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Epiphytic macrolichen communities correspond to patterns of sulfur and nitrogen deposition in the northeastern United States

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Abstract. Atmospheric deposition of sulfur (S) and nitrogen (N) has decreased steadily in the northeastern U.S. since the federal 1970 Clean Air Act was passed, yet deposition remains elevated above natural background levels throughout the region. Epiphytic macrolichens are highly sensitive to air pollution and their status is a good indicator of ecological health. We used deposition modeling for 2000–2013 and multiple metrics of lichen status (i.e., species composition, species richness, thallus condition, lichen sensitivity indices, lichen elemental analysis) to assess air pollution effects at 24 plots in four federally-mandated Class I areas. The areas (Lye Brook Wilderness, VT; Great Gulf and the Presidential Range-Dry River Wildernesses, NH; and Acadia National Park, ME) encompass a range of high to low deposition sites. We developed thallus condition scores and sensitivity groups and indices for S and N based on species patterns using deposition estimates gleaned from a larger, independent data base. Non-metric multidimensional scaling ordinations differentiated forest structure effects on lichen community composition from more complex deposition and elevation effects. Annual mean and cumulative deposition of N correlated strongly with decreases in lichen species richness and N-sensitive species, and poorer thallus condition. Cumulative dry deposition of S yielded the best fit to decreases in thallus condition, poorer community-based S Index values, and absence of many S-sensitive species. Multiple metrics provided consistent evidence that higher depositional loading was associated with greater adverse effects. In general, stronger correlations between present day lichen metrics and cumulative deposition (post-2000), compared to current deposition, emphasize the long-term nature of emissions impacts and continued need to control S and N emissions to restore the ecological health of lichen communities and linked biota.

Keywords: Thallus condition, cumulative deposition, air pollution, epiphyte, cyanolichen, sensitivity rating.

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Deposition of most sulfur (S)- and nitrogen (N)-containing air pollutants has decreased in the northeastern U.S. over the past several decades in response to reductions in emissions of S and N oxides (SO_x and NO_x) achieved through implementation of the U.S. Clean Air Act and similar Canadian legislation. However, reduced nitrogen (NH_x) was not included in that legislation and deposition is locally variable (Vet et al. 2014). Total annual N deposition is often used in calculations of critical loads (Pardo et al. 2011) and correlates better with epiphytic lichen responses than wet deposition alone or any single N-containing depositional compound (Johansson et al. 2010; Jovan et al. 2012). However, the relative harm of different N

