



Challenges characterizing N deposition to high elevation protected areas: A case study integrating instrument, simulated, and lichen inventory datasets for the Devils Postpile National Monument and surrounding region, USA

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ABSTRACT

Excess N deposition is a common stressor of ecological health. Sensitive biota, including many lichens, respond to small differences in atmospheric N deposition. For lands with a conservation mandate, obtaining sufficient N data to evaluate risks is a challenge, especially in Mediterranean or arid landscapes. Managers in the Western U.S. commonly use epiphytic (“tree-dwelling”) lichens to supplement N assessments, although options for higher elevations lacking epiphytes are poorly developed. Managers instead rely on broad-scale air quality simulations like the Total Deposition Model (TDEP). The Sierra Nevada Range is an example where anthropogenic N reaches mid-to-high elevation protected areas but managers lack tools for monitoring at ecologically relevant spatial-scales. Our main goals were to demonstrate how well-studied epiphytic bioindicators can supplement N assessments and recommend saxicolous (“rock-dwelling”) candidates for similar development to improve coverage in higher elevations. As a case study, we characterized N deposition at a small (323 ha) protected area, Devils Postpile National Monument (DEPO), by integrating data from TDEP, air instruments, and assays of %N in the epiphyte *Letharia vulpina*. We used the regional N threshold associated with detrimental effects to epiphytic lichen communities, 2.9 kg N ha⁻¹ yr⁻¹ in throughfall (i.e. under a tree canopy), as a provisional critical load (CL) for indicating areas at risk of ecological impacts. Results clearly showed the need for empirical, diverse, and finer-scaled information, even for an area as small as DEPO. Importantly, simulations from TDEP overestimated dry deposition of oxidized N, making total N estimates nearly twice measured values (6.0 vs 3.03 – 3.66 kg N ha⁻¹ yr⁻¹, respectively). While small, our *L. vulpina* dataset (n = 5) from the Monument indicated highly variable N in throughfall (1.7 – 4.44 kg N ha⁻¹ yr⁻¹), with small-scale drivers, like proximity to the river canyon and the Central Valley, tipping the scale towards CL exceedance. Regional *L. vulpina* assays (n = 355) showed a distinct north-to-south gradient in California where N deposition at DEPO was highly similar to the nearby protected area, Yosemite National Park, where ecological impacts of excess N are well-documented. To expand N bio-monitoring into higher elevation areas, we recommend vetting five widespread saxicolous species, *Rhizoplaca melanophthalma*, *Umbilicaria phaea*, *U. polaris*, *Xanthoparmelia coloradoensis*, and *X. cumberlandia*.

1. Introduction

Nitrogen (N) deposition is a major driver of ecological change in

many parts of the world, including the montane Western U.S. (Bobbink et al., 2010; Clark et al., 2017; Fenn et al., 1998; Pardo et al., 2011). Highly N-sensitive biota respond to small exceedances of background N

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levels, however, obtaining fine-scaled N data for risk evaluation is a management challenge (Blett et al., 2003; Ellis et al., 2013). Instrument-based monitoring networks are too costly and widely-spaced to capture air quality at ecologically relevant scales. Lack of infrastructure, access, and the assumption of pristine conditions, further limit monitoring with instruments in protected areas of the U.S. (i.e. Federal Class 1 Areas - Wilderness, National Parks, and National Monuments), which receive special air quality protections under the Clean Air Act (Greaver et al., 2012). Oftentimes, broad-scale air quality simulation models, like the U. S. Environmental Protection Agency's (EPA) Total Deposition model (TDEP; Schwede and Lear, 2014), provide the sole source of N data for assessments of protected areas.

In semi-arid regions of the montane West, traditional monitoring tools like instruments and simulation models are especially inadequate for assessing ecological risks. A large proportion of N is dry-deposited,

and therefore highly heterogeneous, which means deposition averaged across ecosystem or stand-level scales poorly represents N load at any specific location (Ochoa-Hueso et al., 2011; Tulloss and Cadenasso, 2015). A common strategy federal land managers (FLMs) use, to improve spatial perspectives and provide context for evaluating risks, is supplementing N assessments with measurements of epiphytic ("tree-dwelling") lichens (e.g. Dibble et al., 2016; Fenn et al., 2010; Hoffman et al., 2019; Landers et al., 2008); the U.S. Forest Service (USFS) maintains two large-scale lichen inventories for this purpose (Jovan et al., 2020).

Ideally, N assessments include both instrument and lichen bio-indicator data. Only instruments can show how much N is wet or dry-deposited, what compounds are present, and how tree canopies affect N flux. However, we can use inexpensive assays of tissue N content (%N) in certain lichen species to approximate total N deposition with

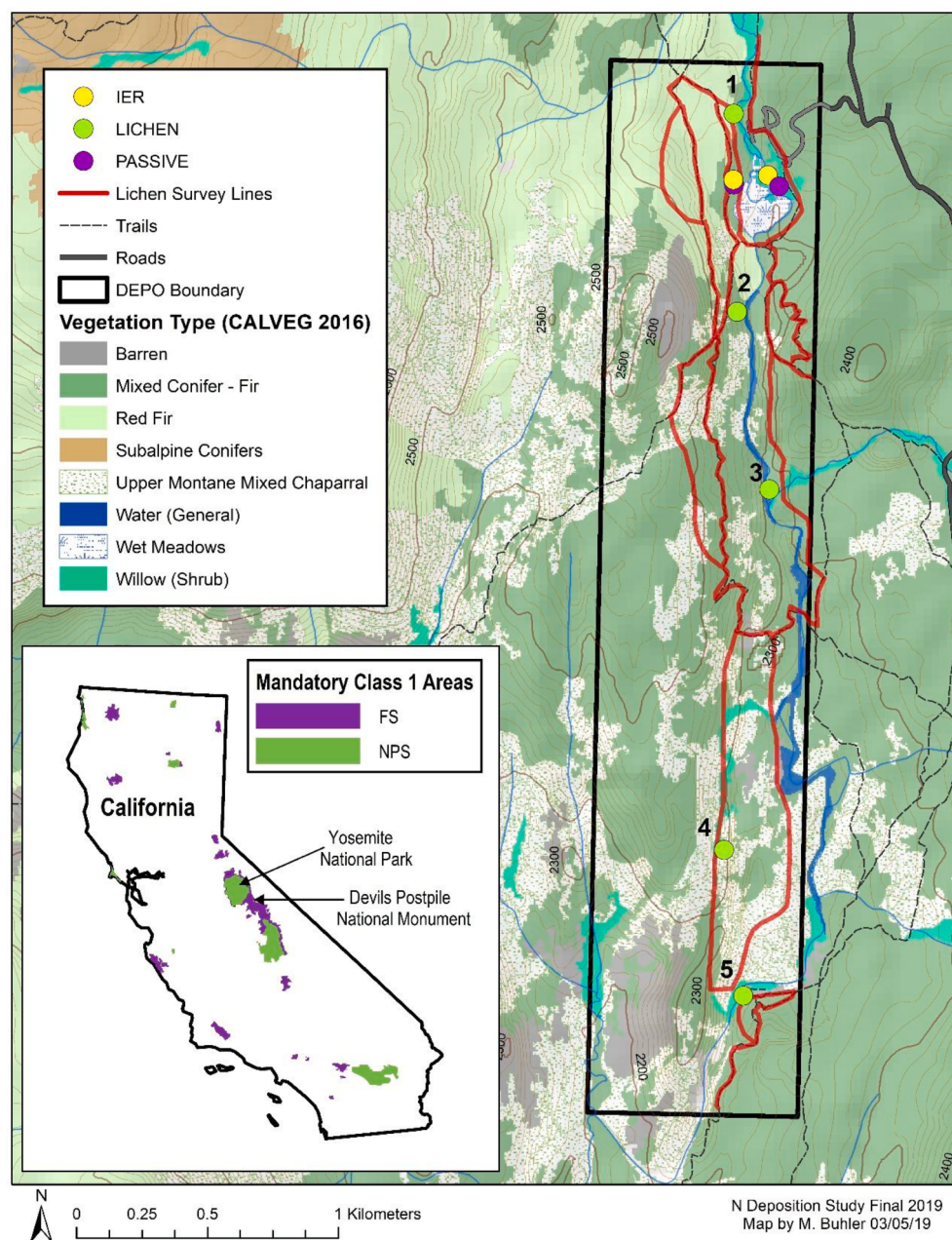


Fig. 1. Vegetation map of Devils Postpile National Monument showing locations of ion-exchange (IER) resins, passive air quality samplers, and collection sites for *Letharia vulpina*. A similar species, *L. columbiana*, was collected at site #2. An inventory of all macrolichen species was conducted in foot-accessible areas of the park as indicated by red traverse lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reasonable accuracy (Hutten, 2015; Root et al., 2013). Increasing N deposition also causes a predictable shift in epiphytic communities from native, N-sensitive species to ‘weedy’ cosmopolitan ones, which FLMs use to define biological effects thresholds, like critical loads (CLs; Fenn et al., 2018a; McMurray et al., 2015), for evaluating the ecological risks of N (Porter et al., 2005; Burns et al., 2008). Species shifts occur at such low N levels (Fenn et al., 2008; Geiser et al., 2019) that FLMs use the associated CLs as guidelines to protect ecosystems as a whole (Fenn et al., 2010; Ellis et al., 2013). The focus on epiphytes, however, means similar tools are lacking for high elevations and other treeless habitats. Saxicolous (“rock-dwelling”) lichens are potential alternatives but are rarely used (although see Fenn et al., 2007; Landers et al., 2008; Perkins et al., 1980; Zschau et al., 2003).

