

Regional Gradients in Lichen Communities of the Southeast United States

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Abstract. *Epiphytic macrolichens were sampled in 203, 0.38 ha plots in the Southeast United States. 176 lichen species were encountered. Gradient analysis revealed two major regional gradients in lichen communities. A multivariate model based on non-metric multidimensional scaling was used to assign gradient scores to plots, based on lichen species composition. The strongest gradient in the lichen communities corresponded to a macroclimatic gradient from the coast through the Piedmont to the Appalachian Mountains. The second major gradient was correlated with air quality, with pollution-tolerant species and lower species richness in urban and industrial areas, and pollution-sensitive species and high species richness in cleaner areas. Epiphytic macrolichens were sparse in urban areas with heavy industry. In many rural areas, lichens were luxuriant and diverse. Species richness was locally variable and only weakly related to the coast-to-mountains gradient, with somewhat higher diversity in the mountains and lower diversity on the Piedmont and coast.*

The Forest Health Monitoring (FHM) program seeks to assess the condition and trend of the forests of the United States (NAPAP 1993; Riitters et al. 1992). FHM is linked with the national sampling grid established by the Environmental Monitoring and Assessment Program (EMAP) of the Environmental Protection Agency. Epiphytic lichen communities were included in FHM because they help to answer several key assessment questions. These questions concern the contamination of natural resources, biodiversity, forest health, and sustainability of timber production.

Hundreds of papers worldwide (chronicled in the series "Literature on air pollution and lichens" in

the *Lichenologist*) and dozens of review papers and books (e.g., de Wit 1983; Nash & Wirth 1988; Richardson 1992; Seaward 1993; Smith et al. 1993; van Dobben 1993) published during the last century, have documented the close relationship between lichen communities and air pollution, especially SO₂ and acidifying or fertilizing nitrogen and sulfur-based pollutants. In a comparison of biological responses between nearby and remote areas surrounding a coal-fired power plant, lichens gave a much clearer response (in terms of diversity, total abundance, and community composition) than either foliar symptoms or tree growth (Muir & McCune 1988). Lichens were one of the few com-

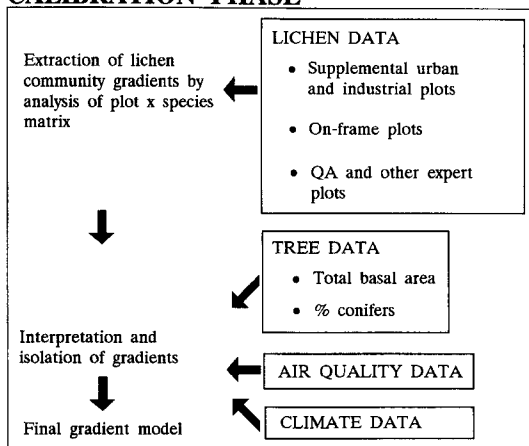
ponents of terrestrial ecosystems to show a clear relationship to gradients of acidic deposition in the eastern United States (NAPAP 1991; Showman 1992). Much of the sensitivity of epiphytic lichens to air quality apparently results from their lack of a cuticle and their reliance on atmospheric sources of nutrition. Although trees may respond to moderate, chronic levels of air pollution deposition, all of the other influences on tree growth, such as variation in soils, make the responses of trees to pollutants difficult to measure in the field. Lichen communities provide, therefore, not only a measure of air pollution impacts upon lichens, but also suggest air pollution impacts on aspects of forest health that are difficult to measure directly.

Elemental content of lichens in the southeastern U.S. has received some study (e.g., Bosserman & Hagner 1981; Kinsman 1990; Walther et al. 1990), but no previous published studies of lichen community response to air pollution have been made in this area. Elsewhere in eastern North America, lichen community response to urban and industrial air pollution has been studied mainly in local urban and industrial areas (LeBlanc et al. 1972; McCune 1988; Muir & McCune 1988; Rao & LeBlanc 1967; Showman 1975, 1981; Will-Wolf 1980). Only Showman (1992) has studied lichen communities on a regional gradient in air quality in North America. In Europe, regional monitoring grids have focussed primarily on elemental analysis of tissues or status of particular species, with only a few large-scale studies analyzing community composition (Bruteig 1993; de Wit 1976; van Dobben 1993).

In addition to their utility as indicators of air quality, epiphytic lichens are an important component of many forests. Lichens often comprise a large portion of the diversity of macrophytic species in a forest. Lichens have numerous functional roles in temperate forests, including nutrient cycling (especially nitrogen fixation in moist forests; Pike 1978) and as components of food webs (Dawson et al. 1987; Maser et al. 1985; Maser et al. 1986; Rominger & Oldemeyer 1989; Servheen & Lyon 1989).

The large-scale sampling of FHM using the EMAP sampling grid allows us to describe regional gradients in lichen community composition as influenced by climate and topography. A multidisciplinary regional sampling grid of this scale is unprecedented in North America, although transcontinental transects in Canada have addressed questions at a similar spatial scale (La Roi 1967; La Roi & Stringer 1976). The current data set extends from Georgia to Virginia, inland to eastern Tennessee. Additional data collected along the whole eastern seaboard in 1994 and 1995 will be analyzed in the future.

CALIBRATION PHASE



APPLICATION PHASE

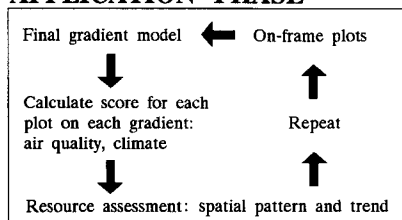


FIGURE 1. Overview of development and application of the lichen community indicator in the Forest Health Monitoring Program.

METHODS

The lichen community indicator is implemented in two phases (Fig. 1): 1) construct a gradient model of lichen communities to isolate and describe climatic and air quality gradients and 2) apply the model to calculate gradient scores for additional plots. Scores for these plots are then used to describe the regional condition and geographic variation in lichen communities. Repeated sampling of these permanent plots will allow us to document changes in the condition of lichen communities over time. All lichen data are archived with the Information Management group for Forest Health Monitoring, Environmental Protection Agency, Las Vegas, Nevada, and at Oregon State University.

We designed the field method for use by non-lichenologists for practical reasons of staffing field crews. Field crews received four days of intensive training in the lichen community method. The method has been closely scrutinized and documented for repeatability (McCune et al. 1997).

Field plots.—The FHM lichen community method determines the presence and abundance of macrolichen species on all standing woody plants in each FHM plot. The field crew collects samples for mailing to lichen specialists. The field methods are described in detail in Tallent-Halsell (1994). Quality assurance (QA) procedures and results are described in Cline (1995) and McCune et al. (1997).

The method has two parts that are performed simultaneously — 1) In each plot, the field crew collects specimens for identification by a specialist, the collection representing the species diversity of macrolichens in the plot

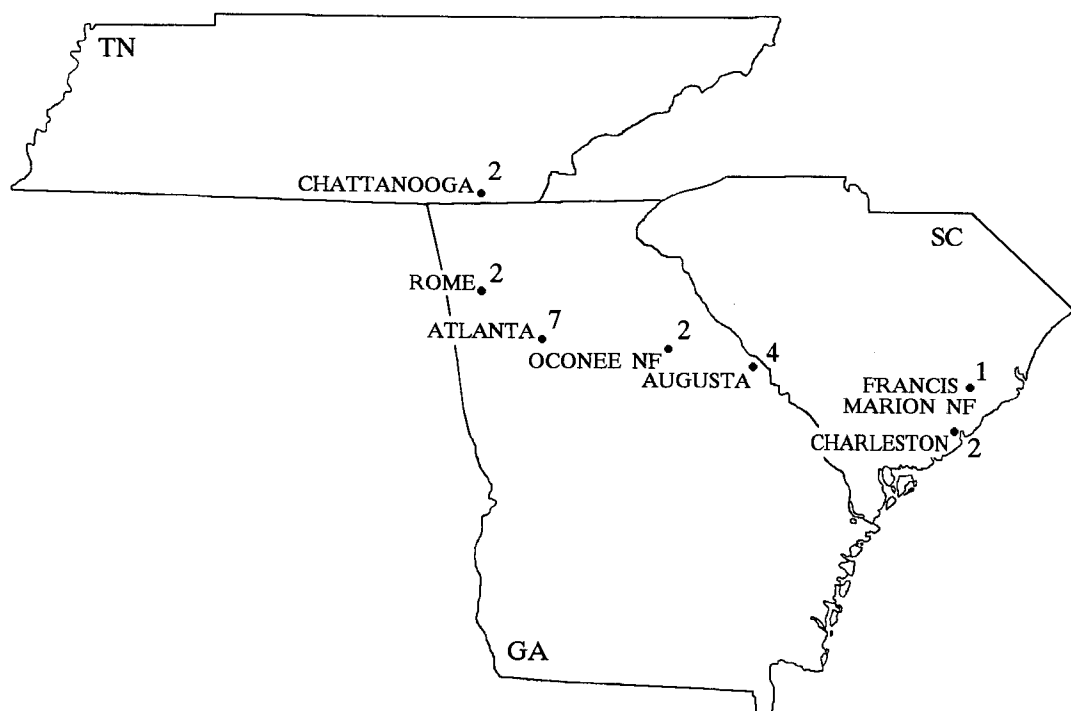


FIGURE 2. Map of supplemental (off-frame) plots, mostly in urban and industrial areas. Numbers indicate the number of plots taken in each area.

as fully as possible. The population being sampled consists of all macrolichens occurring on woody plants, excluding the 0.5 m basal portions of trees and shrubs. Lichens on fallen branches and other lichen litter are included. Given the large plot area, fallen branches always provide a sample of the canopy lichens; and 2) the field crew estimates the abundance of each species using a four-step scale: 1 = rare (< 3 individuals in plot); 2 = uncommon (4–10 individuals in plot); 3 = common (> 10 individuals in plot but less than half of the boles and branches have that species present); and 4 = abundant (more than half of boles and branches in the plot have the subject species present). Note that the field crew need not accurately assign species names to the lichens (that is done later by a specialist), but must be able to distinguish among species.

DATA SOURCES.—*On-frame 1992 and 1993 data.* Lichen community data were collected by summer field crews in 126 on-frame permanent plots in 1992 and 1993, combined. “On frame” means that plots were selected on a formal sampling framework, according to standard sampling protocols for the EMAP hexagonal grid (Messer et al. 1991). Georgia, North Carolina, South Carolina, eastern Tennessee, and Virginia were included. The strict sampling criteria applied to the on-frame data allow regional estimates of lichen community parameters.

QA and training plots by lichen specialists.—Data for six plots in 1992 were collected by our lead lichen specialist in the Southeast (Dey). In 1993 three plots near Asheville were each sampled three times in one season by Dey. One training plot was sampled independently by four lichen specialists. Three additional plots sampled by Dey in 1993 were part of auditing field crews.

Supplemental urban/industrial plots.—Data for 20 off-frame plots (Fig. 2), 17 of these in urban and industrial

settings, were collected in February 1993. The purpose of the supplemental plots was to improve the basis for recognizing lichen indications of either deterioration or improvement in air quality.

Air quality data.—Air quality data from all SO_2 monitoring stations near our urban/industrial sampling sites were extracted from the Aerometric Information Retrieval System (AIRS) through the National Air Data Branch of EPA. Unfortunately, direct monitoring had been so sporadic that we could not use it to calibrate the lichen air quality index developed below. These data are useful, however, in providing a basis for comparison with other studies in other regions. Annual average ambient SO_2 concentrations were fairly low, ranging from about 10–26 $\mu\text{g}/\text{m}^3$.

We also attempted to use other kinds of air quality data, including data on emissions of SO_2 by county and interpolated estimates of nitrate and sulfate deposition. Both of these data sources were eventually rejected. Emissions data for a county cannot readily be used to estimate pollutant deposition in that county, because numerous topographic and locational factors disrupt the relationship between local emissions and local deposition; for example, a plot in a given county may receive most of its atmospheric inputs from other counties.

Nitrate and sulfate data stations are so sparsely distributed that the interpolated values resulting from smoothed regional maps do not accurately portray local deposition of pollutants. For example, although an air pollution signal is clearly expressed by lichen communities in Atlanta, the presence of Atlanta is not discernible on the regional contour maps of sulfate and nitrate deposition.

Lacking useful direct air monitoring data derived from atmospheric sampling, we resorted to simply creating a binary variable indicating plots in urban and industrial

areas (polluted = 1) vs. those in rural areas (polluted = 0). These ratings were later revised on a plot-by-plot basis, based on the gradient model (see below), allowing us to detect polluted rural sites.

Climatic data.—Long-term average climatic data were obtained from two sources: 1) nearest NOAA weather stations using a CD-ROM database, the National Trade Data Bank and 2) for non-urban plots we used summary statistics for climatic divisions (Fovell & Fovell 1993). Each plot was assigned to a climatic division.

DATA STRUCTURE.—Each plot is considered a sample unit. Information from individual species was summarized into synthetic lichen community variables, as described in the "Data reduction" section.

Complete data set.—The complete lichen community data set consists of the 203 plots described above. Data on other variables were included to facilitate the interpretation of the lichen community data. These additional variables were latitude, longitude, state, county, elevation, aspect, slope, topographic position, stand basal area, percent of stand basal area in conifers (dbh > 10 cm), physiographic province, climatic variables, and distance from the Atlantic and Gulf coasts.

Analytical data set.—The analytical data set was a subset of the complete data set that was used to build a gradient model of lichen communities for the Southeast. The analytical data set consists of the QA and training plots taken by the lichen specialist in 1992, the supplemental urban and industrial plots, and the on-frame plots sampled in 1993, for a total of 85 plots. The data collected by the summer field crews in 1992 were not included because of poor quality. Trainees failed to meet data quality objectives, both immediately after training and during the mid-season audit. The poor data quality resulted from too great a work load and insufficient training for the botanists. These problems were largely alleviated in the 1993 field season and the field crews were successfully certified and audited.

On-frame data set.—On-frame data can be used for assessment of regional status and trends because it consists of an unbiased sample (Messer et al. 1991). In contrast, off-frame data, while useful in building a gradient model, cannot be used to answer such questions as, "Is lichen diversity in the southeastern U.S. decreasing through time?"

COMBINING LICHEN ISOMORPHS.—A special problem for lichen community data is the handling of "isomorphs," species that differ in secondary chemical content, but are morphologically nearly identical. Field crews or even lichen specialists would be unlikely to differentiate among isomorphs in the field. Although there is no consensus in the lichenological community on the taxonomic standing of such isomorphs, there are increasing numbers of these "chemical species" being named. Isomorphs often have different geographic ranges and different ecological affinities. In some cases isomorphs are reproductively isolated sibling species; in other cases gene flow between isomorphs has been demonstrated (Culbertson et al. 1988, 1993; DePriest 1994). These isomorphs are, for the most part, readily distinguished in the laboratory with simple chemical tests, and these were used in our identifications. For the practical reason of needing to name thousands of specimens, we did not, however, routinely use thin-layer chromatography to discriminate among isomorphs. Instead, we discriminate among isomorphs in our statistical analysis only when they are separable by spot tests.

The chief advantage to combining the isomorphs would be matching the resolution of the data analysis with the

ability of the field crew to discriminate among species. However, we decided to keep isomorphs separate in the data analysis for several reasons: 1) In most cases only one of a group of isomorphs will be present in a plot; 2) data summaries retain more ecological content if species with similar morphology, but different chemistries and ecologies are kept separate; 3) the distributions of many of these species are poorly known. Regional monitoring programs can make an important contribution to lichenology if chemically-defined species are identified and kept separate.

SPECIES DIVERSITY.—We applied Whittaker's (1972) three kinds of diversity. Alpha diversity is calculated here as the average species richness per plot. Beta diversity is a measure of heterogeneity in the data, which we calculated as the ratio of the total number of species to the average number of species (gamma over alpha). Gamma diversity is the landscape-level diversity estimated as the total number of species across plots.

GRADIENT MODELING.—The dominant gradients in lichen communities were determined using the analytical data set (described above). The gradients were extracted with nonmetric multidimensional scaling (NMS; Kruskal 1964; Mather 1976; McCune & Mefford 1995). NMS has proved one of the most robust and effective methods for multivariate data reduction, especially with species \times sample data and city-block distance measures (Beals 1984; Faith et al. 1987). NMS is well-suited to data that are non-normal or are on arbitrary or discontinuous scales (Mather 1976).

Gradient scores were calculated for each sample unit in the calibration data set. The scores represent positions of each sample unit on each gradient as defined by community composition. These scores were then analyzed for their relationships to other variables (forest structure, air quality, and climate). The gradient model can then be used to score additional plots not included in the analytical data set. This model can be applied to future plots collected "on-frame" (that is, on the EMAP hexagonal grid) in the same region (explained below).

We used NMS with the quantitative version of the Sørensen distance measure. The dimensionality of the data set was first determined by plotting a measure of fit ("stress") to the number of dimensions. A two-dimensional solution was requested of NMS since additional dimensions provided only slight improvement in fit. One hundred iterations were used for each NMS run, using random starting coordinates. Several NMS runs were used for each analysis to ensure that the solution was stable and represented a configuration with the best possible fit. The first two axes were rotated clockwise by 155 degrees. This orthogonal rotation improved interpretability, aligning the frame of the graph with the apparent climatic and air quality gradients.

NMS was used to score lichen plots other than those used in the analytical data set. Instead of rerunning the analysis with each new batch of plots, scores were found for individual plots using the NMS gradient model developed for the analytical data set. Because NMS does not result in a linear "prediction" equation like principal components analysis, a different approach was needed. For each plot, we used an iterative procedure (program NMSCORE) for finding the positions of best fit on both the air quality and climatic gradients. Thus, the gradient model consists of the original data from the analytical data set, the score on each gradient for each plot in the analytical data set, and the algorithm for finding scores for new plots. The algorithm calculates stress for each new plot at each trial location along each gradient. The coordinate of

TABLE 1. Species diversity of epiphytic macrolichens in the southeastern United States. Alpha, beta, and gamma diversity are defined in the text. ¹ Regular field crews, 1993 only; ² specialists only, alpha diversity corrected to crews by 65%; ³ specialists and crews, 1992 and 1993.

	N	Diversity measure		
		alpha (s.d.)	beta	gamma
On-frame ¹				
Mountains	30	16.4 (6.3)	6.5	107
Piedmont	13	12.5 (5.3)	4.3	54
Coastal plain	19	11.9 (4.9)	5.5	66
Off-frame				
urban/industrial ²	17	9.2 (4.9)	4.6	64
QA plots ³	53	22.7 (10.5)	7.0	158

the position with the lowest stress (best fit) on a given gradient is used as the index score for that plot. The best fit is sought with a hierarchical procedure where successively narrower segments of the gradient are searched for the position of best fit. In the application phase (Fig. 1), this procedure requires no decisions on the part of the analyst. Plot scores can thus be calculated mechanically after building the gradient model.

RESULTS AND DISCUSSION

SPECIES DIVERSITY.—A total of 176 epiphytic macrolichen species was observed (Tables 1, 2), along with an additional eight generic categories used when species identifications were impossible (Table 2). Species richness (alpha diversity) ranged from a low of two species in a *Pinus* plantation in an industrial area in Augusta, Georgia, to over 40 species in some plots in the Appalachian foothills. Fewer species were found in urban and industrial areas than in the other plots (Table 1). A weak gradient in species richness was seen from more species in the mountains to fewer species on the coastal plain and piedmont. Gamma diversity was highest in the mountains. Plot-to-plot heterogeneity, as measured by beta diversity, was highest in the mountains and lowest in the piedmont.

The frequency of each species is broken down by data set: on-frame plots, QA plots, and the supplemental off-frame plots (Table 2). Note that 203 plots are included because this table represents the complete data set rather than the analytical data set ($n = 85$; see "Data Structure" above). Much of the diversity was concentrated in the parmelioid genera, including 23 species of *Parmotrema* and 9 species of *Hypotrachyna*. The only fruticose genus with a large contribution to the species count was *Usnea*. The most frequently represented species were, in order, *Punctelia rudecta*, *Flavoparmelia caperata*, *Usnea strigosa*, *Rimelia reticulata*, *Parmotrema hypotropum*, *Hypotrachyna livida*, *Parmelinopsis minarum*, and *Phaeophyscia rubropulchra* (Table 2). Nineteen nitrogen-fixing species

(cyanolichens) were found, the most common being *Leptogium cyanescens*, but none of these was abundant.

LICHEN COMMUNITY GRADIENTS.—Two major gradients captured most of the variance in the lichen communities, the first two dimensions containing 27.5% and 31.5%, respectively, of the information in the analytical data set (cumulative = 59%). Higher dimensions improved the model very little.

Species characteristic of the extremes of these gradients are listed in Table 3. The first gradient corresponds to a macroclimatic gradient from the coast to the Appalachian Mountains. Plots from the Ridge and Valley Province on the west side of the mountains (eastern Tennessee) were more similar to the Piedmont than to the mountains.

The second major gradient (Fig. 3, Table 3) corresponds primarily to a gradient in air quality, with pollution-tolerant species and lower species richness at one end of the gradient, and pollution-sensitive species and high species richness at the other end of the gradient. Plots in urban and industrial areas had fewer species, lower total lichen cover, and higher scores on the second NMS axis, than did most rural plots. In rural areas, lichens were often diverse and luxuriant. Some rural plots fell, however, toward the polluted end of the gradient. These gradients are described in more detail below.

CLIMATIC GRADIENT.—Axis 1 of the NMS ordination corresponded with a regional climatic gradient. The climatic gradient is mainly expressed as differences between the coast and mountains. This difference is most conspicuous in temperature-related climatic variables, the coastal plain being generally warmer, during both summer and winter, than the mountains (Table 4, Fig. 3). All three temperature variables examined (mean annual, July, and January temperatures) were correlated with Axis 1 (Table 4).

The precipitation pattern is more complex, with both the driest areas (e.g., Asheville, NC) and the wettest areas (e.g., Highlands, NC) being in or near the mountains. The southern front of the mountains receives the most precipitation, while sheltered leeward valleys such as Asheville are relatively dry (C. Daly, pers. comm. of results from PRISM model; Daly et al. 1994). This complex and relatively local pattern is responsible for the low correlation of precipitation with the climatic gradient (Axis 1, Table 4). As the density of lichen sampling fills in around the southern Appalachians, a second climatic gradient, related to precipitation in local mountain climates should emerge.

The geographic pattern of the climatic gradient as a whole is shown by mapping scores on the climatic gradient (Fig. 4). If climatic warming occurs

TABLE 2. Frequency of lichen species in the 1992 and 1993 data in the southeastern U.S. Plots on the regular sampling framework ("on-frame") are separated from other plots ("off-frame"). On-frame plots are further broken down by physiographic region: southern Appalachian Mountains (Mts.), Piedmont (Pied.), and coastal plain (Coast. Plain). Off-frame plots include supplemental plots from mainly urban and industrial locations (Suppl.), and plots taken as part of quality assurance (QA) studies, mostly near Asheville, North Carolina. Counts for genera include only those specimens that could not be identified reliably to species.

Species	On-frame			Off-frame		Total
	Mts.	Pied.	Coast. plain	QA	Suppl.	
					0	
<i>Anaptychia palmulata</i>	9	0	0	22	0	31
<i>Anzia colpodes</i>	2	0	0	8	0	10
<i>Bryoria bicolor</i>	0	0	0	1	0	1
<i>Bryoria furcellata</i>	0	0	0	1	0	1
<i>Bulbothrix goebelii</i>	1	3	2	1	0	7
<i>Bulbothrix isidiza</i>	0	0	2	0	0	2
<i>Bulbothrix laevigatula</i>	0	0	3	0	7	3
<i>Candelaria concolor</i>	2	1	1	1		12
<i>Candelaria fibrosa</i>	1	0	0	1	1	3
<i>Canoparmelia amazonica</i>	0	0	2	0	0	2
<i>Canoparmelia caroliniana</i>	15	17	19	18	6	75
<i>Canoparmelia crozalsiana</i>	0	0	1	1	7	9
<i>Canoparmelia cryptochlorophaea</i>	2	0	1	0	2	5
<i>Canoparmelia texana</i>	0	2	5	0	7	14
<i>Canoparmelia</i>	0	0	0	1	0	1
<i>Cetraria americana</i>	0	0	0	3	0	3
<i>Cetraria ciliaris</i>	13	2	0	37	0	52
<i>Cetraria fendleri</i>	2	7	1	1	0	11
<i>Cetraria oakesiana</i>	13	1	0	44	0	58
<i>Cetraria orbata</i>	0	2	0	3	0	5
<i>Cetraria viridis</i>	3	0	0	6	0	9
<i>Cetrelia cetrarioides s.l.</i>	1	0	0	2	0	3
<i>Cetrelia chicitae</i>	3	0	1	3	0	7
<i>Cetrelia olivetorum</i>	5	0	0	5	0	10
<i>Cladonia bacillaris</i>	7	1	2	7	1	18
<i>Cladonia caespiticia</i>	2	0	2	4	0	8
<i>Cladonia chlorophaea s.l.</i>	4	3	1	1	0	9
<i>Cladonia coniocraea</i>	4	1	2	26	0	33
<i>Cladonia cristatella</i>	1	2	4	4	0	11
<i>Cladonia cylindrica</i>	0	0	0	1	0	1
<i>Cladonia didyma</i>	2	0	1	6	0	9
<i>Cladonia floerkeana</i>	0	0	1	0	0	1
<i>Cladonia furcata</i>	0	0	1	0	0	1
<i>Cladonia macilenta</i>	0	1	1	5	0	7
<i>Cladonia mateocyatha</i>	1	0	1	0	0	2
<i>Cladonia ochrochlora</i>	2	0	0	4	0	6
<i>Cladonia parasitica</i>	1	0	2	2	0	5
<i>Cladonia peziziformis</i>	0	1	2	0	1	4
<i>Cladonia ramulosa</i>	5	0	1	3	0	9
<i>Cladonia ravenelii</i>	0	1	0	0	0	1
<i>Cladonia simulata</i>	0	0	1	0	0	1
<i>Cladonia squamosa</i>	4	1	0	13	0	18
<i>Cladonia subradiata</i>	0	0	1	0	1	2
<i>Cladonia vulcanica</i>	2	0	0	4	0	6
<i>Coccocarpia erythroxyli</i>	0	0	1	0	0	1
<i>Coccocarpia palmicola</i>	2	0	2	6	1	11
<i>Collema conglomeratum</i>	0	0	0	1	1	2
<i>Collema nigrescens</i>	1	0	0	3	0	4
<i>Collema subflaccidum</i>	5	0	0	4	1	10
<i>Collema</i>	0	0	0	1	0	1
<i>Dirinaria confusa</i>	1	0	1	0	2	4
<i>Dirinaria picta</i>	0	0	0	0	1	1
<i>Everniastrum catawbiense</i>	0	0	0	8	0	8
<i>Flavoparmelia caperata</i>	41	21	9	53	15	139
<i>Flavopunctelia flaventior</i>	8	1	1	11	3	24
<i>Heterodermia albicans</i>	2	0	0	0	0	2
<i>Heterodermia appalachensis</i>	2	0	3	2	12	19
<i>Heterodermia casarettiana</i>	1	0	0	0	0	1

TABLE 2. Continued.

Species	On-frame			Off-frame		Total
	Mts.	Pied.	Coast. plain	QA	Suppl.	
<i>Heterodermia crocea</i>	1	0	0	0	0	1
<i>Heterodermia hypoleuca</i>	3	0	0	1	0	4
<i>Heterodermia leucomelos</i>	1	0	0	2	0	3
<i>Heterodermia microphylla</i>	1	0	0	1	0	2
<i>Heterodermia obscurata</i>	14	7	9	30	4	64
<i>Heterodermia speciosa</i>	4	1	1	5	6	17
<i>Heterodermia squamulosa</i>	8	0	0	5	0	13
<i>Heterodermia</i>	0	0	0	0	1	1
<i>Hyperphyscia adglutinata</i>	1	0	0	0	0	1
<i>Hypogymnia krogiae</i>	1	0	0	0	0	1
<i>Hypogymnia physodes</i>	3	0	0	11	0	14
<i>Hypotrachyna croceopustulata</i>	0	0	0	7	0	7
<i>Hypotrachyna gondylophora</i>	0	0	0	7	0	7
<i>Hypotrachyna livida</i>	20	22	20	29	4	95
<i>Hypotrachyna osseoalba</i>	0	1	4	0	2	7
<i>Hypotrachyna pseudosinuosa</i>	0	0	0	1	0	1
<i>Hypotrachyna pustulifera</i>	3	1	1	5	7	17
<i>Hypotrachyna revoluta</i>	0	0	0	11	0	11
<i>Hypotrachyna rockii</i>	1	0	0	7	0	8
<i>Hypotrachyna showmanii</i>	2	0	0	13	0	15
<i>Imshaugia aleurites</i>	8	0	0	18	0	26
<i>Imshaugia placorodia</i>	0	1	0	3	0	4
<i>Leptogium austroamericanum</i>	1	0	0	0	1	2
<i>Leptogium corticola</i>	2	0	0	3	0	5
<i>Leptogium cyanescens</i>	4	3	0	6	5	18
<i>Leptogium laceroides</i>	0	0	0	1	0	1
<i>Leptogium teretiusculum</i>	0	0	0	1	0	1
<i>Lobaria pulmonaria</i>	6	0	0	7	0	13
<i>Lobaria quercizans</i>	5	1	0	6	0	12
<i>Lobaria ravenelii</i>	0	0	1	0	0	1
<i>Melanelia halei</i>	1	0	0	6	0	7
<i>Melanelia subaurifera</i>	0	0	0	1	0	1
<i>Menegazzia terebrata</i>	1	0	0	5	0	6
<i>Myelochroa aurulenta</i>	11	6	5	9	6	37
<i>Myelochroa galbina</i>	8	3	1	14	2	28
<i>Nephroma helveticum</i>	1	0	0	2	0	3
<i>Pannaria leucophaea</i>	0	0	0	1	0	1
<i>Pannaria leucosticta</i>	2	0	0	2	0	4
<i>Pannaria rubiginosa</i>	0	0	0	5	0	5
<i>Pannaria tavaresii</i>	1	0	0	2	0	3
<i>Parmelia squarrosa</i>	21	1	0	29	1	52
<i>Parmelia sulcata</i>	3	0	0	11	0	14
<i>Parmeliella triptophylla</i>	1	0	0	2	0	3
<i>Parmelinopsis horrescens</i>	14	3	8	42	3	70
<i>Parmelinopsis minarum</i>	23	17	8	34	7	89
<i>Parmelinopsis spumosa</i>	0	1	0	3	0	4
<i>Parmelinopsis swinscowii</i>	0	0	2	0	0	2
<i>Parmeliopsis hyperopta</i>	0	0	1	0	0	1
<i>Parmotrema arnoldii</i>	5	3	0	2	1	11
<i>Parmotrema austrosinense</i>	0	0	1	0	3	4
<i>Parmotrema chinense</i>	3	1	0	16	0	20
<i>Parmotrema crinitum</i>	9	2	0	18	1	30
<i>Parmotrema cristiferum</i>	0	0	0	0	1	1
<i>Parmotrema dilatatum</i>	4	7	8	4	4	27
<i>Parmotrema eurysacum</i>	3	2	0	11	0	16
<i>Parmotrema gardneri</i>	0	2	0	0	0	2
<i>Parmotrema hypotropum</i>	24	21	10	30	14	99
<i>Parmotrema madagascariaceum</i>	0	0	1	0	0	1
<i>Parmotrema margaritatum</i>	9	1	0	18	0	28
<i>Parmotrema mellissii</i>	4	0	1	7	1	13
<i>Parmotrema michauxianum</i>	4	21	17	19	1	62
<i>Parmotrema perforatum</i>	6	25	18	6	8	63
<i>Parmotrema praesorediosum</i>	0	2	8	1	4	15

TABLE 2. Continued.

Species	On-frame			Off-frame		Total
	Mts.	Pied.	Coast. plain	QA	Suppl.	
<i>Parmotrema rampoddense</i>	1	1	7	0	3	12
<i>Parmotrema rigidum</i>	3	4	6	1	1	15
<i>Parmotrema stippeum</i>	1	0	0	2	0	3
<i>Parmotrema subsumptum</i>	2	0	0	1	0	3
<i>Parmotrema subtinctorium</i>	3	0	1	3	1	8
<i>Parmotrema tinctorum</i>	0	0	7	0	5	12
<i>Parmotrema ultralucens</i>	0	0	1	0	2	3
<i>Parmotrema xanthinum</i>	1	0	0	1	0	2
<i>Parmotrema</i>	1	2	2	1	1	7
<i>Phaeophyscia adiaetola</i>	1	0	0	3	0	4
<i>Phaeophyscia ciliata</i>	2	1	1	3	1	8
<i>Phaeophyscia erythrocardia</i>	0	0	0	1	0	1
<i>Phaeophyscia pusilloides</i>	7	1	1	12	4	25
<i>Phaeophyscia rubropulchra</i>	17	11	4	41	15	88
<i>Phaeophyscia</i>	0	0	0	0	1	1
<i>Physcia aipolia</i>	3	8	4	17	9	41
<i>Physcia americana</i>	3	4	4	14	8	33
<i>Physcia crispa</i>	0	0	2	0	0	2
<i>Physcia millegrana</i>	5	5	3	9	14	36
<i>Physcia neogaea</i>	3	2	0	5	0	10
<i>Physcia pseudospeciosa</i>	0	0	0	0	1	1
<i>Physcia stellaris</i>	10	2	0	17	1	30
<i>Physcia</i>	0	1	0	1	0	2
<i>Physciella chloantha</i>	0	0	0	0	2	2
<i>Physconia detera</i>	0	0	0	0	1	1
<i>Platismatia tuckermanii</i>	10	1	0	19	0	30
<i>Pseudevernia cladonia</i>	0	0	0	2	0	2
<i>Pseudevernia consocians</i>	8	1	0	25	0	34
<i>Pseudocyphellaria aurata</i>	0	0	0	0	1	1
<i>Pseudocyphellaria crocata</i>	0	0	0	2	0	2
<i>Punctelia appalachensis</i>	2	0	1	2	0	5
<i>Punctelia missouriensis</i>	2	1	0	2	0	5
<i>Punctelia rudecta</i>	38	30	21	49	18	156
<i>Punctelia semansiana</i>	8	4	3	9	0	24
<i>Punctelia subrudecta</i>	14	3	1	28	3	49
<i>Punctelia</i>	0	0	0	1	0	1
<i>Pyxine berteriana</i>	1	0	1	0	0	2
<i>Pyxine caesiopruinosa</i>	1	4	4	2	14	25
<i>Pyxine eschweileri</i>	0	1	0	0	3	4
<i>Pyxine soredata</i>	17	3	1	20	4	45
<i>Pyxine subcinerea</i>	0	1	0	0	0	1
<i>Ramalina americana</i>	15	9	6	44	4	78
<i>Ramalina stenospora</i>	1	0	0	0	0	1
<i>Ramalina willeyi</i>	1	0	1	0	2	4
<i>Rimelia cetrata</i>	6	5	11	21	1	44
<i>Rimelia diffractaica</i>	2	0	0	1	0	3
<i>Rimelia reticulata</i>	25	16	19	36	10	106
<i>Rimelia simulans</i>	3	0	0	3	0	6
<i>Rimelia subisidiosa</i>	3	7	15	11	5	41
<i>Sticta weigelii</i>	3	0	0	3	0	6
<i>Usnea aciculifera</i>	4	1	0	0	0	5
<i>Usnea ceratina</i>	5	0	0	10	0	15
<i>Usnea cornuta</i>	7	0	0	5	0	12
<i>Usnea dasaea</i>	5	0	0	8	0	13
<i>Usnea hesperina</i>	5	0	0	14	0	19
<i>Usnea madeirensis</i>	1	0	0	0	0	1
<i>Usnea mutabilis</i>	3	5	5	9	1	23
<i>Usnea occidentalis</i>	1	0	0	2	0	3
<i>Usnea rubicunda</i>	17	3	4	22	0	46
<i>Usnea strigosa</i>	26	29	18	40	7	120
<i>Usnea subfloridana</i>	2	0	0	7	0	9
<i>Usnea subscabrosa</i>	11	0	1	14	0	26
<i>Usnea</i>	0	0	2	9	0	11
Total number of plots	46	35	45	57	20	203
Total number of taxa	124	73	83	137	70	184

TABLE 3. Characteristic epiphytic macrolichens in southeastern United States from Georgia to Virginia, west to east Tennessee.

Pollution tolerant or ubiquitous species	Primarily mountain species
<i>Candelaria concolor</i>	<i>Anaptychia palmulata</i>
<i>Canoparmelia crozalsiana</i>	<i>Cetraria ciliaris</i>
<i>Canoparmelia texana</i>	<i>Cetraria oakesiana</i>
<i>Flavoparmelia caperata</i>	<i>Cetraria viridis</i>
<i>Parmotrema austrosinense</i>	<i>Heterodermia granulifera</i>
<i>Parmotrema hypotropum</i>	<i>Heterodermia squamulosa</i>
<i>Parmotrema gardneri</i>	<i>Imshaugia aleurites</i>
<i>Phaeophyscia pusilloides</i>	<i>Lobaria pulmonaria</i>
<i>Phaeophyscia rubropulchra</i>	<i>Parmelia squarrosa</i>
<i>Physcia aipolia</i>	<i>Parmotrema arnoldii</i>
<i>Physcia americana</i>	<i>Parmotrema margaritatum</i>
<i>Physcia millegrana</i>	<i>Parmotrema subtinctorium</i>
Primarily coastal species	<i>Platismatia tuckermanii</i>
<i>Bulbothrix laevigatula</i>	<i>Pseudevernia consocians</i>
<i>Canoparmelia texana</i>	<i>Punctelia subrudecta</i>
<i>Heterodermia albicans</i>	<i>Pyxine sorediata</i>
<i>Hypotrachyna osseovalba</i>	<i>Usnea ceratina</i>
<i>Parmotrema praesorediosum</i>	<i>Usnea cornuta</i>
<i>Parmotrema rampoddense</i>	<i>Usnea subscabrosa</i>
<i>Parmotrema tinctorium</i>	
<i>Pyxine caesiopruinosa</i>	

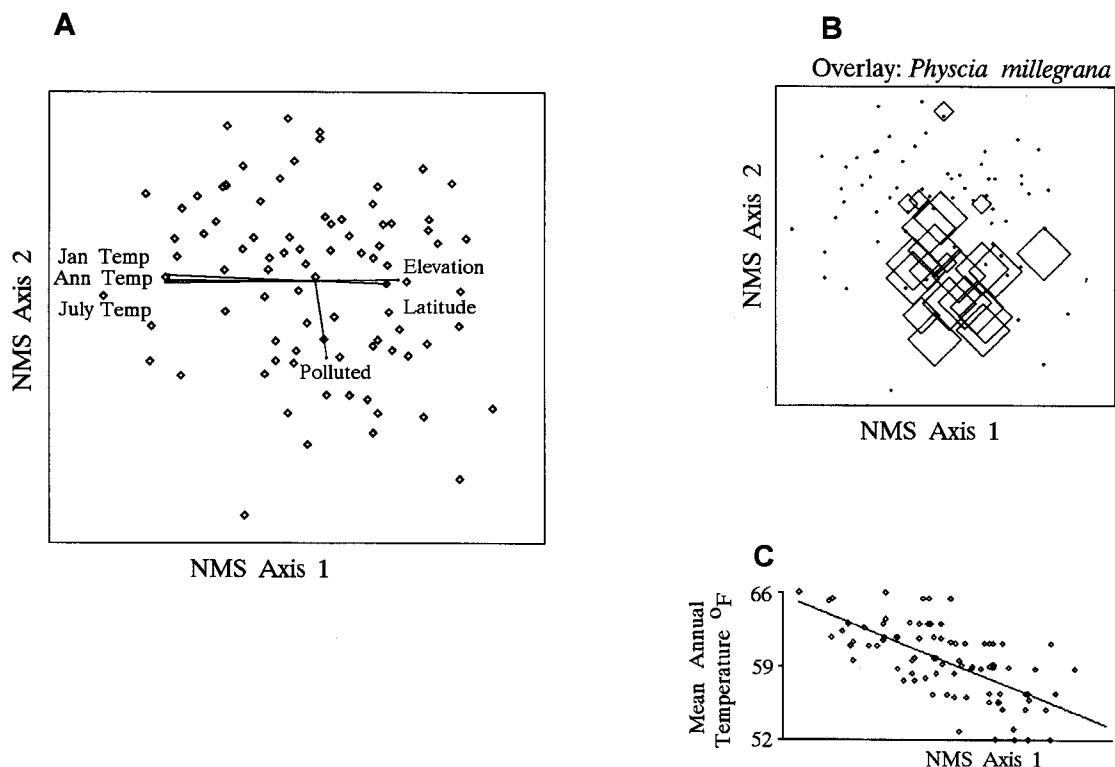


FIGURE 3. Plot scores on lichen community gradients. Axis 1 corresponds to a regional climatic gradient (cool mountain climates to right, warm coastal climates to left). Axis 2 corresponds to an air quality gradient (plots with lower air quality toward the bottom of the graph). A—NMS ordination diagram with radiating environmental vectors from the centroid of points. The length of the line is proportional to the r^2 of the indicated variable with the axes; the direction indicates the direction of increasing values in the graph. B—Overlay of *Physcia millegrana*, a pollution tolerant species. Size of the symbol is proportional to abundance with the smallest symbol meaning absence. C—Overlay of mean annual temperature as a function of score on Axis 1.

TABLE 4. Pearson (r) and Kendall (τ) correlations between site-level variables and lichen community gradients (Axis 1 and Axis 2; see text).

Variable	Axis 1		Axis 2	
	r	τ	r	τ
Urban/industrial or not (1/0)	0.18	0.14	-0.50	-0.40
Latitude	0.47	0.32	-0.06	-0.03
Longitude	0.26	0.16	-0.23	-0.14
Elevation	0.50	0.46	0.08	-0.02
Total tree basal area	0.19	0.12	0.15	0.11
% of basal area in conifers	-0.42	-0.31	0.26	0.15
Sum of lichen abundances	0.34	0.23	0.33	0.20
Lichen species richness	0.32	0.23	0.26	0.16
H' Shannon diversity index	0.29	0.23	0.30	0.16
Mean January temperature	-0.67	-0.49	0.14	0.08
Mean July temperature	-0.66	-0.49	0.00	0.03
Mean annual temperature	-0.66	-0.49	0.08	0.05
Total yearly precipitation	0.05	0.03	0.00	0.03

and influences lichen communities, then the pattern should shift northward in the future.

The climatic gradient is also strongly expressed in the regional distribution patterns of many individual species (examples in Fig. 5). Note that these maps indicate the occurrence of a species, but are not equivalent to range maps. Absence of a species does not mean that species does not occur in that area; rather that the species simply was not recorded for a given plot. The maps do, however, clearly convey the areas in which a species is ecologically prominent.

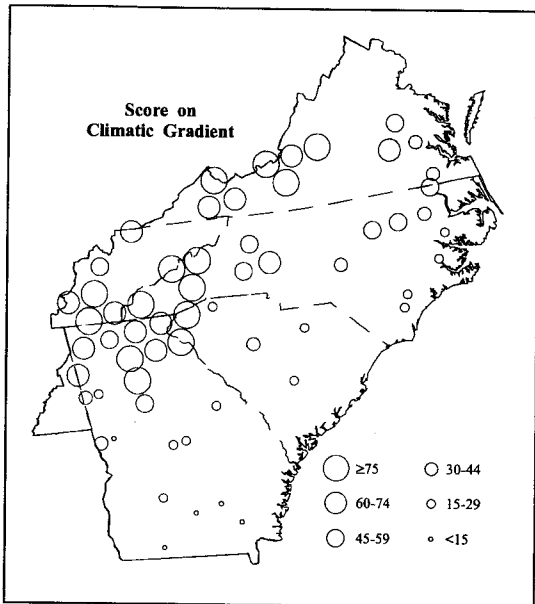


FIGURE 4. Regional distribution of scores on the climatic gradient, as expressed by the lichen community. Numbers are unitless scores on an NMS ordination axis; higher scores correspond to lichen communities indicative of cooler climates.

A weak trend exists in lichen species richness from more species in the cooler (mountain) plots to fewer species in the warmer plots ($r = 0.40$, $n = 85$ for species richness vs. score on the climatic gradient). Plots west of the mountains appear to have species richness similar to the piedmont plots.

The regional pattern in diversity is quite noisy. Species richness is subject to more observer error than scores on the compositional gradients (McCune et al. 1997). In addition to the contribution of observer error, local variation in species richness is likely related to successional status, the proportion of conifers and hardwoods, and air quality.

AIR QUALITY GRADIENT.—Site scores. Sites were scored as to presumed air pollution impact using NMS (Table 5, Fig. 6). Near-urban and industrial areas scored lower, strengthening the interpretation of this gradient as being related to air quality. These areas were clumped near the major urban centers (e.g., Atlanta and Augusta) and at the northern edge of the study area, in northern Virginia. Low scores in the northernmost part of the study area reflect the position of northern Virginia at the edge of the massive swath of air pollution extending from the Ohio River Valley northeast to New England (NAPAP 1993; Ollinger et al. 1993).

Based on the literature, we infer the responsible pollutants to be nitrogen- and sulfur-based acidifying and fertilizing pollutants, but not tropospheric ozone (e.g., McCune 1988; Ruoss & Vonarburg 1995; van Dobben 1993). One might also hypothesize that more frequent disturbance occurs in forests in urban and industrial areas. Disturbance might also reduce lichen diversity and alter species composition. Our urban/industrial sites, however, were often mature forests with natural understories in large city parks and on the edges of golf courses. Furthermore, the species composition of young

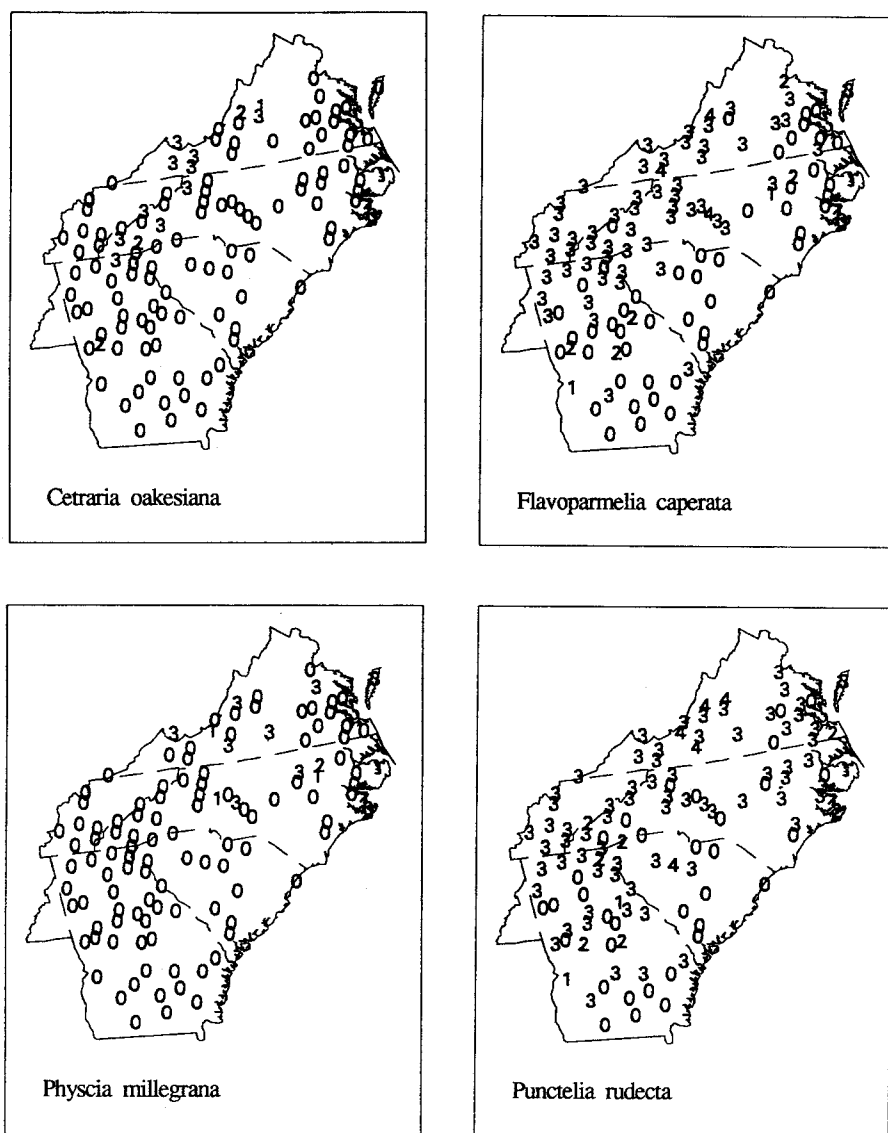


FIGURE 5. Regional distributions of selected individual species of epiphytic lichens: *Cetraria oakesiana* (restricted to mountains), *Flavoparmelia caperata* (widespread and common but less frequent on coast), *Physcia millegrana* (pollution tolerant), and *Punctelia rudecta* (common throughout the region).

stands in clean rural areas differs from that in polluted stands (see "Stand Development" below).

Note that air pollution impact is determined by more than just the ambient air quality. It is well known that in polluted areas of Europe, conifers and other acidic-barked tree species show more extreme loss of epiphytic species than do more basic-barked species, such as *Fraxinus* and many other hardwoods. This contrast is illustrated by a pair of sites in an industrial area of Augusta, Georgia. A site with nearly 84% conifers (a *Pinus* plantation) had only two lichen species, while another plot in an adjoining hardwood stand (2% conifers) had 16 species. At a regional scale, however, percent of the

basal area in conifers was only weakly related to the air quality gradient in lichen communities. Using the proportion of conifers as a covariate did not improve the gradient model.

Air quality in northern Georgia.—Because northern Georgia (north of 33°) was well represented in both the urban/industrial and on-frame data sets, we mapped scores on the air quality gradient in this area (Fig. 7). The relatively low air quality in and near Atlanta is evident as a group of smaller circles. Urban and industrial plots near Rome and Augusta also scored lower than the surrounding areas.

Species scores on air quality gradient.—Corre-

TABLE 5. Plot scores at the low end of the air quality gradient, ordered from more polluted (lowest score) to less polluted (higher score; maximum observed = 112). Responsible pollutants are likely acidifying or fertilizing nitrogen- and sulfur-based pollutants. Sum = sum of lichen abundance codes; S = number of lichen species; H' = Shannon diversity index.

Plot	Score	Sum	S	H'
Augusta, Bowles Rd-pine	-5.7	6	2	0.69
Augusta, Bowles Rd-hardwood	9.9	42	16	2.72
3408432 (just N of Atlanta)	15.0	18	6	1.79
Atlanta, Southbend Park-1	16.6	11	5	1.50
3308481 (just NE of Atlanta)	20.3	15	5	1.61
3208487 (W-central Georgia)	22.5	20	9	2.18
3508511 (E Tennessee)	24.9	17	6	1.78
3508213 (W South Carolina)	25.8	21	7	1.95
Atlanta, Southbend Park-2	26.2	23	10	2.22
Augusta, Lock & Dam	27.2	34	17	2.73
Atlanta, Botanical Gardens-1	29.4	28	13	2.46
Rome, Coosa Park-2	30.4	42	14	2.64
Atlanta, Bobby Jones Golf Course	33.9	41	14	2.64
Atlanta, Botanical Gardens-2	34.7	41	14	2.64
3708012 (western Virginia)	34.9	33	11	2.40
3708137 (western Virginia)	37.5	36	12	2.49
3708046 (western Virginia)	37.9	42	15	2.70
Chattanooga, N Chick. Greenway	38.1	50	18	2.86
3508457 (E Tennessee)	38.3	26	11	2.34

lations (*r*) of individual species with the air quality gradient (second NMS axis) can be used to score species tolerance of air pollution. Some of the species with the highest scores are well known for their tolerance of air pollution (e.g., *Phaeophyscia rubropulchra*, *Physcia millegrana*, and *Candelaria concolor*; see McCune 1988 and Muir & McCune 1988). Air pollution responses for many of the oth-

er more geographically restricted species are poorly known because of the lack of previous lichen community studies in the southeast U.S. Most of the fruticose lichens and cyanolichens thought to be pollution sensitive either showed ambivalent or positive relationships to the air quality gradient.

STAND DEVELOPMENT.—Lichen communities change as a forest develops. Lichens are often conspicuously sparse in very young stands with low basal areas of trees > 10 cm dbh. In this study, two very young stands (total BA < 5 m²/ha) had low lichen species richness (11 and 8 species, respectively). These values are more similar to those of polluted sites than to the rural sites. The effect of these stands on the gradient analysis could be min-

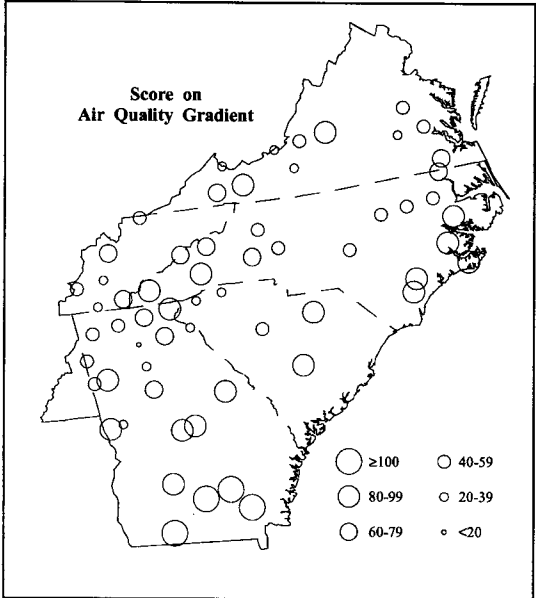


FIGURE 6. Regional distribution of scores on the air quality gradient, as expressed by the lichen community in on-frame plots. Larger circles indicate better air quality.

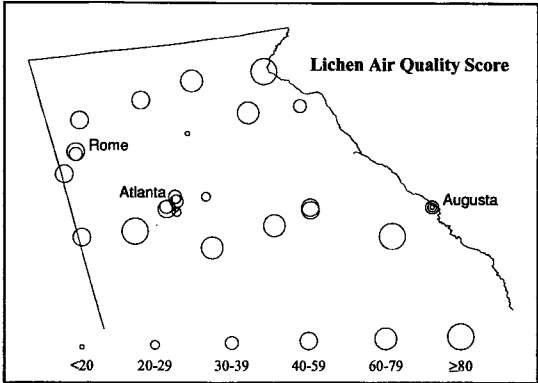


FIGURE 7. Scores on the air quality gradient in northern Georgia as expressed by the epiphytic lichen community. Lower scores indicate lower air quality. Note the lower scores near Atlanta, Augusta, and Rome.

imized by removing plots with total BA < 10 m²/ha. In our case, however, this proved unnecessary. Despite the low diversity in these plots, scores on the second NMS axis indicated good air quality. This demonstrates that the particular species present in young clean-air stands will result in a low air pollution score, even if relatively few species are present.

CONCLUSIONS

Epiphytic macrolichen communities in the southeastern U.S. provided information on several key assessment questions for the Forest Health Monitoring program, including those concerning biodiversity and contamination of natural resources. We found 176 species of epiphytic macrolichens in the 203 plots examined here.

Gradient analysis revealed two major gradients in lichen communities. The first gradient and strongest gradient corresponds to a macroclimatic gradient from the coast to the Piedmont to the Appalachian Mountains and from south to north. This gradient is primarily linked to temperature rather than precipitation, with the southern coast being the warmest. A weak trend appears to exist in species diversity from the mountains to the coast, with the highest diversity in the mountains and lower diversity on the Piedmont and coast. The second major gradient corresponds primarily to a gradient in air quality, with pollution-tolerant species and lower species richness at one end of the gradient, and pollution-sensitive species and high species richness at the other end of the gradient.

Sparse but measurable epiphytic macrolichens were found in urban areas with heavy industry. In remote areas lichens were often luxuriant and diverse. Air pollution impacts on lichen communities were observed near urban and industrial areas in eastern Tennessee, northern Georgia, South Carolina, and in rural Virginia. Difference in species composition allowed us to distinguish between species-poor sites in young, regenerating forest and species-poor sites in areas of low air quality.

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