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Epiphytic macrolichen indication of air quality and climate in interior forested mountains of the Pacific Northwest, USA

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ABSTRACT

Biomonitoring can provide cost-effective and practical information about the distribution of nitrogen (N) deposition, particularly in regions with complex topography and sparse instrumented monitoring sites. Because of their unique biology, lichens are very sensitive bioindicators of air quality. Lichens lack a cuticle to control absorption or leaching of nutrients and they dynamically concentrate nutrients roughly in proportion to the abundance in the atmosphere. As N deposition increases, nitrogen-loving eutrophic lichens become dominant over oligotrophic lichens that thrive in nutrient-poor habitats. We capitalize on these characteristics to develop two lichen-based indicators of air-borne and depositional N for interior forested mountain ecosystems of the Pacific Northwest and calibrate them with N concentration measured in $PM_{2.5}$ at 12 IMPROVE air quality monitoring sites in the study area. The two lichen indices and peak frequencies of individual species exhibited continuous relationships with inorganic N pollution throughout the range of N in ambient $PM_{2.5}$, suggesting that the designation of a critical level or critical load is somewhat arbitrary because at any level above background, some species are likely to experience adverse impacts. The concentration of N in $PM_{2.5}$ near the city of Spokane, Washington was the lowest measured at an instrumented monitoring site near known N pollution sources. This level, 0.37 $\mu g/m^3$/year, served as a critical level, corresponding to a concentration of 1.02% N in the lichen *Letharia vulpina*, which is similar to the upper end of background lichen N concentrations measured elsewhere in the western United States. Based on this level, we estimate critical loads to be 1.54 and 2.51 kg/ha/year of through-fall dissolved inorganic N deposition for lichen communities and lichen N concentration, respectively. We map estimated fine-particulate ($PM_{2.5}$) N in ambient air based on lichen community and lichen N concentration indices to identify hotspots in the region. We also develop and map an independent lichen community-based bioclimatic index, which is strongly related to gradients in moisture availability and temperature variability. Lichen communities in the driest climates were more eutrophic than those in wetter climates at the same levels of N air pollution.

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1. Introduction

Anthropogenic biologically active nitrogen (N) emissions have increased 10-fold since 1860 and represent a major disruption to the global N cycle (Galloway et al., 2004). This excess N is concentrated in Europe, Asia, and North America where food production and combustion of coal and fossil fuels contribute ammonia (NH_3) and nitric oxide emissions (NO, NO_2; Galloway et al., 2004). N deposition has profound effects on human and ecosystem health including decreased water and air quality, eutrophication of freshwater ecosystems, changes in plant community composition, increased soil emissions of nitrogenous greenhouse gases (Fenn et al., 1998), and complex interactions with fire regimes (Fenn et al., 2003a).

N emissions grew with population in the western United States during the past century (Fenn et al., 2003b) and population is projected to continue growing faster in the west than in the rest of the United States (USCB, 2005). However, enforcement of the Clean Air Act has resulted in reductions in nitrate and ammonia deposition in the western United States since the 1990s (CASTNET, 2012). Currently, the forested western mountains remain less impacted by N

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deposition than much of the rest of the country and sources of N emissions in the region are localized around urban, agricultural and industrial areas (Fenn et al., 2003a; Pardo et al., 2011). The effects of localized sources can be difficult to detect at the coarse spatial scale of deposition monitors in the region, especially because many instrumented sites are established at baseline sites far from known pollution sources.

Recent efforts have aimed to increase N deposition monitoring in western states; however, instrumented sites are expensive and their number is limited (Greaver et al., 2012). For example, our study area (Fig. 1) represents 57 million acres, 3% of the total acreage of the contiguous United States, and is served by only 12 active interagency monitoring of protected visual environments (IMPROVE) sites that monitor N in $PM_{2.5}$ near wilderness areas and three National Atmospheric Deposition Program (NADP) sites that monitor precipitation chemistry. Pre-industrial deposition of total N deposition in coniferous forests of the temperate northern hemisphere are estimated to be 0.16–2.13 kg N/ha/year (Holland et al., 1999) and estimates in our study area for 2012 were 1 to 7.2 kg N/ha/year (Schwede and Lear, 2014). To identify changes in N deposition and emerging hotspots in a region with complex topography, a biomonitoring approach has the potential to provide cost-effective and practical information about the distribution of N deposition. Furthermore, biomonitoring provides direct evidence of air pollution effects on sensitive biota and, to the extent that ecological roles of sensitive biota are understood, biomonitoring can help identify broader ecological ramifications of changing air quality.

Lichen community composition and concentration of elemental N in lichen thalli are proven approaches to biomonitoring N deposition patterns in many regions (van Herk et al., 2003; Geiser and Neitlich, 2007; Geiser et al., 2010; Johansson et al., 2012; Jovan et al., 2012; Root et al., 2013). Lichens have a unique biology formed through a symbiosis between a fungus and algae or cyanobacteria. Biomonitoring with lichens is effective because as N deposition increases, nitrogen-loving eutrophic lichens become dominant over oligotrophic lichens that thrive in nutrient-poor habitats. Furthermore, because lichens lack a cuticle to control absorption or leaching of nutrients, they dynamically concentrate nutrients roughly in proportion to the abundance in the atmosphere (Herzig et al., 1989); recent work suggests that lichen N concentration is highly correlated with throughfall dissolved inorganic N deposition (Root et al., 2013).

Lichen communities are also valuable bioclimatic indicators (van Herk et al., 2002; Ellis et al., 2007; Geiser and Neitlich, 2007; Giordani and Incerti, 2008). Because tree-dwelling lichens lack roots to access stored water, their physiology is dependent on humidity and rainfall events occurring at times when temperatures favor photosynthesis (Palmqvist et al., 2008). We expect these organisms to respond more quickly to climate changes than organisms that have structures buffering climatic impacts on their physiology (*e.g.*, roots or cuticles). Some lichens have the potential to become established on newly available substrates within a single year whereas others are more dispersal limited (Sillett et al., 2000). New lichen species can join a community on the time-scale of a decade following forest manipulations that affect micro-climate (Root et al., 2010). Because individual lichen species have different climatic optima, lichen community composition could be used to detect changing climate regimes.

Ecosystems in our region are subject to the one of the steepest precipitation gradients in the contiguous United States. The crest of the Cascades receives greater than 330 cm of precipitation per year while the woodlands 70 km to the east receive only 24 cm per year (PRISM; June 2012; http://www.prismclimate.org). This gradient in moisture availability is coupled with a change in temperature variability; wetter sites have more uniform temperatures throughout days and months whereas drier sites have hot summers and cold winters as well as hot days and cold nights (PRISM). These strong climatic gradients across a relatively contiguous forested ecosystem make the forested western mountains an ideal study area in which to examine climate effects on lichen communities.

