USING EPIPHYTIC MACROLICHEN COMMUNITIES FOR BIOMONITORING AMMONIA IN FORESTS OF THE GREATER SIERRA NEVADA, CALIFORNIA

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Abstract. Chronic, excessive nitrogen deposition is potentially an important ecological threat to forests of the greater Sierra Nevada in California. We developed a model for ammonia bioindication, a major nitrogen pollutant in the region, using epiphytic macrolichens. We used non-metric multidimensional scaling to extract gradients in lichen community composition from surveys at 115 forested sites. A strong ammonia deposition gradient was detected, as evidenced by a high linear correlation with an index of ammonia indicator species conventionally known as "nitrophytes" ($r = 0.93$). This gradient, however, was confounded by elevation ($r = -0.54$). We evaluated three statistical techniques for controlling the influence of elevation on nitrophytes: simple linear regression, nonlinear regression, and nonparametric regression. We used the unstandardized residuals from nonlinear regression to estimate relative ammonia deposition at each plot, primarily because this model had the best fit ($r^2 = 0.33$), desirable asymptotic properties, and it is easy to apply to new data. Other possible sources of noise in the nitrophyte-ammonia relationship, such as substrate pH and acidic deposition, are discussed. Lichen communities indicated relatively high deposition to forests of the southern Sierra Nevada, the Modoc Plateau, as well as in stands near urban areas. Evidence of elevated ammonia was also detected for popular recreation areas such as Sequoia and Yosemite National Parks. Lichen communities from forests in the Tahoe basin, northern Sierra Nevada, southern Cascades, and eastern Klamath Range appeared considerably less impacted. This model will be used for continual assessment of eutrophication risks to forest health in the region.

Keywords: air pollution, ammonia, California, epiphytic lichens, forest health, gradients, indicator species, National Parks, nitric acid, nitrophytes, non-metric multidimensional scaling, Sierra Nevada

1. Introduction

As most forest ecosystems in the northern hemisphere are nitrogen (N) limited, short term atmospheric deposition of anthropogenic N tends to enhance plant productivity (Aber *et al.*, 1989). Chronic exposure to elevated levels, however, can culminate in a syndrome of ecosystem effects known as N saturation, which may include reduced soil fertility, enhanced volatilization of greenhouse gases from the soil, and in extreme cases, forest decline (Aber *et al.*, 1989). Especially within or downwind of agricultural areas, ammonia (NH_3) is typically the dominant component of N deposition. Excess NH_3 has been implicated in various impacts to

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terrestrial ecosystems, such as accelerated needle senescence in conifers, greater susceptibility of trees to frost damage and disease, reduced drought tolerance, reductions in diversity and abundance of ectomycorrhizal symbioses, shifts in herb community composition, and alteration of epiphytic lichen communities (reviewed by Krupa, 2003).

The affinity of certain epiphytic lichen species for NH_3 is well documented in the lichenological literature (e.g. de Bakker, 1989; Jovan and McCune, 2005; van Dobben and de Bakker, 1996; van Herk, 1999, 2001). These indicator species, known as "nitrophytes," are common, conspicuous components of the lichen flora in urban and agricultural landscapes. Van Herk (1999, 2001) found that an index of epiphytic nitrophyte abundance, the Nitrofiele Indicatie Waarde (NIW) could be positively, linearly related to NH_3 deposition in the Netherlands. A similar index developed by Jovan and McCune (2005), is currently used for NH_3 biomonitoring in forests of the greater Central Valley of California. The continual refinement and use of such models is particularly important in the United States where NH_3 is not regularly measured by state and federal air programs.

Epiphytic macrolichen communities are monitored by the Forest Inventory and Analysis Program (FIA) of the United States Department of Agriculture (USDA) to evaluate air quality impacts on forest health. Our main objective was to derive a gradient model, based upon FIA lichen data, to indicate NH_3 deposition in the greater Sierra Nevada (Figure 1). We adapted the methodology of Jovan and McCune (2005) to circumvent a common difficulty with large-scale biomonitoring across mountainous terrain: the tendency for elevation to confound the relationship between indicator species and the environmental factor of interest. In our case, NH_3 varied according to elevation, as did other physiologically important climatic gradients like moisture and temperature.

To extract the influence of elevation from the lichen community response to NH_3, we evaluated the pros and cons of using simple linear regression (SLR), nonlinear regression (NLR), and nonparametric regression (NPR; Bowman and Azzalini, 1997). We used the 'best' approach to adjust the bioindication model and estimate relative NH_3 deposition at 115 FIA forest health monitoring plots. Sites included popular recreation areas in Yosemite and Sequoia National Parks. While we focus on lichens and NH_3, our general methodology could be used for a wide variety of monitoring objectives and indicator organisms.

Degradation of air quality in greater Sierra Nevada forests has become a critical management issue, attributed mainly to the burgeoning tourism industry, forest fires, local agriculture, and long distance transport of pollutants from the highly agricultural and industrialized Central Valley (Figure 1; Cahill *et al.*, 1996; Fenn *et al.*, 2003; National Park Service, 2000). After ozone (O_3), experts consider chronic, excessive N the greatest potential threat to forest health in the region (Fenn *et al.*, 2003). Recent studies suggest NH_3 is the primary constituent of total N deposition (Bytnerowicz and Fenn, 1996; Bytnerowicz and Riechers, 1995; Bytnerowicz *et al.*, 2002; Fenn *et al.*, 2003). Some California forests adjacent to the Los Angeles Basin

Figure 1. Map of greater Sierra Nevada model area. Model boundary is delineated by thick gray line. Thinner black lines indicate Bailey's ecoregions (Bailey 1983). Triangles indicate off-frame plots while circles indicate on-frame plots. NP = National Park.

are already considered N saturated (reviewed in Takemoto *et al.*, 2001) although deposition to the Sierra Range is more moderate, suggesting stands are still in the accumulation phase of the N saturation trajectory (Fenn *et al.*, 2003).

2. Methods

2.1. STUDY AREA

The boundaries of the greater Sierra Nevada model area are based on a previous analysis of epiphytic macrolichen community data from Forest Inventory and Analysis (FIA) plots in northern and central California forests (Jovan and McCune, 2004). Jovan and McCune (2004) used multivariate analysis to group plots into three model areas with relatively similar lichen communities, climate, and topography. The strategy was to reduce environmental variability within the model areas, which may otherwise confound lichen responses to air quality. The Sierra Nevada model area encompasses four ecoregions as defined by Bailey (1983): the Southern Cascades, Modoc Plateau, Northwestern Basin and Range, and Sierra Nevada sections (Figure 1). The northwestern boundary follows the Southern Cascades Section but technically includes high elevation sites in the eastern Klamath Range (>1500 m) that are north of Castle Crags Wilderness and east of Scott Valley. A few plots from small cities in the Sierra Foothills section were also included.

Because the greater Sierra Nevada is mountainous and has a large geographic scope (Figure 1), climate and forest composition were still considerably heterogeneous. Plot elevations ranged from 379 to 2895 m with more than 85% of plots over 1000 m. According to climate maps derived using the Precipitation-elevation Regressions on Independent Slopes Model (PRISM; Daly *et al.*, 1994, 2001, 2002), average annual precipitation tends to increase with elevation (range: ~256 – 2261 mm) with a greater proportion of precipitation falling as snow. Mean annual temperature generally decrease with elevation (~2 – 15.7 C). A notable exception is the cool, high elevation desert of the Modoc Plateau, which lies in the rain shadow of the Klamath Range and southern Cascades.

Most plots occurred in mixed conifer stands dominated by species such as *Abies concolor*, *A. magnifica*, *Calocedrus decurrens*, *Pinus contorta*, *P. jeffreyii*, *P. ponderosa*, and *Pseudotsuga menziesii*. Riparian and low elevation stands often had a hardwood component (e.g. *Alnus rubra*, *Quercus chrysolepis*, *Q. douglasii*, and *Q. wislizenii*). *Ceanothus* spp. and *Arctostaphylos* spp. provided important lichen substrate in the forest understory and in chaparral communities. Vegetation in the Modoc Plateau was more characteristic of the Great Basin, with open stands of *Juniperus occidentalis* and abundant *Artemesia* spp.-steppe.