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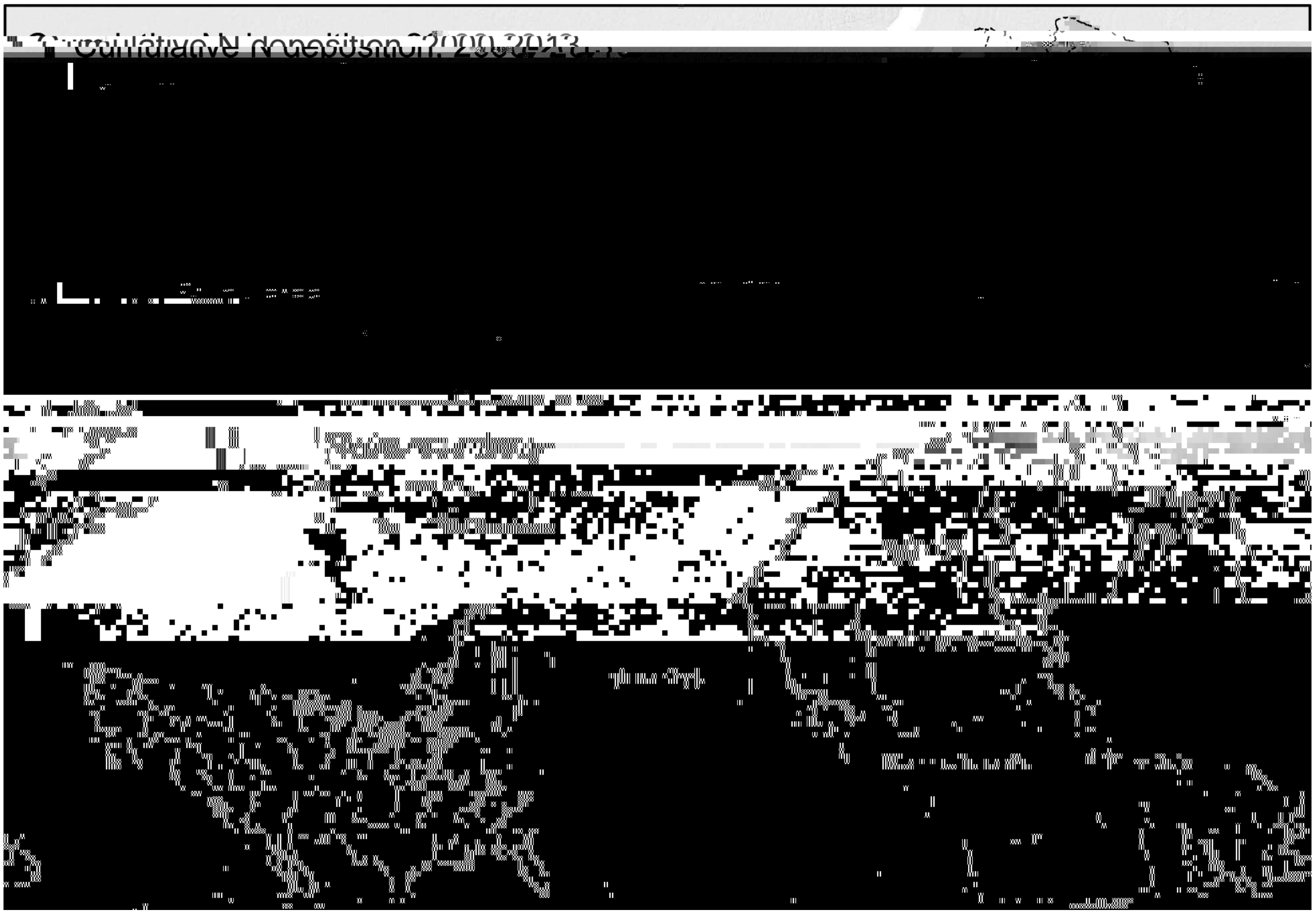

Figure 1. Map of northern New England and New York (NY) showing cumulative deposition (2000–2013) from TDEP for nitrogen at our study areas (four Class I areas): Lye Brook Wilderness (LB), Presidential Range-Dry River Wilderness (DR), Great Gulf Wilderness (GG) and Acadia National Park (AC). Locations of aerosol measuring stations including the station at Whiteface Mountain (WF) in the Adirondack Mountains of NY west of our main study area are also shown. Data sources: NADP (2014), US DOC (2014).

compounds, e.g., reduced N versus oxidized N, to epiphytic lichens remains unclear (Bobbink et al. 2010; Hauck 2010).

For New England states, Hinds & Hinds (2007) demonstrated differences in state-level macro-lichen flora that corresponded with known deposition patterns. Recently, Will-Wolf et al. (2015) used 2002 Community Multi-Scale Air Quality model (CMAQ) total deposition estimates to examine relationships between deposition and Forest Inventory and Analysis (FIA) Lichen Indicator data across New York (NY) and New England. In their data set, lichen composition responded to acidifying S and N inputs, but it proved difficult to separate effects of S from N (Will-Wolf et al. 2015). In our study, we used FIA lichen data and 2002 CMAQ deposition associated with lichen survey sites to develop response curves at the species level and air quality scores for the survey sites. However, our primary focus was evaluating the status of epiphytic macrolichens in four federally mandated Class I areas (areas where air quality will be monitored long-term): Lye Brook Wilderness (LB) in the southern Green Mountains of VT; Great Gulf Wilderness (GG) and the Presidential Range-Dry River Wilderness (DR) in the White Mountains of NH and Acadia National Park (AC) in coastal ME. Deposition in these areas is representative of the regional range for non-urban forests (Fig. 1).

