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Air pollution and climate gradients in western Oregon and Washington indicated by epiphytic macrolichens

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Lichen-based air quality and climate gradients in western Oregon and Washington are responsive to regionally increasing nitrogen availability and to temperature changes predicted by climate models.

Abstract

Human activity is changing air quality and climate in the US Pacific Northwest. In a first application of non-metric multidimensional scaling to a large-scale, framework dataset, we modeled lichen community response to air quality and climate gradients at 1416 forested 0.4 ha plots. Model development balanced polluted plots across elevation, forest type and precipitation ranges to isolate pollution response. Air and climate scores were fitted for remaining plots, classed by lichen bioeffects, and mapped. Projected 2040 temperatures would create climate zones with no current analogue. Worst air scores occurred in urban-industrial and agricultural valleys and represented 24% of the landscape. They were correlated with: absence of sensitive lichens, enhancement of nitrophilous lichens, mean wet deposition of ammonium >0.06 mg l^{-1}, lichen nitrogen and sulfur concentrations >0.6% and 0.07%, and SO_2 levels harmful to sensitive lichens. The model can detect changes in air quality and climate by scoring re-measurements.

Keywords: Climate change; Diversity; Forest health monitoring'; Air quality; Lichen

1. Introduction

Air pollution is a relatively recent concern in the Pacific Northwest. The region's dominant winds originate over relatively clean Pacific Ocean air masses and bring plentiful, cleansing rainfall much of the year (Jackson, 1993). Enforcement of federal laws passed in the 1970s-1990s has reduced point source emissions and per capita vehicular emissions, generally improving urban air quality and bringing most urban areas into compliance for ozone and particulate matter (Estus, 2000; ORDEQ, 2001). On a national scale, the Pacific Northwest is among the cleanest areas for wet deposition of sulfur and nitrogen. Between 1985 and 2003, wet SO_4^{2-} deposition decreased over much of the western Pacific Northwest from 3–9 kg ha^{-1} to <3 kg ha^{-1} (NADP/NTN, 2006). While total wet inorganic nitrogen deposition has increased regionally from <1 kg ha^{-1} to 1–3 kg ha^{-1} since 1985—nearly all due to increases in ammonium deposition—these values are still considerably lower than other parts of the country (NADP/NTN, 2006).

From 1980 to 2000, Oregon and Washington populations grew by 30 and 43%, to 3.4 and 5.9 million people, respectively (US Census Bureau, 2001). Increasing energy needs are poised to negate air quality gains with regard to acidifying, and oxidizing pollutants (Dahlgren, 2000; ORDEQ, 2001); regional intensification of agriculture, particularly animal husbandry, can explain increasing ammonia deposition. Transpacific pollutants enhance regional ozone and NO_x and are predicted to increase with continued population and standard of living increases in Asia (Bertschi et al., 2004). Pacific

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Northwest lichen communities are beginning to experience the adverse effects of nitrogen pollution, with decreases in sensitive taxa and replacement by pollution tolerant or nitrophilous species (Fenn et al., 2003). Thus, while on a national scale the region's pollution profile is fairly clean, parts of the region have begun to mimic other parts of the US (Showman and Long, 1992; Sigal and Nash, 1983) and western Europe (Van Herk et al., 2003) with longer histories of air pollution and a paucity of sensitive taxa.

Climate is also changing, with potentially profound ecological consequences. From 1966 to 1998, mean annual temperatures in western Oregon and Washington increased 0.75–1.2 °C (NOAA, 2005). Mote et al. (2003), comparing eight different climate models, predicted minimum and maximum additional increases of 1.5 and 3.2 °C for Oregon and Washington by 2040. Effects include smaller snowpacks, earlier snow melt, intensified summer drought conditions, higher storm intensities and more frequent coastal flooding (Mote et al., 2003; Shriner and Street, 1997). If air quality and climate are changing, it seems timely to document 21st century baseline conditions from a vegetation perspective.

Lichen elemental content indicates recent environmental loading of depositional and gaseous pollutants (Palomäki et al., 1992; Søchting, 1995). A dynamic equilibrium exists between pollutant accumulation and loss that makes elemental analysis of lichen thalli a sensitive tool for detection of air quality changes (Boonpragob and Nash, 1990). Lichen communities are sensitive to sulfur dioxide (Nash and Gries, 2002) and nitrogen and sulfur-containing acidic compounds in precipitation (Farmer et al., 1992). Some lichens are probably sensitive to ozone, peroxyacetylnitrate and nitrogen oxides, especially if metabolically active during pollution peaks (Ross and Nash, 1983; Scheidegger and Schroeter, 1995; Tarhanen et al., 1997). In contrast, nitrophilous lichens are enhanced by fertilizing and alkalinizing nutrients such as ammonia (Van Dobben et al., 2001; Van Dobben and ter Braak, 1998). Lichens also differ in moisture, temperature, light, nutritional, and dispersal requirements (Sillett et al., 2000). Carefully interpreted, lichen community composition and elemental content of lichen thalli can indicate air quality, climate, and other environmental conditions.

