

Epiphytic macrolichen patterns along an elevation gradient in the White Mountain National Forest, New Hampshire¹

Natalie L. Cleavitt,² Ailís B. Clyne, and Timothy J. Fahey

Department of Natural Resources, Fernow Hall, Cornell University
Ithaca, NY 14853

Abstract. We conducted lichen surveys on mixed broadleaf-conifer plots along an elevation gradient in a northern hardwood forest to test whether current community patterns were more indicative of a gradient in atmospheric inputs of sulfur and nitrogen or a gradient of moisture availability with elevation gain. Our lichen surveys of 12 0.38-ha plots throughout the Hubbard Brook Experimental Forest in north-central New Hampshire revealed four new species records for the state: *Heterodermia squamulosa*, *Hypotrachyna afrorevoluta*, *Parmelia fertilis*, and *Parmotrema arnoldii*. Lichen composition was related to elevation, tree basal area and size of the largest tree. The percent of fruticose lichen species was significantly, positively related to elevation. Species richness also increased with elevation, but was only significantly related to aspect, particularly southness. Species abundance is related positively to tree basal area. The pollution indices were mainly correlated to each other though the sulfur index was correlated to the second ordination axis. Overall, the Hubbard Brook valley appears to have a relatively diverse lichen assemblage related more strongly to plot characteristics than to pollution indices.

Key words: community change, diversity, growth form, macrolichen, pollution indices, water relations

Lichens are complex organisms composed of a symbiosis between fungi and photobionts. These photobionts can be either green algae, or “blue-green” algae (Nitrogen-fixing cyanobacteria), or both types of photosynthesizers. The term cyanolichen refers to those that have cyanobacteria as photobionts. Epiphytic lichens play an important ecological role in the food chain (Asplund *et al.* 2010, Boch *et al.* 2011), as microhabitats for invertebrates (Winchester, Lindo, and Behan-Pelletier 2008; Bokhorst *et al.* 2015), as material

for nest building (Bailey and James 1979, Hayward and Rosentreter 1994), and in water and nutrient cycling (Pike 1978; Knops, Nash, and Schlesinger 1996). They act as bioindicators for air pollution because they are reliant on the air for nutrient intake and have high surface area to volume ratios and, especially cyanolichens, are sensitive to the pH of their substrate and thus to acidification (*e.g.*, Gilbert 1970, McCune 2000). In addition, they have been used as indicators of old-growth forest (Selva 1994, Kuusinen 1996, Sillett *et al.* 2000) and increasingly of climate change response (Aptroot and vanHerk 2007). Indeed, there are efforts underway to refine use of lichens as global indicators of human-induced change (Matos *et al.* 2017).

Patterns in the occurrence of lichen epiphytes can relate to many factors including pollution levels, forest composition and structure (*e.g.*, presence of large trees, broadleaf vs. conifer), and position on the landscape, especially elevation. However, long distance deposition of sulfur (S) and nitrogen (N) also vary with forest composition and elevation (Weathers *et al.* 1988, 2006; Templer *et al.* 2015) with increasing deposition to conifer stands and at higher elevation. Here, we seek to examine variation in several metrics of lichen response: epiphyte composition, abundance, species richness, percent of fruticose species, and indices of pollution sensitive and tolerant species recorded along an elevation gradient of mixed broadleaf and conifer forest plots in the Hubbard Brook Experimental Forest, New Hampshire.

¹ This project was funded by grants from the National Science Foundation (NSF) including a Research Experience for Undergraduates grant to the Hubbard Brook Research Foundation and is a contribution to the Hubbard Brook Ecosystem Study (HBEF). Hubbard Brook is part of the Long-Term Ecological Research (LTER) network, which is supported by NSF. The HBEF is operated and maintained by the USDA Forest Service, Northern Research Station, Newtown Square, PA, USA. This project includes work done by the second author for a senior undergraduate thesis. Scott LaGreca aided with spot tests and finalizing lichen identifications at the Cornell Pathology Herbarium (CUP). Linda Geiser shared her database for developing the lichen sensitivity ratings. Mary Martin created the base map of HBEF with contours. Bob Dirig and two anonymous reviewers provided valuable comments on previous versions.

² Author for correspondence: nlc4@cornell.edu
doi: 10.3159/TORREY-D-18-00021.1

©Copyright 2019 by The Torrey Botanical Society

Received for publication March 23, 2018, and in revised form July 24, 2018; first published January 21, 2019.

In general for lichen epiphytes, there is a positive relationship between species richness and elevation, which is thought to relate to better water relations at higher elevations (Nascimbene and Marini 2015) and to more intensive harvesting of forests at lower elevations (Hofmeister *et al.* 2015; Dymytrova *et al.* 2018). However, inputs of S and N increase substantially (4–6 times higher) at higher elevation sites (Weathers *et al.* 2000, 2006), and this deposition pattern may result in loss of pollution sensitive species at higher elevations. Deposition of N in the White Mountains of New Hampshire have been measured above the critical load for epiphytic lichens at higher elevation sites (4–6 kg ha⁻¹ yr⁻¹; Pardo *et al.* 2011; Templer *et al.* 2015) with particularly acidic cloudwater (Weathers *et al.* 1988). However, the implications of such exceedances on lichen communities have not been well explored at the local scale.

In addition to elevation, deposition is affected by tree composition (broadleaf versus conifer) with conifer trees accumulating higher levels of S and N than broadleaf trees though N deposition is complicated by canopy uptake (Weathers *et al.* 2006; Templer *et al.* 2015). Therefore, if epiphytes in forests along an elevation gradient are negatively impacted by atmospheric deposition, we would expect the greatest impact on pollution sensitive lichen communities in high elevation conifer dominated forests and least impacted communities in low elevation broadleaf dominated forests. For instance, the restriction of *Lobaria pulmonaria* communities with increasing elevation attributed to greater acidic inputs has been shown in Europe (Gauslaa 1995).