A number of studies from the U.S. have recommended specific values that relate N deposition to effects on epiphytic lichen communities. For northern forests, Pardo et al. (2011) recommended a lichen critical load for N of 4–6 kg ha^{-1} yr^{-1}. Concentrations of ammonium nitrates and sulfates in ambient air fine-particulates have correlated strongly with lichen N content and species composition shifts in the western U.S. (Geiser et al. 2010; Root et al.

2015). These researchers also recommended use of IMPROVE aerosol data as a screening tool for exceedance of N critical levels in Class I areas with an annual critical level from 0.37 to 0.51 µg N m^{-3} (Geiser et al. 2010; Root et al. 2015). Healthy lichen communities from “clean” sites in the northwest U.S. corresponded with N concentrations in the lichen *Platismatia glauca* in the range of 0.55 to 0.80% N by dry weight and this range was suggested as a background reference for N effects (Dillman et al. 2007; Glavich & Geiser 2008). However, none of these values have been empirically evaluated for the northeastern U.S., a region lacking in ‘background’ sites (sites not been impacted by air pollution).

Unlike the situation in the western U.S., in the Northeast, nutrient N deposition effects have been compounded and perhaps overshadowed by a legacy of acidic deposition, primarily from sulfuric and nitric acids. In the Northeast, deposition decreases northeasterly from Vermont (VT) through New Hampshire (NH) to Maine (ME) (NADP 2014a,b). Recent improvements to the CMAQ total deposition estimates employ a “hybrid” approach that combines CMAQ output with measured wet and dry deposition, and accounts for topography (Schwede & Lear 2014). Difficult to model variables, such as cloud water deposition at coastal and high elevation plots and forest structure interactions, can significantly influence local deposition to forest environments (Cleavitt et al. 2011; Templer et al. 2015; Weathers et al. 2006), and make accurate modeling of deposition less certain. Epiphytic macrolichens obtain S and N, important and internally mobile macronutrients, from the air and precipitation in dynamic equilibrium with deposition (Boonpragob et al. 1989; Boonpragob & Nash 1990). Nitrogen concentrations in lichens can be used to estimate current levels of total N deposition (Root et al. 2013), making lichen elemental analysis a valuable ground check for modeling data. Lichen response to pollution exposure is a multi-stage process with cumulative effects (Johansson et al. 2010). As pollution increases in toxicity, lichens undergo physiological stress that subsequently affects growth and can cause necrosis of the thallus (Arhoun et al. 2000). Therefore, detailed scoring of thallus condition for all species may be a valuable indicator of pollution stress and help to identify sensitive species.

Species differ in their sensitivity to pollution and therefore pollution tends to homogenizt2.7(el)-2s7.3(vata.)-294.4(Lichen)-3acum eepau mapped in

with ambient wet and dry deposition monitoring data and topography (Schwede & Lear 2014). Annual hybrid total deposition data, referred to as "TDEP", are available at 4 km^2 grid resolution for the years 2000 through 2013, with updates presumably continuing in the future. TDEP total, wet and dry S and N deposition, oxidized and reduced N, and precipitation (Parameter-elevation Relationships on Independent Slopes Model (PRISM), Daly et al. 1994, 2008) data were downloaded from the National Atmospheric Deposition website (NADP 2014a,b) as ESRI ArcGrid^{TM} files. Data were associated with each of the 24 lichen plot locations using ESRI ArcMap^{TM} version 10.2.1. Due to a deposition grid misalignment along the complex Maine coast (Fig. 1), several AC plots fell outside the grid, and were assigned nearest grid-cell values. Any associated error in deposition estimates was likely small as S and N deposition in this area were relatively low and exhibited minimal spatial variability. We represented the deposition environment using two year annual means (S_{ann}, N_{ann}) for the year prior to and year of the plot visit (following Jovan et al. 2012), and cumulative deposition (S_{cum}, N_{cum}), summed from all available years, 2000–2013.

