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Lichen-based indices to quantify responses to climate and air pollution across northeastern U.S.A.

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ABSTRACT. Lichens are known to be indicators for air quality; they also respond to climate. We developed indices for lichen response to climate and air quality in forests across the northeastern United States of America (U.S.A.), using 218–250 plot surveys with 145–161 macrolichen taxa from the Forest Inventory and Analysis (FIA) Program of the U.S. Department of Agriculture, Forest Service. Lichen indicator species for response to climate and air quality were selected using Indicator Species Analysis, correlations with environmental variables, and published literature. Ordinations were used to evaluate the strength and relationships of the final indices. The Pollution Index was calculated for a plot from abundances of 12 tolerant and 45 sensitive indicator species standardized by abundance of all lichen species. The Index was correlated with modeled deposition of acidifying sulfur and oxidized nitrogen and with lichen community ordination pollution axes. Analyses suggested separate response of lichens to fertilizing N (weak statistical support). The Climate Index, from abundances of 19 warmer and 47 cooler climate indicator species, was correlated with modeled minimum January and annual maximum temperatures, and with ordination climate axes. The two indices are statistically independent. Repeat sample variability for each index was 7–14.5% (lower with higher quality data), supporting detection of consistent trends of 16–20% change over time or variation across space. Variability of the Climate Index was more affected by data quality than that of the Pollution Index. The continuous gradient of Pollution Index values suggests the cleanest areas may have air pollution above a critical load to fully protect lichen communities. These Indices can be applied to track lichen responses using other data from our study regions; suitability should be tested before use outside of the study area.

KEYWORDS. Air pollution, air quality, climate, forest, indicator species, lichen, nitrogen, northeastern U.S.A., sulfur.



The study of lichen communities in forested ecosystems allows researchers to address key questions concerning important natural resources, such as biodiversity, response to climate and air quality, ability to provide ecosystem services, and sustainability of timber production (McCune 2000). Lichens have a long history as strong indicators of air quality (Hawksworth & Rose 1976) and have also been used as indicators for forest response to other

environmental factors such as climate (Bates & Farmer 1992; Ellis et al. 2007; Nash 2008; Nimis et al. 2002).

Lichen responses to environmental factors of interest, often represented by the relative abundances of positively and negatively responding species, are used to develop quantitative indices that can be used for large-scale and long-term monitoring of forest ecosystems (Jovan 2008; McCune 2000; Smith et al. 1993; Will-Wolf & Neitlich 2010). The Forest Inventory and Analysis (FIA) Program of the U.S. Department of Agriculture Forest Service has

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included lichens in its inventories of forests of the United States since 1994, to help monitor the status of forested ecosystems.

Air quality ranges from cleaner in remote, mountainous and more northern areas of our study region to poorer in large urban areas like New York City and southwestern New York state (along the northeastern edge of a large area of modeled high air pollution; NADP 2014). Gradients in air quality across the region were stronger in 1994–2004 when field data for this project were collected, than they are now (NADP 2014). Air quality has steadily improved since the early 1990's (US EPA 2014a) with sulfur (S) declining faster than nitrogen (N) deposition, but much variation remains and the entire study area remains affected to some degree by anthropogenic air pollution. No truly pristine areas exist in our study region. Historically, sulfur (SO_x) and acidic nitrogen (NO_x) gaseous air pollutants were important stressors of lichen and plant communities (Bates & Farmer 1992; McCune 1988; Muir & McCune 1988; Richardson 1988; Smith et al. 1993; van Dobben 1993). More recently, the impacts of fertilizing nitrogen (NO_x, NH₄, nitrate and nitrite compounds) have been the focus of research (Fenn et al. 2003a,b; Jovan 2009; Leith et al. 2005; Sillett & Neitlich 1996; van Dobben & ter Braak 1998). We investigated lichen response to both classes of air pollution.

Our main objective was to develop reliable biomonitoring tools for managers that capture region-wide effects on forests of local air quality and climate. The response indices we have developed are the first designed to be applicable across the entire northeastern U.S.A. Several studies have been conducted in eastern North America to evaluate lichen response to air pollution from single point sources (LeBlanc & DeSloover 1970; LeBlanc et al. 1972a; Showman 1975; Will-Wolf et al. 2005, 2010, 2011b), to general air quality in subregions (Brodo 1966; Delendick 1994; Metzler 1980; Showman & Long 1992; Will-Wolf & Jovan 2008), or to particular pollutants (LeBlanc et al. 1972b; McCune 1988).

An index to estimate forest response to local air quality is needed to supplement sparse instrument monitoring networks. The EPA operates more than 120 active monitoring sites (twice as many are inactive) across the study region, but only a third of them monitor N and S pollution and almost 75% of

all monitors are found near large cities (US EPA 2014b). Both air quality and climate are changing over the region (IPCC 2014; US EPA 2014a), although differentiating effects on lichens is a challenge in large-scale analyses. Areas of cooler climate, like montane and northern forests, usually have less urban/industrial development, less agriculture, and generally less air pollution. We tested different modeling approaches to develop statistically independent indices for air quality and climate. Our analyses include strategies for dealing with other common hurdles in air quality biomonitoring studies, such as inadequate pollution measurements for index calibration, uncertainty about indicator species, and determining model sensitivity.

MATERIALS AND METHODS

Model region. The Northeastern FIA Lichen Model Region (NE; **Fig. 1**) encompasses three ecological regions adapted from Bailey's ecoregions (Bailey et al. 1994; Cleland et al. 2007): Eastern Broadleaf Forest (provinces 221 and 222), Northeastern Mixed Forest (province 211) and Adirondack-New England Mountain Mixed Forest (province M211). Eastern Broadleaf Forest plots have warm temperate climate, mostly deciduous/hardwood forests, and relatively lower proportions of natural land cover. Northeastern and Mountain Mixed Forest plots have cool temperate climate, a mixture of deciduous/hardwood and conifer/softwood forests, and relatively higher proportions of natural land cover (**Supplementary Table S1**).

Surveys from project plots. Surveys were from three sources: 523 from standard FIA permanent plots distributed on a systematic grid, 39 from supplemental plots selected from known low and high air quality areas matched by climate across the region, and 126 from training plots used to teach FIA crews protocols for sampling lichens. Many plots have several surveys available, with repeat surveys in the same year or several years apart. Plots with missing ancillary data, with no lichen species found, or with tree basal area (BA) <5 m²/ha were excluded (Will-Wolf et al. 2006). Two full data sets were developed from this reduced pool of 598 surveys, a model development data set and a model evaluation data set.

The model development data set included only one lichen survey per plot and excluded training plots. For plots surveyed more than once, two

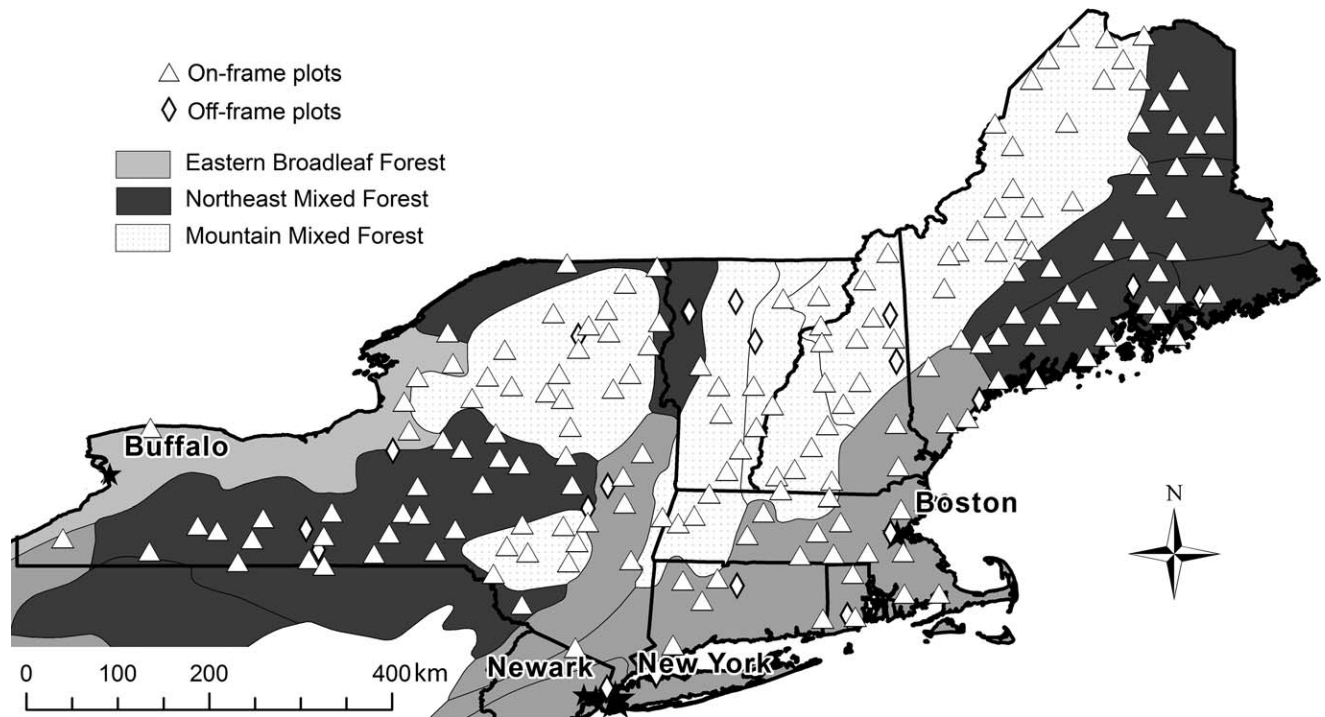


Figure 1. The Northeastern FIA Lichen Model Region (NE) showing ecoregions (shading) and plots used for model development. See text for explanation of distribution gaps. Off-frame plot symbols mostly represent 2 surveys each.

selection criteria were used: 1) the sample with the highest lichen species richness (Lichen R) and 2) samples from 1994–2001 to limit the time span of the model data. To reduce possible geographic bias in the set of 423 plots that remained, standard FIA plots were stratified by location and additional plots were removed to balance representation across the geographic area, with the constraint that the smallest state, Rhode Island, be represented by at least two plots. Each stratum encompassed approximately 0.6 degrees of latitude and longitude, and 100 m elevation range. The 1–2 plots (of no more than 4) with the highest lichen R in each stratum were retained, for an overall removal ratio of slightly less than 1:2. This strategy was chosen for two reasons. First, in quality assessment studies (Patterson et al. 2009), about 60% of tested NE region FIA crew surveys failed to pass the field data criterion (described in the next paragraph) that is based on number of species found. By removing about half of the untested standard crew plot surveys in this way, we were most likely removing many surveys that would have failed if tested. Second, and probably less important, Lichen R can be reduced by local environmental conditions other than pollution and we wished to reduce impact from other factors

(mostly not quantified) as much as possible. Forest isolation (described in section **Plot description and environmental data** below) was sometimes associated with lower Lichen R of a plot for its stratum; no removed plot had notably more forest nearby than other plots in its stratum. The resulting full model development data set had 218 plots with 161 species. Three subsets, described below in section **Response indices** were also extracted from this data set for analyses. Large gaps in distribution of these 218 FIA standard plots (**Fig. 1**) include FIA grid squares where the random permanent plot location was not forested.