In less pollution-impacted areas, occurrence of lichens would be controlled more by microclimate variables such as water availability (Hauck and Spribille 2005, Esseen *et al.* 2016). Water relations in lichens are particularly predictive of occurrence in specific moisture regimes (Liden *et al.* 2010, Gauslaa and Coxson 2011, Esseen *et al.* 2015). Differences in growth form, water holding capacity, and hydration time all relate to water form and availability (Gauslaa 2014, Esseen *et al.* 2015). Fruticose (shrubby) species tend to have low water storage capacity and hold most of their water externally in dense branching patterns. These lichens tend to function best under humid conditions with moderate rainfall and may be unable to grow in high rainfall areas (Esseen *et al.*

2015, 2016) that are critical to cyanolichens with fast hydration and high water storage (Gauslaa 2014). Most foliose (leaf-like) species have greater water holding capacity, which increases with thallus thickness (Esseen *et al.* 2015). In general, rainfall increases with elevation (orographic effect) and the amount of time in a hydrated state tends to be longer for epiphytic lichens (Gauslaa 2014). In addition to increased rainfall, higher elevation plots experience cloudwater inputs and cooler mean annual temperatures that typically foster fruticose lichens (Dymytrova *et al.* 2018).

We use lichen surveys in plots spanning an elevation gain of 420 m to explore two hypotheses that would yield different patterns for lichen communities along an elevation gradient: (a) pollution pattern: greatest reduction in pollution-sensitive species in higher elevation plots and lowest reduction in lower elevation plots, controlling for some conifer component in all plots; and (b) elevation-moisture pattern: increase in species richness and abundance at higher elevation plots with greater presence of fruticose species.

Materials and Methods. **SITE DESCRIPTION.** Hubbard Brook Experimental Forest (HBEF) is a Long-Term Ecological Research (LTER) site in Grafton County, New Hampshire (43°56'N, 71°45'W) with an average January temperature of -8 °C, an average July temperature of 19 °C, and mean annual precipitation of 1,400 mm (Bailey *et al.* 2003). The valley includes 3,160 ha of mixed northern hardwood forest with the highest point of elevation at 1,015 m atop Mt. Kineo. At HBEF, there is an increase of around 70 mm annual precipitation and a decrease of 3.2 °C mean annual temperature for gages with 300 m elevation difference (Bailey *et al.* 2003). The main tree species in the valley are American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britt.), sugar maple (*Acer saccharum* Marsh.), red spruce (*Picea rubens* Sarg.), and balsam fir (*Abies balsamea* (L.) P. Mill.), with the conifer species becoming more dominant at high elevation plots (Schwarz, Fahey, and McCulloch 2003). The forest was disturbed by logging and hurricane damage in the late 19th and early 20th centuries, though higher elevation sites particularly on the north-facing slopes received the least intense disturbance (both human and naturally induced; Cogbill 1989). The soils are mostly well

Table 1. Summary of plot variables for 12 plots in Hubbard Brook valley wide network surveyed for lichens. Eastness and Southness are unitless and derived from the aspect using the sine and cosine, respectively. This creates a linear relationship for Eastness where east = +1 and West = -1 with North and South = 0, and for Southness where South = +1 and North = -1 with East and West = 0. Steepness is the average from five slope measures across the plot.

Plot	Basal area (m ² ha ⁻¹)	Dead BA (%)	Deciduous BA (%)	Birch BA (% of deciduous)	Elevation (m)	Slope (%)	Aspect (°)	Eastness	Southness	Steepness (%)
39	47.76	33.1	13.2	97.1	700	9	18	0.1908	-0.9816	12.9877
40	37.09	33.4	51.0	82.0	730	25	354	-0.3256	-0.9455	28.7585
54	27.53	7.7	62.8	59.7	480	9.5	292	-0.7660	-0.6428	14.4498
56	32.34	9.2	27.9	1.8	480	6	12	-0.6428	-0.7660	5.4353
75	28.60	16.9	61.2	100	805	7	29	0.8290	-0.5592	8.9052
107	26.04	31.3	29.6	84.0	855	18	0	-0.2756	-0.9613	22.0271
121	30.53	11.3	58.8	51.1	510	6	28	0.0698	-0.9976	5.8827
200	30.24	14.2	55.3	50.5	540	5	204	-0.7431	0.6691	6.3499
232	23.09	6.7	58.3	27.7	539	5	25	-0.2079	-0.9781	0.7563
244	36.53	14.3	44.4	100.0	860	15	196	0.0349	0.9994	25.4897
246	34.57	10.2	44.4	97.4	900	12	130	0.5878	0.8090	16.3756
265	22.08	38.0	66.7	42.6	625	12	82	0.9945	0.1045	17.9928

developed, acidic Spodosols (Schwarz *et al.* 2003), although there is considerable landscape variation.

LICHEN SURVEYS. We surveyed and collected lichens from 12 plots in the valleywide plot network (Table 1, Fig. 1, Schwarz *et al.* 2003). The plots were selected to provide a representative sample of the valley, spanning an elevation gradient from 480–900 m while controlling for presence of mixed broadleaf-conifer forest on all plots (Table 1). Plots were selected based on tree composition and were not assessed for lichens prior to the surveys. These plots were surveyed following the Forest Inventory and Analysis (FIA) lichen community protocol (McCune *et al.* 1997, USDA 2004). We used the center of the 0.05-ha valley-wide plots to position our 0.38 ha (34.7 m radius) circular plots.