Area level comparisons to IMPROVE and CSN aerosol data. The Interagency Monitoring of Protected Visual Environments (IMPROVE) network (Eldred et al. 1990; Hand et al. 2011) collects 24-hour aerosol samples of fine particulates (2.5 μm) every third day to assess visibility at Class I areas. Relevant monitors were Acadia (ACAD1), Great Gulf (GRGU1) and Lye Brook (LYBR1 and LYEB1). The EPA Chemical Speciation Network (CSN)

(Eastern Temperate Forest and Northern Forest Level 1 EPA Ecoregions), which includes 1,956 plot surveys independent of the work done here. For each species present in our study, we extracted CMAQ modeled S and N deposition estimates from 2002 (CMAQv5.0.1; the most recent coverage available to us for these sites) for every detection site in a 1992–2012 collection window and calculated the median deposition. We rated the lichen species by the deposition of S and of N at the median quantile for the distribution of detections along each pollution gradient: ‘sensitive’ (, 5 kg ha^{-1} yr^{-1}), ‘intermediate’ (5–10 kg ha^{-1} yr^{-1}), or ‘tolerant’ (. 10 kg ha^{-1} yr^{-1}) (Supplementary Table S1). For each of our 24 plots, N and S community index scores were calculated as: $100^{*} (n_{sensitive} – n_{tolerant})/n_{total}$, where n 5 the number of species for the plot.

Lichen thallus condition scores. We scored the condition of 510 specimens vouchered during the macrolichen surveys on a four point scale 5 0 very poor (thallus surface with extensive damage: convoluted lobes, bleaching, black speckles, pink blotchy areas, or other discoloration and/or damage); 5 1 poor (damage less extensive); 5 2 good (within the normal range for the species); and 5 3 robust (larger thallus often having reproductive structures; Fig. 2). One thallus per voucher was scored and only the main collection for each species on the plot was scored. All scoring was done by J. W. Hinds to minimize observer error. Thallus condition was most variable within DR, GG and LB plots. In these areas, we compared thallus condition of common (defined as present in all three areas in at least two plots per area) and uncommon species (less frequent than as defined for common) to determine whether uncommon species were in worse condition.

Lichen elemental analysis. Samples (20 g) of common species *Hypogymnia physodes*, *Evernia mesomorpha* and *Platismatia glauca* were collected for elemental analysis in August of all years (2009, 2011–2013) following Geiser (2004). In 2009, samples were collected at six locations in AC (two overlapping with lichen survey sites: AC11 and AC18). All collections sites were co-located with previous deposition measurements (McNulty et al. 1990). Samples from GG, DR and LB were collected in 2011–2013 at lichen survey sites (Table 1). Nitrile gloves were worn during collection to reduce contamination, and air-dried specimens were cleaned of debris and non-target lichens with a time-limit of two hours per sample, and shipped to the University of Minnesota Research Analytical Laboratory, St. Paul, MN for total N (LECO FP-528 total N analyzer, LECO Corp., St. Joseph, MI) and total S (LECO SC-132 S analyzer) analysis.

Between means comparisons. We made several comparisons of .6347 -1.4692 TD [(C9.3(N)-487(a)0(t)-4
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N deposition were quantified by regression slopes and percent reduction values, which were examined by paired t-tests. All regressions and ANOVAs were run using JMP Pro 10 (SAS Institute, Cary, NC).

In order to compare the pattern of lichen metric responses to deposition values, linear and nonlinear regression models were compared using three

Figure 5. Lichen diversity partitioning for 24 plots in four Class I areas of the northeastern U.S.: Acadia National Park (AC), Presidential Range-Dry River Wilderness (DR), Great Gulf Wilderness (GG) and Lye Brook Wilderness (LB). foundnugtional Great

luta, *H. revoluta*, *Nephroma laevigatum*, *Parmotrema perlatum*, *Usnea cornuta*, *U. flavocardia* and *U. subrubicunda*. Therefore, we subtracted the occurrence of these species from plot species richness for AC and reanalyzed area differences, which remained significant with AC plots (33.2 6 0.90 species/plot), significantly richer than the other three areas.