2.2. SAMPLING AND SURVEY PROTOCOL

Epiphytic macrolichen communities were surveyed at 115 FIA circular 0.38-ha plots (Figure 1). Ninety-one were permanent "on-frame" plots, located on a 27 km by 27 km FIA hexagonal sampling grid (Messer *et al.*, 1991). On-frame plots occurred on both public and private land, each surveyed once in the summer between 1998–2001. Plots falling on non-forested land or where the landowner restricted access were excluded from the sample, leading to a variable density of plots across the landscape (Figure 1). We surveyed an additional 24 "off-frame" plots in July 2003 (Figure 1), which occurred in residential, urban, and highly recreated areas like National Parks and National Monuments.

Surveys followed the standardized FIA protocol (McCune *et al.*, 1997) employed by Jovan and McCune (2005). Field crews collected specimens of each epiphytic macrolichen occurring above 0.5 m on woody substrates or in the litter. Each species was assigned an abundance class: 1 = rare (<3 thalli), 2 = uncommon (4–10 thalli), 3 = common (>10 thalli present but species occurs on less than 50% of all boles and branches), and 4 = abundant (>10 thalli present and species occurs on more than 50% of all boles and branches). Surveys lasted a minimum of 30 minutes and a maximum of two hours or until ten minutes passed before encountering a different species. Lichen collections were identified by professional lichenologists. The nomenclature of McCune and Geiser (1997) was used for identification of all genera except *Physcia* (Moberg, 2002), *Physconia* (Esslinger, 2000), and *Xanthoria* (Lindblom, 1997). Voucher specimens from off-frame plots reside at the Oregon State University Herbarium (OSC).

Field workers were not required to accurately assign names to lichen species in the field but were trained to differentiate between species based upon morphology during a three day intensive training session. All workers were required to pass a certification exam, for which they had to capture ≥65% of the species found by a professional lichenologist in a practice plot. Crew performance was periodically audited a total of nine times, by "hot checks" (both specialists and field crew surveyed a plot simultaneously) and "blind checks" (specialists re-measured a plot within two months of the crew survey). Field workers always captured at least 65% of the species found by specialists. McCune *et al.* (1997) determined that plot scores on ordination axes were highly repeatable as long as the 65% criterion was met.

2.3. ANALYSIS

Plots without lichens and duplicate surveys from audited plots were excluded from the dataset. For duplicates, we retained the survey conducted by the non-specialist who found the highest species richness. Infrequent species occurring in less than 5% of the plots were excluded from the dataset, which typically improves correlations between ordination axes and environmental variables (McCune and Grace, 2002). After removal of 39 infrequent species, the analysis was based on a total of 52 species in 115 plots (Table I).

Climate data were extracted from the PRISM data (Daly *et al.*, 1994, 2001, 2002) and averaged over 1961 to 1990. Climate variables (annual means) included: precipitation, number of wetdays, relative humidity, dew temperature, mean temperature, maximum temperature, and minimum temperature. Geographic and stand structure variables collected for each plot included elevation, latitude, longitude, total live basal area, basal area of live hardwoods, and basal area of live softwoods.

We derived several variables to describe lichen community gradients: overall lichen species richness, total lichen abundance (sum of all abundance classes per plot), nitrophyte richness, nitrophyte abundance, proportion of nitrophytes (proportion of species richness in nitrophytes), and proportion of nitrophyte abundance (PNA; proportion of total abundance in nitrophytes). The nitrophyte indices were based on Jovan and McCune (2004, 2005) who adopted the designations of Hawksworth and Rose (1970), McCune and Geiser (1997), and van Herk (1999, 2001). Nitrophytes are indicated in Table I. *Flavopunctelia flaventior* is the only designation not supported by at least one of these sources. The determination is

TABLE I

Summary of species found in lichen community plots. (N) designates species considered nitrophilous.% Freq = percentage of plots where the species occurred

	% Frequency	
Species	On-frame ($n = 91$)	Off-frame ($n = 24$)
Ahtiana sphaerosporella	27.5	16.7
Alectoria imshaugii	1.1	4.2
Alectoria sarmentosa	2.2	4.2
Bryoria capillaris	1.1	0.0
Bryoria fremontii	18.7	8.3
Bryoria friabilis	1.1	0.0
Bryoria fuscescens	2.2	0.0
Bryoria pseudofuscescens	1.1	0.0
Bryoria simplicior	2.2	0.0
Bryoria trichodes	1.1	0.0
Candelaria concolor (N)	41.8	83.3
Cetraria canadensis	1.1	0.0
Cetraria chlorophylla	9.9	8.3
Cetraria merrillii	44.0	62.5
Cetraria orbata	19.8	4.2
Cetraria pallidula	4.4	4.2
Cetraria platyphylla	30.8	20.8
Cladonia chlorophaea	1.1	0.0
Collema furfuraceum	5.5	20.8
Collema nigrescens	0.0	4.2
"Dendriscocaulon" sp.	0.0	4.2
Esslingeriana idahoensis	8.8	12.5
Evernia prunastri	15.4	54.2
Flavopunctelia flaventior (N)	1.1	16.7
Hypogymnia enteromorpha	1.1	0.0
Hypogymnia imshaugii	70.3	79.2
Hypogymnia occidentalis	1.1	4.2
Hypogymnia tubulosa	1.1	8.3
Koerberia biformis	0.0	4.2
Leptochidium albociliatum	1.1	0.0
Leptogium cellulosum	0.0	4.2
Leptogium furfuraceum	2.2	0.0
Leptogium lichenoides	6.6	0.0
Letharia columbiana	65.9	58.3
Letharia vulpina	84.6	62.5
Lobaria hallii	1.1	0.0
Melanelia elegantula	34.1	50.0
Melanelia exasperatula	20.9	16.7
Melanelia glabra	16.5	29.2
Melanelia subargentifera	0.0	20.8
Melanelia subelegantula	12.1	12.5

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TABLE I
(*Continued*)

Species	% Frequency	
	On-frame ($n = 91$)	Off-frame ($n = 24$)
Melanelia subolivacea	49.5	79.2
Nodobryoria	0.0	37.5
Nodobryoria abbreviata	50.6	16.7
Nodobryoria oregana	31.9	0.0
Parmelia hygrophila (N)	9.9	12.5
Parmelia pseudosulcata	1.1	0.0
Parmelia saxatilis	1.1	0.0
Parmelia sulcata	23.1	58.3
Parmelina quercina	6.6	20.8
Parmeliopsis ambigua	4.4	4.2
Parmeliopsis hyperopta	3.3	0.0
Peltigera collina	5.5	0.0
Phaeophyscia ciliata	2.2	4.2
Phaeophyscia orbicularis (N)	3.3	29.2
Physcia adscendens (N)	12.1	54.2
Physcia aipolia (N)	8.8	29.2
Physcia biziana	5.5	8.3
Physcia dimidiata (N)	6.6	0.0
Physcia stellaris (N)	5.5	54.2
Physcia tenella (N)	14.3	66.7
Physcia tribacia (N)	0.0	4.2
Physconia americana (N)	13.2	45.8
Physconia enteroxantha (N)	13.2	58.3
Physconia fallax (N)	5.5	29.2
Physconia isidiigera (N)	12.1	45.8
Physconia perisidiosa (N)	16.5	66.7
Platismatia glauca	14.3	25.0
Platismatia herrei	0.0	0.0
Pseudocyphellaria anomala	2.2	0.0
Pseudocyphellaria anthraspis	3.3	0.0
Punctelia perreticulata (N)	0.0	8.3
Ramalina farinacea	0.0	4.2
Ramalina subleptocarpha (N)	2.2	25.0
Tholurna dissimilis	1.1	0.0
Usnea diplotypus	1.1	0.0
Usnea filipendula	9.9	8.3
Usnea lapponica	1.1	0.0
Usnea nidulans	1.1	0.0
Usnea pacificana	2.2	0.0
Usnea scabrata	2.2	0.0
Usnea subfloridana	1.1	0.0
Usnea substerilis	1.1	8.3

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TABLE I

(*Continued*)

Species	% Frequency On-frame ($n = 91$)	Off-frame ($n = 24$)
Vulpicida canadensis	3.3	12.5
Xanthoria candelaria (N)	18.7	12.5
Xanthoria fallax (N)	8.8	25.0
Xanthoria fulva (N)	16.5	37.5
Xanthoria hasseana (N)	12.1	45.8
Xanthoria oregana (N)	19.8	45.8
Xanthoria parietina (N)	2.2	0.0
Xanthoria polycarpa (N)	11.0	62.5

based wholly on the authors' experience in the field wherein this species appears to be a regular component of the nitrophyte community.