Two-hour timed surveys of macrolichens were conducted in each plot. We collected macrolichen species from: recently fallen twigs and branches, live and dead tree boles at greater than 0.5 m from the ground, and fallen tree canopies. Abundance for each species was tallied while surveying and converted to the FIA scale. The FIA abundance codes: 1. Present on one tree, 2. Present on 2–10 trees, 3. Present on more than 10 trees but less than half trees, 4. Present on half or more of trees. The number of species on each plot with abundance ratings of 3 or 4 was used as a metric of lichen abundance. Lichen specimens were returned to the laboratory for spot tests and verified using mainly Hinds and Hinds (2007). Nomenclature was aligned with Esslinger (2018). Specimens were

deposited at the Cornell Plant Pathology Herbarium (CUP).

POLLUTION SENSITIVITY. We used ratings from the U.S. Forest Service National Lichens and Air Quality Database and Clearinghouse curated by Linda Geiser (2018). Species designations correspond to “sensitive” (5 kg ha⁻¹ yr⁻¹), “intermediate” (5–10 kg ha⁻¹ yr⁻¹), or “tolerant” (10 kg ha⁻¹ yr⁻¹) for acidic sulfur deposition and oligotrophic, mesotrophic, and eutrophic for the same classes of nitrogen deposition (Appendix). At the plot level, S and N community index scores were calculated as: $100 * (n \text{ sensitive/oligotrophic} - n \text{ tolerant/eutrophic}) / n \text{ total species with sensitivity ratings}$, where n = the number of species for the plot. Negative index values result when there are more pollution-tolerant than sensitive species on the plot.

GROWTH FORMS. Growth forms have been increasingly used in studies designed to find indicator metrics for human-induced impacts (Giordani *et al.* 2012). For our lichen flora, we differentiated four groups that vary in pollution and desiccation sensitivity: cyanobacteria containing lichens (including tripartite lichens), fruticose chlorolichens lichens, foliose chlorolichens, and *Cladonia* species (squamulose). These groups represent well-recognized lichen growth forms with additional separation of cyanobacteria containing species from other foliose species and have been found useful in a range of ecological studies since Hawksworth and Rose (1970; Appendix). We focused particularly on percentage of the

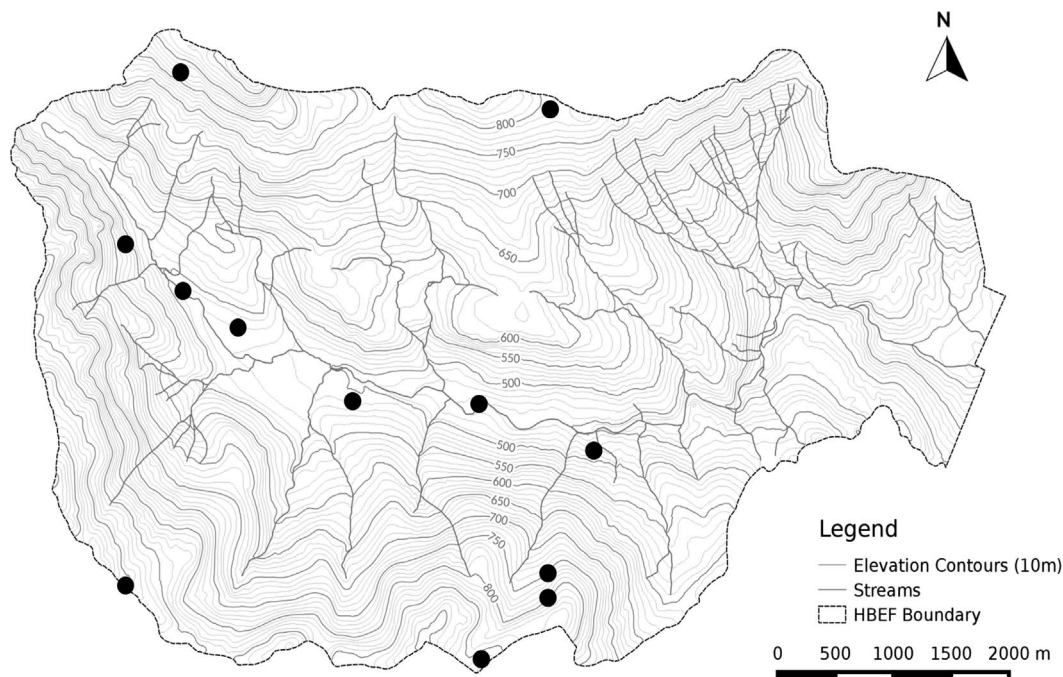


Figure 1. Lichen survey plots (dots) located along an elevation gradient in the Hubbard Brook Experimental Forest, White Mountain National Forest, New Hampshire.

species that are fruticose as an indicator of desiccation sensitivity.

ANALYSIS. Lichen species and plot characteristics data were analyzed using nonmetric multidimensional scaling (NMS), a nonparametric ordination method, in PC-ORD, Version 6.0 (McCune and Mefford 1999). The NMS analysis was run using Sorensen's distance measure with 100 runs using real data and 50 runs of randomized data. The instability criterion was 0.00001 (the probability that a similar final stress could have been found by chance) with 500 as the maximum number of iterations. The final solution was chosen based on the dimensionality with the lowest mean stress from a run comparing randomized to real data (McCune and Mefford 1999). The data set included 12 plots and abundance scores of 66 macrolichens (the one collection of *Menegazzia subsimilis* was included in *M. terrebrata*). Plot variables in the secondary matrix were plot elevation, eastness, southness, slope steepness, percent abundance of deciduous trees (>10 cm diameter at breast height [DBH]), percentage of deciduous tree basal area composed of birch species (to account for change in hardwood species composition with elevation), total basal area,

percentage of basal area represented by dead standing trees, and DBH of the largest tree on the plot (Table 1). In addition, the pollution indices for S and N (see section, Pollution Sensitivity) and percent of fruticose species (see section, Growth Forms) were included in the secondary matrix.