Only eight species of cyanobacteria-containing lichens were found and only one of these (*Lobaria pulmonaria* at GG1) occurred outside of AC, resulting in significantly higher diversity of cyanolichens at AC (Fig. 5). There were 17 species of fruticose lichens, 16 species in the genus *Cladonia* and 53 foliose lichens. Both cyanolichens ($F_{3,20}$ 5 5.11; p 5 0.0087) and fruticose lichens ($F_{3,20}$ 5 3.73; p 5 0.028) were significantly less common outside of AC (Fig. 5). Refer to Cleavitt et al. (2009) and Dibble et al. (2015) for plot species lists and rare species information.

The number of sensitive and tolerant species detected at the sites were strongly correlated ($p < 0.0001$) to total species richness in all cases [N sensitive ($r = 0.931$); S sensitive ($r = 0.886$); S tolerant ($r = 0.773$)] except species tolerant of high N deposition ($r = 0.313$; $p > 0.05$). Nitrogen-tolerant (13 species) and S-sensitive (20 species) lichens were the least frequent classifications. The richness of both S- and N-sensitive species was significantly higher at AC (Fig. 5; Supplementary Table S1).

Lichen indices for S and N. Mean N Index scores were significantly lower (less sensitive and more tolerant species) at LB compared to AC and DR plots (Fig. 6A). Differences in S Index scores across areas were larger than differences in N Index scores. S Index scores were higher (more sensitive and less tolerant species) at AC than GG and LB. At LB, S Index scores were lower and N index scores were much lower than all other areas (Fig. 6A).

Thallus condition scores. Thallus condition declined from AC > DR > GG > LB; ($F_{3,20} = 15.49$; $p < 0.0001$; Fig. 6B). Overall, the contour maps show that most lichen thalli at AC plots were in good condition with a few robust and poor specimens (Fig. 6B). The DR "hour glass" narrows indicating some specimens fall farther below good condition. In contrast, no GG and LB specimens were robust (no scores above 2) and most thalli were in poor condition (Fig. 6B).

Figure 6. Lichen metrics for 24 plots in four Class I areas of the northeastern U.S.: Acadia National Park (AC), Presidential Range-Dry