The model evaluation data set included 250 samples with 139 lichen species, collected from 84 plots surveyed more than once in the same year. These included quality assessment (QA) plots (standard FIA permanent plots) sampled by FIA crew and lichen experts at the same time (“hot audits”), QA plots sampled in the same year by lichen experts blind to crew (“blind checks”), and training plots (Will-Wolf 2007). The criterion to meet the measurement quality objective (MQO) for FIA lichen data on training and QA plots is that crew capture 65% of the number of species (Lichen R) found by the expert (Patterson et al. 2009; USDA FS

2010b). Data were 76 hot audit samples from 35 standard plots (collected 1994–2002), 48 blind check samples from 24 standard plots (collected 1999–2004), and 126 samples from 25 training plots (collected 2000–2004).

Lichen data. Lichen data consisted of abundance indices for each macrolichen species found at each plot. All lichen data were collected according to standard FIA field protocols (USDA FS 2010b) from a single timed (up to 2 hour) survey of lichens on all easily accessible woody substrates above 0.5m in a 0.379 ha (0.937 acre) plot (Will-Wolf 2007; Woodall et al. 2010), with permission from landowners (names and exact locations private by law; Woudenberg et al. 2010). The lichen abundance index has four possible values:

- 1 Rare (1–3 individuals in the plot).
- 2 Uncommon (4–10 individuals in the plot).
- 3 Common (>10 individuals in the plot but fewer than half of the trunks and accessible branches have that species present).
- 4 Abundant (more than half of trunks and accessible branches in the plot have that species present).

This 4-step ordinal abundance scale qualitatively approximates a desirable logarithmic transformation (values 1 and 2 are from counts; 3 and 4 are from proportion of substrates occupied). The method intentionally favors species capture at the expense of precision of abundance estimates; this allows the rapid assessment necessary given the time limit on a survey. The sum of abundance values for all lichen species on a plot is thus more related to multiplication than to simple addition of absolute abundances (pers. comm. Bruce McCune). Across plots both individual and summed abundances are better interpreted as relative rather than absolute indices, since there is wide variation between FIA plots in amount of available substrate per plot (broadly represented by total tree BA; see **Supplementary Table S1**).

All species were identified in the lab by a professional lichenologist from field vouchers, based on morphology and chemical characters. Tools included dissecting microscopes, spot tests and UV lamps. Thin-layer chromatography and light microscopes were not used (Will-Wolf 2009). Taxonomic nomenclature mostly follows Esslinger (2014) except for *Xanthoria polycarpa*, with the caveat that cryptic species were not distinguished. Taxa were thus broader than suggested just by the name in some cases, conforming to concepts described in the 2010

FIA inventory year version of the official online FIA reference file REF_LICHEN_SPP_COMMENTS for treatment of data collected in multiple years (USDA FS 2014a; Will-Wolf & Neitlich 2010). The abundance index value “3” was assigned to about 85% of the species records in the 218-plot data set; the very rare “4” (<1% of records) and the uncommon “1” and “2” values (~14% of records) identified species with notably higher or lower abundance on a plot.

Plot description and environmental data. Plot location data included latitude (lat), longitude (long) and elevation (elev) from field GPS (Woudenberg et al. 2010). Climate variables were 1971–2000 30-year averages interpolated for each plot from the Climate Source model PRISM (Daly & Taylor 2000). In the temperate zone, lichens mostly respond to climate slowly (after 5–40 years) and often indirectly through interactions with other variables and processes (Aptroot 2009; Coppins & Ellis 2010; Insarov & Insarova 2002), so we wanted to avoid any representation in the climate variables of short-term anomalies. Moisture was represented by average annual precipitation (precip) and July relative humidity (rhJul). Temperature was represented by average minimum and maximum annual (AnTmnC, AnTmxC), January (minJan, maxJan), and July (minJul, maxJul) values.

Air quality at a plot was represented by several different variables. Direct pollution measurements could not be used because instrument data and emissions reports were too sparse, as was the case for the FIA southeastern states lichen model (McCune et al. 1997b). One variable was Polluted Sites (Poll), a binary metric contrasting 25 supplemental plots near known pollution sources with 14 supplemental plots far from any pollution source plus all FIA plots. Identified pollution sources included large cities, coal-fired power plants, a paper pulp mill, metal foundries and other heavy industry. All standard FIA plots, most of them rural, were assumed to have no local air pollution sources, as in McCune et al. (1997b).

Modeled 2002 air quality estimates for average annual wet, dry and total deposition (in kg/ha) for sulfur (S), oxidized nitrogen (N), and reduced N were derived from the Community Multiscale Air Quality Modeling System (CMAQ 2010; Tonnesen et al. 2007). Values for each plot were extracted by intersecting plot location and elevation with the 12 km grid coverage of the modeling system. The

CMAQ model averages across climate, elevation, and local pollution measurements from irregularly spaced monitoring stations across an entire 12 km grid cell. Consequently, the modeled pollution variables are correlated to some extent with climate variables, and local pollution signals are obscured.

Land cover was represented by five variables developed in a different study (Will-Wolf et al. 2014a). They are forest cover, forest connectivity, and proportion of area in three cover classes: natural/seminatural, agricultural, or developed land cover. Variables were measured in square neighborhoods centered on each plot, from the National Land Cover Database (Homer et al. 2007; Riitters 2011). Preliminary tests showed a neighborhood size of 15.21 ha was most useful for this project. All variables are ordinal indices ranging from 1–20 where each index value represents a 5% range (e.g., 1 = >0–5%, 20 = 95–100% cover or connectivity).

The plot vegetation variables tree BA (m^2/ha), percentage of tree BA in hardwoods (PcHard), and ecoregion (ecoCD; see above) were extracted from FIA databases (Woudenberg et al. 2010) for standard plots. Equivalent data were obtained by specialists for supplemental and training plots. The lichen community structure variables total number of lichen species (Lichen R) and sum of lichen abundance values (Lichen Sum) were either extracted from FIA databases or calculated from lichen data collected for expert QA, supplemental, and training plots. Summaries by ecoregion for all plot variables are in **Supplementary Table S1**.

Data exploration. We explored patterns of lichen species composition and relationships to environmental variables using nonmetric multidimensional scaling (NMS) ordination with the Bray-Curtis distance measure, in PC-ORD v5.33 (McCune & Mefford 2006). This ordination technique portrays patterns of plots based only on lichen species composition, then secondarily associates environmental variables with lichen community patterns (Legendre & Legendre 1998; McCune & Grace 2002) to facilitate interpretation. We started with the full 218-plot model development data set that had a moderately even distribution across the model region (**Fig. 1**). Plot surveys identified as far outliers based on species composition and lichen species found at fewer than five plots were excluded for ordinations as their data may not accurately reflect lichen response to environmental variables and can

reduce the power of multivariate models. The strength of ordination models was judged based on stability and stress (the extent to which the final solution reflects the original differences between pairs of plots) and on their ecological interpretability.

Composite environmental variables were derived using principal components analysis (PCA) in PC-ORD v5.33 (McCune & Mefford 2006) to assist in interpretation of lichen community patterns. Pearson and Spearman rank correlations between pairs of variables were calculated in SPSS v.21 (2012) to support interpretation of multivariate analyses and to directly evaluate responses of individual lichen species. Only correlations with $r/\rho \geq 0.2$, $p \leq 0.04$ were considered important enough to discuss.

Response indices. We identified lichen species as indicators of pollution or of climate empirically from our own data sets and also by searching the literature. Indices were developed using simple equations and spreadsheet calculations (Microsoft® Excel for Mac 2011). To select indicator species we collated multiple lines of evidence including: 1) results from Indicator Species Analysis (ISA) in PC-ORD v5.33 (McCune & Mefford 2006); 2) simple correlations between species distributions, original environmental variables and ordination-derived variables; and 3) literature reports of species indicator values. Some species uncommon in our data sets and not strongly identified as air quality indicators from our analyses were selected based on published literature for eastern North America (Brodo 1966; Cameron et al. 2007; Delendick 1994; LeBlanc et al. 1972a,b; McCune 1988; McCune et al. 1997b; Metzler 1980; Perlmutter 2010; Showman 1975; Showman & Long 1992; Will-Wolf et al. 2005), and for all of North America (Geiser & Neitlich 2007; Jovan 2008; McCune et al. 1988; Richardson 1988; Wetmore 1983). Other uncommon species with weak support from our data sets were included as climate indicators based on their distribution range (Brodo et al. 2001; Hinds & Hinds 2007). Genus-only taxa were included in the list of selected indicator species if they satisfied two criteria: 1) all tested species in that genus indicated the same extreme of that gradient, and 2) records identifiable only to that genus were included in the model data sets.

We used two subsets of the model development data set for ISA to identify pollution indicators, one with 175 and one with 144 plots. Each subset included only plots close to the latitude and

longitude range of the supplemental plots that were intentionally surveyed in both more polluted and cleaner areas. The excluded plots were mostly in northern Maine in areas with relatively lower air pollution that had no matching plots near local air pollution sources. The 175-plot subset had 141 species and included all FIA plots within the range of the supplemental plots. For the 144-plot subset (also had 141 species), we excluded FIA plots with the lowest Lichen R compared with 2–3 nearby FIA plots. ISA was run on each data subset.

ISA uses grouping variables to assess the association of each species with its strongest group, based on both faithfulness to and prevalence in that group. We developed three variables, Polluted Sites, Acidic Pollution, and Reduced N, each including 3 groups. For Polluted Sites we first assigned plots at known polluted sites to the poorer air quality group. The remainder were stratified by latitude and elevation; those plots with lower than average Lichen R for their latitude and elevation stratum were assigned to the intermediate group while those with higher than average Lichen R were assigned to the cleaner air quality group (plots with low Lichen R associated with other identifiable causes had already been removed). The Acidic Pollution variable used modeled S and oxidized N to define groups while the Reduced N variable used modeled reduced N to define groups. For each grouping variable, the poorer air quality group had fewer plots while the intermediate and cleaner air groups had about equal numbers of plots. ISA was run twice for each grouping variable, once using all groups and once including just the two extreme groups. To account for experiment-wide error, an ISA result with $0.005 < p \leq 0.05$ was considered relatively weak evidence for indication. Twelve ISA analyses of each species in the data sets were conducted in total (3 grouping variables $\times$ 2 group variants $\times$ 2 data sets).

Lists of pollution sensitive or tolerant species were compiled from the 12 ISAs, up to 12 direct pairwise correlation analyses for each species (Correlations of variables Polluted Sites, modeled S, oxidized N, or reduced N with abundance for each species at plots in each of the two ISA data subsets and the full data set) and from literature. We selected indicator species that were supported by at least two strong pieces of evidence ($p < 0.005$ for quantitative results, multiple publications) and we gave more weight to our quantitative results versus literature reports.