Our main goal was to demonstrate how a well-studied epiphytic lichen, *Letharia vulpina* (Wolf lichen; (L.) Hue), can supplement N assessments while also showing the need for bioindicators suitable for higher elevations. At the request of local FLMs, we used Devils Postpile National Monument (DEPO), a remote protected area in the Sierra Nevada Range in California, as a case study. Prior knowledge of N was limited to a single 12 × 12 km pixel in the TDEP simulation model. Meanwhile, a nearby study of epiphytic lichens in Yosemite National Park (NP) indicated highly variable N loads frequently exceeding the CLs detrimental shifts in community composition (Hutten, 2015; Fig. 1). Transitional forests at DEPO are interspersed with sparsely-vegetated rocky zones like those found at higher elevations, allowing us to demonstrate both the benefits and limitations of currently available lichen tools. We placed air quality samplers at two sites, conducted the first lichen inventory in the Monument, and measured %N in *L. vulpina* wherever we found it. Over a decade of using *L. vulpina* assays in the Western U.S. makes this species a handy through line for comparing N across mid-elevation forests, so we use several preexisting datasets from the USFS Lichen Inventories to place N at DEPO along regional deposition gradients across inland montane zones in California, Oregon, and Washington. As a first step towards developing comparable tools for higher zones, we also compile all known preexisting %N data for saxicolous species, and consider species distributions, to recommend candidates for further study in the Sierra Nevada and broader montane West.

2. Methods

DEPO is a relatively small (323 ha) National Monument of significant conservation importance, known for its animal and plant biodiversity (NPS 2015), basalt cliffs, and steep river canyons. It occurs in the Upper Montane forest zone of the Sierra Nevada (Potter, 1998) between 2190 and 2560 m and encompasses 10 vegetation or land types, including many open treeless areas (Fig. 1). Over 85% of DEPO lies within the surrounding Ansel Adams Wilderness area and is adjacent to the John Muir Wilderness area. Like all Class 1 areas in the Central and Southern Sierra, the Monument is downwind of the highly agricultural Central Valley. The Central Sierra also receive air masses from the San Francisco metropolitan area. Several rivers run perpendicular to the west side of the range through deeply incised canyons, with the Upper Middle Fork of the San Joaquin River running north to south through DEPO.

2.1. Simulated N deposition

We used TDEP to simulate N at DEPO, which was represented in the model by a single grid cell. The model output included estimated deposition fluxes for all major chemical compounds of atmospheric N, including organic N pollutants, and for both wet and dry deposition. The Community Multi-scale Air Quality (CMAQ) model has been used widely in the United States for estimating atmospheric deposition at broad scales. More recently the TDEP model gained favor because it combines CMAQ’s simulation capabilities with empirical air quality data where available. As such TDEP is referred to as a hybrid model. TDEP provides

output at a 12- by 12-km grid scale for the continental United States.

2.2. Instrument data

2.2.1. Gas concentrations and branch rinses for dry N deposition

In summer 2015, we installed passive air pollution samplers at two monitoring sites in DEPO, a meadow near Soda Springs (non-wilderness) and an adjacent mixed-conifer stand, for monitoring average concentrations of major N gas species (NO, NO₂, NH₃ and HNO₃). Samplers were deployed at the Meadow site from June 17 to September 24 and at the forest from July 14 to September 24. Exposure periods ranged from 8 to 19 days with an average exposure of 13 days. We used branch rinsing at both sites to determine the surface deposition of reduced N (NH₄⁺) and oxidized N (NO₃⁻). In July 2015, five branches of lodgepole pine (*Pinus contorta*) were rinsed at each site (4 exposure periods with about 1 week duration). Literature-based values of stomatal conductance were used to adjust for internal uptake of nitrogenous compounds.

We used the Empirical Inferential Method (Bytnerowicz et al., 2015) to calculate dry N deposition fluxes from the passive samplers’ concentration data, deposition velocities for gaseous pollutants from Zhang et al. (2003), and leaf area index (LAI). Deposition to leaf surfaces was determined by branch-rinsing and leaf area calculations. The Meadow site had an LAI of 1.09 and the forest site had an LAI of 1.35. LAI for the forested site is a mean of 3 adjacent mixed conifer forest pixels from MODIS images (1.47; 1.30 and 1.14; results provided by Robert Johnson, University of California, Riverside). Total dry deposition of reactive N species was calculated as the sum of all components of surface deposition and stomatal uptake—for the May through October period only. Doubling the summertime dry deposition flux calculated for the forest stand provides a rough estimate of annual dry deposition, albeit with considerable uncertainty because it assumes that dry deposition in winter and summer are similar. This estimate of annual dry deposition was combined with annual wet deposition (we used the average of estimated wet deposition from the bulk deposition flux (bulk × 0.85, see Section 2.2.2, and the TDEP wet deposition value), to arrive at an estimate of total annual N deposition.

2.2.2. Throughfall and bulk for wet and total N deposition

We installed ion exchange resin (IER) collectors (Fenn and Poth, 2004; Fenn et al., 2018b) in the meadow and forest sites to measure total N in throughfall (under *Pinus contorta* canopy) and bulk deposition (i.e. wet deposition in the open meadow). Six replicate IER samplers were used for the meadow sites and 23 for the forest site, which were placed along 4 parallel transects of 3–8 collectors per transect. All samplers remained in place for a total of 12 months. Deposition monitoring began on June 17, 2015. New IER columns were installed on October 30, 2015, and this last set of IER columns were retrieved on June 16, 2016 to complete one year of deposition sampling. This sampling schedule enabled us to calculate both annual and seasonal N flux.

The IER columns absorb ions from precipitation or throughfall samples as the solution percolates through the column. At the end of each sampling period the columns were transported to the laboratory, extracted with 1 N KI and analyzed for NO₃⁻, NH₄⁺, SO₄²⁻ and PO₄²⁻ (the latter as an indicator of possible contamination from bird droppings). Laboratory results of the mass of these ions collected by each column was then extrapolated to elemental deposition flux rates (kg ha⁻¹ yr⁻¹) based on the collection surface area of the sampler funnel or snow tube opening. For further details see Fenn and Poth (2004) and Fenn et al. (2009), Fenn et al. (2018b).

Throughfall is well known to underestimate total N deposition due to the interaction and uptake of reactive pollutants by plant canopies (Avila et al., 2017; Fenn et al., 2013; Gaige et al., 2007; Lovett and Lindberg, 1993). Therefore, we estimated total (wet + dry) N deposition from the throughfall flux data based on assumptions from previous studies showing the approximate levels of canopy uptake of N (Avila et al., 2017; Fenn and Bytnerowicz, 1997). Throughfall-adjusted total

deposition was based on 55% canopy retention of reduced N and 45% canopy retention of oxidized N based on previous work in California (Fenn and Bytnerowicz, 1997) and Spain (Avila et al., 2017), and as constrained by the $\text{NH}_4\text{-N}:\text{NO}_3\text{-N}$ ratios in wet and bulk deposition in this study.

Total N deposition was also estimated by adjusting annual wet N deposition based on the relative proportions of wet vs. dry deposition from multiple years of monitoring at Emerald Lake in Sequoia NP, also a high elevation site in the Sierra Nevada of California with elevated snowfall (Fenn et al., 2009). From this analysis we assumed that 66% of total deposition at DEPO was wet-deposited. We averaged two separate measures of wet deposition at DEPO to estimate total N deposition. For the first, annual wet deposition was calculated using IER bulk deposition from the meadow $\times 0.85$, which is to account for the background dry deposition of N that occurs directly to the funnel deposition collectors. Secondly, we used the wet deposition value from the TDEP model. The total N deposition estimated from the average of these two wet deposition estimates was used to estimate total annual N deposition at DEPO.

2.3. Lichen data

We inventoried macrolichens at DEPO over four days in August 2016, covering all vegetation types and areas accessible by foot (Fig. 1). For each species encountered, we collected a voucher specimen and estimated its abundance across the Monument using broad categories (rare, uncommon, common, abundant) based on the surveyor's judgement. We also surveyed epiphytic lichen communities at two locations, one each near the Meadow and Forest sites, using the standard protocol of the United States Forest Service (USFS) lichen inventories (Jovan et al., 2020). When known, species were assigned to N-sensitivity classes.

2.3.1. *Letharia* at DEPO

Letharia vulpina is the most commonly used species in the Sierra Nevada for measuring %N, although it approaches its upper elevation limit at DEPO. In August 2016, we collected *L. vulpina* wherever found to test for %N using the standard USFS protocol (Fig. 2; Geiser, 2004) and at one site we collected the closely related species *L. columbiana*. In brief,



Fig. 2. *Letharia* was restricted to large *Juniperous occidentalis* trees growing along the San Joaquin river canyon at DEPO. Photo credit: Elisa DiMeglio.

non-powdered nitrile gloves were worn to collect composite samples of about 10 g of dry *Letharia* from 5 or more trees at each site. Compositing many sub-samples helps ensure we capture a reasonable average for %N despite variability amongst individual lichen thalli due to microsite differences affecting exposure. We sealed the lichen in airtight metalized polyester bags. Samples were later processed in a lab to remove any debris and dead tissue. Samples were then dried, ground, and analyzed for N using microwave-assisted digestion (CEM Mars 6 Microwave Digester model 910900) and combustion analysis (Leco 628 Series C/H/N Analyzer model 622-000-000).

2.3.2. Lichen CLs and estimating throughfall N

We used the CL determined by Hutten (2015) for shifts in Sierra Nevada epiphytic communities ($2.9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in throughfall) as a provisional guideline to screen for areas at risk of ecological impacts. We encountered low epiphyte diversity at DEPO, as is natural for that elevation range (Jovan and McCune, 2006), which would obscure observation of local community shifts due to N deposition. Nonetheless, Hutten's CL is for now the best available reference point for transitional, upper montane forests like DEPO. Since the community metrics that define lichen CLs closely track %N in *L. vulpina* (Fenn et al., 2008; Hutten, 2015; Root et al., 2013), we used 1.1%, the % N value corresponding with the CL threshold, to assess the N status of sampling locations relative to the CL.