We use lichen indicators to address four objectives: (1) develop indices for deposition and ambient air concentrations of N-containing air pollutants based on lichen community composition and lichen N concentration; (2) calibrate lichen N pollution indices with instrumented air quality monitoring sites in the region; (3) develop a bioclimatic indicator based on lichen communities that is independent of air pollution impacts; (4) map N pollution and climate bioindicators to allow us to interpret patterns in the region. These indices are developed with a long-term goal of using lichen bioindication to monitor status and trends of air quality and climate in the interior forested mountains of the Pacific Northwest, USA as well as contribute to a broader understanding of the utility of lichens as bioindicators.

2. Methods

2.1. Study area

The study area was in the northwestern United States, in the rain shadow of the Cascade Mountains. We defined the boundaries using the Northwest Forested Mountain Level III ecoregion (EPA, 2012) and county boundaries along the crest of the Cascade Mountains (Fig. 1). Forest composition ranged from montane *Tsuga mertensiana* and *Abies lasiocarpa* forests to mixed conifers including *Pinus ponderosa* and *Pseudotsuga menziesii* at mid-elevations to sparse semi-arid *Juniperus occidentalis* or *Celtis reticulata* woodlands in the driest sites.

2.2. Lichen data

Lichen communities were sampled during 1437 visits to 1006 unique locations (Table A.1). Most plots ($n = 628$) were sampled on a 5.4 km systematic grid by the USDA Forest Service Air Program (Geiser, 2004). We also included 406 plots on a 23 km grid by Forest Inventory and Analysis (Will-Wolf, 2010). Both programs included re-visits for quality control ($n = 139$). Off-frame plots ($n = 264$) established by the USDA Forest Service Air Program targeted polluted areas or atmospheric sampling sites to contribute to model-building.

Lichen abundances were recorded and vouchers were collected on 0.38-ha plots following the Forest Inventory and Analysis (FIA) lichen protocol (Will-Wolf, 2010). Lichen taxonomy was consistent with Esslinger (2011) with a few exceptions. We distinguish the yellow form of *Bryoria fremontii* (historically referred to as *Bryoria tortuosa*, Velmala et al., 2009), because the characteristics distinguishing this growth form may be linked to climatic variables of interest. We followed Miadlikowska et al.'s (2011) designation of *Hypogymnia lophyrea* and *Hypogymnia hultenii.*

At 879 visits, lichen thalli were collected for elemental N measurements. Technicians collected 20 g of one or more species of lichen for total N analysis (Geiser, 2004); typically these data were not available for FIA plots. Because no single lichen species could be found at all plots, a suite of target species included: *Alectoria sarmentosa*, *B. fremontii*, *Bryoria* spp., *Evernia prunastri*, *Hypogymnia imshaugii*, *Hypogymnia inactiva*, *Letharia columbiana*, *Letharia vulpina*, and *Platismatia glauca*. The most frequently-available species was *L. vulpina* (532 visits).

Lichen samples were analyzed with several standard reference materials including digestates of one of two in-house lichen standards of *A. sarmentosa* analyzed every 10th sample. We corrected

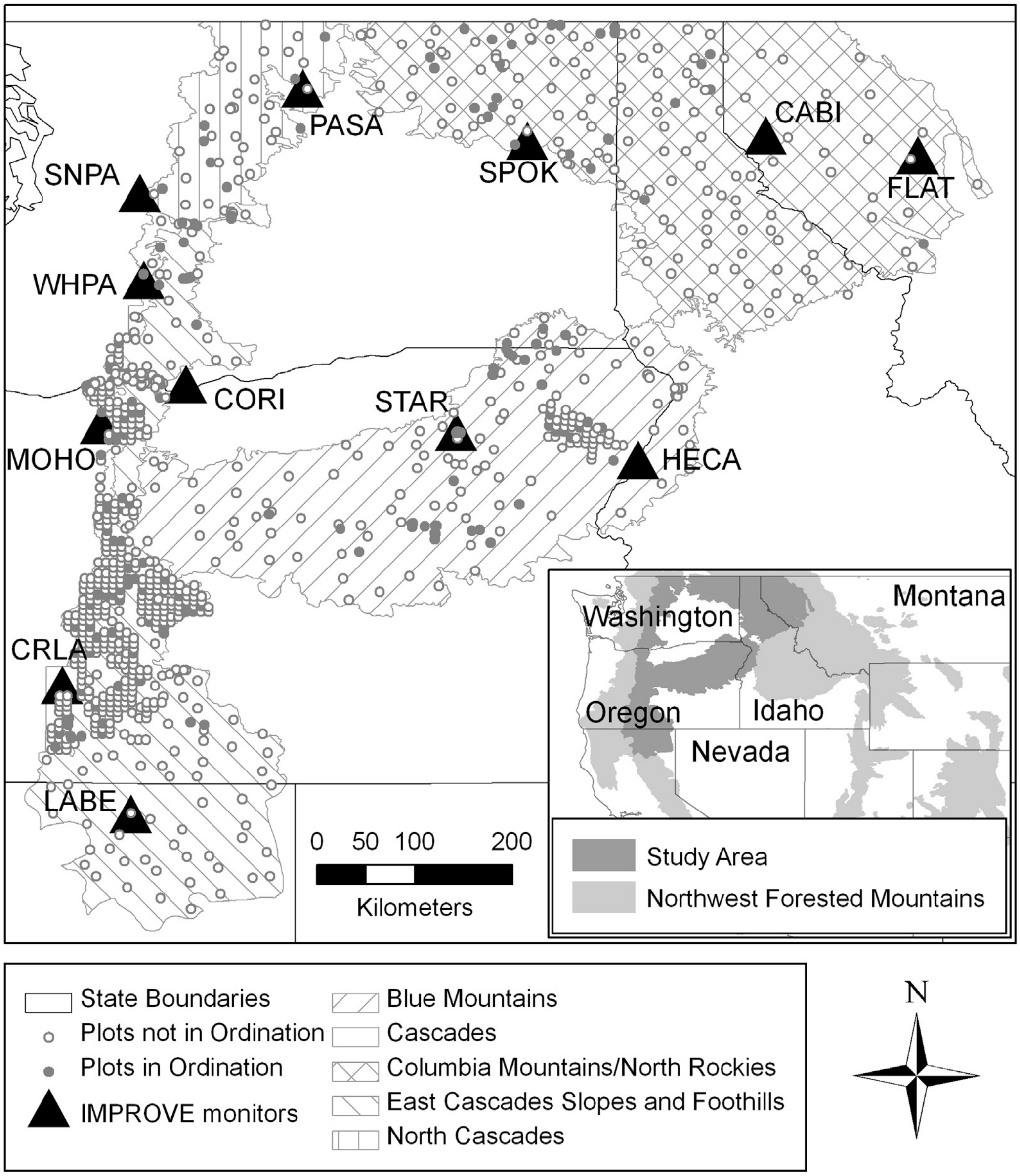

Fig. 1. Inset: Study area in relation to the Northwest Forested Mountains ecoregion of North America. Lichen community composition monitoring plots at 1006 locations sampled between 1993 and 2011. Plots used in ordination are a subset of those measured between 2003 and 2011. IMPROVE air quality monitoring sites are labeled by their acronyms designated by that program.

for differences among lab batches by multiplying all lichen tissue measurements by the factor by which the *A. sarmentosa* standard differed from its grand mean. For example, if the *A. sarmentosa* standard was measured at 90% of its overall average N concentration, we divided all elemental data from that lab batch by 0.9. To estimate lichen N concentration in plots where *L. vulpina* was not available, we used species-specific regressions to predict N concentrations in *L. vulpina* based co-occurrences with other species (Geiser and Neitlich, 2007).