2.3.1. *Ordination*

We used PC-ORD software (version 4.20; McCune and Mefford, 1999) to extract the strongest gradients in lichen community composition following the methodology of Jovan and McCune (2005). Non-metric multidimensional scaling (NMS; Kruskal, 1964) ordination with Sørensen distance measure was conducted on a matrix of sample units by species abundance. The data underwent 999 runs, each consisting of a maximum of 500 iterations. We selected the ordination solutions with the lowest stress for a given dimensionality. Among those, we chose the final solution using a stress improvement criterion of five. In other words, a solution with n dimensions was favored over a solution with $n-1$ dimensions only if the additional axis reduced stress by five or more.

The final solution was evaluated against a Monte Carlo test of 500 runs with randomized data to determine whether patterns were stronger than would be expected by chance. We calculated coefficients of determination between original plot distances and distances in the final ordination solution to determine how much variability in lichen community composition was represented by the NMS axes (McCune and Grace, 2002). We used orthogonal rotation to maximize correlations of NMS axes to environmental and lichen community variables. Ordination scores for plots and species were visualized in scatterplots. Species scores were calculated by a single weighted averaging step (McCune and Grace, 2002).

2.3.2. *Elevation Models and Air Quality Score Adjustment*

To extract elevation effects, we adjusted the lichen community response to NH_3 with a strategy similar to McCune *et al.* (1998). They used the standardized residuals from a simple linear regression (SLR) of elevation on an index of pollution indicator species as "adjusted air scores". We modeled the relationship between PNA and elevation using three methods: SLR, nonparametric regression (NPR) with a local mean model, and nonlinear regression (NLR) with the following 3-parameter generalized sigmoid curve:

$$Y = \frac{a}{1 + (\text{Elevation}/c)^b}$$

where Y is the fitted value, a is the upper asymptote, b is a coefficient, and c is the elevation at the inflection point. We compared the applicability, ease of communication and use, performance, and inherent bias along the response curve of each statistical approach. The unstandardized residuals from the "best" approach served as estimates of relative NH_3 deposition at each plot, hereafter referred to as "air scores." We used SPSS (2001) to conduct the NLR and HyperNiche (McCune and Mefford, 2004) for the SLR and NPR.

We included NPR as it can resolve complex response curves. Unlike traditional regression, NPR does not calculate coefficients for a mathematical function relating the response variable to predictors. Instead model building iteratively optimizes model fit without reference to a specific global model form. The investigator specifies a local model or kernel function (Bowman and Azzalini, 1997). The local model defines how plots are weighted for a prediction at a given point in the habitat space and specifies the shape of the function used to fit points. We used a local mean estimator and Gaussian kernel function to relate proportion of nitrophytes to elevation. We selected a minimum average neighborhood size of 3 plots. The standard deviation (tolerance) of the kernel function was optimized by cross-validated coefficients of determination (xr^2), the statistic we used to evaluate model fit.

3. Results and Discussion

3.1. ORDINATION RESULTS

The non-metric multidimensional scaling (NMS) ordination had two axes with a final stress and instability of 20.05 and 0.03, respectively. Minimum stress of the ordination was lower than would be expected by chance ($p < 0.005$). Axis 1 explained most of the variability in lichen community structure ($r^2 = 0.57$) while axis 2 was relatively weak ($r^2 = 0.24$). As axis 2 appeared primarily driven by climatic gradients, it will not be fully discussed further in this paper (Figure 2 and Table II).

The high linear correlations of nitrophyte abundance ($r = 0.84$) and proportion of nitrophyte abundance (PNA; $r = 0.93$) to axis 1 suggest ammonia (NH_3) is a major factor driving this lichen community gradient (Figure 2 and Table II). Indices of nitrophyte richness were similarly correlated (Table II). Although NH_3 deposition

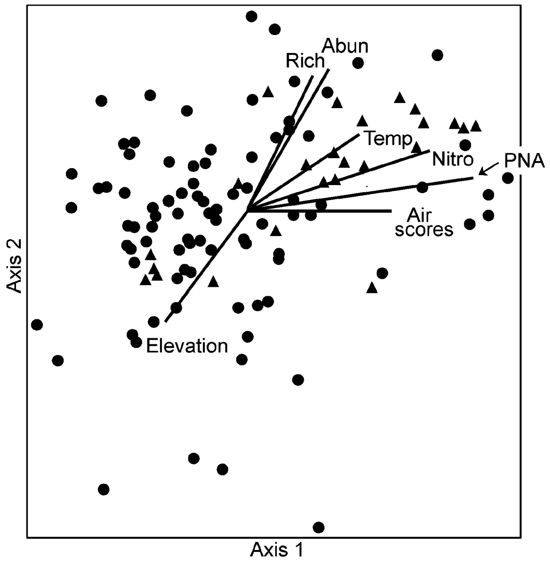

Figure 2. Ordination joint plot with environmental and lichen community variables overlaid. Triangles indicate off-frame plots while circles indicate on-frame plots. Vector lengths and directions indicate correlations with the ordination. Most vectors with $r^2 > 0.25$ are shown. To prevent crowding, related variables with overlapping vectors of similar strength are designated by a single label: Temp (temperature) represents dew temperature, mean temperature, minimum temperature, and maximum temperature; Nitro includes nitrophyte diversity and abundance; and PNA includes proportion of species richness and lichen abundance at a plot in nitrophytes. Abbreviations for other environmental vectors are: Rich = total lichen species richness, Abun = total lichen abundance (sum of abundance codes), and Air scores = air quality scores adjusted for elevation.

data were not available for model calibration, our interpretation is strongly supported by the lichenological literature (Benfield, 1994; de Bakker, 1989; Jovan and McCune, 2005; van Dobben and de Bakker, 1996; van Herk, 1999, 2001). The PNA index was strongly, positively related to estimated NH_3 deposition in the greater Central Valley (Jovan and McCune, 2005). Likewise, Van Herk (1999, 2001) found a comparable relationship between atmospheric NH_3 and Nitrofiele Indicatie Waarde (NIW) scores in the Netherlands, calculated as the mean abundance of nitrophytes over ten *Quercus robur* trees. Most of our nitrophyte designations are consistent with the NIW and as would be expected, all of these species had moderate to high scores on axis 1 (Figure 3).

We must consider, however, that nitrophytes were probably also responding to climatic variability (Figure 4). As anticipated, elevation also had an appreciable correlation with axis 1 ($r = -0.54$; Figure 2) as did climatic variables normally patterned on elevation, like temperature and precipitation (Table II). We are unaware of a documented "upper elevation limit" for nitrophytes. Nonetheless, epiphytic lichen diversity and abundance generally tend to decrease with increasing elevation

TABLE II

Summary of correlation coefficients for correlations between ordination axes and topographic, environmental, and lichen community variables

	r	
Variable	Axis 1	Axis 2
Longitude	0.21	−0.39
Latitude	−0.32	0.17
Elevation	−0.54	−0.63
Dew temperature	0.63	0.55
Maximum temperature	0.60	0.60
Mean temperature	0.67	0.55
Minimum temperature	0.67	0.45
Humidity	−0.06	0.13
Wetdays	−0.46	0.10
Precipitation	−0.19	0.31
Total live basal area	−0.28	0.07
Hardwood basal area	0.47	0.21
Softwood basal area	−0.35	0.52
Species richness	0.52	0.72
Total lichen abundance	0.57	0.73
Proportion of nitrophyte abundance	0.93	0.37
Proportion of nitrophyte richness	0.91	0.36
Nitrophyte abundance	0.84	0.49
Nitrophyte richness	0.83	0.50
Adjusted air scores	0.75	0.02

in the study area, as clearly illustrated by the almost diametrically opposed richness, abundance, and elevation vectors in the ordination (Figure 2).