For ISA to identify climate indicators, we restricted the model development data set to 191 plots with 161 species by excluding all plots where poor air quality was demonstrated. PCA on the plot environmental data for these 191 plots with a centered variance-covariance cross products matrix (each factor contributes in proportion to its own variance) was used to extract an axis suitable to use as a synthetic climate variable (Legendre & Legendre 1998; McCune & Grace 2002). We assigned plots to four equal-sized southern/warm to northern/cool climate groups based on each of three grouping factors: latitude and elevation, the PCA-derived synthetic climate variable, or the two strongest modeled temperature factors: maximum annual temperature and minimum January temperature. ISA was run with each grouping factor and with either all groups or only the two extreme groups. Six ISA analyses of each species were conducted in total (3 grouping variables $\times$ 2 group variants).

Species identified as indicators of either the warmest or the coolest groups from the 6 ISAs, from direct correlation analyses, and from literature were added to the list of potential indicator species. Six pairwise correlations were calculated for each species: between each species abundance and latitude, modeled maximum annual temperature, or modeled minimum January temperature, for both the full 218-plot dataset and the 191-plot climate subset. The synthetic PCA climate variable was correlated with species in the 191-plot data subset, making a total of seven correlations per species. Again, selected indicator species were supported by two or more strong pieces of evidence and we gave more weight to our quantitative results versus literature.

Assess reliability of response indices. Using the 84 plots in the model evaluation data set with 250 repeat samples, we first calculated response indices from formulas we developed using indicator species. Next, we calculated deviation of crew sample index from expert sample index for each plot (McCune et al. 1997a). Average deviation for each plot was calculated separately for passing crew samples and those that failed to meet the FIA standard MQO. Average deviations (sign ignored) and bias (sign included) of crew index values from the expert, plus full variability including the expert, for samples from the same plot were compared to assess the resample variability and establish the reliability for each index.

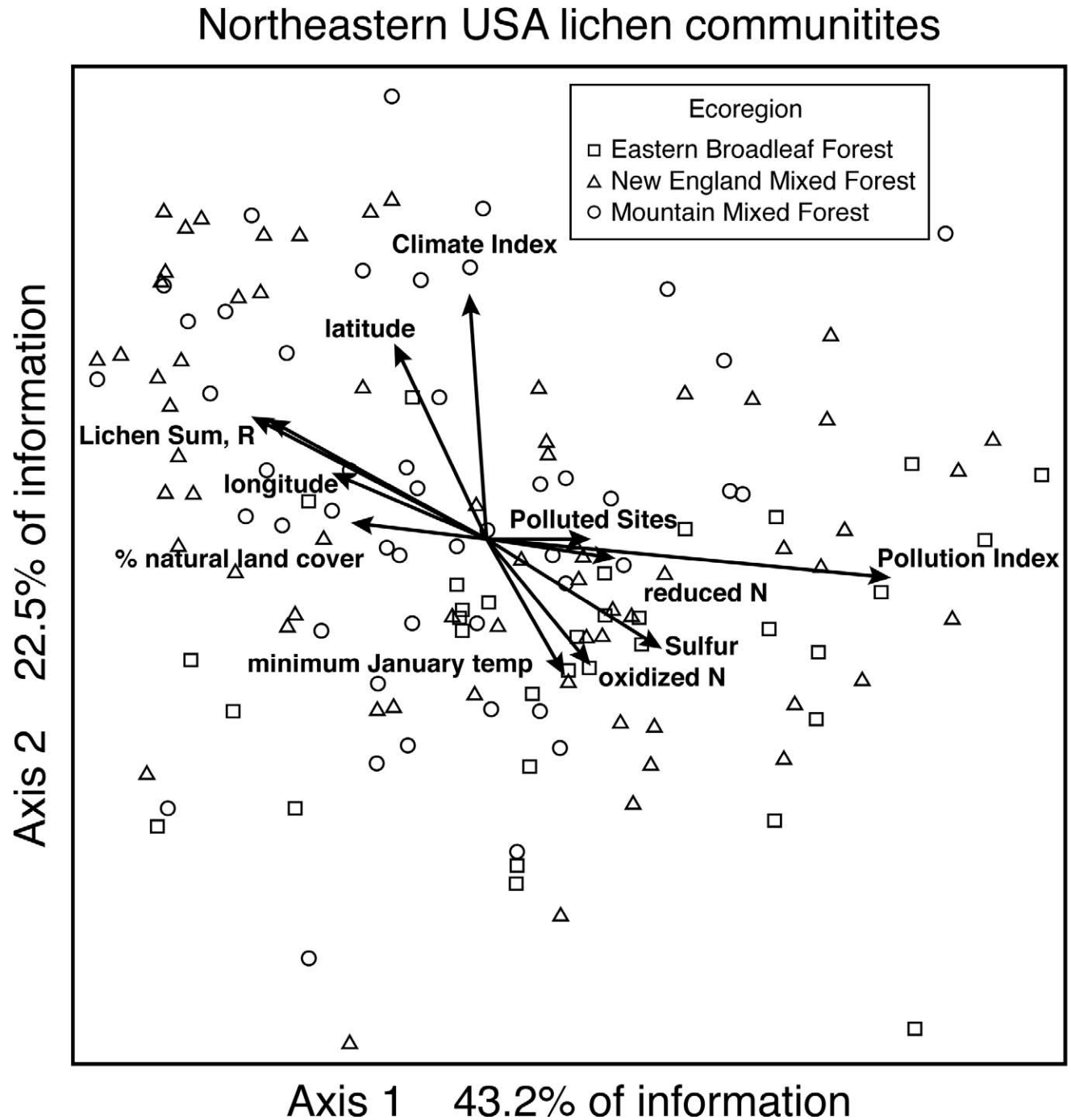


Figure 2. NMS ordination of 144 plots with 44 species, emphasizing pollution response.

An additional 5% (to represent unstudied variability or changes in plot conditions over time that affect lichen species composition) was added to the calculated resample variability to develop estimates for the amount of change in plot conditions over time that can be detected by each index to support interpretation of how lichens indicate environmental conditions and identify regional trends.

RESULTS AND DISCUSSION

Data exploration and insights. A biplot of the strongest NMS air quality ordination helps visualize the correlation structure between lichen community gradients, climate, air quality, and land use (**Fig. 2**: 144 plot data subset, 44 species at >5 plots; significant 3d solution captured 79.9% of original information; final stress 18.73; final instability

0.004). Indices from this ordination were too unreliable for use to directly monitor trends. Repeat sample variability of a plot Pollution Index from Axis 1 was 35–40%, requiring consistent change of 40–45% of the full Index range to detect a trend, too high to be useful for monitoring. Climate variables had Pearson correlation $r^2 = 0.231$ – 0.314 with Axis 2, indicating this axis was unsuitable for a Climate Index because 65–70% of lichen variation was unrelated to climate. While this ordination was inadequate for development of response indexes, it was the only fair comparison of the relative importance of air quality and climate to lichens, suggesting that air quality accounted for almost twice as much variation in lichen communities as did climate. Attempts to develop independent pollution and climate indexes followed the analysis steps recommended by Will-Wolf & Neitlich (2010). The best single ordination from the full 218-plot model development data set had both climate and air pollution variables strongly correlated with a single axis, as did the best ordination from the 175-plot data subset emphasizing air quality response. The most robust climate ordination, from the 191-plot data subset emphasizing climate response, had repeat sample variability of the strongest Climate Index axis higher than that reported above for the best air quality ordination.

Pairwise correlations of environmental variables with each other illustrated general environmental patterns across the region. The full data set and all three data subsets were used for different steps in model development; each was a valid but incomplete representation of relationships among lichens, air quality and climate. So we have reported ranges of correlations between environmental variables for multiple data sets as our most accurate estimates of relationships. Co-occurrence of lower air pollution and cooler climate was very strong across the region based on our variables (r/ρ 0.35–0.8 for 144 plots, 0.6–0.86 for 218 plots, $p < 0.005$). Lichen species richness and abundance increased with both cooler climates (r/ρ 0.4–0.6 for 144, 191, or 218 plots, $p < 0.01$) and cleaner air quality (r/ρ 0.37–0.6 for 144, 175, or 218 plots, $p < 0.01$). Temperature variables co-varied strongly (r/ρ 0.85–0.95) for the full data set and all three data subsets; they were strongly correlated with latitude, less with elevation. Minimum January temperature was the most strongly correlated with lichen community compo-

sition ($r/\rho = 0.5$ – 0.7 with relevant ordination axes, $p < 0.005$). Relative humidity was mostly independent of temperature, was strongly correlated with longitude (largest ρ 0.72 for 218 plots, $p < 0.0005$), and might independently influence lichen community composition somewhat. Plots with more nearby natural land cover (the strongest correlations of the five land cover variables) usually had cooler climates, more lichens and less air pollution (significant but weak correlations). Attempts to stratify plots based on amount of natural land cover failed to strengthen analyses. Axis 2 from PCA of environmental variables (191-plot data subset) represented 22.7% of all variation among environmental variables, for evaluation of climate indicator species. It was most strongly correlated with elevation (Pearson $r^2 = 0.719$) and temperature (Pearson $r^2 = 0.513$ – 0.653), and was weakly correlated (Pearson $r^2 < 0.2$) with all non-climate variables including air pollution.

Preliminary results suggested possibly different responses by lichens to acidic and fertilizing N air pollution. Modeled sulfur (S) and oxidized nitrogen (N) had similar relationships to lichen community composition, illustrated by their vectors on the air quality ordination (**Fig. 2**; correlation $r = 0.5$ – 0.6 with Axis 1). They were strongly correlated with each other (r/ρ 0.86–0.9, $p < 0.0005$) and with modeled temperature (r/ρ 0.5–0.7, $p < 0.0005$) for different data sets. In contrast, modeled reduced N was less correlated with S and oxidized N (r/ρ 0.6–0.8, $p < 0.0005$), much less correlated with modeled temperature (r/ρ 0.3–0.53, $p < 0.01$) for the same data sets, and had a different weaker relationship to lichen community composition as illustrated by its separated and shorter vector on **Fig. 2**. Its apparent closer alignment with the Pollution Index there was a side effect of its lack of correlation with climate; both S and oxidized N had stronger correlations with Axis 1 of **Fig. 2** and directly with the Pollution Index (see section **Pollution index evaluation** below). Lichen species richness and abundance had stronger negative correlations with S (ρ -0.56 to -0.6 , 144 plots) than with N variables (oxidized N the stronger; ρ -0.42 to -0.46 , 144 plots). Low correlations of lichen species richness and abundance with the binary variable Polluted Sites (ρ -0.37 to -0.46 , 144 plots) plus the weak relationship of the latter to lichen community composition (short vector on **Fig. 2**) suggested our assumption of

relatively cleaner air quality at most standard FIA plots was not valid for this region. Polluted Sites correlated most strongly with modeled S, suggesting it represented primarily acidic air pollution.