Because our study hypotheses are focused specifically on responses to elevation, the lichen metrics: species richness, lichen abundance, N-Index, S-Index and percent of fruticose species were further examined by linear regression to determine the strongest relationship to elevation. To put our findings in context, we further compared lichen metrics between plots at HBEF and those measured previously using the same methods (Cleavitt *et al.* 2015) at eight plots also within the White Mountain National Forest (WMNF). Because of unequal sample sizes (12 vs. 8 plots), nonparametric Wilcoxon comparisons were used. Regressions and Wilcoxon tests were run in JMP Pro 13 for Windows (SAS Institute Inc., Cary, NC).

Results. Surveys of 12 plots (0.38 ha) in the HBEF documented 67 species of macrolichens including nine fruticose species and only two cyanolichens (Fig. 2; Appendix). Twelve of the

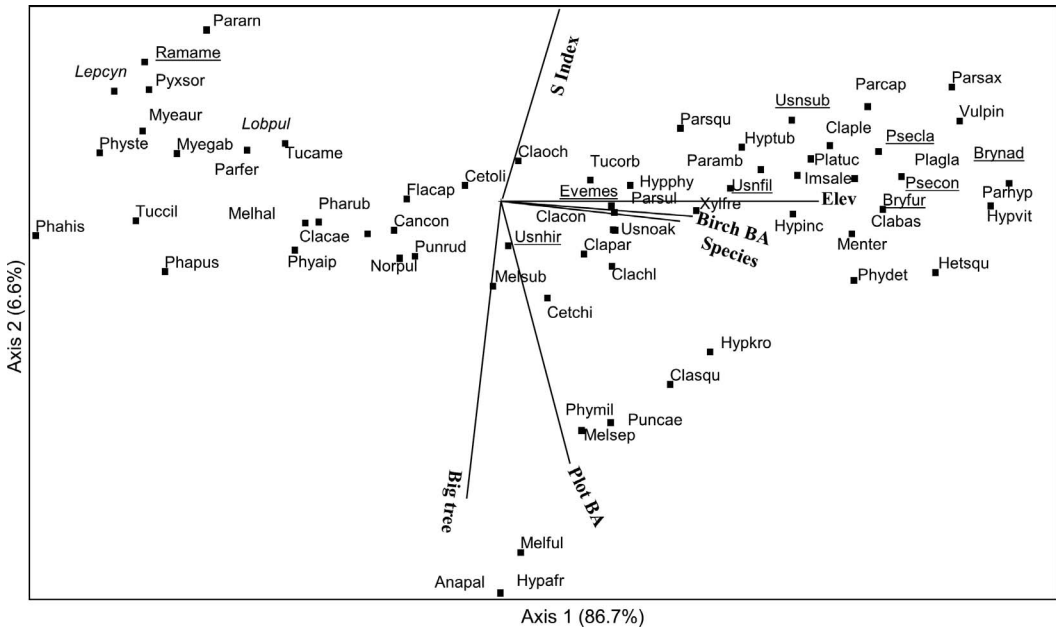


Figure 2. Nonmetric multidimensional scaling ordination of lichen species with vectors for plot variables significantly related to the axes. Lichen species are abbreviated by the first three letters of their generic and specific epithets. Full species names are given in the Appendix. Species in *italic* are cyanobacteria containing lichens. Species that are underlined are fruticose in growth form. Vector abbreviations are: Elev (elevation), birch BA (% of hardwood basal area represented by birch species), Species (number of species recorded), Plot BA (basal area of trees on plot), Big tree (diameter of largest tree on plot), S Index (index calculated from number of species sensitive to or tolerant of sulfur deposition).

species are listed as regionally rare (Hinds and Hinds 2007). The five rarest (R1) species found in our surveys include four new state records for New Hampshire: *Heterodermia squamulosa*, *Hypotrachyna afrorevoluta*, *Parmelia fertilis*, and *Parmotrema arnoldii*. The rare and common species were balanced with 10 species occurring only in one plot and 10 species occurring in 11 or more plots. Four species occurred in all 12 plots: *Evernia mesomorpha*, *Flavoparmelia caperata*, *Hypogymnia physodes*, and *Usnocetraria oakesiana* (see Appendix).

Most (93.3%) of the variation in species composition was explained by two axes in the NMS ordination, with the majority of variation (Axis 1: 86.7%) related to elevation and related changes in tree composition, and a smaller amount of variation (Axis 2: 6.6%) related to S index, basal area, and DBH of the largest tree (Fig. 2). Thirty-one of the 66 species were significantly correlated to one of the ordination axes (Fig. 2). Of these, 18 species increased and 7 species decreased with elevation (Axis 1), while 6 species increased

on plots with higher basal area and a larger tree present (Axis 2; Fig. 2).

The percent of fruticose lichens was positively correlated with plot steepness ($r^2 = 0.901$; $P < 0.0001$), elevation ($r^2 = 0.639$; $P = 0.0253$) and birch basal area ($r^2 = 0.587$; $P = 0.0448$). Species richness was correlated to plot southness ($r^2 = 0.6468$; $P = 0.0230$). Lichen abundance was better predicted by plot basal area ($r^2 = 0.650$; $P = 0.0221$) and birch basal area ($r^2 = 0.7564$; $P = 0.0044$). Lichen abundance was the only lichen metric that differed between HBEF and other WMNF plots (data not shown; $\chi^2 = 4.50$; d.f. = 1; $P = 0.0339$). The pollution indices were most strongly correlated to one another ($r^2 = 0.6637$; $P = 0.0186$). Only the S index was significantly related to lichen species composition patterns (Fig. 2). The pollution indices were not significantly related to any other plot characteristics.