Preliminary analyses gave us confidence that lichen N concentrations were informative of spatial variability and were consistent even when different target species were measured. For *L. vulpina*, differences among plots accounted for 87% of the variance in elemental N, within-plot variability accounted for 12% and variability in lab replicates accounted for 2%. The average difference between measured and predicted N in *L. vulpina* based on other target species was −0.009% N (SD = 0.226% N, n = 358). The correlation between measured N in *L. vulpina* and predicted by other lichens in plots with co-occurrence was 0.73.

2.3. Air pollution, climate and forest data

Ambient-air nitrate and sulfate concentrations in fine particulates less than 2.5 μm in diameter ($PM_{2.5}$) were measured at 12 atmospheric sampling sites (Fig. 1) every third day for 24 h (IMPROVE; June 2012; http://vista.cira.colostate.edu/improve). We calculated N concentrations assuming that nitrates and sulfates were balanced by ammonia as NH_4NO_3 and $(NH_4)_2SO_4$. We include data for three years preceding lichen sampling. We linked these sites to lichen plots by selecting the three closest plots within 20 km; in some cases fewer than three plots fell within the desired radius.

Climate variables included climatic moisture deficit (CMD), continentality, December minimum temperature, August maximum temperature, annual relative humidity, and annual precipitation (Table 1). CMD was downloaded for 1981–2010 from climateWNA (July 2014; http://www.climatewna.com) and is a synthetic climate variable intended to quantify drought stress associated with climatic conditions. CMD is calculated as the sum of the

Table 1
Variables included in models and their relationship with the ordination axes (when $R^2 \geq 0.12$). For most variables, R^2 is listed for 171 plots included in the ordination subset of the dataset; community compositions are fitted into the calibration ordination for 24 plots near IMPROVE air quality monitoring sites to evaluate those variables.

Acronym	Full name	Units	R^2 NMS1	R^2 NMS2
Lichen elemental				
Nlevu	N in *Letharia vulpina*	%	0.12	
Plot				
Lat	Latitude	dd		0.25
Long	Longitude	dd		
Lichen community				
SpRich	Species richness	Species		0.49
ComIndex	Community N index	*ln*(deposition)	0.84	
Forest structure				
Age	Age of oldest tree or dominant cohort	years		
ConiBA	Conifer basal area	m^2/ha		0.23
HdwdBA	Hardwood basal area	m^2/ha		
Climate				
Cont	Continentality	°C		0.32
PptAnn	Annual precipitation	cm		0.46
Rhann	Annual relative humidity	%		0.35
Tmaaug	Maximum August temperature	°C		
Tmidec	Minimum December temperature	°C		0.14
CMD	Climatic moisture deficit	mm		0.34
Air quality measurements				
ImpN	N in $PM_{2.5}$ measured at IMPROVE sites	μg/m^3/year	0.50	

monthly difference between atmospheric evaporative demand and precipitation (Wang et al., 2012). Continentality is a measure of temperature variability calculated as the difference between the maximum August and December minimum temperatures. Other climate variables were extracted from parameter-elevation regressions on individual slopes model (PRISM; June 2012; http://www.prismclimate.org) on an 800-m^2 grid resolution between 1971 and 2000 for plots sampled between 1993 and 2002 and between 1979 and 2008 for plots sampled between 2003 and 2011. For both time periods, we used a thirty-year averages to describe average conditions experienced by fairly long-lived organisms. We ended the thirty-year averages in the middle of the sampling round to best represent plots sampled in that round.

Basal area of conifers and hardwoods were recorded for each plot as well as a presence/absence variable indicating presence of a hardwood tree species. Forest age was measured differently in different phases of the inventory programs. Since a single large, old tree can support a diversity of additional lichens on a plot, we sought tree ages for the oldest measured tree in the plot. When this was not available, we used the estimated age of dominant trees.

2.4. Analysis

We developed a community-based index by categorizing lichen N concentrations, calculating the relative frequency of each species in each category and fitting a smoothed regression line through those points to identify the lichen N concentration associated with each species' peak relative frequency (McCune and Geiser, 2009; http://gis.nacse.org/lichenair/?page=sensitivity) excluding uncommon species and those with ambiguous relationships (details in Appendix B). For each plot with lichen N concentration data, we used the calibration equation developed in Root et al. (2013) to estimate throughfall deposition, which is the amount of dissolved inorganic nitrogen (DIN) collected in ion exchange resin tubes under a forest canopy (Fenn and Poth, 2004). We averaged the natural logarithm of predicted throughfall N deposition associated with species' peak frequencies to calculate a lichen community-based index of air quality that could be interpreted in deposition units by exponentiating. We included plots for analysis only if they included at least five modeled species.

To calibrate lichen indices with measurements at instrumented air quality monitoring stations, we used simple linear regression using the lm function in the software R (R Development Core Team, 2014). The response variables included lichen elemental N and lichen community index and the predictor variable was N measured in fine particulates ($PM_{2.5}$) at IMPROVE air quality monitoring sites. We log-transformed variables as necessary to improve variance and distributional assumptions and included CMD and annual precipitation as potential covariates.

To relate the two lichen air quality indices to each other, we used a linear mixed model in the lmer package in the software R (R Development Core Team, 2014) with the lichen community index as the response, lichen N concentration as the predictor, and CMD and annual precipitation as potential covariates. Since several plots in this dataset had community and lichen N concentration measurements for revisits in each round, we included plot as a random effect and selected a final model with all terms significant based on a drop in deviance test. We report the marginal R^2, which is the variation represented by the fixed effects (*L. vulpina* N and annual precipitation) only (Nakagawa and Schielzeth, 2013).

We sought to independently isolate community composition gradients related to air quality and climate, which were confounded in preliminary analyses. For example, there were several low-elevation hardwood-dominated plots with high lichen N concentration whereas very few of the high elevation conifer-dominated plots had high lichen N concentration. To isolate the gradients of interest, we sought a dataset with a balanced number of plots in each combination of climate, hardwood presence, and lichen N concentration. We subsampled our dataset using a systematic sample of up to ten plots in each of 18 categories of elevation, hardwood presence, and lichen N concentration for a total of 171 plots measured between 2003 and 2011.