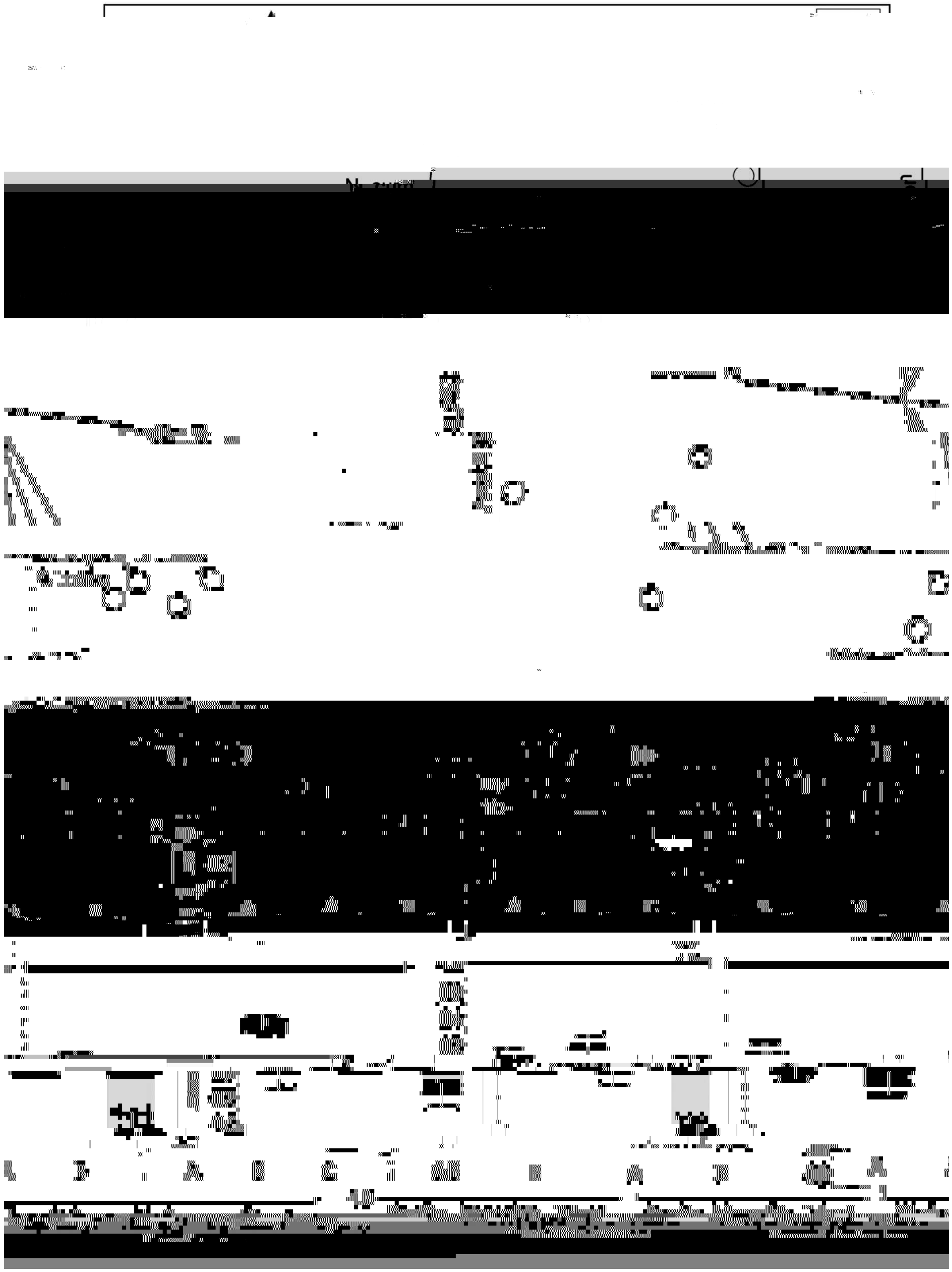

Figure 7. A. NMS ordination of 24 plots in four Class I areas by lichen composition with joint bi-plot of variables with 0.30 or higher r^2 to one of the ordination axes. Plots are coded by study area. Bi-plot vector variable abbreviations are: elevation (Elev), S cumulative deposition 2000–2013 (Scum), annual dry S deposition (Dry Sann), annual total N deposition (Nann), N cumulative deposition 2000–2013 (Ncum), percent broadleaf density (Broadlf%), percent conifer density (Conifer%), and thallus condition score (Condition). B. Relationships of S indicator species to the ordination axes by

Comparison of lichen elemental values

and GG, were reversed for TDEP estimates and lichen elemental content (Figs. 3C & 6C). Recent work from the northwest U.S. have demonstrated the integrative nature of lichen elemental concentrations (Root et al. 2013). The elevation and topographic complexity of the DR and GG plots would increase the importance of cloud water inputs; the CMAQ model does not account for cloud water. The strong correspondence of all other independent lichen metrics with the pattern of DR being slightly cleaner than GG argues that the lichen N contents were more representative of lichen exposures than the TDEP data in this instance, and that lichen elemental analyses can serve as a valuable tool to calibrate deposition modeling efforts in complex terrain.

The relationship between lichen elemental content and aerosol N was difficult to assess with only four monitoring stations. However, the relationship between lichen N and aerosol N for the northeastern states does not seem to be as tight as the relationship reported by Geiser et al. (2010) or Root et al. (2015) for the northwestern states. This difference may be, in part, because particulate NO_3 and total particulate N are a small fraction (typically 5–10% at our northeastern sites), but it may represent a better surrogate of total N deposition in the Northwest than in the Northeast, where sources contributing to particle formation and deposition are more variable in space and time.