A small contingent of non-nitrophilous species, such as *Ahtiana sphaerosporella*, *Letharia vulpina*, *L. columbiana*, and *Cetraria merrillii*, usually dominate high-elevation forests throughout the Cascades and Sierra Nevada ranges. These high-elevation habitats are arguably harsher from a lichen's perspective, due to factors like lower temperatures (Figure 2) and higher proportions of precipitation falling as snow (not measured; Figure 4). Nitrophyte distributions in particular may be also be affected by the scarcity of hardwood substrates at mid to high elevations (Figure 4). Nitrophytes are not exclusively associated with hardwoods but there is evidence that richness and abundance within a community are positively affected by the chemical properties of hardwood bark, to be discussed further in the “Effect of natural bark pH” subsection.

Confounding thus occurs as NH_3 varies with elevation (Figure 4). Ammonia emissions sources are more concentrated in the low elevation foothills. This geographic belt, especially in the south, has a greater density of cities, larger cities, more farms, and more ranching (Momsen, 2001; Figure 4). Additionally, foothill

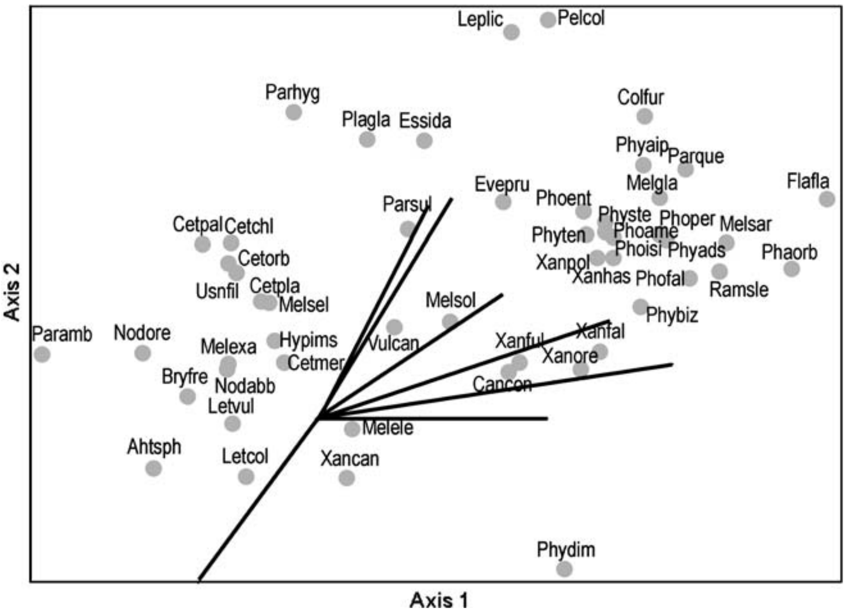

Figure 3. Ordination joint plot with environmental and lichen community variables overlaid as vectors. Gray circles indicate species' centroids (i.e. species scores along axes 1 and 2). Names are abbreviated to the first three letters of the genus and species epithet with the following exceptions: Melsar = *Melanelia subargentifera*, Melsel = *Melanelia subelegantula*, Melsol = *Melanelia subolivacea*.

forests are nearest to the highly agricultural Central Valley where NH_3 emissions are high and lichen communities characteristically dominated by nitrophytes (Jovan and McCune, 2004, 2005). Ammonia has a high deposition velocity so a high proportion is deposited locally, just downwind of the emissions source (Asman and van Jaarsveld, 1992). Direct monitoring data do show higher bulk N deposition at lower elevation forests of the western Sierra Nevada (Bytnerowicz *et al.*, 2002; reviewed in Fenn *et al.*, 2003) although few comparable data are available for NH_3 specifically.

3.2. MODEL ADJUSTMENT

A scatterplot between elevation and PNA showed a relationship resembling either a straight line or sigmoid curve (Figure 5). According to a simple linear regression (SLR), elevation represented 31% of the variance in the PNA ($p < 0.001$; Figure 5). A one hundred-meter increase in elevation is associated with an average decrease of 2.7% in PNA (95% confidence interval: 1.9% to 3.5%). Nonlinear regression (NLR) explained slightly more variability in the data ($r^2 = 0.33$; Table III) but yielded a more complex sigmoid model (Figure 5). Hyperniche fit an approximately sigmoid curve to the nonparametric regression (NPR) model with a cross-validated r^2 of

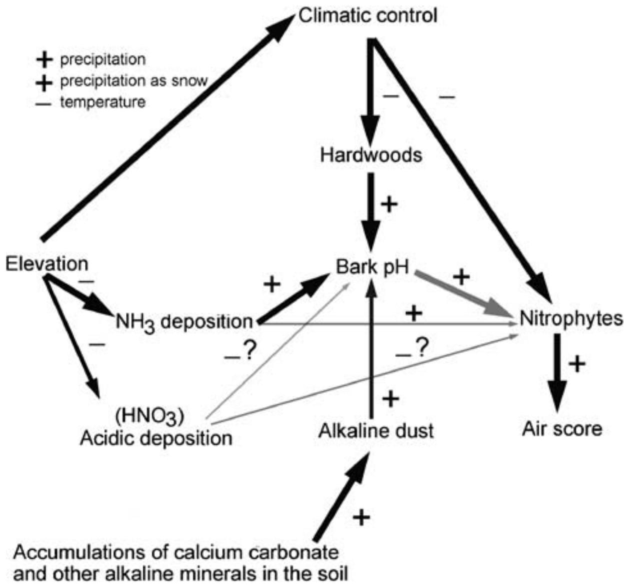

Figure 4. Hypothesized environmental effects on nitrophytes in the greater Sierra Nevada model area. Anticipated positive (+) and negative (−) correlations are noted above each arrow. Arrow thickness indicates expected effect size. We emphasize the hypothesis that the nitrophyte-NH_3 relationship is mediated by bark pH although the other predominant mechanism (NH_3 affects nitrophytes directly) is also included in the diagram. Gray arrows indicate understudied phenomena or effects for which there are competing hypotheses. Alkaline dust is typically associated with the soil taxonomic order Aridisols. It is diagrammed independently of climatic variables because the formation of Aridisols is associated with both climatic (aridic soil moisture regime and a thermic to cryic soil temperature regime) and non-climatic factors (e.g. composition of soil parent material, site geologic history).

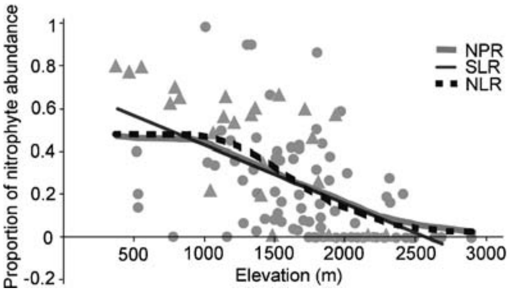

Figure 5. Regressions of proportion of nitrophyte abundance on elevation with three methods: nonparametric regression (NPR), simple linear regression (SLR), and nonlinear regression (NLR). Gray triangles indicate off-frame plots and gray circles indicate on-frame plots.

TABLE III

Best fit values for parameters of generalized sigmoid model found by nonlinear regression of proportion of nitrophyte abundance on elevation. SE = standard error

Parameter	Estimate	SE	95% Confidence interval
Asymptote	0.48	0.06	0.37 to 0.60
Inflection point	1690	108	1476 to 1904
Slope	5.91	1.89	2.17 to 9.66

0.26 (Figure 5). The NPR response curve was based upon an average neighborhood size of 36 and an optimized tolerance (standard deviation) of 252 m for elevation. This tolerance means that points within ± 252 m elevation of a target point are given the most weight in the local mean.

Simple linear regression appeals in its ease of application, ease of communication, and generally good fit to the data (Table IV). Yet the model is fatally flawed since the regression line crosses the x-axis (Figure 5). Thus, a plot higher than 2600 m would need to have an impossible negative abundance of nitrophytes to be assigned a low air score, a low air score being roughly equivalent to low NH_3 deposition for a given elevation. The remaining two models yielded similar response curves but we favored NLR because it had the better fit to the data and additional plots could be easily fit with the regression equation (Table IV).