Regional gradient models of the USDA Forest Inventory and Analysis (FIA) Program Lichen Indicator (USDA-Forest Service, 2004) differentiate lichen community responses to air pollution and climate from other environmental variables. Systematically sampled survey data can be scored along air pollution and climate gradients and used to assess conditions and monitor change across forested lands in the United States. Gradient models and initial assessments are complete for the southeastern states (McCune et al., 1997a), California (Jovan and McCune, 2005) and Colorado (McCune et al., 1998) and in preparation for the Mid-Atlantic, inland Northwest, and New England. This study presents a Pacific Northwest model using lichen data collected from 1994 to 2001.

We show that lichen community composition is a practical tool to assess and monitor air quality and climate change in western Oregon and Washington by: (1) modeling epiphytic macrolichen community response; (2) scoring air quality and climate at 1416 sites; (3) interpolating scores to map air quality and climate zones, quantifying effects in biological terms; (4) listing indicator species; and (5) discussing the relationship between scores and ambient pollutants, wet deposition, lichen thallus chemistry, and predicted changes in climate.

2. Methods

2.1. Study design

The FIA lichen indicator is implemented by modeling lichen community gradients in relationship to air quality, climate and other environmental variables. The model is then applied to the entire dataset to calculate air quality and climate scores (Fig. 1) and assess regional condition and spatial variation. Repeated sampling documents changes in community condition over time. Our model applies to western Oregon and Washington from the Pacific Ocean to the crest of the Cascade Range, demarcated by county boundaries (Fig. 2).

2.2. Lichen community data

From 1994 to 2001, trained field observers collected vouchers and estimated abundance of each epiphytic macrolichen detected during 1549 surveys on 891 'on-frame' and 525 'off-frame' circular 0.38 ha plots (Table 1) following the FIA lichen community protocol (USDA-Forest Service, 2004). On-frame data are used to make regional inferences about status and trends

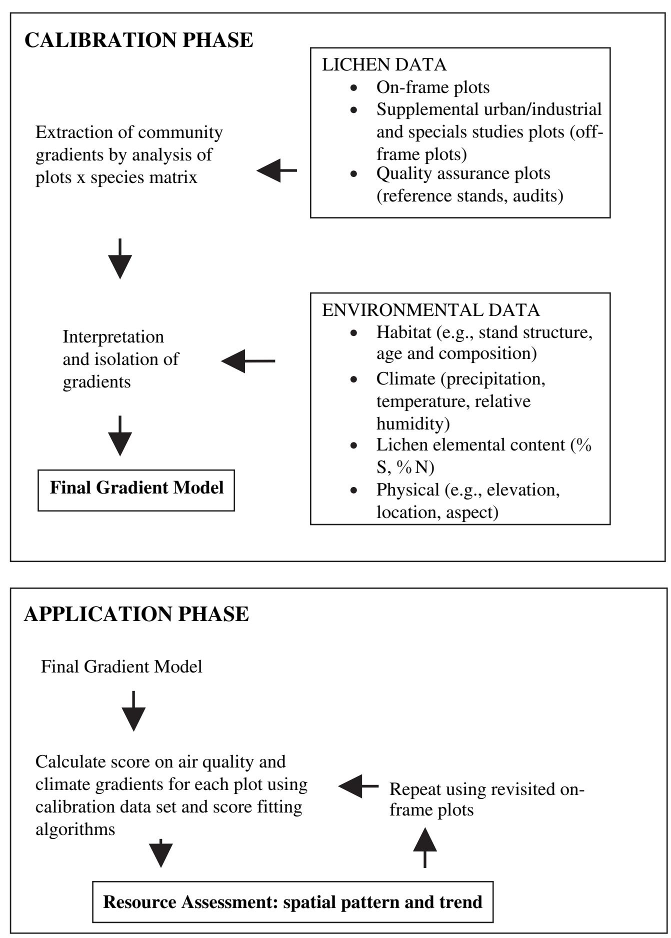

Fig. 1. Overview of the development and application of US Forest Service/Forest Inventory Analysis lichen indicator gradient models.