We used ordination, which distills community composition into dominant gradients, to model lichen community associations with air quality and climate gradients. Our ordination technique was nonmetric multidimensional scaling (NMS; Kruskal, 1964) in PC-Ord (McCune and Mefford, 2010) with Sørensen (Bray-Curtis) distance, no penalty for tied ranks and rotation to principal axes. We used the slow-and-thorough autopilot settings in which the configuration was optimized using 250 runs with lichen community data. We evaluated 1D to 6D solutions, selecting the dimensionality where adding a further dimension would reduce the final stress by less than 5% of the highest possible stress, and where a randomization test with 250 runs determined that the final stress smaller than expected by chance alone ($p < 0.05$). We interpreted environmental variables on the ordination using vectors with length and direction related to the correlation between variables and ordination axis scores. We mapped species locations on the ordination using their centroids. To relate ordination scores to N concentrations in $PM_{2.5}$ at IMPROVE air quality monitoring sites, we calculated ordination scores for plots matched with those sites using PC-Ord's NMS Scores algorithm (McCune and Mefford, 2010) and regressed ordination scores on N concentrations in $PM_{2.5}$ at IMPROVE air quality monitoring sites. We rigidly rotated the ordination to maximize interpretation of air quality gradients along axis 1 and climate along axis 2 and developed a lichen climate indicator by using PC-Ord's NMS Scores algorithm (McCune and Mefford, 2010) to score all lichen community plots along ordination axis 2.

3. Results

3.1. Lichen communities

We observed 172 lichen species in the study area (Table A.2). Of these, the richest genera were *Bryoria*, *Cladonia*, *Hypogymnia*, the Physciaceae, and *Usnea*. Within-plot species richness ranged from 0 to 43 with a median of 15. The frequencies of lichens in plots sampled systematically across all land ownerships (P3) allow inference about the relative frequencies of occurrence on forested lands across the study area (Table A.2). The lichen community index gradient ranged from plots with more oligotrophic to more eutrophic lichen species (Table B.2). Most species with high N index values were substantially more frequent in plots sampled off the systematic sampling grids, suggesting that off-grid plots successfully targeted polluted sites.

3.2. Calibration of lichen indices

Lichen N concentrations were successfully related to N concentration in $PM_{2.5}$ at IMPROVE air quality monitoring sites ($R^2 = 0.65$, Fig. 2A, Table 2) with no covariates exhibiting a significant effect on the relationship ($p = 0.60$ and 0.68 for annual precipitation and CMD). The lichen community index was also correlated with N concentration at IMPROVE air quality monitoring sites, however, CMD was a significant covariate in this relationship ($p = 0.03$, Fig. 2B, Table 2) but annual precipitation was not ($p = 0.26$). Although both lichen indices were strongly related to N concentration in $PM_{2.5}$ at instrumented IMPROVE air quality monitoring sites, they were less strongly related to each other and annual precipitation improved the model (marginal $R^2 = 0.32$, Fig. 2C, Table 2).

3.3. Calculation of critical levels

There was no sharp threshold in lichen communities or N concentration as related to N concentrations in $PM_{2.5}$, which made selecting a lichen response threshold a judgment call (Fig. 2B). Lichen communities did not appear to be strongly impacted by N concentration below 0.37 μg N/m^3/year, the concentration at the IMPROVE air quality monitoring site near the city of Spokane, Washington. This site had the lowest ambient air N concentration of those established near known N pollution sources. Sites with lower ambient air N concentrations were near wilderness areas thought to be at essentially background N concentration levels. Thus, we considered the ambient air concentration measured at the Spokane IMPROVE air quality monitoring site (0.37 μg N/m^3/year in $PM_{2.5}$) to be our lowest measured estimate of above-background ambient air N concentrations. And, because lichens were responsive at this level, we interpreted it as a critical level.

We used the regressions (Table 2) to determine lichen index values corresponding to the designated critical level of 0.37 μg N/m^3/year in $PM_{2.5}$ (Table 3). The N concentration in *L. vulpina* at the critical level was 1.02% (95% confidence interval (CI) = 0.85 to 1.20). Using the relationship developed in Root et al. (2013), this concentration corresponds to throughfall DIN of 2.52 kg ha/year. The low and high ends of the confidence interval correspond to a range of 1.77 to 3.47 kg DIN/ha/year.

The lichen community index value at the critical level for N concentration in $PM_{2.5}$ and median CMD (410 mm) was 0.43 (95% CI = 0.10 to 0.76). This community index can be exponentiated for an estimate of throughfall DIN (see Appendix B for details) and corresponds to 1.54 kg DIN/ha/year (95% CI = 1.11 to 2.14; Table 3).

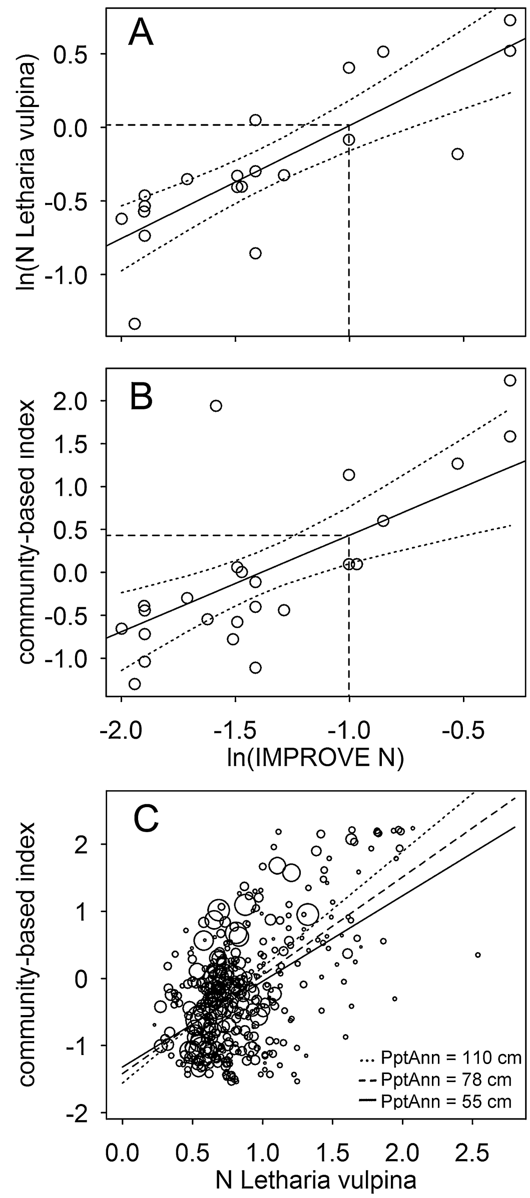

Fig. 2. (A) Relationship N concentration in *Letharia vulpina* and N concentrations in $PM_{2.5}$ at IMPROVE air quality monitoring sites with dotted lines representing 95% confidence intervals. Dashed vertical line represents N concentration at the Spokane IMPROVE air quality monitoring sites (0.37 μg/m^3/year) and dashed horizontal line represents the corresponding lichen concentrations (1.02%). (B) Relationship between lichen community N index and N concentrations in $PM_{2.5}$ at IMPROVE air quality monitoring sites at climatic moisture deficit = 410. The horizontal dashed line shows the community index level (0.43) corresponding to the Spokane site. (C) Relationship between the two lichen-based bioindicators across the entire dataset at three levels of annual precipitation (PptAnn) with point sizes proportional to annual precipitation. Detailed model descriptions in Table 2; natural logarithms symbolized by *ln*.