In some instances, we converted %N to throughfall estimates using Root's (2013) calibration model (a) to express assay results in more relatable terms. Root found *L. vulpina* from California and Oregon correlated highly with throughfall ($R^2 = 0.74$). The uncertainty of throughfall predictions was very low around small N values like CLs but increased as N levels increased, especially beyond $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. For our one *L. columbiana* collection, we used Hutten's (2015) interspecies calibration equation (b) to first convert % N to the equivalent in *L. vulpina*. Final lichen-based estimates of throughfall deposition are reported in $\text{kg N ha}^{-1} \text{ yr}^{-1}$.

- (a) $\ln(\text{throughfall N}) = 0.886 + 1.968 * \ln(\%N \text{ in } Letharia \text{ vulpina})$
- (b) $\%N \text{ in } Letharia \text{ vulpina} = 0.9424 (\%N \text{ in } Letharia \text{ columbiana}) - 0.0017$

2.3.3. Regional *Letharia* datasets

We assembled 4 regional *L. vulpina* datasets, mostly from the USFS Lichen Inventories, to compare with DEPO's results (Table 1). This includes all publically available data from the Sierra Nevada as well as intensively sampled data collected above 2000 m at Yosemite NP (Hutten, 2015). Most data from the Sierra Region came from the USFS Forest Inventory and Analysis Program (FIA), which samples lichens on a systematic grid of forested plots. We included forested sites just north and south of the Range, as well as data from the USFS Air Resources Management Program (ARM) from Wilderness Areas in Oregon and Washington. A similar dataset wasn't available for wilderness in California.

2.3.4. Saxicolous candidates

To recommend saxicolous species for higher elevations, we consulted with field guides, the Consortium of North American Lichen Herbaria website (accessed June 2019), the USFS Lichen Inventories, and unpublished pilot datasets (Table 1). We also conducted reconnaissance hikes to eight Wilderness Areas in the Sierra Nevada (Summer 2019) to note saxicolous species' distributions. We found replicated %N data for three of the species we recommended, and compared repeatability with replicates from regional *L. vulpina* datasets (Table 1). We focused only on macro-lichens because crustose species are difficult to handle.

Table 1

Regional datasets for %N in *Letharia vulpina* and saxicolous candidates. Data sources are listed in decreasing order of their contribution. USFS = U.S. Forest Service, FIA = Forest Inventory and Analysis Program, ARM = Air Resource Management Program. Most data from the USFS Lichen Inventories may be downloaded from <http://gis.nacse.org/lichenair> (see also Jovan et al. 2020). In most cases, 'replicated %N data' consisted of a primary sample and one replicate.

Species	Region	Description	Contributing datasets	Timeframe
<i>Letharia vulpina</i>	Sierra Region (n = 86)	All available %N data for the Sierra Region, including 11 sites in the Southern Cascades and 9 in the Los Angeles Basin. High Yosemite sites are treated separately.	USFS FIA Lichen Inventory (Jovan and Carlberg 2007); Kings River Landscape Study (Jovan et al. unpublished); Sierra wilderness transect (Cisneros et al., unpublished); Western Airborne Contaminant Assessment Project (Landers et al. 2008), DEPO (this study)	2004–2016
<i>Letharia vulpina</i>	High Yosemite (n = 109)	All %N data greater than 2000 m elevation	National Park Service (Hutten 2015)	2010–2011
<i>Letharia vulpina</i>	Wilderness in Oregon and Washington (n = 160)	All available %N data	USFS ARM Lichen Inventory	1993–2013
<i>Letharia vulpina</i>	National Forests in Oregon, Washington, and California (n = 149 pairs)	Replicated %N data	USFS ARM Lichen Inventory, and including all field and lab replicates from the datasets above.	1993–2013
<i>Rhizoplaca melanophthalma</i>	San Bernardino and Sierra Nevada (n = 7 pairs)	Replicated %N data	Saxicolous data from San Bernardino (Kovasi et al. unpublished) and Sierra wilderness transect (Cisneros et al. unpublished) pilots.	2013–2014
<i>Umbilicaria phaea</i>	San Bernardino (n = 9 pairs)	Replicated %N data	Saxicolous data from San Bernardino pilot (Kovasi et al. unpublished)	2014
<i>Xanthoparmelia cumberlandia</i>	National Forests in Colorado, Idaho, Oregon, and Washington (n = 36 pairs)	Replicated %N data	Saxicolous data from USFS ARM lichen inventory	1994–2012

3. Results

3.1. Instruments vs TDEP

Overall, most empirical measurements indicated reduced-to-oxidized N ($\text{NH}_4\text{-N}:\text{NO}_3\text{-N}$) ratios greater than one, or greater than two, depending on the measurement. Results were fairly consistent within similar modes of measurement; ratios for summertime N gas concentrations at the meadow and forest sites were 1.2 and 1.4, respectively, while ratios for deposition measurements (not including inferential dry deposition calculated values) ranged from 2.1 to 2.5 (Fig. 3, Table 2). While TDEP's ratio for wet N deposition was close (2.62), the ratio for total simulated N deposition was quite low at 0.82; Table 2). Accordingly, TDEP's ratio for annual dry deposition (0.40) was also substantially lower than ours based on the inferential method (0.98 and 1.22). The summertime surface deposition of NH_4^+ and NO_3^- to *Pinus contorta* at the Meadow site (0.094 and 0.150 $\text{uEq m}^{-2}\text{h}^{-1}$) and Forest

site (0.077 and 0.105 $\text{uEq m}^{-2}\text{h}^{-1}$) were similar, leading to ratios for branch rinses that fell in the middle (0.63 and 0.73).

Throughfall N deposition measured at the Forest site was 1.7 $\text{kg N ha}^{-1}\text{yr}^{-1}$ and bulk deposition at the adjacent meadow was 2.1 $\text{kg N ha}^{-1}\text{yr}^{-1}$. Our estimates of total N deposition flux based on these measurements were higher than wet or throughfall deposition alone (Table 2). Throughfall N adjusted for percent canopy uptake gave a total deposition estimate of 3.7 $\text{kg N ha}^{-1}\text{yr}^{-1}$ while bulk deposition adjusted for percent total deposition occurring as wet gives a similar estimate (3.0 $\text{kg N ha}^{-1}\text{yr}^{-1}$). The corresponding TDEP estimate for total N deposition flux was higher at 6.0 $\text{kg N ha}^{-1}\text{yr}^{-1}$. When broken down into wet vs dry deposition, TDEP's wet estimate (2.21 $\text{kg N ha}^{-1}\text{yr}^{-1}$) was basically equal to ours (i.e. bulk; 2.1 $\text{kg N ha}^{-1}\text{yr}^{-1}$) while TDEP's dry estimate (3.79 $\text{kg N ha}^{-1}\text{yr}^{-1}$) was much higher than our estimate for the 6-month growing season using the inferential method (1.1 and 0.8 $\text{kg N ha}^{-1}\text{yr}^{-1}$ for Meadow and Forest, respectively; Supplementary Table 3). Doubling our values to better approximate annual deposition, as the

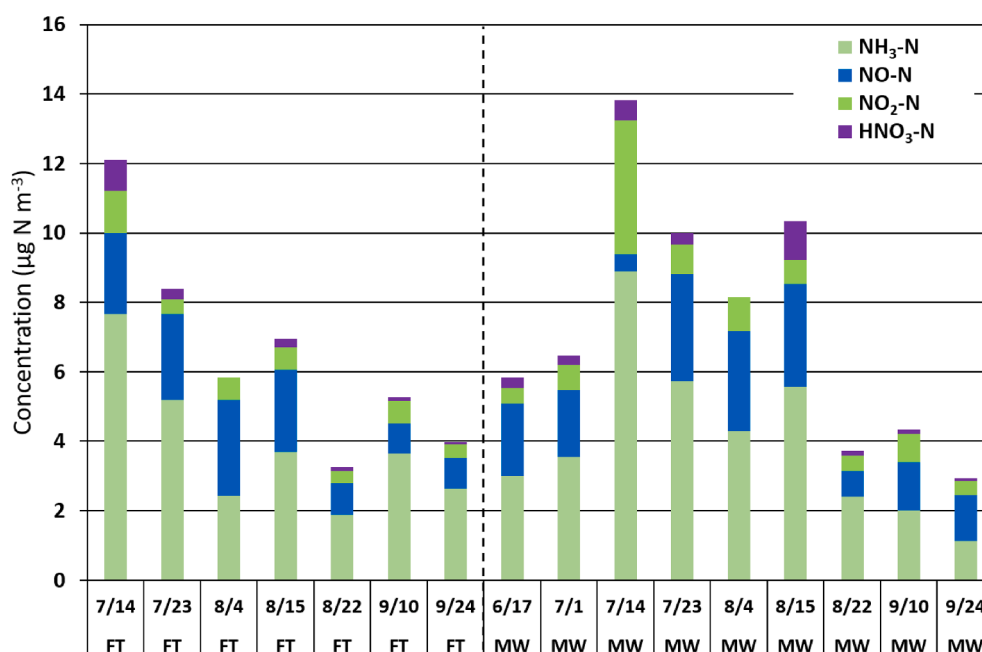


Fig. 3. Average concentrations of gaseous N pollutants at the Forest (FT) and Meadow (MW) sites in summer 2015 measured by passive monitors.

Table 2

Comparison of deposition fluxes at DEPO from modeled, measured, and lichen-based estimates. $\text{NH}_4\text{-N}:\text{NO}_3\text{-N}$ is the ratio of reduced to oxidized forms of nitrogen.

Deposition Method ¹	Total N	Reduced N	Oxidized N	$\text{NH}_4\text{-N}:\text{NO}_3\text{-N}$
TDEP-dry deposition	3.79	1.09	2.7	0.4
TDEP-wet deposition	2.21	1.6	0.61	2.62
TDEP-total deposition	6	2.69	3.3	0.82
Throughfall deposition	1.74	1.18	0.57	2.07
Bulk deposition	2.1	1.45	0.66	2.2
	3.66	2.62	1.04	2.52
Total deposition: Throughfall-adjusted ²	3.03			
Total deposition: Bulk-adjusted ³				
Throughfall deposition: <i>Letharia</i> -estimated	3.71	N/A	N/A	N/A
Dry deposition to meadow: Empirical Inferential Method, summer season ⁴	1.09	0.54	0.55	0.98
Dry deposition to forest: Empirical Inferential Method, summer season ⁴	0.82	0.45	0.37	1.22
$\text{NH}_3:\text{NO}_y$ ratio for gaseous pollutants in meadow: summer season ⁵				1.2
$\text{NH}_3:\text{NO}_y$ ratio for gaseous pollutants in forest: summer season ⁵				1.4

¹ Unless otherwise stated, deposition refers to annual deposition ($\text{kg N ha}^{-1} \text{yr}^{-1}$).

² Throughfall-adjusted deposition is based on 55% canopy retention of reduced N and 45% canopy retention of oxidized N based on previous work in California (Fenn and Bytnerowicz 1997) and Spain (Avila et al., 2017), and as constrained by the $\text{NH}_4\text{-N}:\text{NO}_3\text{-N}$ ratios in wet and bulk deposition in this study.

³ Estimated total N deposition is based on the assumption that 66% of total deposition was as wet deposition based on multiple years of wet and dry deposition data at Emerald Lake in Sequoia National Park, also a high elevation Sierra Nevada site with elevated snowfall (Fenn et al., 2009). Wet deposition was estimated as bulk deposition in the meadow $\times 0.85$ to account for the background dry deposition directly to the funnel collector; Using this estimate of wet deposition and the wet deposition value from the TDEP model, we estimated total N deposition as 2.71 and 3.35 $\text{kg N ha}^{-1} \text{yr}^{-1}$, respectively. Value shown is the mean of these two estimates.

⁴ Dry deposition fluxes for the 2015 summer season were determined for a 182 day time period (May - October).

⁵ NO_y is the sum of HNO_3 , NO and NO_2 . Units for all of these gaseous pollutants are expressed as unit of N.

TDEP estimate represents, still yields considerably lower dry deposition estimates. Estimated total N deposition calculated from inferential dry deposition (summer value $\times 2$) plus wet deposition, yields an estimated total annual N deposition value of 3.8 $\text{kg N ha}^{-1} \text{yr}^{-1}$, which is within the range of the other estimates for total N deposition.

3.2. Lichen data

As expected due to elevation, epiphytes were relatively rare at DEPO. In the park-wide lichen survey, only 7 of 39 macro-lichen species we encountered were epiphytes (Supplementary Tables 1 & 2). Among the 31 saxicolous species found, two common ones (*Rhizoplaca melanophthalma* and *Umbilicaria phaea*) have been used in California to a limited extent in pilot studies for %N assays (Table 1).

3.2.1. *Letharia* at DEPO

Because of the high snow line in much of the park, *Letharia* typically grew high on the trees or was found decomposing in the litter, which is avoided for %N analysis. Accessible *Letharia* only occurred on exposed *Juniper occidentalis* trees on cliffs overlooking the San Joaquin River or on granite buttresses over canyons (Fig. 2). Nitrogen measured in *L. vulpina* ($n = 4$) and *L. columbiana* ($n = 1$) samples ranged from 0.99 to

1.36 %N, corresponding with an estimated throughfall range of 2.39 to 4.44 $\text{kg N ha}^{-1} \text{yr}^{-1}$ (Table 3). Only the two northernmost throughfall values were below the CL threshold for epiphytic lichens. These included IER-measured throughfall from the Forest site and the northernmost *L. vulpina* site (1.7 and 2.39 $\text{kg N ha}^{-1} \text{yr}^{-1}$ respectively; Fig. 1).

3.2.2. Regional N gradient

Regional data gathered for *L. vulpina* ($n = 355$) spanned a wide range of %N values (0.29 – 2.66) corresponding with an estimated throughfall N range of 0.21 to 16.63 $\text{kg N ha}^{-1} \text{yr}^{-1}$ (Table 4, Fig. 4). The range of the Sierra Nevada Range itself was wide (0.63 – 2.23 %N), with adjacent plots to the north (Southern Cascades range: 0.51 – 0.94 %N) and south (L.A. Basin range: 1.8–2.66 %N) filling in the lowest and highest values, respectively. Using the 1.1% N threshold as a reference point, about 70%, 55%, and 7% of sites in the High Yosemite, Sierra region, and northern Wilderness Areas, respectively, were above the epiphytic lichen CL. Data from DEPO match the Yosemite average (1.2 %N), falling just below the Sierra Range average (1.27 %N). Oregon and Washington Wilderness Areas, which are much farther from large urban and industrial areas averaged, 0.75 %N. Lichen and TDEP-based deposition estimates were broadly similar, with lichens picking up considerable small-scale variability evidenced most clearly in the intensive High Yosemite sample (Fig. 5).

3.2.3. Saxicolous candidates

We recommended five saxicolous species for further study based on availability in the Sierra Region, widespread distribution across the Western U.S. (Table 5), ease of use, and extent of prior use by others. We found field replicate data for three candidates (*Rhizoplaca melanophthalma*, *Umbilicaria phaea*, *Xanthoparmelia cumberlandia*). All had lower average and max relative standard deviations (RSDs) compared to *L. vulpina* (Table 6), although this may be due to their small, geographically-limited datasets (Table 1). Lab replicates were too few to interpret except for *L. vulpina* where average lab RSD was considerably less than for field replicates (1.94% and 8.95%, respectively), as is typical for assays. Differences in tissue N concentrations among *L. vulpina* field replicates had a strongly, positively-skewed distribution averaging 0.1% N ($\text{SD} = 0.119\%$; Fig. 6). Over 80% of *L. vulpina* field replicates differed by less than 0.15 %N, and larger differences were not consistently associated with higher %N sites as might be expected.

4. Discussion

Our N assessment at DEPO touched on two fundamental aspects of N regime (N composition and amount), two major vegetation types (mixed conifer and wet meadow), two topographic positions (exposed canyon and cliff-side vs interior forested sites), and fall loosely on a north-to-south gradient along the San Joaquin River Canyon with increasing proximity to the Central Valley where most N emissions originate. We collected much more data than is typical for assessments in Class 1 areas, underscoring the need for more empirical, diverse, and finer-scaled information - even within areas as small as DEPO.

Table 3

Assay results and throughfall estimates ($\text{kg N ha}^{-1} \text{yr}^{-1}$) from *Letharia* collected at DEPO. See Fig. 1 for site locations. Due to low availability, only one composite sample was analyzed per site. For information about repeatability of %N measurements, please see Table 6.

Species	Site	%N	Estimated throughfall	Elevation (m)
<i>Letharia vulpina</i>	1	0.99	2.39	2316
<i>Letharia columbiana</i>	2	1.36*	4.44	2329
<i>Letharia vulpina</i>	3	1.21	3.53	2281
<i>Letharia vulpina</i>	4	1.33	4.24	2278
<i>Letharia vulpina</i>	5	1.28	3.95	2232

*converted to equivalent in *L. vulpina*

Table 4

Summary statistics for regional *L. vulpina* datasets. The intensive High Yosemite dataset is listed separately from the broader Sierra Region in which it occurs. Throughfall estimates are in kg N ha⁻¹ yr⁻¹.

Region (Subregion)	%N			Estimated throughfall		
	Min	Ave	Max	Min	Ave	Max
Sierra region	0.51	1.30	2.66	0.64	4.07	16.63
(Sierra Nevada Range)	0.63	1.27	2.23	0.98	3.88	11.76
(S. Cascades)	0.51	0.75	0.94	0.64	1.38	2.15
(L.A. Basin)	1.80	2.19	2.66	7.71	11.34	16.63
High Yosemite	0.88	1.21	1.80	1.89	3.53	7.71
OR & WA wilderness	0.29	0.75	1.94	0.21	1.36	8.94

4.1. Instruments vs TDEP

Air monitors provided a very different picture of N composition and total deposition than TDEP, showing the critical importance of ground-truthing modeled data. Almost all measurements show N at DEPO is richer in NH₄-N than NO₃-N, although NH₄-N dominance varied depending on what state the N was in (i.e. as wet deposition, dry deposition, or a gas) and whether N interacted with plant surfaces. The NH₄-N:NO₃-N ratios for throughfall, throughfall-adjusted total N deposition, bulk N deposition, and TDEP wet deposition (Table 3) were all within the expected range for sites in the Sierra Nevada Range, whereas ratios for TDEP dry and total deposition flux estimates were much lower (e.g. 5.5- and 2.7-fold lower than bulk deposition ratios; Fenn et al., 2003a, 2003b). The over-estimation of NO₃-N in dry deposition (e.g. 3.2-fold greater than adjusted throughfall deposition) explains the low ratios as well as why simulated N deposition nearly doubled empirical estimates, signaling significantly higher potential for ecological degradation to an area protected by a conservation mandate. Similar issues were documented for TDEP in other remote, semi-arid montane areas (McMurray et al., 2015; Pardo et al., 2011; Fenn, unpublished data). The issue probably originates from the documented two-fold over-estimation of NO_x emissions in the EPA National Emissions Inventory (Travis et al., 2016), which provides the foundation for TDEP modeling N deposition.

The seeming discrepancy between the much lower NH₄-N:NO₃-N ratios measured for branch rinses (0.63 and 0.73) and total summertime dry deposition fluxes (1.0 and 1.2) probably results from high stomatal uptake of NH₃ and low deposition to surfaces. A summertime study in southern California forests showed NH₃ uptake was an important component of the dry deposition flux, similar to NH₄⁺ deposition to foliar surfaces (Bytnerowicz et al., 2015). Empirical evidence suggests reduced forms of N deposited to plant surfaces are often preferentially retained at higher rates than oxidized forms of N, particularly in more arid climates.

While all empirical estimates of total N fell within a narrow range, the estimate based on bulk deposition (3.03 kg N ha⁻¹ yr⁻¹) is likely the most reliable flux estimate at the pixel-scale because it does not include the complex interactions of atmospheric N with the plant canopy, as does throughfall, branch rinsing, the TDEP simulation, and the inferential calculations. The limitations of bulk deposition measurements are that mainly only wet deposition is measured, and the challenge of efficiently capturing snowfall in winter, particularly in canopy-free locations during windy conditions (Fenn et al., 2015). Although not a flux measurement per se, presumably the single most reliable measurement overall is the NH₄:NO₃ ratio in the bulk deposition samples (2.2), which can be used as a constraint in calculating total N deposition, as we did to arrive at the number 3.03 kg N ha⁻¹ yr⁻¹.

4.2. Lichen data

4.2.1. *Letharia* at DEPO

While small, the *L. vulpina* dataset from DEPO expanded our understanding of N deposition in the Monument and hints that small-scale drivers tip the balance towards CL exceedance. The large contribution of

dry deposition to N regimes in the West makes this heterogeneity commonplace in areas receiving anthropogenic N (Ochoa-Hueso et al., 2011). The interplay of three possible drivers at DEPO may be worth further exploration: 1) proximity to river canyons, 2) vegetation-pollutant interactions, and 3) proximity to the Central Valley. Since deposition at DEPO spans the epiphytic lichen CL, arguably the smaller details of where and why higher deposition occurs take on greater importance.

1. Abundant *Letharia* was only found at exposed sites along canyons, which represent a more intense deposition environment than interior sites in the mixed conifer forest. The San Joaquin River canyons act as a conduit, allowing polluted air masses from the Central Valley to penetrate deep into the Range as (Bytnerowicz et al., 2013; Cisneros et al., 2010). This phenomenon was also clearly observed with intensively sampled *Letharia* spp in nearby Yosemite National Park (Hutten, 2015).
2. Vegetation-atmospheric pollutant interactions can also enhance or moderate N loads through accumulation of dry deposition on plant surfaces and canopy uptake of N. For example, throughfall N measured by IERs at the Forest site was about 50% lower than bulk deposition in the adjacent meadow. Uptake by the large, open-grown *J. occidentalis* where *L. vulpina* grew is possible but hasn't been studied. However, it's well-known that open-grown trees, or 'discontinuities' in general (e.g. forest edges) tend to be hotspots of N deposition (Perakis and Kellogg, 2007; Tulloss and Cadenasso, 2015; Weathers et al., 2001).
3. The two northernmost values for throughfall, one by *L. vulpina* and one by IER samplers, were the only ones falling beneath the epiphytic lichen CL. Cisneros et al. (2010) measured a similar, larger-scale gradient decreasing along an elevational transect from the Sierra foothills, through DEPO, up to the Sierra crest. Thus a smaller-scale south to north deposition gradient at DEPO is also possible. In future monitoring efforts we recommend prioritizing the southern edge of the monument for placing air samplers.

Hutten's (2015) work in the relatively epiphyte-rich mixed conifer stands of Yosemite is a more ideal demonstration of the benefits of finely-scaled datasets (n = 301). Abundant target species enabled modeling of major %N drivers, like elevation and topographic position, and production of an interpolated map describing deposition in unprecedented spatial detail (10 m²). As also posited for DEPO, smaller-scale drivers relating mostly to interactions with vegetation surfaces were also suspected to be influential, but occurred beneath the intended stand-level scale of the Yosemite study. The large sample size and ability to interpolate helped smooth out these sources of variability beneath the manager's level of concern. To further explore deposition patterns in DEPO and similar, patchily forested habitats, adding saxicolous target species may help capture a more representative picture of N effects. For higher elevation areas and others lacking trees and tall vegetation, a lower sampling intensity may be sufficient.

4.2.2. Regional N gradient

Major benefits of *L. vulpina* assays include a long tenure of use in N assessments and high robustness to climatic differences compared to community-based lichen metrics (Root et al., 2013). Thus, large regional datasets like those in this study are valuable resources for interpreting local N loads within a broader geographic context. Lichen and TDEP estimates of N tracked well at the large-scale (Fig. 5), both showing a prominent north to south N deposition gradient consistent with prior studies in the Sierra Nevada and inland S. California montane areas (Fenn et al., 2008; Jovan and McCune, 2006; Jovan et al., 2012). The *Letharia*-based map also reflects the substantial influence of microenvironments on local-scale deposition similar to that noted by Tulloss and Cadenasso (2015) for California's dry oak-savannah habitats.

While averages were the same, the small DEPO dataset spanned an

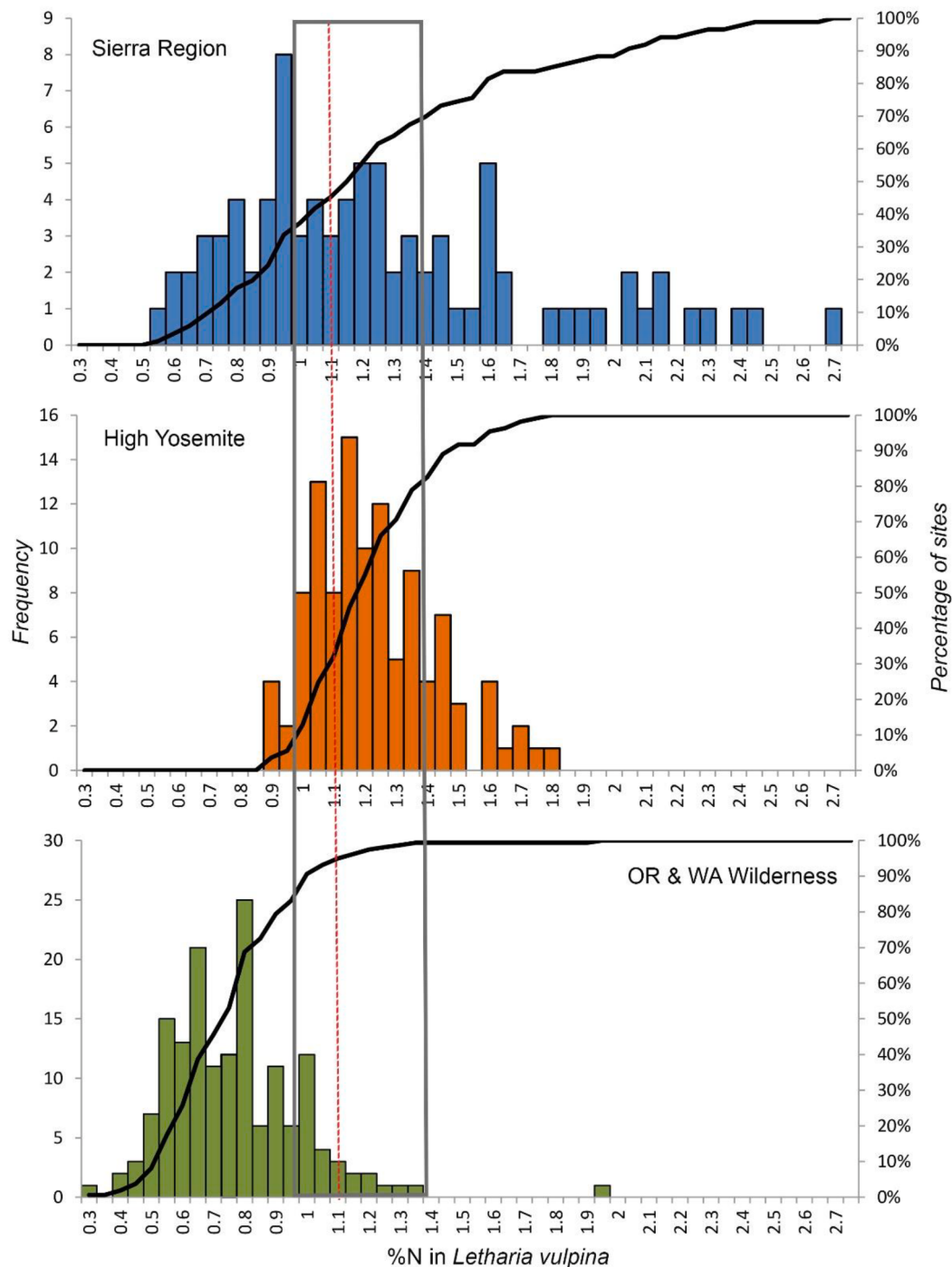


Fig. 4. Cumulative frequency graphs for %N in *Letharia vulpina* from the Sierra region, High Yosemite (pictured separately), and Wilderness Areas in OR and WA. The red dotted line is the %N associated with the CL for detrimental impacts to epiphytic lichen communities. The gray box indicates the range of %N values measured at DEPO. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

impressive 61% of the range from the much larger High Yosemite dataset, and was more than 3x greater than the overall standard deviation among regional field replicates (Fig. 6). Some heterogeneity is surely due to error although high assay repeatability suggests small differences in %N are potentially meaningful. Again, additional data-points would be needed to further interpret this apparent complexity.

4.2.3. Saxicolous candidates

More than 25 years of data collection and research under the USFS Lichen Inventories help FLMs use both assay and community-based lichen tools to meet air monitoring directives (Jovan et al., 2020).