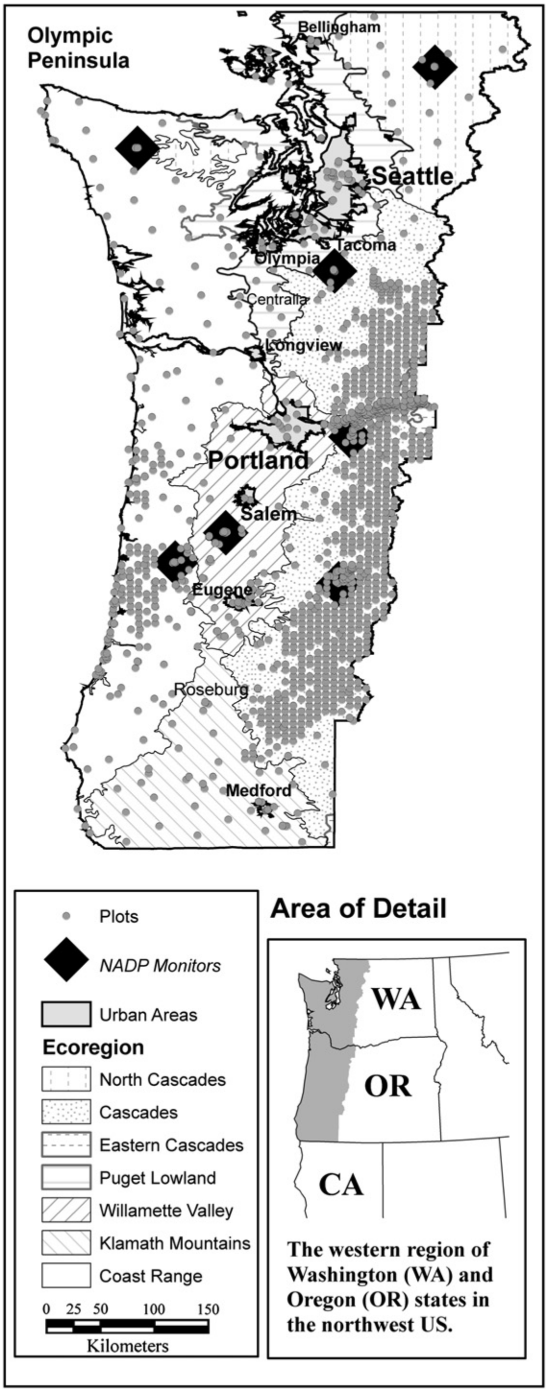

Fig. 2. Ecoregions, lichen plots, and wet deposition monitoring locations in the study area.

because they comprise an unbiased sample (Messer et al., 1991). Off-frame data supplement model development, rare species capture, and point density for response maps.

Lichens were identified using McCune and Geiser (1997), Lindblom (1997), and Halonen et al. (1998) from morphology, spot tests, and thin layer chromatography (White and James, 1985); taxonomy followed Esslinger (1997). Species of *Bryoria, Cladonia, Collema, Fuscopannaria, Leptogium, Physcia, Usnea*, and *Xanthoria* with <4 occurrences, having high potential indicator value at the genus level, were lumped with genus-only collections (Table 2). Other vouchers identifiable only to genus (~4% of identifications) and species with <4 occurrences were excluded from analysis.

2.3. Lichen elemental data

At most plots (Table 1) 20 g samples of two species were gathered for total sulfur, nitrogen and lead analysis following Geiser (2004). Each sample is large in order to be representative of the population, which, presumably consists of similar numbers of old and young individuals over time. Target species were *Alectoria sarmentosa, Evernia prunastri, Hypogymnia enteromorpha, H. inactiva, H. imshaugii, Letharia vulpina*, and *Platismatia glauca*. Multiple target species were needed because no one lichen could be found at all sites. The 97.5% quantile (0.59% N) for the nitrogen concentration distribution in *Platismatia glauca* collected in on-frame national forest plots (FIA P1)—assumed to be clean—was used to distinguish nitrogen-enhanced from unenhanced plots. *Platismatia glauca* was collected at 121 of 293 plots used to develop the gradient model. To utilize lichen chemistry data from the remaining plots, species-specific linear regression models were constructed to predict *P. glauca* values from other lichens based on co-occurrence. On average, predicted values differed from *P. glauca* values by .010% N (SD 0.10% N). If the measured (or predicted value when *P. glauca* did not occur on the plot) averaged >0.59% N, the site was considered nitrogen-enhanced. Linear regression models were also used to predict '% S in *P. glauca*' on plots where *P. glauca* was absent. Measured (or predicted) values >0.073% S were considered enhanced. Lead is not a nutritional constituent of lichens and values >15 $\mu g\ g^{-1}$ were considered enhanced; the two species average was the plot value.

2.4. Climate, pollution, and other environmental data

Estimates of mean annual precipitation, relative humidity, dew point, maximum August and minimum December temperatures, continentality (the difference between maximum August and minimum December temperatures) and annual days with precipitation were determined using layers generated by climate source (Daly and Taylor, 2000) parameter-elevation regressions on individual slopes model (PRISM) at a 2 km^2 cell resolution. Mean annual days of marine fog at 100 m above ground level and annual temperature were obtained from the 90 m^2 cell US Forest Service potential natural vegetation model for predicting environmental variables across Pacific Northwest landscapes (Lipow et al., 2004).