To score plots, one first calculates the PNA from the lichen community data using the nitrophyte designations in Table I:

$$\text{PNA}_i = \frac{\sum_{j=1}^{S} x_{ij} w_j}{\sum_{j=1}^{S} x_{ij}}$$

where S = number of species, x_{ij} = the abundance of species j in plot i, and w_j = a vector of binary values indicating whether each species is a nitrophyte ($w_j = 1$) or not ($w_j = 0$). Plot elevation in meters is plugged into the following NLR equation to find the expected proportion of nitrophytes, the fitted value (Y):

$$Y = \frac{0.48}{1 + (\text{Elevation}/1689)^{5.91}}$$

The final air score is the unstandardized residual from the NLR model multiplied by 100:

$$\text{Air quality score} = 100\,(\text{PNA} - Y)$$

Air scores are interpreted as the percentage of nitrophytes above or below what is expected for a given elevation, so higher scores indicate relatively higher NH_3 deposition.

TABLE IV

Comparison of pros and cons for three different modeling approaches. NPR = nonparametric regression

Criteria	Simple linear regression	NPR local mean	Nonlinear regression
Ease of application	New response values can easily be predicted using the regression equation	NPR does not generate an equation so the investigator must use statistical software to estimate new values.	New response values can easily be predicted using the regression equation
Ease of communication	This technique is the easiest to communicate, being mechanistically simple and commonly used	NPR is the most difficult to communicate, being a statistical approach that is unfamiliar to many.	Nonlinear regression is a more common analysis technique than NPMR in biological studies. However, the investigator must determine which mathematical function is most appropriate for modeling and justify that choice.
Fit (r^2 or xr^2)	$r^2 = 0.31$	$xr^2 = 0.26$	$r^2 = 0.33$
Fit (areas of bias)	The regression line crosses the x-axis, meaning plots at elevations above 2600 m will always be scored as having poor air quality.	More low elevation plots (~250 to 1000 m) would be classified as having poor air quality scores relative to the linear model. Please see description of bias for nonlinear regression.	Scoring by the nonlinear model is less conservative than the linear and NPR models at mid elevations (1000 to 1570 m): proportionally fewer plots would be classified as having better air quality than expected for a given elevation. The opposite is true for plots between 1700 and 2270 m. However, these differences are slight.

3.3. INTERPRETATION OF AIR SCORES AND SOURCES OF VARIABILITY

The vector for air scores was strongly correlated with NMS axis 1 ($r = 0.75$) and aligned closely with the nitrophyte indices (Figure 2). Most plots scoring on the extreme high end of axis 1 were off-frame, and thus were located in urban, residential and heavy recreation areas (Figure 2). We would logically expect higher NH_3

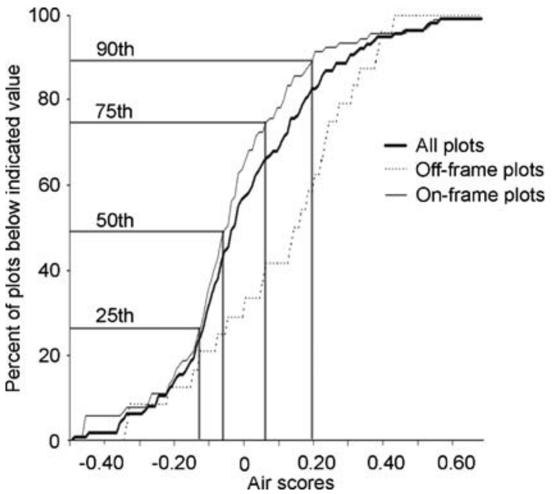

Figure 6. Cumulative frequency distribution of air scores. Data are divided into the 25th, 50th, 75th, and 90th percentiles for on-frame plots. Higher scores indicate worse air quality.

deposition in areas with higher human activity due to: 1) emissions from motor vehicle catalytic converters, which constitute a major NH_3 source in California (Committee on the Environment and Natural Resources Air Quality Research Subcommittee, 2000); 2) point source emissions from industry; 3) biomass burning (i.e. emissions from wood stoves, campfires, forest fires); and 4) the presence of farms and livestock.

The cumulative frequency of air scores shows that considerably more off-frame plots had poor (high) air scores than on-frame plots (Figure 6). The 25th, 50th, 75th, and 90th percentiles were based on scores for on-frame plots only (Figures 6 and 7) since the FIA program will not re-sample and track lichen communities at off-frame plots. The median air score for on-frame plots was −0.06, and 50% scored between −0.13 to 0.06 (Figure 6). The median for off-frame plots was much higher at 0.15, with 50% of plots scoring between −0.07 and 0.24.

Air scores may have a linear relationship to NH_3 deposition as the PNA had a linear relationship to estimated NH_3 in the adjacent greater Central Valley (Jovan and McCune, 2005). The related NIW index was also linearly related to NH_3 deposition in the Netherlands (van Herk, 1999, 2001). By controlling for confounding factors associated with elevation (Figure 4), we have indeed improved our chances of capturing this simple linear relationship. On the other hand, this adjustment could have extracted some useful information from the model since, as discussed earlier, NH_3 probably varies as a function of elevation. Ideally we have retained that variability in the PNA although we'd need NH_3 measurements to gauge our success.

There remain two potentially important sources of noise in our data, both relating closely to the alleged mechanism of the nitrophyte-NH_3 association. As the name "nitrophyte" implies, lichenologists have long held the notion that these species

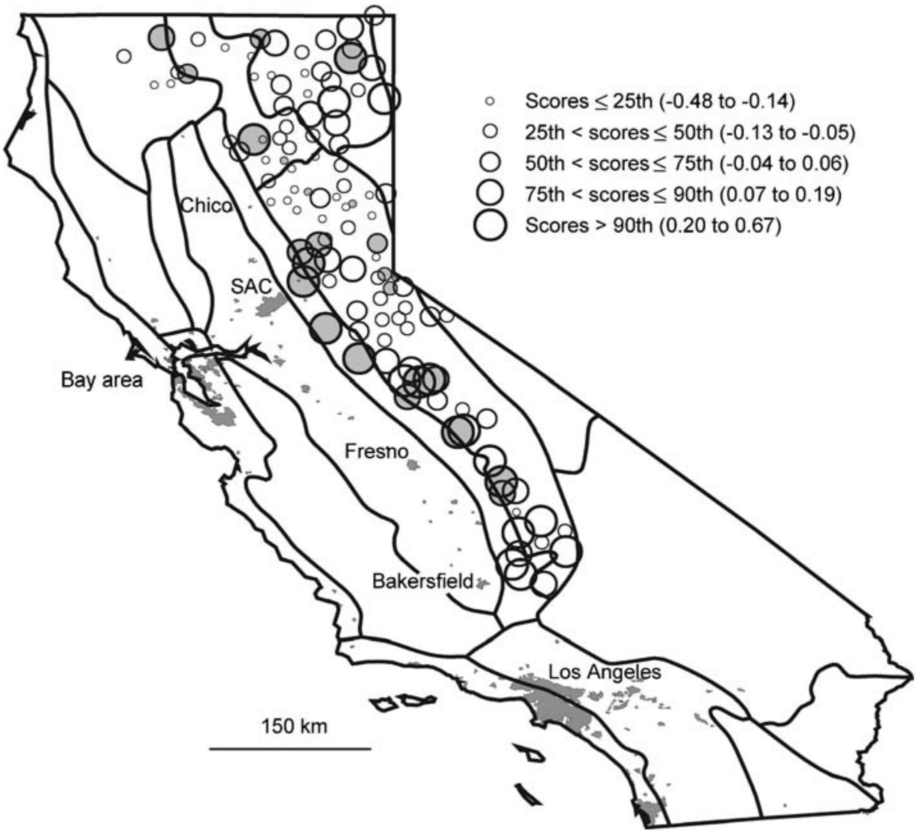

Figure 7. Map of air scores. Circles represent lichen community plots. Classes are based upon the 25th, 50th, 75th, and 90th percentiles of air scores at on-frame plots. Off-frame plots and urban areas are shaded gray. SAC = Sacramento.

require abundant N. Yet there is considerable evidence for an alternative mechanism: that nitrophytes are primarily promoted by substrates with high pH rather than high N content (van Dobben and de Bakker, 1996; van Dobben and ter Braak, 1998; van Herk, 1999, 2001). Being the only alkaline gas in the atmosphere, nitrophyte abundances are often easily tied to NH_3 concentrations (e.g. van Herk 1999, 2001; Jovan and McCune, 2005) presumably via raising bark pH (Figure 4). This appears to be the favored mechanism, suggested by its prominence in the lichenological literature over the last decade. Yet there certainly is no consensus (van Haluwyn and van Herk, 2002).