Discussion. Lichens are highly sensitive indicators of air pollution because of their nutrient acquisition strategy that directly exposes them to atmospheric deposition. Over the past 30 years,

steady improvement in air quality and reductions in acid deposition have been recorded in the northeastern United States, including the site of the present study, the Hubbard Brook Experimental Forest (Likens, Driscoll, and Buso 1996; data online at National Atmospheric Data Program [NADP] 2018). The lack of correspondence between elevation and indices for S and N made existence of a pollution pattern with elevation unlikely at this site. The changes in lichen metrics were more in support of the increased moisture response with elevation as percent of fruticose species increased significantly with elevation and species richness tended to increase. However, lichen abundance did not significantly increase with elevation and related more strongly to basal area of trees, particularly birch basal area.

The HBEF has a relatively diverse lichen assemblage. In comparison with areas surveyed using identical methods, HBEF plots were similar to other plots in the White Mountain National Forest, and all were much poorer in cyanolichens than plots in Acadia National Park (Cleavitt *et al.* 2015). The finding of four new lichen records for the state by surveying an area less than 5 ha could either suggest that New Hampshire is severely under collected or that there has been some recovery of the lichen flora though not in the most pollution sensitive group, the cyanolichens. The only epiphytic cyanobacteria containing lichens recorded in our surveys were the most common in the region, *Leptogium cyanescens* and *Lobaria pulmonaria*. Hinds and Hinds (2007) present evidence of decline in cyanolichens in New Hampshire; however, the lack of site-specific historic data precludes certainty about the cause of low cyanolichen diversity. Overall, the legacy of S deposition and attendant acidification is more apparent than N deposition in agreement with other plots in the Northeast (Cleavitt *et al.* 2015) and with differences in S and N inputs measured on site (Weathers *et al.* 1988, Likens *et al.* 1996).

Our surveys also recovered 10 species published as old growth indicators (Selva 1994, Hinds and Hinds 2007): *Anaptychia palmulata*, *Cetrelia chicitae*, *Cetrelia olivetorum*, *Hypogymnia tubulosa*, *Hypogymnia vittata*, *Lobaria pulmonaria*, *Menegazzia terrebrata*, *Myelochroa aurulenta*, *Normandina pulchella*, and *Pseudevernia cladonia*. This high number of old growth indicators agrees with the inability to statistically

distinguish between the structure and composition of the forest at HBEF (average age 100 yr) and the known old growth forest at the nearby Bowl Natural Area (Schwarz *et al.* 2001). The importance of basal area and large-tree DBH in the lichen composition of HBEF is also reflective of the presence of older pockets of trees within the valley. Similarly, the relationship of lichen abundance to basal area may reflect higher abundance in plots with less historical disturbance, allowing more time for the accumulation of lichen biomass on these plots.

Conclusion. Overall, the greater number of pollution sensitive species in the higher elevation plots suggests that atmospheric inputs are not currently restricting the occurrence of these species. Low levels of N ($3\text{--}5\text{ kg ha}^{-1}\text{ yr}^{-1}$) have been shown to be beneficial for growth of some fruticose species (Esseen *et al.* 2016). Perhaps under the more optimal moisture conditions at these higher elevation sites, the lichens are less vulnerable to damage from moderate exceedance of S and N inputs. The degree to which optimal water relations could ameliorate pollution effects deserves further study.

Literature Cited

- APROOT, A. AND C. M. VAN HERK. 2007. Further evidence of the effects of global warming on lichens, particularly those with *Trentepohlia* phycobionts. *Environ. Pollut.* 146: 293–298.
- ASPLUND, J., P. LARSSON, S. VATNE, AND Y. GAUSLAA. 2010. Gastropod grazing shapes the vertical distribution of epiphytic lichens in forest canopies. *J. Ecol.* 98: 218–225.
- BAILEY, R. H. AND P. W. JAMES. 1979. Birds and the dispersal of lichen propagules. *Lichenologist* 11: 105–106.
- BAILEY, A. S., J. W. HORNBECK, J. L. CAMPBELL, AND C. EAGER. 2003. Hydrometeorological database for Hubbard Brook Experimental Forest: 1955–2000. General Technical Report NE-305. United States Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA. 36 p.
- BOCH, S., D. PRATI, S. WERTH, J. RÜETSCHLI, AND M. FISCHER. 2011. Lichen endozoochory by snails. *PLoS One* 6: e18770.
- BOKHORST, S., J. ASPLUND, P. KARDOL, AND D. A. WARDLE. 2015. Lichen physiological traits and growth forms affect communities of associated invertebrates. *Ecology* 96: 2394–2407.
- CLEAVITT, N. L., J. W. HINDS, R. L. POIROT, L. H. GEISER, A. C. DIBBLE, B. LEON, R. PERRON, AND L. H. PARDO. 2015. Epiphytic macrolichen communities correspond to patterns of sulfur and nitrogen deposition in the northeastern United States. *Bryologist* 118: 304–324.