No high resolution data exist for air pollutants in western Oregon and Washington. State monitors are confined to urban areas; other monitors are widely spaced. We used dry weight N and S concentrations in lichen thalli to indicate availability of N and S to lichen communities. Each plot was also assigned a binary variable for pollution: "polluted" if the plot was within the boundaries of an urban area (but lacked elemental analysis data) or if % N in *Platismatia glauca* was >0.59%; "clean" if otherwise. To relate lichen elemental content and lichen-community based air scores (see Section 2.5 for description of air score derivation) to wet deposition of nitrate, ammonium and sulfate ions, we installed 3–6 plots within 2 km of each of seven National Atmospheric Deposition Program (NADP) monitors in the study area (Fig. 2) (NADP/NTN, 2006).

The dataset also included plot coordinates, state, county, elevation, aspect, slope, quadratic mean diameter of trees >2.5 cm diameter, basal area of live trees, % basal area in conifers and hardwoods, year, mean age of dominant trees, lichen species richness, coast distance, and Omernik's (1986) US Environmental Protection Agency Level III eco-regions.

2.5. Analyses

Using the inferential on-frame FIA P3 data subset (Table 1), we calculated: α-diversity, the average species richness per plot; γ-diversity, the landscape-level diversity estimated by the total number of species, and γ/α, a measure of heterogeneity (Whittaker, 1972).

Elevation, precipitation, and hardwood basal area were confounded in pilot ordinations of the complete lichen community dataset; urban- industrial and agricultural areas are generally in the lowest, driest parts of the region, where forests are dominated by hardwoods. To isolate the air pollution signal, the model development dataset was systematically selected for comparable numbers of clean and polluted plots across all elevation, hardwood basal area, and

Table 1
Lichen community data sources

Plot type[a]	Geographic area	Plots	Surveys	Plots in model	Element analysis	Years	Reference
On-frame FIA P3	Study area 23 km grid	198	252	19	Some	1997–2001	This paper
On-frame FIA p1	National forest 5.4 km grid	693	745	155	Yes	1993–2001	This paper
Off-frame	Columbia River Gorge	117	141	51	Yes	1993–2001	This paper
Off-frame	Major cities	96	98	35	Yes	1995–1998	This paper
Off-frame	Blue River Adaptive Management Area, western Cascades, Oregon	22	22	0	No	1999	Berryman, 2002
Off-frame	Immediate coast	65	65	9	No	1998–2000	Glavich et al., 2005
Off-frame	Bureau of Land Management, Oregon Coast and Cascade Ranges	121	121	0	No	1994–1997	Neitlich and McCune, 1997; Peterson and McCune, 2003
Off-frame	Rural and semi-rural in study area	65	66	9	Yes	1995–2001	This paper
Off-frame	Within 2 km of NADP monitors	39	39	15	Yes	1998	This paper
	Totals	1416	1549	293			

[a] On-frame plots are part of the US Forest Service Forest Inventory and Analysis permanent plot framework covering all United States forests, public and private. Pacific Northwest P1 plots are centered on the crosshairs of a 5.4 km square grid; P3 plots are randomly located inside 23 km diameter hexagonal grid cells. Off-frame plots are not part of the framework, permanently marked, or randomly located. All plots were 0.38 ha and were surveyed for lichens by certified observers following the Forest Health Monitoring Lichen Indicator protocol (USDA-Forest Service, 2004).

precipitation ranges (Table 3). The dominant gradients in lichen communities were then extracted using non-metric multidimensional scaling (NMS) in PC-ORD (McCune and Mefford, 1999). NMS is a robust, effective non-parametric method for multivariate reduction of community data (Mather, 1976).

Using NMS "slow and thorough" settings and Sorenson distance measures, we chose a three-dimensional solution with best final stress (17.53) and instability (0.023) based on 270 runs of 400 iterations—120 with real data and 150 with randomized data. We rotated the ordination to maximize alignment of % N in *Platismatia glauca* with Axis 1 and climatic variables with Axis 2. The final air and climate score for each plot was its position on Axes 1 and 2, respectively. NMS was then used in predictive mode ("simultaneous fitting of new plots to axes") to score the 1123 remaining plots. Scores for replicate surveys were averaged to yield a single score per plot. The score-fitting algorithm calculates stress for each new plot at each trial location along each gradient choosing the lowest stress location as the final position. In the application phase (Fig. 1), re-measurement scores are mechanically calculated using the gradient model and score-fitting routine.

Air scores were block-kriged to interpolate a response surface. Spatial autocorrelation between air scores using the robust variogram estimator (Cressie and Hawkins, 1980) revealed directional dependence. Theoretical variograms were constructed for north-south and east-west directions using a nested, Gaussian model to predict unsampled locations. Predictions for 3 km^2 cells covering the study area used the 30 nearest data points, averaging 16-point blocks. Climate scores were kriged in Arc GIS 9 using the Gaussian semi-variogram model and a variable search radius including 20 points (ESRI, 2004).