Many studies document epiphyte relationships to N using dose–response curves, enabling managers to operationalize these N-sensitive organisms via CLs for tracking the status of protected lands. Much work is needed to develop similar tools using saxicolous communities. To our knowledge, no studies yet classify these species into N sensitivity groups or attempt to define relationships to deposition. We recommend focusing first on the simpler challenge of developing reliable, cost-effective %N assay protocols, and second on investigating CLs for saxicolous communities specific to upper montane and higher ecosystems.

As for the five assay candidates recommend for further study, overlapping distributions and varied preferences for moisture, exposure, and

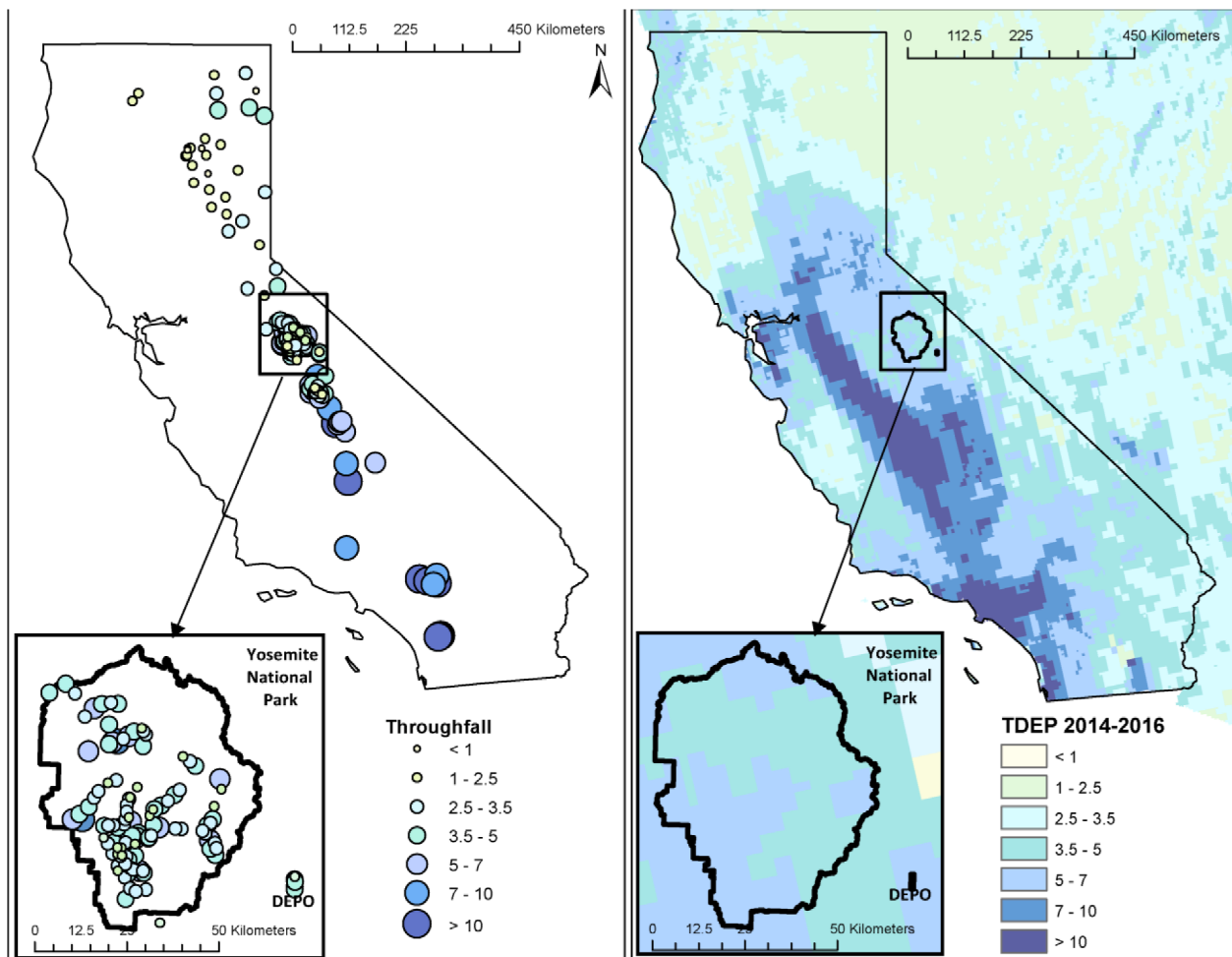


Fig. 5. Regional maps showing lichen-estimated N in throughfall (left) and total N predicted by TDEP averaged across 2014–2016 (right). Deposition above 2.9 kg N ha⁻¹ yr⁻¹ exceeds the epiphytic lichen CL.

Table 5
Summary of habitat and distributions for saxicolous candidates based on the Consortium of North American Lichen Herbaria website and field guides (Hale and Cole, 1988; McCune and Geiser, 2009; Sharnoff, 2014).

Species	Authority	Maximum Elevation	Habitat in CA and Sierra Nevada	Distribution
<i>Rhizoplaca melanophthalma</i>	(DC.) Leuckert	4206 m	On exposed to sheltered acidic rock at all elevations. Widespread across the state in montane and subalpine forests.	Widespread and common across the Western U.S.
<i>Umbilicaria phaea</i>	Tuck.	3170 m	On exposed to somewhat shaded non-calcareous rock outcrops and talus. Common at low to mid elevations, less frequent at high elevations.	The most common species of <i>Umbilicaria</i> in the state, widespread across Western North America. Most widespread of all target species.
<i>Umbilicaria polaris</i>	(Schol.) Zahlbr.	4400 m	On exposed to somewhat sheltered rock, common at subalpine to alpine elevations.	Widespread across the Western U.S. at high elevations.
<i>Xanthoparmelia coloradoensis</i>	(Gyeln.) Hale	3658 m	Widespread on rock, moss over rock, and soil. Fairly common at mid to high elevations, usually in exposed to somewhat sheltered sites.	Most common in central to southern California in drier habitats.
<i>Xanthoparmelia cumberlandia</i>	(Gyeln.) Hale	3170 m	On rock or sometimes overgrowing moss or litter over rock. Common mostly at low to mid elevations in forested and steppe regions.	Widespread across the Western U.S., probably the most common <i>Xanthoparmelia</i> species in California.

nutrient availability ensure geographic coverage in the Sierra Region and probably much of the high elevation West (Table 5). Field reconnaissance to high elevation Wilderness Areas in the Sierra Nevada in 2019 supported our recommendations and led to adding *Umbilicaria polaris* to better capture alpine sites. At the other extreme, the *Xanthoparmelia* species are common in lower elevation treeless areas, and so would help link saxicolous datasets across elevational zones. Our analysis of pre-existing pilot datasets for three of the candidate species

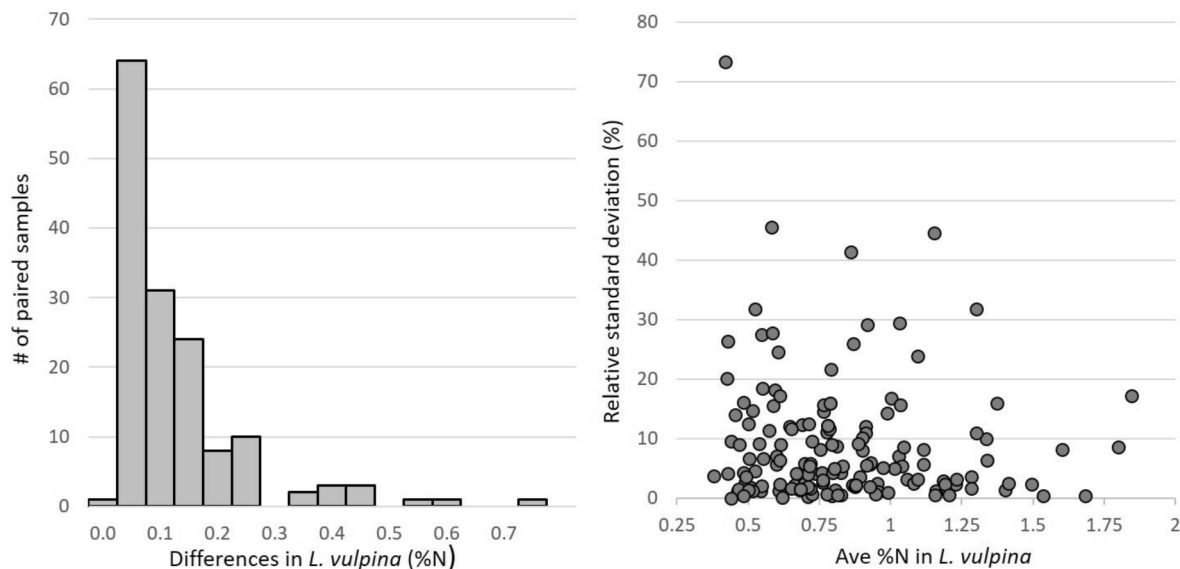
suggested assays were repeatable. However, due to the small size and narrow geographic range of datasets, we recommend including all five species in an expanded repeatability analysis and explore calibrating %N between target species, including *Letharia* spp.

4.3. Land management and policy implications

The large spatial variance shown in this and many other studies

Table 6Summary statistics for replicated %N datasets. RSD = $\pm$ relative standard deviation.

Species	n	%N			Field RSD			Lab RSD	
		Min	Ave	Max	Min	Ave	Max	n	Ave
<i>Letharia vulpina</i>	149	0.20	0.83	1.91	0.00	8.95	73.32	96	1.94
<i>Rhizoplaca melanophthalma</i>	7	1.11	1.48	1.97	1.78	7.70	14.14	1	0.02
<i>Umbilicaria phaea</i>	9	1.11	1.71	2.80	1.07	3.82	12.31	—	—
<i>Xanthoparmelia cumberlandia</i>	36	0.84	1.34	2.19	0.00	6.93	25.24	9	2.23

**Fig. 6.** Histogram (left) and relative standard deviations (right) of %N between paired *Letharia vulpina* field replicates ($n = 149$) from USFS land in Oregon, Washington, and California.

demonstrate the need to better capture N-deposition across the landscape of the Sierra Nevada. Deposition models could be improved with a more rigorous ground-truthing of current estimations, although where fine-scale deposition maps are needed for ecosystem protection in areas such as DEPO, simulation models are not expected to have this capability in the foreseeable future. Current widely-used simulation models provide deposition estimates at 12×12 to 50×50 km grid scales (Schwede and Lear, 2014; Simpson et al., 2012). The CMAQ model was parameterized at a $4 \text{ km} \times 4 \text{ km}$ grid scale for two-thirds of California (Tonnesen et al., 2007; Fenn et al., 2010), which improved capability to map areas in exceedance of CLs and other N response thresholds. But even such finer scale simulation modeling did not overcome the inherent limitations. For instance, CMAQ data for areas of the Sierra Nevada exposed to N deposition greater than $6 \text{ kg ha}^{-1} \text{ yr}^{-1}$ had to be adjusted upward based on empirical throughfall data from the region (Fenn et al., 2010) to better reflect actual values.

Thus, the importance of on-the-ground measurements for finer-scale risk management cannot be understated. In the Sierra Nevada, river canyons are likely transport corridors of anthropogenic emissions where increased monitoring of N deposition would be beneficial. Such topographic and other micro-site factors mentioned in this study cause the high fine-scale variability in N deposition observed at DEPO, and is expected wherever dry deposition or cloudwater deposition are important drivers of atmospheric deposition (Weathers et al., 2006). This is particularly relevant in arid and semiarid areas of Western North America, but even in mesic climates, dry deposition is an important atmospheric deposition input (Lindberg et al., 1986; Lovett and Lindberg, 1993). As demonstrated in this study, ambient air concentration measurements and deposition monitors (e.g. IER samplers, passive samplers) can be used in conjunction with low-cost lichen assays to enhance N assessments in areas of interest. Lichen assays calibrated to

monitoring data can then be used to greatly increase the capacity to estimate spatial distribution of N-deposition in Wilderness and other remote areas.

5. Conclusions

Monitoring assessments establish the need for management actions. Therefore, the availability of N data for landscape, stand-level, or smaller spatial scales is essential for protected areas where the goal is preserving the natural state of the land. Hundreds of studies document cascading effects from excess N deposition, making it a common stressor of ecosystems affected by the airsheds of developed areas. Using lichens as an inexpensive screening tool helps capture finer-scaled patterns and optimize placement of instruments or other monitoring resources. Many of the most pristine protected areas are remote, at high elevations, and above tree line, where very little is known about deposition. These systems are also the least buffered against the effects of chronic atmospheric inputs of acidifying and eutrophying atmospheric deposition. If saxicolous lichens can be used for reliable assays, and perhaps also for defining CLs, bio-monitoring in these underserved areas would greatly improve the ability of managers to assess potential ecological risks.

CRedit authorship contribution statement

Sarah Jovan: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization. **Mark E. Fenn:** Conceptualization, Methodology, Investigation, Writing - original draft. **Monica Buhler:** Investigation, Visualization. **Andrzej Bytnerowicz:** Conceptualization, Methodology, Investigation, Writing - original draft. **Adrienne Kovasi:** Formal analysis. **Martin Hutten:** Resources. **Elisa DiMeglio:** Investigation. **Donald Schweizer:** .

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

- Avila, A., Aguilera, L., Izquieta-Rojano, S., García-Gómez, H., Elustondo, D., Santamaría, J.M., Alonso, R., 2017. Quantitative study on nitrogen deposition and canopy retention in Mediterranean evergreen forests. *Environ. Sci. Pollut. Res.* 24, 26213–26226.
- Blett, T., Geiser, L., Porter, E., 2003. Air Pollution-Related Lichen Monitoring in National Parks, Forests, and Refuges: Guidelines for Studies Intended for Regulatory and management purposes. U.S. Dept. of the Interior Technical Report NPSD 2292. 25 pp.
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinnerby, S., Davidson, E., Dentener, F., Emmett, B., Erismann, J.-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., De Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.* 20, 30–59.
- Burns, D.A., Blett, T., Haeuber, R., Pardo, L.H., 2008. Critical loads as a policy tool for protecting ecosystems from the effects of air pollutants. *Front. Ecol. Environ.* 6, 156–159.
- Bytnerowicz, A., Burley, J.D., Cisneros, R., Preisler, H.K., Schilling, S., Schweizer, D., Ray, J., Dulen, D., Beck, C., Auble, B., 2013. Surface ozone at the Devils Postpile National Monument receptor site during low and high wildland fire years. *Atmos. Environ.* 65, 129–141.
- Bytnerowicz, A., Johnson, R.F., Zhang, L., Jenerette, G.D., Fenn, M.E., Schilling, S.L., Gonzalez-Fernandez, I., 2015. An empirical inferential method of estimating nitrogen deposition to Mediterranean-type ecosystems: the San Bernardino Mountains case study. *Environ. Pollut.* 203, 69–88.
- Cisneros, R., Bytnerowicz, A., Schweizer, D., Zhong, S., Traina, S., Bennett, D.H., 2010. Ozone, nitric acid, and ammonia air pollution is unhealthy for people and ecosystems in southern Sierra Nevada, California. *Environ. Pollut.* 158, 3261–3271.
- Clark, C.M., Bell, M.D., Boyd, J.W., Compton, J.E., Davidson, E.A., Davis, C., Fenn, M.E., Geiser, L., Jones, L., Blett, T.F., 2017. Nitrogen-induced terrestrial eutrophication: cascading effects and impacts on ecosystem services. *Ecosphere* 8, e01877.
- Dibble, A.C., Hinds, J.W., Perron, R., Cleavitt, N., Poirot, R.L., Pardo, L.H., 2016. Monitoring air quality in Class I wilderness areas of the Northeastern United States using lichens and bryophytes. *Gen. Tech. Rep. GTR-NRS-165*. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 44 p.
- Ellis, R. A., Jacob, D. J., Sulprizio, M. P., Zhang, L., Holmes, C. D., Schichtel, B. A., Blett, T., Porter, E., Pardo, L. H., Lynch, J. A., 2013. Present and future nitrogen deposition to national parks in the United States: critical load exceedances. *Atmos. Chem. Phys.* 13, 9083–9095.
- Fenn, M.E., Bytnerowicz, A., 1997. Summer throughfall and winter deposition in the San Bernardino Mountains in Southern California. *Atmos. Environ.* 31, 673–683.
- Fenn, M.E., Allen, E.B., Weiss, S.B., Jovan, S., Geiser, L.H., Tonnesen, G.S., Johnson, R.F., Rao, L.E., Gimeno, B.S., Yuan, F., Meixner, T., Bytnerowicz, A., 2010. Nitrogen critical loads and management alternatives for N-impacted ecosystems in California. *J. Environ. Manage.* 91, 2404–2423.
- Fenn, M.E., Bytnerowicz, A., Schilling, S.L., Ross, C.S., 2015. Atmospheric deposition of nitrogen, sulfur and base cations in jack pine stands in the Athabasca Oil Sands Region, Alberta, Canada. *Environ. Pollut.* 196, 497–510.
- Fenn, Mark E., Bytnerowicz, Andrzej, Schilling, Susan L., Vallano, Dena M., Zavaleta, Erika S., Weiss, Stuart B., Morozumi, Connor, Geiser, Linda H., Hanks, Kenneth, 2018. On-road emissions of ammonia: an underappreciated source of atmospheric nitrogen deposition. *Sci. Total Environ.* 625, 909–919.
- Fenn, M. E., Poth, M. A., Aber, J. D., Baron, J. S., Bormann, B. T., Johnson, D. W., Lemly, A. D., McNulty, S. G., Ryan, D. E., Stottlemeyer, R., 1998. Nitrogen excess in North American ecosystems: Predisposing factors, ecosystem responses, and management strategies. *Ecological Applications* 8:706–733.
- Fenn, M.E., Poth, M.A., Bytnerowicz, A., Sickman, J.O., and Takemoto, B.K. 2003b. Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra Nevada. pp. 111–155 In: Bytnerowicz, A., Arbaugh, M.J., Alonso, R. (eds.), *Developments in Environmental Science, Volume 2: Ozone Air Pollution in the Sierra Nevada: Distribution and Effects on Forests*. Elsevier, Amsterdam.
- Fenn, M.E., Jovan, S., Dr., Yuan, F., Geiser, L., Meixner, T., Gimeno, B.S., 2008. *Environ. Pollut.* 155: 492–511.
- Fenn, M.E., Sickman, J.O., Bytnerowicz, A., Clow, D.W., Molotch, N.P., Pleim, J.E., Tonnesen, G.S., Weathers, K.C., Padgett, P.E., and Campbell, D.H., 2009. Methods for measuring atmospheric nitrogen deposition inputs in arid and montane ecosystems of western North America. In: Legge, A.H. (ed.), *Developments in Environmental Science, Vol. 9: Air Quality and Ecological Impacts: Relating Sources to Effects*. Elsevier, Amsterdam pp. 179–228.
- Fenn, M.E., Bytnerowicz, A. and Schilling, S.L. 2018a. Passive monitoring techniques for evaluating atmospheric ozone and nitrogen exposure and deposition to California ecosystems. *Gen. Tech. Rep. PSW-GTR-257*. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 129 p.
- Fenn, M.E., Poth, M.A., 2004. Monitoring nitrogen deposition in throughfall using ion exchange resin columns: A field test in the San Bernardino Mountains. *J. Environ. Qual.* 33, 2007–2014.
- Fenn, M.E., Haeuber, R., Tonnesen, G.S., Baron, J.S., Grossman-Clarke, S., Hope, D., Jaffe, D.A., Copeland, S., Geiser, L., Rueth, H.M., Sickman, J.O., 2003. Nitrogen emissions, deposition, and monitoring in the western United States. *Bioscience* 53, 391–403.
- Fenn, M.E., Geiser, L., Bachman, R., Blubaugh, T.J., Bytnerowicz, A., 2007. Atmospheric deposition inputs and effects on lichen chemistry and indicator species in the Columbia River Gorge, USA. *Environ. Pollut.* 146, 77–91.
- Fenn, Mark E., Ross, Christopher S., Schilling, Susan L., Baccus, William D., Larrabee, Michael A., Lofgren, Rebecca A., 2013. Atmospheric deposition of nitrogen and sulfur and preferential canopy consumption of nitrate in forests of the Pacific Northwest, USA. *For. Ecol. Manage.* 302, 240–253.
- Gaige, E., Dail, D.B., Hollinger, D.Y., Davidson, E.A., Fernandez, L.J., Sievering, H., White, A., Halteman, W., 2007. Changes in canopy processes following whole-forest canopy nitrogen fertilization of a mature spruce-hemlock forest. *Ecosystems* 10, 1133–1147.
- Geiser, L. H., Nelson, P. R., Jovan, S. E., Root, H. T., Clark, C. M., 2019. Assessing Ecological Risks from Atmospheric Deposition of Nitrogen and Sulfur to US Forests Using Epiphytic Macrolichens. *Diversity* 11:87.
- Geiser, L.H., 2004. Manual for monitoring air quality using lichens on national forests of the Pacific Northwest. USDA-Forest Service Pacific Northwest Region, Portland, OR. R6-NR-AQ-TP-1-04.
- Greaver, Tara L., Sullivan, Timothy J., Herrick, Jeffrey D., Barber, Mary C., Baron, Jill S., Cosby, Bernard J., Deerhake, Marion E., Dennis, Robin L., Dubois, Jean-Jacques B., Goodale, Christine L., Herlihy, Alan T., Lawrence, Gregory B., Liu, Lingli, Lynch, Jason A., Novak, Kristopher J., 2012. Ecological effects of nitrogen and sulfur air pollution in the US: what do we know? *Front. Ecol. Environ.* 10, 365–372.
- Hale, M. E., and Cole, M., 1988. *Lichens of California*. Berkeley: U of California. Print. California Natural History Guides; 254 pages.
- Hoffman, Abigail S., Albeke, Shannon E., McMurray, Jill A., Evans, R. David, Williams, David G., 2019. Nitrogen deposition sources and patterns in the Greater Yellowstone Ecosystem determined from ion exchange resin collectors, lichens, and isotopes. *Sci. Total Environ.* 683, 709–718.
- Hutten, M.A., 2015. Yosemite Region nitrogen Deposition Patterns in the Composition of Lichen Communities. Ph.D. Dissertation. Oregon State University, Department of Botany and Plant Pathology.
- Jovan, S., Carlberg, T., 2007. Nitrogen content of *Letharia vulpina* tissue from forests of the Sierra Nevada, California: geographic patterns and relationships to ammonia estimates and climate. *Environ. Monit. Assess.* 129, 243–251.
- Jovan, S., Will-Wolf, S., Geiser, L.H., Dillman, K., Haldeman, M., Shory, R., 2020. User guide for the National Forest Inventory and Analysis lichen database (ver1.0). *Gen. Tech. Rep. PNW-GTR-988*. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 82p.
- Jovan, S., McCune, B., 2006. Using epiphytic macrolichen communities for biomonitoring ammonia in forests of the greater Sierra Nevada, California. *Water Air Soil Pollut.* 170, 69–93.
- Jovan, Sarah, Riddell, Jennifer, Padgett, Pamela E., Nash III, Thomas H., 2012. Eutrophic lichens respond to multiple forms of N: implications for critical levels and critical loads research. *Ecol. Appl.* 22, 1910–1922.
- Landers, D.H., Simonich, S.L., Jaffe, D.A., Geiser, L.H., Campbell, D.H., Schwindt, A.R., Schreck, C.B., Kent, M.L., Hafner, W.D., Taylor, H.E., Hageman, K.J., Usenko, S., Ackerman, L.K., Schrlau, J.E., Rose, N.L., Blett, T.F., Erway, M.M., 2008. The Fate, Transport, and Ecological Impacts of Airborne Contaminants in Western National Parks (USA). EPA/600/R-07/138. U.S. Environmental Protection Agency, Office of Research and Development, NHEERL, Western Ecology Division, Corvallis, Oregon.
- Lindberg, S.E., Lovett, G.M., Richter, D.D., Johnson, D.W., 1986. Atmospheric deposition and canopy interactions of major ions in a forest. *Science* 231.
- Lovett, Gary M., Lindberg, Steven E., 1993. Atmospheric deposition and canopy interactions of nitrogen in forests. *Can. J. For. Res.* 23, 1603–1616.
- McCune, B. and Geiser, L., 2009. *Macrolichens of the Pacific Northwest*, 2nd Edition. Oregon State University Press. 504 pages.
- McMurray, Jill A., Roberts, David W., Geiser, Linda H., 2015. Epiphytic lichen indication of nitrogen deposition and climate in the northern rocky mountains, USA. *Ecol. Ind.* 49, 154–161.
- Ochoa-Hueso, Raúl, Allen, Edith B., Branquinho, Cristina, Cruz, Cristina, Dias, Teresa, Fenn, Mark E., Manrique, Esteban, Pérez-Corona, M. Esther, Sheppard, Lucy J., Stock, William D., 2011. Nitrogen deposition effects on Mediterranean-type ecosystems: an ecological assessment. *Environ. Pollut.* 159, 2265–2279.