After the failure of ordination models to develop sufficiently independent and reliable response indices, our final approach was to develop a climate index and a pollution index, each from different models based on selected lists of indicator species. This approach proved successful. The best ordination models informed the development of both indices.

Air quality model—Pollution index. Many species had significant responses to both acidic air pollution and reduced N from our analyses; published reports often suggested species were generally responsive to air pollution without distinguishing between classes of compounds. Based primarily on the direct correlations reported in the previous section, we interpreted that species responses to modeled S, oxidizing N, or the variable Polluted Sites all represented responses primarily to acidic air pollution. We interpreted that species response to modeled reduced Nitrogen probably was the best representation from our study of species response to fertilizing Nitrogen air pollution in general.

Selection of final indicator species (**Table 1**) favored pollution-tolerant species with cool climate distributions and pollution-sensitive species with warm climate distributions. Indicator species that were both pollution-tolerant and warm climate indicators, or were both pollution-sensitive and cool climate indicators, fostered correlation between the air quality and climate response indices. Several of the selected species were assigned to only one of the possible indicator lists, based on the relative strengths of their responses within the NE model region. This semi-quantitative selection process that emphasized response to air quality coincident with relative indifference to climate or with climate response counter to the region-wide correlation between higher pollution and warmer climate, was required to ensure the statistical independence of the two indices so the Pollution Index could be used without needing to quantitatively account for response to climate and vice versa. Preliminary tests of several indices developed using all species, or longer lists of species with any evidence of response either to any form of air pollution (S, both forms of

N, or Polluted Sites), or only to acidic air pollution (S, acidic N, or Polluted Sites), resulted in indices too strongly correlated with climate variables (Pearson $r^2 > 0.5$). Preliminary tests of several indices with shorter indicator lists of only those species with very strong responses (in either or both directions), either to any form of pollution or only to acidic pollution, resulted in indices with notably higher repeat sample variability (~ 25 – 30% of full index range) that did not support trend monitoring as well as our final index. *Flavoparmelia caperata* is an example of our emphasis on our own quantitative results; it is reported in literature as both sensitive and tolerant to air pollution, although we included it as an indicator relatively sensitive to air pollution based on several quantitative results (**Table 1**). Another potentially counter-intuitive result is our selection of both *F. caperata* and *Punctelia rudecta* as pollution sensitive indicators, but selection of the closely-related species, *Flavopunctelia flaventior*, as a pollution tolerant indicator. Evidence for the pollution tolerance of *F. flaventior* was relatively weak (**Table 1**), but this species had one correlation with cool climate (not included under climate in **Table 1**) and helped to fill our need for cool-climate pollution-tolerant indicators to support a Pollution Index independent from climate.

Our best Pollution Index, based on the full selected indicator species list in **Table 1** of 12 taxa tolerant and 45 taxa sensitive to acidic pollution, was calculated from this equation:

Pollution Index

$$= 1 + \left(\frac{\sum \text{abundance acidic tolerant species} - \sum \text{abundance of acidic sensitive species}}{\sum \text{abundance all species}} \right)$$

where “acidic” is Sulfur + acidic Nitrogen pollution. “1” was added to the quotient so the formula always returns a positive value for the index. Values of this Index can range from 0 for cleanest air and/or lowest risk of pollution impact in the region (only cleaner air indicators found), to 2 for dirtiest air and/or highest risk of pollution impact (only polluted air indicators found). The smallest calculated value for the 218 plot data set was 0.2432, so the actual index range was less than is possible. Indicator species

Table 1. Indicator species for air quality or climate determined using Indicator Species Analysis (ISA), correlations (Corr), and North American literature reports (NA lit). Selected pollution indicator species are either sensitive (S) or tolerant (T) to acidic air pollution; selected climate indicator species are associated with either warmer (W) or cooler (C) temperature. Species with ¹ after the letter in either of the Selected Species columns had equally strong response to fertilizing N pollution. **Pollution indication codes:** 1 = generally pollution sensitive, 2 = sensitive to acidic pollution, 3 = sensitive to fertilizing N pollution, 4 = generally tolerant, 5 = tolerant of acidic pollution, 6 = tolerant of fertilizing total N, 7 = tolerant of reduced N. Numbers are in order of strength, stronger (est) to left. **Climate indication codes:** c = cooler or w = warmer, N = northern distribution, E NA = eastern, SE = southeastern. A number or letter for an indication code followed by “(1)” is supported by only one strong result; all others are supported by at least two strong results. All ISA have $p \leq 0.05$; ~50% of results have $p \leq .005$. Correlation results have $r/\rho \geq 0.2$, $p \leq 0.04$; ~40% of results have $p \leq 0.005$. To summarize indicator strength, stronger Selected Species have their letter in bold; the weaker are in regular text. Abbreviations: N = number of plots, of total 218 for most species. Species with * after the N column value were in only the 250-sample model evaluation data set.

Indicator species	N	Air quality indicators			Selected species	Climate indicators			Selected species
		ISA	Corr	NA lit		ISA	Corr	NA lit	
<i>Ahtiana aurescens</i>	14						c	N	C
<i>Bryoria</i> sp.	4						c		C
<i>Bryoria capillaris</i>	4		2,3			c		N	C
<i>Bryoria furcellata</i>	51	1,2,3	2,3	2	S ¹	c		N	C
<i>Bryoria fuscescens</i>	6	3,1	2,3	3		c		N	C ¹
<i>Bryoria nadvornikiana</i>	13	1,2,3	2,3			c	c		C
<i>Bryoria trichodes</i> sensu lato	5		2	2	S	c(1)	c(1)	N	C
<i>Candelaria concolor</i>	42	5,7,4	7	4,5,6	T ¹				
<i>Cetrelia olivetorum</i>	17						c	N	C
<i>Cladonia chlorophaea</i> gp	38	1,2	2,3	4	S	c			
<i>Cladonia cristatella</i>	15	4		4	T		w	E NA	W
<i>Cladonia macilenta</i> var <i>bacillaris</i>	14						w	E NA	W
<i>Cladonia squamosa</i>	7	1	2	6	S				
<i>Collema nigrescens</i>	2					c(1)	c(1)	E NA	C
<i>Collema subflaccidum</i>	4		3,2			c		E NA	C
<i>Evernia mesomorpha</i>	112	2,1,3	2,3,1		S ¹	c	c		C
<i>Flavoparmelia caperata</i>	123	1,2,3	1	1,2,4,6	S	w	w		W
<i>Flavopunctelia flaventior</i>	5	4(1)	4(1)		T				
<i>Flavopunctelia soledica</i>	2			1	S				
<i>Heterodermia speciosa</i>	7		2,3			c		E NA	C
<i>Hyperphyscia adglutinata</i>	1*			1,4	T				
<i>Hypogymnia krogiae</i>	15	2,1,3	2,3			c	c	N	C
<i>Hypogymnia physodes</i>	142	1,2,3	2,3,1	4,5,6	S ¹	c			
<i>Hypogymnia tubulosa</i>	19	2,1,3	2,3	2	S ¹	c			
<i>Imshaugia aleurites</i>	36	1,3,2	3,2	1	S ¹	c			
<i>Leptogium cyanescens</i>	20	2,3,1	3,2	1	S ¹		w	E NA	W
<i>Leptogium saturninum</i>	4		3,2	3		c		N	C
<i>Lobaria pulmonaria</i>	46	2,1,3	2,3	1,2,3	S ¹	c	c		C
<i>Lobaria quercizans</i>	26	1,3,2	2,3	1	S ¹	c			
<i>Melanelixia fuliginosa</i>	15			2,6			c	N	C ¹
<i>Melanelixia subaurifera</i>	131	2,1,3	2,3,1	2	S	c			
<i>Melanohalea halei</i>	8					c	c		C
<i>Melanohalea olivacea</i>	5					c		N	C
<i>Melanohalea septentrionalis</i>	31	2,1,3	2,3			c	c		C
<i>Menegazzia terebrata</i>	8	3,1	2,3	2,3	S ¹				
<i>Myelochroa galbina</i>	56	2,1,3	2,3	2	S ¹	c			
<i>Nephroma helveticum</i>	3			1,2,3	S ¹	c			
<i>Nephroma resupinatum</i>	1			1,2,3	S ¹				
<i>Parmelia saxatilis</i>	6	3(1)	3(1)				w		W ¹
<i>Parmelia squarrosa</i>	81	2,1,3	2,3,1	1,2,3	S ¹		w		W
<i>Parmelia sulcata</i>	190	2(1)	2(1)	4,5,6	T ¹	c		N	C
<i>Parmeliopsis ambigua</i>	15	1	2,3		S ¹	c			

Table 1. Continued.

Indicator species	N	Air quality indicators				Climate indicators			
		ISA	Corr	NA lit	Selected species	ISA	Corr	NA lit	Selected species
<i>Parmeliopsis capitata</i>	15	2(1)	2(1)			c			C
<i>Parmeliopsis hyperopta</i>	7		2,			c	c		C
<i>Parmotrema</i> sp.	3*						w		W
<i>Parmotrema crinitum</i>	2			6			w	SE	W ¹
<i>Parmotrema hypotropum</i>	5		2		S	w	w		W
<i>Parmotrema margaritatum</i>	3*						w		W
<i>Parmotrema perforatum</i>	3		5			w	w		W
<i>Parmotrema perlatum</i>	2						w		W
<i>Phaeophyscia hirtella</i>	2			1	S				
<i>Phaeophyscia pusilloides</i>	67			1,4,5	T		c		C
<i>Phaeophyscia rubropulchra</i>	151		5,7	4,5	T				
<i>Physcia adscendens</i>	19	4,5,7	7,5	5,6	T ¹				
<i>Physcia aipolia</i>	24			4,6			c		C
<i>Physcia millegrana</i>	98	4,5,7	5,7,4	4,5,6,7	T ¹	w	w		W
<i>Physcia stellaris</i>	71			4,5,6					
<i>Physciella chloantha</i>	6	4,5,7	4		T				
<i>Physconia detersa</i>	41	1		1	S	c	c		C
<i>Physconia leucoleiptes</i>	9	4,5,7	4		T ¹		c		C
<i>Platismatia glauca</i>	28	1,3,2	2,3		S	c			C
<i>Platismatia tuckermanii</i>	46	2,1,3	2,3,1	1	S ¹	c			
<i>Pseudevernia consocians</i>	4						c		C
<i>Pseudocyphellaria crocata</i>	4		2,3	1,3	S ¹	c			
<i>Punctelia caseana</i>	28		5			w		E NA	W
<i>Punctelia rudecta</i>	138	1,3,2	1,3,2	4,6	S ¹		w	E NA	W
<i>Pyxine soorediata</i>	45	1,3,2	2,3	1	S ¹	c			C
<i>Ramalina americana</i>	22	2,1,3	2,3	2	S ¹	c			
<i>Ramalina dilacerata</i>	16	1,2,3	2,3			c		N	C
<i>Ramalina roesleri</i>	3			3		c		N	C ¹
<i>Tuckermannopsis americana</i>	43	1,3,2	2,3		S				
<i>Tuckermannopsis ciliaris</i>	12		2,3	1	S ¹	c			
<i>Tuckermannopsis orbata</i>	36	1,2,3	2,3		S	c	c		C
<i>Usnea</i> sp.	17					c	c		C
<i>Usnea cavernosa</i>	1			1	S		c	N	C
<i>Usnea ceratina</i>	10	1,2,3	3,2	1,2	S ¹	c			C
<i>Usnea filipendula</i>	11	1	2,3			c		N	C
<i>Usnea fulvoreagens</i>	4		2	1	S		w		W
<i>Usnea glabrata</i>	1						c		C
<i>Usnea glabrescens</i>	2			1	S		c		C
<i>Usnea hirta</i>	59	2,1,3	2,3,1		S	c		N	C
<i>Usnea longissima</i>	4			1	S ¹	c		N	C
<i>Usnea mutabilis</i>	4				S		w		W
<i>Usnea occidentalis</i>	4				S		c		C
<i>Usnea strigosa sensu lato</i>	10	1			S	w	w		W
<i>Usnea subfloridana</i>	52	2,1,3	2,3,1		S ¹	c		N	C
<i>Usnea trichodea</i>	5	1			S		w		W
<i>Usnocetraria oakesiana</i>	71	1,2,3	1,2,3	1,4	S	c	c		C
<i>Vulpicida pinastri</i>	35	3,1,2	2,3		S		c		C
<i>Xanthomendoza fallax</i>	1*			4,6	T ¹				
<i>Xanthomendoza hasseana</i>	5			6			c		C
<i>Xanthoria polycarpa</i>	5	1		2,6		c(1)	c(1)		C