Table 2
Linear regression models relating lichen bioindicator values to N concentrations in $PM_{2.5}$ at instrumented IMPROVE air quality monitoring sites. Variable names are listed in Table 1 Natural logarithms are symbolized by *ln*. The regression between lichen N concentration and the community N index also included a random term for plots because several were revisited; the R^2 value reflects the marginal R^2, which is the variation represented by the fixed effects only (lichen N concentration and precipitation).

Response	n	R^2_{adj}	Term	Estimate	SE	p
$ln(\text{Nlevu}) = \beta_0 + \beta_1 \times ln(\text{ImpN})$	20	0.65	β_0	0.78	0.19	<0.001
			β_1	0.77	0.13	<0.001
$\text{ComIndex} = \beta_0 + \beta_1 \times ln(\text{ImpN}) + \beta_2 \times \text{CMD}$	25	0.63	β_0	0.91	0.60	0.147
			β_1	1.12	0.27	<0.001
			β_2	0.0016	0.0007	0.035
$\text{ComIndex} = \beta_0 + \beta_1 \times \text{Nlevu} + \beta_2 \times \text{PptAnn} + \beta_3 \times \text{PptAnn} \times \text{Nlevu}$	389	0.32	β_0	−1.08	0.22	<0.001
			β_1	0.83	0.23	0.006
			β_2	−0.004	0.002	0.106
			β_3	0.008	0.003	0.025

Table 3
Lichen index values at the critical level of 0.37 μg N/m^3/year in $PM_{2.5}$ at IMPROVE air quality monitoring sites (Index threshold value), their 95% confidence intervals (CI), $PM_{2.5}$ N at the endpoints of the confidence interval ($PM_{2.5}$ range), and the estimated throughfall dissolved inorganic N deposition based on calibration using the model developed by Root et al. (2013). Deposition estimates were calculated at the endpoints of the 95% confidence intervals for the lichen indices. Estimates based on the community index are based on CMD = 410 mm, the median of the dataset at IMPROVE air quality monitoring sites; at sites with higher CMD, lichen community index values were higher (see Table 2).

Lichen index	Index threshold value	CI	$PM_{2.5}$ range (μg N/m^3/year)	Deposition (kg N/ha/year)	Deposition range (kg N/ha/year)
N concentration	1.02% N	0.852–1.20	0.29–0.46	2.51	1.77–3.47
Community index	0.43	0.10–0.76	0.27–0.49	1.54	1.11–2.14

Lichen communities were more eutrophic in moisture-stressed sites even where N concentration was apparently at background levels (Table 2). For example, at 0.37 μg N/m^3/year in $PM_{2.5}$, the community index was −0.126 (corresponding to an estimated 0.88 kg DIN/ha/year) at CMD = 59 and 0.96 (corresponding to an estimated 2.62 kg DIN/ha/year) at CMD = 746, the minimum and maximum for the dataset.

3.4. Community ordination and climate

Ordination of lichen community composition allowed us to decouple air quality and climate-related gradients, as evidenced by the nearly perpendicular climate and air quality vectors in the ordination (Table 1, Fig. 3). The ordination successfully reduced the 171 species to two primary gradients, representing 82.5% of the variation in community structure with 25.0% on the first axis and 57.4% on the second and the axes were 97% orthogonal. The lichen community air quality index was strongly related to the first ordination axis (R^2 = 0.84; Table 1). N concentration measured at IMPROVE air quality monitoring sites was also strongly related to the first ordination axis (R^2 = 0.50; Table 1) whereas lichen N concentration was only moderately related to this axis (R^2 = 0.12). Visual examination of the position of species on the ordination suggested an interpretable trend of oligotrophic to eutrophic species along the first axis (Fig. B.2).

The second ordination axis was strongly related to a climate gradient described by a positive association with annual precipitation and relative humidity and a negative association with climatic moisture deficit and continentality (Table 1; Fig. 3). This represents a gradient from dry climates with high temperature variability to wetter climates with more homogeneous temperature regimes. Species richness was greatest in wet suboceanic climates. Hardwood plots were well-distributed along both gradients in lichen community composition with the exception of the high end of axis 1; no conifer-only plots could be found in the most polluted areas. Oligotrophic, mesotrophic, and eutrophic lichen species could be found across the climate gradient with fewer eutrophs in the wettest sites (Fig. B.2).

3.5. Mapping air quality and climate indices

Both lichen air quality indices were elevated in Columbia River Gorge and Snake River Canyon, northeastern California, and near urban and agricultural centers such as Spokane, Washington and Bend, Oregon (Fig. 4). Air quality indices were lowest in the Cascade Mountains, indicating better air quality. While the community and lichen N concentration indices differed on some plots, the broad pattern was similar. The climate index based on the second axis of the ordination tracked annual precipitation (Fig. 5) and described a gradient from dry, continental sites in the lowlands to moist, suboceanic sites in the Cascade and Rocky Mountains.

4. Discussion

Developing bioindicators of air quality was expected to be a challenge in this region because climatic gradients are quite strong and most sites are relatively clean compared with much of the rest of North America (Fenn et al., 2003a). Despite these challenges, lichen indices proved successful in uncovering subtle patterns in air quality. Both indices detected elevated N pollution near agricultural areas of the Palouse region and Columbia Basin in east-central Washington that were likely to be impacted by ammonia and are consistent with earlier research (Fenn et al., 2003a). Near Spokane, Washington and Bend, Oregon, urban sources of NO_x likely contribute to elevated lichen air quality indices. The Columbia River Gorge is impacted by air drainage from urban areas and agriculture (Fenn et al., 2007), which may also be the case at Hell's Canyon along the Snake River. Plots with high index values in otherwise clean regions were typically established close to small point sources with localized emissions. The Rocky Mountains in northern Idaho and northeast Oregon show more eutrophic communities than would be expected based on known N pollution sources. A hint of this pattern is also seen in earlier lichen indicator work (Fenn et al., 2003a) and models (Fenn et al., 2003b) but was not explored in depth. This region was less intensively sampled than Oregon and Washington; detailed sampling including instrumented sites, throughfall monitors or lichen N concentration may improve our understanding of the lichen communities in northern Idaho.

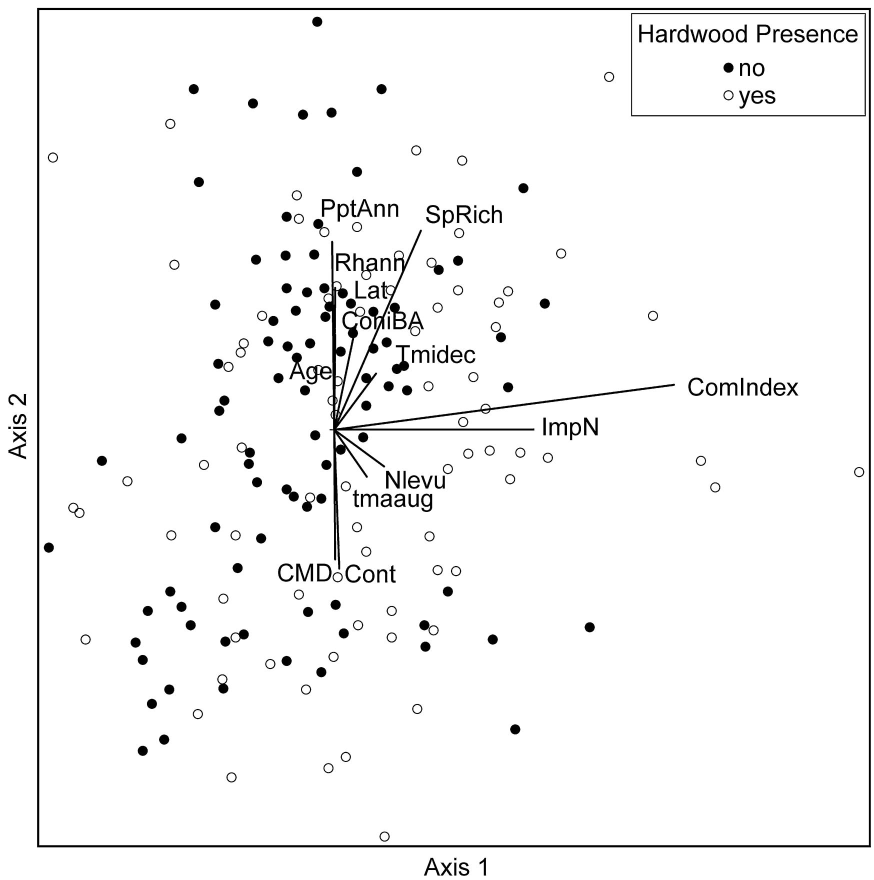

Fig. 3. Lichen community ordination for a subset of 2003–2011 plots; points represent plots in species space. Vectors represent a post-hoc overlay of environmental variables and are longer for stronger relationships. Acronyms and strength of relationships between environmental variables and ordination scores can be found in Table 1.

4.1. Comparing lichen bioindicators

Both indices that we examined, elemental N concentration in *L. vulpina* and the lichen community index, were strongly related to N concentration in $PM_{2.5}$ at instrumented IMPROVE air quality monitoring sites. However, they were not as strongly related to each other (Table 2), suggesting that other sources of variability impact these indices differently. Our models suggested that precipitation and CMD had a greater influence on lichen community composition as compared with lichen N concentration. At the same level of N concentration in $PM_{2.5}$, sites experiencing more moisture stress showed more eutrophic lichen communities. Both indices are potentially subject to other sources of variability such as seasonality of precipitation, substrate, age, dispersal, forest structure, temperature seasonality, fog, and site history. Finding similar patterns using these different lichen indices strengthens the value of lichen indicators by providing multiple lines of evidence to identify impacted sites.

4.2. Impact of climatic moisture deficit on community index

The impact of CMD on the community indicator was unexpected; an integrated measure of moisture stress that combines temperature and precipitation was biologically intuitive but has not been used as a covariate in previous lichen bioindicator studies. Our models suggest that at the same level of N concentration, more moisture-stressed sites have more eutrophic lichen communities; others have similarly found that sites with lower precipitation (Geiser et al., 2010) or elevation (Jovan and McCune, 2005) have more eutrophic communities. Geiser et al. (2010) and Jovan and McCune (2005) use this information to infer that drier or lower elevation climates should have lower critical loads to maintain the same level of eutrophication of the lichen community. However, if communities are naturally more oligotrophic at wet sites, by allowing a higher critical load at those sites, communities undergo substantially more change to reach the critical load than they would at dry sites. We advocate holding the critical level of pollution constant and allowing the community composition index at the critical level to vary with climate. This ensures a similar magnitude of community shift at sites approaching the critical level, and avoids sanction of dramatic changes at wet sites or biologically unimportant shifts at dry sites.

4.3. Deposition measurement accuracy

In an area where many pollution sources are localized, bioindicators can be sensitive to small-scale patterns. For example, in the Columbia River Gorge, plots close to the river showed higher pollution levels than those a short distance away. This area is a major conduit for NO_x pollution from the city of Portland in the summer and NH_3 pollution from agriculture to the east in winter (Fenn et al., 2007). At the fine scale of lichen plots, the spatial pattern of pollution can be clearly differentiated; however, these patterns may be difficult to detect using interpolated models. We considered using interpolated models (*e.g.*, CMAQ, Appel et al., 2011; NADP, 2012) for calibration but favored using concentration at instrumented IMPROVE air quality monitoring sites, which were more strongly related to lichen indices as has been found for some other lichen bioindicator studies (Geiser et al., 2010; McMurray et al., 2013). Other studies in California (Jovan

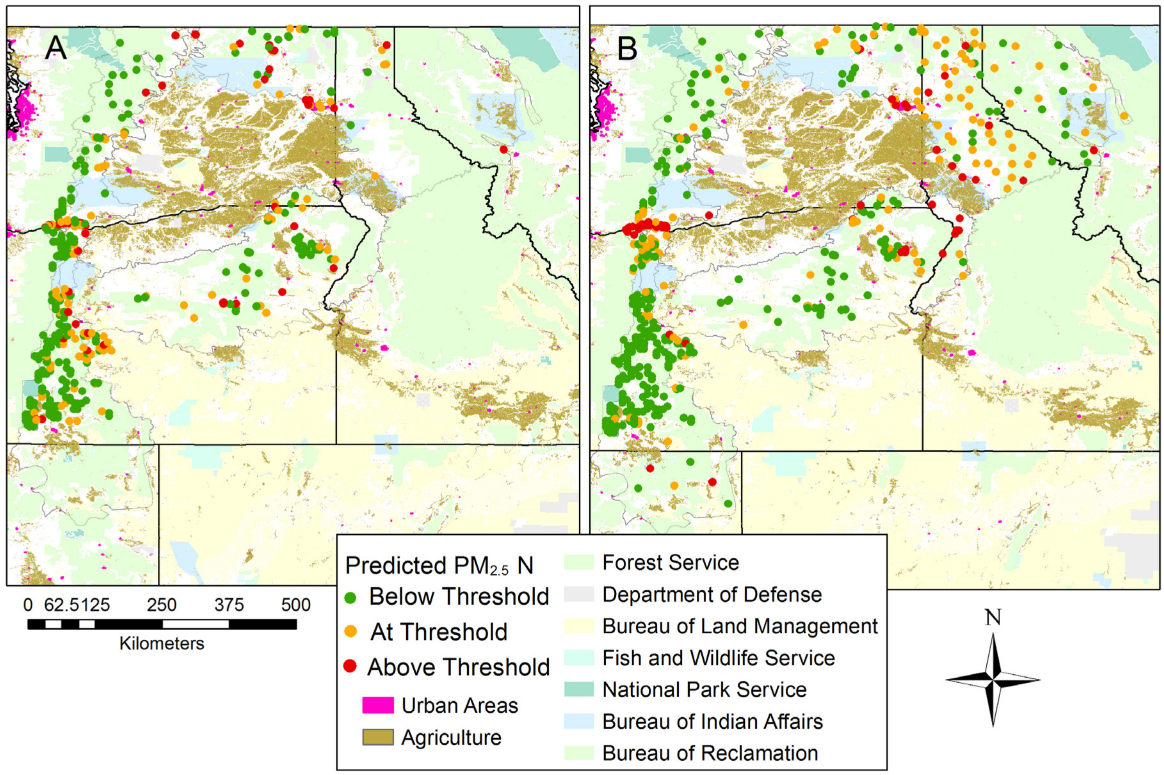

Fig. 4. Maps of estimated N concentration in $PM_{2.5}$ for plots sampled in 2003–2011 using the lichen N concentration index (A) and lichen community index after correcting for climatic moisture deficit (B). The yellow plots are within the 95% confidence interval corresponding to the critical level of 0.37 $\mu g/m^3$/year (Table 3); red plots are higher than this interval and green are lower. The background agriculture layer is based on 2006 data from the Multi-Resolution Land Characterization (http://www.mrlc.gov/nlcd06_data.php, 8/6/2012).

and McCune, 2005) and the western Pacific Northwest (Geiser and Neitlich, 2007) were more successful at calibrating lichen bioindicators with interpolated deposition models, likely because those regions have stronger, broader scale pollution patterns.

4.4. Considerations identifying critical levels and loads

The two lichen indices and peak frequencies of individual species exhibited continuous relationships with inorganic N pollution throughout the range of N in ambient $PM_{2.5}$ and through-fall deposition. This continuous response suggests that the designation of a critical level or critical load is somewhat arbitrary because at any level above background, some species are likely to experience adverse impacts. This pattern is consistent with previous lichen studies (Geiser and Neitlich, 2007; Geiser et al., 2010; Jovan et al., 2012) and grassland communities (Payne et al., 2013).

Natural background N deposition in the region was likely quite variable and eutrophic species were historically a part of the flora. Pre-industrial background deposition was estimated to be 0.16–2.13 kg N/ha/year (Holland et al., 1999) and estimated fine particulate nitrate concentrations to be 0.028 and 0.112 $\mu g/m^3$/year (Trijonis, 1990). Many sites within the region are within the range of natural pre-industrial N deposition; however, the lowest $PM_{2.5}$ N concentration in our dataset was 0.136 $\mu g/m^3$/year at Crater Lake National Park, above the estimated historic range of concentration. Our estimated critical loads between 1.11 and 2.14 kg DIN/ha/year overlap the likely historic N deposition and reflect a continuous response to N pollution, suggesting that adverse effects on lichen communities can be observed as soon as N deposition exceeds the historic range of variability.

4.5. Comparisons with other critical levels and loads

Our estimated threshold index value of 1.02% N in *L. vulpina* is consistent with other lichen bioindicator work. For example, in the Pacific Northwest the 97.5% quantile of the distribution of lichen concentrations at presumably clean sites estimates a threshold N concentration of 1.03% N in *L. vulpina* (Fenn et al., 2008; The United States Forest Service National Lichen and Air Quality Database, http://gis.nacse.org/lichenair/index.php?page=cleansite). McMurray et al. (2013) estimated a slightly higher threshold of 1.12% in *L. vulpina* in study sites in Wyoming. The critical level for concentration affecting lichen community composition for the western Pacific Northwest is 0.52 $\mu g/m^3$/year in $PM_{2.5}$ (Geiser et al., 2010), which is slightly higher than our estimate, perhaps reflecting the wetter climate.

Our estimated critical loads are slightly lower than those estimated using lichen bioindicators in nearby regions but not the lowest for all bioindicators; for example, wet deposition exceeding 1.5 kg N/ha/year has been linked to changing diatom communities in Rocky Mountains lakes (Baron et al., 2011). The total deposition critical load for lichen communities in the western Pacific Northwest varies from 2.7 at dry sites to 9.2 kg total N/ha/year at wetter sites (Geiser et al., 2010). However, as most of our sites are drier, we would expect critical loads east of the Cascade Crest to be at the low end of that range. Based on a similar threshold for N concentration in *L. vulpina*, Fenn et al. (2008) estimated a critical load of 3.1 kg total N/ha/year. McMurray et al. (2013) observed strong effects on Wyoming lichen communities, including bleaching and necrosis at 4 kg DIN/ha/year. Critical levels and loads estimated for our region are substantially lower than those in most European studies (*e.g.*,