- Pardo, Linda H., Fenn, Mark E., Goodale, Christine L., Geiser, Linda H., Driscoll, Charles T., Allen, Edith B., Baron, Jill S., Bobbink, Roland, Bowman, William D., Clark, Christopher M., Emmett, Bridget, Gilliam, Frank S., Greaver, Tara L., Hall, Sharon J., Lilleskov, Erik A., Liu, Lingli, Lynch, Jason A., Nadelhoffer, Knute J., Perakis, Steven S., Robin-Abbott, Molly J., Stoddard, John L., Weathers, Kathleen C., Dennis, Robin L., 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. *Ecol. Appl.* 21, 3049–3082.
- Perakis, Steven S., Kellogg, Chev H., 2007. Imprint of oaks on nitrogen availability and $\delta^{15}\text{N}$ in California grassland-savanna: a case of enhanced N inputs? *Plant Ecol.* 191, 209–220.
- Perkins, D.F., Millar, R.O., Neep, P.E., 1980. Accumulation of airborne fluoride by lichens in the vicinity of an aluminium reduction plant. *Environ. Pollut. Series A, Ecol. Biol.* 21, 155–168.
- Porter, E., Blett, T., Potter, D. U., Huber, C., 2005. Protecting Resources on Federal Lands: Implications of Critical Loads for Atmospheric Deposition of Nitrogen and Sulfur. *Bioscience* 55:603–612.
- Potter, D.A., 1998. Forested communities of the upper montane in the central and southern Sierra Nevada. USDA Forest Service General Technical Report PSW-GTR-169, Pacific Southwest Research Station, Albany, California, USA.
- Root, Heather T., Geiser, Linda H., Fenn, Mark E., Jovan, Sarah, Hutten, Martin A., Ahuja, Suraj, Dillman, Karen, Schirokauer, David, Berryman, Shanti, McMurray, Jill A., 2013. A simple tool for estimating throughfall nitrogen deposition in forests of western North America using lichens. *For. Ecol. Manage.* 306, 1–8.
- Schwede, Donna B., Lear, Gary G., 2014. A novel hybrid approach for estimating total deposition in the United States. *Atmos. Environ.* 92, 207–220.
- Sharnoff, S., 2014. *A Field Guide to California Lichens*. New Haven: Yale UP. Print. 405 pages.
- Simpson, D., Benedictow, A., Berge, H., Bergstrom, R., Emberson, L.D., Fagerli, H., Flechard, C.R., et al., 2012. The EMEP MSC-W chemical transport model - technical description. *Atmos. Chem. Phys.* 12, 7825–7865.
- Tonnesen, G., Wang, Z., Omary, M., and Chien, C.-J., 2007. Assessment of nitrogen deposition: Modeling and habitat assessment. California Energy Commission, PIER Energy-Related Environmental Research. CEC-500-2006-032. <http://www.energy.ca.gov/2006publications/CEC-500-2006-032/CEC-500-2006-032.PDF>.
- Travis, K.R., Jacob, D.J., Fisher, J.A., Kim, P.S., Marais, E.A., et al., 2016. Why do models overestimate surface ozone in the Southeast United States? *Atmos. Chem. Phys.* 16, 13561–13577.
- Tulloss, Elise M., Cadenasso, Mary L., 2015. Nitrogen deposition across scales: hotspots and gradients in a California savanna landscape. *Ecosphere* 6, 1–12.
- Weathers, Kathleen C., Cadenasso, Mary L., Pickett, Steward T.A., 2001. Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conserv. Biol.* 15, 1506–1514.
- Weathers, Kathleen C., Simkin, Samuel M., Lovett, Gary M., Lindberg, Steven E., 2006. Empirical modeling of atmospheric deposition in mountainous landscapes. *Ecol. Appl.* 16, 1590–1607.
- Zhang, L., Brook, J.R., Vet, R., 2003. A revised parameterization for gaseous dry deposition in air-quality models. *Atmos. Chem. Phys.* 3, 2067–2082.
- Zschau, T., Getty, S., Gries, C., Ameron, Y., Zambrano, A., Nash III, T.H., 2003. Historical and current atmospheric deposition to the epilithic lichen *Xanthoparmelia* in Maricopa County, Arizona. *Environ. Pollut.* 125, 21–30.