Table 2. Repeat-sample variability for Climate and Pollution Indexes from plots sampled between 1994 and 2005. Positive bias for the Pollution Index means the crew sample rates the plot as more polluted than the expert sample; negative bias means the opposite. Positive bias for the Climate Index means the crew sample rates the plot as in cooler climate than the expert sample; negative bias means the opposite. Range for the Pollution Index is 0.2432–2 (range 1.7568) and is 0–2 (range 2) for the Climate Index. Average bias (% of model range) is calculated from original signed values for deviation from expert; average deviation (% of range) is calculated with sign ignored.

Training plots			Standard plots	
Pollution Index				
Field quality status	pass MQO	fail MQO	pass MQO	fail MQO
No. plot samples	87	16	47	16
90% of deviations	within 11.3% of model range	within 13.8% of model range	within 10.8% of model range	within 14.8% of model range
Average bias	0.012 (0.68%)	0.093 (5.28%)	−0.012 (0.69%)	−0.066 (3.74%)
Average deviation	0.111 (6.29%)	0.131 (7.47%)	0.099 (5.62%)	0.121 (6.88%)
Climate Index				
Field quality status	pass MQO	fail MQO	pass MQO	fail MQO
No. plot samples	87	16	47	16
90% of deviations	within 9.7% of model range	within 16.1% of model range	within 12.2% of model range	within 16.7% of model range
Average bias	−0.005 (0.26%)	−0.032 (1.59%)	0.007 (0.33%)	−0.166 (8.32%)
Average deviation	0.101 (5.10%)	0.179 (8.94%)	0.107 (5.35%)	0.246 (12.28%)

abundance index was entered into the formula to allow the index to be affected by relative abundances of tolerant versus sensitive indicators as well as their presence. This increased the sensitivity of the index and reduced number of ties in index values, since many plot samples included at least one species in each response class.

Our strongest index for response to fertilizing N pollution, using 14 tolerant taxa and 30 sensitive taxa, was not sufficiently independent of the acidic pollution index (correlations with the “acidic” Pollution Index were $r/\rho = 0.89$ – 0.94 from different data sets) to recommend for use. Twenty-nine (including five very common species) of the 57 Pollution Index indicator species were equally strong indicators in the same direction for response to fertilizing N pollution, while five of 15 additional indicators for response to fertilizing N pollution were also equally strong climate indicators (**Table 1**, sensitive: *Bryoria fuscescens*, *Parmotrema crinitum*, *Ramalina roesleri*; tolerant: *Melanelixia fuliginosa*, *Parmelia saxatilis*). The 10 remaining species were notably stronger indicators for response to fertilizing N (sensitive: *Anaptychia palmulata*, *Leptogium austroamericanum*, *L. corticola*, *Lobaria scrobiculata*, *Ramalina thrausta*; tolerant: *Cladonia macilenta*, *Melanohalea elegantula*, *Physcia stellaris*, *Xanthomendoza hasseana*, *Xanthoria polycarpa*), evaluated as described in Methods.

Pollution index evaluation. Quantitative evaluation of the pollution model was based on three criteria: 1) Is the Pollution Index reliable enough to

support useful pattern and trend analysis? 2) Is it sufficiently representative of air quality and independent of climate response? 3) Do non-model plots fit adequately to the model when tested?

- 1) Reliability and repeatability. These aspects of our acidic pollution index were tested using the model evaluation data set of 250 samples at 84 plots. Repeatability of indices for training plots and standard plots were evaluated separately; training plots at only a few sites represented a narrower range of environmental conditions and focused on crew performance at the beginning of a season, while standard plots represented much of the available range of environmental conditions (**Fig. 1**, **Supplementary Table S1**), as well as crew performance in the context of routine sampling conditions and stresses during the field season.

Training and field season repeatability varied slightly. For training, the average unsigned deviation and signed bias of crew values from passing samples were notably smaller than for failing samples (**Table 2**). Passing samples had little bias, while failing samples had positive bias: they recorded a plot to be, on average, 5.3% of index range more polluted than the expert. For standard plots, again the average unsigned deviation and signed bias of passing values were smaller than for failing samples, by about the same margin as for training samples. Passing samples again had little bias, while failing samples had more bias, but this time it was negative: a plot was recorded as about 4% less polluted than the expert. Crew performance on field season QA evaluation was stronger than at training, for both passing and failing samples.

Table 3. Pollution Index, with environmental and lichen community variables plus Climate Index, summarized by five categories spanning equal parts of the full Pollution Index range of 1.7568 (0.2432–2) for 218 model plots. Category 1 includes plots with the cleanest air (Cln); category 6 includes plots with the most polluted air (Poll). “Avg” = average ($\pm$ 1 standard deviation); “Rng” = actual range, reported for most variables. Pollution Index is mapped by category in Fig. 4A.

Category		Pollution Index	Polluted plots	Total S, kg/ha	Oxidized N, kg/ha	Reduced N, kg/ha	Index, % natural land cover	No. of lichen taxa	Sum of lichen abundance	Climate Index
1 (Cln)	Avg	0.446 ($\pm$ 0.086)	2 of 69	6.4 ($\pm$ 2.5)	4.6 ($\pm$ 1.7)	1.9 ($\pm$ 0.8)	17.9 ($\pm$ 2.0)	20.1 ($\pm$ 8.1)	52.1 ($\pm$ 20.1)	1.288 ($\pm$ 0.256)
(N=69)	Rng	0.243–0.593	plots	3.6–13.3	2.7–9.5	1.1–5.3	9–20	6–37	16–95	0.440–1.833
2	Avg	0.776 ($\pm$ 0.108)	2 of 62	9.4 ($\pm$ 3.4)	6.6 ($\pm$ 2.2)	2.7 ($\pm$ 1.0)	16.7 ($\pm$ 3.4)	12.5 ($\pm$ 4.8)	30.8 ($\pm$ 11.0)	1.068 ($\pm$ 0.295)
(N=62)	Rng	0.605–0.941	plots	3.9–18.4	2.5–14.1	1.2–6.3	5–20	3–22	8–55	0.250–1.781
3	Avg	1.092 ($\pm$ 0.101)	6 of 54	11.8 ($\pm$ 3.6)	7.7 ($\pm$ 1.9)	3.0 ($\pm$ 0.9)	14.3 ($\pm$ 4.1)	9.4 ($\pm$ 4.0)	22.5 ($\pm$ 8.8)	0.990 ($\pm$ 0.272)
(N=54)	Rng	0.950–1.306	plots	4.6–24.2	3.3–13.5	1.3–5.2	5–20	2–19	5–44	0.353–1.600
4	Avg	1.481 ($\pm$ 0.104)	10 of 22	13.0 ($\pm$ 2.6)	7.9 ($\pm$ 1.8)	3.6 ($\pm$ 1.0)	9.9 ($\pm$ 5.8)	6.7 ($\pm$ 2.3)	17.1 ($\pm$ 5.8)	1.085 ($\pm$ 0.221)
(N=22)	Rng	1.333–1.667	plots	8.6–16.5	4.7–13.6	2.4–6.6	1–18	3–13	8–30	0.667–1.692
5 (Poll)	Avg	1.916 ($\pm$ 0.122)	5 of 11	19.9 ($\pm$ 13.3)	9.5 ($\pm$ 3.8)	4.3 ($\pm$ 2.1)	10.6 ($\pm$ 4.8)	3.8 ($\pm$ 1.8)	10.7 ($\pm$ 5.6)	1.016 ($\pm$ 0.585)
(N=11)	Rng	1.714–2.0	plots	6.8–45.9	4.6–15.9	1.7–8.1	1–15	1–7	2–21	0.0–2.0

With most deviations (including experts and failing crew) within 11–15% of the model range (Table 2) and adding 5% for variation over time from other sources, the Pollution Index would need to change on average by 16–20% of the model range in a consistent direction to detect a trend over time or a pattern across a large region. A reasonable extrapolation is that an entire set of standard FIA plots whose data quality matches that estimated from tests ($\sim$ 40% passing) would have variability about 13% of model range, and bias about 2%. Evaluation of passing repeat samples indicated that if at least 90% of samples met the field MQO, bias would be negligible, repeat sample variability would be about 6%, and a consistent trend or variation in pattern of 12% or less could be detected.

- 2) Sufficiently representative of air quality and independent of climate response. Of all variants tested, our Pollution Index had the strongest correlation with lichen response as represented by the air quality ordination (Fig. 2). The Pollution Index captured 37% of the variation in lichen community composition as represented by axis 1 (i.e., Pearson correlation $r^2 = 0.853$ of the index with ordination Axis 1 * $r^2 = 0.432$ between axis 1 distances between plots and total distances, to represent the total information captured by Axis 1, Fig. 2). The Pollution Index also had strong direct correlations with other pollution variables ($r^2=0.3$ – 0.5 with S, weaker with acidic N; $r^2=0.2$ – 0.37 with reduced N) in the four model data sets that confirmed greater linkage of our index with acidic air pollution. The index had only weak correlations with our Climate Index (see below): $\rho^2 = 0.066$ (144 plots) to $\rho^2 = 0.144$ (218 plots). These small non-significant correlations clearly indicate that

the Pollution and Climate Indices are adequately independent of one another. Plots in the 218-plot data set were assigned to 5 classes based on their Pollution Index score (equal range for each class) and were compared against values for other variables and the Climate index (Table 3) for plots in that class. Averages for pollution and lichen community description variables by Pollution index class showed clear trends of lower lichen diversity and more pollution with higher values of the Pollution Index. In contrast, Climate Index values did not follow that trend; only for Pollution Index class 1 were the Climate Index average and range skewed toward cooler plots. Many plots in Pollution Index class 1 were excluded from the two pollution model development data subsets to increase the likelihood of developing a Pollution Index independent of climate. The Pollution Index was negatively correlated ($\rho = -0.52$ to -0.58 , $p < 0.0005$) with an index representing proportion of natural land near a plot (the strongest of our land cover variables), and the class average for our index of natural land cover decreased as pollution increased. This suggests carefully blocked field site design will be needed for studies that seek to identify independent responses of lichens to air quality and landscape pattern.

- 3) Good fit of non-model plots to model. Application of a response index is often facilitated by defining an extrapolation limit for future index values, and providing a quantitative benchmark to decide when and where the index/model fits poorly to new plot data. For the FIA Program extrapolation limits for response indices have been suggested to be about 10% beyond the full model range of the index; evaluation of fit depends on the type of model (Will-Wolf &

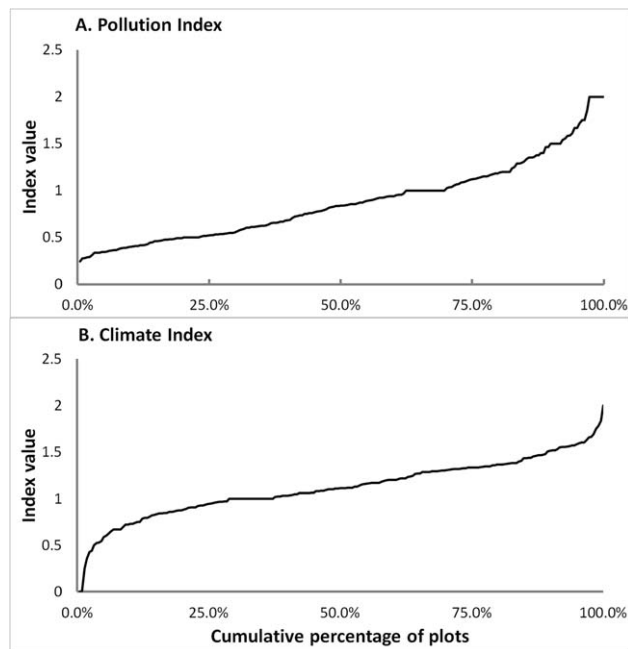


Figure 3. Cumulative distributions of New England (NE) region lichen response indices. **A.** The Pollution Index. **B.** The Climate Index.

Neitlich 2010). For the full 218-plot model development data set, the Pollution Index ranged from a maximum of 2 for the most polluted plots to a minimum of 0.2432 for the relatively cleanest plot, with a full range of 1.7568. Since the maximum value of 2 for the Pollution Index was recorded for model plots, it is not possible for a plot to have a value beyond an upper extrapolation limit. The estimated minimum 10% extrapolation value is 0.0676, so a plot value lower than this would be possible. However, the minimum possible value of “0” for this Pollution Index, indicating a plot had only pollution-sensitive indicator lichen species, is a reasonable outcome given the large number of indicator species defined as sensitive and the few defined as tolerant. Since values below the 10% extrapolation limit would thus be reasonable for the Index, we do not recommend excluding them from analyses.

The cumulative distribution of Pollution Index values for the full 218-plot data set (**Fig. 3A**) showed a reasonably linear increase over the first two thirds of its range, increasing nonlinearly after that to plateau at the maximum value (7 plots). Of the 598 unique plot samples we analyzed from 257 plots in all data sets, only one plot repeat sample had none of the acidic pollution indicator species, no additional plots had the maximum Index value, and none had a value below the model minimum. So the model, based on

indicator species from a maximum of 218 model plots and index range defined from those plots, fitted well to the 380 non-model plot samples we tested.

If the proportion of plots lacking any indicator species increases notably over time or when the index is applied to areas outside the model region, then fit of the model should be reevaluated. If the proportion of plots with the maximum or minimum value is greatly increased over what we found, then the Pollution Index becomes insensitive at that end of the gradient. No standard way to evaluate fit of an index from an indicator species model has been recommended for the FIA Program (Will-Wolf & Neitlich 2010).

Pollution index interpretation. Evaluation confirmed that the Pollution Index was sufficiently independent of the final Climate Index to support separate evaluations of response to pollution and climate without considering the other variable. Detection of a consistent pattern of about 16–20% change over time even with only moderately reliable field data is small enough to be useful for trend analysis over the entire model region. Approximate bias for the full model set given our estimated data quality was about 1% more polluted than actual. For the set of all 589 standard crew samples available for the region, the bias might be about 2–3% more polluted than actual.

The greater sensitivity of Pollution Index values at the upper end of the Pollution gradient (but before the Index reached its maximum value; **Fig. 3A**) was almost entirely related to lower lichen species richness (**Table 3**, categories 4 and 5), where the presence or absence of each species that is not a pollution-tolerant indicator had a strong effect on index value. Plots with maximum value 2 (Index not sensitive to differences between plots) had 5 or fewer species, and all but one of the more polluted plots (**Table 3**, categories 4 and 5) had 10 or fewer species. The sensitivity of this index could be extended at the polluted end by scoring plots with value 2 somewhat higher depending on how many of the pollution indicators are found; a plot with only one pollution-tolerant indicator species probably has worse air quality than a plot with five pollution-tolerant indicator species. A related strategy to extend sensitivity at the cleaner end of the gradient would be more difficult to devise, since more versus fewer pollution-sensitive indicator species might well signal response to a factor other than air quality.

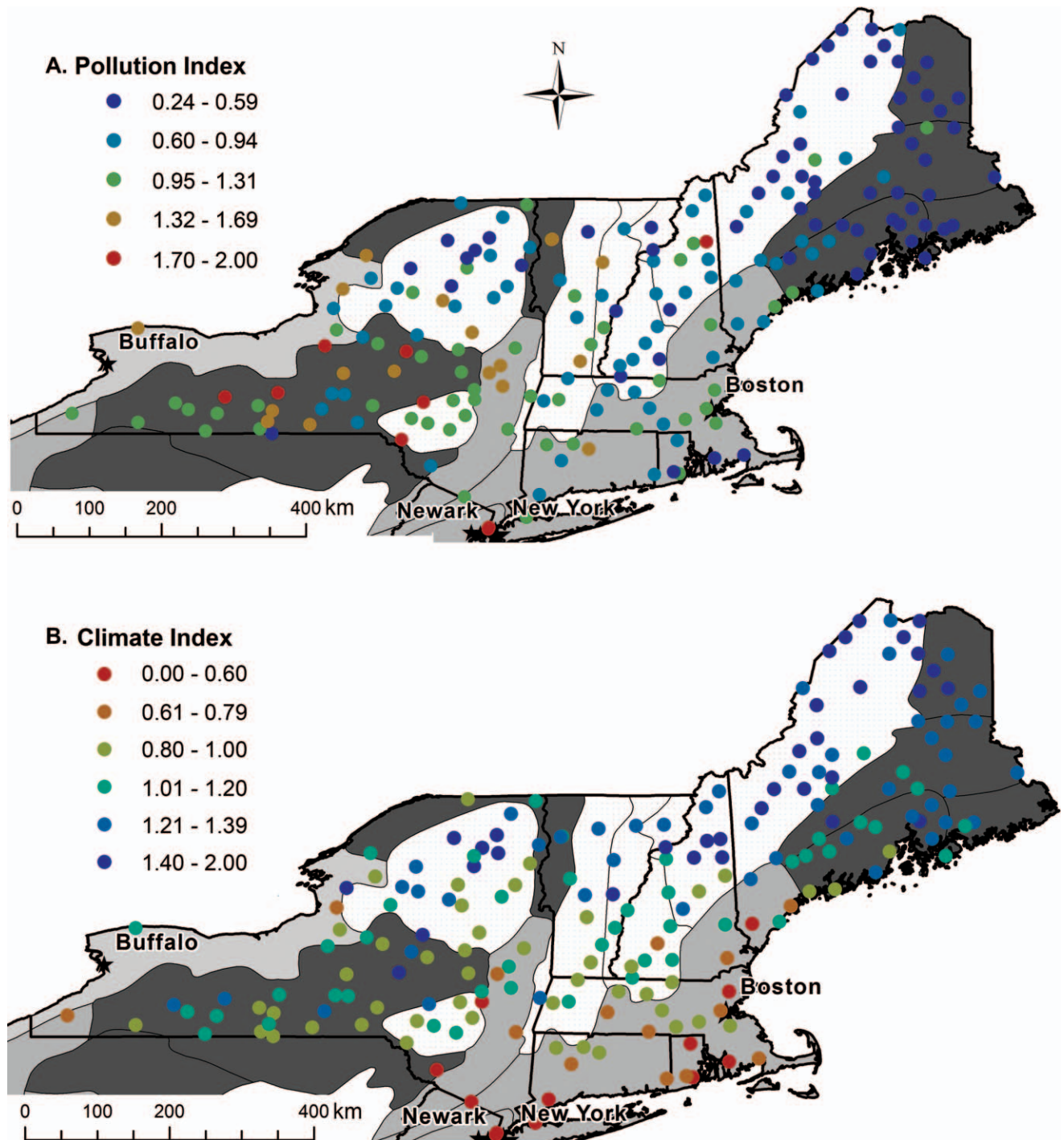


Figure 4. A. Map of Pollution Index values. B. Map of Climate Index values. Categories from Table 3 (for A) or Table 4 (for B). See Fig. 1 for identification of ecoregions indicated by shading. See text for explanation of categories.

The map of Pollution Index (**Fig. 4A**) by sites and category from **Table 3** shows poorer air quality (higher values) in “upstate” New York than near the coast—only New York City itself has red dots for the highest Index class. With the improvement of air quality since the 1960s–1980s (US EPA 2014a), the

highest regionally modeled acidic air pollution (NADP 2014) in our project area is now in southwestern New York state, rather than along the coastal urban/industrial corridor. Pollution Index values reflect this trend as well as indicating other local areas with air quality issues.

Climate model—Climate index. Using procedures similar to those explained for the air quality model, selection of final indicator species favored, first, climate indicator species indifferent to air quality; second, cool climate indicator species that are pollution-tolerant and warm climate indicator species that are pollution-sensitive; and third, selection of species for only one of the indices, to develop statistically-independent indices. Again, we chose this semi-quantitative method for compiling our final lists of indicator species in **Table 1** to reduce correlation between the indices.

Our best Climate Index (of several tested similarly to the procedures summarized for the Pollution Index) from the full set of 19 warm climate and 47 cold climate indicator taxa in **Table 1** was calculated from this equation:

Climate Index

$$= 1 + \left(\frac{\sum \text{Abundance of cool climate species} - \sum \text{Abundance of warm climate species}}{\sum \text{Abundance all species}} \right)$$

“1” is added to the quotient so the formula always returns a positive value for the index. Value can range from 0 for warmest climate (only warm climate indicators present) to 2 for coolest climate (only cool climate indicators present). Index values for the 218-plot model data set spanned the full potential range of 0 to 2. Again, indicator species abundance was entered into the formula to increase index sensitivity and reduce ties, since many plot samples included at least one species in each response class.

Climate index evaluation. Quantitative evaluation of the climate model was based on three criteria, as for the air quality model: 1) Is the Climate Index reliable enough to support useful pattern and trend analysis? 2) Is it sufficiently representative of climate response and independent of air quality response? 3) Do non-model plots fit adequately to the model when tested?

- 1) Reliability and repeatability. For our Climate Index, this was evaluated using the same set of 250 repeat samples at 84 plots as for the Pollution Index. Repeatability of indices for training plots and standard plots were again evaluated separately.

Training and field season variability differed for the Climate Index (**Table 2**). For training, the average unsigned deviation and signed bias of the

passing crew values was slightly smaller than for failing samples. Passing samples had relatively little bias, while failing samples had weak negative bias; they recorded a plot as about 1.5% warmer on average compared to the expert. For standard plots, the average unsigned deviation and signed bias of passing crew values were notably smaller than for failing crew samples. Passing samples had relatively little bias, while failing samples had much stronger negative bias; they recorded a plot as about 8% warmer on average compared to the expert. Crew performance for passing samples on field season QA evaluation was slightly weaker than at training. It was, however, much weaker for failing samples, with much stronger bias and more deviation from expert than were training samples.

With most deviations (including experts and failing crew) within 12–17% of model range (**Table 2**) and adding 5% for variation over time from other sources, the Climate Index must deviate on average by 17–22% of model range in a consistent direction, to detect a trend over time or a geographical pattern. A reasonable extrapolation from bias estimates is that an entire set of standard plots whose data quality matches those of our standard FIA plots would be estimated to be about 2–4% warmer than they should. Evaluation of passing repeat samples indicates that if at least 90% of samples meet the field MQO, bias would be negligible, repeat sample variability would be about 5.5%, and a consistent trend of 15% or less could be detected.

- 2) Representative of climate response and independent of air quality response. This index had the strongest correlations with climate variables (Pearson $r^2 = 0.546$ – 0.553 with temperature, weaker with PCA climate), lichen community composition (12% of variation; Pearson correlation $r^2 = 0.523$ with ordination Axis 2 * $r^2 = 0.225$ of total information represented on Axis 2 of the air quality ordination, **Fig. 2**) and was the least correlated with the Pollution Index of all variants tried. As presented above, the Pollution and Climate Indices are only weakly correlated and thus adequately independent of one another. Using the 218-plot data set, plots were divided into 6 classes based on their Climate Index values, for comparison with values of other variables and the Pollution index (**Table 4**) for plots in each class. Classes 1 and 6 each span 0.6 of full Climate Index range to compensate for few plots having values near each extreme; classes 2 through 5 each span ~ 0.2 of full index range. While climate and lichen community description variables varied with the Climate Index, variation of Pollution Index values at these plots did not. Only for classes 5 and 6 (cooler climates) did average Pollution

Table 4. Climate Index, with environmental variables and Pollution Index, summarized by six categories of the full Climate Index range of 0–2 for 218 model plots. Categories 1 and 6 each span ~0.6 units of full range; categories 2–5 each span ~0.2 units of full range. Category 1 includes warmest climate plots (W); category 6 includes coolest climate plots (C). Avg = average (± 1 standard deviation); Rng = actual range, reported for most variables. Climate Index is mapped by categories in Fig. 4B.

Category	Climate Index	Latitude	Min January temp	July relative humidity	Index, % natural land cover	No. of lichen taxa	Sum of lichen abundance	Pollution Index
1 (W) (N=12)	Avg	41.67°N (± 0.80)	−7.7°C (± 2.6)	71.1% (± 2.9)	13.3 (± 5.3)	5.7 (± 3.3)	15.2 (± 9.1)	1.092 (± 0.488)
	Rng	40.77–43.41°	−11.6 to −4°	68–77%	1–18	1–10	2–29	0.480–2.0
2 (N=17)	Avg	42.34°N (± 0.69)	−9.5°C (± 1.8)	71.0% (± 3.1)	13.2 (± 5.7)	9.8 (± 4.1)	25.5 (± 9.7)	0.920 (± 0.300)
	Rng	41.48–43.63°	−13.0 to −6.6°	67–76%	1–18	3–18	9–44	0.50–1.50
3 (N=52)	Avg	42.90°N (± 0.88)	−11.8°C (± 2.0)	68.3% (± 2.4)	14.4 (± 4.4)	10.4 (± 5.0)	25.4 (± 11.0)	1.038 (± 0.344)
	Rng	40.93–44.96°	−15.7 to −5.5°	65–76%	1–18	4–22	9–54	0.405–2.0
4 (N=51)	Avg	43.52°N (± 1.0)	−12.8°C (± 2.3)	69.5% (± 2.7)	14.8 (± 4.6)	13.3 (± 6.6)	32.8 (± 16.7)	0.943 (± 0.410)
	Rng	41.80–45.54°	−18.3 to −8.0°	63–74%	5–20	3–31	8–84	0.290–2.0
5 (N=51)	Avg	44.68°N (± 1.15)	−15.4°C (± 2.6)	69.4% (± 2.6)	16.9 (± 3.6)	16.3 (± 9.2)	42.0 (± 23.2)	0.733 (± 0.442)
	Rng	42.32–47.19°	−19.5 to −10.2°	64–75%	4–20	3–37	9–86	0.243–2.0
6 (C) (N=35)	Avg	45.17°N (± 1.20)	−16.9°C (± 2.4)	69.4% (± 2.2)	18 (± 2.7)	16.4 (± 8.9)	41.8 (± 23.4)	0.666 (± 0.383)
	Rng	42.80–47.19°	−21.3 to −12.0°	65–74%	10–20	2–36	5–95	0.342–2.0

Index show a bias toward cleaner plots. Seven of the known polluted sites are in these two climate classes, though many of the cleaner air plots in these two classes were excluded from the pollution model data subsets. The strong increases of species richness and abundance with climate category reflect response to air quality as well as to climate in the full data set; species richness patterns in **Tables 3 & 4** mirror patterns in the lichen community ordination (**Fig. 2**) to illustrate that species richness responded strongly to both air quality and climate. Responses of lichen community variables primarily to climate are discussed in the next section. The Climate Index was positively correlated ($\rho = 0.44$ – 0.46 , $\rho^2 = 0.19$ – 0.21 , $p < 0.0005$) with an index for proportion of natural land near a plot (the strongest of the land cover variables) and average natural land cover index increased (more land cover in this class) with cooler climates. This correlation was notably weaker than for the Pollution Index; there appears less need to consider Climate Index interaction with land cover pattern when both are investigated.

- 3) Extrapolation limits and model fit. The full 218-plot model development data set (polluted plots included) had 2 plots with Climate Index value 0 and one plot with value 2, spanning the full possible range of the index, so the recommended 10% extrapolation limit does not apply. All of the 598 samples we analyzed from 257 plots had at least one climate indicator species and no additional samples had either the maximum or minimum value. Cumulative distribution of Climate Index values for the 218-plot data set (**Fig. 3B**) shows a reasonably linear increase over much of its range, with nonlinear increases near both ends of the gradient. Few plots had the extreme values, and the nonlinear increases reflect the greater sensitivity of the Index toward the extremes. So the model fits well to the non-model plots we tested. If the proportion of plots with none of the indicator species increases notably over time or when the index is applied to areas outside the model region, then fit of the model should be reevaluated. If the proportion of plots with the maximum or minimum value is greatly increased in a set of plots, then the Climate Index becomes insensitive at that end of the gradient.

Climate index interpretation. The Climate Index met reasonable reliability criteria even when plots that failed the program MQO were included. Repeat sample variability for the Climate Index of 7–12.5% of model range supports detection of a consistent pattern of 15–18% change over time even with only moderately reliable field data. The final

Climate and Pollution Indices developed from indicator species were more strongly correlated with lichen community composition (vectors longer, **Fig. 2**) and more independent of each other (angle between vectors close to 90°) on that best air quality ordination (our most suitable analysis for comparison of relationships between the two indices) than were other variables related to climate or air quality.

The sensitivity of Climate Index values at the extremes was partly related to lichen species richness, as with the Pollution Index. The 12 Climate Index category 1 plots had quite low species richness (**Table 4**), and several of the 12 plots with the highest values (part of category 6) had relatively low species richness as well. The three plots with Climate Index values of 0 or 2 had low species richness and high Pollution Index values, but only a few of the other low richness plots at Climate Index extremes had high Pollution Index values so other causes are likely involved. Several of the 12 plots closest to the cold end of the Climate Index had species richness higher than average (**Table 4**, category 6), showing that species richness alone did not place a plot near the cold end of the gradient. The map location in **Fig. 4B** of sites by Climate Index category from **Table 4** matches eco-regions reasonably well; most of the red and orange dots are in Eastern Deciduous Forest, the warmest of the three (**Supplementary Table S1**). Low diversity plots in category 6 were not consistently mismatched with category of nearby higher diversity plots on **Fig 4B** (data not shown), further support for the robustness of the Climate Index.

The Climate Index had weak positive correlations with lichen species richness (Lichen R: Pearson $r^2 = 0.12$, $p < 0.0001$) and sum of abundance (Lichen Sum: Pearson $r^2 = 0.13$, $p < 0.0001$) from the 191-plot data subset with known polluted plots excluded (similar results from the best climate ordination), while the Pollution Index still had strong negative correlations with them even in that data subset ($r^2 = 0.39$ and 0.43 , $p < 0.0001$). These direct correlations clearly support that Lichen R and Lichen Sum varied less with climate than they did with air quality, similar to the patterns in the **Fig. 3** ordination. The apparently strong links in **Table 4** of diversity with cooler climate reflect some bias from inclusion there of polluted plots more frequent toward the south. Increases of Lichen R and Sum with cooler climate independent of response to air quality have been

reported in another eastern U.S.A. study (McCune et al. 1997b), though the opposite pattern has been seen in northwestern U.S.A. and California (Geiser & Neitlich 2007; Jovan & McCune 2004). It is possible that Lichen R and Sum in our study area do not actually vary much at all with climate; they might perhaps rather be linked with more natural land cover nearby, that was relatively independent of the Pollution Index but had weak positive correlation with the Climate Index (see previous section). Will-Wolf et al. (2014a) found that air quality and amount of nearby forest cover appeared to predict Lichen R in 1994–2005 FIA data more strongly than did climate, in three eastern U.S.A. geographic regions that overlap our study area.