We linearly regressed air scores and lichen element content at NADP plots with mean annual wet deposition of nitrates, ammonia, sulfates and pH recorded by the respective NADP monitor in the 3 year period preceding the lichen survey. The adjusted r^2 value and F-test p-values indicated correlation strength and significance.

PC-ORD's Indicator Species Analysis (ISA) identified lichens associated with clean, intermediate and polluted plots in the calibration data set. The three groups were defined by air score ranges in which 90%, 50% and 10% of plots had a binary air pollution rating of "clean". ISA (Dufrene and Legendre, 1997) combines species abundance and faithfulness of occurrence within each group with a Monte Carlo statistical significance technique to produce indicator values for each species in each group. We selected air quality classes from the distribution of air scores at sites supporting sizeable populations (>25 individuals ha^{-1}) of the indicator species with broadest geographic distributions. ISA also identified lichens associated with four climate zones pre-selected by natural breaks. Natural breaks (Jenks, 1967), also known as Jenks' optimization, is the default ArcGIS classification algorithm (ESRI, 2004). Break points maximize similarity of within-class values by identifying relatively big jumps in the data values. The algorithm calculates classes based on the smallest possible total error (the sum of absolute deviations about the class median or, alternatively, the sum of squared deviations about the class mean). The climate ISA was performed on clean plots only and on all plots in the calibration data set to learn the effects of enhanced nitrogen availability on lichen communities within each climate zone.

The lichen community method has been closely scrutinized for repeatability (McCune et al., 1997b; Jovan and McCune, 2005). Quality assurance and training procedures are described in McCune and Neitlich (2001). The measurement quality objective (auditor air score – observer air score/gradient length × 100) is <12%, where gradient length is the difference between the highest and lowest air score in the complete dataset. Of 126 audited surveys, the mean difference between auditor and observer gradient scores was 6.1%. Only three audits out of 73 (4%) observer gradient scores were >12%. Data are archived by USDA-Forest Service FIA Information Management (USDA-Forest Service, 2005).

3. Results

3.1. Lichen diversity

A total of 227 epiphytic macrolichen species were observed (Table 2). Greatest species diversity was found in *Usnea, Cladonia*, the Physciaceae, *Bryoria, Hypogymnia, Peltigera, Cetraria* s.l., *Ramalina* and *Xanthoria*. Species richness (α-diversity) ranged from 0 to 50. Highest mean α-diversity occurred in Oregon's Willamette Valley and Cascades ecoregions (Table 4). Washington had lower α-diversity than Oregon, especially in the densely populated Puget Lowlands where little mature forest remains. Low α-diversity was

Table 2
Detection and frequency of epiphytic macrolichens in western Oregon and Washington forests