3.3.1. *Effect of Natural Bark pH*

“Natural” variability in bark pH (i.e. unaffected by pollutant deposition), thus, probably adds noise to the nitrophyte-NH_3 relationship. This effect can be tempered by sampling lichen communities from a single tree species like van Herk (1999, 2001). Yet such restriction is often impossible, as in our case, when modeling a sizeable, topographically heterogeneous area. At such large spatial scales, the predominance of hardwoods at sampled plots is important to consider (Figure 4) as hardwood bark, in general, is naturally more alkaline than conifer bark (e.g. Barkman, 1958). Conceivably, conifers must intercept more NH_3 deposition to achieve the same nitrophyte loading, all else being equal. Natural pH effects on our air scores should have been considerably subdued by adjusting the model for elevation, since hardwood basal area decreases with elevation (Table II and Figure 4). Accordingly, a post hoc SLR of hardwood basal area on air scores showed only a weak correlation ($r^2 = 0.09$; $p < 0.01$). Regardless, natural variability in bark pH may be an important source of noise in large-scale models.

3.3.2. *Acidic Deposition Effect?*

Ammonia and acidic deposition may have antagonistic effects on nitrophyte abundance (van Dobben, 1983; van Dobben and ter Braak, 1998; Figure 4). This hypothesis has not been rigorously tested although it seems worthy of consideration, given the evidence that substrate pH plays an intermediary role in the lichen-NH_3 association. Of particular import in the greater Sierra Nevada is nitric acid (HNO_3), a major component of acidic deposition in California (California Environmental Protection Agency, 2000; Takemoto *et al.*, 1995). As discussed by Jovan and McCune (2005), the relationship between lichens and HNO_3 is virtually unknown. The lack of comprehensive HNO_3 monitoring data for northern and central California has so far precluded any informative investigation.

We expect NH_3 is the primary factor controlling nitrophyte abundance in our study area. Nitrogen-apportionment data for the southwestern Sierra Nevada show NH_3 makes a far greater contribution to total N deposition than HNO_3 (Bytnerowicz and Riechers, 1995; Bytnerowicz *et al.*, 2002). We also know that reduced N compounds (NH_x) dominate N deposition where measured in the western Sierra Nevada (Fenn *et al.*, 2003). Additionally, the geographic distribution of air scores coincides well with known NH_3 deposition and land use patterns as described below in the "Distribution of air scores" section. Even so, without additional pollutant data, we cannot conclude with certainty that HNO_3 has no effect.

3.3.3. *Effects of Other Major Pollutants*

Other major anthropogenic pollutants probably have little, if any, influence on air scores. Jovan and McCune (2005) found that the PNA was independent of ozone (O_3) and nitrogen dioxide (NO_2) concentrations, which are both high in parts of the greater Sierra Nevada. Sulfur dioxide (SO_2) effects are also unlikely as ambient levels in California are beneath the threshold at which research suggests even the most sensitive lichen species respond (Peterson *et al.*, 1992). Direct measurements from the California Air Resources Board monitoring network show annual means that are usually below 3 ppb in northern and central California. Nitrophyte sensitivities to various common air pollutants are reviewed more elaborately by Jovan and McCune (2005).

3.4. DISTRIBUTION OF AIR SCORES

More than half of the plots scoring above the 90th percentile were concentrated in the southern Sierra Nevada adjacent to the San Joaquin Valley (Figure 7). Accordingly, a high proportion of both on and off-frame plots in this region scored above the 75th percentile (Figure 7), which is consistent with preexisting data regarding NH_3 deposition and emission patterns. Over 50% of estimated NH_3 emissions from fertilizers and confined cattle operations in California originate in the San Joaquin Valley (California Air Resources Board, 1999; Potter *et al.*, 2001). Reduced N pollutant deposition along a north-south transect in the Sierra Nevada is highest in the southwestern part of the range (reviewed in Fenn *et al.*, 2003). Some low-elevation chaparral watersheds in the region are showing early signs of N saturation (Fenn *et al.*, 2003). These results complement Jovan and McCune (2005), who suggested that epiphytic lichen communities in the San Joaquin Valley were, overall, the most severely impacted by NH_3 in the greater Central Valley.

Other plots scoring above the 75th percentile include off-frame plots downwind of the Sacramento metropolitan area, Alturas in the Modoc Plateau, and Yreka near the Interstate-5 corridor (Figure 7). Several plots in the Modoc plateau also had PNA greater than 10% of the expected value. Even though this area is relatively remote and sparsely populated (approximately 43,300 in total), agriculture is a major land use. Modoc and Lassen host the highest acreage in farms relative to all other counties in the study area (Momsen, 2001). Because this region is relatively arid, however, calcareous or alkaline dust may also promote nitrophytes (Figure 4), a phenomenon inferred by Gilbert (1976), Loppi and Pirintsos (2000), Neitlich *et al.* (2003) and van Herk (1999).

Otherwise, lichen community data suggest that NH_3 deposition is comparatively low at most on-frame plots in the northern third of the study area (Figure 7). The same general pattern was found for total N deposition, which is low in northern forests (2–4 kg N/ha/year; Blanchard and Michaels, 1994) relative to sites in the southwestern Sierra Nevada (2–17 kg N/ha/year; reviewed in Fenn *et al.*, 2003). All but one plot scoring below -0.20 occur in this region. Lichen communities at many of these plots were diverse, resembling what we'd expect at mixed conifer stands with low NH_3 deposition. At plots scoring below the 25th percentile especially, communities were typified by high abundances and diversity of *Hypogymnia*, *Cetraria*, *Melanelia*, *Nodobryoria*, *Letharia* and common instances of *Bryoria fremontii*, *Evernia prunastri*, *Parmelia sulcata*, and *Usnea filipendula*.

Most of these genera contain species van Herk identifies as sensitive to NH_3 deposition, known as acidophytes (1999, 2001). As expected, these species tended to have low scores along axis 1 (Figure 3). There is recent evidence that ammonium, the reaction product of NH_3, may also have deleterious effects on acidophytes (van Herk *et al.*, 2003) although more investigation is needed before we can truly capitalize upon this relationship for bioindication. We did not employ acidophyte-based indices primarily because this group is poorly defined for North America. These species are indirectly involved in the PNA, however, via the relativisation of nitrophyte abundance by total lichen abundance.

A better understanding of acidophyte ecology should be a priority for bioindication efforts in the United States as these are the most vulnerable species in NH_3-affected forests and would likely be the first to disappear. Some North American candidates such as the *Bryoria* species play crucial functional roles in western forest ecosystems, for instance, serving as major wildlife forage (elk, caribou, deer, flying squirrels), nesting materials (many bird species and rodents), and invertebrate habitat.

3.4.1. *Tahoe Basin*

High elevation plots near the Tahoe Basin also had low air scores (-0.15 to -0.03; Figure 7) even though local N deposition is implicated, at least partly, in the decrease in lake clarity observed over the last five decades (Cahill *et al.*, 1996; Jassby *et al.*, 1994). Our inability to detect analogous evidence of eutrophication with nitrophytes is probably because high-elevation oligotrophic lakes like Lake Tahoe have extremely low N critical loads. Nitrogen deposition (4–5 kg N/ha/year; *Fenn et al.*, 2003) is actually low relative to the southwestern Sierras. Likewise, phosphorous is also believed to be an important fertilizing agent in the lake (reviewed in Fenn *et al.*, 2003) but would not be likely to affect nitrophile abundance. A third consideration is that NO_x compounds make up a large proportion of total local N deposition (Fenn *et al.*, 2003).