- COGBILL, C. V. 1989. Hubbard Brook revisited. Unpubl. manuscript.
- DYMYTROVA, L., U.-B. BRÄNDLI, C. GINZLER, AND C. SCHEIDEGGER. 2018. Forest history and epiphytic lichens: Testing indicators for assessing forest autochthony in Switzerland. *Ecol. Indicators* 84: 847–857
- ESSEEN, P.-A., T. OLSSON, D. COXSON, AND Y. GAUSLAA. 2015. Morphology influences water storage in hair lichens from boreal forest canopies. *Fungal Ecol.* 18: 26–35.
- ESSEEN, P.-A., M. EKSTROM, B. WESTERLUND, K. PALMQVIST, B. G. JONSSON, A. GRAFSTROM, AND G. STAHL. 2016. Broad-scale distribution of epiphytic hair lichens correlates more with climate and nitrogen deposition than with forest structure. *Can. J. For. Res.* 46: 1348–1358
- ESSLINGER, T. L. 2018. A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada, Version 22. *Opuscula Philolichenum* 17: 6–268.
- GAUSLAA, Y. 1995. The Lobarion, an epiphytic community of ancient forests threatened by acid rain. *Lichenologist* 27: 59–76.
- GAUSLAA, Y. 2014. Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens. *Lichenologist* 46: 1–16.
- GAUSLAA, Y. AND D. COXSON. 2011. Interspecific and intraspecific variations in water storage in epiphytic old forest foliose lichens. *Botany* 89: 787–798.
- GEISER, L. 2018. Air pollution sensitivity ratings for macrolichens in the eastern U.S. Retrieved September 18, 2018 from National Lichens and Air Quality Database and Clearinghouse, United States Forest Service, Washington, DC. <http://gis.nacse.org/lichenair/index.php?page=e_sensitivity>.
- GILBERT, O. L. 1970. A biological scale for the estimation of sulfur dioxide pollution. *New Phytol.* 69: 629–634.
- GIORDANI, P., G. BRUNIALTI, G. BACARO, AND J. NASCIBENE. 2012. Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems. *Ecol. Indicators* 18: 413–420.
- HAUCK, M. AND T. SPRIBILLE. 2005. The significance of precipitation and substrate chemistry for epiphytic lichen diversity in spruce-fir forests of the Salish Mountains, northwestern Montana. *Flora* 200: 547–562.
- HAWKSWORTH, D. L. AND F. ROSE. 1970. Qualitative scale for estimating sulphur dioxide air pollution in England and Wales using epiphytic lichens. *Nature* 227: 145–148.
- HAYWARD, G. D. AND R. ROSENRETER. 1994. Lichens as nesting material for northern flying squirrels in the northern Rocky Mountains. *J. Mammal.* 75: 663–673.
- HINDS, J. W. AND P. L. HINDS. 2007. *Macrolichens of New England*. New York Botanical Garden, Bronx, NY.
- HOFMEISTER, J., J. HOSEK, M. BRABEC, D. DVORAK, M. BERAN, H. DECKEROVA, J. BUREL, M. KRIZ, J. BOROVICKA, J. BETÁK, M. VASUTOVA, J. MALICEK, Z. PALICE, L. SYROVATKOVA, J. STEINOVA, I. CERNAJOVA, E. HOLA, E. NOVOZAMSKA, L. CIZEK, V. IAREMA, K. BALTAZIUK, AND T. SVOBODA. 2015. Value of old forest attributes related to cryptogam species richness in temperate forests: A quantitative assessment. *Ecol. Indicators* 57: 497–504.
- KNOPS, J. M., T. H. NASH, AND W. H. SCHLESINGER. 1996. The influence of epiphytic lichens on the nutrient cycling of an oak woodland. *Ecol. Monogr.* 66: 159–179.
- KUUSINEN, M. 1996. Cyanobacterial macrolichens on *Populus tremula* as indicators of forest continuity in Finland. *Biol. Conserv.* 75: 43–49.
- LIDEN, M., A. V. J. CABRAJIC, M. OTTOSSON-LOFVENIUS, K. PALMQVIST, AND T. LUNDMARK. 2010. Species-specific activation time-lags can explain habitat restrictions in hydrophilic lichens. *Plant Cell Environ.* 33: 851–862.
- LIKENS, G. E., C. T. DRISCOLL, AND D. C. BUSO. 1996. Long-term effects of acid rain: Response and recovery of a forest ecosystem. *Science* 272: 244–246.
- MATOS, P., L. GEISER, A. HARDMAN, D. GLAVICH, P. PINHO, A. NUNES, A. M. V. M. SOARES, AND C. BRANQUINHO. 2017. Tracking global change using lichen diversity: Towards a global-scale ecological indicator. *Methods Ecol. Evol.* 8: 788–798.
- MCCUNE, B. 2000. Lichen communities as indicators of forest health. *Bryologist* 103: 353–356.
- MCCUNE, B. AND M. J. MEFFORD. 1999. PC-ORD: Multivariate analysis of ecological data, Version 6.0. MJM Software, OR, Glendon Beach, OR. Available online at <<https://www.pcord.com/>>. Last accessed September 18, 2018.
- MCCUNE, B., J. P. DEY, J. E., PECK, D. CASSELL, K. HEIMAN, S. WILL-WOLF, AND P. N. NETLICH. 1997. Repeatability of community data: Species richness versus gradient scores in large-scale lichen studies. *Bryologist* 100: 40–46.
- [NADP] NATIONAL ATMOSPHERIC DEPOSITION PROGRAM. 2018. Retrieved September 18, 2018, from U.S. Environmental Protection Agency, Washington, D.C. <<http://nadp.slh.wisc.edu/data/sites/siteDetails.aspx?net=AMON&id=NH02>>.
- NASCIBENE, J. AND L. MARINI. 2015. Epiphytic lichen diversity along elevational gradients: Biological traits reveal a complex response to water and energy. *J. Biogeogr.* 42: 1222–1232.
- PIKE, L. H. 1978. Importance of epiphytic lichens in mineral cycling. *Bryologist* 81: 247–257.
- PARDO, L. H., M. E. FENN, C. L. GOODALE, L. H. GEISER, C. T. DRISCOLL, E. B. ALLEN, J. S. BARON, R. BOBBINK, W. D. BOWMAN, C. M. CLARK, B. EMMETT, F. S. GILLIAM, T. L. GREAVER, S. J. HALL, E. A. LILLESKOV, L. LIU, J. A. LYNCH, K. J. NADELHOFFER, S. S. PERAKIS, M. J. ROBIN-ABBOTT, J. L. STODDARD, K. C. WEATHERS, AND R. L. DENNIS. 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. *Ecol. Appl.* 21: 3049–3082.
- SCHWARZ, P. A., T. J. FAHEY, C. W. MARTIN, T. G. SICCAMA, AND A. BAILEY. 2001. Structure and composition of three northern hardwood-conifer forests with differing disturbance histories. *For. Ecol. Manag.* 144: 201–212.
- SCHWARZ, P. A., T. J. FAHEY, AND C. E. MCCULLOCH. 2003. Factors controlling spatial variation of tree species abundance in a forested landscape. *Ecology* 84: 1862–1878.
- SELVA, S. B. 1994. Lichen diversity and stand continuity in the northern hardwoods and spruce-fir forests of northern New England and western New Brunswick. *Bryologist* 97: 424–429.