Scientific name	On-frame P3 plots (211 surveys)		All plots (1549 surveys)
	Detected	Freq	Detected
Ahtiana pallidula	9	4.3	142
Ahtiana sphaerosporella	0	<0.5	12
Alectoria imshaugii	28	13.3	280
Alectoria lata	0	<0.5	9
Alectoria sarmentosa	84	39.8	882
Alectoria vancouverensis	13	6.2	108
Bryoria spp.	36	17.1	240
Bryoria bicolor	0	<0.5	8
Bryoria capillaris	75	35.5	582
Bryoria fremontii	11	5.2	81
Bryoria friabilis	22	10.4	274
Bryoria furcellata	0	<0.5	5
Bryoria fuscescens	37	17.5	300
Bryoria glabra	4	1.9	234
Bryoria lanestris	0	<0.5	1
Bryoria pseudocapillaris	4	1.9	14
Bryoria pseudofuscescens	19	9.0	208
Bryoria spiralifera	0	<0.5	7
Bryoria subcana	1	0.5	6
Bryoria tortuosa	2	0.9	7
Bryoria trichodes	7	3.3	135
Bunodophoron melanocarpum	0	<0.5	1
Candelaria concolor	16	7.6	105
Cavernularia hultenii	17	8.1	256
Cavernularia lophyrea	6	2.8	97
Cetraria aculeata	0	<0.5	1
Cetrelia cetrarioides	12	5.7	63
Cladonia spp.	25	11.8	85
Cladonia albonigra	4	1.9	4
Cladonia bellidiflora	4	1.9	15
Cladonia carneola	4	1.9	24
Cladonia chlorophaea, C. merochlorophaea	7	3.3	77
Cladonia cornuta	0	<0.5	7
Cladonia fimbriata	29	13.7	147
Cladonia furcata	1	0.5	16
Cladonia macilenta	1	0.5	18
Cladonia norvegica	9	4.3	15
Cladonia ochrochlora, C. coniocraea	70	33.2	380
Cladonia phyllophora	0	<0.5	2
Cladonia pocillum	0	<0.5	2
Cladonia pyxidata	2	0.9	6
Cladonia squamosa	40	19.0	268
Cladonia sulphurina	1	0.5	5
Cladonia transcendens	72	34.1	344
Cladonia umbricola	10	4.7	32
Cladonia verruculosa	2	0.9	11
Collema spp.	0	<0.5	7
Collema furfuraceum	1	0.5	19
Collema nigrescens	3	1.4	14
Dendriscocaulon intricatulum	1	0.5	2
Erioderma sorediatum	0	<0.5	17
Esslingeriana idahoensis	29	13.7	222
Evernia prunastri	104	49.3	632
Flavoparmelia caperata	0	<0.5	1
Flavopunctelia flaventior	0	<0.5	4
Fuscopannaria/Pannaria spp.	1	0.5	1
Fuscopannaria ahlneri	0	<0.5	2
Fuscopannaria leucostictoides	0	<0.5	36
Fuscopannaria mediterranea	2	0.9	11
Fuscopannaria pacifica	4	1.9	89
Heterodermia leucomela	0	<0.5	12
Heterodermia sitchensis	0	<0.5	1
Heterodermia speciosa	0	<0.5	2
Hypocenomyce castaneocinerea	2	0.9	58
Hypocenomyce friesii	0	<0.5	9
Hypocenomyce leucococca	0	<0.5	1
Hypocenomyce scalaris	5	2.4	31
Hypogymnia apinnata	68	32.2	591
Hypogymnia austerodes	0	<0.5	4
Hypogymnia unknown sp. #1	0	<0.5	1
Hypogymnia duplicata	6	2.8	19
Hypogymnia enteromorpha	133	63.0	1066
Hypogymnia heterophylla	1	0.5	39
Hypogymnia imshaugii	90	42.7	798
Hypogymnia inactiva	116	55.0	1047
Hypogymnia metaphysodes	37	17.5	353
Hypogymnia occidentalis	53	25.1	358
Hypogymnia oceanica	2	0.9	80
Hypogymnia physodes	129	61.1	1050
Hypogymnia rugosa	3	1.4	64
Hypogymnia tubulosa	85	40.3	848
Hypotrachyna revoluta	1	0.5	6
Hypotrachyna sinuosa	54	25.6	345
Kaernefeltia californica	0	<0.5	20
Kaernefeltia merrillii	19	9.0	115
Leioderma sorediatum	0	<0.5	4
Leptochidium albociliatum	0	<0.5	1
Leptogium spp.	2	0.9	9
Leptogium brebissonii	0		26
Leptogium cellulosum	0	<0.5	1
Leptogium lichenoides	0	<0.5	18
Leptogium palmatum	1	0.5	21
Leptogium polycarpum	10	4.7	77
Leptogium pseudofurfuraceum	0	<0.5	4
Leptogium saturninum	1	0.5	19
Letharia columbiana	2	0.9	27
Letharia vulpina	42	19.9	325
Lobaria hallii	0	<0.5	14
Lobaria linita	1	0.5	1
Lobaria oregana	19	9.0	337
Lobaria pulmonaria	53	25.1	457
Lobaria scrobiculata	13	6.2	129
Melanelixia fuliginosa	40	19.0	149
Melanelixia glabra	0	<0.5	11
Melanelixia subargentifera	0	<0.5	7
Melanelixia subaurifera	24	11.4	245
Melanohalea elegantula	0	<0.5	18
Melanohalea exasperatula	35	16.6	243
Melanohalea subelegantula	4	1.9	99
Melanohalea subolivacea, M. multispora	12	5.7	62
Menegazzia terebrata, M. subsimilis	35	16.6	213
Nephroma bellum	2	0.9	133
Nephroma helveticum	16	7.6	215
Nephroma laevigatum	8	3.8	110
Nephroma occultum	1	0.5	21

(*continued on next page*)

Table 2 (*continued*)