3.4.2. *Sequoia and Yosemite National Parks*

The model indicated elevated NH_3 deposition in the southern National Parks, Sequoia and Yosemite, where plots received a mixture of high air scores. The plot along the Lower Kaweah river in Sequoia had the highest score (0.39) while the plot at Turtleback Dome in Yosemite, located above the parking lot of a popular viewpoint, also scored well above the 90th percentile (0.35). The plots at Yosemite Village (0.21), the hub of commerce and heavy traffic congestion in the park, and at Lookout Point in Sequoia National Park (0.11) were somewhat lower (Figure 7). These results are congruent with previous air quality work conducted in Sequoia National Park. Bytnerowicz *et al.* (2002) found elevated NH_3 at the Lower Kaweah site (seasonal mean $= 2.6\,\mu g/m^3$) although deposition at a lower elevation site not sampled in our study, Ash Mountain, was even higher ($4.5\,\mu g/m^3$). Other studies have documented relatively high N deposition in canopy throughfall in Sequoia National Park (6–15 kg N/ha/yr; reviewed in Fenn *et al.*, 2003). Nitrogen deposition patterns in Yosemite National Park are less well known.

Some air pollution in these forests probably originates from the San Joaquin Valley. However, tourism is likely an additional major source of NH_3 emissions and other air pollutants. According to the National Park Service (NPS), 1.4×10^6 people visited Sequoia and 3.3×10^6 people visited Yosemite in 2002 alone. In addition to area sources of pollution (e.g. hotels, campsites, housing developments, sewage treatment facilities), motor vehicle exhaust is recognized as a major ecological threat in both parks, but especially in the Yosemite Valley (National Park Service, 2000). Plans to restrict use of private vehicles in Yosemite have been the recent focus of a heated debate among visitors, lawmakers, and NPS managers. Baum *et al.* (2000) suggested that scientists have underestimated the contribution of motor vehicle exhaust to NH_3 deposition. They found that, on average, a car emits 94 mg/km traveled. Emissions have dramatically increased since the widespread adoption of 3-way catalytic converters for NO_x control. Back in 1981, for instance, Pierson and Brachaczek (1983) calculated an emission rate of $1.3 \pm 3.5\ \mathrm{mg/km}^{-1}$.

4. Conclusions

Forest Inventory and Analysis plots adjacent to the San Joaquin Valley as well as plots near some urban areas indicate relatively high ammonia (NH_3) deposition. Epiphytic lichen communities near Yosemite and Sequoia National Parks also show strong evidence of NH_3 enrichment. Overall, NH_3 deposition appears to be low in most rural plots in our study area, outside the southwestern Sierra Nevada. The severity of NH_3 impacts to lichen communities on the Modoc Plateau remains unclear until we better understand the contributions of alkaline dust versus NH_3 to nitrophyte abundance. We anticipate that air scores are affected minimally by nitric acid (HNO_3) deposition. Nevertheless, future biomonitoring work in the greater Sierra Nevada should include concurrent lichen community surveys and short-term passive monitoring of NH_3 and HNO_3 to clarify this assumption.

Ammonia bioindication is very important for the greater Sierra Nevada where nascent signs of N saturation have been detected in some southern chaparral communities (Fenn *et al.*, 2003). Comprehensive direct NH_3 monitoring is lacking even though much of the study area regularly intercepts polluted air masses from the highly agricultural and industrialized Central Valley (Cahill *et al.*, 1996). Local emissions are expected to increase as the human population in the Sierra Nevada alone is forecasted to increase by 1.5 to 2.4 million people by 2040 (University of California SNEP Science Team and Special Consultants, 1996).

Lichens provide an excellent, inexpensive alternative for estimating fine-scale distributions of NH_3. Because of its high deposition velocity (Asman and van Jaarsveld, 1992), NH_3 is difficult to accurately map without a high density of monitoring locations. Tracking epiphytic lichen communities with the presented Forest Inventory and Analysis (FIA) bioindication model is an important first step towards determining eutrophication risks to forest health in the region. Ultimately we envision this modeling approach as a stepping stone to more sophisticated bioindication, namely towards models that yield more quantitative NH_3 estimates.

Such an accomplishment, however, greatly hinges upon our progress identifying and controlling for major sources of noise in the nitrophyte-NH_3 relationship.

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References

Aber, J. D., Nadelhoffer, K. J., Steudler, P. and Melillo, J. M.: 1989, 'Nitrogen saturation in northern forest ecosystems', *BioScience* **39**, 378–386.

Asman, W. A. H. and van Jaarsveld, J. A.: 1992, 'A variable-resolution transport model applied for NH_x for Europe', *Atmos. Environ.* **26**, 445–464.

Bailey, R. G.: 1983, 'Delineation of ecosystem regions', *Environ Manage.* **7**, 365–373.

Barkman, J. J.: 1958, *Phytosociology and Ecology of Cryptogamic Epiphytes*, Van Gorcum, Assen, Germany, pp. 628.

Baum, M. M., Kiyomiya, E. S., Kumar, S., Lappas, A. and Lord, H., III: 2000, 'Multicomponent remote sensing of vehicle exhaust by dispersive absorption spectroscopy. 1. Effect of fuel type and catalyst performance.' *Environ. Sci. Technol.* **34**, 2851–2858.

Benfield, B.: 1994, 'Impact of agriculture on epiphytic lichens at Plymtree, east Devon', *Lichenologist* **26**, 91–94.

Blanchard, C. L. and Michaels, H.: 1994, 'Regional Estimates of Acid Deposition Fluxes in California', *Final Report No.A132–149*. Air Resources Board, Sacramento, California, USA, pp. 98.

Bowman, A. W. and Azzalini, A.: 1997, '*Applied Smoothing Techniques for Data Analysis*', Clarendon Press, Oxford, UK, pp. 204.

Bytnerowicz, A. and Fenn, M.: 1996, 'Nitrogen deposition in California forests: a review', *Environ. Pollut.* **92**, 127–146.

Bytnerowicz, A. and Riechers, G.: 1995, 'Nitrogenous air pollutants in a mixed conifer stand of the western Sierra Nevada, California', *Atmos. Environ.* **29**, 1369–1377.

Bytnerowicz, A., Tausz, M., Alonso, R., Jones, D., Johnson, R. and Grulke, N.: 2002, 'Summer-time distribution of air pollutants in Sequoia National Park, California', *Environ. Pollut.* **118**, 187–203.

Cahill, T. A., Carroll, J. J., Campbell, D. and Gill, T. E.: 1996, 'Chapter 48: Air Quality,' in *Status of the Sierra Nevada*, U.S. Geological Survey Digital Data Series, Sierra Nevada Ecosystem Project, Final Report to Congress, vol. II., University of California Centers for Water and Wildland Resources, Davis, CA, USA, pp. 1227–1261. http://ceres.ca.gov/snep/pubs/web/PDF/VII_C48.PDF

California Air Resources Board: 1999, 'Estimates of Ammonia Emissions from Beef and Dairy Cattle in California', *Review draft*, Planning and Technical Support Division, California Air Resources Board, Sacramento, CA, USA, pp. 42.

California Environmental Protection Agency: 2000, 'Atmospheric Acidity Protection Program: Final Assessment', *Report*, California Air Resources Board, Sacramento, CA, USA, pp. 37. http://www.arb.ca.gov/research/acid-dep/AAPPrpt.pdf

Committee on the Environment and Natural Resources Air Quality Research Subcommittee: 2000, 'Atmospheric Ammonia: Sources and Fate; a Review of Ongoing Federal Research and Future Needs', *Air Quality Research Subcommittee Meeting Report*, NOAA Aeronomy Laboratory, Boulder, CO, USA, pp. 19.

Daly, C., Neilson, R. P. and Phillips, D. L.: 1994, 'A statistical-topographic model for mapping climatological precipitation over mountainous terrain', *J. Appl. Meteorol.* **33**, 140–158.

Daly, C., Taylor, G. H., Gibson, W. P., Parzybok, T. W., Johnson, G. L. and Pasteris, P.: 2001, 'High-quality spatial climate data sets for the United States and beyond', *T. A.S.A.E.* **43**, 1957–1962.

Daly, C., Gibson, W. P., Taylor, G. H., Johnson, G. L. and Pasteris, P.: 2002, 'A knowledge-based approach to the statistical mapping of climate', *Climate Res.* **22**, 99–113.

De Bakker, A. J.: 1989, 'Effects of ammonia emission on epiphytic lichen vegetation', *Acta Bot. Neerl.* **38**, 337–342.

Esslinger, T. L.: 2000, 'A key for the lichen genus *Physconia* in California, with descriptions for three new species occurring within the state', *Bulletin of the California Lichen Society* **7**, 1–6.