- SILLETT, S. C., B. McCUNE, J. E. PECK, T. R. RAMBO, AND A. RUCHTY, A. 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecol. Appl.* 10: 789–799.
- TEMPLER, P. H., K. C. WEATHERS, A. LINDSEY, K. LENOIR, AND L. SCOTT. 2015. Atmospheric inputs and nitrogen saturation status in and adjacent to Class I wilderness areas of the northeastern US. *Oecologia* 177: 5–15.
- [USDA] UNITED STATES DEPARTMENT OF AGRICULTURE. 2011. Phase 3 Field Guide – Lichen Communities, Version 5.1. Accessed September 18, 2018. Forest Inventory and Analysis Program, United States Forest Service, Washington, DC. <<https://www.fia.fs.fed.us/library/field-guides-methods-proc/>>.
- WEATHERS, K. C., G. E. LIKENS, F. H. BORMANN, S. H. BICKNELL, B. T. BORMANN, B. C. DAUBE, JR., J. S. EATON, J. N. GALLOWAY, W. C. KEENE, K. D. KIMBALL, W. H. McDOWELL, T. G. SICCAMA, D. SMILEY, AND R. A. TARRANT. 1988. Cloudwater chemistry from ten sites in North America. *Environ. Sci. Technol.* 22: 1018–1028.
- WEATHERS, K. C., G. M. LOVETT, G. E. LIKENS, AND R. LATHROP. 2000. The effect of landscape features on deposition to Hunter Mountain, Catskill Mountains, New York. *Ecol. Appl.* 10: 528–540.
- WEATHERS, K. C., S. M. SIMKIN, G. M. LOVETT, AND S. E. LINDBERG. 2006. Empirical modeling of atmospheric deposition in mountainous landscapes. *Ecol. Appl.* 16: 1590–1607.
- WINCHESTER, N. N., Z. LINDO, AND V. M. BEHAN-PELLETIER. 2008. Oribatid mite communities in the canopy of montane *Abies amabilis* and *Tsuga heterophylla* trees on Vancouver Island, British Columbia. *Environ. Entomol.* 37: 464–471.

Appendix

Traits of 67 macrolichen species occurring in 12 plots surveyed at Hubbard Brook Experimental Forest. Frequency is the number of plots where the species occurred and abundance is the mean abundance score for the species across the plots. Abundance scores 1–4 as explained in the methods section. Growth forms were foliose, fruticose, squamulose, and cyanolichen (in the broad sense). Three sensitivity classes (1 = lowest levels; 3 = highest levels) for sulphur (S) and nitrogen (N) pollution were extracted from sensitivity ratings for the Eastern Region (Geiser XXXX) from species occurrence in plots with varying levels of S and N deposition. Species that were not rated are marked as NR.