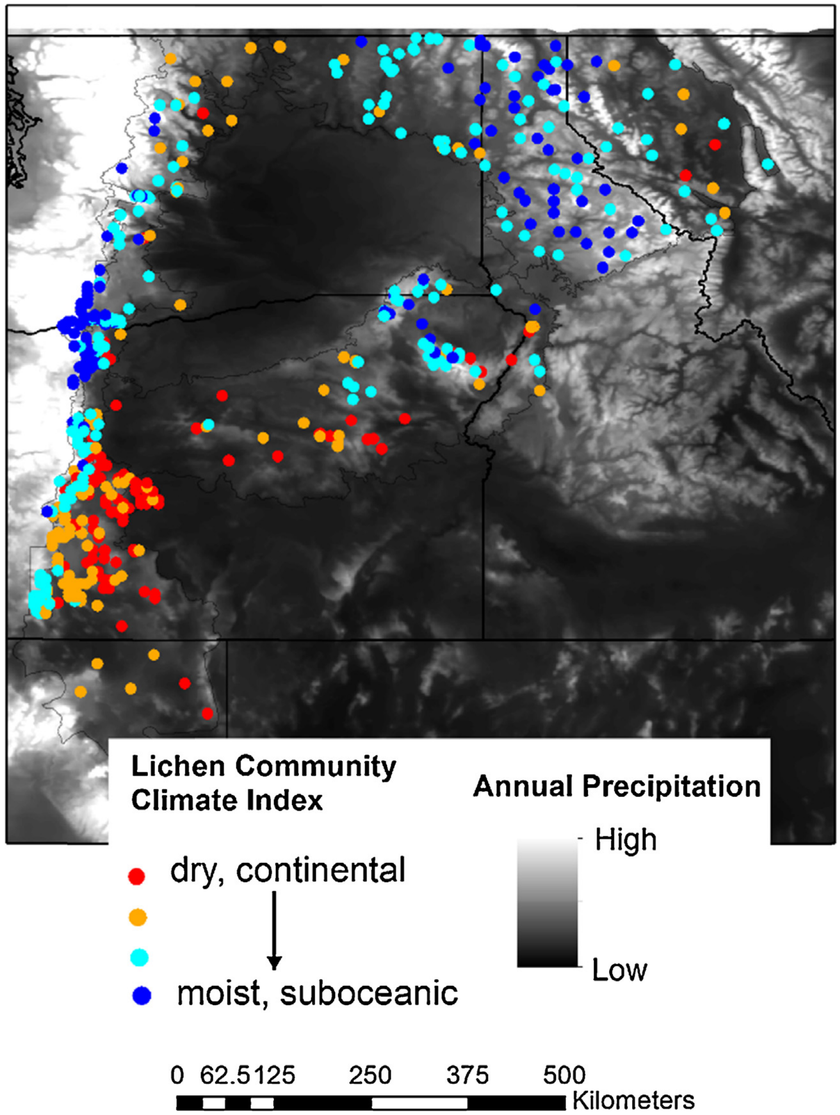

Fig. 5. Map of lichen community climate index values with mean annual precipitation in the background (PRISM).

Bobbink et al., 2003; Pinho et al., 2012), likely because background levels of deposition in our study area were substantially lower and therefore we are able to detect earlier community responses.

4.6. Eutrophs and oligotrophs

Critical loads based on eutrophic or oligotrophic lichen species have been developed for several regions in the western United States and Europe (*e.g.*, Geiser and Neitlich, 2007; Jovan et al., 2012). Our species categorizations were broadly similar to others' (Jovan et al., 2012; McCune and Geiser, 2009) but included several minor differences in classifications (Table B.2). Despite the potential for regional differences in sensitivity associated with climate, eutroph and oligotroph designations are remarkably consistent across study areas in the western US (Jovan et al., 2012). However, classifications may also depend on the range of deposition values within the study area. For example, in a study in Portugal where deposition ranged from 17.9 to 381.7 kg N/ha/year, *Ramalina farinacea* was considered to be an oligotroph (Pinho et al., 2012); in our study this species was associated with the most eutrophic sites with a peak frequency at 9.5 kg N/ha/year. A benefit to using a continuous indicator, as we did, is that it may be more sensitive to the uniqueness of each species' response and is less impacted by arbitrary cut-offs used to classify species as oligotrophs or eutrophs. Despite this advantage, designating eutrophs, mesotrophs, and oligotrophs added to the interpretability to the lichen community index.

4.7. Climatic gradients

The strongest climate gradient was associated with a shift from dry regions with high temperature variability to wetter sites with more homogeneous temperatures. This pattern is consistent with several other lichen studies; for example, Italian lichen communities were strongly patterned by a combination of temperature and moisture regimes (Giordani and Incerti, 2008). Similarly, precipitation and temperature range (oceanicity) were the dominant climatic predictors of lichen communities in the UK (Ellis et al., 2007). In the western Pacific Northwest, lichen communities were strongly related to continentality, December minimum temperature and relative humidity (Geiser and Neitlich, 2007). Unlike in coastal regions of the USA (McCune et al., 1997; Geiser and Neitlich, 2007), lichen communities in our study area were much more strongly related to moisture availability than any of the temperature variables except continentality. Because CMD estimates are readily available in the study region and have been projected into the future for a variety of climate change scenarios (Wang et al., 2012), this relationship can be used to interpret potential future climate changes.

CMD is expected to increase throughout our study area in the next decades (Wang et al., 2012); for example, based on four representative model projections averaged across 2070–2099, CMD was projected to increase by 107 mm at one study site in our area (Dodson and Root, 2014). Because sites with higher CMD have lower species richness of epiphytic lichens and more eutrophic communities, this may have a detrimental impact to lichen communities. We also expect an accompanying decline in ecosystem functions of epiphytic lichens, particularly as those important as forage or in nutrient cycling (alectorioids and cyanolichens; McCune and Geiser, 2009) are among the species most associated with mesic climates in our study area. However, it is possible that the overall lichen flora will not decline in overall diversity because crustose soil-dwelling species can be quite abundant and diverse in dry, continental woodland and steppe habitats (Root et al., 2011). This pattern could parallel an observed long-term trend in the UK where lichen richness is increasing as tropical species move north even though boreal and arctic species are declining (van Herk et al., 2002). Thus the ecological roles of lichen communities may change from those associated with forest macrolichens to other functional groups such as crustose lichens.

Exceptions to overall climatic patterns of species richness and community composition may be indirectly affected by climate or land-use changes in the future. For example, many plots with fewer than 5 species experienced stand-replacing wildfire or tree harvesting. In the coming decades, a greater area of our region is expected to be affected by stand-replacing wildfires as a result of past fire suppression and more extreme climatic events such as drought (Wimberley and Liu, 2014). While lichens can be quite sensitive to subtle changes in climate, conversion of forest to other vegetation types denies epiphytic species their habitat. This indirect effect of climate change may have a substantial impact on lichen communities and complicate interpretations of their community composition and richness in relation to direct climate effects.

5. Conclusion

We developed two lichen-based indicators of air pollution from N: lichen N concentration in *L. vulpina* and a lichen community index. Both were well-calibrated with N concentrations in $PM_{2.5}$ at instrumented IMPROVE air quality monitoring sites in the region and both were continuous in their relationship with N concentration. We propose a critical level of 0.37 $\mu g/m^3$/year N in $PM_{2.5}$ based on impacts at concentrations above this level observed at the Spokane, Washington monitoring site. Lichen communities were more eutrophic in moisture-stressed sites regardless of air quality. Lichen indices highlighted enhanced N near agricultural areas, urban and industrial areas. They also detected impacts in the narrow canyons along the Columbia and Snake Rivers where N-enriched air drains from agricultural and urban areas.

Lichens species richness and community composition were strongly related to climate gradients including climatic moisture deficit and continentality independently from air quality impacts. High lichen species richness was associated with moist sites with more consistent temperatures across days and months. We expect that climate change will cause declines in epiphytic macrolichen diversity and biomass as a result of decreased moisture availability (less suitable climate) and more frequent, higher intensity fires (less suitable habitat or time to rebuild populations). Furthermore, because more eutrophic lichen communities are associated with both moisture stress and air quality, climate change may exacerbate the effects of N pollution.

Flora and fauna of northwestern forests have co-evolved within defined nutrient availability and climate regimes. We have shown that nutrient nitrogen enhancements and dry climates are associated with reduced occurrence of widespread oligotrophic forage (alectoriods), matrix (cetrarioids, *Platismatia, Hypogymnia*) and cyano (*Lobaria*, *Peltigera, Pseudocyphellaria, Nephroma, Sticta*) lichens. These lichens currently provide important forage, nesting materials, and habitat for mammals, birds, and invertebrates—fauna which are, in turn, interdependent. Thus declines in widespread nutrient- and climate-sensitive macrolichens, can have broad ecological repercussions for the habitat quality and resiliency of northwestern forests.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2015.01.029.

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