

AN ABSTRACT OF THE DISSERTATION OF

Martin A. Hutten for the degree of Doctor of Philosophy in Botany and Plant Pathology presented on October 20, 2014.

Title: Yosemite Region Nitrogen Deposition and Patterns in the Composition of Lichen Communities.

Abstract approved: _____
Bruce McCune

This dissertation describes patterns in epiphytic macrolichen community composition along a nitrogen deposition gradient in the Yosemite region of the Sierra Nevada in California. This region is part of the largest federal air quality Class 1 designated air-shed in the western United States, covering the entire crest of the Sierra Nevada, and is protected under the Clean Air Act. Aside from the westernmost foothills, most of the region is federally designated Wilderness and has been subjected to few direct human impacts. The main air pollutants are nitrogen compounds which are carried eastward by prevailing winds from emission sources in the Central Valley. For more than a decade, measurements of nitrogen deposition at the Yosemite National Atmospheric Deposition Program station have been near or above the published lichen critical load; the quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge. A California-wide deposition model predicts that critical load exceedance has become the norm throughout the western slope of the central and southern Sierra Nevada.

The principal objectives of the study were to determine the threshold response level of epiphytic lichen communities to nitrogen deposition and to map where that deposition level is exceeded in the Yosemite area. I measured throughfall nitrogen deposition at 12 sites for one year and related it to the accumulation of nitrogen in the thalli of the lichens *Letharia vulpina*, *Letharia columbiana*, and *Evernia prunastri*. I then measured the accumulation of nitrogen by lichens at nearly 300 additional locations throughout the study area to calibrate a model for lichen nitrogen accumulation at the landscape level. I extrapolated the calibration model to estimate N inputs at a high level of resolution throughout the study area. In 38 intensive study sites along the nitrogen deposition gradient, I conducted detailed assessments of the composition of epiphytic

macrolichen communities to evaluate the apparent responses to elevated nitrogen deposition. I combined the data from two independent sampling techniques: a standard, semi-quantitative, stand-level method; and a new quantitative, branch-level assessment method to determine a lichen critical load for the coniferous forests in the study area. Concurrent with the branch lichen community assessment, I measured the pH and conductivity of the branch bark to address persistent questions in the literature about the role of the ionic environment of the substrate in mediating the response of lichen communities to nitrogen deposition.

Both lichen community assessment methods revealed similar trends in the composition of lichen communities along the nitrogen deposition gradient. Lichen communities exposed to low N deposition levels were dominated by species adapted to low nitrogen inputs and had a low species richness and abundance of lichen eutrophs. Exposure to elevated nitrogen deposition was associated with lichen communities that were increasingly eutroph-dominated. There was weak evidence for a decline of lichen oligotrophs on conifer branches with increasing nitrogen deposition. Lichen substrate pH and electrical conductivity were not correlated with nitrogen deposition, and the abundance of individual lichen species, including eutrophs, was not correlated with substrate pH or conductivity. Therefore, the increase in eutrophs was likely a direct consequence of elevated nitrogen deposition.

The lichen community work demonstrated that lichen thallus nitrogen concentrations standardized to *Letharia vulpina* equivalents exceeding 1.1% dry-weight were associated with major changes in the composition of lichen communities. This corresponded to 2.9 kg inorganic nitrogen ha⁻¹ yr⁻¹ (wet + dry); the empirical critical load determined in this study. Throughfall deposition measurements from this study, and deposition measurements at the Yosemite National Atmosphere Deposition Program station verify that nitrogen deposition reached or exceeded that critical load at 12 locations in the study area. The lichen thallus nitrogen accumulation model, which included hundreds of local calibration points, suggested the critical load is exceeded in at least 68% of the study area, including more than 70% of the area designated as federal air quality Class 1 air-sheds.

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YOSEMITE REGION NITROGEN DEPOSITION AND PATTERNS IN THE
COMPOSITION OF LICHEN COMMUNITIES.

by
Martin A. Hutten

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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.

Martin A. Hutten, Author

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YOSEMITE REGION NITROGEN DEPOSITION AND PATTERNS IN THE COMPOSITION OF LICHEN COMMUNITIES

CHAPTER 1: INTRODUCTION

Yosemite National Park and nearby portions of the Sierra and Stanislaus National Forests are part of the largest federal air quality Class 1 designated air-shed in the western United States; an area covering the entire crest of the Sierra Nevada in California. Federal Class 1 air-sheds include specific national parks, national wilderness areas, and national monuments granted special air quality protections under Section 162(a) of the federal Clean Air Act in 1977.

The Central Valley of California, one of the most productive agricultural areas in the world, lies directly to the west of this region; less than 1% of the nation's total farmland, fertile soils and extensive irrigation systems produce more than 8% of the monetary value of agricultural output in the U.S. (Reilly, 2008). Nearly half of all fruits, nuts, and vegetables consumed in the US are produced in California (CDFA, 2012) and primarily in the Central Valley. Such productivity and growth are sustained with significant inputs of energy and fertilizers.

High levels of ammonia (NH_3) are emitted from mainly agricultural sources in the Central Valley. In the atmosphere, ammonium (NH_4^+) and NO_x emissions from fossil fuel combustion (e.g., traffic) and wildfires are important constituents of smog-forming aerosols that contribute substantially to ambient fine particulate matter in the atmosphere (Cox, Delao, Komorniczak, & Weller, 2009; Nowak et al., 2012). In the San Joaquin Air District, the prevalence of such aerosols has resulted in the District's designation of non-attainment with the national 24-hour $\text{PM}_{2.5}$ standard, since the establishment of the standard in 1997 (Cox et al., 2009). Aerosols such as NH_4NO_3 are stable enough for transport across long distances and contribute substantially to view-shed degradation (Trijonis, 1990), common in the Sierra Nevada (Fenn et al., 2003). These aerosols also play an important role in the elevated atmospheric (N) deposition in the Sierra Nevada.

Forested ecosystems in the western US are adapted to low concentrations of $\pm 0.2 \mu\text{g m}^{-3}$ fixed nitrogen (N) in ambient air (Trijonis, 1990). Background N-deposition varies with annual precipitation (Williams & Tonnessen, 2000) and canopy scavenging (i.e., forest cover and leaf area), and may have averaged $\pm 0.69 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Holland et al., 1999). These levels are currently exceeded throughout California (Fenn et al., 2010).

While fixed nitrogen is a nutrient, high deposition rates result in ecological harm (Fenn et al., 2010; Fenn et al., 2003; Volpe et al., 2006). The quantitative estimate of an exposure to one or

more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge is termed a critical load (CLO) or critical level (CLE; Nilsson & Grennfelt, 1988) and is derived from observations on ecosystem responses (Burns et al., 2008; NADP, 2008; Pardo et al., 2011; Porter et al., 2005). Critical levels and CLO's are becoming an increasingly important tool in air quality management (Glavich & Geiser, 2008; Porter & Johnson, 2007). In terrestrial habitats, CLO's for N are generally lowest for lichens and bryophytes, and increase from mycorrhizal fungi to herbaceous plants, shrubs, and trees (Pardo et al., 2011), but for a given receptor, the CLO may differ among ecosystems and between regions. The sensitivity of lichens is related to their symbiotic nature and the lack of a protective outer cuticle; absorption of both nutrients and pollutants occurs over much of their outer surface from predominantly aerial sources (Nimis, et al., 2002). For nitrogen in California, previous CLO estimates for epiphytic macrolichen communities were 3.1, and 5.5 kg N ha⁻¹ yr⁻¹ for mixed coniferous forest and oak woodlands, respectively (Fenn et al., 2008).

Pollutant loadings in excess of the CLO affect the composition of the lichen communities. Individual species differ substantially in their nutrient requirements and sensitivity to pollutants (Geiser, 2004; Hyvärinen et al., 1992; Park et al., 2003), so that the composition of lichen communities provides detailed information about local nutrient and pollution regimes. Increased N deposition results in an increased richness and abundance of eutrophs: lichens that thrive in nutrient rich environments (McCune & Geiser, 2009). Lichen oligotrophs require environments with a low nutrient availability and will decline under increasing N deposition regimes, while lichen mesotrophs have an intermediate nutrient requirement.

Deposition modeling in California suggests that throughfall N deposition exceeds previously estimated lichen CLO for coniferous forests in all but the easternmost portion of the Yosemite region of the Sierra Nevada (Fenn et al., 2010). Unfortunately, N deposition is prohibitively difficult and expensive to quantify at the landscape level. Within the study area, routine measurements are made only at the NADP station (CA99) in Yosemite National Park, where N deposition levels have been near the lichen CLO for at least a decade. Lichen thallus N concentration levels have a strong, positive correlation with throughfall N deposition (Fenn et al., 2008; Geiser et al., 2010; Geiser & Neitlich, 2007; Root et al., 2013) and may have potential as a proxy for deposition mapping at a lower cost than instrumental monitoring. Such methods are important to develop because N-related ecological impacts are pervasive throughout the region. Just south of the Yosemite region in the southern Sierra Nevada at Sequoia and Kings Canyon National Parks, impacts on lichen communities are more severe than those observed in the

Yosemite region (Fenn, Haeuber, et al., 2003). To the north, Lassen National Park is thought to be less impacted; however, data are limited and elevated lichen N levels were documented on the southern flank of Lassen Peak in 2010 (M.A. Hutten, unpublished data).

Many lichen species are also sensitive to the acidity of their substrate; bark pH has long been regarded as an important factor in influencing the composition of natural epiphytic lichen floras (Barkman, 1958; Schmidt et al., 2001). Consequently, bark pH is frequently measured and identified as a strong environmental driver in the composition of lichen communities (e.g., Mitchell et al., 2005; van Herk, 2001). Historic pollution regimes of sulfur, and more recently NH_3 , have a strong effect on the bark ionic environment, resulting in complex effects on the composition of lichen communities and their post-pollution recovery (Larsen et al., 2007; Spier et al., 2010). Because the Yosemite region study area does not have a long pollution history, the NH_4^+ and NO_3^- -dominated pollution regime provided a unique opportunity to study the role of substrate pH in mediating the response of epiphytic lichen communities to N pollutants.

SPECIFIC OBJECTIVES

In Chapter Two, I determine the threshold response level of epiphytic lichen communities to nitrogen pollutants in the coniferous forests that dominate the region. Chapter Three focuses on the primary objective of this study, the determination of the geographic extent of the area where the nitrogen CLO is exceeded. This required a detailed assessment of N inputs at the landscape level. Secondly, the chapter describes how N deposition can be modeled using lichen thallus N concentration as a proxy for N deposition with high resolution, at low cost, and with minimal impacts. In Chapter Four, I evaluate the role of substrate pH and substrate conductivity in the composition of epiphytic lichen communities of coniferous forest along a nitrogen pollution gradient.

CHAPTER 2: YOSEMITE REGION NITROGEN DEPOSITION IN RELATION TO LICHEN COMMUNITY COMPOSITION

Martin A. Hutten, Bruce McCune

Environmental Pollution
-Submission pending-

ABSTRACT

Yosemite National Park and nearby portions of the Sierra and Stanislaus National Forests in California are designated federal Class air quality 1 areas that are afforded the highest level of protection under the U.S. Clean Air Act (1977). Throughfall measurements and modeling suggest that nitrogen (N) deposition exceeds the critical load for epiphytic lichen communities in large portions of the area, but lichen community impacts have not been demonstrated. We measured lichen thallus N-concentration levels as a proxy for atmospheric N deposition in 38 study sites, and used a stand-level, semi-quantitative method, as well as a new branch-level quantitative assessment method to evaluate the composition of lichen communities. The data from the two lichen assessment methods were combined to evaluate N associated responses of the lichen community. Lichen thallus N levels were standardized to *Letharia vulpina* dry-weight equivalents and ranged from 0.9 to 2.2%; corresponding to a throughfall deposition of 1.9 to 11.5 kg inorganic N (wet + dry) ha⁻¹ yr⁻¹. Along this gradient of increasing N deposition there was a community shift toward increased eutroph richness and abundance and an increased eutroph-to-oligotroph abundance ratio. Lichen community composition shifted markedly at a lichen thallus N level above 1.1%, corresponding to 2.9 kg inorganic throughfall N (wet + dry) ha⁻¹ yr⁻¹, which was thus determined to be the critical load. Increasing N deposition was associated with a weak absolute decline in oligotroph abundance on conifer branches that was not detected by the stand-level method. At N deposition regimes leading to lichen thallus N levels $\geq 1.5\%$ (5.4 kg N ha⁻¹ yr⁻¹), the eutroph *Candelaria pacifica* typically proliferated on > 50% of the branch surfaces.

Highlights: ► Yosemite region N deposition ranged from 1.9 to 11.5 kg N ha⁻¹ yr⁻¹; well above natural background levels. ► Branch and stand-level lichen community assessment methods yielded comparable results. ► Eutroph richness and abundance and the eutroph-to-oligotroph abundance ratio were positively correlated with the N accumulation in lichen thallus. ► The empirical critical load for epiphytic lichen communities in coniferous forests was determined to be 1.1% N (dry-weight), corresponding to throughfall N (wet + dry) of 2.9 kg ha⁻¹ yr⁻¹. ► Monitoring the relative abundance of *Candelaria pacifica* on dead conifer branches may allow for rapid identification (< 1 hour per site) of areas that exceed the N critical load.

Keywords: Air pollution effects, Air quality, California ecosystems, Community shifts, Critical loads of N, Eutrophication, Lichen eutrophs, Nitrogen deposition.

INTRODUCTION

Nitrogen (N) emissions and atmospheric deposition have increased significantly in the last century (Bobbink et al., 2010), and N compounds rank among the most significant pollutants worldwide. A variety of human activities readily elevate naturally low ambient N levels of about $0.2 \mu\text{g m}^{-3}$ (Trijonis, 1990). While fixed N is a nutrient, excess N results in ecological consequences (Fenn et al., 2010; Vitousek et al., 1997). The quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge is termed a critical load (CLO) or critical level (CLE; Nilsson & Grennfelt, 1988), and is derived from observations on ecosystem responses (Burns et al., 2008; NADP, 2008; Pardo et al., 2011; Porter et al., 2005). Critical levels and CLO's are becoming an increasingly important tool in air quality management and in communicating ecological impacts (Glavich & Geiser, 2008; Porter & Johnson, 2007). CLE's are ambient air concentrations expressed in ppm or $\mu\text{g m}^{-3}$, whereas CLO's refer to deposition loadings that are typically expressed in terms of $\text{kg ha}^{-1} \text{yr}^{-1}$ of wet or total deposition. In aquatic habitats, diatoms are most sensitive to N deposition, resulting in the lowest CLO. In terrestrial habitats, CLO's for N are generally lowest for lichens and bryophytes, and increase from mycorrhizal fungi to herbaceous plants, shrubs, and trees (Pardo et al., 2011), but for a given receptor, the CLO may differ among ecosystems and between regions. The sensitivity of lichens is related to their symbiotic nature and the lack of a protective outer cuticle; absorption of both nutrients and pollutants occurs over much of their outer surface from predominantly aerial sources (Nimis, et al., 2002). For nitrogen, CLO estimates for epiphytic macrolichen communities range from a deposition of 3 to $9 \text{ kg N ha}^{-1} \text{yr}^{-1}$, as modeled by USEPA Community Multiscale Air Quality (CMAQ), increasing with mean annual precipitation in western Oregon and Washington forests (Geiser et al., 2010). In Mediterranean climates of California, the CLO estimates are 3.1 and $5.5 \text{ kg N ha}^{-1} \text{yr}^{-1}$ for mixed coniferous forest and oak woodlands, respectively (Fenn et al., 2008). Ecosystems in the western US are adapted to low concentrations of $\pm 0.2 \mu\text{g m}^{-3}$ fixed nitrogen (N) in ambient air (Trijonis, 1990). Background N-deposition varies with annual precipitation (Williams & Tonnessen, 2000) and canopy scavenging (i.e., forest cover and leaf area), and may have averaged $\pm 0.69 \text{ kg N ha}^{-1} \text{yr}^{-1}$ (Holland et al., 1999). These levels are currently exceeded throughout California (Fenn et al., 2010).

Pollutant deposition often has a strong, positive correlation with dry-weight pollutant concentration (% dry-weight) in the thalli of epiphytic lichens (Fenn et al., 2008; Geiser et al., 2010; Geiser & Neitlich, 2007; Root et al., 2013), which makes lichen thallus an excellent

integrated air sampler for elemental analyses (Geiser, 2004). Individual species differ substantially in their sensitivity to pollutants (Geiser, 2004; Hyvärinen et al., 1992; Park et al., 2003) so that the composition of lichen communities also provides detailed information about local pollution regimes.

In the Yosemite region, measurements of N deposition at the National Atmospheric Deposition Program (NADP) air quality monitoring site (Hodgdon: CA99), field measurements (Root et al., 2013; unpublished data M.A. Hutten), and deposition models (Fenn et al., 2010; Hutten & McCune, 2014b) approached or exceeded the N CLO levels established for lichens of coniferous forests in California (Fenn et al., 2008). Nitrogen pollutants favor eutrophic species, lichens that thrive in nutrient rich environments (McCune & Geiser, 2009), so that the richness and abundance of eutrophs increase with N deposition. Lichen oligotrophs require environments with a low nutrient availability and will decline under increasing N deposition regimes, while lichen mesotrophs have an intermediate nutrient requirement. Casual observations in the study area showed apparent eutrophication effects in lichen communities on conifer. The eutroph lichen *Candelaria pacifica* is so abundant that it coats branches yellow throughout the foothill woodlands west of Yosemite, and outside the study area, for instance in the ‘Giant Forest’ of Sequoia National Park (pers. observations); one of the most magnificent forests in the world. It is unknown whether or not lichen oligotrophs have been affected. Losses in lichen oligotroph diversity and abundance are thought to take place prior to the establishment of eutrophs in the UK (Wolseley et al., 2006) and in the Pacific Northwest (Geiser & Neitlich, 2007). A regional N deposition model shows that the CLO of $3.1 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for epiphytic lichens (Fenn et al., 2008) is exceeded throughout the western slope of the Yosemite region of the Sierra Nevada. While this includes a large portion of the area designated as federal air quality Class 1, virtually no lichen community impact studies have been conducted. Our research therefore had three objectives:

- (1) quantify the N deposition regime at the stand-level;
- (2) characterize the composition of lichen communities in relation to the N deposition regime with two independent methods, the standard stand-level semi-quantitative method and a new branch-level quantitative method, and compare their relative performance and sensitivity;
- (3) determine a lichen community response threshold and corresponding throughfall N CLO for epiphytic lichen communities in the coniferous forests of the study area.

MATERIALS AND METHODS

Study Area: The study area is about 820,000 ha and includes Yosemite National Park and a portion of the adjoining Stanislaus and Sierra National Forests, on the west slope of the Sierra

Nevada in central California, USA. The hydrographic boundary of the Sierra Nevada crest and the boundary with Mono County delimit the northeastern boundary, and the Madera-Fresno county line bounds the southeast (Figure 2-1). Our major focus was Yosemite National Park, but we extended the study area westward, toward pollution emission sources in the Central Valley. The western extent of the study area follows the lower distributional limit of the mixed-conifer forest type (Anderson et al., 1976), which is approximated by the western boundary of the Sierra and Stanislaus National Forests. The terrain in the study area is mountainous, with elevations ranging from 260 m along the western boundary to well over 3000 m close to the crest. Along this steep elevation gradient, climate and forest composition change profoundly.

Climate: The study area is characterized by long, hot, and dry summers that are more pronounced at lower elevations. January and July daily maximum temperatures average 13°C and 33°C at low elevations, respectively, and 2°C and 19°C at the passes along the Sierra Nevada crest, respectively. The bulk of the precipitation occurs during late fall and winter. Mean annual precipitation ranges from 40 cm at the lowest elevations to about 140 cm at some high-elevation sites (data extracted from interpolated 800 m PRISM climate normals 1971-2000, Daly et al., 2008, PRISM Climate Group 2004). Yosemite Valley, at 1190 m elevation, received an annual average of 104 cm of snow during the same period¹.

Vegetation: At the lowest elevations in the study area, the vegetation is a mix of chaparral and foothill woodlands (*Quercus* and *Pinus*). Montane zone vegetation is characterized by extensive mixed-conifer forest (*Abies*, *Calocedrus*, *Pinus*, and *Pseudotsuga*), including groves of *Sequoiadendron* and some of the tallest pines in the world. Subalpine forests (*Juniperus*, *Pinus*, and *Tsuga*) finally give way to high elevation rock barrens around 2500 m.

Air Quality: Sulfur dioxide concentrations averaged $\leq 0.5 \mu\text{g m}^{-3}$ annually since 1995 with highest recorded bi-weekly averages $< 2 \mu\text{g m}^{-3(2)}$. This is well below the ‘no-effect level’ reported for lichens in the Netherlands (Sparrius, 2007) and the response threshold of 5-15 ppb for sensitive lichens in the Pacific Northwest (McCune & Geiser, 2009). Ammonia (NH_3) is not routinely monitored by established air quality monitoring networks, but annual concentrations averaged around $0.94 \mu\text{g m}^{-3(3)}$; just below the CLE of $1 \mu\text{g m}^{-3}$ established by the United Nations Economic Commission for Europe for lichens and bryophytes in Europe (Batty & Hallberg, 2010). Monthly ambient air concentrations averaged $> 1 \mu\text{g NH}_3 \text{ m}^{-3}$ during the dry season (June-

¹ Yosemite Park Hdqtrs COOP station: ID 049855

² CASTNET YOS404, Turtleback Dome: measurement period: Oct 1995 – Febr 13

³ AMoN: CA44, Turtleback Dome: measurement period: Mar 2011 – Sept 13

September), and peaked at $2.6 \mu\text{g m}^{-3}$ during July³, just below levels that would result in detectable alteration of the lichen community, if sustained (van Herk, 2001; Wolseley et al., 2006). Critical levels and critical loads are typically lower in the U.S. than in Europe (Pardo et al., 2011), consequently NH_3 may play a role in the lichen responses in the study area, particularly in areas closest to emission sources in the Central Valley. Total N deposition averaged 3.1 and 3.5 kg N (wet + dry) $\text{ha}^{-1} \text{yr}^{-1}$ in 2010 and 2011, respectively. This rate has been relatively stable for little over one decade, especially when accounting for the influence of annual precipitation. The ionic forms of N, especially NH_4^+ and NO_3^- , are the largest constituents of total N deposition in the study area. Modeled throughfall N deposition in the study area ranged 2-9 kg N $\text{ha}^{-1} \text{yr}^{-1}$ (Fenn et al., 2010). Between 2010 and 2011, throughfall N deposition ranged 2.8 to 4.7 kg N $\text{ha}^{-1} \text{yr}^{-1}$ for 12 sites within Yosemite National Park (Root et al., 2013; unpublished data M.A. Hutten) which were measured using methods described by Fenn & Poth (2004). Modeling based on lichen thallus N-concentration levels indicated a throughfall range of 1.8 to 12.3 kg N $\text{ha}^{-1} \text{yr}^{-1}$ (Hutten & McCune, 2014b).

Site Selection: We non-randomly placed 38 plots throughout the study (Figure 2-1; Appendix A). We aimed for a representative, well-distributed sampling of habitats throughout the study area and intentionally co-located a plot with the NADP air quality monitoring site (Hodgdon: CA99), and another plot with the CASTNET air quality monitoring site (Turtleback Dome: YOS404). Other criteria for plot selection included the availability of sufficient target lichens from which to collect thallus samples for elemental content analysis, and a distance from roads ≥ 50 m. Our study was focused on conifer-dominated forest, therefore we rejected plots that had more than a few overstory hardwoods. Plot elevation ranged from 307-2821 m, and 80% of the plots were over 1000 m.

Local N Deposition: Thallus sampling was accomplished during dry and stable weather at the end of the dry season in 2010 and 2011 to avoid season-related fluctuations in lichen thallus N levels (Bruteig, 1993) as is common practice (Blett et al., 2003; Jovan & Carlberg, 2007; Saros et al., 2010). In each plot, we collected lichen thalli using methods developed by Geiser (2004). Healthy target lichen thalli (species enumerated below) were collected from coniferous tree boles and branches using latex gloves to avoid contamination. Each composite sample had a target field weight of 10 g and consisted of a single air-tight polyester bag with lichen individuals of the same species collected from at least six different trees. In the office, the lichens were spread on paper to air dry and to remove debris including bark, other lichen species, and necrotic thallus, resulting in a final weight of approximately 7 g (air dry) per sample. Samples were analyzed at the University

of Minnesota Research Analytical Laboratory during the winter following the field collection. There, samples were ground and dried to constant weight. Lichen thallus N levels (% dry-weight; hereafter: % dw) were then estimated using a LECO FP-528 N Analyzer (Dumas-method: Lee et al., 1996; Yeomans & Bremner, 1991).

We employed a variety of quality assurance measures. Within-site sampling error was estimated by collecting four replicate composite samples in 12 plots within a 2-week period during the spring of 2011 (Table 2-1). We frequently split unnecessarily large samples to get an indication of the N variability within the sample. Field replicates and sample splits were averaged for final plot-level estimates. The lab routinely addressed measurement precision and accuracy by reanalyzing the digestate of the first sample in a batch, and every 10th sample thereafter. This resulted in lab replicates which were averaged for final plot-level estimates. The laboratory also verified measurement accuracy by referencing NIST⁴ peach-leaf and apple-leaf standards for the first sample in a batch and every 10th sample thereafter.

Under the same deposition regime, the thalli of different lichen species may accumulate N at different rates (Hutten & McCune, 2014b; Root et al., 2013). Therefore, we focused only on three species, the minimum number of species necessary to canvas the study area. We used *Letharia vulpina* (LEVU) in 30 plots, *Letharia columbiana* in two high elevation plots (14, and 35), and *Evernia prunastri* at three low elevation plots (36, 37, and 38; Figure 2-2). When LEVU was not available, we predicted N levels in LEVU thalli from the N levels of *Letharia columbiana* or *Evernia prunastri* using simple linear regression (Hutten & McCune, 2014b). For plot 5, the fall sample was compromised and we estimated fall 2010 N levels by dividing spring N (% dw)/0.86, the average decrease in N levels measured across the winter period in 11 plots (Table 2-1).

Lichen Community Composition: For a different research project, we developed a quantitative branch-level lichen community assessment method (Hutten & McCune, 2014a). These data provided an opportunity to compare the relative sensitivities of the branch-level method with the standard, semi-quantitative stand-level method used by Forest Inventory and Analysis (FIA, 2006) in detecting patterns in lichen community composition along the N deposition gradient.