Lichen species	Abbreviation in ordination	Frequency	Abundance	Growth form	S class	N class
<i>Anaptychia palmulata</i> (Michaux) Vainio	Anapal	1	1	foliose	3	NR
<i>Bryoria furcellata</i> (Fr.) Brodo & D. Hawksw.	Bryfur	2	1	fruticose	2	1
<i>Bryoria nadvornikiana</i> (Gyelnik) Brodo & D. Hawksw.	Brynad	2	1.5	fruticose	1	1
<i>Candelaria concolor</i> (Dickson) Stein	Cancon	2	1	foliose	1	2
<i>Cetrelia chicitae</i> (W. L. Culb.) W. L. Culb. & C. F. Culb.	Cetchi	3	1	foliose	1	1
<i>Cetrelia olivetorum</i> (Nyl.) W. L. Culb. & C. F. Culb.	Cetoli	11	1.25	foliose	1	1
<i>Cladonia caespiticia</i> (Pers.) Flörke	Clacae	11	2	squamulose	3	3
<i>Cladonia chlorophaea</i> (Flörke ex Sommerf.) Sprengel	Clachl	9	1.6	squamulose	1	1
<i>Cladonia coniocraea</i> (Flörke) Sprengel	Clacon	10	2	squamulose	NR	NR
<i>Cladonia macilenta</i> Hoffm.	Clamac	2	1	squamulose	3	3
<i>Cladonia ochrochlora</i> Flörke	Claoch	11	1.27	squamulose	3	NR
<i>Cladonia parasitica</i> (Hoffm.) Hoffm.	Clapar	3	1	squamulose	NR	NR
<i>Cladonia pleurota</i> (Flörke) Schaerer	Claple	1	1	squamulose	NR	NR
<i>Cladonia squamulosa</i> (Scop.) Hoffm.	Clasqu	3	1	squamulose	1	1
<i>Evernia mesomorpha</i> Nyl.	Evemes	12	2.2	fruticose	1	1
<i>Flavoparmelia caperata</i> (L.) Hale	Flacap	12	1.92	foliose	3	3
<i>Heterodermia squamulosa</i> (Degel.) W. L. Culb.	Hetsqu	1	1	foliose	3	3
<i>Hypogymnia incurvoides</i> Rass.	Hypinc	6	2.2	foliose	NR	NR
<i>Hypogymnia krogiae</i> Ohlsson	Hypkro	6	1.2	foliose	2	1
<i>Hypogymnia physodes</i> (L.) Nyl.	Hypphy	12	2.1	foliose	2	1
<i>Hypogymnia tubulosa</i> (Schaerer) Hav.	Hyptub	5	1.4	foliose	2	1
<i>Hypogymnia vittata</i> (Ach.) Parrique	Hypvit	2	1	foliose	NR	NR
<i>Hypotrachyna afrorevoluta</i> (Krog & Swinscow) Krog & Swinscow	Hypafr	1	1	foliose	NR	NR
<i>Imshaugia aleurites</i> (Ach.) S. F. Meyer	Imsale	6	1.7	foliose	1	1
<i>Leptogium cyanescens</i> (Rabenh.) Körber	Lepcyn	3	1.3	cyanolichen	1	1
<i>Lobaria pulmonaria</i> (L.) Hoffm.	Lobpul	5	1.4	cyanolichen	1	1
<i>Melanelixia glabrata</i> (Lamy) Sandler & Arup	Melgla	2	2	foliose	3	3
<i>Melanelixia subaurifera</i> (Nyl.) O. Blanco et al.	Melsub	11	1.5	foliose	2	1
<i>Melanohalea halei</i> (Ahti) O. Blanco et al.	Melhal	9	1.7	foliose	3	1
<i>Melanohalea septentrionalis</i> (Lyngé) O. Blanco et al.	Melsep	1	1	foliose	1	1
<i>Menegazzia subsimilis</i> (H. Magn.) R. Sant.	Menter	1	1	foliose	1	1
<i>Menegazzia terebrata</i> (Hoffm.) A. Massal.	Menter	2	1	foliose	NR	NR
<i>Myelochroa aurentata</i> (Tuck.) Elix & Hale	Myeaur	6	2.5	foliose	3	3
<i>Myelochroa galbina</i> (Ach.) Elix & Hale	Myegal	2	1	foliose	1	1
<i>Normandina pulchella</i> (Borrer) Nyl.	Norpul	2	1	squamulose	NR	NR
<i>Parmelia fertilis</i> Müll. Arg.	Parfer	2	1	foliose	NR	NR
<i>Parmelia saxatilis</i> (L.) Ach.	Parsax	4	2	foliose	NR	2
<i>Parmelia squarrosa</i> Hale	Parsqu	9	2.1	foliose	1	1
<i>Parmelia sulcata</i> Taylor	Parsul	11	2.6	foliose	NR	1
<i>Parmeliopsis ambigua</i> (Wulfen) Nyl.	Paramb	2	1	foliose	2	1
<i>Parmeliopsis capitata</i> R. C. Harris ex J. W. Hinds & P. L. Hinds	Parcap	4	1.25	foliose	2	1
<i>Parmeliopsis hyperopta</i> (Ach.) Arnold	Parhyp	2	1	foliose	1	1
<i>Parmotrema arnoldii</i> (Du Rietz) Hale	Param	1	1	foliose	NR	NR
<i>Phaeophyscia hispida</i> (Ach.) Essl.	Phahis	1	1	foliose	1	2

Appendix

Continued.

Lichen species	Abbreviation in ordination	Frequency	Abundance	Growth form	S class	N class
<i>Phaeophyscia pusilloides</i> (Zahlbr.) Essl.	Phapus	3	1.7	foliose	NR	2
<i>Phaeophyscia rubropulchra</i> (Degel.) Essl.	Pharub	10	2.8	foliose	3	3
<i>Physcia aiipolia</i> (Ehrh. ex Humb.) Fürnr. var. <i>aiipolia</i>	Phyaip	2	1	foliose	1	3
<i>Physcia millegrana</i> Degel.	Phymil	1	1	foliose	3	3
<i>Physcia stellaris</i> (L.) Nyl.	Physte	4	1	foliose	1	2
<i>Physconia detersa</i> (Nyl.) Poelt	Phydet	3	1	foliose	NR	NR
<i>Platismatia glauca</i> (L.) W. L. Culb. & C. F. Culb.	Plagla	6	2.3	foliose	2	1
<i>Platismatia tuckermanii</i> (Oakes) W. L. Culb. & C. F. Culb.	Platuc	3	1.3	foliose	1	1
<i>Pseudevernia cladonia</i> (Tuck.) Hale & W. L. Culb.	Psecla	4	1.5	fruticose	3	3
<i>Pseudevernia consocians</i> (Vainio) Hale & W. L. Culb.	Psecon	5	1.4	fruticose	NR	3
<i>Punctelia caseana</i> Lendemmer & Hodgkinson	Puncae	2	2	foliose	3	3
<i>Punctelia rudecta</i> (Ach.) Krog	Punrud	11	2.2	foliose	3	3
<i>Pyxine sorediata</i> (Ach.) Mont.	Pyxsor	4	1.5	foliose	NR	1
<i>Ramalina americana</i> Hale	Ramame	3	1	fruticose	1	1
<i>Tuckermannopsis americana</i> (Sprengel) Hale	Tucame	5	1	foliose	1	1
<i>Tuckermannopsis ciliaris</i> (Ach.) Gyelnik	Tuccil	1	1	foliose	3	1
<i>Tuckermannopsis orbata</i> (Nyl.) M. J. Lai	Tucorb	2	1	foliose	2	1
<i>Usnea dasopoga</i> (Ach.) Nyl.	Usndas	7	1.4	fruticose	1	1
<i>Usnea hirta</i> (L.) Weber ex F. H. Wigg.	Usnhir	6	1	fruticose	2	1
<i>Usnea subfloridana</i> Stirton	Usnsub	3	1.7	fruticose	1	1
<i>Usnocetraria oakesiana</i> (Tuck.) M. J. Lai & C. J. Wei	Usnoak	12	3	foliose	NR	1
<i>Vulpicida pinastri</i> (Scop.) J.-E. Mattsson & M. J. Lai	Vulpin	4	1.25	foliose	1	1
<i>Xylospora friesii</i> (Ach.) Bendiksbj & Timdal	Xylfri	2	1.5	squamulose	NR	NR