Clearly the reliability of field data affected the precision with which climate response trends over time or across regions could be detected, and affected the magnitude of general bias toward scoring plots as warmer than actual. There was stronger deterioration in accuracy and precision of the Climate Index for failed plots than there was for the Pollution Index (**Table 2**). Assuming about 40% of all FIA crew surveys passed the data quality criterion, in the 191-plot data subset surveys for 30–40 of the 139 selected crew plots might have failed the field MQO (no known failing samples were included and many crew plots with low species richness for their area had been excluded). From calculations that Climate Index values for failing plots were about 8% warmer than the expert, bias for the full model data set was probably no more than 2% warmer than actual. For the set of all 589 standard crew plots available for the region, this bias would probably be about 4% warmer.

CONCLUSIONS

We achieved our objective to develop Pollution and Climate Indices for the northeastern U.S.A. that are sufficiently robust and independent to be used for pattern and trend analysis of forest response to the two drivers separately. As illustrated in **Fig. 4**, even though the two indices are statistically independent of each other, their geographic patterns overlap substantially, reinforcing the strong geographic covariance of climate and air quality in this region during the field data collection period of the study. This pattern highlights an important limitation on interpretation: each index represents only that aspect of lichen response to air quality or

climate that is independent of the other factor, not all lichen response to either air quality or climate. Our study also presents one more example of how lichen species richness is a poor indicator of response to a single driver across large geographic regions, since it was linked to several different kinds of disturbance as well as to environmental gradients. Through extensive empirical testing we, like Goldilocks, eventually arrived at “just the right” set of individual species as indicators for response to either pollution or climate to develop indices that were both independent of one another and sufficiently reliable to support useful monitoring of trends.

Each index had repeatability sufficiently low to support reasonable assessment of trend analysis. Variability was somewhat higher for our indices than for the 6–12% repeat sample variation reported for other published FIA lichen models (Geiser & Neitlich 2007; Jovan & McCune 2004, 2005, 2006; McMurray et al. 2013; McCune et al. 1997a; McCune et al. 1998). Our estimates that consistent trends of 15–20% could be detected even with the moderate level of data quality achieved by northeastern FIA data (Patterson et al. 2009) are still small enough to be useful for trend analysis over the entire model region. Tradeoffs in the sensitivity of the two indices to data quality for precision and accuracy suggested that the two indices probably have about equal value for trend analysis with moderate data quality. While the Pollution Index had slightly higher variability and thus lower precision overall, it had higher accuracy overall because failing crew samples had only slightly higher (and inconsistent) bias than did samples that passed the minimal field MQO. In contrast, the Climate Index had lower variability and thus higher precision overall, but probably lower accuracy than the Pollution Index with data of only moderate quality because failing samples had notably higher consistent bias toward scoring plots as warmer than recorded by passing samples. Thus the Climate Index would benefit more from improvement in data quality than would the Pollution Index. With better data quality both indices could detect changes of similarly smaller magnitude: 10–15%.

We did not achieve our goal to develop pollution indices sufficiently distinctive to represent different responses of lichens to acidic air pollution and to fertilizing Nitrogen (N) pollution. Differential responses of lichen communities to estimated and

modeled Sulfur (S) and oxidized N pollution versus estimated reduced N pollution are suggested by our multivariate analyses and pairwise correlations, but the sets of indicator species for the two classes of pollution were not distinct enough to support statistically independent indices. Our results support the interpretation that our final Pollution Index reflects response to S plus oxidized N more strongly, and response to reduced N and probably total N less strongly; this interpretation is preliminary without good independent data on local air quality. With S declining, but both oxidized and reduced N remaining relatively high in eastern U.S.A. (CMAQ 2010; NADP 2014), distinguishing more accurately how the different forms of air pollution affect lichen communities here is an important research agenda. Other FIA studies have reported that pollution loads at plots estimated from measured lichen thallus element content (Geiser & Neitlich 2007; McCune et al. 1998; Root et al. 2013; Will-Wolf et al. 2014b) or directly measured canopy throughfall (Jovan & McCune 2006; Jovan et al. 2012) correlate more strongly with lichen community responses than do regionally modeled air quality variables. Lichen tissue element concentrations have provided efficient estimates for pollution load at standard FIA plots (Geiser & Neitlich 2007; Will-Wolf et al. 2014b) and from other eastern U.S.A. studies (i.e., Olmez et al. 1985; Will-Wolf et al. 2005). Data on local air quality would support better evaluation of the effects of different classes of air pollution on lichen communities and better discrimination among lichen species as indicators for different kinds of air pollution. It is important to conduct such studies very soon in the eastern U.S.A., to support more accurate forest health evaluation and facilitate improved management and conservation efforts.

Our Pollution and Climate Indices can be applied quite simply to any lichen community sample from a new or different set of plots in the northeastern U.S.A. states. Reliance on sets of indicator species rather than more complicated mathematical models to which plots are fitted requires only spreadsheet calculation, so ability to identify lichens is the primary expertise needed to apply the indices. Some constraints should be followed in using our indices for other projects. These indices should be applied with caution outside our project boundaries; the indicator value of listed species might well change in different ecological

conditions or when evaluated at a different spatial scale. The species *Flavoparmelia caperata* illustrates how indicator value of a species is context-dependent rather than absolute. It is a common species in eastern North America across a wide range of natural environments (Brodo et al. 2001), and has been cited as an indicator of warming climate in Europe (Søchting 2004). It was quantitatively supported in this study as both a warmer climate and a relatively pollution sensitive indicator (Table 1). However, in a study comparable in both scale and methods of an adjacent area to the south (Will-Wolf et al. 2014b), *F. caperata* was not found to be an indicator of response to either climate or air quality. Interpretation of patterns and trends using our indices should emphasize results across many plots and not focus on individual plots, given the variability of the indices. To enhance comparability of index values, field and analysis protocols should be similar to ours: 1) search intensity and size of search area should at least generally match procedures for the FIA program; 2) only macrolichen taxa should be counted for index calculation; 3) macrolichen taxa should be defined using rules similar to those for the FIA program (cryptic species should not be counted separately, for instance). Searching more intensely, searching larger areas, and/or listing many cryptic species separately for calculations might all bias index values calculated from our formulas. Since many indicator species are fairly common and many non-indicator species are uncommon, all of these practices can shift index value toward the center of the FIA index range by increasing the value of the equation denominator and thus reducing the impact of indicator species abundance on the index value. Use of different protocols for estimating abundance would likely not bias the indices, since abundances are automatically standardized by plot within each equation. Use of only presence data would reduce the sensitivity and increase the variability of each index, perhaps rendering them too imprecise for useful monitoring of trends.

Critical loads (CLs) for lichen communities have been proposed for western U.S.A. (Fenn et al. 2003a,b; Jovan et al. 2012; McMurray et al. 2013), but not yet for eastern U.S.A. A CL is a pollution load below which sensitive responders, like lichens, are expected to be unharmed. From our study we could not clearly identify a pollution threshold associated with the onset of damage to lichen communities; we saw continuous change in lichen

communities (Fig. 3) and gradual increase of our Pollution Index with increases in regionally averaged air pollution (Table 3) rather than abrupt threshold responses. The presence of pollution-tolerant indicator lichen species at many plots in the cleanest air class (Table 3), plus the continuous gradient of our Pollution Index values, tempt us to suggest that the CLs for S and acidic N (and probably also for fertilizing total and reduced N) have probably been exceeded even in the cleaner portions of our study area. Such a conclusion could be supported by national deposition models (CMAQ 2010; NADP 2014) that show the lowest regionally averaged amounts in eastern U.S.A. of both N and S are at least 2–3 times higher than in remote areas of western U.S.A. and parts of Canada. However, conclusions are premature since we do not have direct local measurements of pollutants to compare with our lichen responses. Targeted studies of lichen response linked to direct local pollutant measurement plus re-measurement of lichen communities to evaluate change over time will be needed to support establishment of CLs for eastern U.S.A. lichen communities.

Resurvey of lichens at FIA project plots soon (10–15 years after the surveys used in our study) would likely show interesting trends. Air quality has improved somewhat, and climate has continued to change. Will-Wolf et al. (2011a) found that across eastern U.S.A. and in some subregions, lichen species richness varied more with air quality than with climate. Our results suggested similar patterns for variability of both lichen species richness and lichen species composition in our study area. Since S deposition has continued to decline in the region since our lichen surveys while both forms of N remain relatively high, a reasonable prediction might be that lichen response to acidic pollution will show improvement and response to fertilizing N might have become the more important air quality issue. One caveat supported by previous studies is that lichen recovery after improvement in air quality often does not follow the exact reverse of lichen degradation and loss as air quality worsens (e.g., Bates & Farmer 1992; Bates et al. 2001; Gunn et al. 1995; Liška & Herben 2008; McClenahan et al. 2012; Nash & Gries 2002; Showman 1997; Shrestha et al. 2012; van Dobben 1996); availability and success of propagules is a minor part of lichen loss, but a much more important component of recovery. This caveat

also applies to monitoring response to climate change; loss of species may track climate but colonization by new species may be linked with several drivers. While nearby forest cover was not a major factor affecting lichen response in our study, it has been more strongly linked with lichen species richness (Will-Wolf 2014a) and composition (Will-Wolf et al. 2005) in other eastern U.S.A. studies. Amount of nearby forest cover linked to lichen dispersal ability or local establishment success might become a more important factor explaining composition of epiphytic lichen communities as air quality continues to improve but climate also continues to change. A targeted study to better stratify plots by air quality, climate and land cover would be needed to explore possible independent effects of land cover pattern on lichens in this region.

Our project contributes substantially to improvements in evaluation of indicator lichen species for use to estimate response of biological communities to environmental factors. We have followed the recommendation of Dufrêne & Legendre (1997) to include indicators for response to both ends of a gradient of interest, a practice still not as common as it should be. Whittet & Ellis (2013) documented much subjectivity in choice of indicator lichen species in the past and called for more quantitative support for the selection of indicator species and interpretation of the environmental conditions they represent. We have illustrated an obvious limitation of quantitative analysis; the results can differ with different data sets for the same project area even when the data sets overlap. Since almost all identified lists of indicator species are intended for use beyond the original project, addressing this limitation is almost always worthwhile. We chose to develop robust lists of species from multiple quantitative analyses as well as literature and have in addition selected indicators from a candidate list to best meet our explicitly stated goals. This strategy has quantitative support while it overcomes the limitations of a single analysis; it also compensates for limited species capture at a site from timed samples. Both considerations are likely to be important for species-based response indices intended for application across a large region.

In summary, broad appropriate application of our Pollution and Climate Indices should enhance the ability of scientists and managers to quantify response of forest lichens and forest ecosystems in general to air quality and climate in the northeastern U.S.A. region.

They are simple and useful tools to independently track response of forest lichens and forest ecosystems to changes in air pollution and climate of the region.

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Supplementary documents online:

Supplementary Table S1. Summary of plot characteristics by ecoregion. Values for most are mean (SE if appropriate), range. For “polluted plots” value is % of plots near a known pollution source. Units are listed as appropriate; several are unitless indexes; lichen species richness is count of species on plot. Abbreviations: ecoCD = ecoregion code; max = maximum; min = minimum; n = number of plots.