Scientific name	On-frame P3 plots (211 surveys)		All plots (1549 surveys)
	Detected	Freq	Detected
Nephroma parile	3	1.4	47
Nephroma resupinatum	16	7.6	164
Niebla cephalota	0	<0.5	6
Nodobryoria abbreviata	12	5.7	59
Nodobryoria oregana	61	28.9	582
Normandina pulchella	6	2.8	48
Pannaria rubiginella	0	<0.5	1
Pannaria rubiginosa	0	<0.5	3
Parmelia hygrophila	81	38.4	758
Parmelia pseudosulcata	12	5.7	164
Parmelia saxatilis	12	5.7	99
Parmelia squarrosa	1	0.5	36
Parmelia sulcata	150	71.1	1072
Parmeliopsis ambigua	16	7.6	194
Parmeliopsis hyperopta	79	37.4	801
Parmotrema arnoldii	11	5.2	86
Parmotrema chinense	7	3.3	68
Parmotrema crinitum	1	0.5	18
Peltigera aphthosa	1	0.5	7
Peltigera britannica	2	0.9	20
Peltigera canina	0	<0.5	3
Peltigera collina	33	15.6	317
Peltigera degenii	1	0.5	3
Peltigera leucophlebia	1	0.5	3
Peltigera membranacea	0	<0.5	36
Peltigera neckeri	0	<0.5	8
Peltigera neopolydactyla	2	0.9	25
Peltigera pacifica	2	0.9	8
Peltigera praetextata	0	<0.5	2
Peltigera rufescens	0	<0.5	6
Phaeophyscia hirsuta	0	<0.5	1
Phaeophyscia orbicularis	1	0.5	16
Phaeophyscia rubropulchra	0	<0.5	1
Physcia adscendens	21	10.0	241
Physcia aipolia	28	13.3	172
Physcia caesia	1	0.5	1
Physcia dimidiata	1	0.5	2
Physcia dubia	0	<0.5	3
Physcia stellaris	1	0.5	12
Physcia tenella	24	11.4	115
Physconia americana	5	2.4	29
Physconia enteroxantha	5	2.4	39
Physconia isidiigera	2	0.9	45
Physconia perisidiosa	11	5.2	64
Platismatia glauca	166	78.7	1317
Platismatia herrei	100	47.4	950
Platismatia lacunosa	2	0.9	29
Platismatia norvegica	17	8.1	177
Platismatia stenophylla	71	33.6	786
Polychidium contortum	2	0.9	23
Pseudocyphellaria anomala	20	9.5	311
Pseudocyphellaria anthraspis	21	10.0	260
Pseudocyphellaria crocata	9	4.3	154
Pseudocyphellaria rainierensis	0	<0.5	18
Psoroma hypnorum	0	<0.5	6
Punctelia perreticulata	0	<0.5	4
Ramalina dilacerata	33	15.6	182
Ramalina farinacea	98	46.4	652
Ramalina intermedia	0	<0.5	1
Ramalina menziesii	0	<0.5	31
Ramalina obtusata	0	<0.5	1
Ramalina pollinaria	1	0.5	6
Ramalina roesleri	2	0.9	35
Ramalina subleptocarpha	1	0.5	44
Ramalina thrausta	2	0.9	41
Sphaerophorus globosus	98	46.4	839
Sticta fuliginosa	16	7.6	185
Sticta limbata	10	4.7	160
Sticta weigelii s. l.	2	0.9	32
Sulcaria badia	2	0.9	6
Tholurna dissimilis	0	<0.5	1
Tuckermannopsis chlorophylla	114	54.0	950
Tuckermannopsis orbata	102	48.3	846
Tuckermannopsis platyphylla	37	17.5	475
Tuckermannopsis subalpina	3	1.4	25
Usnea sp., *U. pacificana*, *U. nidulans*, *U. wasmuthii*, *U. diplotypus*, *U. substerilis*	72	34.1	502
Usnea cavernosa	5	2.4	18
U. cornuta, *U. fragilescens*	20	9.5	184
U. filipendula, *U. madeirensis*, *U. chaetophora*	107	50.7	721
U. flavocardia and *U. ceratina*	69	32.7	395
U. glabrescens, *U. fulvoreagens*	6	2.8	55
Usnea glabrata, *U. esperantiana*	27	12.8	239
Usnea gracilis	1	0.5	27
Usnea hirta	3	1.4	20
Usnea lapponica	22	10.4	73
Usnea longissima	10	4.7	67
Usnea rubicunda	0	<0.5	15
Usnea scabrata	33	15.6	338
Usnea subfloridana	44	20.9	218
Vulpicida canadensis	13	6.2	105
Waynea californica	1	0.5	1
Xanthoria/*Xanthomendoza* spp.	3	1.4	8
Xanthomendoza fallax, *X. borealis*, *X. fulva*, *X. oregana*	9	4.3	44
Xanthomendoza hasseana, *X. montana*, *Xanthoria polycarpa*	39	18.5	233
Xanthoria candelaria	5	2.4	33
Xanthoria parietina	1	0.5	12
Count of taxa identified to species	163		227

Detections (Detected) are the number of plots in which the subject species was found. Frequency (Freq) is the percentage of on-frame USFS-FIA (P3) plots in which the species was detected; frequency in western Oregon and Washington can be inferred from this value. Taxa that were difficult to distinguish are listed in the same rows.

associated with very young stands, very high elevation sites, and the most polluted urban environments. Maximum species richness (>45) occurred in low-mid elevations with intermediate nutrient availability and trees >100 years old (12 plots, all

Table 3
Group membership and environmental ranges of plots in the model development data subset

