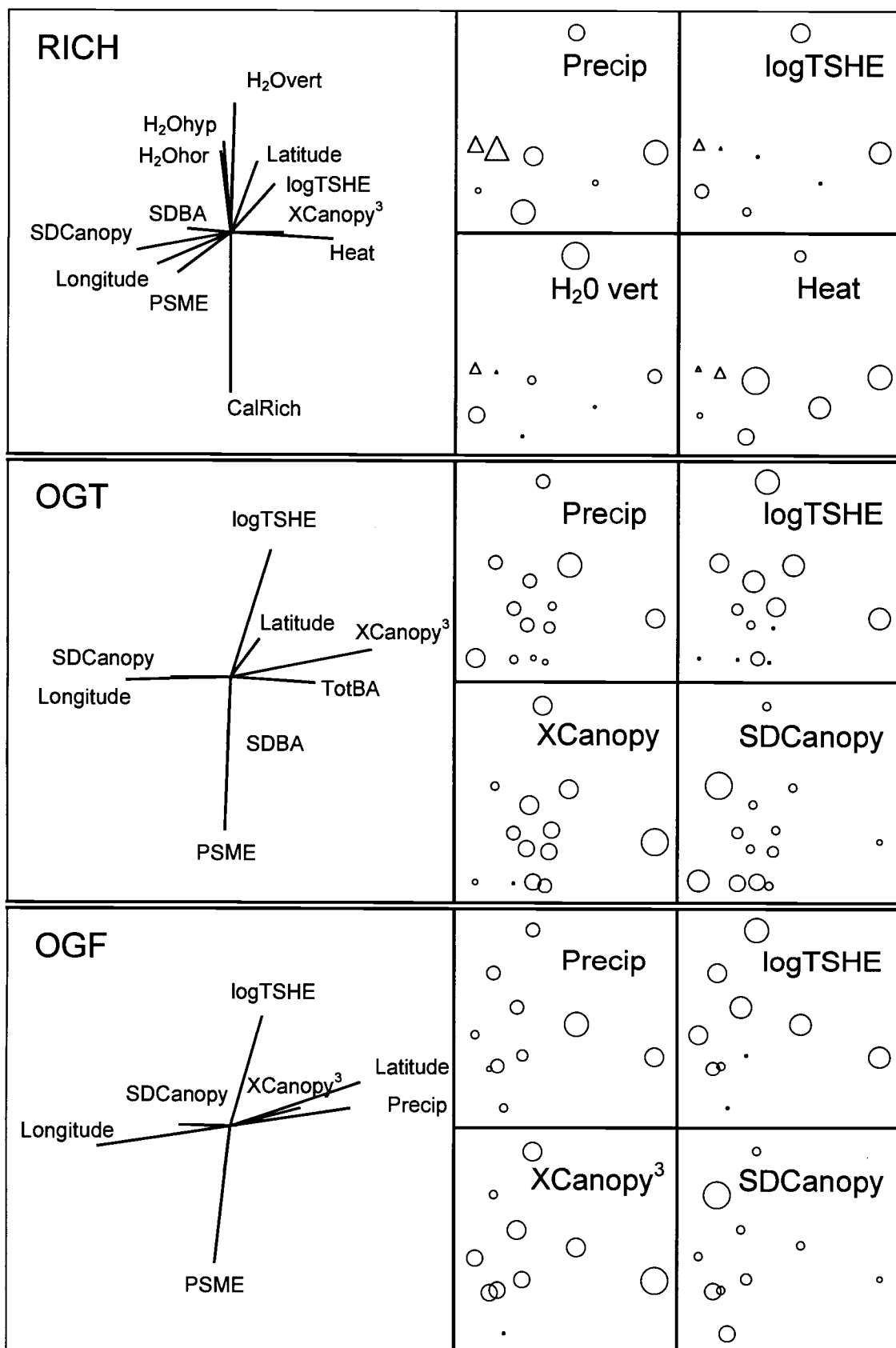
Structural variables correlated only weakly with calicioid communities. The large variation in species richness forms a gradient in the ordination that may obscure other gradients in the calicioid communities. To more closely examine the relations of environment to species composition, ordinations were made for data with limited variation in species richness. Three subsets of the data were ordinated: plots with nine or more calicioid species (RICH), plots containing old-growth forest or young forest with remnant old-growth trees (OGT), and plots containing undisturbed old-growth forest (OGF). With few plots remaining ( $n = 8, 13, \text{ or } 10$ , respectively), the correlations were often sensitive to the influence of a single plot. Thus, each ordination revealed slightly different sets of environmental variables correlated with two axes (Figure 4.4). RICH included two plots without old trees; both were legacy plots.

RICH had an X axis correlated with a suite of structural variables: heat index, the *Tsuga* gradient, canopy density, gappiness, and heterogeneity in tree basal area. Heat index and canopy density measures all related to understory exposure, increasing light and decreasing humidity. As already discussed, the *Tsuga* gradient may also relate to understory exposure. The Y axis resembled the X axis of the whole data set ordination in the correlations with calicioid richness and latitude. However, a correlation with precipitation was lacking, while there were added correlations with measures of distance from perennial water (streams or ponds). Overlaying the ordination with the most strongly correlated measure of distance from water revealed that the correlation was an artifact of a single plot high on the Y axis.

OGT also had correlations that focused on how the canopy affects the understory. The X axis correlated with average canopy density, gappiness, and the total basal area of the stand (stand density). The *Tsuga* gradient was correlated with the Y axis of the ordination. Although precipitation did not correlate with the ordination, the overlay suggests that a single plot low on both X and Y axes prevented correlation.

OGF eliminated the plot that inhibited a correlation with precipitation in the OGT ordination. The X axis was dominated by correlations with precipitation and latitude, much like the ordination of the whole data set. However, some correlation with average canopy density and gappiness remained.

**Figure 4.4** Ordination of plots in species space from subsets of the data (species with less than two occurrences removed). For each ordination, correlation vectors and four variable overlays are shown. **RICH**: ordination of the data set restricted to plots with nine or more calicioid species. **OGT**: ordination of the data set restricted to plots with old-growth trees. **OGF**: ordination of the data set restricted to plots in old-growth forests. Symbols code for presence (circles) or absence (triangles) of old-growth trees in the plot. Symbol size corresponds to the value of the variable. Distance to the nearest perennial water body horizontally, vertically, and diagonally ( $H_2O_{hor}$ ,  $H_2O_{vert}$ , and  $H_2O_{diag}$ ) were measured from plot locations on U.S.G.S. 7.5 minute quadrangle maps. Abundance of *Pseudotsuga menziesii* (PSME) is from our basal area measures. Other variables are explained in the methods and Figure 4.3.



**Figure 4.4**

Many of the species sampled had clear distributions over important environmental variables (Figure 4.5). Most had the highest frequency of occurrence among sites with relatively low precipitation, little *Tsuga heterophylla*, and a relatively high heat index. This pattern refutes part *a* of the second hypothesis, that calicioids would associate with high humidity stands. There was a less distinct tendency for species to occur in sites with intermediate canopy density, which is partly compatible with part *b* of the second hypothesis, that calicioids would associate with increasing gappiness in forest structure. Most of the sites which possessed characters optimal for calicioid diversity were in the southern half of the sampling region. It is difficult to determine the exact meaning of the *Tsuga* gradient for calicioid communities. Increasing *Tsuga* should correspond to decreased understory exposure, but it correlated with the OGT and OGF ordinations independently of other measures that relate to understory exposure.

## **DISCUSSION**

### **Diversity of Calicioid Species**

Calicioids are most diverse in stands with old forest structures both in Oregon and elsewhere (Tibell 1992; Selva 1994; Holien 1996; Kuusinen and Siitonen 1998). Congruent with Holien (1996), most of our calicioids inhabited deeply textured bark and were restricted to the side of tree trunks not wetted by rain. The intermediate diversity that we found in the legacy plots, and high diversity in old growth, support the idea that calicioid diversity increases with stand continuity. However, the use of calicioids as indicators of stand continuity (Tibell 1992; Selva 1994) would not be appropriate in our region since so many species are scarce in high precipitation forests with high concentrations of *Tsuga*. Measuring stand continuity with calicioid richness could imply that many 600 yr old, undisturbed forests, which generally have a high proportion of *Tsuga*, have less continuity than many 250 yr old, moderately disturbed forests.

Despite the general similarity in calicioid diversity patterns between our study in western Oregon and studies in Fennoscandia, some specific patterns differed. For

**Figure 4.5** Scatterplots for species with three or more occurrences, across the dominant environmental variables. **(Upper-block)** Axes represent the contribution of *Tsuga heterophylla* to basal area (log transformed) and the estimated annual rainfall. **(Lower-block)** Axes represent average canopy density (transformed by  $x^3$ ) and heat index. Symbols code for presence (circles) or absence (triangles) of old-growth trees in the plot. Symbol size corresponds to the value of the variable or presence of the species.

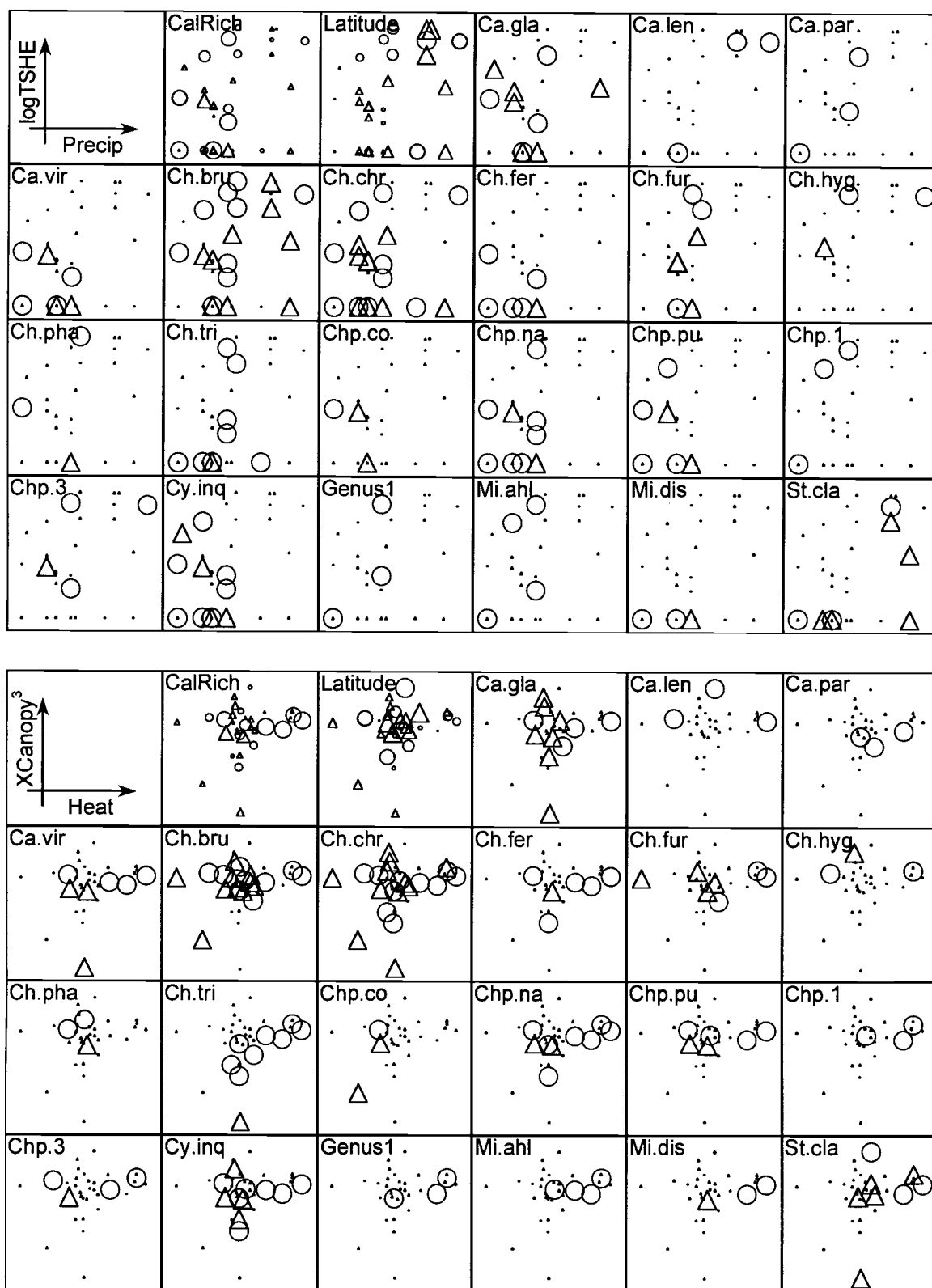


Figure 4.5

example, three of the indicators of long forest continuity in Sweden (Tibell 1992) were encountered in this investigation: *Calicium adaequatum*, *Chaenotheca laevigata*, and *Chaenothecopsis nana*. We found a clear association between *Chaenothecopsis nana* and old-growth forest. *Chaenotheca laevigata* was too infrequent to establish a solid relationship with old-growth. We found *Calicium adaequatum* only twice, but both times in young stands. In Oregon *C. adaequatum* occurs mainly on twigs in lowland hardwood stands (unpublished data) and is more abundant than in Sweden. *Phaeocalicium populneum* (Brond. ex Duby) A. F. W. Schmidt was also identified as a rare indicator of forest continuity in Sweden. Although we did not encounter *P. populneum* in this investigation, it frequents both old and young *Populus trichocarpa* in western Oregon valleys (Peterson and Rikkinen 1999). These disparate associations probably reflect differences in climate, forests, and landscape history between Sweden and Oregon.

Most wood-inhabiting species were on sheltered sides, or in hollows, of snags. Logs are poor calicioid substrate in much of western Oregon because they are rapidly overgrown by bryophytes and even sheltered microhabitats may be too humid for colonization. Similarly, logs are poor substrates for calicioids in humid habitats in Norway (Holien 1996).

Several species occurred on wolf trees. Although wolf trees that are formed by advance regeneration from the previous stand could be deceptively old (Oliver and Larsen 1996), the bark of their trunks should not be much older than that of surrounding young trees. The occurrence of some calicioids on wolf trees may indicate that the size of the trunk may be more important than bark characteristics for colonization by these species, perhaps by protecting some bark from rain interception. Future studies to elucidate the microhabitat requirements of calicioids should examine these trees.

## Environmental Gradients

Given that calicioid diversity can be so high in humid, boreal forests (Holien 1996; Kruys and Jonsson 1997), the correspondence between species richness and low precipitation, southern sites is surprising. However, we need to be cautious in comparing

*Pseudotsuga* and *Tsuga* forests of the Pacific Northwest with *Picea* and *Pinus* forests of Fennoscandia. The canopy depth and average precipitation of a typical coniferous forest in our region may exceed the maximum found in northern Europe. Average canopy density may also be significantly greater. It may be that the most shaded, humid forests studied in Fennoscandia would resemble our more open, low precipitation sites in western Oregon. The sites that Tibell (1992) used in Sweden all have less precipitation (maximum = 0.96 m) than those used in our study (minimum = 1.20 m). Similarly, the area Holien (1996) studied in Norway averages 0.90 m of precipitation. Data for canopy depth and gappiness are not available from these studies.

Most previous ecological studies of calicioid communities (Hyvärinen et al. 1992; Selva 1994; Holien 1996; Kruys and Jonsson 1997; Kuusinen and Siitonen 1998) covered relatively small regions compared with this study or have not examined the influence of many landscape-scale environmental gradients. Holien (1996) considered environmental gradients in Norway over an area 12 X 12 km. In that study, ordination suggested that species richness might be related to decreasing slope and more southwestern aspects (our 'Heat' variable combined these), but the correlations were weak compared to other variables. Holien found that one species, *Chaenotheca subroscida* (Eitner) Zahlbr., was associated with high elevations; our elevation gradient was too limited for detecting associations. The one wide-ranging study that did examine environmental gradients (Tibell 1992) concluded that human impacts obscured any correlations with the macroenvironment due to greater impacts in southern Sweden. Tibell also provides a good discussion of the relative importance of macro- and microclimate for calicioids and other crustose lichens.

Relationships of calicioids to several environmental gradients (Figure 4.5) suggest that these gradients could be used to predict calicioid species occurrences. For example, a late-successional or old-growth site with about 2.5 m of annual precipitation would probably not harbor *Cyphelium inquinans*, but would have a good chance of harboring *Stenocybe clavata*. Predicting the occurrence of calicioids is the subject of another paper (Peterson et al. 2000c).

## Notes on Selected Species

The goals of this study included improving our understanding the composition of the calicioid flora in the Pacific Northwest and the habitats of the species. We found several species that are not yet described. These would appear to be endemic to our region, however they may eventually be found in other parts of the world, particularly understudied regions such as eastern Asia. Many species in our flora showed clear habitat associations. Some of these associations differed slightly from other parts of the world.

**Hardwood-twig species.** Since the sites focused on conifer forests, we did not encounter many hardwood twig species. *Calicium adaequatum* was found at two sites on *Alnus rubra*, and *Stenocybe fragmenta* was found at one site on *Rhamnus purshiana*. All trees harboring them were less than 200 yrs of age. Within the Pacific Northwest it is unlikely that either species is associated with old forest structure, although an important habitat for *C. adaequatum* in our region is the twigs of late-successional *Quercus garryana* (unpublished data).

**Resinicolous species.** The only species found on resin in this study was *Chaenothecopsis nana*, which occasionally occurred on small patches of dried *Pseudotsuga menziesii* resin. In these instances it also occurred on adjacent bark and the apothecia produced on the resin usually appeared less vigorous, so it should not be considered a true resinicolous species. True resinicolous species do exist in the Pacific Northwest (Rikkinen 1999), but none were collected as of the time of our sampling. Resinicolous species may have been present in some sites, but overlooked due to lack of knowledge of their habitats.

***Calicium adpersum*.** This species was found only once, on the bark of an old *Pseudotsuga menziesii*. The species appears to be rare in Oregon.

***Calicium glaucellum*.** *C. glaucellum* occurred on a wide range of substrates. It occurred mostly on the bark of old trees and on wood of old snags, but occasionally grew on the bark of trees less than 200 yrs old.

***Calicium lenticulare*.** This species was encountered only on wood of old snags.

***Calicium parvum*.** There are few collections of this species in Oregon but this may be due to misidentification as *C. glaucellum*. Similar to *C. glaucellum*, we found it both on wood and bark.

***Calicium viride*.** This species is well known from areas east of the Cascade crest. In our sampling on the west side, *C. viride* had a very strong association with low precipitation areas with little *Tsuga heterophylla*, and did not occur in stands with high canopy density or low heat index. This species was sometimes difficult to recognize because the thallus is pale, containing less pigment, when shaded.

***Chaenotheca brunneola* and *C. chrysocephala*.** *C. brunneola* and *C. chrysocephala* are the two species in this study that occurred over a wide range of habitats and were collected frequently from trees less than 200 yrs old. Whether or not they are limited to trees of at least late-successional status (ca. 80-200 yrs old; USDA and USDI 1994) is not determinable without additional sampling of late-successional and younger stands. More research should be conducted to identify what tree age is required for colonization by these species. *C. brunneola* responded differently from *C. chrysocephala* to the *Tsuga* gradient. *C. brunneola* was most frequent among stands with a high *Tsuga* content, while *C. chrysocephala* was most frequent in stands with a low *Tsuga* content.

***Chaenotheca furfuracea*.** This species has unusual habitat requirements. We found it on a variety of substrates (wood, bark, roots, rock, and soil) under overhangs formed by the roots of tipped-over trees or by the butt of large tree trunks on a steep slope.

***Chaenotheca hygrophila*.** *C. hygrophila* is currently considered a valid species (Tibell 1999) and is morphologically distinguished from *C. brunneola* by morphology of the thallus and excipulum. We found it in varied sites that match the distribution of *C. brunneola*.

***Chaenotheca trichialis*.** Like *Calicium viride*, this species associated with dry, open sites. It was sometimes difficult to identify in shaded situations due to poor thallus development.

***Chaenothecopsis consociata*.** *C. consociata* is thought to be a parasite specific to *Chaenotheca chrysocephala*; all specimens that we found appeared to have that

relationship. *C. consociata* differed from most species found in this study in that it occurred in sites with a low heat index (Figure 4.5). Our impression is that it is a northern species occurring in Oregon primarily in cool habitats.

***Chaenothecopsis nana*.** This abundant species occurred almost exclusively on the bark of old-growth *Pseudotsuga menziesii*. We collected this species twice from apparently young trees but both were wolf trees near old-growth forest.

***Chaenothecopsis cf. nigra*.** *C. nigra* has not been reported in North America. The small specimens found in this study are not adequate for confidently adding it to the North American checklist (Esslinger and Egan 1995).

***Chaenothecopsis* sp. 1.** This species had ca. 0.5 mm tall apothecia and frequently formed tall, narrow capitula with a slight bluish pruina reminiscent of *C. fennica* (Laurila) Tibell. Spores were 6-9  $\mu\text{m}$  long with a distinct septum. It grew saprophytically, usually hidden in cracks within the bark of old-growth *Pseudotsuga menziesii* in relatively dry forests with a high heat index.

***Chaenothecopsis* sp. 2.** This species anatomically resembled *C. pusilla*, but differed by having spores ca. 8-12  $\mu\text{m}$  in length. Macroscopically, it appeared very similar to *C. nana* in stature and habitat.

***Chaenothecopsis* sp. 3.** This one closely resembled *C. pusilla*, but was distinguishable by its diminutive size ( $< 0.5$  mm) and unusual habitat. It grew saprophytically, deep in tiny fissures in the bark of old-growth trees.

***Cyphelium inquinans*.** We were surprised that *C. inquinans* did not occur in any sites with high precipitation, as it is often thought to have a broad ecological amplitude. Like *Chaenotheca brunneola* and *Ch. chrysocephala*, it occurred on relatively young trees, though not as frequently as the prior species.

***Phaeocalicium* sp. 1.** This distinctive calicioid was collected at one site, on *Alnus rubra*, and had mature non-septate spores, 8-10  $\mu\text{m}$  in length. It is probably rare, as it has not been collected outside this study. It will be described when additional specimens become available.

**Species 1.** This is a very unusual calicioid fungus that will be described as a new genus. The stalk and excipulum were covered with dense, hyaline, hair-like hyphae resembling those of *Chaenothecopsis pilosa* Tibell and K. Kalb (see Tibell and Ryman

1995). The excipulum contained a reddish pigment that reacted green in KOH like several *Chaenothecopsis* and other members of the Mycocaliciaceae. It differed from known members of the Mycocaliciaceae by having spore walls that are deeply fluted, resembling some Myxotrichiaceae (Onygenales *sensu lato*) and the ascal tip is not distinctly thickened. Efforts are underway to analyze the DNA and determine its proper placement in the Ascomycota. Inclusion of this fungus with calicioids is tentative, but reasonable based on morphology and ecology. We found it only on the bark of old-growth or wolf-like *Pseudotsuga menziesii*, usually in tiny fissures going deep into the bark, and often close to *Chaenothecopsis* sp. 3.

***Stenocybe clavata*.** This species, endemic to the Pacific Northwest, has an unusual ecology. It appears to be bimodal, occurring at the ends of the precipitation gradient. In the high precipitation sites it may occur more frequently on younger trees and is much more tolerant of the presence of *Tsuga heterophylla*. The species also occurs frequently on *Picea sitchensis* close to the Coast (unpublished data).

## Management Implications

Calicioid diversity is strongly associated with old-growth trees and legacy structures. The high diversity of calicioids in the Pacific Northwest may be due to the relatively large areas of old forest remaining in the region. Perpetuation of most species will require old-growth reserves.

Retention of some old-growth trees during harvest of old forests might help sustain diverse calicioid communities. However, there was considerable variation in calicioid richness among our three young stands with remnant old trees, so the value of retention may be inconsistent. For some calicioids, retention of large, old, decorticate snags and advance regeneration for future wolf trees may increase colonization prior to the reacquisition of old-growth trees. It is important to recognize that large, old, decorticate snags are not a renewable resource in forests where trees are not allowed to live for several hundred years and die naturally. In much of Oregon's managed forests,

large snags will eventually decompose, but will not be replaced as long as these stands remain in rotation.

If calicioid species receive protection buffers under the Northwest Forest Plan (USDA and USDI 1994) or other regulations, the buffers must be large. Calicioids may be sensitive to microhabitat light conditions (Rikkinen 1995) and we found correlations between calicioid communities and stand characters that could influence understory light conditions. Alteration of the microhabitat light conditions could degrade habitat quality. Removal of the forest canopy near a protected species, or even thinning within the buffer, could alter these light conditions. However, understory thinning may occasionally be useful within a buffer to prevent an insurgence of *Tsuga heterophylla* or other shade tolerant trees.

#### **ACKNOWLEDGEMENTS**

We thank Leif Tibell and Jouko Rikkinen for assistance and advice concerning calicioid taxonomy, and The Portland Garden Club for funding a visit to those experts. Andrea Ruchty and Abbey Rosso provided greatly appreciated field assistance. Field work was performed with funding from the US Geological Survey Division of Biological Resources and the U.S.G.S. Forest Rangeland Ecosystem Research Center.

## Chapter 5

### Modeling Occurrence over a Landscape for Multiple, Poorly Understood Species

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For Submission to *Ecological Applications*,  
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## **ABSTRACT**

Our challenge was to model occurrence for 58 species. The habitats of these species are not well understood, so we needed a method that allows results to be conveniently updated as additional information (sampling) becomes available and not require user-intensive rebuilding of complicated models. We also wanted to avoid parametric methods because our data do not fit parametric assumptions. The method we developed uses an empirical window technique, similar to kernel estimation. The windowing method estimates the probability of occurrence for each species at a target site using the species's frequency of occurrence among sampled sites neighboring the target site within an environmental matrix. The method automatically accounts for interactions between environmental variables and allows all species to be predicted from the same combination of variables. Our environmental matrix included seven variables that were available as GIS coverages for western Oregon. We determined the optimal combination of variables (model) by comparing species lists from sampled sites with predictions for the sites. Predictions for each sampled site were calculated with that site removed from the data set. The optimal model consisted of all seven variables. For continuous variables, the window half-width was equal to 30% of the gradient width in the variable. Across all seven variables (dimensions) the window occupied 1.62 % of the environmental space. This allowed validation of 85 of our 97 sampled sites with more than 70% of predictions performing better than our most predictive null model. Microhabitat was not well represented by our environmental matrix, but it is very important for calicioid occurrence, so we believe that the results could be improved by increasing the representation of microhabitat characteristics in the model. Further, adding more sampled sites could allow us to use a narrower window, possibly improving the results.

## **INTRODUCTION**

Modeling the occurrence of species in unsampled sites or across landscapes may be of great use in the conservation of rare, sensitive, or ecologically valuable species.

The value of models may be greater for species about which little is known.

Unfortunately, the less that is known about species, the simpler the models must be and the less confidence can be placed in the models. Still, land management decisions affecting rare, sensitive, or ecologically valuable species, should make maximal use of the available information.

One such group is the calicioids (formerly the order Caliciales). This group includes many lichenized and non-lichenized fungi that associate closely with old forest structures (usually > 200 yrs old), which qualifies them for survey and management protocols on federal lands in the Pacific Northwest (PNW; USDA and USDI 1994). Surveying and identifying the numerous species in the PNW is difficult. Species are found in the field by their fruiting bodies: generally a small (average < 1 mm tall), pin-like perennial ascomata. Identification, particularly of non-lichenized species, frequently requires microscopic examination of spore morphology and other anatomic structures. In short, surveying all species of calicioids occurring in all forests proposed for logging is impractical.

As an alternative, we set out to find a method which would allow us to predict a species list for an unsampled forest stand (target site), based on data from previously sampled stands. Such a method would allow us to assist the survey process by providing potential species lists that could guide surveyors. The models could also allow exploration of potential consequences to species resulting from stand management actions. We expanded our goals to include mapping the estimated probability of occurrence for each species across the western Oregon landscape.

Species modeling projects often utilize parametric curve-fitting methods such as regression; these are impractical for our project for several reasons. Difficulties in sampling these tiny organisms force us to measure species occurrence as presence/absence, and many are infrequently present. While logistic regression would work well with the presence/absence data, its parametric nature is not appropriate for our data.

Also important to us was the ability to update model output as more information becomes available from additional sampled sites. Typical forms of regression require user-intensive model building that would need to be repeated to incorporate any new

data. Such models would need to be built for each species separately. Repeating the modeling process for numerous species, each time a new site or group of sites was sampled, would be very time consuming. We sought a method that would immediately adapt to new data points.

Finally, proper modeling of species response curves over environmental gradients can be complicated. If sampling occurs over broad environmental gradients, species responses to those gradients will rarely appear linear. Interactions between gradients may also exist. Such species responses are difficult to model with regression techniques. At least one of our species, *Stenocybe clavata*, may even have a bimodal distribution (Peterson and McCune 2000d, impossible to model with regression without an extensive data set and a complex equation).

We set out to develop a non-parametric method that can estimate probabilities directly from empirical data, respond to non-linear distributions of species over environmental gradients, and be easily updated as further sites are sampled.

## **METHODS**

### **Modeling Method**

Our solution was to predict species occurrence at a target site from its proportion of occurrence among previously sampled sites within an ecological neighborhood (sites similar to the target site). The ecological neighborhood is determined by constructing a window into the data that is centered on the target site. The method is similar to kernel estimation (Silverman 1986) which is often used for density estimation and curve smoothing. The primary difference between our method and kernel estimation is that our method incorporates absence information. Our method also resembles the one used by MacArthur et al. (1962) to predict bird census from three habitat characteristics.

We first assume that the probability of each species occurring at a site is a function of the environmental variables:

$$p = f(e_1, e_2, \dots e_n)$$

where  $p$  is the probability of occurrence and  $e_j$  are environmental variables. Dispersal is omitted from the equation. This omission may not bias the results much if the species disperse rapidly over distances. Spore morphology (Tibell 1994) and a study of habitat islands (Kruys and Jonsson 1997) suggest that calicioids have little difficulty with long distance dispersal. For dispersal-limited species with data sets that have thorough spatial coverage, geographic coordinates could be included among the environmental variables, making results depend on proximity to known sites.

We estimate probability from sampled sites within the windows of each variable simultaneously. A sampled site is within all windows for quantitative variables when:

$$\left(|t_1 - s_1| \leq h_1\right) \text{AND} \left(|t_2 - s_2| \leq h_2\right) \text{AND} \dots \left(|t_n - s_n| \leq h_n\right) = \text{TRUE}$$

where  $t_j$  is the value of the  $j^{\text{th}}$  quantitative habitat variable for the target stand,  $s_j$  is the value of the  $j^{\text{th}}$  habitat variable for the sampled stand, and  $h_j$  is the half-width of the window for the  $j^{\text{th}}$  habitat variable. For qualitative variables (e.g. binary variables) the site is within the windows when:

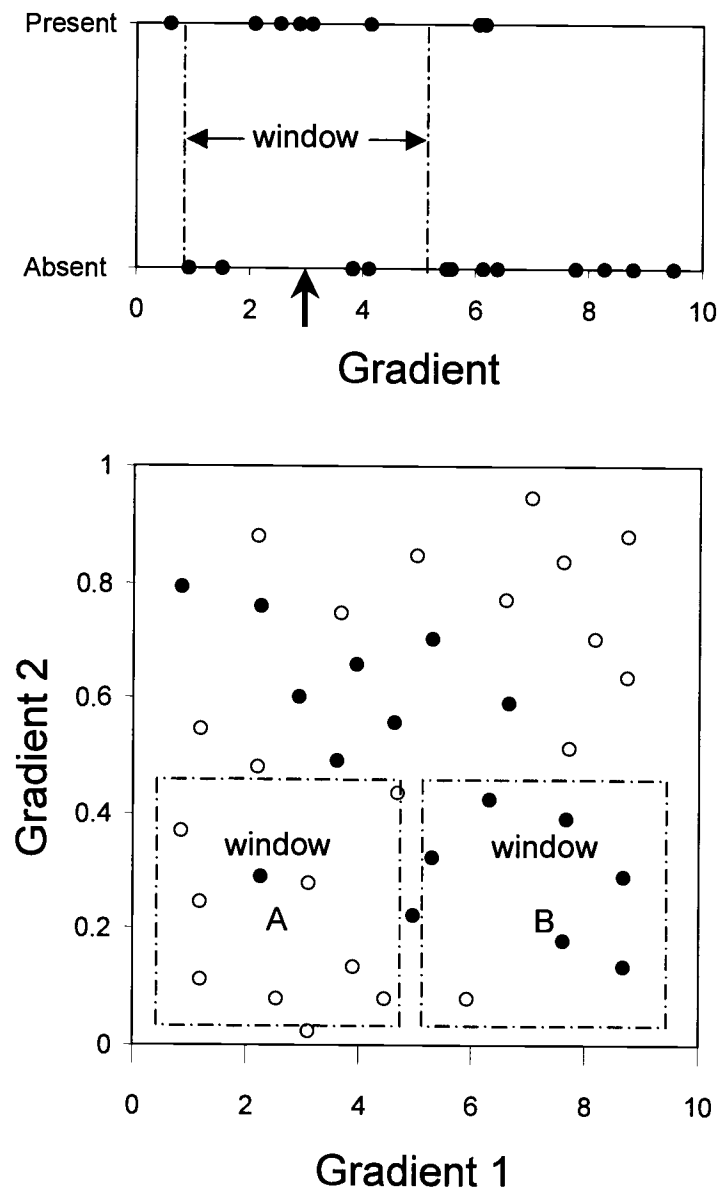
$$(t_1 = s_1) \text{AND} (t_2 = s_2) \text{AND} \dots (t_n = s_n) = \text{TRUE}$$

where  $t_j$  is the value of the  $j^{\text{th}}$  habitat variable for the target stand, and  $s_j$  is the value of the  $j^{\text{th}}$  habitat variable for the sampled stand.

The combination of these windows creates a hypercube within the multidimensional space formed by the environmental variables. This hypercube is centered on the target site. The estimated probability of occurrence for a species in the target site ( $\hat{p}$ ) is:

$$\hat{p} = \frac{\sum_{i=1}^n v_i}{n}$$

where  $n$  is the number of sites within the hypercube and  $v_i$  is the presence (1) or absence (0) value for the species at the  $i^{\text{th}}$  site within the window. Note that other values for  $v_i$  are possible, but the estimate would be in the units of those values (e.g. if cover values were used, the equation would estimate the cover value for the target site). A diagrammatic representation of the method is presented for one and two dimensions in Figure 5.1.



**Figure 5.1** Diagrammatic representation of the windowing method in one and two dimensions. The upper graph demonstrates windowing on a single gradient, or dimension (X axis), for presence (1) and absence (0) data. The estimated probability of presence at a target stand with a gradient value of 3 (arrow) and  $h = 0.25$  of the gradient length equals  $5/9$ , or  $0.56$  (note: some plotted points overlap). The lower graph demonstrates windowing over two gradients, or dimensions, for presence (solid circles) and absence (empty circles) data. The estimated probability of presence at target stand A is  $1/9$ , or  $0.11$ . The estimated probability of presence at target stand B is  $6/7$ , or  $0.86$ . The two gradients have an important interaction that would not be clear if each was examined independently.

## Sampled Sites and Species

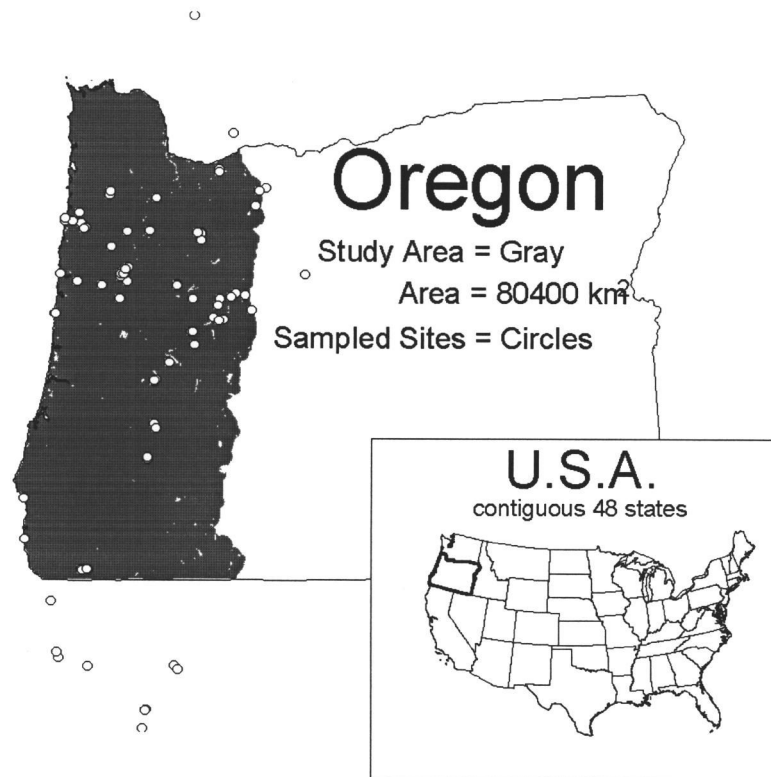
Sampled sites were obtained from data used in the Cascade Mountain Range study of Peterson and McCune (2000d; 32 sites) and from stand inventories performed by Peterson, Rikkinen, or both (65 sites). All sites were in western Oregon or neighboring regions (Figure 5.2). Neighboring regions were included to improve resolution on gradients near the extremes found in western Oregon. Sites ranged from 30 to 1620 m elevation and from 89 cm to 470 cm estimated annual precipitation (PRISM model; Daly et al. 1994). Stand compositions included conifers, hardwoods, or both. Most inventoried stands were either late-successional (with a majority of dominant trees aged 80-200 yrs old) or old-growth (with a majority of dominant trees aged 200 yrs or more). The data from Peterson and McCune included a mix of young (50-80 yrs), late-successional, and old-growth stands. Late-successional and old-growth stands occupy a much higher proportion of our data than of the current landscape in western Oregon.

The sampling for the Cascade study (Peterson and McCune 2000d) was restricted to a circular plot with an area of 0.38 ha and was positioned for macrolichen studies (Peterson and McCune 2000a; 2000b), without consideration of calicioid communities. Plots were placed in four predetermined stand types: (1) unthinned stands aged 60-110 yrs, (2) commercially thinned stands aged 60-110 yrs, (3) old-growth stands more than 200 yrs old, and (4) macrolichen diversity hotspots of various ages. The first three stand types were upland stands except for one old-growth stand, while the hotspots were often riparian.

Stand inventories were not restricted to formal plots, but generally covered an area comparable to the Cascade study samples. Inventories were confined to areas of uniform stand structure and topography. Inventories were opportunistic and often closer to highways and populated places than the Cascade sampling. The inventoried stands spanned a wider range of stand types, including purely hardwood stands, than the Cascade sampling which focused on conifer forests.

During the Cascade sampling, direct measures were taken in the field for slope, aspect, forest composition (basal area of conifer and hardwood trees), and canopy density. For the current effort, slope and aspect were transformed into a single heat index

## Study Area and Sampled Sites



**Figure 5.2** Study region (gray) and sampled sites (circles).

(see Peterson and McCune 2000d), and forest composition was transformed into presence or absence of conifers and hardwoods. Stand age was obtained from a previous study using the same sites (Bailey and Tappeiner 1998). Comparable environmental data for stand inventories was not always available. Among other site notes, the presence of conifer and hardwood trees was recorded for all inventories. Slope and aspect were often lacking, so for all stand inventories the heat index was obtained by locating the site on our GIS coverage for heat index (below). The descriptions of canopy density were later approximated with 25, 50, 75, or 100 percent canopy cover. Inventoried stand ages were classified as young (< c. 40 yrs), intermediate (c. 40-79), late-successional (c. 80-200), and old-growth (> c. 200 yrs), as best determinable by stand structures including trunk diameter, branch size, and understory development with additional consideration of effects from elevation, water availability, and soils. Trunk diameter is a poor predictor of tree age, so it is important to note that trunk diameter was not the only basis for age classification. Only forested sites were sampled. For all sites, elevation was obtained either from USGS 7.5-minute topographic quadrangle maps or from our GIS elevation coverage (below). Annual precipitation was estimated for all sites from the PRISM GIS layer (below).

Approximately 90 species of calicioids are known to occur in the region and our sampled sites harbor about 75 of them. Several of these have been omitted from this modeling effort due to taxonomic issues; a few have been combined into species groups to retain compatibility of species concepts over the time of sampling and between samplers. The *Chaenotheca brachypoda* group includes that species plus one other that is likely to be described into the genus *Sclerophora*. The *Chaenotheca brunneola* group includes *C. hygrophila* Tibell, possibly *Chaenotheca spheroccephala* Nád., and maybe another undescribed species. The *Chaenothecopsis tasmanica* group may include *C. nigra* Tibell and a third undescribed species. The final list of species and groups included 58 taxa (Table 5.1). Since no identification guides exist for calicioids in Oregon, species identification relied on numerous taxonomic works for outside regions (Tibell 1975, 1977, 1980; Noble 1982; Tibell 1982, 1984; Middelborg and Mattsson 1987; Tibell 1987, 1991; Titov and Tibell 1993; Tibell and Ryman 1995; Tibell 1996a, 1996b).

**Table 5.1** Species list and statistics. Occ = number of occurrences among the 97 sampled sites.  $\bar{I}_2$  = improvement over the NULL2 model. %<sub>2</sub> = percent of estimations with positive  $I_2$ . Odds = odds ratio for positive values of  $I_2$ . P = one-tailed p-value for the odds ratio being greater than one.

Species	Occ	$\bar{I}_2$	% <sub>2</sub>	Odds	P
<i>Calicium abietinum</i> Pers.	11	0.0004	57.6	1.361	0.1997
<i>C. adaequatum</i> Nyl.	14	0.0475	67.1	2.036	0.0179
<i>C. adspersum</i> Pers.	4	-0.0017	50.6	1.024	0.5308
<i>C. glaucellum</i> Ach.	43	0.0350	55.3	1.237	0.2963
<i>C. lenticulare</i> Ach.	18	0.0701	74.1	2.864	0.0010
<i>C. parvum</i> Tibell	6	-0.0014	68.2	2.148	0.0119
<i>C. salicinum</i> Pers.	9	0.0121	76.5	3.250	0.0003
<i>C. viride</i> Pers.	24	0.0862	67.1	2.036	0.0179
<i>Chaenotheca brachypoda</i> (Ach.) Tibell	10	0.0452	85.9	6.083	0.0000
<i>C. brunneola</i> (Ach.) Müll. Arg. GROUP	61	0.1107	63.5	1.742	0.0525
<i>C. chlorella</i> (Ach.) Müll. Arg.	6	0.0043	63.5	1.742	0.0525
<i>C. chrysocephala</i> (Turner ex Ach.) Th. Fr.	45	0.0351	56.5	1.297	0.2455
<i>C. cinerea</i> (Pers.) Tibell.	1				
<i>C. ferruginea</i> (Turner & Borrer) Mig.	23	0.0722	72.9	2.696	0.0016
<i>C. furfuracea</i> (L.) Tibell	37	0.1096	65.9	1.931	0.0263
<i>C. gracillima</i> (Vainio) Tibell	21	0.0722	72.9	2.697	0.0018
<i>C. hispidula</i> (Ach.) Zahlbr.	3	0.0070	77.6	3.474	0.0002
<i>C. laevigata</i> Nád.v.	10	0.0114	72.9	2.696	0.0018
<i>C. olivaceorufa</i> Vainio	11	0.0417	68.2	2.148	0.0119
<i>C. phaeocephala</i> (Turner) Th. Fr.	18	0.0475	61.2	1.576	0.0955
<i>C. stemonea</i> (Ach.) Müll. Arg.	16	0.0498	60.0	1.500	0.1246
<i>C. trichialis</i> (Ach.) Th. Fr.	38	0.0863	65.9	1.931	0.0263
<i>C. xyloxena</i> Nád.v.	10	0.0084	68.2	2.148	0.0119
<i>Chaenothecopsis consociata</i> (Nád.v.) A. F. W. Schmidt	10	-0.0058	52.9	1.125	0.4096

**Table 5.1, Continued**

<i>C. debilis</i> (Turner & Sm.) Tibell	15	0.0283	64.7	1.833	0.0376
<i>C. edbergii</i> Selva & Tibell	1				
<i>C. epithallina</i> Tibell	8	0.0257	56.5	1.297	0.2455
<i>C. nana</i> Tibell	25	0.1083	70.6	2.400	0.0048
<i>C. pusilla</i> (Ach.) Schmidt	37	0.1035	65.9	1.931	0.0263
<i>C. pusiola</i> (Ach.) Vainio	16	0.0110	64.7	1.833	0.0376
<i>C. rubescens</i> Vainio	1				
<i>C. rubina</i> Tibell	5	-0.0135	48.2	0.932	1.0000
<i>C. savonica</i> (Räs.) Tibell	18	-0.0015	52.9	1.125	0.4096
<i>C. sitchensis</i> Rikkinen	5	0.0146	75.3	3.046	0.0006
<i>C. sp. 1</i>	5	-0.0127	61.2	1.576	0.0955
<i>C. tasmanica</i> GROUP	10	0.0235	70.6	2.400	0.0048
<i>C. tsugae</i> Rikkinen	3	0.0014	65.9	1.931	0.0263
<i>C. ussuriensis</i> Titov	8	0.0001	47.1	0.889	0.4096
<i>C. viridialba</i> (Kremp.) A. F. W. Schmidt	1				
<i>C. viridireagens</i> (Nádv.) A. F. W. Schmidt	6	-0.0052	62.4	1.657	0.0716
Species 1	4	-0.0055	56.5	1.297	0.2455
<i>Cybebe gracilentia</i> (Ach.) Tibell	8	0.0003	58.8	1.429	0.1594
<i>Cyphelium inquinans</i> (Sm.) Trevis.	40	0.1012	63.5	1.741	0.0525
<i>C. pinicola</i> Tibell	3	0.0090	87.1	6.727	0.0000
<i>Microcalicium ahlneri</i> Tibell	18	0.0278	56.5	1.297	0.2455
<i>M. arenarium</i> (Hampe ex A. Massal.) Tibell	2	-0.0029	63.5	1.742	0.0525
<i>M. disseminatum</i> (Ach.) Vainio	20	0.0374	48.2	0.932	1.0000
<i>Mycocalicium subtile</i> (Pers.) Szat.	34	0.0763	63.5	1.742	0.0525
<i>Phaeocalicium compressulum</i> (Szatala) A. F. W. Schmidt	3	0.0173	89.4	8.444	0.0000

**Table 5.1, Continued**

<i>P. populneum</i> (Brond. ex Duby) A. F. W. Schmidt	3	0.0169	85.9	6.083	0.0000
<i>Sclerophora peronella</i> (Ach.) Tibell	7	0.0027	74.1	2.864	0.0010
<i>Sphinctrina leucopoda</i> Nyl.	1				
<i>Stenocybe clavata</i> Tibell	24	0.0949	63.5	1.742	0.0525
<i>S. fragmenta</i> E. B. Peterson & Rikkinen	1				
<i>S. major</i> (Nyl.) Körber	9	0.0454	69.4	2.269	0.0077
<i>S. pullatula</i> (Ach.) Stein	12	0.0368	62.4	1.656	0.0716
<i>Thellomma ocellatum</i> (Körber) Tibell	1	0.0019	95.3	20.2500	0.0000

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## Landscape Data

We obtained an elevation coverage from the Forest and Rangeland Ecosystem Science Center (FRESC) at Oregon State University, that was assembled from USGS 30 m digital elevation models. A heat index was derived from the elevation coverage by first deriving aspect and slope, then calculating the heat index with the equation used by Peterson and McCune (2000d). The slope values were limited to a maximum of 45° to prevent systematic error in the equation.

We downloaded the PRISM model of estimated annual rainfall (Daly et al. 1994; <http://www.ocs.orst.edu/prism/>) for Oregon in polygon format. We first projected it into UTM coordinates, then converted it to a grid with a cell size of 25 m to match the finest resolution WODIP data (below). The 25 and 100 m resolutions are much finer than the resolution of the PRISM, so the values were interpolated.

We obtained forest cover data from the Bureau of Land Management's Western Oregon Digital Image Project (WODIP; USDI 1998). This provided data for all of Oregon west of the Cascade Mountain crest, derived from 1993 Landsat Thematic Mapper satellite data. The data were in grid format (25 X 25 m pixels) with unique values for all combinations of forest type (conifer, hardwood, or mixed), tree size classes (based on diameter at breast height), canopy layering (single or multi-layered), and canopy density (10 % increments). From this, we extracted several separate coverages: presence/absence of conifers, presence/absence of hardwoods, trunk diameter size class, and canopy density.

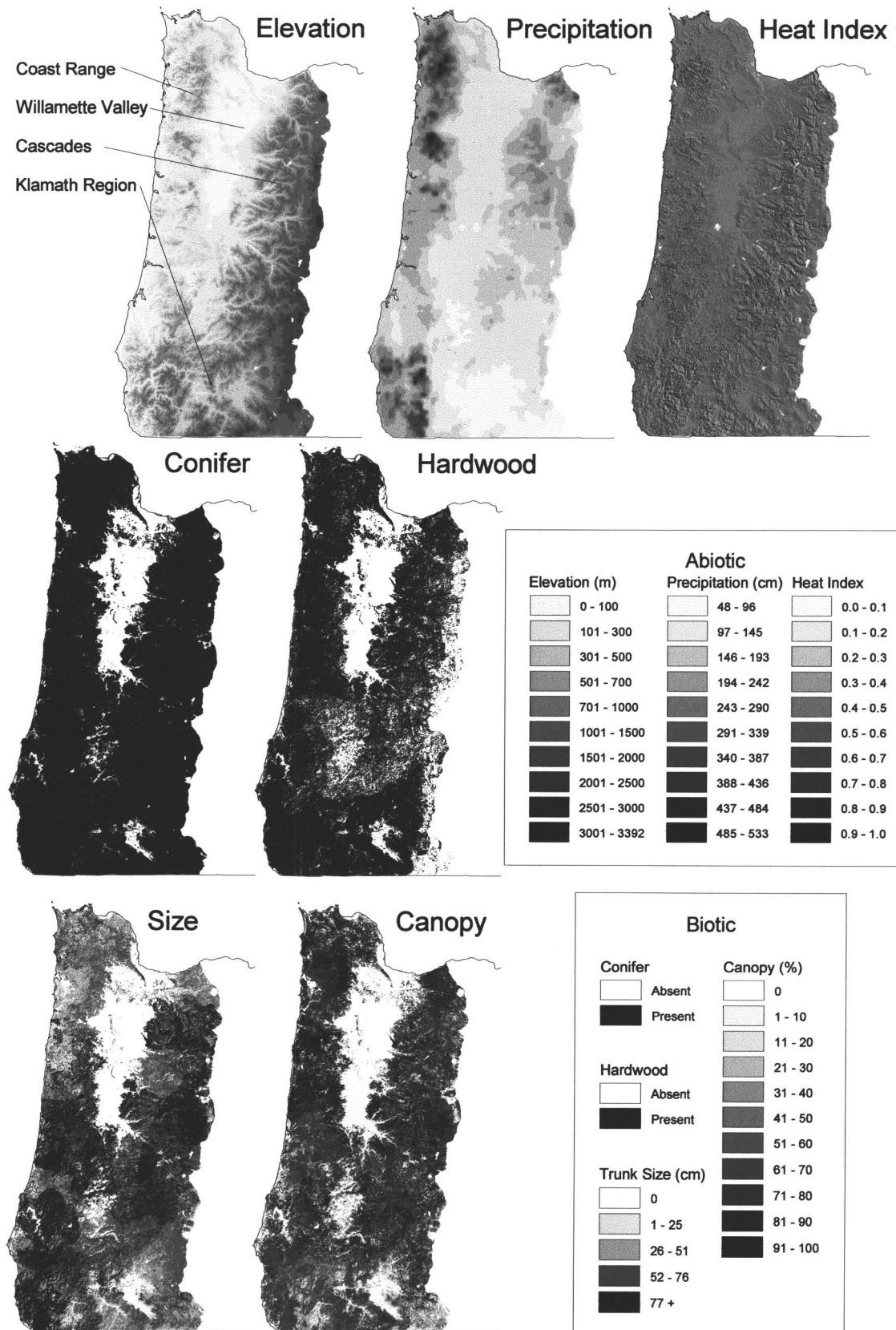
Although measurements of diameter at breast height form a poor substitute for tree or forest age, we know of no landscape-wide coverage for forest age. Thus we were forced to use the WODIP size class data in lieu of forest age. We equate the largest size class in the WODIP coverage (> 77 cm) with old-growth forest (< 200 yrs), the second largest class (52-76 inches) with late-successional forest (80-200 yrs), and the smaller two size classes with young forests (< 80 yrs). An alternative form of the size class data was also considered, in which the two smaller categories and the two larger categories were each combined to form a binary coverage relating to younger (< 80 yrs) vs older forests (> 80 yrs).

The analysis to map estimated probabilities of all species across all of western Oregon was performed with a 100 m pixel resolution in order to save computing time. The maps covered western Oregon, eastward a little beyond the crest of the Cascade mountain range (Figure 5.3). The 30 m resolution coverages (elevation and heat index) were resampled with the nearest neighbor algorithm to a cell size of 100 m. The 25 m resolution coverages (estimated annual precipitation and all WODIP-derived coverages) were aggregated to the 100 m pixel resolution. Aggregation was performed for conifer and hardwood presence/absence coverages by using the maximum value of aggregated pixels. Precipitation, canopy density, and tree size-class were aggregated by the mean value of the pixels; others were aggregated by the maximum value. Tree size-class was considered for aggregation by maximum value, but that increased the percent of forested pixels in the largest size-class (Table 5.2). This increase was due to many scattered, isolated pixels with the largest size class, and may not appropriately represent old-growth forest.

GIS coverages were manipulated using Arc/View 3.2 (ESRI 1999) with ESRI's Spatial Analyst 1.1 extension, and the Spatial Tools 3.2 extension, freely available from <http://www.esri.com>. Software for the modeling method is available at <http://www.geocities.com/ecomodeler/model/SpOcc.html>.

### **Model Validation and Variable Selection**

Model validation was performed by comparing the occurrences of species in sampled sites with model predictions for the species at the same site. Each sampled site was removed from the data, one at a time, and its environmental parameters were used to define a target site. Predictions were made for species at this target site with the model under consideration (MODEL) and two null models. For the NULL1 model, estimated probability for each species was set to 0.50. For the NULL2 model, estimated probability for each species was set to the proportion of occurrences of the species within the data set. Species with only a single occurrence were removed, as they would automatically be estimated at 0 for MODEL and NULL2 when validating the site at which they did occur.



**Figure 5.3** GIS coverages for model input.

**Table 5.2** Effect of aggregation methods on the tree size-class coverage. Values given are percents of forested pixels in size-classes. Original WODIP data (Original) has a pixel resolution of 25 m. Coverages were aggregated to a 100 m resolution by the maximum value of aggregated pixels (100 m, Maximum) and by the mean value with the result rounded up (100m, mean, rnd up).

Size Class	Original	100 m, Maximum	100 m, mean, rnd up
1	26.511 %	6.835 %	19.592 %
2	42.123 %	29.599 %	42.122 %
3	26.624 %	44.369 %	33.642 %
4	4.742 %	19.198 %	4.644 %

**Table 5.3** Model selection and validation. For all models,  $h$  is 25 percent unless otherwise noted.  $N$  = number of sampled sites that could be validated with the model.  $\bar{I}_1$  = improvement of estimations with the model over the NULL1 model.  $\%_1$  = percent of estimations with positive  $I_1$ .  $\bar{I}_2$  = improvement of estimations with the model over the NULL2 model.  $\%_2$  = percent of estimations with positive  $I_2$ .  $I_2R$  = odds ratio for positive values of  $I_2$ .  $P$  = one-tailed p-value for the odds ratio being greater than 1. The highest values for validation measures are in bold. The chosen optimal model is both in bold and italicized.

Model	N	$\bar{I}_1$	$\%_1$	$\bar{I}_2$	$\%_2$	$I_2R$	P
elevation	97	0.2587	97.2	0.0069	64.2	1.793	0.00000
precipitation	97	0.2558	97.2	0.0040	60.6	1.539	0.00000
heat index	97	0.2496	97.2	-0.0022	21.5	0.274	0.00000
conifer p/a	97	0.2565	96.9	0.0048	58.1	1.386	0.00000
hardwood p/a	97	0.2533	97.2	0.0016	56.2	1.280	0.00000
size/age class (4 categories)	96	0.2583	97.7	0.0073	45.8	0.846	0.00002
size/age class (2 categories)	97	0.2598	97.4	0.0081	35.1	0.472	0.00000
Canopy	97	0.2567	97.1	0.0049	61.2	1.578	0.00000
elevation + precipitation	97	0.2618	96.7	0.0101	68.5	2.178	0.00000
elevation + precipitation + heat index	97	0.2617	96.6	0.0099	58.2	1.139	0.00000
conifer + hardwood	97	0.2575	97.2	0.0058	60.0	1.501	0.00000
conifer + hardwood + size/age class (2)	96	0.2649	97.3	0.0137	57.3	1.341	0.00000
conifer + hardwood + size/age class (4)	95	0.2623	97.4	0.0118	56.1	1.277	0.00000
conifer + hardwood + size/age class (2) + canopy	93	0.2713	97.1	0.0198	62.3	1.653	0.00000
conifer + hardwood + size/age class (4) + canopy	87	0.2647	96.7	0.0148	56.6	1.304	0.00000
elevation + precipitation + conifers + hardwood + size/age class(2)	91	0.2722	96.5	0.0216	65.7	1.919	0.00000
elevation + precipitation + conifers + hardwood + size/age class(4)	89	0.2729	96.6	0.0221	63.4	1.732	0.00000

**Table 5.3, Continued**

elevation + precipitation + conifers + hardwood + size/age class(2) + canopy	85	0.2772	95.6	0.0284	69.9	2.323	0.00000
elevation + precipitation + conifers + hardwood + size/age class(2) + canopy	80	0.2768	95.1	0.0298	70.1	2.344	0.00000
<b>elevation + precipitation + heat + conifers + hardwood + size/age class(2) + canopy:</b>							
h = 100 %	96	0.2649	97.3	0.0138	57.3	1.341	0.00000
h = 95 %	96	0.2650	97.3	0.0138	57.4	1.346	0.00000
h = 90 %	96	0.2650	97.3	0.0138	57.0	1.330	0.00000
h = 85 %	96	0.2653	97.4	0.0141	58.0	1.379	0.00000
h = 80 %	96	0.2655	97.3	0.0143	57.7	1.367	0.00000
h = 75 %	96	0.2658	97.4	0.0146	58.1	1.388	0.00000
h = 70 %	96	0.2674	97.4	0.0162	60.6	1.538	0.00000
h = 65 %	96	0.2671	97.4	0.0159	60.6	1.538	0.00000
h = 60 %	96	0.2657	97.4	0.0148	59.5	1.468	0.00000
h = 55 %	96	0.2647	97.3	0.0140	59.0	1.441	0.00000
h = 50 %	94	0.2651	97.3	0.0145	61.1	1.568	0.00000
h = 45 %	94	0.2663	97.1	0.0157	62.7	1.684	0.00000
h = 40 %	91	0.2683	97.4	0.0192	65.7	1.913	0.00000
h = 35 %	90	0.2710	97.2	0.0228	67.1	2.038	0.00000
h = 34 %	88	0.2810	96.4	0.0321	73.5	2.774	0.00000
h = 33 %	87	0.2795	96.3	0.0313	72.9	2.690	0.00000
h = 32 %	87	0.2813	96.6	0.0331	72.9	2.686	0.00000
h = 31 %	85	0.2799	96.5	<b>0.0323</b>	72.9	2.556	0.00000

**Table 5.3, Continued**

<b>h = 30 %</b>	<b>85</b>	<b>0.2799</b>	<b>96.5</b>	<b>0.0323</b>	<b>72.2</b>	<b>2.596</b>	<b>0.00000</b>
<i>h</i> = 29 %	83	0.2783	96.4	0.0301	70.9	2.438	0.00000
<i>h</i> = 28 %	82	0.2777	96.3	0.0300	70.8	2.422	0.00000
<i>h</i> = 27 %	81	0.2765	95.7	0.0295	70.4	2.381	0.00000
<i>h</i> = 26 %	80	0.2768	95.2	0.0298	70.9	2.439	0.00000
<i>h</i> = 25 %	<b>80</b>	<b>0.2768</b>	<b>95.1</b>	<b>0.0298</b>	<b>70.1</b>	<b>2.344</b>	<b>0.00000</b>
<i>h</i> = 20 %	76	0.2742	93.8	0.0283	68.2	2.140	0.00000
<i>h</i> = 15 %	63	0.2887	96.1	<b>0.0355</b>	67.4	2.070	0.00000
<i>h</i> = 10 %	48	0.2870	94.8	0.0350	72.0	2.571	0.00000
<i>h</i> = 5 %	13	0.2708	83.8	0.0221	68.6	2.186	0.00000
<i>h</i> = 0 %	2	0.4200	96.0	<b>0.1246</b>	97.0	32.333	0.00000F
elevation + precipitation + heat + conifers + hardwood + ageclass(4) + canopy:	72	0.2738	94.0	0.0271	65.6	1.906	0.00000

The improvement ( $I$ ) of MODEL was then calculated by measuring how much closer it was to the actual species value (presence or absence) than were NULL1 and NULL2:

$$\text{IF (present): } I_1 = \hat{p}(\text{MODEL}) - \hat{p}(\text{NULL1})$$

$$I_2 = \hat{p}(\text{MODEL}) - \hat{p}(\text{NULL2})$$

$$\text{IF (absent): } I_1 = \hat{p}(\text{NULL1}) - \hat{p}(\text{MODEL})$$

$$I_2 = \hat{p}(\text{NULL2}) - \hat{p}(\text{MODEL})$$

where  $\hat{p}(\text{MODEL})$  is the estimated probability from MODEL,  $\hat{p}(\text{NULL1})$  is the estimated probability from NULL1, and  $\hat{p}(\text{NULL2})$  is the estimated probability from NULL2. Improvement values over NULL1 and NULL2 ( $\bar{I}_1$  and  $\bar{I}_2$ , respectively) were averaged over all species, and over all validated sites. Counts were also kept for the number of positive improvements among the species for a site, and averaged over all sites. A ratio of the total number of positive improvements over all sites to the total number of zero and negative improvements was used to calculate an odds ratio for site improvement over a null model with a 0.5 chance of improvement.

Variable selection was performed by a manual forward-selection search for the combination of variables and size of  $h$ . The optimal model was determined by the improvement of the probabilities over null models (Table 5.3). We further restricted the optimal model to values of  $h$  that allowed validation of at least eighty percent of the sampled sites. We began with  $h = 0.25$  (25 percent of the length of continuous variables). Abiotic and biotic variable models were first examined separately. These were then combined, and variables that had been eliminated from the abiotic and biotic models were reexamined for model improvement. Finally, the alternate size-class variable was swapped into the model to verify which form worked best. Once the model variable selection was complete, different values of  $h$  were investigated at intervals of 0.05, then at intervals of 0.01 within the 0.05 intervals adjoining the optimal value.

## **RESULTS**

### **Model Validation**

The optimal model included all seven environmental variables with  $h = 0.30$  (30 percent; Table 5.3). Forest age was used in the two-class form. The hypercube (environmental neighborhood) occupies a volume equal to 1.62 percent of the volume defined by the variables. This model allowed validation of 85 out of 97 sampled sites (12 sites had no other sites within their window). Fifty of the 58 species occurred at more than one site and were thus included in the validation. Of the estimated probabilities calculated for all 50 species over the 85 validated sites, 72 % were closer to the real species values at the sites than the NULL2 model. However the average improvement over NULL2 showed that probability estimations from MODEL were only 0.03 closer on average to the real presence or absence (one or zero) values.

Validations run for individual species over the 97 sites showed that model improvement ( $\bar{I}_2$ ) varied considerably (Table 5.1). For nine of the species, the optimal model had no improvement over the NULL2 model (minimum  $\bar{I}_2 = -0.01$ ). Five species had  $\bar{I}_2 > 0.10$ . The amount of improvement in predictions for a species is positively correlated with the number of occurrences in the data (Figure 5.4). The percent of predictions with positive improvement bears little relation to the number of occurrences in the data except that there is more scatter for the rarer species. The odds ratio, which is an exponential function of the percent of predictions with positive  $\bar{I}_2$  (Figure 5.4 inset) also has no relation to the number of occurrences.

### **Maps of Species over the Landscape**

The GIS data we obtained for input to the model covered 80,387 km<sup>2</sup> of land in western Oregon at a resolution of 1 ha. Of these, the WODIP data showed 63,150 km<sup>2</sup> were forested. Calicioid communities could be estimated from our data set for

**Figure 5.4** Relationships between validation measures and number of occurrences.

**Figure 5.5** Summary output from model. **Sites In** is the number of sampled sites used to estimate probabilities for a site (pixel). **Ave. Pr.** is the average probability over all 58 species for a site. **Ave. Odds** is the average odds ratio over all 58 species for a site. **Sig. Spp.** is the number of species at a site which have significantly a high odds ratios.

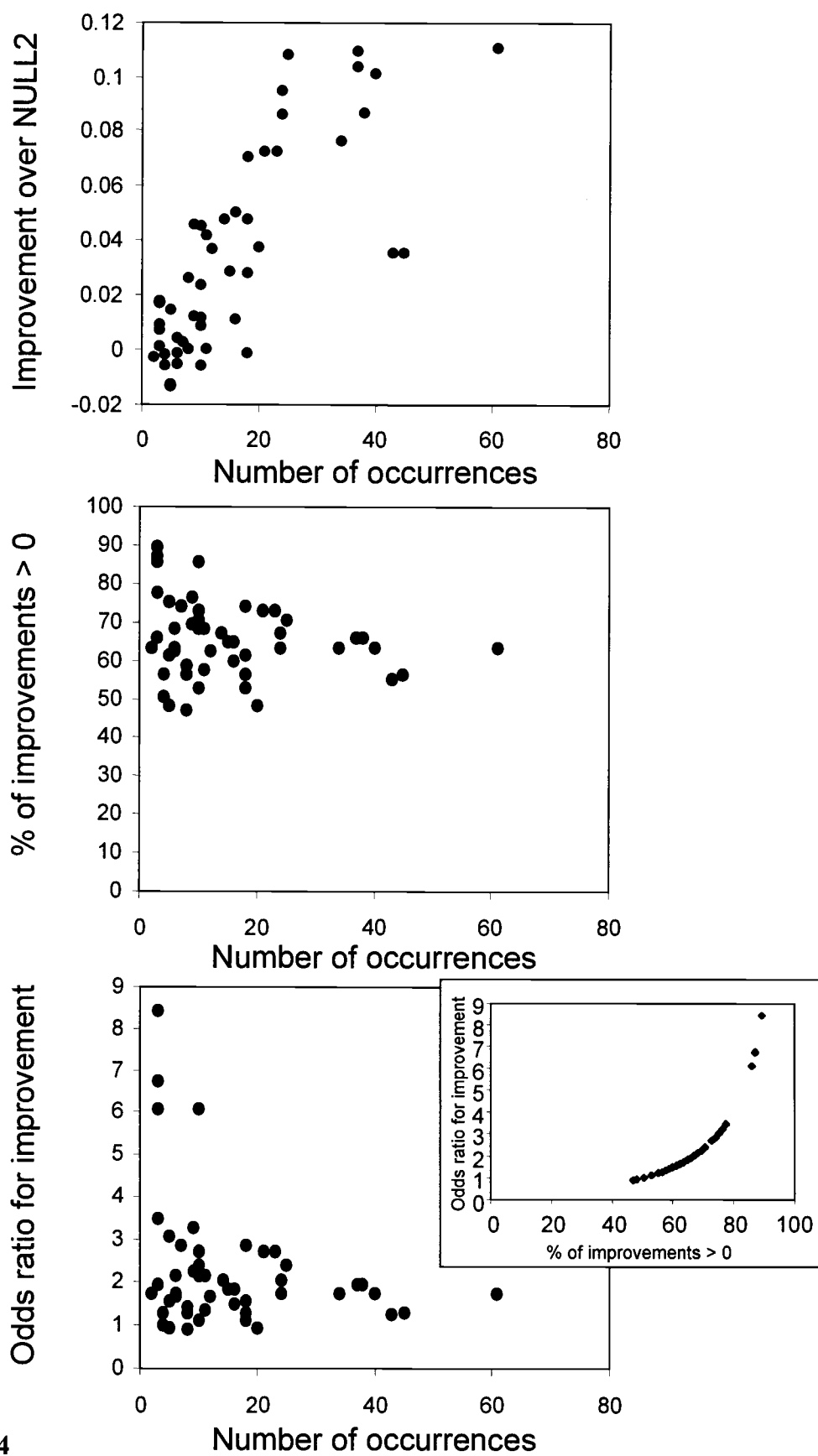
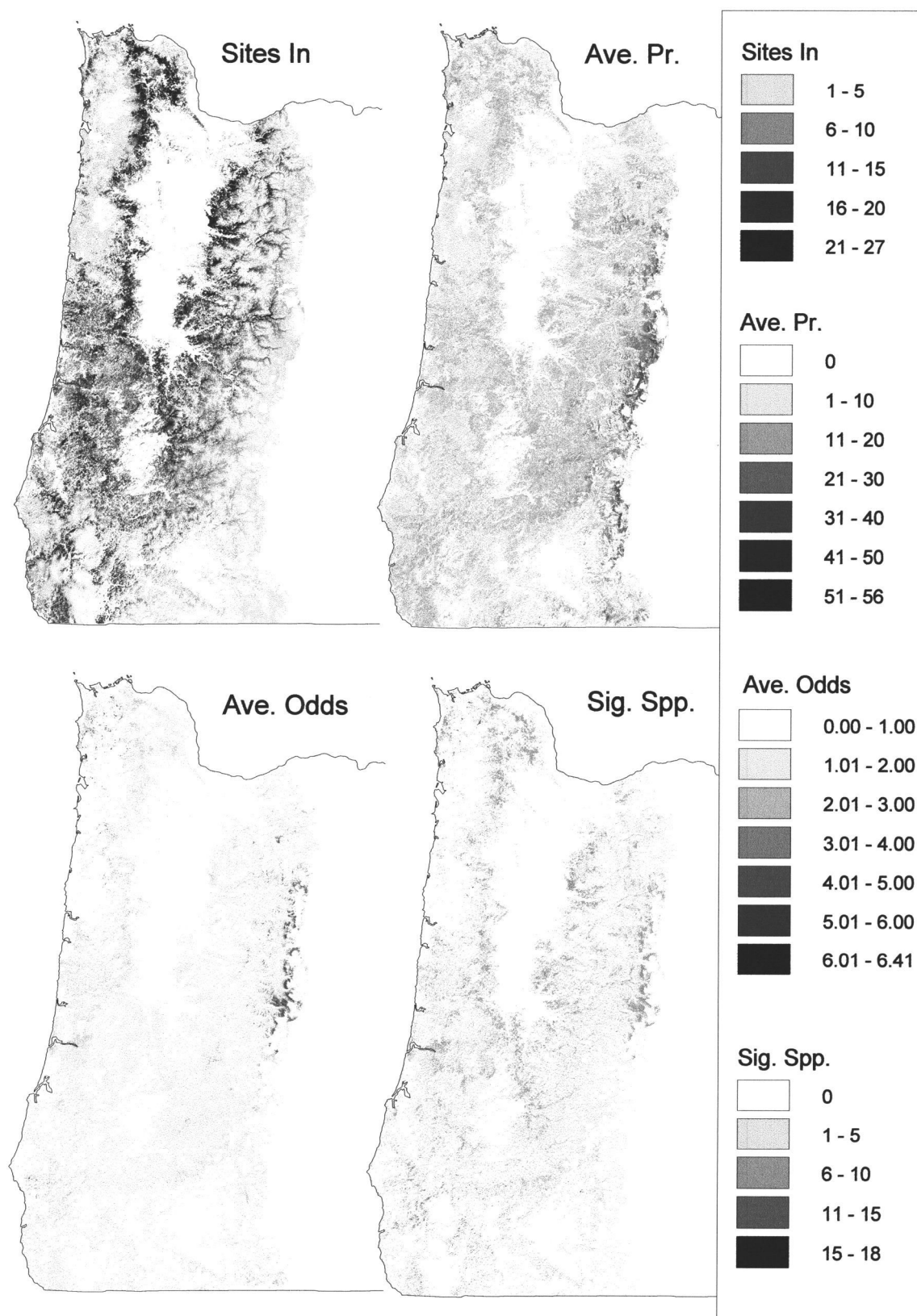


Figure 5.4



**Figure 5.5**

42,536 km<sup>2</sup> (Figure 5.5). Since we excluded non-forested sites in our data, calicioid communities for these could not be predicted. Lack of woody substrate required by calicioids would prevent most species from occurring in such sites. A few species capable of inhabiting old untreated fence posts might occur in non-forested sites, but at a low frequency that would result in a very low probability. The lack of predictions for many forested sites reflect the low variety of young forests in our sample and missing combinations of values for variables.

For the 42536 km<sup>2</sup> in which we were able to predict calicioid occurrences, the number of sampled sites within the environmental neighborhood ranged from 1 to 27. Map pixels incorporating the higher number of sampled sites were concentrated in foothills and low mountains surrounding the Willamette Valley (Figure 5.5).

Average estimated probability of species for a site was greatest in the dry, high-elevation sites near the crest of the Cascade Mountains and on their east slope. Average odds ratio maps differed from average estimated probability in that the sites with highest average odds ratios were heavily concentrated in the low elevation foothills near the Willamette Valley. The map of the number of species at a site with a statistically significant high odds ratio ( $S$ ;  $p \leq 0.05$ , one-tailed, Fisher's Exact Test) was similar to the map of average odds ratio ( $AVE \hat{p}$ ). The major difference was that the highest values of  $S$  (14-16 significant species) were much more restricted to old forests at rather low elevations (500 - 600 m), with moderately high estimated annual precipitation (c. 200 cm) and open but continuous canopies (ca. 70% coverage). The presence or absence of hardwoods bore surprisingly little relevance to  $S$ , considering that many species are restricted to hardwoods. Those species, however, tend to occur in hardwood forests lacking conifers.

## **DISCUSSION**

### **Modeling Concept**

This modeling method does not rely on parametric assumptions; instead it extracts probabilities directly from the data. As a result it should be responsive to complicated, non-linear distributions of species over environmental gradients. There is little problem with using the same combination of environmental variables for all species. If a species does not respond to the amount of annual precipitation, it should have a roughly uniform ratio of presences to absences over that environmental gradient which would approximate its ratio within the entire data set. The only detrimental effect is a reduction in the number of sampled sites remaining in the environmental neighborhood, due to forming a window on an extra dimension in the environmental space.

By combining windows over each variable with the AND logical operator, we form a multidimensional environmental neighborhood (the hypercube). Since all sites within the neighborhood are simultaneously within each variable's individual neighborhood, interactions between the environmental variables are automatically accounted for (Figure 5.1). When modeling occurrence with many standard techniques such as regression, consideration of variable interactions is costly in terms of degrees of freedom and parsimony. Small data sets such as ours limit the number and form of interactions that might be included in regression models.

Occurrence at previously sampled sites within the window could be used with a weighted averaging to place greater weight on those in close proximity to the target site, as is often done with kernel estimation (Silverman 1986). However, considering sampled sites simply as inside (or outside) the window has the advantage that the method can be used in conjunction with odds ratio statistics. This allows a statistical comparison of the odds of a species occurring at a site within the environmental neighborhood (hypercube) with the odds of it occurring in sites outside the neighborhood. Thus we can determine if the neighborhood of the target contains exceptionally good sites for the species, suggesting that the target site is also exceptional.

For conservation issues, this use of odds ratios has an advantage over using estimated probabilities directly. Estimated probabilities are related to the frequency of species in the whole data set, so using average estimated probabilities of species to determine conservation value biases toward common species. Odds ratios rely only on the *ratio* of the frequency inside the neighborhood to the frequency outside. To illustrate the comparison between average estimated probability ( $AVE \hat{p}$ ) and the number of species with a significantly high odds ratio ( $S$ ), consider a case of predicting three species at two sites (Table 5.4). Species A is rather common and has a frequency of 0.6 in the data set. Species B and C are rare and each have a frequency of 0.02 in the data set. At site 1, the estimated probability ( $\hat{p}$ ) of species A is 0.80 while for species B and C,  $\hat{p} = 0.00$ . The odds ratio is not significantly high for any species ( $S = 0$ ). At site 2,  $\hat{p} = 0.20$  for all three species and the odds ratio is significantly high for B and C ( $S = 2$ ). While  $AVE \hat{p}$  at site 1 (0.27) is higher than at site 2 (0.20), the number of species with a significantly high odds ratio ( $S$ ) is zero for site 1 and two for site 2. Thus, site 2 is an exceptionally good site for more species than site 1. Preservation of site 1 would most likely conserve species A but not B or C. Preservation of site 2 might not conserve any species, but it will have a better chance of conserving the rare species, and preservation of several sites like site 2 will likely conserve all of them. Identification of site 2 for conservation would not be possible using average estimated probabilities alone.

## Model Output

Maps of estimated probability and odds ratio significance were mostly compatible with previous knowledge of the species responses to environmental gradients (Peterson and McCune 2000d). For example, *Calicium viride* is well known for occurring in relatively dry open forests in the PNW and becomes most abundant in drier areas to the south and east. The maps from our model reflect this (Figure 5.6). *Chaenotheca hispidula* is an uncommon species that has been found only on old *Quercus* trees in or near the Willamette Valley and is also appropriately mapped (Figure 5.6).

**Table 5.4** Hypothetical prediction of three species at two sites to demonstrate using the number of species at a site with statistically significant high odds ratios ( $S$ ) versus the average estimated probability of occurrence ( $AVE \hat{p}$ ).

	Sp. A	Sp. B	Sp. C	Average $\hat{p}$	Conservation value
overall freq.	0.60	0.02	0.02		
Site 1:					
$\hat{p}$	0.80	0.00	0.00	0.27	good for one common species
odds ratio sig.?	no	no	no		
Site 2:					
$\hat{p}$	0.20	0.20	0.20	0.20	good for two rare species
odds ratio sig.?	no	yes	yes		

**Figure 5.6** Results for *Calicium viride* and *Chaenotheca hispidula*, mapping estimated probability of occurrence (**Pr.**) and one-tailed significance for high odds ratio (**Odds p-value**). Circles indicate sampled sites where the species was present.

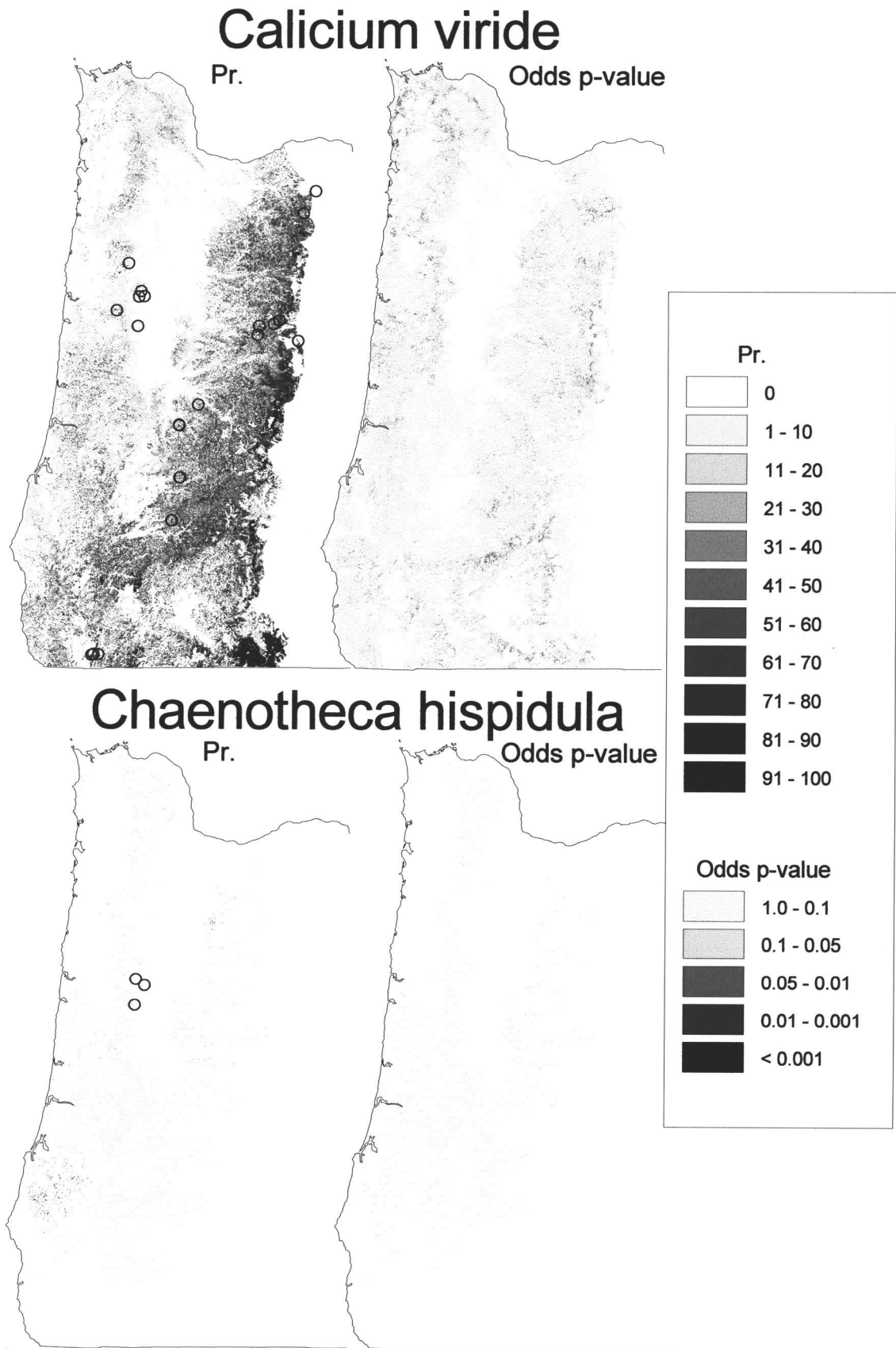


Figure 5.6

However, some maps do not reflect what is known about the species.

*Chaenothecopsis sitchensis* is a non-lichenized species known only to occur on resin of *Picea sitchensis*, a tree species restricted to the coast in Oregon. The modeled maps show only low estimated probabilities for the species at best. These areas are both along the coast and at inland low elevations around the Willamette Valley (Figure 5.7). Such errors should be expected when modeling a host-specific species with data that lacks information on the presence of the host. Model performance could be easily and dramatically improved for a target stand of known tree species composition.

The response to non-linear distributions was not entirely satisfactory. *Stenocybe clavata* is thought to have a bimodal distribution, occurring in both wet and dry forests, but not in intermediate forests (Peterson and McCune 1999c). The map of estimated probability of occurrence for this species (Figure 5.7) indicates only a slight suggestion of this bimodal distribution. The highest estimated probabilities are concentrated both in the wet northern Coast Range and the dry southern part of western Oregon. However, intermediate sites have only slightly lower estimated probabilities. Significant odds ratios show even less of the bimodality, as they are more focused on the wet northern Coast Range forests and the western edge of the Willamette Valley.

The imprecise response of predictions to this bimodal distribution is due to the large value of  $h$ . As the number of our sampled sites increases, we should be able to decrease  $h$ . This should increase precision, clarifying complicated distributions over gradients (Figure 5.8), while maintaining good validation measures for most sampled plots. Higher improvements over NULL2 were achieved by using  $h = .15$  and  $.10$ , though this allowed validation of only 63 and 48 sites, respectively. It is interesting that even better improvement ( $\bar{I}_2$ ) was seen with  $h = 0$ , though only two sites could be validated (these occupied the same point in environmental space). If increasing the number of sampled sites does allow us to decrease the value of  $h$ , then model performance (as measured by  $\bar{I}_2$ ) and resolution of complicated environmental-response curves should increase.

Still, a large  $\bar{I}_2$  may be difficult to achieve. In the one dimensional demonstration of the windowing technique, a pattern is intuitively present. Our method

**Figure 5.7** Results for *Chaenothecopsis sitchensis* and *Stenocybe clavata*, mapping estimated probability of occurrence (**Pr.**) and one-tailed significance for high odds ratio (**Odds p-value**). Circles indicate sampled sites where the species was present.

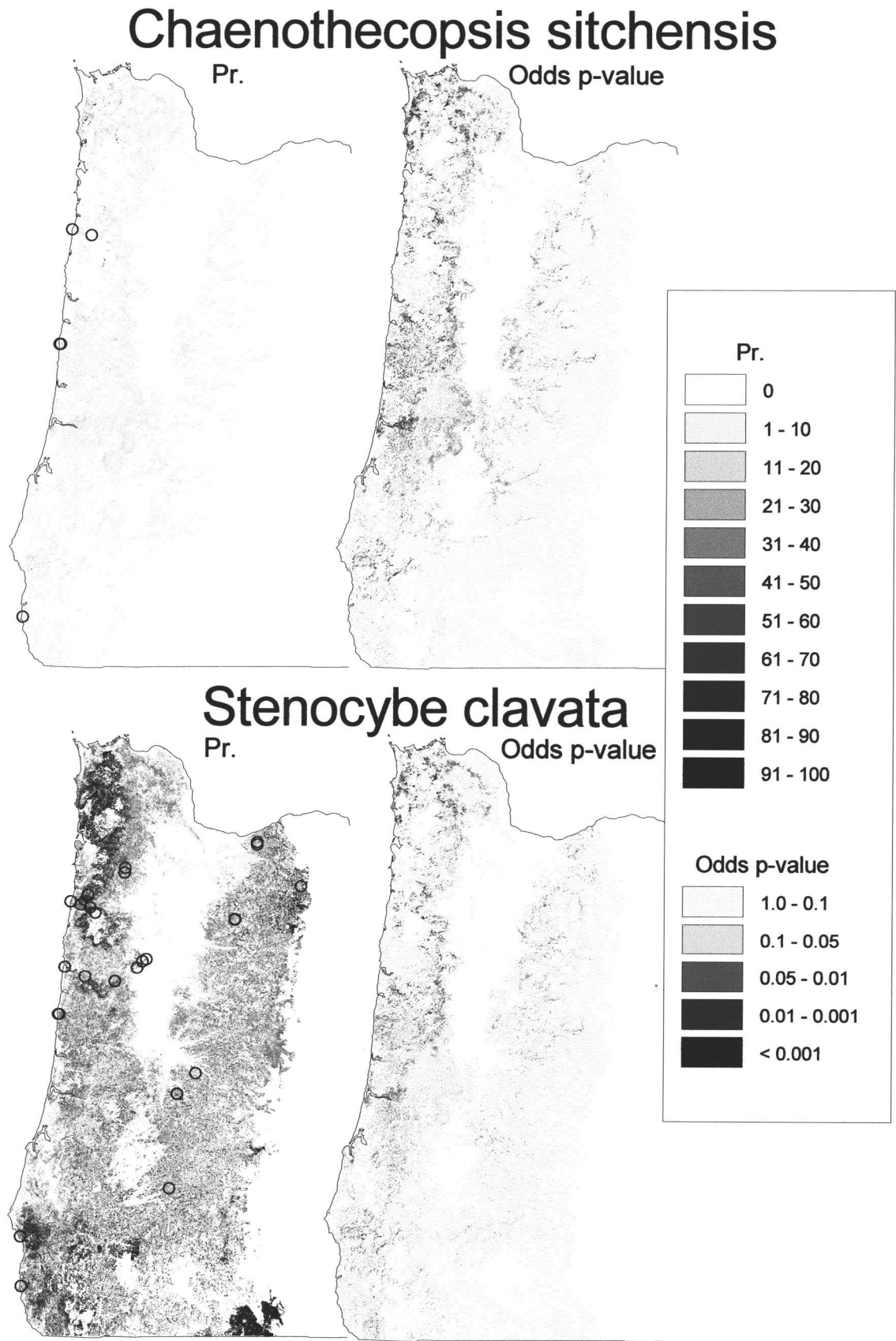
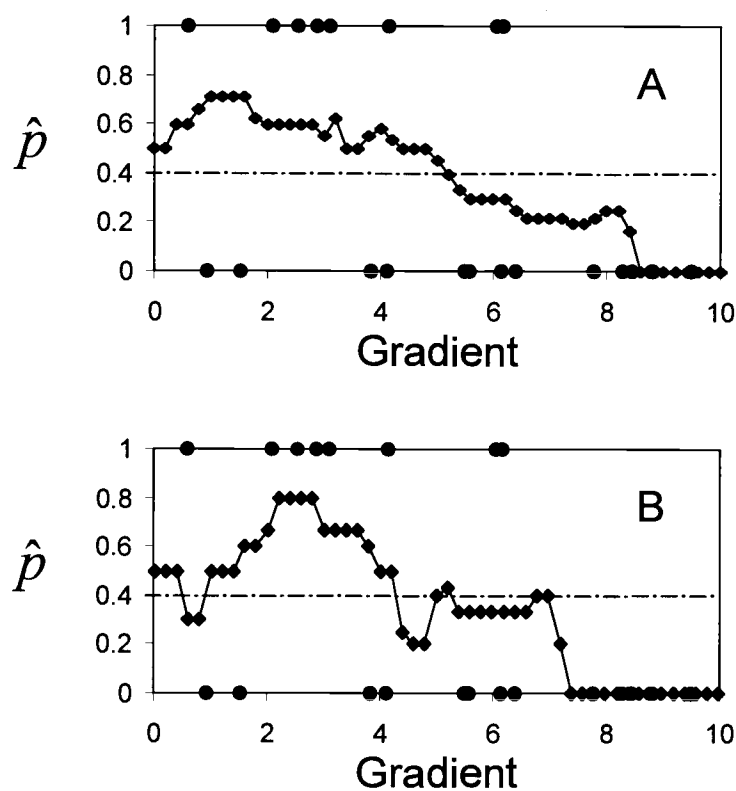


Figure 5.7

calculates a reasonable appearing response curve (Figure 5.8a). If this example is validated,  $\bar{I}_2 = 0.08$  and 70 % of the predictions have a positive improvement. The comparison between quantitative estimated probabilities and the binary presence/absence values may automatically lead to low improvement values in most situations, particularly with high values of  $h$ . By halving the value of  $h$  for the demonstration graph (Figure 5.8b), a higher resolution of the response curve is achieved and the improvement value doubles to 0.15. The percent of positive improvements remains steady. Since our sparse data set requires a high value of  $h$ , our  $\bar{I}_2$  of 0.03, and positive improvement for 72 % of predictions, is respectable.

Another factor that may be relevant to the overall low values of model performance may be the nature of calicioid habitat requirements. Most species are very substrate-specific (Hyvärinen 1992) and sensitive to light conditions (Rikkinen 1995). It may be that the importance of the microhabitat outweighs the macroenvironment in determining suitable habitat. The variables that were available as GIS coverages all describe the stand macroenvironment. It is possible that modeling calicioid occurrence will never have great success rates while using the macroenvironmental predictors that are available on a landscape level. For example, *Calicium glaucellum* most frequently occurs in dry, open forests (Peterson and McCune 2000d), but was found at one of our highest annual precipitation sites on a sun-baked tree trunk at the edge of a forest gap. Small gaps are measurable, and in the future may be accurately represented in high resolution GIS coverages. However, it is unlikely that measures of bark texture and pH, which may influence calicioid communities (Hyvärinen 1992), could ever become available as GIS coverages. More precise measurement of tree or forest age in our sampled sites, and a legitimate GIS coverage for forest age would be of great use. Several species occur primarily on large, old snags (Holien 1996; Kruys and Jonsson 1997, Peterson and McCune 2000d). While we did have information on the presence of snags for our sampled sites, such information is not currently available in GIS coverages. Some species, particularly those occurring on hardwood twigs or on conifer resin, are limited to only a few host species. Thus, information on the species-level forest composition might be useful in future models.



**Figure 5.8** Response curves to the one-dimensional demonstration graph (Figure 1) for two different values of  $h$ . Curves are formed by plotting the estimated probability at 0.2 unit intervals along the gradient. Estimated probabilities are displayed with diamonds. Presences and absences at sampled sites are displayed with circles. The dotted line represents the overall frequency of the hypothetical species (corresponds to the NULL2 model). **A.**  $h = 0.30$ . **B.**  $h = 0.15$ .

Using two age classes led to better model performance than using four age classes. Many of the inventoried late-successional sites (80-200 yrs of age) had exceptional structural diversity. This may have biased the late-successional stands to resemble old-growth more closely than would typical late-successional stands. Therefore the grouping of late-successional and old-growth stands should not imply that calicioid communities are fully developed prior to the onset of old-growth forest conditions.

In determining optimal habitats for conservation, using the number of species with significantly high odds ratios ( $S$ ) provided much different results from using average estimated probabilities ( $AVE \hat{p}$ ). The highest  $AVE \hat{p}$  values were in high elevation, dry sites in the Cascade Mountains, and on their east slope, while the highest values of  $S$  were in low elevation old forests with relatively open canopies. The dry Cascade and east-slope sites had moderate values of  $S$ . The average odds ratio provides still different results with high values in the dry Cascade and east-slope sites, but the highest values in some of the wettest sites in the northern Coast Range. However, the average odds ratio is a poor measure of conservation value for sites as it is very sensitive to influence from just one or a few exceptional species. The number of significant species ( $S$ ) is the measure least sensitive to bias, that we have examined. We believe it is the most useful for determining the conservation value of a site.

The low-elevation old forests that form the most valuable habitats for calicioids are also the forests that have been most impacted historically by logging. However, a number of such sites do remain and will be important for conserving calicioid diversity in the Pacific Northwest. One of these sites, Little Sinks Research Natural Area (44° 50.3 N, 123° 26.4 W), harbors higher diversity of calicioids than any other stand known in region (over 30 species). This low-elevation site has an old forest with canopy gaps enforced by ponds. By itself, Little Sinks is not likely the cause of the large number of significant species predicted for these habitats because the sites with the highest number of species are predicted from over 20 sites.

## Utility of the Modeling Method

The utility of this method is very high for modeling numerous species simultaneously. It offers conveniences of using the same combination of environmental variables for all species and the automatic inclusion of variable interactions. Effort is required in data acquisition and in determining the optimal model. Otherwise, use of the method is limited mainly by computing resources. Computing effort increases linearly with the number of environmental variables, the number of sampled sites, and the number of sites or pixels to make predictions for. We used a Windows 98 PC computer with a 500 MHz AMD Athelon processor and 128 MB RAM. Since the version of the software we used loads all GIS maps entirely into memory, large maps require heavy use of virtual memory, which slows the analysis. Therefore we divided our region into five subregions and ran the model on each consecutively. Generating Estimated probability maps for all 58 species over a subregion at a resolution of 100 m required about 20 hrs, or about four days for all of western Oregon.

For our specific test application, we identified three significant weaknesses with our data that likely caused the low improvement over the NULL2 model: (1) substrate and microhabitat are of great importance to calicioids while we had only macroenvironment variables for predictors, (2) our data set was small considering the size and heterogeneity of western Oregon, and (3) our data set consisted mainly of older coniferous forests, under representing other forest types in Oregon. The modeling method may work better for organisms where the available macroenvironment variables have more direct influences on species occurrence and for data sets that are more representative of the landscape. The non-parametric nature, avoidance of curve fitting for potentially complex responses, and automatic inclusion of interactions are valuable benefits of this method.

## ACKNOWLEDGEMENTS

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## Chapter 6

### Conclusions

The studies contained in this dissertation increased our knowledge of how lichen communities vary between stand types and across the western Oregon landscape, and proposed a method to predict species occurrence.

Chapter two examined macrolichen communities in old stands, young stands, and young stands that were thinned 10 to 25 yrs earlier to accelerate tree growth. Differences in lichen communities between thinned and unthinned stands were small. In thinned stands, alectorioid lichens were slightly higher in abundance, *Hypogymnia imshaugii* was more frequent, and there was lower landscape-level species richness. Old growth macrolichen communities were distinctly different from communities in the two young stand types. Seven species associated with old-growth forested plots, including the nitrogen-fixing lichen *Lobaria oregana* and several forage-providing alectorioid lichens. The presence of remnant old trees apparently increases the occurrence of old-growth associates in young stands.

Lichen communities varied over the landscape, particularly between the Coast and Cascade Mountain Ranges. The difference between mountain ranges corresponded to climatic gradients, particularly annual precipitation. Successional patterns in macrolichen communities also appeared to differ between the ranges. Lastly, we found evidence that suggests air pollution may impact lichen communities in some parts of these mountain ranges.

Chapter three compared macrolichen communities in suspected hotspots of high macrolichen diversity with those in more typical young and old stands. The hotspots averaged five species more than the young and old stands. Hotspots fell into three general categories: riparian zones, upland hardwood gaps, and rock outcrops. Macrolichen communities in riparian zones were most different from the young and old stands. These hotspots harbored communities with particularly high richness of nitrogen-fixing cyanolichens; 16 cyanolichen species associated specifically with riparian zones.

Chapter four focused on calicioid communities within the Cascade Mountain Range. The goals of this study included gaining basic information on the calicioid taxa

that occur in our region and examining ecological patterns in calicioid communities. In addition to the information presented in this dissertation, sampling for chapter four contributed to range extensions for several species (Peterson and Rikkinen 1999), the recent description of *Stenocybe fragmenta* (Peterson and Rikkinen 1998), and the growing awareness of five more undescribed species that are discussed in the chapter. I hope to publish descriptions for at least four of these new species soon, so that proper names can be used for them in the final publication of chapter four.

Calicioid species richness was closely associated with old growth trees. In young forests, calicioids appear to be fostered by the presence of legacy structures, such as old snags and wolf trees. These wolf trees were probably formed by advance regeneration left behind from a previous stand. Such structures may increase continuity between the current stand and previous stands. Many calicioid species frequented old stands with low annual precipitation and high understory exposure. In some regions of the world, calicioid richness can be used to index stand continuity; environmental gradients would severely distort such an index if used in the Pacific Northwest.

Chapter five proposed a modeling method to predict species occurrence by using the apparent responses of species to habitat characters and environmental gradients. The specific goal was to estimate the probability of occurrence for a species in a new (target) site. We used the proportion of the species' occurrences among sampled sites that fell within an ecological neighborhood around the target site. This simple method avoids parametric assumptions, provides easy updating of models as additional sites are sampled, and automatically accounts for interactions among predictor variables. It can be linked with GIS data and software to map probability of occurrence across landscapes.

For identifying conservation value of sites, using the average probability of occurrence may bias toward common species. Instead, the number of species estimated to have significantly high odds of occurring may better identify valuable conservation sites, as the odds are relative to sites outside the environmental neighborhood. Data on calicioids demonstrated that the modeling method outperforms our null models even when the species being modeled have substrate requirements that are not easily described on a stand-level.

This dissertation has several implications for forest managers. As we have known for some time, lichen communities vary with the age of a forest. Many old-growth associates perform valuable ecosystem functions. The important nitrogen-fixing lichen *Lobaria oregana* and several forage-providing alectorioids are most abundant in old growth. This dissertation confirms that the association of these lichens with old-growth forest occurs widely across the western Oregon landscape.

Cyanolichens in general were once thought to associate with old growth, as does *Lobaria oregana*. This dissertation corroborates an emerging shift in our understanding of cyanolichens by showing that most nitrogen-fixing cyanolichens differ from *L. oregana* in their habitat association. These cyanolichens are found most abundantly in riparian zones. The reason for this association is still uncertain but likely involves the increased humidity of riparian zones or the altered light environment caused by concentrations of hardwood trees.

Preservation of old growth forests and riparian buffer zones, along with retention of green trees in managed forests, will probably form the foundation of maintaining lichen diversity in the Pacific Northwest. This foundation can be built upon in several ways. Community diversity in managed forests may be promoted through cutting prescriptions that encourage structural diversity. Modeling tools, such as the method for predicting species occurrence that is proposed in chapter five, will also be useful. This modeling method can help managers to locate important habitat for conservation. It can also be used to predict changes in lichen communities that may result from different management options, thus improving decision making abilities.

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