FIA Stand-level Method (hereafter: FM): Described in detail in the FIA field methods manual (FIA, 2006), the first author and two trained field assistants collected epiphytic macrolichens (hereafter: lichens) from woody substrates within arm's reach above 0.5 m from the

⁴ National Institute for Standards and Technology

ground, within a 0.38-ha circular plot (36.6 m radius). Freshly fallen lichens on the ground were also collected. Each species was assigned an abundance code: 1 for infrequent lichens (1-3 thalli); 2 for uncommon lichens (4-10 thalli); 3 for common lichens (> 10 thalli and occurring on < 50% of all available boles and branch substrates in the plot); and 4 for abundant lichens (> 10 thalli and occurring on > 50% of boles and branches). The minimum survey duration was 30 min. and the maximum duration was two hrs. Within that period, surveys are terminated when the plot has been fully surveyed, and the surveyor failed to encounter another species within 10 min.

Branch Method (hereafter: BM): In each plot, we collected 10 1-m branch segments from 10 trees of the same species. We targeted branch lichen communities because they were shown to be more responsive to (NH₃) pollution than tree bole lichen communities (Wolseley et al., 2006). We narrowed our efforts to corticated dead branches because they are easy to collect and tend to be good lichen substrate, perhaps in part because the process of bark flaking slows (Barkman, 1958). Branches needed to be within reach from the ground or freshly fallen. We rejected branches without lichens if branches with lichens were available. To minimize differences imparted by branch size, bark thickness, bark texture, etc., we targeted branches 10 - 45 mm in diameter. We measured branch diameter at each end with electronic calipers, and determined the age of the branch apex under a dissecting microscope. Due to the major elevation gradient of the study area, it was necessary to use eight different conifer species: *Abies concolor* (17 plots), *A. magnifica* (8 plots), *Pinus sabiniana* (5 plots), *P. ponderosa* (4 plots), *P. attenuata* (1 plot), *Juniperus occidentalis* (1 plot), *Pseudotsuga menziesii* (1 plot), and *Tsuga mertensiana* (1 plot). To score lichen abundance, we used a linear quadrat with 100 1-cm squares and recorded the presence of each lichen species, or group of similar species, in each cm² on the upper surface of the branch. This resulted in a branch abundance between 0-100 for each lichen species. *Candelaria pacifica* frequently preferred the lower surface of the branches and therefore was independently scored on the lower surface of the branch which also yielded a combined total abundance for *Candelaria pacifica*. We grouped species difficult to identify to the species level when young, e.g., *Melanohalea*, and *Melanelixia* species as ‘Melanelioid’ (Table 2-2). In the text and tables we refer to these groups as single species, e.g., ‘branch species richness’ will refer to species but also include groups of species.

We derived analogous lichen indices for each method to describe and evaluate the trophic status and composition of the lichen community (Table 2-3). The trophic status of individual lichen species follows those reported in McCune & Geiser (2009). The designation of *Flavopunctelia flaventior* follows that of Jovan & McCune (2006) and is supported by our

experience in the study area where this species appears to be a regular component of the eutrophic community. We were unable to identify our (few) young tufted *Usnea* spp. We considered them mesotrophs based on their occurrence in N affected (riparian) habitat. Three species of *Usnea* are known to occur in the study area: a pendulous oligotroph, a tufted mesotroph, and a tufted species without trophic designation (Hutten et al., 2013). For the FM, we analyzed plot-level variables including and excluding lichen occurrences on hardwoods.

Critical Load Determination: To determine a lichen community N-deposition response threshold, we combined data from both methods into a single matrix that included 12 lichen community predictors: PNA, PMA, POA, Erich, and EO ratio from both methods; and BM Oabun, and BM *Candelaria pacifica* total abundance (top + bottom; Table 2-3).

Nomenclature: Names of vascular plants conform to the Jepson Manual (Baldwin et al., 2012). Lichen collections were identified by the first author, using keys and nomenclature in McCune & Geiser (2009) with the following exceptions: revisions in the genus *Leptogium* by (Otálora et al., 2008); *Parmelia barrenoae* Divakar, M. C. Molina & A. Crespo, which was recently added to the flora of North America (Hodkinson et al., 2010); and *Platismatia wheeleri* Goward, Altermann & Björk, a recently described taxon (Lumbsch et al., 2011). Lichen vouchers reside at the Yosemite National Park Herbarium (YM).

Statistical and Spatial Analysis: We quantified throughfall N deposition from lichen thallus N concentration (% dw) using the calibration equation: $\ln(\text{throughfall N}) = 0.886 + 1.968 * \ln(\text{N \% dw in } Letharia\ vulpina)$ from Root et al. (2013) which includes data from the study area. For three plots (28, 33, and 34) lichen thallus N measurements were unavailable and we estimated LEVU N (% dw) from a throughfall deposition model (Fenn et al., 2010) using the same equation. Estimating LEVU-equivalent N levels from other lichen species and the deposition model added an unquantified additional error to the lichen N-level estimates for these locations.

We characterized the substrate characteristics of branch lichen communities with a three-level Analysis of Variance (ANOVA) in XLSTAT[®]-Pro (Version 2014.1.10, Addinsoft, Inc., Brooklyn, NY, USA) among 38 plots with sites as random factor and species as fixed factor with 10 branches nested within sites. We used simple linear regression (SLR) in Microsoft[®] Excel 2013 to evaluate lichen community indices that characterized lichen community composition in relation to the N deposition regime. The indices ignored six macrolichens without a previously established trophic status. These species had low abundances and little potential to influence results. The BM indices also ignored crustose lichens due to mixed sensitivity to N. Infrequent

species that occurred in fewer than six plots were excluded. One plot (27) had a much lower lichen thallus N level than expected from the lichen community structure and N deposition models (Fenn et al., 2010; Hutten & McCune, 2014b) and was removed from the analysis. This resulted in matrices with 37 plots and 29 species, and 37 plots and 21 species for the FM and BM, respectively. The BM eutroph-to-oligotroph abundance ratio (EO) required log transformation, which necessitated adding 0.01 to all scores to avoid division by zero. Transformation of the FM EO ratio was not necessary, but enabled a direct comparison of this index between methods. We used Non-Metric Scaling (NMS: Kruskal, 1964; Mather, 1976) in PC-ORD (McCune & Mefford, 2006) to visualize patterns in lichen community composition. For a given dimensionality, we evaluated the strength of the ordination solution with the lowest stress by comparing it to the outcome of a randomization test with 250 runs. The final ordination diagram was rotated orthogonally to maximize correlations of axes to environmental variables.

We evaluated the utility and sensitivity of the BM and FM by comparing the relative performance of lichen indices with SLR. We also directly compared the resemblance of the FM and BM data matrices with a Mantel test in PC-ORD. A large positive and significant standardized Mantel statistic (r) would indicate that the two methods give similar results, whereas a small, non-significant r statistic would suggest that the community composition is unrelated or unstable. For Mantel and NMS, we used the Sørensen (Bray-Curtis) and Euclidean (Pythagorean) distance measures for FM and BM matrices, respectively.

The lichen community response threshold and corresponding throughfall N CLO were determined with Non-Parametric Multiplicative Regression (NPMR; McCune, 2006) in Hyperniche (McCune & Mefford, 2008). NPMR allows iterative exploration of models for landscape N inputs without the need to assume a particular relationship between response and predictor variables. We preferred models with only lichen community predictors to maximize the regional applicability of our results. To visualize eutroph proliferation at N deposition levels exceeding the lichen CLO, we also carried out multiple linear regression in Hyperniche.

Maps were created with Environmental Systems Research Institute (ESRI, Redlands, California) ArcGIS desktop version 10.1 software.

RESULTS

Local N deposition Regimes: Lichen thallus N levels ranged from 0.89-2.20 (% dw LEVU equivalents), corresponding to a throughfall deposition range of 1.93-11.45 kg N ha⁻¹ yr⁻¹ across 38 plots (Figure 2-1, Appendix B). Only four plots had lichen thallus N levels < 1.1 (% dw LEVU equivalents), corresponding to a throughfall deposition below the lichen CLO of 3.1 kg N

ha⁻¹ yr⁻¹ estimated by Fenn et al. (2008). Observed lichen thallus N levels ranged broadly among plots compared to within-plot lichen N variation, and laboratory accuracy and precision were high compared to the within-plot lichen N variation (Table 2-4). We did not directly assess the within-sample variation, but opportunistic sample splits suggested that it can be high (Table 2-4). Lichen thallus N levels fluctuated seasonally and annually. Spring N levels were 0.2% dw lower than fall N levels ($p < 0.05$, one-tailed paired t-test; Table 2-1). Lichen thallus N levels appeared to be higher in the fall of 2010 than in the fall of 2011, however our data are not well suited to address inter-annual patterns since we did not replicate the sampling in the spring of 2010.

Lichen Community: A total of 65 epiphytic lichen species were documented, 11 of which occurred exclusively on hardwoods. The oligotroph LEVU and the eutroph *Candelaria pacifica* occurred in more than 75% of all plots sampled. LEVU demonstrated a remarkable ecological amplitude, occurring over 98% of the elevation gradient (309-2821 m). Of the 65 species recorded, 24 species were eutrophs, 18 were mesotrophs, 18 were oligotrophs, and the trophic status of 5 species was not previously designated (Table 2-2). Lichen communities in stands with low lichen thallus N levels were characterized by low eutroph richness, PNA, and EO. When lichen thallus N levels were high, eutrophs such as *Candelaria pacifica* and *Physcia* spp. proliferated. *Xanthomendoza* and *Xanthoria* species were also more abundant, but remained minor community components even at the upper end of the N deposition gradient observed.

Branch Method: Among all sites, a total of 27 lichen species and species groups (hereafter: species) were recorded that were consolidated to 21 species and groups prior to analyses (Table 2-2). Mean plot richness was 7.2, ranging from a minimum of zero at two plots above 2500 m (plot 5, 31) to a maximum of 14 species at 900 m elevation (plot 32). *Candelaria pacifica* was the most common eutroph, present in > 75% of the plots. It proliferated at lichen thallus N levels ≥ 1.5 (% dw LEVU equivalents) coloring branches yellow. Melanelioids were the most common mesotrophs, and LEVU was the most common oligotroph, present in more than 70% of all plots sampled. Branch characteristics were characterized by Hutten & McCune (2014a): mean branch diameter of corticated dead conifer branches was 1.4 cm at the branch tip and 2.4 cm at the base, and did not differ among tree species (3-level nested ANOVA; $F = 2.33$; $p = 0.077$; $n = 4$), but did differ among sites within species (3-level nested ANOVA; $F = 20.15$; $p < 0.0001$; $n = 32$). Mean age (at branch death) was just over 17 yrs, ranging from 10-yr old *Pinus ponderosa* branches to 35 yr-old *Tsuga mertensiana* branches. Branch age differed among tree species (3-level nested ANOVA; $F = 3.81$, $p < 0.021$, $n = 3$), as well as between sites within species (3-level nested ANOVA; $F = 7.88$; $p < 0.0001$; $n = 28$).

Method Comparison: The FM and BM distance matrices had a minor positive relationship (Mantel Statistic $r = 0.294$, $p = 0.005$) which was also reflected by the results of the analysis of each method individually. The FM indices for lichen thallus N levels were consistently weakened by excluding the hardwood lichen component; henceforth, references to FM lichen indices include conifer and hardwood lichens. The correlation of BM indices was consistently weakened by the inclusion of two high elevation plots with low lichen thallus N levels that lacked branch lichens. Lichen thallus N levels $> 1.1\%$ dw were positively correlated with eutroph richness. The FM pattern was stronger than the BM ($R^2 = 0.458$ vs. 0.344) due to a greater range in FM eutroph richness (p -values ≤ 0.0001 ; Figure 2-3, Table 2-3). Lichen thallus N levels $> 1.1\%$ dw were also positively correlated with PNA for both methods ($R^2 = 0.505$ and 0.375 for FM and BM, respectively; p -values < 0.0001 ; Figure 2-3, Table 2-3). FM PNA responded at slightly lower N levels than BM PNA. Lichen thallus N levels $> 1.1\%$ dw were also positively correlated with EO for both methods; $R^2 = 0.498$ and 0.497 for FM and BM, respectively ($p < 0.0001$; Figure 2-3, Table 2-3). At a given N level, BM and FM EO ratios may be quite different, e.g., at high N levels, the BM community was more eutroph saturated than the FM. Both methods also captured a weaker pattern of proportional oligotroph decline with lichen thallus N levels $> 1.1\%$ dw (Figure 2-3, Table 2-3). The FM data did not show a decline in absolute abundance of oligotrophs with increasing lichen thallus N levels. BM data did show a decline in absolute oligotroph abundance ($R^2 = 0.107$, $p < 0.05$; Table 2-3); however, the inclusion of plots without branch lichens weakened the pattern.

Ordination of plots in species space yielded comparable results between the FM and BM: both suggested a two-dimensional solution with a minimum stress (11.9 and 7.8 for the FM and BM, respectively; Table 2-6) lower than expected by chance (p -values < 0.001 from randomization tests) and final solution instabilities < 0.001 . The two axes explained most of the variability in lichen community structure; total $R^2 = 0.87$ and 0.95 for FM and BM, respectively. Axis 1 explained most of the variability in the community in both methods, $R^2 = 0.71$ and 0.69 for FM and BM, respectively. Axis 2 was relatively weak in both methods and is not further discussed. The nearly 3 km vertical elevation gradient confounded the relationship between lichen community structure and lichen thallus N levels, i.e., there was no separation of climatic variables and the N gradient in either method. Lichen thallus N level was a weaker predictor of lichen community structure than elevation, easting, or temperature (Figure 2-4, Table 2-6).

Critical Load Determination: To determine the CLO for epiphytic lichen communities we used the strongest two-predictor model identified by NPMR, a local linear model that

predicted lichen thallus N levels from FM EO and BM PNA with tolerances 0.800 and 0.081, respectively ($xR^2 = 0.668$, Average Neighborhood Size (ANS) = 5.8). The model suggested lichen thallus N levels < 1.1 (% dw LEVU equivalents), corresponding to a throughfall N deposition of $2.9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, were associated with lichen communities characterized by FM EO ratio's < 0.1 and BM PNA $\leq 11\%$ (Figure 2-5). At lichen thallus N levels > 1.1% dw epiphytic lichen communities were positively associated with FM EO and BM PNA; however, FM EO responded before BM PNA. At relatively low lichen thallus N levels, BM PNA spanned a considerable range, but at lichen thallus N levels above 1.5% dw the range narrowed toward higher BM PNA. At lichen thallus N levels < 1.1% dw, eutroph richness and abundance on conifer branches was low. The regular presence of more than one or two eutroph species on conifer branches suggested the lichen CLO was approached or exceeded (not shown). *Candelaria pacifica* was occasionally present at low stand-level N deposition; then largely restricted to specific microhabitats, e.g., boles of inclined trees, bird perches, or substrates below high leaf-area canopy throughfall areas. Regular occurrence of *Candelaria pacifica* on dead corticate conifer branches, i.e., branch abundance > 200 in a 10 branch sample (combining scores from upper and lower branch surfaces), suggested that the CLO at the stand-level was exceeded (Figure 2-6, Figure 2-7).

DISCUSSION

The lichen N-level data confirmed or extended the geographic area modeled by Fenn et al. (2010) as being above the CLO (Figure 2-1). Three plots suggested a slightly lower local N level than those modeled by Fenn et al. (2010).

Lichen thallus N concentration was a convenient proxy for throughfall N deposition. Minor seasonal fluctuations did occur (e.g., early June N levels are 86% of the N levels in mid-September), but may be avoided by restricting the sampling to periods with dry and stable weather. About 85% of the total annual inorganic N deposition occurred as wet deposition in both 2010 and 2011 (NADP CA99; Hodgdon), therefore N accumulation in lichens during the dry summers may appear counter-intuitive. The N concentration of ambient air during the summer was twice that of the wet period; total NO_3^- and NH_4^+ averaged 1.83 and $0.46 \mu\text{g m}^{-3}$ in the dry season, respectively, vs. 0.90 and $0.23 \mu\text{g m}^{-3}$ during the wet season, respectively across all years⁵. When precipitation occurred, average NO_3^- and NH_4^+ concentrations in rain water were more than twice as high during the dry period than in the wet period; 2.25 and 0.62 mg L^{-1} vs.

⁵ CASTNET YOS404: Turtleback Dome.

0.86 and 0.27 mg L⁻¹⁽⁶⁾. Differences may be greater under forest canopies when rainwater washes down accumulated pollutants. Thus, lichen thallus N levels likely increased due to ongoing dry and incidental wet deposition while lichens are largely too dry to metabolize N for growth and respiration, resulting in a net N accumulation during the summer.

The branch and stand-level lichen assessments both effectively, and relatively inexpensively, demonstrated comparable lichen community patterns associated with excess N deposition. This was remarkable considering that the two methods differed by over seven orders of magnitude in the size of the observational unit (1 cm² for BM vs. 4208 m² for FM). Nevertheless, there were some important differences:

- (1) FM PNA increased at a lower N level than BM PNA, suggesting that the FM would detect the initial eutroph proliferation earlier than the BM.
- (2) At a given N level, the EO ratio at the stand and branch-level may be quite different, e.g., at high N levels the branch community was more eutroph-dominated relative to the stand-level overall. Because the FM covers more microhabitats, including those less susceptible to eutroph proliferation, this was not surprising.
- (3) The BM recorded fewer species than FM, and the necessary consolidation into species groups weakened the ability of the BM to track trends in species richness relative to the FM.
- (4) The FM effectively demonstrated a major apparent increase of eutroph abundance with increasing N inputs, but did not capture a decline in the absolute abundance of oligotrophs. This may be attributable to a relatively low average stand-level oligotroph richness and abundance, which makes detecting an absolute decline more difficult with the ranked abundances of the FM.
- (5) At the plot level, the FM score can be significantly influenced by even a minor hardwood component. Removing hardwood lichens consistently reduced BM sensitivity to the N deposition gradient, suggesting that hardwood lichen communities responded to excess N before conifer lichen communities. This effect needs further study as hardwood lichen CLO's in California are higher than conifer lichen CLO's.

The methods have unique operational strengths and weaknesses regarding time and expertise needed. Both methods require approximately two hours to conduct in the field when branches are readily available, such as in open old-growth forests of the study area. In forest types with poor branch access (e.g., recently burned forest; snow-pruned high-elevation forest; dense, second-growth forest), the BM would be much more time-consuming and challenging. The BM also

⁶ NADP CA99; Hodgdon

requires a trained lichenologist to correctly identify and quantify small and poorly developed lichen thalli. This constraint could be overcome by collecting and sending sample branches to an expert for analysis, with an increase in processing time. Further improvements to the BM might include measurement of N at the branch-level via branch-segment rinsing (Jovan et al., 2012). In contrast, the FM may be reliably performed by well-trained, non-lichenologists (McCune et al., 1997), but requires significant additional time for laboratory identifications by a lichenologist.

Our results support a lichen thallus N level of 1.1 (% dw LEVU equivalents), corresponding to a throughfall N deposition of $2.9 \text{ kg ha}^{-1} \text{ yr}^{-1}$ as the CLO above which epiphytic lichen communities in coniferous forests of the study area will be increasingly affected. Our empirical determination of the lichen CLO in the study area is comparable with a prior determination for lichens in coniferous forest in California (Fenn et al., 2008) and rests predominantly on the proliferation of eutrophs which elevated lichen community indices such as PNA and EO. While we think of the response of epiphytic lichen community to increasing N deposition as more or less continuous, at throughfall deposition levels above $2.9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, eutrophs such as *Candelaria pacifica* occupied a much wider range of microhabitats. The ecological niche ‘width’ of eutrophs was not directly captured by our indices, but served as an empirical indicator. It may be useful to develop a niche-width metric, in future work.

We anticipated an absolute decline in oligotroph abundance with increasing N deposition, but only the branch-level method detected a weak decline in oligotroph abundance. It is likely that the complex distribution of many oligotroph species on the landscape made pattern detection more difficult. In the study area, oligotroph richness and abundance was generally low except in cool and moist sites. Low oligotroph richness could have reduced the ability of the ranked abundance system (stand-level method) to detect a decline relative to the absolute abundance system (branch-level method). However, assuming immaculate air quality, it is highly unlikely that the same abundance of cyanolichens and oligotrophs found in the western Pacific Northwest could naturally occur in the greater Central Valley for strictly climatic reasons (Jovan, 2008). Because our data did not reveal major trends in lichen oligotroph abundance, it is possible that significant losses have not yet occurred; i.e., increases in eutroph richness and abundance on conifer substrates may occur before or concurrent with the decline of oligotrophs. If major oligotroph losses occurred prior to this study, it would follow that the CLO determined in this study would need to be adjusted downward. Regardless, the fate of lichen oligotrophs warrants further study and while our network of plots may serve as a useful reference point, it may be necessary to specifically target habitats with high oligotroph diversity.

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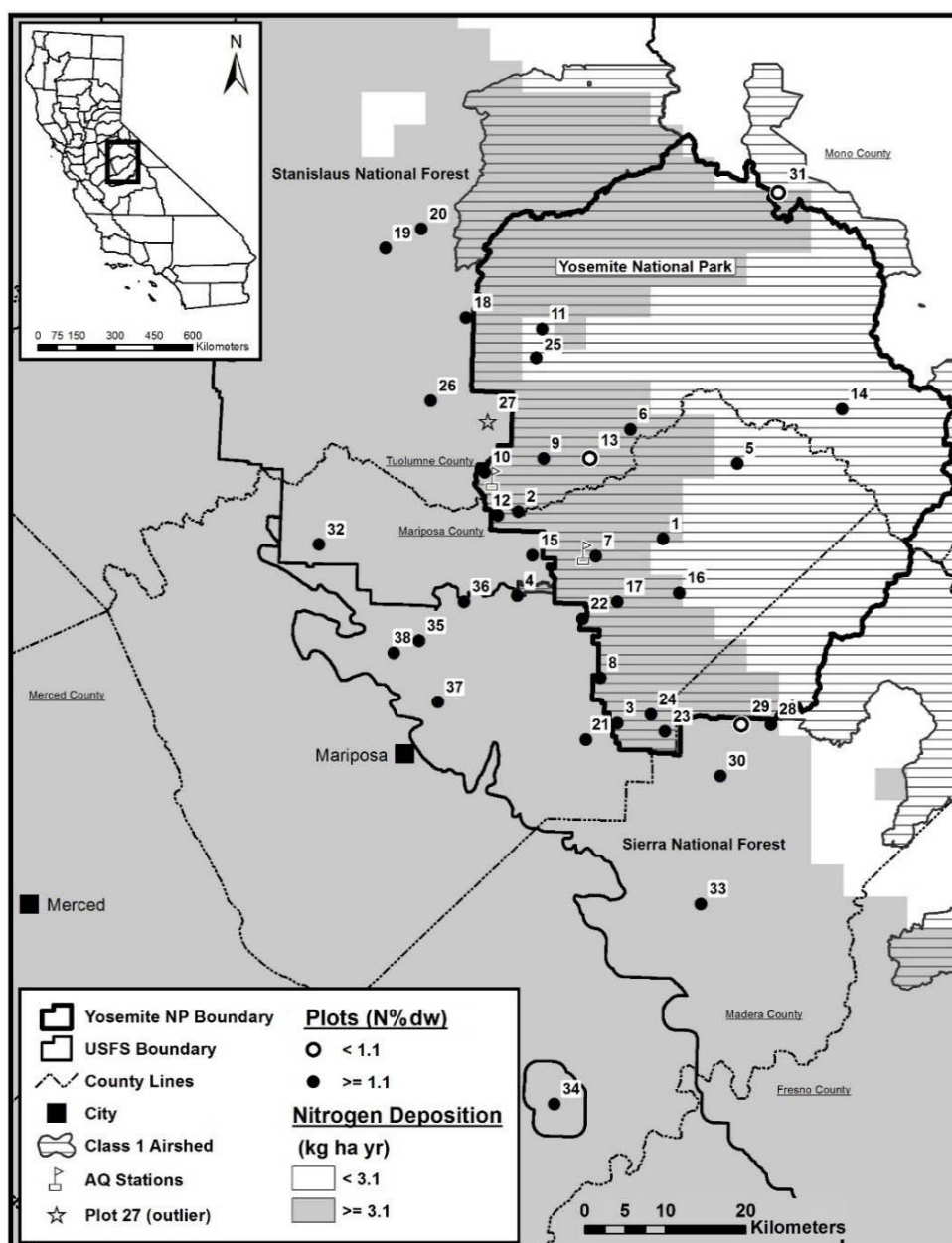


Figure 2-1: Map of the study area and modeled N deposition estimates.

The study area encompasses Yosemite National Park and the NW and SW portion of the Sierra and Stanislaus National Forest, respectively. One plot is just east of the Sierra Nevada crest, on the Humboldt-Toiyabe National Forest (plot 31). We co-located one plot with the NADP air quality monitoring site (plot 10, Hodgdon: CA99), and another with the CASTNET air quality monitoring site (plot 7, Turtleback Dome: YOS404). Designated federal air quality Class 1 area is identified with hatch marks and gray-shaded areas received > 3.1 kg throughfall N ha⁻¹ yr⁻¹ (Fenn et al., 2010); the N CLO for lichens in coniferous forests in California as estimated by Fenn et al., (2008). Plots with open or closed circles had lichen thallus N levels (as measured in this study) below or above the Fenn et al., (2008) N CLO for lichens, respectively. Plots 28, 33, and 34 used data from the deposition model to estimate the plot lichen thallus N concentration.

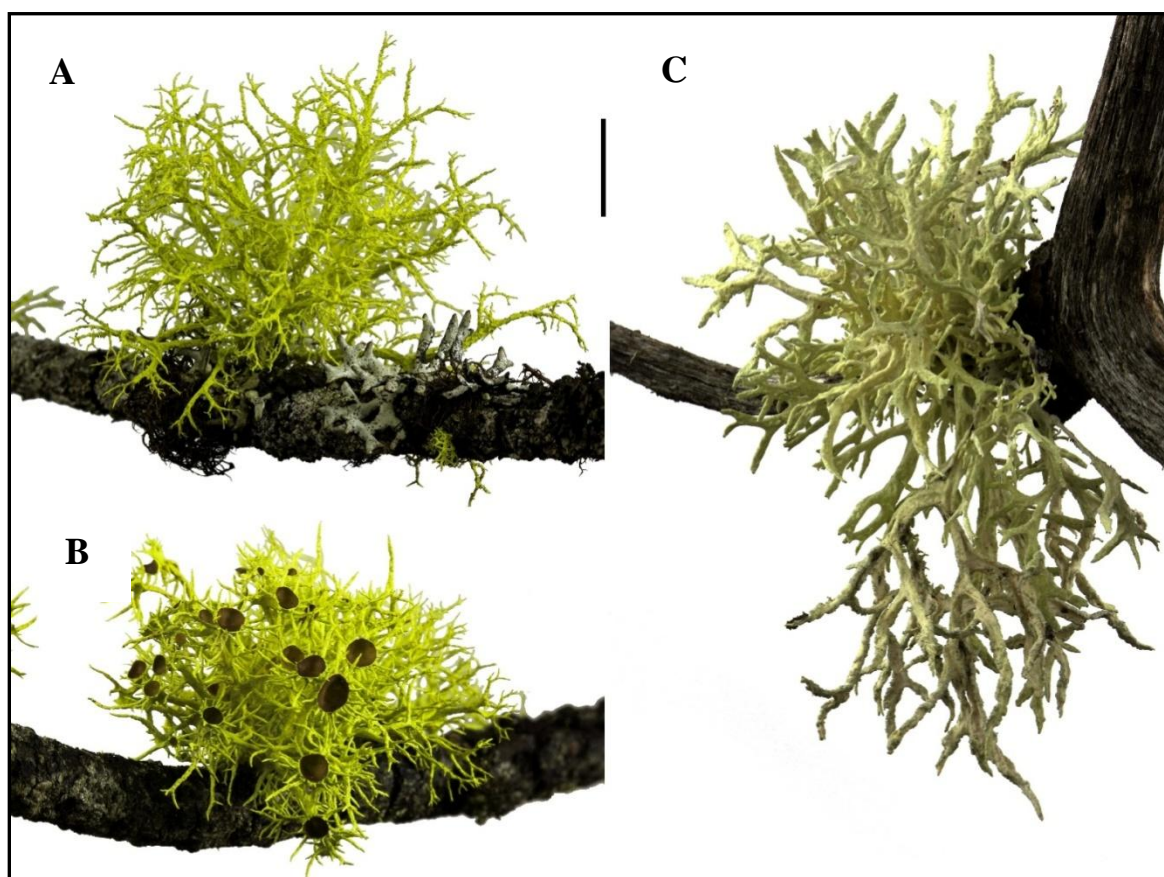


Figure 2-2: The lichen species used to estimate N deposition from lichen thallus N levels. **A:** *Letharia vulpina*, **B:** *Letharia columbiana*, and **C:** *Evernia prunastri*, each scaled to 1 cm (vertical bar).

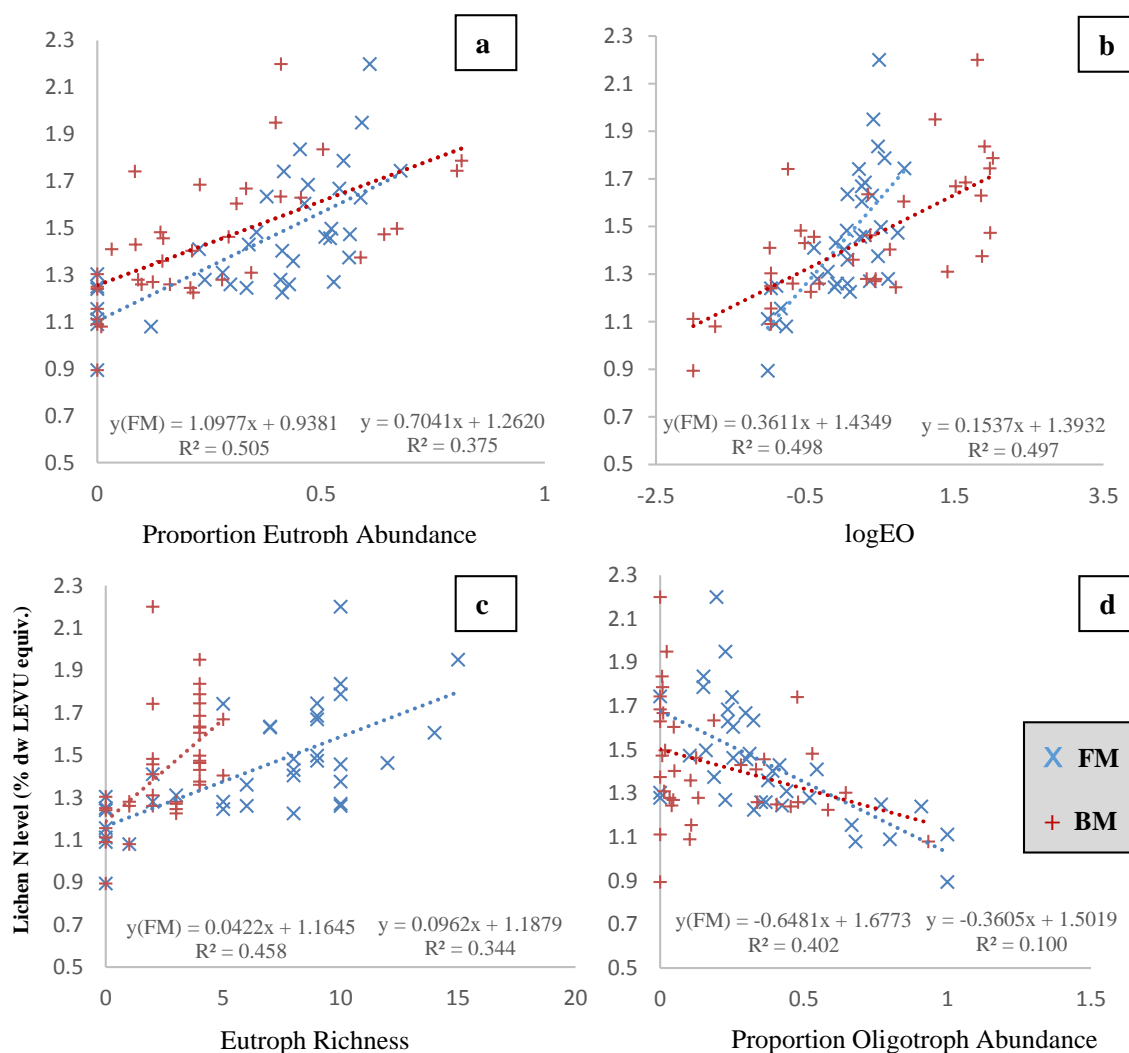


Figure 2-3: The relative performance of lichen indices between methods.

The relative performance of select lichen indices between FM and BM using simple linear regression analysis with lichen thallus N level (% dw *Letharia vulpina* equivalents) on the vertical axis. Shown on the horizontal axis are: **a**) Proportion Eutroph Abundance (PNA); **b**) Eutroph to Oligotroph ratio (logEO; logtransformed), where the FM excluded one high elevation plot (14) that lacked both eutrophs and oligotrophs, resulting in a log-transformation outlier that was removed; **c**) Eutroph richness; and **d**) Proportion Oligotroph Abundance (POA), where the BM pattern was weakened by the inclusion of two high elevation plots with low lichen thallus N levels that lacked branch lichens. All p-values ≤ 0.0001 except BM POA ($p = 0.057$; Table 2-3).

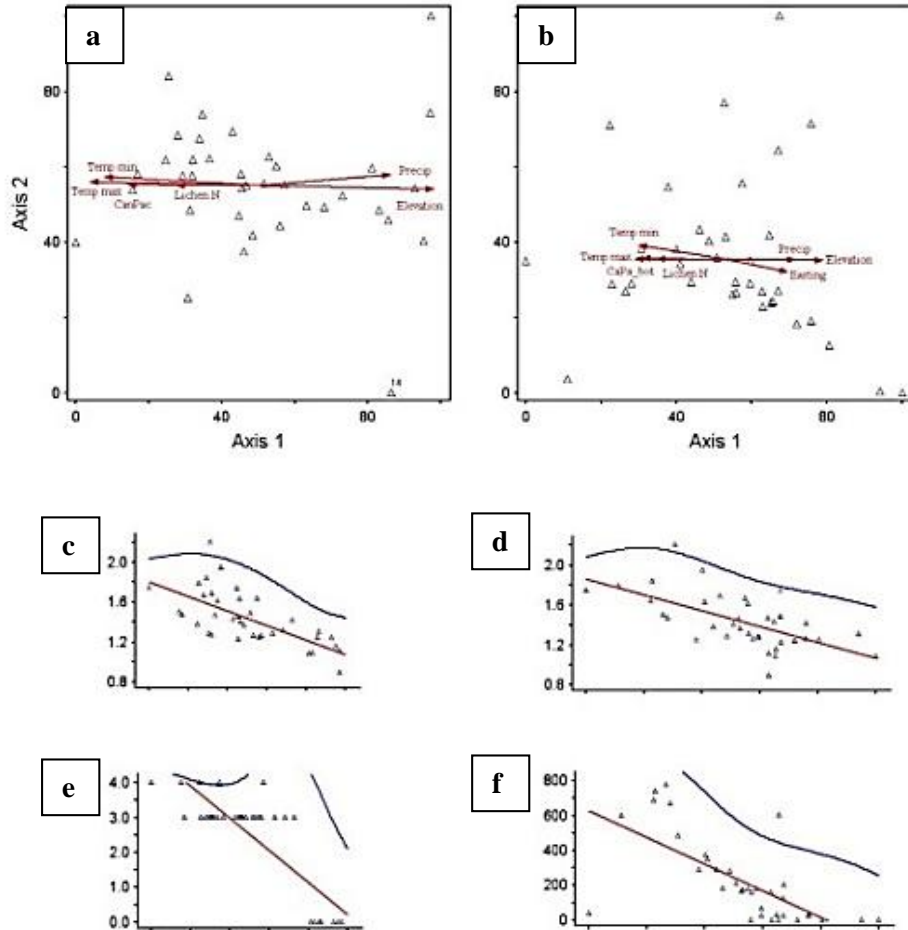


Figure 2-4: Comparison of ordination of FM and BM plots in species space.

Results from ordination (NMS) of the FM (a) and the BM (b) in species space further summarized in Table 2-5. Joint plot vectors representing correlation of lichen thallus N levels with ordination axis 1 shown for FM (c) and BM, respectively (d). Scatterplots of the abundance of *Candelaria pacifica* along ordination axis 1 scores shown for FM (e) and BM, respectively (f). The blue envelope lines in c-f display the approximate upper bound of the overlay variable, which include about 95% of the plotted points with respect to the ordination axis. See Table 2-6 for correlations with environmental variables.

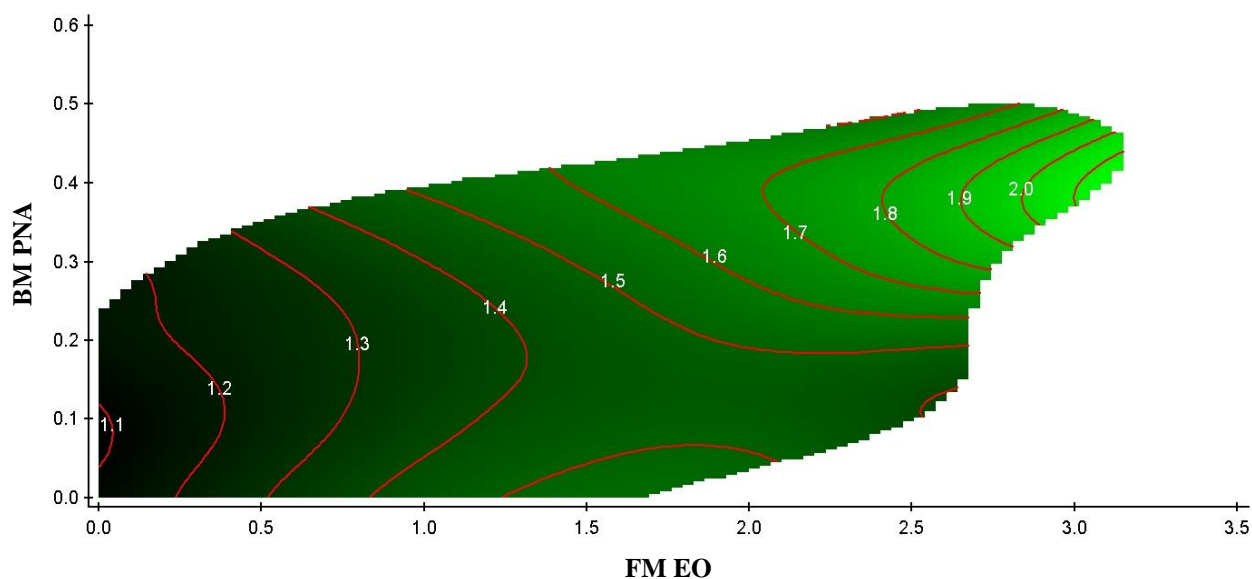


Figure 2-5: Lichen thallus N level model with predictors FM EO and BM PNA.

The lichen CLO was determined from a local linear model (NMPR) that combined FM and BM indices to estimate lichen thallus N levels (% dw *Letharia vulpina* equivalents): $xR^2 = 0.657$, ANS 5.8 FM EO tolerance 0.800 and BM PNA tolerance 0.081.

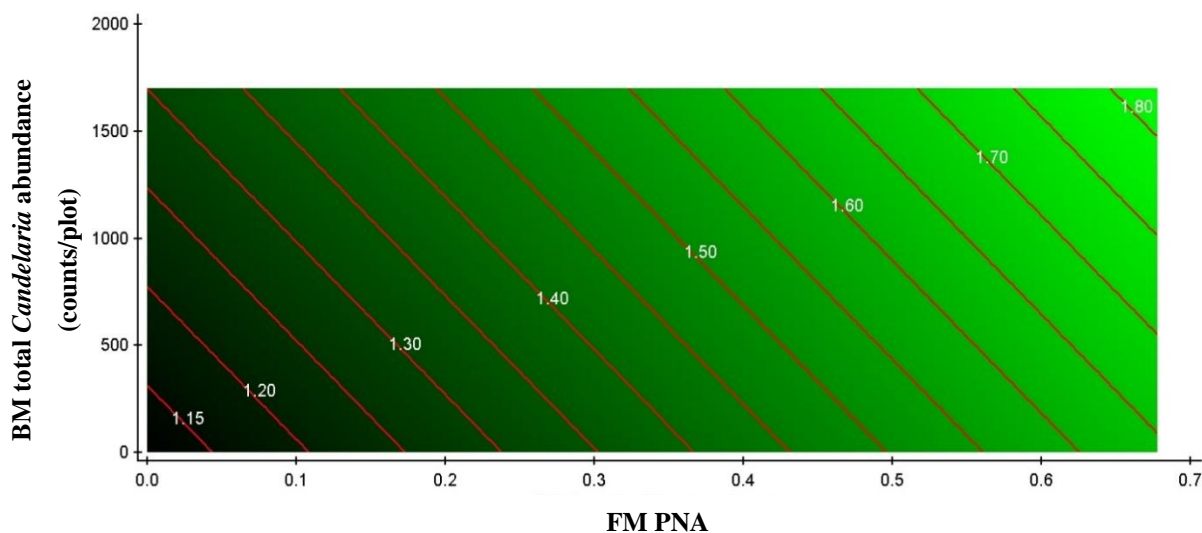


Figure 2-6: Multiple linear regression model for lichen thallus N level with FM PNA and BM *Candelaria* abundance.

Multiple linear regression model predicting lichen thallus N levels (% dw LEVU equivalents) from FM PNA and BM total *Candelaria pacifica* abundance (top and bottom), $R^2 = 0.543$: $1.1165 + \text{FM PNA} (0.7732) + \text{Candelaria pacifica} (0.0001)$.



Figure 2-7: Typical N-affected branch lichen communities.

Photographs of branches in N-affected western portions of the study area. For each 25 cm long segment the upper and lower branch surfaces are shown: **a)** *Pinus sabiniana* at 1.5% N dw., corresponding to $5.4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (BLM MRA, plot 38), **b)** *Pinus attenuata* at 1.8% N dw., corresponding to $7.1 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Feliciano, plot 35), and **c)** *Pinus sabiniana* at an estimated $6.3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Fenn et al., 2010) from Cathey's Valley at the western limit of the study area. The yellow coating is the lichen eutroph *Candelaria pacifica*.

Table 2-1: Seasonal and annual differences in lichen thallus N levels.

Lichen thallus N level quality assurance data (% dw in *Letharia vulpina* equivalents). The spring 2011 (June) replication effort was carried out to determine method sampling error. The fall sampling combined data \leq km (fall 2009-2011). The spring N level for plot 9 was unusually low and considered an outlier.

PLOT #	Spring 2010	Fall	Fall SE	Spring 2011	Spring SE	Spring 2010/ 2011
1	1.51 (n = 1)	1.66 (n = 4)	0.084	1.40 (n = 4)	0.085	1.08
2	1.41 (n = 1)	1.48 (n = 2)	0.088	1.32 (n = 4)	0.042	1.07
3	1.47 (n = 1)	1.69 (n = 1)	-	1.51 (n = 4)	0.039	0.97
4	1.41 (n = 1)	1.37 (n = 3)	0.054	1.24 (n = 4)	0.043	1.14
5	1.46 (n = 1)	-	-	1.31 (n = 4)	0.059	1.11
6	1.28 (n = 1)	1.24 (n = 2)	0.170	1.09 (n = 4)	0.032	1.17
7	1.41 (n = 1)	1.46 (n = 3)	0.092	1.33 (n = 4)	0.043	1.06
8	1.33 (n = 1)	1.27 (n = 2)	0.020	1.10 (n = 4)	0.061	1.21
9	(0.71 (n = 1))	1.26 (n = 1)	-	1.10 (n = 4)	0.069	
10	1.34 (n = 1)	1.40 (n = 3)	0.022	1.24 (n = 4)	0.083	1.08
11	1.71 (n = 1)	1.74 (n = 3)	0.037	1.29 (n = 4)	0.035	1.33
13		1.08 (n = 2)	0.070			
14	1.38 (n = 1)	1.30 (n = 2)	0.212	1.03 (n = 4)	0.116	1.34
			0.085		0.059	1.14

Table 2-2: Lichen species recorded by method.

The lichen Trophic Status according to McCune & Geiser (2009), and Jovan & McCune (2006) for *Flavopunctelia flaventior*, where: E = eutroph (also known as nitrophyte), O = oligotroph (also known as acidophyte), and M = mesotrophs (also known as neutrophyte). Plots refers to the total number of plots where a species was recorded. HW only species occurred exclusively on hardwood substrates in the stand-level method (FM). Range identifies the minimum and maximum elevation where the species was recorded. The total abundance is the sum of abundance scores for the FM, and the total score for the branch-level method (BM). The score for *Candelaria pacifica* is reported as the total counts for the lower + upper branch surface.

Scientific Name	Trophic Status	Elevation Range, m	FM			BM	
			Total abundance	# Plots	HW only	Total abundance	# plots
<i>Ahtiana sphaerosporella</i>	O	1571-2519	24	12		463	6
<i>Alectoria sarmentosa</i>	O	1893	1	1		-	-
<i>Bryoria fremontii</i>	O	1348-2184	4	2		15	1
<i>Candelaria pacifica</i>	E	309-2225	95	32		6414/8686	31/30
<i>Cetraria chlorophylla</i>	M	1821-1893	1	2		-	-
<i>Cetraria merrillii</i>	O	361-2517	57	27		169	13
<i>Cetraria pallidula</i>	O	1348	1	1		2	1
<i>Cetraria orbata</i>	O	1039-2184	15	9		485	10
<i>Cetraria platyphylla</i>	O	914-2184	26	12			
<i>Cladonia coniocraea</i>		1821	1	1		-	-
<i>Cladonia fimbriata</i>		1039-1282	4	2		-	-

<i>Collema furfuraceum</i>	E	361-1252	8	5	X	-	-
<i>Collema nigrescens</i>	E	750-1252	9	5	X	-	-
<i>Evernia prunastri</i>	E	469-2023	14	20		379	8
<i>Flavopunctelia flaventior</i>	E	361-1571	7	4		57	2
<i>Flavopunctelia soredica</i>	E	750	2	1		-	-
<i>Hypogymnia imshaugii</i>	O	361-2517	73	30		3666	23
<i>Hypogymnia tubulosa</i>	M	914	2	1		6	1
<i>Leptochidium albociliatum</i>	O	914-1157	1	2	X	-	-
<i>Letharia columbiana</i>	M	834-2726	71	26		-	-
<i>Letharia gracilis</i>		1282	1	1		-	-
<i>Letharia vulpina</i>	O	361-2821	100	35		3273	28
<i>Melanelixia californica</i>	M	309-2023	42	16		5181	31
<i>Melanelixia subargentifera</i>		309-1951	6	5			
<i>Melanohalea exasperatula</i>	M	852-2225	20	8			
<i>Melanohalea multispora</i>	M	309-1354	10	4			
<i>Melanohalea subelegantula</i>	E	852-2225	40	17			
<i>Melanohalea subolivacea</i>	M	361-2137	53	20			
<i>Nephroma helveticum</i>	O	914-1039	2	2	X	-	-
<i>Nodobryoria oregana</i>	M	914-2821	61	26		54	10
<i>Normandina pulchella</i>		750-1157	6	4	X	-	-
<i>Parmelia barrenoae</i>	E	469-2023	37	19		197	9
<i>Parmelia hygrophila</i>	M	1868	1	1		-	-
<i>Parmelina coleae</i>	E	361-1951	38	18		-	-
<i>Parmeliopsis ambigua</i>	O	1282-1893	3	3		-	-
<i>Peltigera collina</i>	M	914	1	1	X	-	-
<i>Phaeophyscia ciliata</i>	E	1157-1589	9	5	X	-	-
<i>Phaeophyscia orbicularis</i>	E	361-1821	7	4		-	-
<i>Physcia adscendens</i>	E	361-1951	50	24		858	19
<i>Physcia aipolia</i>	E	309-1747	30	12			
<i>Physcia biziana</i>	E	309	1	1			
<i>Physcia dimidiata</i>	E	309	1	1			
<i>Physcia rhizinata in ed.</i>	E	1039-1157	3	2			
<i>Physcia stellaris</i>	M	309-1821	38	18			
<i>Physcia tenella</i>	E	605-2023	28	14		61	10
<i>Physconia americana</i>	M	852-1747	15	6			
<i>Physconia californica</i>	M	309	1	1			
<i>Physconia enteroxantha</i>	E	309-2023	47	20			
<i>Physconia fallax</i>	M	309-1821	14	8			
<i>Physconia isidiigera</i>	M	309-1951	31	13			
<i>Physconia perisidiosa</i>	E	361-1821	36	16		100	2
<i>Platismatia glauca</i>	M	914-1868	5	3			
<i>Platismatia wheeleri</i>	M	750-914	4	2		-	-
<i>Ramalina farinacea</i>	E	1348-1868	5	3		-	-
<i>Scytinium cellulosum</i>	O	1157-1282	3	2	X	-	-
<i>Scytinium lichenoides</i>	O	914-1455	6	3	X	-	-
<i>Scytinium tacomae</i>	O	361-1455	7	5		-	-
<i>Scytinium teretiusculum</i>	O	914-1039	3	2	X	-	-
<i>Usnea sp.*</i>	M	361-1951	11	8		159	2
<i>Vulpicida canadensis</i>	O	361-1354	13	7		10	2
<i>Waynea californica</i>		750-1252	9	5	X	-	-
<i>Xanthomendoza fallax</i>	E	309-1951	6	3		348	20
<i>Xanthomendoza fulva</i>	E	309-1951	27	13			
<i>Xanthomendoza hasseana</i>	E	469-1821	44	20			
<i>Xanthoria polycarpa</i>	E	309-1893	20	10			
Crustose lichens						20188	36

Table 2-3: Indices derived to analyze patterns in the lichen community composition.

Lichen community indices used to analyze stand-level data (FM) and branch-level data (BM) for species with known trophic status (Table 2-2). Correlation of lichen indices with lichen thallus N levels (% dw in LEVU equivalents) from simple linear regression: * = p-value < 0.05, ** = p-value ≤ 0.001, and *** = p-value ≤ 0.0001. The performance of several BM indices was affected by inclusion of two plots with low lichen thallus N levels without branch lichen occurrences.

FM	BM	Description	FM plot mean min-max (avg)	BM plot mean min-max (avg)	Correlation with lichen thallus N levels (R ² :
	Trich	Total lichen species richness	1 – 33 (14.8)	0 – 14 (7.0)	0.336*** / 0.107*
	Erich	Eutroph species richness	0 – 15 (6.5)	0 – 5 (2.6)	0.458*** / 0.344***
	MRich	Mesotroph species richness	0 – 7 (3.4)	0 – 4 (1.2)	0.333** / 0.179*
	Orich	Oligotroph species richness	0 – 10 (4.4)	0 – 5 (2.3)	0.004 / 0.061
	Eabun	Total plot eutroph abundance	0 – 39 (15.5)	0 – 2327 (434)	0.492*** / 0.316**
	Mabun	Total plot mesotroph abundance	0 – 25 (8.5)	0 – 527 (141)	0.508** / 0.188*
	Oabun	Total plot oligotroph abundance	0 – 27 (10.7)	0 – 813 (217)	0.001 / 0.107*
	Tabun	Total plot lichen abundance	2 – 67 (35.6)	0 – 2898 (1336)	0.331** / 0.323**
N/A	CaPa_bot	<i>Candelaria pacifica</i>	N/A	0 – 775 (229)	0.405***
N/A	CaPa_top	<i>Candelaria pacifica</i>		0 – 958 (169)	0.202*
N/A	CAND	<i>Candelaria pacifica</i>		0 – 1695 (397)	0.314**
	PNA	Proportion eutroph (also known as nitrophytes) of total abundance	0 – 0.68 (0.37)	0 – 0.81 (0.26)	0.505*** / 0.375***
	PMA	Proportion mesotroph of total lichen abundance	0 – 1.0 (0.25)	0 – 0.35 (0.10)	0.003 / 0.109*
	POA	Proportion oligotroph of total lichen abundance	0 – 1 (0.37)	0 – 0.91 (0.18)	0.402*** / 0.100
	EO	Log(Eabun/Oabun)	-2 – 0.83 (-0.02)	-2 – 3.37 (0.28)	0.498*** / 0.497***

Table 2-4: Comparison of sources of variability and sampling error in the measurement of lichen thallus nitrogen.