Group membership				Complete data set[a]	Model development data subset			
Group	Polluted[b]?	Elevation	HW[c]?	Plots	Plots	% N in Platismatia glauca (dry weight)	Precipitation (cm year^{-1})	Elevation (m)
1	0	Low	0	100	28	0.26–0.58	46–406	0–223
2	0	Low	1	59	28	0.28–0.57	79–323	0–229
3	0	Mid	0	243	30	0.24–0.52	114–452	244–640
4	0	Mid	1	51	29	0.33–0.58	86–343	244–610
5	0	High	0	613	31	0.30–0.54	74–381	671–1524
6	0	High	1	38	23	0.32–0.58	97–381	671–1463
7	1	Low	0	55	29	0.63–1.20	69–229	18–223
8	1	Low	1	109	30	0.95–1.20	71–241	2–229
9	1	Mid	0	20	13	0.60–0.70	91–282	244–625
10	1	Mid	1	38	28	0.59–1.20	53–259	244–604
11	1	High	0	23	19	0.59–0.90	140–328	671–1554
12	1	High	1	5	5	0.62–0.73	84–323	701–853
Total				1338	293			

The model scores air quality and climate at forested sites in western Oregon and Washington based on the lichen species present and their abundances. Approximately equal numbers of plots from the complete data set were randomly assigned to each group in the model development subset. Balancing the groups improved the model's ability to differentiate air pollution-related lichen community responses from responses to low elevation, low precipitation and high hardwood cover.
[a] There were 1338 plots with complete environmental data.
[b] See Section 2.4 for explanation of binary pollution assignments; 0, clean; 1, polluted.
[c] HW, % basal area in hardwood trees is >20%; 0, no; 1, yes.

in Oregon). Landscape diversity was highest in Oregon's Klamath Mountains and Western Cascades; heterogeneity was highest in Washington's Coast Range and Puget Lowland. At least two species, pollution tolerant *Phaeophyscia rubropulchra* (from east Portland) and the nitrophyte, *Xanthoria parietina* (from Portland, Willamette Valley, Tillamook coastal dairy land, and Columbia River Gorge vicinities), are probably not native to the Pacific Northwest.

Frequency in the P3 on-frame plots (Table 2) can be used to infer frequency in the study area. Of the 53 cyanolichens, a highly air-pollution sensitive group, only 54% were detected in P3 plots and 84% occurred in <5% of P3 plots. By contrast, 78% of non-cyanolichens were detected in P3 plots. Representing 24% of the total species diversity, cyanolichens accounted for a disproportionate share of rare species, making them especially vulnerable to extirpation in air-pollution affected areas.

3.2. Community gradients

The NMS ordination explained 84% (37, 37 and 9% on axes 1, 2, and 3) of the variance in the lichen community dataset. The final orthogonalities were 100% in Axis 1 vs. 2, 98% in Axis 1 vs. 3, and 100% in Axis 2 vs. 3. The model successfully separated pollution from other environmental variables (Fig. 3 and Table 5). All three pollution variables (% N and % S in lichen thalli, and polluted or not) were strongly positively correlated with Axis 1. Lack of polluted sites in the highest precipitation areas (Table 3), caused a small negative correlation of precipitation with the pollution axis; r^2 values of other Axis 1 variables were <0.21. Axis 2 was strongly correlated with decreasing minimum December temperatures, mean annual temperature, relative humidity, and increasing continentality, elevation, longitude, and coast distance. Axis 3 had little

Table 4
Comparison of species diversity of epiphytic macrolichens by ecoregion and state

On-frame FIA plots	Coast R. WA	Coast R. OR	Puget Lowlands WA	Will. V. OR	Klamath OR	W. Casc. WA	W. Casc. OR	S. Casc. OR	E. Casc. WA	E. Casc. OR	WA ave.	OR ave.
α-diversity	13.7[b]	18.8	14.2[c]	24.5	20.8	16.2[b]	24.3	21.6	22.1[b]	22.0[b]	15.5[a]	21.7
α-diversity SD	7.0	8.5	7.7	9.9	10.2	5.4	8.6	9.9	6.7	6.1	6.9	9.1
β-diversity	5.8	5.0	5.6	3.1	5.2	5.4	4.1	2.7	2.7	3.0	7.5	6.9
γ-diversity	79	94	79	75	108	87	101	59	59	66	116	149
N	24	29	26	11	32	38	29	5	7	10	95	116

Ecoregions are US EPA Level III Provincial Ecoregions (Omernik, 1986) partitioned by state for comparison purposes. Coast R., Coast Range; Will. V., Willamette Valley; Klamath, Klamath Mountains; W. Casc., Western Cascades and North Cascades; S. Casc., Southern Cascades; E. Casc., Eastern Cascades; WA, Washington State; OR, Oregon State. