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A Landscape-level Analysis of Epiphytic Lichen Diversity in Northern and Central California: environmental predictors of species richness and potential observer effects

Sarah Jovan
Department of Botany and Plant Pathology,
Oregon State University, Corvallis, OR 97331
e-mail: <jovans@bcc.orst.edu>

Abstract. *In this study, patterns in epiphytic lichen species richness in northern and central California are modeled using regression techniques. Several climatic, geographic, and stand characteristic variables were included in the analysis to determine the best predictors of richness. Because the data were collected by multiple people, the potential for observer effects to impact data quality is also investigated. A stepwise linear regression identified longitude, maximum temperature (mean annual), and overstory tree diversity as the best predictors of species richness, together explaining about 30% of the variability in the data. Accounting for data collector identity raised the percentage of variability explained to 51%.*

Introduction

The purpose of this study is to investigate epiphytic lichen diversity in northern and central California. This region of California has a diverse flora that consists of many distinct communities spanning the complex set of climatic and topographic gradients that thread throughout the landscape. The cyanolichen and *Usnea* rich communities characteristic of the humid, cool forests of the northwestern coastline are starkly different than the high and dry communities of the Sierras where brilliant *Letharia* species and *Hypogymnia imshaugii* predominate. The complex landscape provides a wide range of habitats, which in turn support a wide variety of epiphytic communities.

Defining the conditions that promote a high diversity of epiphytic lichens within any landscape is a particularly daunting task as each species has individualistic tolerances to environmental conditions, in many cases making distributional patterns complex and difficult to predict. Moreover many factors are known to influence the establishment of epiphytic lichen species. The general importance of climatic factors such as precipitation, relative humidity, and temperature are well documented.

The importance of various stand characteristics and structural heterogeneity to species diversity is also well studied. Some degree of substrate specificity is common for many species, making the composition of the tree community important to lichen establishment. In the Oregon Cascades, Neitlich and McCune (1997) demonstrated that hardwood patches in young (~50 yrs) mixed conifer forests had higher species richness than areas where hardwoods were absent. Hardwoods often support a different lichen flora than the conifer counterparts (Neitlich & McCune, 1997; Kuusinen, 1996; Becker, 1980), thereby increasing epiphytic lichen diversity in the stand overall. Older trees and snags often support a distinguished flora as well (Neitlich & McCune, 1997; Sillett & Goslin, 1999; Gustafsson et al, 1992). Some lichen species, known as late-successional or old-growth associated, occur more abundantly or even exclusively in older stands (Gustafsson et al, 1992; McCune, 1993; Rosso et al, 2000; Lesica et al, 1991).

These are but a small sample of the habitat qualities that lichenologists have found to be important to lichens. Collecting data for all potentially pertinent variables is infeasible, so deciding upon a set of target variables must be done judiciously.

Observer Effects

Data spanning a broad spatial scale, as these data do, are often collected by multiple people. Four different people surveyed the lichen communities for this project. Naturally each surveyor has his/her own unique abilities, experience and education relevant to the nature of the data collection. There is concern that results of broad scale sampling of lichen community composition are not repeatable, that the numbers of species found and estimated characteristics of their distributions in the sample area vary greatly between observers. A study by McCune et al (1997) directly addressed this question using the same sampling protocol as used for the data analyzed here. They found that species richness captured in a plot varied considerably between the different surveyors, and that inequities in past experience with lichens and the local lichen flora greatly affected the surveyor's ability to accurately estimate species richness. Whenever multiple surveyors collect data for a study, particularly when the focus is a statistic sensitive to uncommon species, the effect of observer identity must be estimated to evaluate data quality.

Objectives

The objectives of this study are twofold: (1) to determine what environmental factors are the best predictors of species richness within the study area (Figure 1) using a multiple linear regression on a diverse set of 17 explanatory variables and (2) to determine how much additional variability in species richness is explained when surveyor identity is included in the model. Pinning down the exact conditions that support high or low lichen diversity, especially at the broad landscape level of northern and central California, would be nearly impossible. However, I will attempt to identify a general set of environmental conditions for which one would expect a higher diversity of species.

Methods

FHM Methodology for Collecting Community Data

Lichen community data were collected by four surveyors under the direction of the Forest Health Monitoring (FHM)/Forest Inventory Analysis (FIA) programs (for field protocol see McCune et al, 1997). Over three years (1998-2000), the surveyors visited 153 permanent 0.4 hectare circular plots and documented the presence of all epiphytic macrolichen species. Plots were dispersed throughout Northern and Central California on a sampling grid (Figure 1).

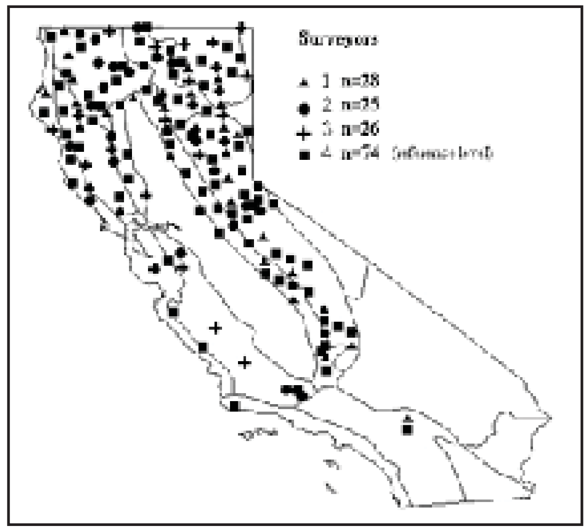

Figure 1: Map depicting sampled plots. Different symbols indicate the surveyor who collected the data.

Determining a model for predicting species richness

Stepwise multiple linear regression was used to select which group of environmental variables were the best predictors of species richness. To determine the most parsimonious model from a set of 17 environmental variables, the "forward" variable selection setting was used (S-plus software package). The annual means of precipitation, humidity, temperature, and dewpoint temperature were considered. The maximum and minimum yearly temperature, annual number of wetdays (number of days when precipitation occurred) and the Conrad index of continentality (Tuhkanen, 1980) were also included. All climate data was derived from the PRISM model (Daly et al, 1994). Geographic variables included were: elevation, longitude, and latitude. The following set of variables describing the stand structures of the plots was also analyzed: overstory diversity of trees, hardwood species diversity, conifer species diversity, total basal area, hardwood basal area, and conifer basal area.

A more complex (saturated) model including interaction terms between the variables selected by the stepwise regression was fit to the data. The saturated model was compared to the original model without interaction terms using an extra sums of squares F-test.

After accounting for all potentially important environmental and stand-related variables, indicator variables representing the four different surveyors were added to the accepted model and analyzed with a multiple linear regression. As each person surveyed a geographically dispersed set of plots, there should be essentially no confounding correlations between the indicator variables and the environmental variables (Figure 1). The new model was again compared to a saturated model, which included all possible second order interactions between the indicator variables and main effects using an extra sums of squares F-test.

Investigation of Correlation Structure Among Environmental Variables
One would expect several of the environmental variables (i.e., maximum temperature and mean temperature or precipitation and longitude), to be highly correlated. Because they explain approximately the same variability in species richness, the stepwise regression technique selects only the variable with the greatest contribution to the correlation of determination (R^2) of the model. Thus, one variable was removed from the model and substituted by a correlated variable. A series of multiple linear regressions were run on these permutations of the final model to investigate the underlying correlation structure among the environmental variables.

Results

Species Richness Model
The forward stepwise regression identified longitude (p<0.001), maximum temperature (p<0.001), and tree species diversity (p<0.001) as the best predictors of species richness. The second regression suggested that observer identity was also asociated with species richness as coefficients of all surveyor indicator variables in the model were statistically significant (Table 1). In total, the three environmental predictor variables explained about 30% of the variability in species richness between plots (R^2=.30). Addition of the surveyor indicator variables resulted in an increase of variability explained by the model to .51 (R^2) in total. In all cases, the more complex models with interaction terms between the variables did not greatly improve the fit of the model (p>.05 for all extra SS F-tests and interaction term coefficients). Thus, the final model from the multiple linear regression analysis was: species richness ~ longitude + maximum yearly temperature + tree species diversity + SURVEYOR.

Table 1: Regression results for final model

Source	Value	Std. Error	Pr(>|t|)
Intercept	-195.17	35.5378	<.001
Longitude	-1.6452	0.3	<.001
Maximum Temperature	0.0487	0.0126	<.001
Overstory Diversity	1.2287	0.3292	<.001
Crewmember 1	-5.5194	1.1931	<.001
Crewmember 2	-9.2352	1.2606	<.001
Crewmember 3	-2.3785	1.2364	0.0563

At fixed values of all other explanatory variables in the model, a one-unit decrease in longitude is associated with an average decrease in species richness by about 1.6 species (95% confidence interval: -2.24 to –1.05 species). On average, species richness is expected to increase by one species for every 20 degree increase in maximum temperature with all other variables held fixed (95% confidence interval for 20 degree increase in maximum temperature: .48 to 1.48 species). For each additional tree species on a plot, species richness will increase, on average, by 1.2 species (95% C.I.: .577 to 1.88 species). Surveyor identity also related to species richness detected. In reference to the surveyor who found (on average) the highest diversity of species per plot, the other crewmembers found 2.4 (95% C.I.: .06 to 4.82), 5.5 (95% C.I.: 3.15 to 7.85), and 9.2 (95% C.I.: 6.71 to 11.69) fewer species per plot.

Investigation of Correlation Structure among environmental variables

Any one of the variables relating to moisture (precipitation, # wetdays, humidity) could be substituted for the main effect "longitude" in the final model to generate a comparable model with only a slightly lower coefficient of determination (R^2 ranged from .44 to .48). Substituting maximum temperature with the other variables related to temperature (minimum temperature, mean temperature, Conrad index of continentality) likewise generated comparable models (R^2 ranged from .47 to .49). Elevation, (usually thought to be a complex gradient involving both moisture and temperature), could also be substituted for maximum temperature (R^2=.49). All of the variables relating to stand characteristics were interchangeable with overstory tree diversity (R^2 ranged from .48 to .49) except the basal area of hardwoods, which had a non-significant coefficient (p=.215) and resulted in a lower coefficient of determination for the model (R^2=.45). In all cases the regression coefficient of the substituted variable and the coefficients of the other variables were statistically significant (p<.01).

Discussion

Environmental Predictors of Species Richness

Interpretation of the species richness model generated in this study must be done cautiously. Even though the variables selected by the stepwise regression are the best predictors, they are only part of an intercorrelated set of variables associated with species richness. Because any variable from the moisture subset could be substituted for longitude to generate a model with a similarly high correlation coefficient, longitude may be thought of as a reflection of an underlying west to east moisture gradient. (Longitude doesn't "act" upon lichens although moisture level does). As moisture tends to decrease as you proceed east (longitude decreases), one would expect species richness to also decrease.

Figure 2 includes maps of California that present species richness (Fig. 2(a)), elevation (Fig. 2(b)), precipitation (Fig. 2(c)), maximum temperature (Fig. 2(d)), and overstory tree diversity (Fig. 2(e)) per plot. Because the model for predicting species richness is multivariate, there would not be perfect correspondence between the species richness of a plot and any environmental predictor considered singly. Nonetheless, the relationships between species richness and the environmental predictors

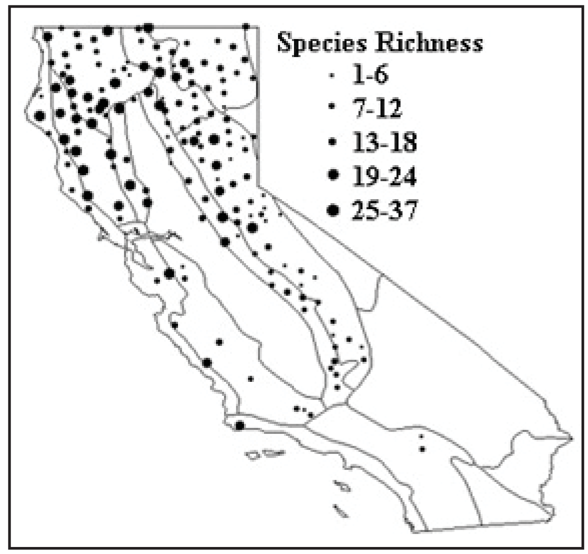

Figure 2(a)

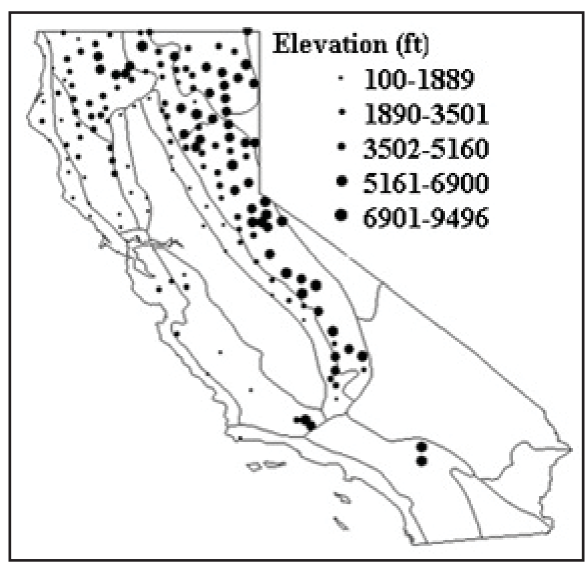

Figure 2(b)

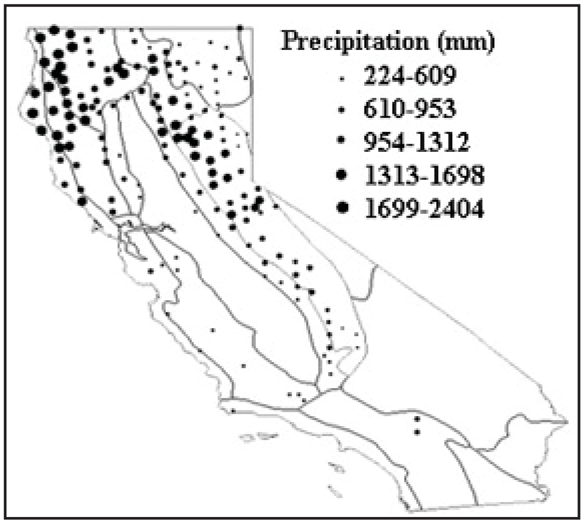

Figure 2(c)

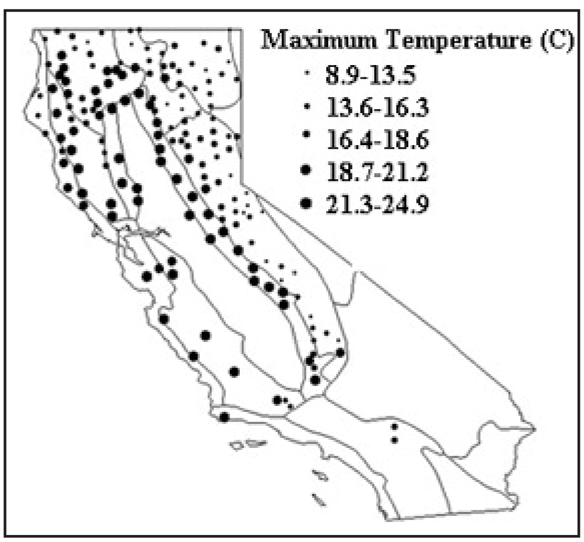

Figure 2(d)

are generally evident by comparing any two of the maps. The trends suggested by the model are most clear by comparing the two most climatically extreme regions in the study area: the species-rich northwest coast (where moisture is abundant, temperatures low, elevation low and overstory diversity high) and the relatively species poor Sierras (where arid, hot conditions prevail, elevation is high, and overstory diversity is low).

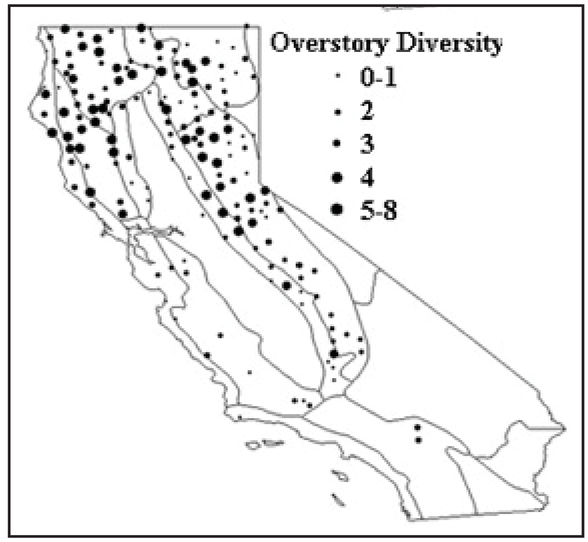

Figure 2(e)

Observer Effects

The FHM/FIA program has a standard method for ensuring data quality for projects like this one. All surveyors undergo training and certification. The trainee must find 65% of the species captured by a professional lichenologist. Those who failed the certification are given further training and repeat the test until passing. Periodically during the field season, the surveyors are audited. Lichen data from some plots is re-measured and sometimes both crew and experts survey the plot to compare species capture rates. This system works well for one intended use of the data, which involves using lichen community composition to evaluate air quality in the area. Gradient scores based upon community composition were more repeatable and consistent than species richness (McCune et al, 1997).

The results of this study agree with the findings of McCune et al (1997) regarding species richness. Surveyor identity explained about 21% of the variability in species richness, strongly suggesting a large inconsistency among surveyors. It is probable that the data were biased towards abundant species, resulting in the under-collection of rare, infrequent, or cryptic species that closely resemble others. Because climatic and geographic factors were included in the model before adding in the surveyor indicator variables, the effects of these variables were controlled. Thus the likelihood that observed differences in surveyor performance were confounded by environmental factors is low.

Recommendations for Future Attempts at Modeling Species Richness

Repeatable, accurate measures of macrolichen species richness are difficult to obtain for large plots. At large spatial scales the list of potentially important environmental variables can be quite large, especially when the study area is topographically and climatically complex like California. As demonstrated in this study, climatic factors and broad stand characteristics like tree diversity are only a small part of the full story.

Longitude, maximum temperature, and overstory diversity explained only a total of 30% of the variability in species richness between plots, a disappointing amount even considering the wide geographic spread of plots. It is inevitable that many other relevant factors were overlooked with the coarse-grained approach that was used in this study. Due to a lack of complete data for the plots, potentially important habitat features such as age, stand disturbance history, canopy cover, local air quality and a measure of riparian influence were not included. Future attempts to model macrolichen species richness should incorporate a more elaborate set of variables including those mentioned above.

The potential for measurement error in the environmental data to weaken the model also needs consideration. All climate variables in this study were estimated on a 4 by 4 km grid over California. Direct weather data from monitoring stations were used to extrapolate climate estimates to other areas, based upon a regression-based model that adjusts for the effect of elevation (Daly et al, 1994). A Gaussian filter was then used to estimate climate within the 4 by 4 km grid cells. Although it would be difficult to quantify, some degree of error in the climate data is expected.

Also discovered here, observer effects can introduce much unwanted variability or "noise" into the data. Administration of a more rigorous lichen training, hiring crews with more prior experience with lichen surveys, and raising the standards of species capture during certification and audits would help improve the repeatability of species richness estimates. Having surveyors visit randomly chosen plots or a geographically dispersed set of plots is also a form of insurance. Much like the effect of averaging, inaccurate surveys are essentially "diluted" by the more accurate surveys, minimizing regional bias. Most importantly, however, this strategy allows the analyst to detect and quantify observer effects.

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Special Notice

The following communications have been received by the Society:

Macrolichens of the Siskiyous, June 18-21, Course #: W8, Instructor: Ron Hamill

The Siskiyous are recognized as one of the most biologically diverse regions of the world. The abundance of forest types and unique geology of the Siskiyous are reflected in the richness of the lichen flora. This course will focus on the ecology and alpha-taxonomy of macrolichens of the region. Functional groups, morphological and chemical characters will be discussed and used for identification. Field trips to different habitats will be followed by identification sessions. Geared to all levels of experience. As microscopy, use of dichotomous keys and handling of reagents are necessary for proper identification, prior experience is helpful but not obligatory. Beginners should be overwhelmed but don't have to worry about getting everything, while advanced lichen lovers will likely learn a few things too. Tuition $160.

For more information and registration visit the Website: <http://www.siskiyou.org/sfi/class_toc_02.html>.

2002 EAGLE HILL FIELD SEMINARS ON THE COAST OF MAINE

Crustose Lichens: Special Topics, July 14-20, 2002, Instructor: Dr. Irwin M. Brodo

Emphasis-concentration on limited number of lichen groups, with in-depth studies using monographs and advanced literature; special attention to *Lecanora*, *Ochrolechia*, *Lecidea*, *Porpidia*, and *Rhizocarpon*: chemistry and identification of local sterile crustose lichens: participants invited to bring problem crustose lichens with them for study and discussion.

For more information and registration visit the Website: <http://maine.maine.edu/~eaglhill>.