¹ Samples collected in the spring of 2010 and 2011. ² Specimen splits were conducted opportunistically and do not optimally address the within-sample variation.

³ National Institute for Standards and Technology.

Variation	Description	# reps	# sites	St. Dev.
Within-plot	Within plot replicates, spring 2011	4	12	0.118
Between years	Same plot same season, different years ¹	2	10	0.124
Within-sample	Specimen split ²	2	25	0.065
Lab precision	Lab repeat analysis sample duplicate	2	39	0.019
Lab accuracy	Lab analysis of NIST ³ standards	-	40	0.041

Table 2-5: Summary of ordination analysis (NMS).

Both ordination solutions were rotated on lichen thallus N level in the environmental matrix to maximize correlation with ordination axis 1.

	Dimen -sion	Solution total R²	Axis 1 strength R²	Lichen N% dw loading on axis 1 r (R²)	Stress	Plots	Species
FM	2	0.871	0.712	-0.666 (0.443)	11.92	37 (excl. plot 27)	29 species in > 5 plots
BM	2	0.954	0.686	-0.615 (0.379)	7.78	37 (excl. plot 27)	21 species in > 5 plots

Table 2-6: Correlation (Pearson) of major environmental variables with ordination axis 1.

Coordinates are Universal Transverse Mercator (UTM: NAD83 Zone 11N).

		FM	BM
Code	Description	r	r
Easting	UTM Easting (m)	0.626	0.561
Northing	UTM Northing (m)	0.354	0.275
Elevation	Elevation (m)	0.956	0.711
Canclos	Canopy Closure (%)	0.011	0.022
Tmax	Average annual maximum temperature (°C)	-0.954	-0.701
Tmin	Average annual minimum temperature (°C)	-0.913	-0.687
Precip	Precipitation (mm)	0.826	0.599
Lichen N	Lichen thallus N level (% dw LEVU equivalents)	-0.673	-0.615
CanPac	<i>Candelaria pacifica</i> abundance (branch bottom)	-0.844	-0.674

**CHAPTER 3: MAPPING NITROGEN POLLUTION USING LICHEN
THALLI IN THE YOSEMITE REGION OF THE SIERRA NEVADA,
CALIFORNIA**

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Ecological Applications
-Submission pending-

ABSTRACT

Yosemite National Park and nearby portions of the Sierra and Stanislaus National Forests in California are designated as federal air quality Class 1 and are afforded the highest level of protection under the Clean Air Act (1977). Local measurements of throughfall nitrogen (N) deposition, deposition modeling, and studies of the composition of epiphytic macrolichen communities suggested that the lichen critical load was exceeded. This effort is the first in estimating the geographic area of critical load exceedance at high level of resolution with lichen thallus N levels as predictor.

We estimated stand-level N inputs from lichen thallus N levels at 301 locations throughout the study area. With these data, we calibrated a lichen thallus N concentration model to extrapolate corresponding N deposition to the landscape level at a high level of resolution. Lichen thallus N levels were standardized to *Letharia vulpina* dry-weight equivalents and ranged from 0.85 to 2.28% corresponding to a throughfall deposition of 1.8 to 12.3 kg inorganic N (wet + dry) ha⁻¹ yr⁻¹. More than 82% of the lichen thallus samples had N levels > 1.1%, corresponding to a previously identified lichen critical load of 2.9 kg throughfall N ha⁻¹ yr⁻¹. Modeling of lichen thallus N levels across the landscape suggested that the lichen critical load for epiphytic macrolichens in coniferous forests has been exceeded in at least 68% of the study area, including all of the foothills and montane areas across the west slope of the Yosemite area Sierra Nevada. The measurement of lichen thallus N levels was a cost-effective alternative method for estimating stand-level total N deposition, and lichen thallus N levels can be used to estimate landscape level N inputs at a high level of resolution.

Highlights: ► Yosemite region lichen thallus N concentration ranged from 0.85 to 2.28% (dry-weight *Letharia vulpina* equivalents), corresponding to a throughfall deposition of 1.8 to 12.3 kg inorganic N (wet + dry) ha⁻¹ yr⁻¹. ► The critical load of 2.9 kg throughfall N ha⁻¹ yr⁻¹ was reached or exceeded in at least 68% of the study area, and in 71% of the federal air quality Class 1 designated area. ► Lichen thallus N levels are useful for mapping N deposition at a high level of resolution.

Keywords: Air pollution effects, Air quality, California ecosystems, Community shifts, Critical loads, Eutrophication, Epiphytic lichens, Nitrogen deposition.

INTRODUCTION

Yosemite National Park and nearby portions of the Sierra and Stanislaus National Forest are part of the largest federal air quality Class 1 designated air-shed in the western United States, protected under the Clean Air Act, covering the entire crest of the Sierra Nevada in California. Federal land managers are charged with direct responsibility to protect the air quality and related values of Air Class 1 lands under the Clean Air Act.

West of the Sierra Nevada lies the Central Valley of California, one of the most productive agricultural areas in the world. Here, less than 1% of the nation's total farmland, fertile soils, and extensive irrigation systems produce more than 8% of the agricultural output in monetary value (Reilly, 2008). Nearly half of all fruits, nuts, and vegetables consumed in the US are produced in California (CDFA, 2012) and primarily in the Central Valley.

Such productivity and growth are sustained with significant inputs of energy and fertilizers with concomitant emissions that are regulated by California State Air Districts. The San Joaquin Valley Air District (District) lies upwind of Yosemite National Park and covers the southern half of the Central Valley. The District has made major progress toward attaining federal air quality standards. It is challenged however, not only by the emissions associated with intensive agriculture, animal feeding operations, and dairy farms, but also by rapid rates of population growth and high-density traffic. The population in the District is projected to increase from 2.6 million in 2000 to nearly six million in 2035, and the number of vehicle miles is projected to increase 209% during the same period (Cox et al., 2013). Vehicle fuel combustion is responsible for 83% of nitrogen oxides (NO_x) emissions at the state level. While they have been decreasing at the District, local emissions are still high. For example, Fresno County lies just southwest (downwind) of the study area and had an annual emission of 74 tons of NO_x per day in 2010, ranking 7th highest among California counties (Cox et al., 2013). Fresno County also has high ammonia (NH_3) emissions; with an annual average of 69 tons per day it ranked 2nd highest among California counties. The majority of the NH_3 emissions ($\pm 92\%$) originate from agricultural sources and are expected to remain relatively constant (Cox et al., 2013).

In the atmosphere, ammonium (NH_4^+) and NO_x emissions from fossil fuel combustion (e.g., traffic) and wildfires are important constituents of smog-forming aerosols that contribute substantially to ambient fine particulate matter in the atmosphere (Cox et al., 2009; Nowak et al., 2012). In the San Joaquin Air District, the prevalence of such aerosols has resulted in the District's designation of non-attainment with the national 24-hour $\text{PM}_{2.5}$ standard, since the establishment of the standard in 1997 (Cox et al., 2009). Aerosols such as NH_4NO_3 are stable

enough for transport across long distances and contribute substantially to view-shed degradation (Trijonis, 1990) that is common in the Sierra Nevada (Fenn et al., 2003), and also play an important role in the elevated atmospheric nitrogen (N) deposition in the Sierra Nevada.

Ecosystems in the western US are adapted to low natural ambient N levels of about $0.2 \mu\text{g m}^{-3}$ (Trijonis, 1990). Natural background N-deposition data are not available for the study area, but may have averaged $\pm 0.69 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Holland et al., 1999) depending on annual precipitation (Williams & Tonnessen, 2000) and canopy scavenging (i.e., forest cover and leaf area). These levels are currently exceeded throughout California (Fenn et al., 2010).

While fixed nitrogen is a nutrient, high deposition rates are ecologically harmful (Fenn et al., 2010; Fenn et al., 2003; Volpe et al., 2006). The quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge is termed a critical load (CLO) or critical level (CLE; Nilsson & Grennfelt, 1988), derived from observations on ecosystem responses (Burns et al., 2008; NADP, 2008; Pardo et al., 2011; Porter et al., 2005). Critical levels and CLO's are becoming an increasingly important tool in air quality management and in communicating ecological impacts (Glavich & Geiser, 2008; Porter & Johnson, 2007).

CLE's are ambient air concentrations expressed in ppm or $\mu\text{g m}^{-3}$, whereas CLO's refer to depositional loadings typically expressed in terms of $\text{kg ha}^{-1} \text{ yr}^{-1}$ of wet or total (wet + dry) deposition. In aquatic habitats, diatoms are most sensitive to N deposition, hence have the lowest CLO (Saros et al., 2010). In terrestrial habitats, CLO's for N are generally lowest for lichens and bryophytes, and increase from mycorrhizal fungi to herbaceous plants, shrubs, and trees (Pardo et al., 2011), but for a given receptor, the CLO may differ among ecosystems and between regions.

The sensitivity of lichens is related to their symbiotic nature and the lack of a protective outer cuticle; absorption of both nutrients and pollutants occurs over much of their outer surface from predominantly aerial sources (Nimis, et al., 2002). The National Atmospheric Deposition Program (NADP: CA99, Hodgdon) station located in Yosemite National Park has measured N deposition levels near the lichen CLO estimates for coniferous forests in California (Fenn et al., 2008; Hutten & McCune, 2014c) for at least a decade. A throughfall N deposition model developed for California (Fenn et al., 2010) suggest that the CLO is exceeded in the western half of the Yosemite Sierra Nevada. At 11 sites in Yosemite National Park, and one site in the Sierra National Forest, Hutten and McCune measured throughfall N deposition for one year (2010-2011), using methods developed by Fenn & Poth (2004). Throughfall deposition ranged from 2.8 to $4.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Root et al., 2013; unpublished data M.A. Hutten). Throughfall N deposition

was positively correlated with thallus N levels of several epiphytic macrolichen species (Root et al., 2013) and was also correlated with the species composition of lichen communities (Fenn et al., 2008; Geiser et al., 2010; Geiser & Neitlich, 2007). In the study area, apparent impacts to lichen community composition were correlated with a N deposition gradient identified via lichen thallus N levels at 38 sites (Hutten & McCune, 2014b).

The primary objective of this study was to evaluate the utility of lichen thallus N-concentration data to provide a more complete spatial pattern of atmospheric N deposition throughout the Yosemite region of the Sierra Nevada. We specifically aimed to determine the geographic extent of the area where the lichen critical load has been exceeded. Similar work has been attempted without success elsewhere (Raymond et al., 2010), but with the existing regional calibration of lichen thallus N concentration and throughfall-N deposition (Root et al., 2013) and nonparametric modeling techniques, we aspired to develop a cost effective, and low-impact method for potential future use. This work is important because high resolution deposition data are needed (Glavich & Geiser, 2008), and quantifying N-deposition using standard ion-exchange resin (IER) methodology (Fenn & Poth, 2004) is expensive and time-consuming. In the Sierra Nevada, N-related impacts are already more severe farther south in Sequoia National Park (Fenn et al., 2003), e.g., deposition rates of $4.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ are modelled for the ‘Giant Forest’ (Fenn et al., 2010). To the north, Lassen National Park is thought to be less impacted; however, data are limited and elevated lichen N levels were documented on the southern flank of Lassen Peak in 2010 (M.A. Hutten, unpublished data). Detailed information on N inputs across the Yosemite region may help managers understand changing landscape dynamics, e.g., increases in the invasiveness of exotic annual grasses (Fenn et al., 2010), and improve the ability of managers to engage the public.

MATERIALS AND METHODS

Study Area: The study area is about 820,000 ha and includes Yosemite National Park and a portion of the adjoining Stanislaus and Sierra National Forests on the west slope of the Sierra Nevada in central California, USA. The hydrographic boundary of the Sierra Nevada crest and the boundary with Mono County delimits the northeastern boundary and the Madera-Fresno county line bounds the southeast (Figure 3-1). Our major focus was Yosemite National Park, but we extended the study area westward, toward pollution emission sources in the Central Valley. The western extent of the study area follows the lower distributional limit of the mixed-conifer forest type (Anderson et al., 1976) which is approximated by the western boundary of the Sierra and Stanislaus National Forests. The terrain in the study area is mountainous, with elevations

ranging from 260 m along the western boundary to well over 3000 m close to the crest. Along this steep elevation gradient, climate and forest composition change profoundly.

Climate: The study area is characterized by long, hot, and dry summers that are more pronounced at lower elevations. January and July daily maximum temperatures average 13°C and 33°C at low elevations, respectively, and 2°C and 19°C at the passes along the Sierra Nevada crest, respectively. The bulk of the precipitation occurs during late fall and winter. Mean annual precipitation ranges from 40 cm at the lowest elevations to about 140 cm at some high-elevation sites (data extracted from interpolated 800 m PRISM climate normals 1971-2000, Daly et al., 2008, PRISM Climate Group 2004). Yosemite Valley, at 1190 m elevation, received an annual average of 104 cm of snow during the same period⁷.

Vegetation: At the lowest elevations in the study area, the vegetation is a mix of chaparral and foothill woodlands (*Quercus* and *Pinus*). Montane zone vegetation is characterized by extensive mixed-conifer forest (*Abies*, *Calocedrus*, *Pinus*, and *Pseudotsuga*), including groves of *Sequoiadendron* and some of the tallest pines in the world. Subalpine forests (*Juniperus*, *Pinus*, and *Tsuga*) finally give way to high elevation rock barrens around 2500 m.

Air Quality: Sulfur dioxide concentrations averaged $\leq 0.5 \mu\text{g m}^{-3}$ annually since 1995 with highest recorded bi-weekly averages $< 2 \mu\text{g m}^{-3}$ ⁽⁸⁾. This is well below the ‘no-effect level’ reported for lichens in the Netherlands (Sparrius, 2007) and the response threshold of 5-15 ppb for sensitive lichens in the Pacific Northwest (McCune & Geiser, 2009). Ammonia (NH_3) is not routinely monitored by established air quality monitoring networks, but annual concentrations averaged around $0.94 \mu\text{g m}^{-3}$ ⁽⁹⁾; just below the CLE of $1 \mu\text{g m}^{-3}$ established by the United Nations Economic Commission for Europe for lichens and bryophytes in Europe (Batty & Hallberg, 2010). Monthly ambient air concentrations averaged $> 1 \mu\text{g NH}_3 \text{ m}^{-3}$ during the dry season (June-September), and peaked at $2.6 \mu\text{g m}^{-3}$ during July¹⁰; just below levels that would result in detectable alteration of the lichen community if sustained (van Herk, 2001; Wolseley et al., 2006). Critical levels and critical loads are typically lower in the U.S. than in Europe (Pardo et al., 2011), consequently NH_3 may play a role in the lichen responses in the study area, particularly in areas closest to emission sources in the Central Valley. Total N deposition averaged 3.1 and 3.5 kg N (wet + dry)^{8,10} $\text{ha}^{-1} \text{ yr}^{-1}$ in 2010 and 2011, respectively. This rate has been relatively stable for little over a decade, especially when accounting for the influence of annual precipitation. The

⁷ Yosemite Park Hdqtrs COOP station: ID 049855

⁸ CASTNET YOS404, Turtleback Dome: measurement period: Oct 1995 – Febr 13

⁹ AMoN: CA44, Turtleback Dome: measurement period: Mar 2011 – Sept 13

¹⁰ NADP CA99, Hodgdon: measurement period: Oct 1995 – Febr 13

ionic forms of N, especially NH_4^+ and NO_3^- , are the largest constituents of total N deposition in the study area. Modeled throughfall N deposition in the study area ranged 2-9 kg N ha⁻¹ yr⁻¹ (Fenn et al., 2010). Between 2010 and 2011, throughfall N measurements ranged 2.8 to 4.7 kg N ha⁻¹ yr⁻¹ for 12 sites within Yosemite National Park (Root et al., 2013; unpublished data M.A. Hutten) using methodology described by Fenn & Poth (2004). Lichen thallus N-levels corresponded to a range of 1.8 to 11.5 kg throughfall N ha⁻¹ yr⁻¹ for the study area (Hutten & McCune, 2014b).

Site Selection: We collected lichen thallus N-level data at 301 locations throughout the study area (Figure 3-1). Criteria for site selection included the availability of sufficient target lichens for element content sampling, distance from roads ≥ 50 m, few overstory hardwoods, and a good dispersion throughout the study area in general. Due to the remote nature of much of the study area and our reliance on volunteers, relatively accessible areas of Yosemite National Park were more densely covered than other parts of the study area. The effort included lichen N-level data from 38 locations where Hutten & McCune (2014b) studied the impacts of N deposition on epiphytic lichen community composition (hereafter: ‘intensive plots’; Appendix A).

Lichen Thallus N Levels: Thallus sampling was accomplished during dry and stable weather at the end of the dry season in 2010 and 2011 to avoid season-related fluctuations in lichen thallus N concentration (Bruteig, 1993) as is common practice (Blett et al., 2003; Jovan & Carlberg, 2007; Saros et al., 2010). In each plot, we collected lichen thalli using methods developed by Geiser (2004). Healthy target lichen thalli (species enumerated below) were collected from coniferous tree boles and branches using latex gloves to avoid contamination. Each composite sample had a target field weight of 10 g and consisted of a single air-tight polyester bag with lichen individuals of the same species collected from at least six different trees. In the office, the lichens were spread on paper to air dry and to remove debris including bark, other lichen species, and necrotic thallus, resulting in a final weight of approximately 7 g (air dry) per sample. Samples were analyzed at the University of Minnesota Research Analytical Laboratory during the winter following the field collection. There, samples were ground and dried to constant weight. Lichen thallus N levels (% dry-weight; hereafter: % dw) were then estimated using a LECO FP-528 N Analyzer (Dumas-method: Lee et al., 1996; Yeomans & Bremner, 1991). We employed a variety of quality assurance measures that were described in detail by Hutten & McCune (2014c).

Under the same deposition regime, lichen species may accumulate N at different rates (Root et al., 2013). Therefore, we focused only on three species, the minimum number of species necessary to canvas the study area. We relied predominantly on *Letharia vulpina* (LEVU); a

widespread and abundant species in the Sierra Nevada, and set this species as our measurement standard. In locations where LEVU was unavailable, we predicted thallus N levels for LEVU from either *Letharia columbiana* or *Evernia prunastri* using simple linear regression after verifying that a linear model was appropriate.

Lichen thallus N concentration had a strong, positive correlation with throughfall N deposition (Root et al., 2013), and throughfall N deposition is strongly correlated with shifts in the composition of lichen communities (Fenn et al., 2008; Geiser et al., 2010; Geiser & Neitlich, 2007). We estimated throughfall N from lichen thallus N (% dw LEVU equivalents) using a calibration equation, $\ln(\text{throughfall N}) = 0.886 + 1.968 * \ln(\text{N in } Letharia\ vulpina)$, from Root et al. (2013).

Statistical and Spatial Analysis: To estimate atmospheric N deposition from lichen thallus N concentration across the landscape required the use of three lichen species. We estimated *Letharia vulpina* equivalent N levels from *Letharia columbiana* and *Evernia prunastri* thalli collected in sites where two or three target species were available using Simple Linear Regression (SLR; Microsoft® Excel 2013). We increased the range and utility of our regression models by including lichen thallus N level data from the regional U.S Forest Service Air Resource Management Airlichen Database (USDA-USFS, 2013). These data introduced a single major outlier that was removed prior to analysis. Estimating LEVU-equivalent N levels from other lichen species added an unquantified additional error to the lichen N-level estimates for these locations.

We evaluated the utility of lichen thallus N concentration in estimating N deposition at the landscape level with Non-Parametric Multiplicative Regression (NPMR; McCune, 2006) in Hyperniche (McCune & Mefford, 2008). NPMR permits iterative exploration of models without the need to assume a particular relationship between response and predictor variables. We used basic environmental predictor variables including precipitation and temperature, and topographical variables including elevation, slope, aspect, and Topographic Position Index (TPI; Jenness, 2006; Figure 3-1). Strong aggregation of sampling points in the predictor space necessitated the use of conservative settings to control model overfitting. Aggregation to 1000 m site groups did not improve model fit.

Spatial analyses were carried out using Environmental Systems Research Institute (ESRI, Redlands, California) ArcGIS desktop version 10.0 software.

Nomenclature: Nomenclature follows McCune & Geiser (2009) for lichens, and the Jepson Manual (Baldwin et al., 2012) for vascular plants.

RESULTS

Lichen thallus N-level data was quantified at 301 locations (Figure 3-1) spanning an elevation gradient from 329 to 3073 m. Some 96% of the sampling locations were above 1000 m elevation. Above 2500 m, lichens were more sparsely distributed and frequently out of reach. We relied predominantly on LEVU thalli that were abundant across the study area (273 locations). At seven low elevation locations only *Evernia prunastri* was available, and at nine high-elevation locations only *Letharia columbiana* was available. We regressed N accumulation in *Evernia prunastri* and *Letharia columbiana* to *Letharia vulpina* with data from 32 locations in the study area where two or three target species were available. The data from the study area poorly represented low thallus N levels and we augmented our regressions with data from Oregon, Washington, and other regions in CA (USDA-USFS, 2013) to strengthen the relationships (Figure 3-2, Table 3-2).

Among the 301 locations, lichen thallus N levels ranged between 0.85 - 2.28 (% dw in LEVU equivalents), corresponding to a deposition range of 1.8 – 12.3 kg ha⁻¹ yr⁻¹. Ninety percent of all samples had N levels higher than 1.03%, the threshold considered to be “elevated N status” by Jovan and Carlberg (2007). More than 82% had N levels exceeding 1.1%, the lichen critical load determined for the study area (Hutten & McCune, 2014c).

We first constructed a simple model with only easting and northing as predictors of lichen thallus N levels to evaluate how well a ‘distance to emission source model’ accounted for lichen thallus N levels; this model had limited strength ($xR^2 = 0.256$, Average Neighborhood Size (ANS) 23.6, with tolerances for northing and easting 3731 and 6852 m, respectively). Model results suggested that N-contaminated air reached farther east into the study area along the Merced and the Tuolumne River corridors than elsewhere (Figure 3-3).

Considering the limited strength of the ‘distance to source’ model, we added other predictors (Table 3-1). The best overall model was a two-predictor model with elevation and TPI (Figure 3-4). While the overall strength of the two-predictor model was modest ($xR^2 = 0.349$, ANS 25.5, with tolerances 247 and 27 for elevation and TPI, respectively), the standard error of the residuals for lichen thallus N levels against elevation and TPI was 0.044 (or 0.21 N% in dw LEVU equivalents), adequate for deposition estimation in the study area considering the standard deviation for lichen tissue sampling (0.118% N in (LEVU dry-weight equivalents).

We extrapolated the lichen thallus N model with elevation and TPI to the landscape with a conservative Minimum Neighborhood Size (MNS) setting of 6.4. This model generated estimates for 68% of the study area, but for the remaining area our thallus N sampling was too

sparse to generate estimates with such conservative settings. Where estimates were made, the model suggested the nitrogen CLO for lichens was exceeded throughout, including 71% of the air quality Class 1 designated area. We used a less conservative model ($MNS = 1$), to estimate N deposition in the remainder 32% of the study area. With the combination of the two model settings, a small area at the easternmost extreme of the study area ($\pm 0.5\%$ of the total surface area) remains at or below a deposition of $2.9 \text{ kg throughfall N ha}^{-1} \text{ yr}^{-1}$, i.e., the lichen CLO was exceeded in more than 99% of the study area (Figure 3-5).

DISCUSSION

At the landscape scale, lichen thallus N levels were correlated with elevation and topographic position. While the overall strength of the model that predicted lichen thallus N levels based on elevation and TPI was modest, we did not anticipate a strong relationship due to the complexity of the terrain and because we did not measure many factors that influence N deposition and accumulation in lichen thalli at regional and local scales (e.g., wind direction, speed, turbulence, canopy complexity, leaf area, branch and/or stem-flow, lichen growth). Because of the strong west-to-east elevation gain, elevation (and temperature gradients) accounts for distance to pollution sources as well as regional and diurnal airflow patterns along the major west to east-oriented valleys. Nitrogen accumulation was higher in valley bottoms and on ridges than at mid-slope locations. The effect was stronger at low elevations and gradually weakened at higher elevations. Increased lichen N accumulation on ridges may be related to greater contact with N-contaminated air and boundary layer effects. The increased N accumulation in valleys compared to mid-slope locations may be related to diurnal airflow patterns and temperature inversions, resulting in concentration and movement of N-rich air masses in and along valleys. This effect may weaken with increasing distance to emission sources due to the progressive mixing of the air masses. In fact, at the highest elevations, valley bottoms showed a slightly lower N accumulation relative to mid-slope and ridge positions. This may be related to increased humidity and fertility in valleys, with consequently increased metabolic use of N by lichens and trees (direct foliar uptake of N), rather than to sheltering from N deposition.

In scaling up to the landscape level, we observed model tolerances with a characteristic spatial scale of about 4 and 7 km for longitudinal and latitudinal distance, respectively. These distances may guide future sampling grids and provide caution against traditional kriging which assumes the variance is equal in all directions.

Lichen thallus N levels have a strong positive correlation with throughfall N deposition (Root et al., 2013) and thallus sampling is highly repeatable (Hutten & McCune, 2014c).

Nevertheless, values substantially lower or higher than expected from nearby lichen N-level sampling did occur which resulted in large residuals in our model for Yosemite region lichen thallus N levels. NPMR is insensitive to outlier values with large datasets such as these, but minor modifications to the thallus sampling protocol and site selection may further improve the accuracy of N deposition estimation via lichen thallus N concentration levels.

- The *Letharia* thalli in the study area were often very large; the minimum number of thalli permitted in the element sampling protocol (Geiser, 2004) typically satisfied the 10 g field target weight. There is little research on the range of N-level variability in individual lichen thalli at the site level, but we presume it is relatively high (Hutten & McCune, 2014c). Requiring a larger minimum number of individual thalli for each composite lichen N sample, and balancing the maximum relative contribution of large individual thalli into a composite sample should be considered in future work.
- Detailed notes taken for each composite sample suggested that unusually low lichen thallus N levels may occur when thalli were collected from litterfall, boles without foliage (i.e., snags), or boles with a branch architecture that directs canopy throughfall away from the bole.
- There may be potential for denitrification when moist field samples are stored for too long in airtight bags. During laboratory processing we recorded a vinegar-like odor in a few samples that returned unexpectedly low N levels.
- Unexpectedly high lichen thallus N levels may result from contamination with animal excrement, fire suppression retardant drops, or sampling from decumbent branches that funnel high levels of throughfall.
- Our practice to sample thalli ≥ 50 m from roads largely avoided local emission contributions from affecting the model (i.e., traffic); however, large positive model residuals occurred at the Yosemite Big Oak Flat entrance station, and several major intersections that are known for traffic congestion. In future work, larger buffers should be considered for such areas.

We visually compared the geographic area where our model predicted that lichen critical load has been exceeded with a California-wide N deposition model (Fenn et al., 2010). Our higher resolution model (10-m versus 4000-m), with hundreds of local calibration points, suggested the California-wide deposition model slightly underestimates the area where the critical load has been exceeded, primarily at higher elevations in the study area. Nevertheless, both models provide independent evidence for landscape-wide exceedances of the CLO for lichens.

It is likely that current N-deposition regimes will be sustained for many years which will have a range of serious ecological consequences. Among the most sensitive known terrestrial

organisms, the fate of lichen oligotrophs under a sustained, elevated N deposition regime is uncertain, given that many species are already restricted to cool, moist refuges.

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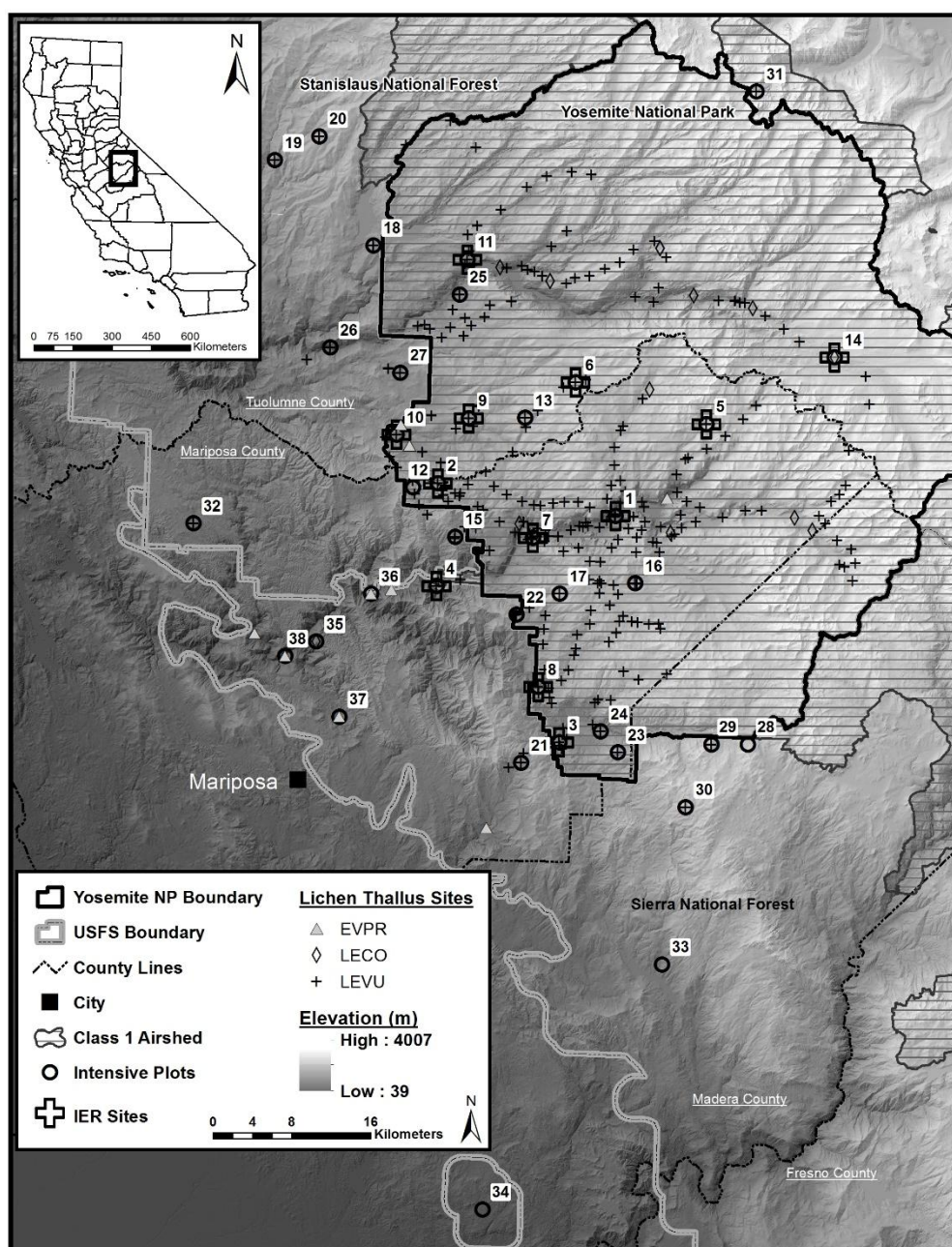


Figure 3-1: Map of the study area and lichen thallus N sampling locations.

The study area encompasses Yosemite National Park, and the NW and SW portion of the Sierra and Stanislaus National Forest, respectively. One of the intensive sites was located just on the eastern slope of the Sierra Nevada crest, on the Humboldt-Toiyabe National Forest (plot 31). Lichen thallus N-level data were collected in 301 localities. Hatch marks identify the area designated as federal air quality Class 1.

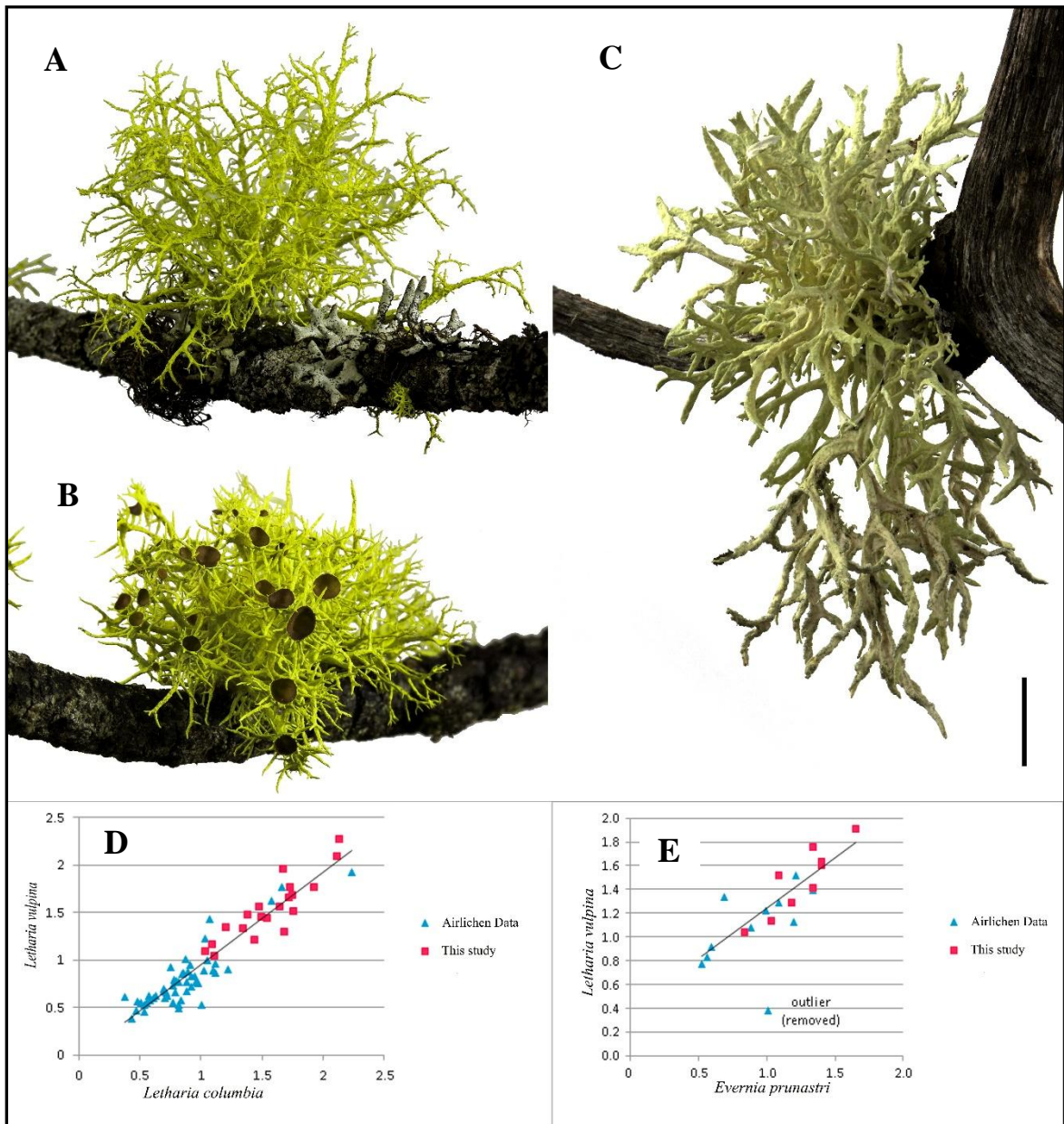


Figure 3-2: Lichen species and lichen thallus N level correlations between species.

A: *Letharia vulpina*, **B:** *Letharia columbiana*, and **C:** *Evernia prunastri*, all scaled to 1 cm (vertical bar). **D:** Relationship between the thallus N levels (% dw) of *Letharia columbiana* on the X-axis, and the thallus N levels (% dw) of *Letharia vulpina* on the Y-axis. **E:** The relationship between the thallus N levels (% dw) of *Evernia prunastri* on the X-axis, and the thallus N levels (% dw) of *Letharia vulpina* on the Y-axis. The regression equations are shown in Table 3-2.

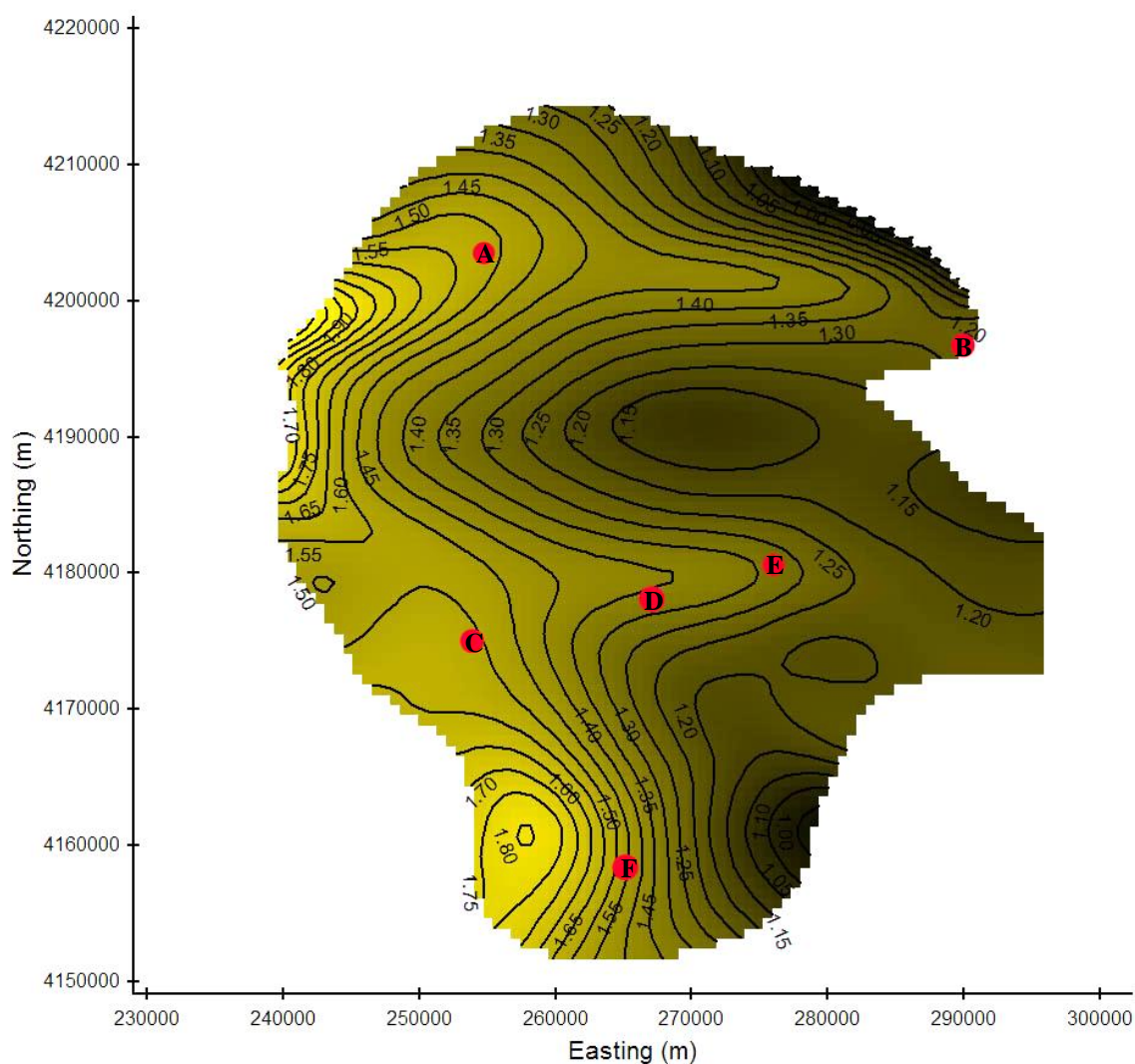


Figure 3-3: Distance to N pollution emission sources model for lichen thallus N levels. Local linear model for lichen thallus N levels (as proxy for N deposition), shown as 'contour lines', with easting and northing as predictors. Coordinates are Universal Transverse Mercator in NAD 83, zone 11N. Model $xR^2 = 0.256$, ANS 23.6, with tolerances 3731, and 6852 m for northing and easting, respectively. White areas lacked sufficient data for estimates and are largely outside of the study area. Reference points: **A**: Hetch Hetchy at O'Shaughnessy Dam; **B**: Tuolumne Meadows; **C**: El Portal; **D**: Yosemite Valley at El Capitan; **E**: Yosemite Valley at Half Dome; **F**: Wawona.

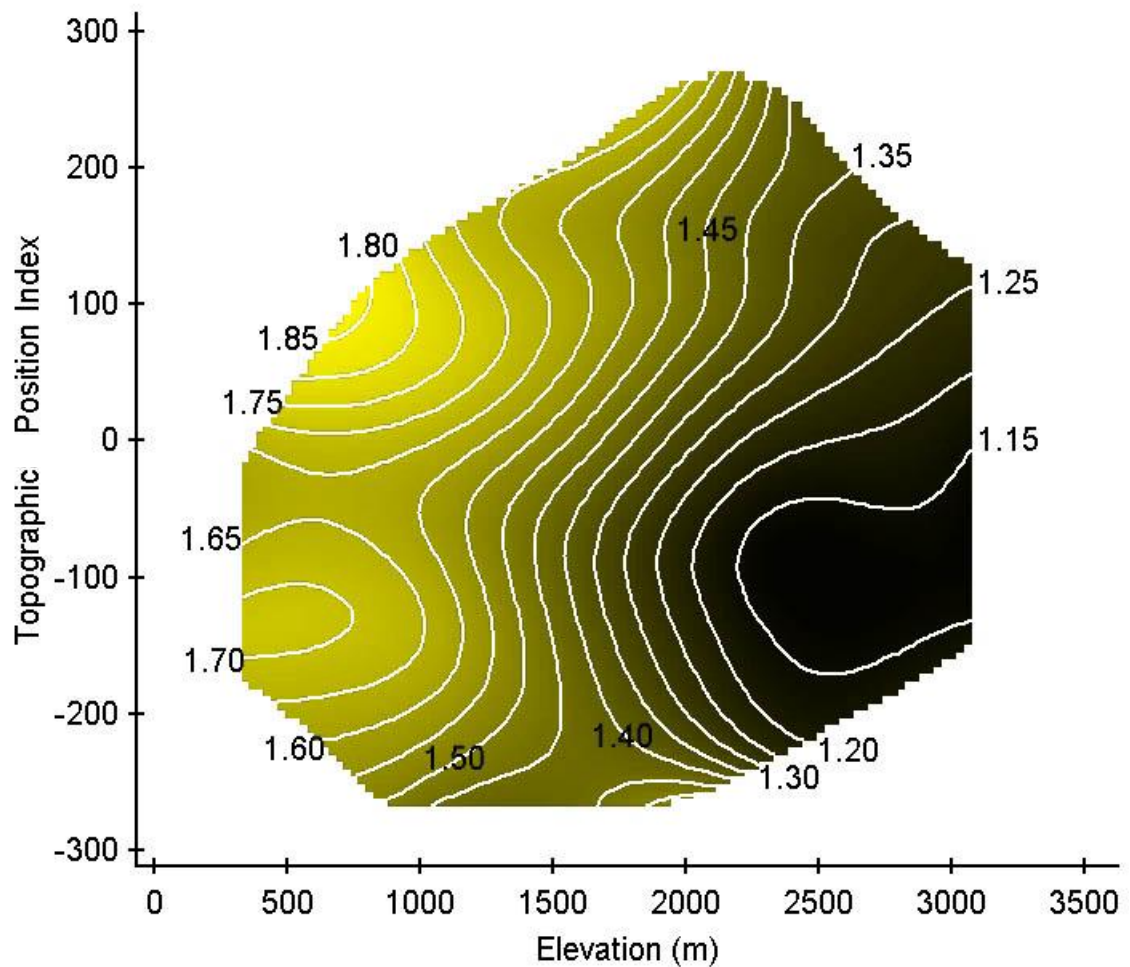


Figure 3-4: Topographic model for lichen thallus N levels.

Local linear model for lichen thallus N levels (% dw LEVU equivalents), shown as 'contour lines', with elevation and Topographic Position Index (TPI) as predictors. High TPI values suggest proximity to a summit or ridge and low values suggest proximity to a valley bottom. TPI values near zero are either mid-slope or flat areas (Jenness, 2006). Model $xR^2 = 0.349$, ANS 25.5, with tolerances for elevation and TPI 247 and 27, respectively, and a Minimum Neighborhood Size = 5. White areas lacked sufficient data for estimates.

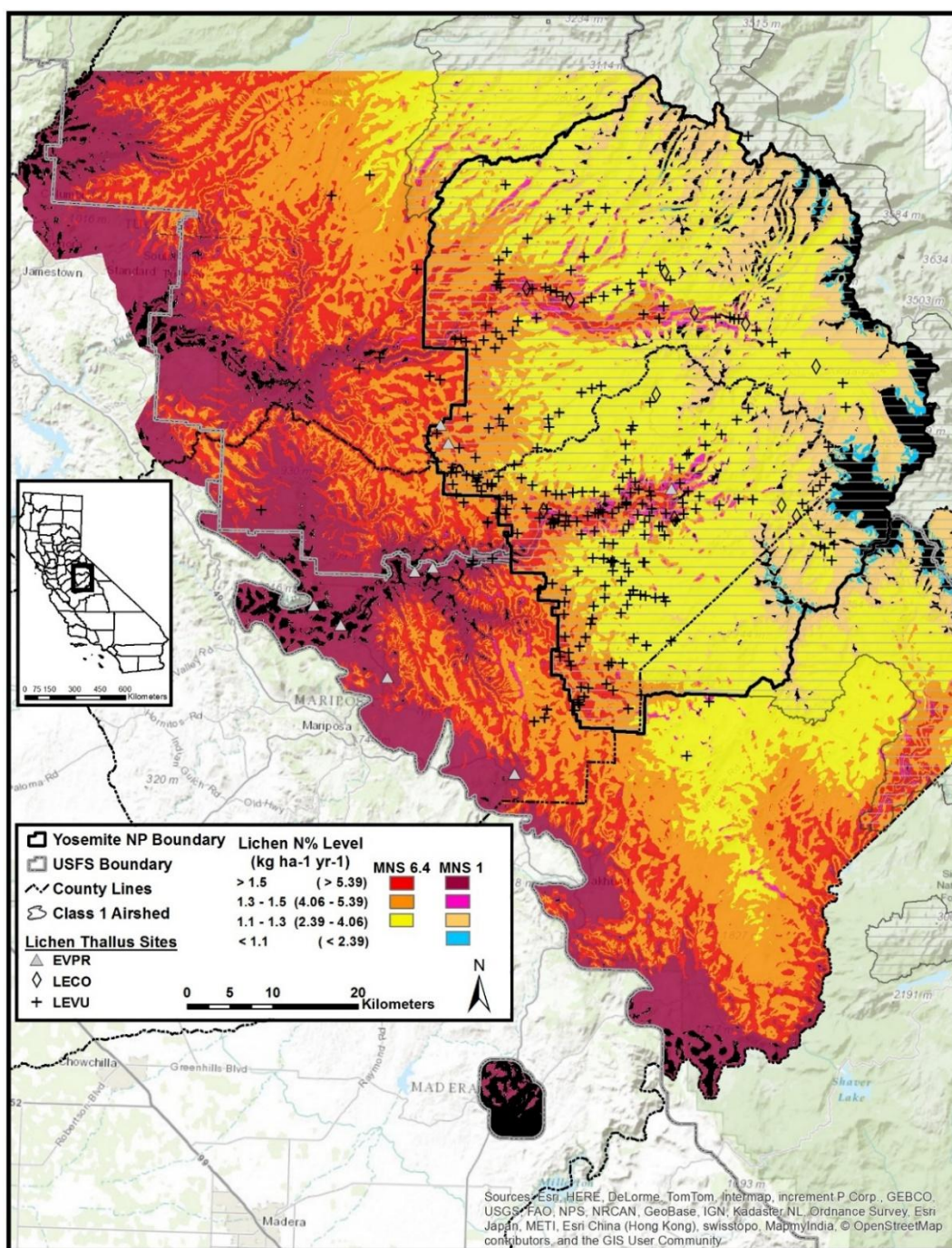


Figure 3-5: Nitrogen deposition map from model estimates for lichen thallus N-levels with elevation and TPI as predictors.

Model extrapolations for lichen thallus N levels (% dw LEVU equivalents) and corresponding throughfall N deposition in kg N ha⁻¹ yr⁻¹ from a conservative two-predictor model with MNS 6.4 (Figure 3-4) supplemented with a less conservative version (MNS = 1) to expand the geographic coverage. No model extrapolations were made for areas in black. Hatch marks identify air quality Class 1 areas.

Table 3-1: Names and definitions of variables considered for lichen N-level modeling.

PRECIPITATION	
precip1-12:	Mean monthly precipitation in January-December (mm)
annPRE:	Mean annual precipitation (mm)
dryPRE:	Mean annual precipitation during dry period from June through September (mm)
wetPRE:	Mean annual precipitation during wet period from October through May (mm)
TEMPERATURE	
TMAX1-12:	Mean maximum temperature in January-December (°C)
TMAX14:	Mean annual maximum temperature (°C)
TMIN1-12:	Mean minimum temperature in January-December (°C)
TMIN14:	Mean annual minimum temperature (°C)
TOPOGRAPHY	
Slope:	Average slope of the plot (°)
PDIR:	Potential annual direct incident radiation ($\text{MJ cm}^{-2} \text{ yr}^{-1}$; McCune, 2007)
Heatload:	Index for aspect with zero being coolest and one as warmest (McCune, 2007)
Solar Radiation:	ArcGIS 10.0
TPI:	Topographic Position Index (Jenness, 2006). High values suggest proximity to a summit or ridge. Low values suggest proximity to a valley bottom. TPI values near zero are either mid-slope or flat areas.

Table 3-2: Simple linear regression models relating lichen thallus N levels between species pairs.

The equations combine data from the study area with data from Oregon, Washington, and elsewhere in California (Airlichen Database; USDA-USFS, 2013).

Model	N-level		
	R_{adj}^2	datapoints	p-value
N in <i>L. vulpina</i> = 0. 0.9424(N in <i>L. columbiana</i>) - 0.0017	0.87	73 (22 this study)	< 0.001
N in <i>L. vulpina</i> = 0.8050(N in <i>E. prunastri</i>) + 0.4270	0.76	21 (11 this study)	< 0.001

**CHAPTER 4: ARE LICHEN COMMUNITY RESPONSES TO
ELEVATED NITROGEN DEPOSITION MEDIATED BY
SUBSTRATE ACIDITY?**

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The Lichenologist
-Submission pending-

ABSTRACT

Yosemite National Park and nearby portions of the Sierra and Stanislaus National Forests in California are designated federal air quality Class 1 areas. Measurements and modeling of nitrogen deposition suggest however that the critical load for epiphytic lichen communities of coniferous forests is exceeded throughout the area. The deposition gradient near established lichen community response thresholds provided an opportunity to clarify the role of substrate pH in mediating lichen community responses to elevated nitrogen deposition. We estimated throughfall nitrogen deposition from the nitrogen concentration in lichen-thalli at 38 study sites along the deposition gradient. We applied a new branch-level quantitative method to evaluate the composition of lichen communities relative to lichen nitrogen concentration, branch-surface pH, lab pH, and electrical conductivity. Lichen nitrogen concentration ranged from 0.9 to 2.2 percent dry-weight in *Letharia vulpina* equivalents, corresponding to a throughfall nitrogen deposition of 1.9 to 11.5 kg nitrogen ha⁻¹ yr⁻¹. Branch surface pH and branch laboratory pH were correlated but differed substantially. Substrate pH measures were not correlated with electrical conductivity. Differences between pH and conductivity measurements were largely controlled by tree species and to lesser extent by site differences. Individual lichen species occupied substrates with a wide range in pH and conductivity. The abundance of lichen eutrophs was positively correlated with the lichen thallus nitrogen concentration, but was not correlated with substrate pH or conductivity. Our results provided little evidence for a substantial alteration of substrate pH and conductivity by ammonium-nitrate dominated N depositional loads near the lichen critical load. Instead, epiphytic lichen communities were apparently directly affected by increased nitrogen availability.

Highlights: ► Ammonium-nitrate dominated nitrogen deposition has no apparent effect on the bark ionic environment at deposition levels near the lichen critical load. ► Under this deposition regime, bark pH and electrical conductivity play an insignificant role in the composition of conifer-branch lichen communities. ► Lichen eutrophs apparently responded directly to nitrogen inputs and not to branch pH or electrical conductivity, even on the relatively acidic (mean plot surface pH: 3.5 – 4.9) conifer substrates in the study area.