Fenn, M. E., Poth, M. A., Bytnerowicz, A., Sickman, J. O. and Takemoto, B. K.: 2003, 'Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra Nevada', in A. Bytnerowicz, M. J. Arbaugh and R. Alonso (ed.) *Ozone Air Pollution in the Sierra Nevada–Distribution and Effects on Forests*, Elsevier Science Ltd., Oxford, UK, pp. 111–155.

Gilbert, O. L.: 1976, 'An alkaline dust effect on epiphytic lichens', *Lichenologist* **8**, 173–178.

Jassby, A. D., Reuter, J. E., Axler, R. P., Goldman, C. R. and Hackley, S. H.: 1994, 'Atmospheric deposition of nitrogen and phosphorus in the annual nutrient load of Lake Tahoe (California-Nevada)', *Water Resour. Res.* **30**, 2207–2216.

Jovan, S. and McCune, B.: 2004, 'Regional variation in epiphytic macrolichen communities in northern and central California forests', *The Bryologist* **107**, 328–339.

Jovan, S. and McCune, B.: 2005, 'Bioindication of Air Pollution in the Greater Central Valley of California, U.S.A. with Epiphytic Macrolichen Communities', *Ecol. Appl.*: in press.

Krupa, S. V.: 2003, 'Effects of atmospheric ammonia (NH_3) on terrestrial vegetation: a Review', *Environ. Pollut.* **124**, 179–221.

Kruskal, J. B.: 1964, 'Non-metric multidimensional scaling: a numerical method', *Psychometrika* **29**, 115–129.

Lindblom, L.: 1997, 'The genus *Xanthoria* (Fr.) Th. Fr. in North America', *Journal of the Hattori Botanical Laboratory* **83**, 75–172.

Loppi, S. and Pirintsos, S. A.: 2000, 'Effect of dust on epiphytic lichen vegetation in the Mediterranean area (Italy and Greece)', *Israel Journal of Plant Science* **48**, 91–95.

McCune, B. and Geiser, L.: 1997, '*Macrolichens of the Pacific Northwest*', Oregon State University Press and U.S.D.A. Forest Service, Corvallis, OR, USA, pp. 386.

McCune, B. and Grace, J. B.: 2002, '*Analysis of Ecological Communities*', MjM Software, Gleneden Beach, OR, USA, pp. 300.

McCune, B. and Mefford, M. J.: 1999, '*Multivariate Analysis on the PC-ORD System'*, Version 4, MjM Software, Gleneden Beach, OR, USA.

McCune, B. and Mefford, M. J.: 2004, '*Hyperniche. Nonparametric Multiplicative Habitat Modeling*', Version 1.00.60 beta, MjM Software, Gleneden Beach, OR, USA.

McCune, B., Rogers, P., Ruchty, A. and Ryan, B.: 1998, 'Lichen communities for forest health monitoring in Colorado, USA', *Report to the USDA Forest Service*, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR, USA, pp. 30.

McCune, B., Dey, J. P., Peck, J. E., Cassell, D., Heiman, K., Will-Wolf, S. and Neitlich, P. N.: 1997, 'Repeatability of community data: species richness versus gradient scores in large-scale lichen studies', *The Bryologist* **100**, 40–46.

Messer, J.J., Linthurst, R.A. and Overton, W.S.: 1991, 'An EPA program for monitoring ecological status and trends', *Environ. Monit. Assess.* **17**, 67–78.

Moberg, R.:2002, 'Physcia', in T. H. Nash III, B. D. Ryan, C. Gries and F. Bungartz (ed.) *Lichen Flora of the Greater Sonoran Desert Region I*, Lichens Unlimited, Arizona State University, Tempe, AZ, USA, pp. 358–373.

Momsen, J. H.: 2001, 'Agriculture in the Sierra', in *Status of the Sierra Nevada*, U.S. Geological Survey Digital Data Series, Sierra Nevada Ecosystem Project, Final Report to Congress, vol. II., University of California Centers for Water and Wildland Resources, Davis, CA, USA, pp. 497–528. http://ceres.ca.gov/snep/pubs/web/PDF/VII_C17.PDF

National Park Service: 2000, 'Final Yosemite Valley Plan, Supplemental Environmental Impact Statement', Online report, National Park Service, Yosemite National Park, CA, USA. http://www.nps.gov/yose/planning/yvp/seis/index.html

Neitlich, P., Rogers, P. and Rosentreter, R.: 2003, 'Lichen Communities Indicator Results from Idaho: Baseline Sampling, *General Technical Report RMRS-GTR-103*, US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA, pp. 14.

Peterson, J., Schmoldt, D., Peterson, D., Eilers, J., Fisher, R. and Bachman, R.: 1992, 'Guidelines for evaluating air pollution impacts on class I wilderness areas in the pacific northwest', *General Technical Report PNW-GTR-299*, US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, USA, pp. 83.

Pierson, W. R. and Brachaczek, W. W.: 1983, 'Particulate Matter Associated with Vehicles on the Road. II.', *Aerosol Sci. Tech.* **2**, 1–40.

Potter, C., Krauter, C. and Klooster, S. 2001. Statewide Inventory Estimates of Ammonia Emissions from Native Soils and Chemical Fertilizers in California. *Final report for Contract # ID: 98-716*, California Air Resources Board, Sacramento, CA, USA, 96 pp. ftp://ftp.arb.ca.gov/carbis/reports/l522.pdf

'*SPSS for Windows*', Rel. 11.0.1: 2001, SPSS Inc., Chicago, Il, USA.

Takemoto, B. K., Bytnerowicz, A. and Fenn, M. E.: 2001, 'Current and future effects of ozone and atmospheric nitrogen deposition on California's mixed conifer forests', *Forest Ecol. Manag.* **144**, 159–173.

Takemoto, B. K., Croes, B. E., Brown, S. M., Motallebi, N., Westerdahl, F. D., Margolis, H. G., Cahill, B. T., Mueller, M. D. and Holmes, J. R.: 1995, 'Acidic deposition in California: findings from a program of monitoring and effects research', *Water Air Soil Pollut.* **85**, 261–272.

University of California SNEP Science Team and Special Consultants:1996, 'Chapter 2: People and Resource Use', in *Status of the Sierra Nevada*, U.S. Geological Survey Digital Data Series, Sierra Nevada Ecosystem Project, Final Report to Congress, vol. I., University of California Centers for Water and Wildland Resources, Davis, CA, USA, pp. 17–45. http://ceres.ca.gov/snep/pubs/web/PDF/v1_ch02.pdf

Van Dobben, H. F.: 1983, 'Changes in the epiphytic lichen flora and vegetation in the surroundings of Hertogenbosch (The Netherlands) since 1900', *Nova Hedwigia* **37**, 691–719.

Van Dobben, H. F. and de Bakker, A. J.: 1996, 'Re-mapping of lichen biodiversity in The Netherlands: effects of decreasing SO_2 and increasing NH_3', *Acta Bot. Neerl.* **45**, 55–71.

Van Dobben, H. F. and ter Braak, C. J. F.: 1998, 'Effects of atmospheric NH_3 on epiphytic lichens in the Netherlands: The pitfalls of biological monitoring', *Atmos. Environ.* **32**, 551–557.

Van Haluwyn, C. and van Herk, C. M.: 2002, ‘Bioindication: the community approach’, in P. L. Nimis, C. Scheidegger, and P. A. Wolseley (ed) *Monitoring with Lichens-monitoring lichens*, IV. Earth and Environmental Sciences vol. 7, Kluwer Academic Publishers, Dordrecht, the Netherlands, pp. 39–64.

Van Herk, C. M.: 1999, ‘Mapping of ammonia pollution with epiphytic lichens in the Netherlands’, *Lichenologist* **31**, 9–20.

Van Herk, C. M.: 2001, ‘Bark pH and susceptibility to toxic air pollutants as independent causes of changes in epiphytic lichen composition in space and time’, *Lichenologist* **33**, 419–441.

Van Herk, C. M., Mathijssen-Spiekman, E. A. M., de Zwart, D.: 2003, ‘Long distance nitrogen air pollution effects on lichens in Europe’, *Lichenologist* **35**, 347–359.