While lichen elemental analysis seems a good companion to estimated deposition values, the sampling is time (cleaning samples) and money (analyzing samples) intensive. Perhaps more importantly, we were often limited by the availability of lichens and could not match species across sites. All of these factors limited our sample sizes (N5 10 for *Evernia*, N5 14 for foliose spp.), which in turn limited our ability to detect significance of relationships between thallus elemental content and other variables (Supplementary Table S2).

Response to deposition. Lichen metrics were generally better correlated with cumulative deposition than annual deposition (Table 6). The pattern across areas was similar for N_{ann} and N_{cum} deposition making differentiation between models difficult (Table 5). None of the metrics related well to S_{ann}, and this is explainable in part because AC plots were surveyed in (2005–2006) when S deposition at AC was higher and closer to 2011–2013 deposition at all other sites, therefore leaving little variability in S_{ann} between areas (Fig. 3B). The differences in patterns of S_{ann} and S_{cum} across the areas resulted in clearer differentiation of cumulative estimates as a better fit to lichen metrics (Table 6). In our study, dry S deposition related more closely to patterns in lichen metrics than total or wet S deposition. Dry deposition of S may be more harmful to lichens, both because it has the potential to become highly concentrated when the thallus is rehydrated, and because it largely originates from SO_2, which has a long history of toxicity to lichens

For forms of the N inputs, there was limited evidence from our study that oxidized N was more relevant than total N (Tables 5 & 6). In the northeastern U.S., the ratio of reduced to oxidized N has been increasing over time, but oxidized N still accounts for over half of total N deposition at all of our plots. If upwind NO_x emissions continue to decrease more rapidly than NH_x emissions, future northeastern N deposition will likely be dominated by reduced N, similar to large sections of the central and western U.S. and Europe. Low bark pH at our study plots resulting from the legacy of acidifying S inputs is reflected in bark pH values (3.80–5.98) at our cleanest Acadia plots (data from red maple and red spruce; Cleavitt et al. 2011). Jovan et al. (2012) suggest that nitrophytes (N-tolerant) responded to total N regardless of bark pH within their study range (bark pH 4.8–6.1). Even so, based on measures from AC, bark pH at our western sites are likely lower than 4.8, and at least some nitrophytes are limited by low pH and may respond faster if NH_4 contributes more to N inputs over time.

Comparison to critical values. The critical load of 4–6 kg yr^{-1} ha^{-1} of total N deposition recommended for epiphytic lichens in the Northern Forest Ecoregion highest scores at AC and the lowest scores at LB (Fig. 6A ties across the areas have always existed regardless of deposition impacts? For instance, could the plots in VT simply always have lacked species regarded as sensitive to air pollution for other reasons such as distance from the coast? Examination of historical specimens in Hinds & Hinds (2007) convincingly demonstrated that many sensitive species were previously known from VT and NH. Their data lends support to our supposition that patterns reported here are largely from deposition effects. In addition, we subtracted species restricted to the coast (eight species listed under Species richness) from the AC plot diversity and maintained significant differences in lichen richness between areas.

Conclusions. Lichen communities in all four Class I areas appeared adversely affected by air pollution despite significant decreases in annual deposition loading over the past 14 years. This pattern appears related to the legacy of cumulative deposition effects, which related more clearly to lichen metrics. At AC, the “cleanest” area, impacts were evident only as a negative S-Index score and high number of S-tolerant species. In addition, AC was the only area that has recently had annual deposition loadings below the published lichen N critical loads, and has lichen thallus S and N concentrations below clean-site thresholds. In contrast, the continued higher depositional loading of pollutants to LB over time have resulted in lower lichen richness, poorer thallus condition, and higher

Bennett, J. P. & C. M. Wetmore. 1997. Chemical element concentrations in four lichens on a transect entering Voyageurs National