Keywords: Air pollution effects, Air quality, Bark acidity, Bark conductivity, California ecosystems, Eutrophication, Epiphytic lichens, Nitrogen deposition.

INTRODUCTION

Ecosystems in the western US are adapted to low concentrations of $\pm 0.2 \mu\text{g m}^{-3}$ fixed nitrogen (N) in ambient air (Trijonis, 1990). Background N-deposition varies with annual precipitation (Williams & Tonnessen, 2000), and canopy scavenging (i.e., forest cover and leaf area), and may have averaged $\pm 0.69 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Holland et al., 1999), but such levels are exceeded throughout California (Fenn et al., 2010).

While fixed N is a nutrient, high deposition rates result in ecological harm (Fenn et al., 2010; Fenn et al., 2003; Volpe et al., 2006). The quantitative estimate of one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge is termed a critical load (CLO), or critical level (CLE; Nilsson & Grennfelt, 1988) and is derived from observations on ecosystem responses (Burns et al., 2008; NADP, 2008; Pardo et al., 2011; Porter et al., 2005). Critical levels and CLO's are becoming an increasingly important tool in air quality management (Glavich & Geiser, 2008; Porter & Johnson, 2007). CLE's are ambient air concentrations expressed in ppm or $\mu\text{g m}^{-3}$, whereas CLO's refer to depositional loadings expressed in terms of $\text{kg ha}^{-1} \text{ yr}^{-1}$ of wet or total (wet + dry) deposition. In terrestrial habitats, CLO's for N are generally lowest for lichens and bryophytes, and increase from mycorrhizal fungi to herbaceous plants, shrubs, and trees (Pardo et al., 2011), but for a given receptor, the CLO may differ among ecosystems and between regions.

The vulnerability of lichens is related to their symbiotic nature and the lack of a protective outer cuticle; absorption of both nutrients and pollutants occurs over much of their outer surface from predominantly aerial sources (Nimis, et al., 2002). The sensitivity of lichens was recognized as early as the 19th century, when dramatic shifts in species communities in major cities in Europe were attributed to acidic air pollution mainly from sulfur-containing compounds (e.g., Stirton, 1874). Individual species differ in their sensitivity, so that the species composition of lichen communities may provide detailed information of local air quality. The N CLO estimates for epiphytic macrolichen communities range from a deposition of 3 to 9 $\text{kg N ha}^{-1} \text{ yr}^{-1}$, as modeled by USEPA Community Multiscale Air Quality (CMAQ), increasing with mean annual precipitation in western Oregon and Washington forests (Geiser et al., 2010). In Mediterranean climates of California, Fenn et al. (2008) estimated lichen CLO ranging from 3.1 and 5.5 $\text{kg throughfall N ha}^{-1} \text{ yr}^{-1}$, for mixed coniferous forest and oak woodlands, respectively.

Lichens are also sensitive to the ionic environment of their substrate, i.e., the pH and electrical conductivity (EC) of bark; some lichen species exhibited such fidelity to their bark ionic environment that lichenologists have adopted terms such as acidiphily and acidophytes to

describe lichens that prefer acidic bark substrates (Barkman, 1958; Du Rietz, 1945; van Herk, 1999). Bark pH is regarded as one of the important factors determining the composition of natural epiphytic lichen floras (Mitchell et al., 2005; Schmidt et al., 2001; van Herk, 2001), e.g., the natural development of the *Lobaria*-rich communities on *Quercus* is thought to be bark pH dependent (Bates et al., 1990; Gauslaa, 1985; Kermit & Gauslaa, 2001).

The ionic status of bark substrates varies naturally with tree species and changes in soil type (Farmer et al. 1991; Kermit and Gauslaa 2001) and measurement location within a tree. The main driver for within-tree differences in bark pH and EC are natural atmospheric processes that leach the non-living outer bark. This results in a substantially lower surface pH and EC compared to inner bark (Gauslaa & Holien, 1998; Legrand et al., 1996), a decline in pH with increasing bark age (Bates, 1992; Ellis & Coppins, 2007; Farmer et al., 1991), and a higher pH and EC of twigs than larger branches or the bole (Leith et al., 2005; Wolseley et al., 2006). The pH and EC of twigs and boles also increase with measurement height within several conifer species (Kermit & Gauslaa, 2001; Legrand et al., 1996) which may be related to reduced exposure to throughfall leachate with increasing measurement height. The bark pH of *Quercus* boles was shown to vary seasonally (Farmer et al., 1991) and it is possible that even the epiphytes themselves influence the substrate pH (Barkman, 1958; Gauslaa & Holien, 1998; Kermit & Gauslaa, 2001).

Several methods and modifications are used to assess bark pH, and the different methods may yield substantially different results (Kermit and Gauslaa 2001; Schmidt et al. 2001), leading Farmer et al. (1990) to call for standardization. Several authors hypothesize that only the pH of the immediate surface is important for lichens (Schmidt et al. 2001; Spier et al. 2010) since lichens depend on precipitation, canopy drip, and stem flow as their main sources of nutrients (Barkman, 1958; Hale, 1983). However, it has not been definitively demonstrated which method is best correlated with lichen community structure.

The deposition of dust from natural and unnatural sources may affect the bark ionic environment, e.g., dust in cities from concrete building demolition (Fuller & Green, 2004), proximity to quarries or roads (Gilbert, 1976; Marmor & Tiina, 2007), or dust from open habitats including arable land (Kricke & Loppi, 2002). The bark of some species may be more vulnerable to perturbation than others; alkaline roadside dust shifted the naturally acidic bark pH of *Pinus sylvestris* from 3.0 to 5.7 (Marmor & Tiina, 2007) but in the same study the naturally more sub-neutral bark pH of *Tilia cordata*, pH 4.6, was unaffected.

Atmospheric pollutants may affect the bark ionic environment and cause indirect effects to lichen communities (Gilbert, 1986; Hauck et al., 2001; Hawksworth & Rose, 1970). High SO₂

and NH_4 pollution levels increased the EC of *Quercus* bark from 100 - 160 to 500 - 900 $\mu\text{S cm}^{-1}$ at urban sites in the Netherlands (van Herk, 2001). In the nineteen sixties in western Europe, sulfur dioxide (SO_2) loadings up to 50 $\text{kg ha}^{-1} \text{yr}^{-1}$ strongly acidified tree bark e.g., *Quercus* bole pH dropped as low as 2.9 (Bates et al. 1990) whereas pH 3.7 - 5.0 was considered to be normal by Barkman (1958). These emissions resulted in dramatic distributional shifts even among lichen species otherwise relatively insensitive to SO_2 (Purvis et al. 2007) because bark pH influences speciation and bioavailability of sulfur (Gilbert, 1986). Low bark pH renders lichens more vulnerable to SO_2 (Türk & Wirth, 1975) and other potentially toxic elements (Larsen et al., 2007) so that lichen communities effectively become more pH dependent in the presence of significant SO_2 . Small tree branches may be more vulnerable to perturbation than tree boles (Wolseley et al., 2006), perhaps due to a low buffering capacity.

Once altered, bark substrate pH does not readily recover after pollution is mitigated; high SO_2 loadings through the 1970's have left a legacy of acidified bark surfaces in European forests that apparently limited eutroph colonization (Larsen et al., 2007; van Dobben & ter Braak, 1998; van Herk, 2001). Under these conditions, the abundance of lichen eutrophs (syn. nitrophytes) was more limited by bark pH than by N availability (e.g., van Dobben and ter Braak 1998; van Herk 2001). During the initial recovery, trees with a naturally high bark pH, e.g., *Salix* spp. and *Fraxinus* spp., were recolonized first (Larsen et al., 2007). On the more acidic bark of *Quercus* spp., recovery was more rapid on younger trees (van Herk, 1999). While high SO_2 regimes in Europe have been gradually lowered since the nineteen eighties, total N deposition remained high and NH_3 emissions, which elevate bark pH, have increased. The western European pollution history is unique, and the applicability of the lichen and substrate pH research to conditions in the western US is uncertain at best. Findings from the dynamic post SO_2 recovery period into an environment with high total N deposition and high NH_3 exposure may be difficult to replicate. For example, Larsen et al. (2007) found that after a period of significantly improved air quality in London, fewer than half of the eutrophs showed any preference for higher bark pH. More recently, Spier et al., (2010) reported that oligotrophs are growing among eutrophs in the Netherlands, and that there is no longer a clear relationship between eutrophs, oligotrophs (syn. acidiphytes) and bark acidity. Eutrophs may grow well on acidic substrates in the UK (Wolseley et al., 2006), the Los Angeles Basin (Jovan et al., 2012), and the central Sierra Nevada. In the LA Basin, eutroph abundance on *Quercus* was not related to substrate pH, but to levels of several N pollutants (Jovan et al., 2012). Eutrophs may be more sensitive to N than bark pH under low SO_2 and NH_3 deposition regimes, and at high NH_3 (and SO_2) concentrations, the effect may be

predominantly on substrate pH (Sutton et al., 2009). The complexity of (legacy) effects prompted Wolseley et al. (2006) to study lichens on twigs rather than boles because they are a barometer of current atmospheric conditions, whereas lichens on boles may carry a relict flora reflecting previous conditions.

The air quality conditions in the Yosemite region of the Sierra Nevada provided a unique opportunity to clarify the role of substrate pH in mediating lichen community responses to increasing N inputs without complicating effects from past sulfur pollution. The area is designated as federal air quality Class 1 and is afforded the highest level of protection in the U.S. under the Clean Air Act (1977). The history of air pollution impacts to lichens is short; total N deposition levels above current estimates of the lichen CLO (Fenn et al., 2008; Hutten & McCune, 2014c) have been maintained for little more than one decade¹¹.

The primary objective of this study was to determine the role of the substrate ionic environment in the responses of epiphytic lichen communities to an N deposition gradient near the lichen CLO. Our secondary objective was to evaluate the relative performance of measures of pH and EC in explaining the lichen community composition and to extend previous work to conifer substrates; almost all published work relates to hardwood substrates.

MATERIALS AND METHODS

Study Area: The study area is about 820,000 ha and includes Yosemite National Park and a portion of the adjoining Stanislaus and Sierra National Forests on the west slope of the Sierra Nevada in central California, USA. The hydrographic boundary of the Sierra Nevada crest and the boundary with Mono County delimits the northeastern boundary and the Madera-Fresno county line bounds the southeast (Figure 4-1). Our major focus was Yosemite National Park, but we extended the study area westward, toward pollution emission sources in the Central Valley. The western extent of the study area follows the lower distributional limit of the mixed-conifer forest type (Anderson et al., 1976) which is approximated by the western boundary of the Sierra and Stanislaus National Forests. The terrain in the study area is mountainous, with elevations ranging from 260 m along the western boundary to well over 3000 m close to the crest. Along this steep elevation gradient, climate and forest composition change profoundly.

Climate: The study area is characterized by long, hot, and dry summers that are more pronounced at lower elevations. January and July daily maximum temperatures average 13°C and 33°C at low elevations, respectively, and 2°C and 19°C at the passes along the Sierra Nevada

¹¹ NADP station CA99; Hodgdon

crest, respectively. The bulk of the precipitation occurs during late fall and winter. Mean annual precipitation ranges from 40 cm at the lowest elevations to about 140 cm at some high-elevation sites (data extracted from interpolated 800 m PRISM climate normals 1971-2000, Daly et al., 2008; PRISM Climate Group 2004). Yosemite Valley, at 1190 m elevation, received an annual average of 104 cm of snow during the same period¹².

Vegetation: At the lowest elevations in the study area, the vegetation is a mix of chaparral and foothill woodlands (*Quercus* and *Pinus*). Montane zone vegetation is characterized by extensive mixed-conifer forest (*Abies*, *Calocedrus*, *Pinus*, and *Pseudotsuga*), including groves of *Sequoiadendron* and some of the tallest pines in the world. Subalpine forests (*Juniperus*, *Pinus*, and *Tsuga*) finally give way to high elevation rock barrens around 2500 m.

Air Quality: Sulfur dioxide concentrations averaged $\leq 0.5 \mu\text{g m}^{-3}$ annually since 1995 with highest recorded bi-weekly averages $< 2 \mu\text{g m}^{-3}$ ⁽¹³⁾. This is well below the ‘no-effect level’ reported for lichens in the Netherlands (Sparrius, 2007) and the response threshold of 5-15 ppb for sensitive lichens in the Pacific Northwest (McCune & Geiser, 2009). Ammonia (NH_3) is not routinely monitored by established air quality monitoring networks, but annual concentrations averaged around $0.94 \mu\text{g m}^{-3}$ ⁽¹⁴⁾; just below the CLE of $1 \mu\text{g m}^{-3}$ established by the United Nations Economic Commission for Europe for lichens and bryophytes in Europe (Batty & Hallberg, 2010). Monthly ambient air concentrations averaged $> 1 \mu\text{g NH}_3 \text{ m}^{-3}$ during the dry season (June-September), and peaked at $2.6 \mu\text{g m}^{-3}$ during July⁽¹⁴⁾; just below levels that would result in detectable alteration of the lichen community, if sustained (van Herk, 2001; Wolseley et al., 2006). Critical levels and critical loads are typically lower in the U.S. than in Europe (Pardo et al., 2011), consequently NH_3 may play a role in the lichen responses in the study area, particularly in areas closest to emission sources in the Central Valley. Total N deposition averaged 3.1 and 3.5 kg N (wet + dry)^{13,15} $\text{ha}^{-1} \text{yr}^{-1}$ in 2010 and 2011, respectively. This rate has been relatively stable for little over one decade, especially when accounting for the influence of annual precipitation. The ionic forms of N, especially NH_4^+ and NO_3^- , are the largest constituents of total N deposition in the study area. Between 2010 and 2011, throughfall N measurements ranged 2.8 to 4.7 kg N $\text{ha}^{-1} \text{yr}^{-1}$ for 12 sites within Yosemite National Park (Root et al., 2013; unpublished data M.A. Hutten) using methodology described by Fenn & Poth (2004). Modeled

¹² Yosemite Park Hdqtrs COOP station: ID 049855

¹³ CASTNET YOS404, Turtleback Dome: measurement period: Oct 1995 – Febr 13

¹⁴ AMoN: CA44, Turtleback Dome: measurement period: Mar 2011 – Sept 13

¹⁵ NADP CA99, Hodgdon

throughfall N deposition estimates for the study area ranged 2 - 9 kg N ha⁻¹ yr⁻¹ (Fenn et al., 2010) and 1.8 - 12.3 kg N ha⁻¹ yr⁻¹ (Hutten & McCune, 2014b). The annual average pH of rainwater ranged between 5.5 and 5.7 since 2003¹⁶.

Site Selection: We non-randomly placed 38 plots throughout the study area (Figure 4-1; Appendix A). We aimed for a representative, well-distributed sampling of habitats throughout the study area and intentionally co-located a plot with the NADP air quality monitoring site (Hodgdon: CA99), and another with the CASTNET air quality monitoring site (Turtleback Dome: YOS404). Other criteria for plot selection included the availability of sufficient target lichens from which to collect thallus samples for elemental content analysis, and a distance from roads \geq 50 m. Our study was focused on conifer-dominated forest, therefore we rejected plots that had more than a few overstory hardwoods. Plot elevation ranged from 307-2821 m, and 80% of the plots were over 1000 m.

Local N Deposition: Lichen thallus N concentration has a strong, positive correlation with throughfall N deposition (Root et al., 2013), therefore, we used lichen thallus N-levels as a proxy for N deposition. Lichen thallus sampling was accomplished during dry and stable weather at the end of the dry season in 2010 and 2011 to avoid season-related fluctuations in lichen thallus N levels (Bruteig, 1993) as is common practice (Blett et al., 2003; Jovan & Carlberg, 2007; Saros et al., 2010). In each plot, we collected lichen thalli using methods developed by Geiser (2004). Healthy target lichen thalli (species enumerated below) were collected from coniferous tree boles and branches using latex gloves to avoid contamination. Each composite sample had a target field weight of 10 g and consisted of a single air-tight polyester bag with lichen individuals of the same species collected from at least six different trees. In the office, the lichens were spread on paper to air dry and to remove debris including bark, other lichen species, and necrotic thallus, resulting in a final weight of approximately 7 g (air dry) per sample. Samples were analyzed at the University of Minnesota Research Analytical Laboratory during the winter following the field collection. There, samples were ground and dried to constant weight. Lichen thallus N levels (% dry-weight; hereafter: % dw) were then estimated using a LECO FP-528 N Analyzer (Dumas-method: Lee et al., 1996; Yeomans & Bremner, 1991). We employed a variety of quality assurance measures that were described in detail by Hutten & McCune (2014c).

Under the same deposition regime, lichen species may accumulate N at different rates (Root et al., 2013). Therefore, we focused only on three species, the minimum number of species necessary to canvas the study area. We relied predominantly on *Letharia vulpina* (LEVU; 30

¹⁶ CASTNET YOS404, Turtleback Dome

plots); a widespread and abundant species in the Sierra Nevada, and set this species as our measurement standard. We used *Letharia columbiana* in two high elevation plots (14, 35) and *Evernia prunastri* at three low elevation plots (36, 37, and 38; Figure 4-1). In locations where LEVU was unavailable, we predicted thallus N levels for LEVU from either *Letharia columbiana* or *Evernia prunastri* using simple linear regression models developed by Hutten & McCune (2014b).

Lichen Community Composition: In each plot, we collected 10 1-m branch segments from 10 trees of the same species. We targeted branch lichen communities because they were shown to be more responsive to (NH₃) pollution than tree bole lichen communities (Wolseley et al., 2006). We narrowed our work to corticated dead branches because they are easy to collect and tend to be good lichen substrate, perhaps in part because the process of bark flaking slows (Barkman, 1958). Branches needed to be within reach from the ground or freshly fallen. We rejected branches without lichens if branches with lichens were available. To minimize differences imparted by branch size, bark thickness, bark texture, etc., we targeted branches 10 - 45 mm in diameter. We measured branch diameter at each end with electronic calipers, and determined the age of the branch apex under a dissecting microscope. Due to the major elevation gradient of the study area, it was necessary to use eight different conifer species: *Abies concolor* (17 plots), *A. magnifica* (8 plots), *Pinus sabiniana* (5 plots), *P. ponderosa* (4 plots), *P. attenuata* (1 plot), *Juniperus occidentalis* (1 plot), *Pseudotsuga menziesii* (1 plot), and *Tsuga mertensiana* (1 plot). To score lichen abundance, we used a linear quadrat with 100 1-cm squares, and recorded the presence of each lichen species, or group of similar species, in each cm² on the upper surface of the branch. This resulted in a branch abundance between 0-100 for each lichen species. *Candelaria pacifica* frequently preferred the lower surface of the branches and therefore was independently scored on the lower surface of the branch which also yielded a combined total abundance for *Candelaria pacifica*. We grouped species difficult to identify to the species level when young, e.g., *Melanohalea*, and *Melanelixia* species as ‘Melanelioid’ (Table 4-1). In the text and tables we refer to these groups as single species, e.g., ‘branch species richness’ will refer to species but also include groups of species.

We derived lichen indices to describe and evaluate the trophic status and composition of the lichen community (Appendix B). The trophic status of individual lichen species follows those reported in McCune & Geiser (2009; Table 4-1). The designation of *Flavopunctelia flaventior* follows that of Jovan & McCune (2006) and is supported by our experience in the study area where this species appears to be a regular component of the eutrophic community. We were

unable to identify our (few) young tufted *Usnea* spp. We considered them mesotrophs based on their occurrence in N affected (riparian) habitat. Three species of *Usnea* are known to occur in the study area: a pendulous oligotroph, a tufted mesotroph, and a tufted species without trophic designation (Hutten et al., 2013).

Substrate Ionic Environment: We characterized the acidity of the same lichen branches on which we determined lichen species abundance using three commonly used methods: branch surface flathead pH (hereafter: surface pH), laboratory bench pH (hereafter: lab pH), and electrical conductivity (hereafter: EC).

Surface pH: Branch surface pH was measured in the field during dry and stable weather in summer and fall of 2010. Occasionally, branches were collected, stored in the laboratory, and measured within a few weeks. We used an unmodified ExStik™ PH100 flat surface electrode pH meter and methodology described by Larsen et al. (2007). The pH meter was calibrated prior to each session using two buffer solutions (pH 4 and pH 7). We anticipated high within-branch and within-site variation, and measured five points per one-meter branch segment. Measurements were five cm from the thinnest end of the branch segment, then at 25, 50, 75, and 95 cm. Each measurement targeted a spot directly on the upper surface of corticate dead branches without macrolichens, wetted with a few drops of 0.1 M KCl dissolved in deionized water. We allowed enough time for the pH meter reading to stabilize (i.e., retain a reading to ± 0.01 pH for about 3 s). Lichens occurred only on decorticate branches in one high elevation plot dominated by JUOC, and lichen community data and surface pH measurements were taken *in situ*, on decorticate portions of live branches.

Lab pH and EC: We used California State certified instruments; a ‘Hach Sension 4’ pH meter, and a ‘Hach Sension 7’ conductivity meter, that were calibrated to 3 points every morning prior to measurements. We modified the methodology developed by Kermit & Gauslaa (2001). Since green algal lichens can be more acidic than the bark (Gauslaa & Holien, 1998), we first scraped any lichens from the thinnest 10 cm of branch segments that had been stored in the laboratory for about one year. Using a razor blade, we removed the outer bark into ≤ 1 mm thin slices. We opted not to pulverize the bark because it results in pH measurements much higher than surface pH measures (Kermit & Gauslaa, 2001), and we aimed to capture a lab pH measurement most reflective of the lichen substrate. For each branch segment, we weighed 0.5 g of bark slices into a sample using a micro-balance. The sample was suspended in 20 ml of deionized water for one hour. Tests identified that suspension pH stabilized after about 30 minutes (without KCl or agitation).

Statistical and Spatial Analysis: We characterized the substrate acidity of branch lichen communities with a three-level Analysis of Variance (ANOVA) in XLSTAT®-Pro (Version 2014.1.10, Addinsoft, Inc., Brooklyn, NY, USA) among 38 plots with sites as random factor and species as fixed factor with 10 branches nested within sites for lab pH and EC. We used a four-level nested ANOVA for surface pH with sites as random factor, species as fixed factor within sites, and branches nested within sites as an additional factor. Five repeat measurements of pH were nested within each branch.

To analyze patterns in lichen community structure, we used Non-Parametric Multiplicative Regression (NPMR: McCune & Mefford, 2008; McCune, 2006) to iteratively explore models without the need to assume a particular relationship between response and predictor variables. The matrix included 37 plots and 15 lichen community variables after the removal of one outlier (plot 27) that had unusually low N levels (% dw). The matrix included two high-elevation plots without branch lichens (5, 31). Indices of the community trophic status ignored six infrequent species with low abundances for which the trophic status was uncertain. We removed species that occurred in fewer than three plots and the multispecies group of crustose lichens because they introduced noise from mixed sensitivity to N enrichment.

We used nonmetric multidimensional scaling (NMS: Kruskal, 1964; Mather, 1976, using in PC-ORD; McCune & Mefford, 1999) to ordinate plots in species space and used overlay environmental variables, including lichen thallus N levels. The Euclidean (Pythagorean) distance measure retained sensitivity to differences in absolute abundance. We selected the ordination solution with the lowest stress for a given dimensionality. A Monte Carlo test of 250 runs with randomized data evaluated the strength of patterns in the NMS solution. The final ordination diagram was rotated orthogonally to maximize correlations of axes to environmental variables.

Maps were created with Environmental Systems Research Institute (ESRI, Redlands, California) ArcGIS desktop version 10.0 software.

RESULTS

Local N Deposition Regimes: Lichen thallus N ranged from 0.89-2.20% dw (LEVU equivalents) in the fall 2010 (mid Sept-mid Oct), corresponding to 1.93-11.45 kg throughfall N ha⁻¹ yr⁻¹ across 38 plots (Appendix B; Hutten and McCune 2014a). The range in lichen thallus N levels observed across the study area was high compared to the mean within-site standard deviation of 0.118% N (LEVU dry-weight equivalents). Lab accuracy and precision were high with mean standard deviations of 0.04 and 0.02% N (dry-weight), respectively.

Branch Lichen Communities: Branch mean diameter was 1.4 cm at the younger end, and 2.4 cm at the older end of the branch segment. Mean age at time of branch death was just over 17 years and ranged from 10-year-old PIPO branches to 35-year-old TSME branches. Branch size did not differ across tree species ($p < 0.077$; $F = 2.3$; 3-level nested ANOVA; Table 4-2), but did differ across sites within tree species ($p < 0.0001$). Branch age differed across tree species as well as across sites within tree species ($p < 0.0001$; 3-level nested ANOVA; $F = 7.9$; Table 4-2).

A total of 27 lichen species and species groups (hereafter: species) were recorded and consolidated to 18 species prior to analysis (Table 4-1). Total lichen richness declined with increasing elevation. Mean plot richness was 7.2, ranging from zero at two plots above 2500 m (plots 5, 31) to a maximum of 14 species at 900 m elevation (plot 32). *Candelaria pacifica* was the most common eutroph, present in 80% of all plots sampled. ‘Melanelioids’ were the most common lichen mesotrophs, and LEVU was the most common oligotroph, present in > 85% of all plots sampled.

Substrate Ionic Environment: Branch surface pH differed among tree species and the tree-species level represented 83% of the total model variance ($p < 0.0001$, $F = 11.5$, 4-level nested ANOVA; Table 4-2, Figure 4-3). Surface pH did differ between sites within tree species and between individual branches within sites but these represented only a small proportion of the overall model variance (both $p < 0.0001$; $F = 17.8$ and 20.8 , respectively). Since we typically conducted pH measurements on only a single tree species per site, our nested design likely attributed some site level variance to tree species.

The variance distribution was very similar for lab pH; 73% of the total model variance occurred between tree species ($p < 0.0003$, $F = 7.1$, 3-level nested ANOVA; Table 4-2) and about 11% occurred between sites within tree species ($p < 0.0001$, $F = 17.9$). Surface pH is correlated with lab pH at the plot / tree species level ($R^2 = 0.561$ from SLR, $y(\text{lab pH}) = 0.4943(\text{surface pH}) + 3.1267$), but lab pH is always substantially higher than surface pH (Figure 4-2, Figure 4-3).

Conductivity was low and ranged between 40 - 130 $\mu\text{S cm}^{-1}$. The majority of the variance distribution, about 62%, was again between tree species ($p < 0.0001$, $F = 9.2$, 3-level nested ANOVA; Table 4-2, Figure 4-3). Only about 7% of the variance occurred between sites within tree species ($p < 0.0001$, $F = 4.1$) and when compared to pH measures, a larger amount of variance, 31%, occurred between branches within sites and species. There was no correlation between surface pH and EC at the plot level, except for ABMA ($R^2 = 0.665$ from SLR). Neither surface pH, lab pH, nor EC was correlated with branch age or branch size at the plot level.

Lichen Communities and the Substrate Ionic Environment: Considering that only 5% of the variance occurred at the (1-m) branch-level (Table 4-2), we assumed the branch mean surface pH to be sufficiently representative for the substrate pH of each of the lichen species recorded on the branch. We further assumed that lab pH and lab EC, measured only once per branch, would have a similarly low if not lower within-branch variance. We then analyzed the surface pH, lab pH, and EC range of each lichen species (and species groups), and for oligotrophs, mesotrophs and eutrophs as groups. Individual lichen species occurred on branches across a broad range of surface pH, lab pH and EC values (Figure 4-2, Table 4-1). Analysis in NPMR did not detect evidence for a relationship of eutroph abundance with branch pH, nor EC, at either plot or branch-level, even after the removal of branches without eutrophs (not shown). At the plot level, the Proportion eutroph (syn. Nitrophyte) lichen Abundance (PNA) was associated with the N levels in lichens ($xR^2 = 0.448$, Average Neighborhood Size (ANS) = 9.3, tolerance = 0.08 PNA units).

Ordination at the plot level yielded a strong two-dimensional solution ($0.99 R^2$) with a low minimum stress of 5.5. Ordination axis 1 is much stronger than axis 2, $R^2 = 0.89$ and 0.09 , respectively. In overlays, surface pH, lab pH, and EC were weakly associated with ordination axes (Table 4-3). Lichen thallus N levels (% dw) had a modest association with axis 1 ($R^2 = 0.325$; Figure 4-4, Table 4-3).

DISCUSSION

While we lack a local unpolluted reference level, it appears unlikely that past or present pollutant loadings have substantially altered the natural pH range of branch-lichen bark substrates in the study area. Branch surface pH in the study area is similar to that of several of the same conifer species in Lassen Volcanic National Park (Hutten, unpublished data), which lies 400 km N of the study area and receives N deposition levels below the lichen CLO (NAPD station data CA96: Manzanita Lake). Furthermore, the average plot surface pH range is similar to the range of *Picea abies* branch communities unaffected by pollutants in Norway; pH 3.5 – 5.0 (Kermit & Gauslaa, 2001) vs. pH 3.5 – 4.7 in the study area. The lack of any relationship of easting and elevation, as surrogates for distance to emission sources, also suggests that N pollutants have little to no effect on branch substrate pH; however, the large number of tree species used may have obscured a pattern.

The influence of alkaline dust on the lichen communities in the study area is thought to be minor for a number of reasons. The predominant soil types in the study area are granite-derived; exposed clay-rich metamorphic soils, which are more likely to have an alkaline dust

effect, occur only in the foothills. Furthermore, our smooth-barked target branches had a relatively low dust retention capability and a low EC range. While we expected dead branches to have a relatively low EC, the range we observed was much lower than reported for live *Pinus* spp. in northern Spain (Santamar & Mart, 1997) and live *Abies* and *Picea* boles in France (Legrand et al., 1996). Substantial alkaline dust deposits would have likely maintained a higher substrate EC and pH.

Eutroph abundance was not associated with surface pH, lab pH, or EC, on a variety of conifer species along an NH_4NO_3 dominated N-deposition regime approaching and exceeding established CLO's for epiphytic lichens in coniferous forests in California (Fenn et al., 2008; Hutten & McCune, 2014c). At the relatively low N deposition levels in the study area compared to western Europe, lichen eutroph presence and abundance was correlated with N inputs, consistent with Sutton et al. (2009) and Jovan et al. (2012), but in contrast with the majority of the European literature. Lichen eutroph preference for substrates with high pH in western Europe is likely attributable to substantially higher SO_2 and/or NH_3 exposure relative to the western U.S. For similar reasons, the (higher) western European critical load values are not be broadly applicable to the U.S. (Glavich & Geiser, 2008), emphasizing the tremendous research value of relatively pristine ecosystems in the western U.S.

Surface and lab pH values were positively correlated, but lab pH was always substantially higher, in line with other authors (Gauslaa & Holien, 1998; Legrand et al., 1996), even though we did not pulverize bark. Like Legrand et al. (1996), we found that conductivity was not correlated with acidity (except in ABMA). According to Legrand, EC predominantly depends on, and is negatively correlated with bark age, or rather bark thickness, as outer tissues are exposed to more leaching and gradually lose their buffering capacity. Our data showed a negative correlation of plot mean EC with plot mean branch size (as surrogate for bark thickness), but the pattern was not statistically significant.

We were unable to determine the pH or EC measure that correlated best with branch-lichen community composition because lichen species were unresponsive to either pH or EC, despite the broad range in measured values. Considering the high levels of natural variability in substrate pH and EC, it seems unlikely that common lichen epiphytes would be particularly sensitive to these measures under normal air-quality conditions. Although we believe our findings are likely to be broadly applicable, it would be desirable to assess whether our results, and those of Jovan et al. (2012), extend to maritime climates.

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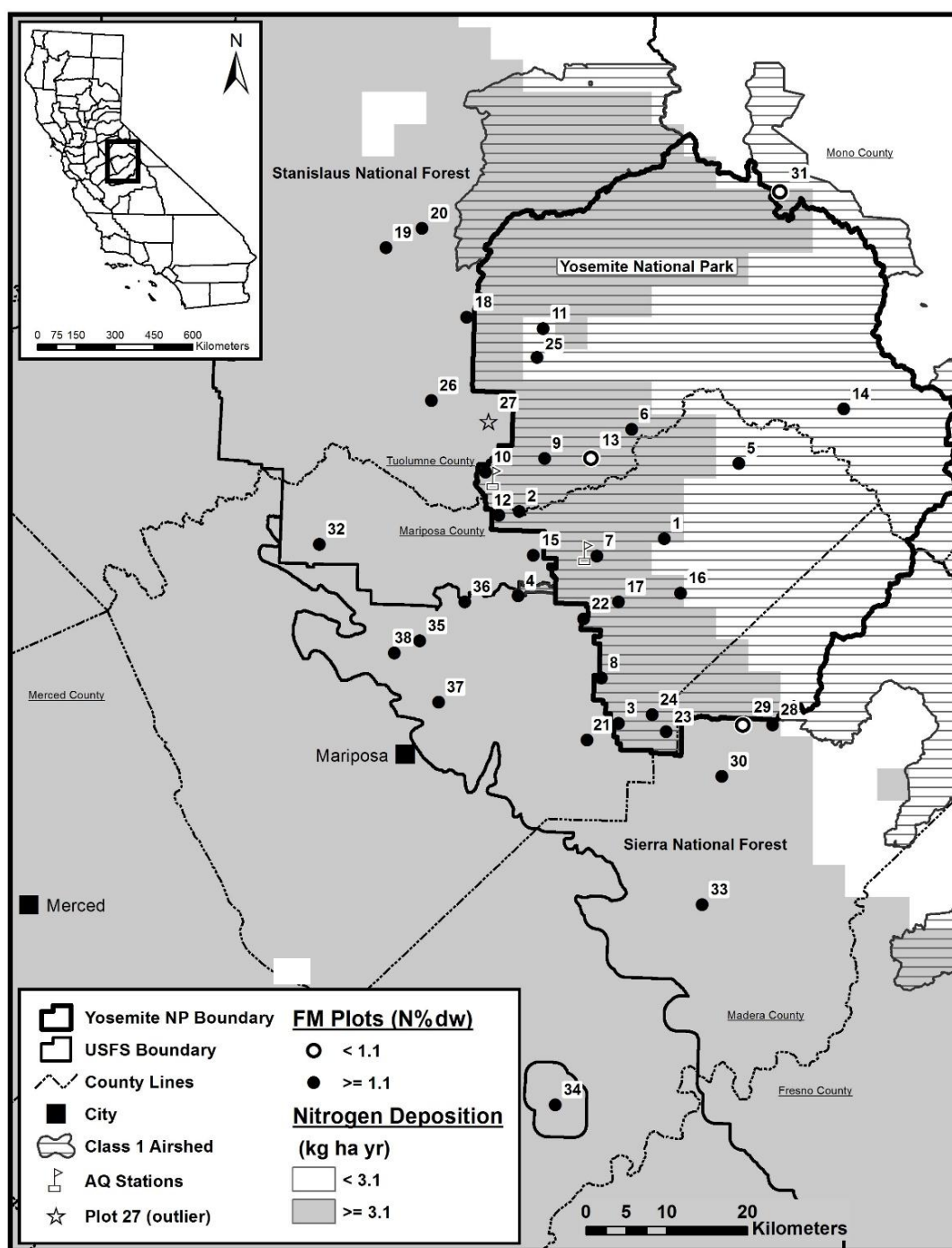


Figure 4-1: Map of the study area and plot locations.

The study area encompasses Yosemite National Park, and the NW and SW portions of the Sierra and Stanislaus National Forests, respectively. Hatch marks identify the area designated as federal air quality Class 1. Gray-shaded areas received $> 3.1 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Fenn et al., 2010); the lichen critical load for coniferous forest determined by Fenn et al., (2008). Plot symbols reflect lichen thallus N levels above and below 1.1% N (LEVU dry-weight equivalents), corresponding to $2.9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, the critical load determined by Hutten & McCune (2014c). Plots 28, 33, and 34 used N deposition model estimates (Fenn et al., 2010) to estimate lichen thallus N levels.

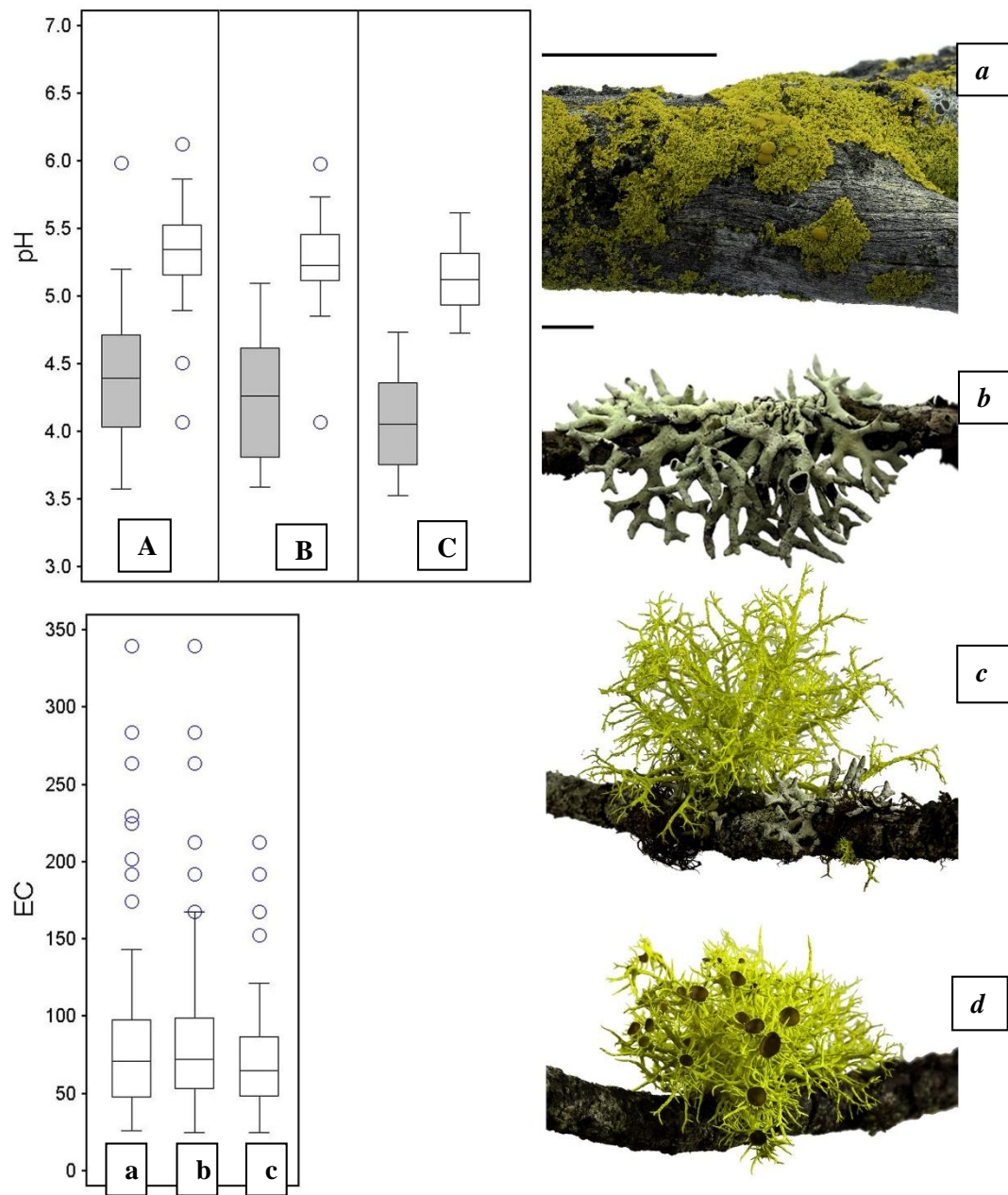


Figure 4-2: Substrate pH and EC preferences of three common lichen species.

Upper left: Boxplots of branch substrate pH (gray) and lab pH (white) for: **A)** *Candelaria pacifica*, **B)** *Hypogymnia imshaugii*, and **C)** *Letharia* spp. (mostly *Letharia vulpina*).

Whiskers are the 5th and 95th percentiles, outliers are > 1.5 times the interquartile range.

Lower left: The branch EC range of species in A-C at upper left, shown in a-c, respectively.

Right: Species images: a) *Candelaria pacifica* (scale bar = 1 cm), b) *Hypogymnia imshaugii*, c) *Letharia vulpina*, and d) *Letharia columbiana*. Images b-d were scaled to scale bar = 1 cm in b.

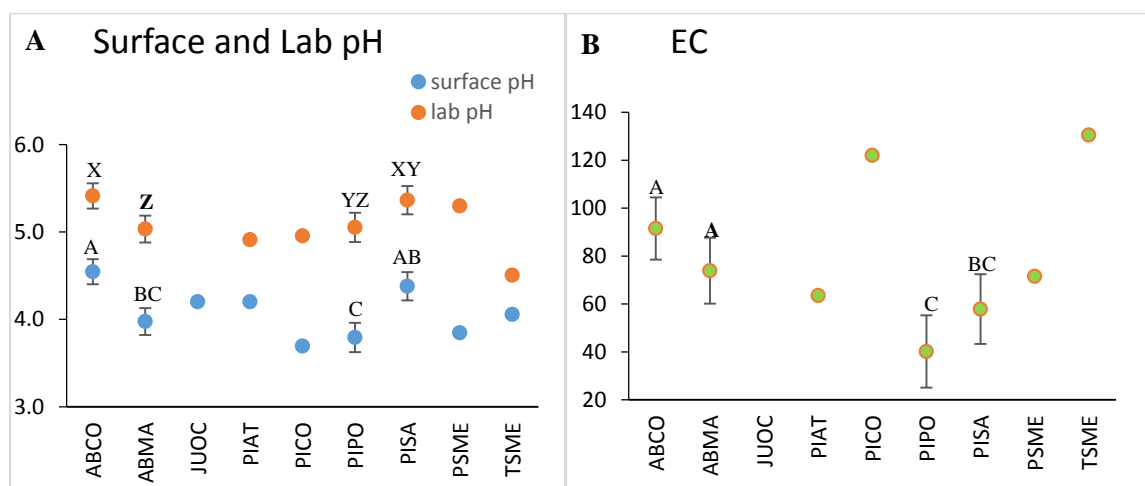


Figure 4-3: Substrate pH and EC for different tree species.

Comparison of means surface pH, lab pH and EC for nine different tree species from nested-ANOVA. Error bars represent one standard error above and below the plot mean. Species without bars were measured in only one or two plots. Identical letters above means indicate the means between tree species did not differ significantly (Tukey's multiple comparison test, i.e., HSDs). **A.** Surface and lab pH, and **B.** EC ($\mu\text{S cm}^{-1}$). The lab pH and EC of JUOC were not measured.

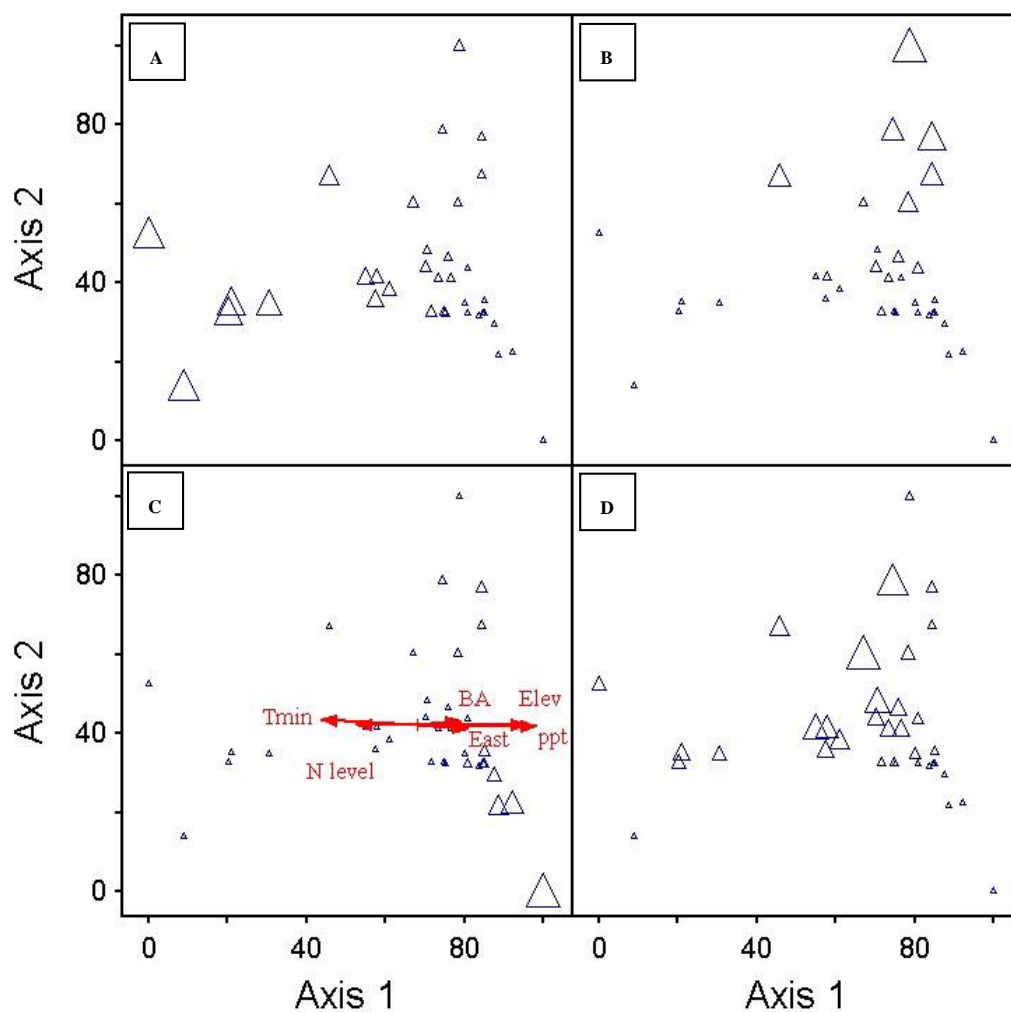


Figure 4-4: Ordination of plots in species space.

Symbol size represents the abundance of four common lichen species in each plot: **A)** total abundance (top +bottom) of *Candelaria pacifica*, **B)** *Hypogymnia imshaugii*, **C)** *Letharia* spp. (mainly *Letharia vulpina*), and **D)** melanelioids. Vectors shown in C apply to A-D and depict strength and direction of correlation between environmental variables and patterns in the composition of the lichen community. Only vectors with $R^2 > 0.15$ with ordination axis 1 or 2 are shown; variable names and correlation strengths are shown in Table 4-3.

Table 4-1: Lichen species recorded on conifer branches.

Species and groups recorded on 379 conifer branches in 38 plots. N rating is the lichen trophic status: E) eutrophs (also known as nitrophytes), O) oligotrophs (also known as acidophytes), and M) mesotrophs (also known as neutrophytes). Elevation range is the minimum and maximum elevation recorded for the species. Abundance is the total number of cm² squares where a species or consolidated group was present. *Candelaria pacifica* abundance is reported as total for lower/upper branch surface. Plots identifies the total number of plots where a species was recorded. The range of surface pH, lab pH, and EC are the minimum and maximum values measured for a given species with the total number of branches measured.

Scientific Name	N Rating ¹	Elevation Range (m)	Abundance	Plots	Surface pH	Lab pH	EC
					range min-max (n = number of branches)		
<i>Ahtiana sphaerosporella</i>	O	2184-2519	463	6	3.2-4.6 (n = 39)	4.5-5.5	33-152
<i>Bryoria fremontii</i>	O	2184	15	1	3.9-4.0 (n = 3)	4.6-4.8	79-107
<i>Candelaria pacifica</i>	E	309-2225	6414/8686	31/30	3.3-6.0 (n = 290)	4.1-6.1	12-339
<i>Cetraria merrillii</i>	O	361-2519	169	13	3.2-5.2 (n = 48)	4.7-5.9	26-212
<i>Cetraria pallidula</i>	O	1282	2	1	4.4-4.8 (n = 2)	5.0-5.1	191-212
<i>Cetraria orbata</i>	O	1190-1893	485	10	3.9-5.7 (n = 17)	5.1-6.1	49-263
<i>Cetraria platyphylla</i>	O	1252					
<i>Evernia prunastri</i>	E	361-1455	379	8	3.3-5.2 (n = 34)	4.1-5.9	12-229
<i>Flavopunctelia flaventior</i>	E	750-914	57	2	3.3-3.9 (n = 8)	4.7-5.2	22-78
<i>Hypogymnia imshaugii</i>	O	914-2519	3666	23	3.3-5.3 (n = 118)	4.1-6.0	17-339
<i>Hypogymnia tubulosa</i>	M	914	6	1	3.7-3.8 (n = 2)	4.7-4.9	24-36
<i>Letharia columbiana</i>	M	1564-2137	201	6	3.4-5.7 (n = 33)	4.8-5.6	41-141
<i>Letharia vulpina/Letharia sp.</i>	O	1039-2364/ 469-2726	3273/2611	28/15	3.3-4.7 (n = 66)/ 3.2-5.1 (n = 101)	4.5-5.7/ 4.6-5.7	12-140/ 22-212
<i>Melanelixia californica</i>	M	309-2225	5181	31	3.3-5.7 (n = 226)	4.1-6.0	12-339
<i>Melanelixia subargentifera</i>							
<i>Melanohalea exasperatula</i>	M						
<i>Melanohalea multisporea</i>	M						
<i>Melanohalea subelegantula</i>	E						
<i>Melanohalea subolivacea</i>	M						
<i>Nodobryoria oregana</i>	M	914-2430	54	10	3.4-5.1 (n = 25)	4.1-5.7	914-
<i>Parmelina coleae</i>	E	309-1550	431	9	3.4-5.4 (n = 39)	4.5-5.9	16-157
<i>Parmelia barrenoae</i>	E	750-1589	197	9	3.3-4.6 (n = 30)	4.1-5.7	12-229
<i>Physcia adscendens</i>	E	605-1984	858	19	3.9-5.2 (n = 31)	4.9-6.0	28-201
<i>Physcia aipolia</i>	E	309-1868			3.7-6.0 (n = 64)	4.8-6.0	16-174
<i>Physcia biziana</i>	E						
<i>Physcia dimidiata</i>	E						
<i>Physcia rhizinata in ed.</i>	E						
<i>Physcia stellaris</i>	M						
<i>Physcia tenella</i>	E						
<i>Physconia americana</i>	M	309-1868	61	10	4.1-6.0 (n = 31)	4.9-6.0	31-114
<i>Physconia californica</i>	M						
<i>Physconia enteroxantha</i>	E						
<i>Physconia fallax</i>	M						
<i>Physconia isidiigera</i>	M						
<i>Physconia perisidiosa</i>	E						
<i>Platismatia glauca</i>	M	914-1039	100	2	3.7-3.8 (n = 6)	4.1-5.2	17-45
<i>Platismatia wheeleri</i>	M						
<i>Usnea sp.</i>	O	750-914	159	2	3.3-4.6 (n = 18)	4.1-5.4	19-78
<i>Vulpicida canadensis</i>	O	361-750	10	2	3.3-4.6 (n = 5)	4.7-5.4	22-85
<i>Xanthomendoza fallax</i>	E	361-2023	50	10	3.9-6.0 (n = 43)	4.9-6.0	28-263
<i>Xanthomendoza fulva</i>	E						
<i>Xanthomendoza hasseana</i>	E						
<i>Xanthoria polycarpa</i>	E	309-2225	193	10	3.5-5.7 (n = 37)	5.0-5.9	33-283
Crustose lichens		309-2726	20188	36	3.2-6.0 (n = 360)	4.1-6.1	12-339

Table 4-2: The variance distribution of lichen substrate measures across study design levels.
Results from nested ANOVA of surface pH, laboratory pH, laboratory EC, branch size, and branch age measurements.

Surface pH

Level	df	Variance		F	F crit	p value
Between tree species	3	0.9953	81%	11.5109	2.9113	< 0.0001
Sites within tree species	31	0.0865	7%	17.8296	1.4852	< 0.0001
Branches within sites	339	0.0879	7%	20.7640	1.1460	< 0.0001
Spots within branches	1518	0.0576	5%			
	1891	1.2272				

Lab pH

Level	df	Variance		F	F crit	p value
Between tree species	4	0.2676	78%	7.1115	2.6684	< 0.0001
Sites within tree species	32	0.0376	11%	17.9249	1.4794	< 0.0001
Branches within sites	325	0.0379	11%			
	361	0.3431				

EC

Level	df	Variance		F	F crit	p value
Between tree species	4	2789.9612	62%	9.2076	2.6684	< 0.0001
Sites within tree species	32	303.0072	7%	4.0771	1.4792	< 0.0001
Branches within sites	327	1398.6898	31%			
	363	4491.6582				

Branch size

Level	df	Variance		F	F crit	p value
Between tree species	4	0.5040	50%	2.3319	2.6684	0.0769
Sites within tree species	32	0.2161	21%	20.1498	1.4775	< 0.0001
Branches within sites	343	0.2927	29%			
	379	1.0128				

Branch age

Level	df	Variance		F	F crit	p value
Between tree species	3	92.3426	64%	3.8089	2.9466	0.0208
Sites within tree species	28	24.2437	17%	7.8834	1.5209	< 0.0001
Branches within sites	253	26.8783	19%			
	284	143.4645				

Table 4-3: Description and correlations of environmental variables and lichen species with ordination axes.

Environmental vectors with $R^2 > 0.15$ and species in bold are shown in the ordination (NMS) diagram of plots in species space in Figure 4-4. Coordinates are Universal Transverse Mercator (UTM; NAD 83 Zone 11N).

Environmental Matrix		Axis 1		Axis 2	
Code	Description	r	R ²	r	R ²
N level	Lichen thallus N level (% dw LEVU equiv.)	-0.56	0.32	0.02	0.00
East	UTM easting (m)	0.51	0.26	-0.14	0.02
North	UTM northing (m)	0.37	0.13	0.02	0.00
Elev	Plot elevation (m)	0.74	0.55	0.00	0.00
Slope	Plot slope (degrees)	-0.05	0.00	0.03	0.00
Aspect	Plot aspect (degrees)	0.19	0.04	-0.12	0.01
BA	Plot basal area (m ² ha ⁻¹)	0.47	0.22	0.14	0.02
CanClos	Canopy closure (%)	0.20	0.04	0.15	0.02
Age	Average branch age (yrs)	0.00	0.00	-0.13	0.02
EC	Electrical conductivity (mS cm ⁻¹)	0.27	0.07	0.25	0.06
LabpH	Lab pH	-0.20	0.04	0.29	0.08
Surface	Surface pH	-0.24	0.06	0.28	0.08
Precip	Average annual precipitation (mm)	0.78	0.60	-0.07	0.01
Tmin	Average annual minimum temp (°C)	-0.70	0.49	0.17	0.03

Species Matrix		Axis 1		Axis 2	
Code	Description	r	R ²	r	R ²
CAND	<i>Candelaria pacifica</i> (total)	-0.99	0.98	-0.05	0.00
MELA	Melanelioids	-0.31	0.09	0.43	0.19
PhysciaT	<i>Physcia</i> spp.	-0.53	0.29	0.07	0.01
XantTOT	Xanthorioids	-0.52	0.27	0.07	0.00
HyIm	<i>Hypogymnia imshaugii</i>	0.14	0.02	0.83	0.69
VuCo	<i>Vulpicida canadensis</i>	-0.54	0.29	-0.27	0.07
LETH	<i>Letharia</i> spp.	0.46	0.21	-0.53	0.28
USNE	<i>Usnea</i> spp.	-0.27	0.07	-0.22	0.05
FLAV	<i>Flavopunctelia</i> spp.	-0.40	0.16	-0.27	0.07
CeMe	<i>Cetraria merillii</i>	-0.12	0.01	-0.15	0.02
PHYSCO	<i>Physconia</i> spp.	-0.20	0.04	0.12	0.01
PLAT	<i>Platismatia</i> spp.	0.03	0.00	-0.06	0.00
EvPr	<i>Evernia prunastri</i>	-0.43	0.19	-0.27	0.07
NODO	<i>Nodobryoria oregana</i>	0.30	0.09	-0.28	0.08
ParmTot	<i>Parmelia</i> spp.	0.00	0.00	-0.12	0.01

CHAPTER 5: GENERAL CONCLUSIONS

The Yosemite region is part of the largest federal air quality Class 1 designated air-shed in the western United States, protected under the Clean Air Act, covering the entire crest of the Sierra Nevada. Aside from the foothills, the region is federally designated Wilderness and has been subjected to few direct human impacts. One of the principal ecological concerns is the deposition of excess nitrogen (N) from anthropogenic emissions in the Central Valley carried eastward into the mountains by prevailing winds. The National Atmospheric Deposition Program (NADP) station in Yosemite has measured N deposition levels near and above established lichen critical loads for more than a decade. A California-wide N-deposition model predicts such levels have become the norm throughout the foothills and montane areas west of the central and southern Sierra Nevada crest. Primary objectives of this study were: to quantify throughfall-N deposition, to establish a threshold N-response level of sensitive lichen communities (i.e., the lichen critical load), and to determine the geographic extent of the area where the lichen critical load is exceeded.

Between 2010 and 2011, we quantified total inorganic nitrogen (wet + dry) throughfall deposition levels at 12 sites where we also collected lichen thallus N data; deposition ranged from 2.8 to 4.7 kg N ha⁻¹ yr⁻¹. Measuring deposition using standard Ion Exchange Resin (IER) methodology is prohibitively time consuming and expensive. Therefore, we calibrated our IER throughfall deposition data with co-located lichen N-level data as part of a collaborative multi-state effort (Root et al., 2013). This enabled the use of lichen thallus N levels as a proxy for N deposition; a more cost effective and low-impact method to quantify N inputs.

To expand the measurement of N inputs to the landscape level required the use of three different lichen species. Consequently, it was necessary to first correlate the N levels of the three different lichens; *Letharia columbiana* and *Evernia prunastri* to *Letharia vulpina*, with data from localities where the species co-occurred because lichen species may accumulate N at different rates. The species calibration data from the study area were supplemented with data available from other parts of the western U.S. to extend the accumulation relationships across a broader range of N deposition. We then standardized lichen thallus N-concentration data to the most common lichen used, *Letharia vulpina* (LEVU), and collected lichen thallus N data in 301 locations throughout the study area. Lichen thallus N levels ranged from 0.85 to 2.28% (LEVU dry-weight equivalents), corresponding to a deposition range of 1.8 to 12.3 kg N ha⁻¹ yr⁻¹. More than 82% of the lichen thallus samples had N levels > 1.1% which we determined to be the

threshold response level for epiphytic lichen communities in the coniferous forests in the study area.

We modeled standardized lichen thallus N levels and extrapolated N inputs to the study area. The results show that the east-west aligned watersheds of the Merced and Tuolumne River are conduits for contaminated air to flow farther east than elsewhere. In the final model, owing to the strong west-to-east elevation gain in the study area, elevation accounted for the distance to emission sources as well as prevailing airflow patterns. The Topographic Position Index was an additional predictor with a minor contribution to the model. It adjusted for higher N accumulation in valley bottoms and on ridges relative to mid-slope locations. This effect was stronger at low elevations and gradually weakened at higher elevations, perhaps due to the progressive mixing of the air masses.

Under low natural N deposition regimes, lichen communities of coniferous forests are dominated by mesotrophs and oligotrophs. At the stand-level, the richness and abundance of eutrophs is low, and eutroph occurrence on conifer substrates is typically limited to specific microhabitats. With elevated N inputs the affected lichen composition shifts at a threshold N deposition level that is termed the lichen critical load. In the study area, the empirical critical load was determined at lichen thallus N levels $> 1.1\%$ (LEVU dry-weight equivalents), corresponding to a throughfall N deposition of $2.9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. Determining a critical load for the study area ensured the applicability of our inferences about excess N exposure (relative to the lichen critical load) from our N-deposition model for the study area. It also validated previous lichen critical load research, necessary in future studies and emissions regulation.

The determination of the critical load was based on two lichen community indices: the abundance ratio of eutrophs to oligotrophs, measured at the stand-level, and the proportion of the total lichen abundance dominated by eutrophs, measured at the branch-level. We think of the response of the epiphytic lichen community to elevated N as more or less continuous; however, at throughfall deposition level $> 2.9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ eutrophs such as *Candelaria pacifica* occupy a wider range of microhabitats, setting in motion a major shift in the character of the lichen community. We anticipated an absolute decline in oligotroph abundance with increasing N deposition, but only the branch-level method detected a weak decline in oligotroph abundance. It is likely that the complex distribution of many oligotroph species on the landscape made pattern detection more difficult. In the study area, oligotroph richness and abundance was generally low except in cool and moist sites. Low oligotroph richness could have reduced the ability of the ranked abundance system (stand-level method) to detect a decline relative to the absolute

abundance system (branch-level method). However, assuming immaculate air quality, it is highly unlikely that the same abundance of cyanolichens and oligotrophs found in the western Pacific Northwest could naturally occur in the Yosemite region for strictly climatic reasons (Jovan, 2008). The fact that our data did not reveal major trends in lichen oligotroph abundance may suggest that significant losses have not yet occurred, i.e., increases in eutroph richness and abundance on conifer substrates occur before or concurrent with the decline of oligotrophs. Alternatively, if N exposure related losses of oligotrophs occurred prior to this study, the CLO would need further downward adjustment. Regardless, the fate of lichen oligotrophs in the Yosemite region warrants additional study. Our network of plots may serve as a reference point in the future; however, due to complex oligotroph distribution on the landscape, specific targeting of habitats with high oligotroph diversity may be necessary.

When lichen community composition shifts, it is not always apparent whether it is a direct response to increased N deposition, an indirect effect through an alteration of the lichen substrate imposed by the pollutant, or a combination of both. We determined branch acidity and electrical conductivity; measures correlated with lichen community composition in other pollution studies. Each measure varied at several levels of scale, but there was no evidence for any relationship of lichen community composition with measures of pH or conductivity. Consequently, it appeared that ammonium-nitrate-dominated N deposition is associated with direct changes in the lichen community composition and that such exposure apparently does not substantially alter the acidity or conductivity of the lichen substrate.

Two techniques developed during this study may be broadly applicable to other work. The branch lichen assessment method may be fine-tuned into a rapid assessment tool to provide direct feed-back about the N status of the lichen community. The regular presence of more than one or two eutroph species on conifer branches suggests that the lichen critical load is approached or exceeded. Specifically, the abundance and distribution of the eutroph *Candelaria pacifica* may provide insights when measured quantitatively with the branch-assessment method. This species may be present in specific micro-habitats at N deposition regimes below the critical load; however, when it proliferates as a regular part of the conifer branch lichen community (e.g., > 200 counts per 10x 1-m branch sample), it is likely that the lichen critical load has been exceeded ($R^2 = 0.405$; from simple linear regression of lichen thallus N levels with *Candelaria pacifica* abundance measured on the lower branch surface). Such rapid assessments may be useful for instance in providing instant feedback to managers of conservation areas seeking field verification of local N inputs above or below the lichen critical load, or to scientists seeking a

low-cost method of estimating N deposition. The other technique developed during this study that may be broadly applicable is the modeling of lichen thallus N levels to estimate landscape level N inputs at a high level of resolution.

Yosemite is one of the oldest and most well-known National Parks in the country, and it is surprising how little lichen work has been done in the region. This study is the first to systematically assess epiphytic lichen community composition and to quantify the apparent impacts of N pollutants on lichen communities at the landscape scale. The studies presented in this dissertation determined the lichen critical load for N deposition in the Yosemite region and demonstrate this threshold is exceeded in 68% of this region of the Sierra Nevada, including 72% of the air quality Class 1 designated area. These findings have broad implications. Land managers have been primarily concerned with the impacts of ammonium-based aerosols on regional haze, although visibility issues have diminished somewhat in recent years. For the untrained eye, it is not as easy to appreciate the gradual alteration of lichen communities at the landscape scale, yet impacts are visually apparent throughout the foothills of the Yosemite region, deep into heart of Yosemite Valley and in the Giant Forest of Sequoia National Park well south of the study area.

The sheer beauty of Yosemite inspires and humbles millions of people every year. This creates an opportunity, if not a responsibility for land managers to engage the public about the ecological effects and pervasiveness of excess N deposition. Current N deposition regimes are likely to be sustained for many years and are likely to have a range of serious ecological consequences. Among the most sensitive known terrestrial organisms, the fate of lichen oligotrophs under a sustained, elevated N deposition regime is uncertain, given that many species are already restricted to cool and moist refuges. As the consequences of human activity bear down with the wind and rain, there will be no simple solutions. One important piece is the need to interpret and share with visitors the complex and far reaching ecological stories of today, just as John Muir was compelled to tell the story that led to the preservation of Yosemite more than 100 years ago.

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APPENDICES

APPENDIX A: LICHEN PLOT CHARACTERISTICS.

East and North are Universal Transverse Mercator (NAD 83, zone 11N). Slope is measured in degrees, Aspect as degrees E of N; Can Clsr is the forest canopy closure as percent closed. BA is Basal Area, HW is hardwood BA in $\text{m}^2 \text{ha}^{-1}$. For explanation of species acronyms see Appendix B. Ownership: Yosemite National Park unless indicated: San Joaquin Experimental Range^a, Bureau of Land Management, Merced River Recreation Area^b, private^c, Sierra National Forest^{*}, Stanislaus National Forest^{**}, Humboldt-Toiyabe National Forest^{***}.

Plot	Plot Name	East	North	Elevation(m)	Topogr. Position	Slope	Aspect	Can Clsr	BA m^2/ha	Hw BA	Plot Basal Area composition
1	Yellow Pines	270119	4179505	1190	lower slope	1	324	60	40.40	6.82	ACMA(5%)CADE(22%)POBA(1%)PIPO(72%)QUKE(1%)
2	Crane Flat Lookout	252115	4182859	1951	upper slope	10	28	47	44.08	0.00	ABCO(23%)CADE(2%)PILA(75%)
3	Chowchilla Mt Rd	264418	4156570	1353	mid slope	15	90	80	86.32	3.19	ABCO(40%)CADE(20%)PILA(6%)PIPO(30%)QUKE(3%)
4	El Portal [*]	251966	4172411	605	ridge top	30	72	30	14.23	6.45	PISA(94%)QUWI(6%)
5	Snow Creek	279333	4188833	2562	lower slope	2	208	60	54.18	0.00	ABMA(12%)PICO(78%)PIMO(8%)TSME(2%)
6	Siesta Lake	266063	4193049	2364	mid slope	5	348	45	45.91	0.00	ABMA(68%)PICO(24%)PIMO(8%)
7	Turtleback Dome	261742	4177335	1589	upper slope	15	345	70	40.40	27.27	CADE(32%)PILA(2%)PIPO(20%)PSME(18%)QUKE(27%)
8	Mosquito Creek	262308	4162190	1251	mid slope	20	347	85	77.13	4.76	CADE(32%)PIPO(21%)PSME(42%)QUKE(5%)
9	Aspen Valley	255248	4189431	1893	mid slope	3	60	80	98.25	0.00	ABCO(64%)CADE(32%)PILA(5%)
10	Hodgdon	247939	4187757	1455	mid slope	20	64	55	47.75	13.46	CADE(17%)PILA(17%)PIPO(52%)QUKE(13%)
11	Hetch Hetchy	255105	4205515	1563	mid slope	6	164	50	35.81	5.13	CADE(41%)PIPO(54%)QUKE(5%)
12	Merced Grove	249601	4182410	1758	upper slope	14	152	62	62.44	4.41	ABCO(25%)CADE(7%)PILA(18%)PIPO(46%)QUKE(4%)
13	Tioga Rd	260979	4189469	2184	mid slope	7	209	45	56.01	0.00	ABMA(97%)PICO(2%)PIPO(2%)
14	Tuolumne	292335	4195602	2726	mid slope	35	164	25	42.24	0.00	JUOC(100%)
15	Little Nellie ^{**}	253883	4177416	1549	mid slope	15	80	55	26.63	17.24	CADE(10%)PILA(3%)PIPO(69%)QUKE(17%)
16	Mono Meadow	272120	4172707	2137	mid slope	25	45	60	49.59	0.00	ABCO(89%)PIJE(11%)
17	Glacier PT, GrouseCr	264445	4171637	2225	mid slope	20	14	60	53.26	0.00	ABMA(100%)
18	W Lake Eleanor	245585	4206947	1586	ridge top	12	106	61	52.34	3.51	ABCO(7%)CADE(12%)PILA(14%)PIPO(63%)QUKE(4%)
19	Bourland CR ^{**}	235588	4215580	1747	ridge top	12	100	60	63.36	8.70	CADE(20%)PILA(4%)PIPO(67%)QUKE(9%)
20	W-Hells Mt ^{**}	240078	4217992	1983	mid slope	25	328	65	41.78	0.00	ABCO(96%)PILA(4%)
21	Chowchilla West [*]	260549	4154503	1571	mid slope	10	290	80	47.75	1.92	ABCO(58%)CADE(21%)PILA(4%)PIPO(15%)QUKE(2%)
22	YOSE West	260082	4169525	1868	mid slope	11	8	85	89.99	0.00	ABCO(72%)CADE(13%)PILA(14%)
23	MariposaGrove	270344	4155551	2023	upper slope	25	44	65	41.78	0.00	ABCO(27%)CADE(10%)PIJE(7%)PILA(56%)
24	SF Merced Riv	268593	4157675	1282	lower slope	15	12	87	56.01	0.00	CADE(37%)PILA(7%)PIPO(24%)PSME(33%)
25	O'shaughnessy	254313	4201971	1207	mid slope	18	260	20	4.13	22.22	PISA(78%)QUWI(22%)
26	Early Intake	241216	4196611	834	mid slope	35	170	45	10.10	27.27	PISA(73%)QUWI(27%)
27	MiddleFork TR	248284	4194059	1347	lower slope	7	159	85	89.99	0.00	ABCO(35%)CADE(29%)PIPO(37%)
28	NGravellyFordMine [*]	283513	4156368	2519	mid slope	12	22	70	99.17	0.00	ABMA(99%)PICO(1%)
29	WGravellyFordMine [*]	279844	4156367	2517	mid slope	18	210	70	98.25	0.00	ABMA(100%)
30	S IronMt [*]	277227	4150019	2430	mid slope	20	188	75	67.95	0.00	ABMA(100%)
31	PeelerLake ^{***}	284412	4222549	2820	lower slope	25	0	50	48.67	0.00	PICO(21%)PIMO(9%)TSME(70%)
32	DutchCreek ^{**}	227341	4178787	914	lower slope	2	320	92	51.42	3.57	CADE(25%)PILA(36%)PIPO(36%)QUKE(4%)
33	BassLake [*]	274819	4134085	1038	mid slope	13	269	90	59.69	7.69	ABCO(2%)CADE(52%)PILA(3%)PIPO(35%)QUCH(5%)Q
34	Fresno [*]	256604	4109245	308	lower slope	0	0	21	14.23	12.90	PISA(87%)QUSP(13%)
35	Feliciano ^o	239778	4166805	852	ridge top	28	335	65	21.12	36.96	PIAT(63%)QUWI(37%)
36	Savage ^{**}	245349	4171629	469	mid slope	30	127	66	17.91	0.00	PISA(100%)
37	Midpines KOA ^c	242114	4159185	750	lower slope	0	0	50		0.00	PIPO, PISA, QUKE
38	BLM MRA ^b	236626	4165317	361	lower slope	22	120	60	23.42	35.29	PISA(65%)QUWI(35%)

APPENDIX B: NITROGEN REGIME AND LICHEN INDICES BY PLOT.

The 38 lichen community plots with Lichen N level in N % dry-weight in LEVU equivalents, with corresponding Total N deposition as throughfall N in kg ha⁻¹ yr⁻¹. FIA method indices include the hardwood component. HW Rich is the % richness exclusive to hardwoods. Acronyms: ABCO = *Abies concolor*, ABMA = *Abies magnifica*, ACMA = *Acer macrophyllum*, CADE = *Calocedrus decurrens*, JUOC = *Juniperus occidentalis*, PIAT = *Pinus attenuata*, PICO = *Pinus contorta*, PILA = *Pinus lambertiana*, PIPO = *Pinus ponderosa*, PISA = *Pinus sabiniana*, POBA = *Populus balsamifera*, PSME = *Pseudotsuga menziesii*, QUCH = *Quercus chrysolepis*, QUKE = *Quercus kelloggii*, QUSP = *Quercus* sp., QUWI = *Quercus wislizeni*, TSME = *Tsuga mertensiana*. Branch diameter in cm.

Plot	Plot name	lichen N level	Total N dep.	FIA Method							Branch Method								
				Rich-ness	HW Rich	T abun	E abun	O abun	EO	PNA	Tree Sp.	branch diam.	Rich-ness	T abun	E abun	M abun	O abun	EO	PNA
1	Yellowpines	1.7	6.6	16	25%	37	20	11	1.8	0.54	ABCO	1.1	10	646	296	26	9	32.9	0.33
2	Crane Flat Lookout	1.5	5.3	19	26%	45	16	14	1.1	0.36	ABCO	1.1	6	830	136	31	511	0.3	0.14
3	Chowchilla Mt Rd	1.7	6.8	21	14%	51	24	12	2.0	0.47	ABCO	1.0	6	1116	309	384	0	44.6	0.23
4	El Portal	1.4	4.5	17	71%	48	27	9	3.0	0.56	PISA	1.1	7	503	676	232	0	74.4	0.59
5	Snow Creek	1.1	3.0	1	0%	2	0	2	0.1	0.00	ABMA	1.0	0	0	0	0	0	0.0	0.00
6	Siesta Lake	1.2	3.7	6	0%	11	0	10	0.1	0.00	ABMA	1.6	6	904	0	0	411	0.1	0.00
7	Turtleback Dome	1.5	5.1	18	39%	50	26	15	1.7	0.52	PSME	1.0	8	1169	201	478	494	0.4	0.15
8	Mosquito Creek	1.3	3.9	20	40%	53	28	12	2.3	0.53	PSME	1.3	9	1172	165	205	61	2.7	0.12
9	Aspen Valley	1.3	3.8	21	0%	49	21	18	1.2	0.43	ABCO	1.0	6	1002	194	184	404	0.5	0.16
10	Hodgdon	1.4	4.7	18	50%	46	19	18	1.1	0.41	ABCO	1.1	10	1066	280	195	65	4.3	0.21
11	Hetch Hetchy	1.7	7.2	13	46%	36	15	9	1.7	0.42	PIPO	2.0	8	558	51	35	290	0.2	0.08
12	Merced Grove	1.2	3.6	17	18%	46	19	15	1.3	0.41	ABCO	1.0	9	1058	287	51	782	0.4	0.21
13	Tioga Rd	1.1	2.8	10	0%	25	3	17	0.2	0.12	ABMA	1.2	9	881	8	11	830	0.0	0.01
14	Tuolumne	1.3	4.1	1	0%	3	0	0	0.0	0.00	JUOC	5.2	2	1037	0	0	670	0.1	0.00
15	LittleNellie	1.6	6.3	12	67%	34	20	8	2.5	0.59	ABCO	1.0	7	971	689	264	0	72.3	0.45
16	MonoMeadow	1.3	4.1	10	0%	25	9	11	0.6	0.36	ABCO	1.0	5	492	256	43	10	25.6	0.34
17	GlacierPT_GrouseCr	1.4	4.8	8	0%	22	5	12	0.4	0.23	ABMA	1.0	9	1120	37	3	385	0.1	0.03
18	W_JakeEleanor	1.4	4.4	14	21%	32	14	12	1.2	0.44	ABCO	1.0	9	1208	203	203	147	1.4	0.15
19	BourlandCR	1.3	3.7	13	31%	33	11	14	0.8	0.33	ABCO	1.0	7	1197	311	527	60	5.2	0.21
20	W_HellsMt	1.3	3.9	9	0%	25	6	13	0.5	0.24	ABCO	1.1	8	937	360	212	171	2.1	0.28
21	ChowchillaWest	2.0	9.0	27	7%	66	39	15	2.6	0.59	ABCO	1.4	7	1054	664	312	38	17.5	0.40
22	YOSEwest	1.6	6.4	18	0%	37	14	12	1.2	0.38	ABCO	1.0	8	1351	911	266	416	2.2	0.41
23	MariposaGrove	1.3	3.8	15	0%	37	11	13	0.8	0.30	ABCO	1.1	7	1393	153	121	742	0.2	0.10
24	SFMercedR	1.4	4.9	25	28%	65	22	27	0.8	0.34	ABCO	1.0	11	1162	106	108	350	0.3	0.09
25	O'shaughnessy	1.3	3.9	11	64%	22	9	0	4.1	0.41	ABMA	1.0	6	860	86	104	31	2.8	0.09
26	EarlyIntake	2.2	11.5	17	71%	46	28	9	3.1	0.61	PISA	1.5	5	1038	690	384	0	64.3	0.41
27	MiddleForkTR	1.0	2.3	16	0%	33	20	8	2.9	0.61	ABCO	1.4	8	1037	932	14	223	4.2	0.49
28	NGravellyFordMine	1.2	3.2	3	0%	9	0	6	0.2	0.00	ABMA	1.6	6	1037	0	0	112	0.1	0.00
29	WGravellyFordMine	1.1	2.9	6	0%	15	0	12	0.1	0.00	ABMA	3.8	3	1001	0	0	103	0.1	0.00
30	S_IronMt	1.3	3.8	6	0%	13	0	10	0.1	0.00	ABMA	2.1	4	1470	0	0	596	0.1	0.00
31	PeelerLake	0.9	2.0	2	0%	6	0	6	0.1	0.00	TSME	1.0	0	0	0	0	0	0.0	0.00
32	DutchCreek	1.6	6.2	33	55%	67	31	17	1.8	0.46	PIPO	1.5	14	1028	418	254	63	6.6	0.31
33	BassLake	1.5	5.1	26	54%	55	28	14	2.0	0.51	PIPO	1.4	10	540	183	31	78	2.3	0.29
34	Fresno	1.7	7.2	16	6%	31	21	0	6.8	0.68	PISA	1.2	7	1203	2327	137	0	94.4	0.80
35	Feliciano	1.8	8.0	21	43%	53	24	8	3.0	0.45	PIAT	1.6	9	1191	1204	189	15	80.3	0.50
36	Savage	1.5	5.2	16	6%	39	22	4	5.5	0.56	PISA	1.2	9	842	1431	194	15	95.4	0.64
37	Midpines_KOA	1.8	7.6	19	47%	40	22	6	3.7	0.55	PIPO	1.3	10	838	1979	78	19	104.2	0.81
38	BLM MRA	1.5	5.4	20	45%	44	23	7	3.3	0.52	PISA	0.9	9	758	1457	170	37	39.3	0.67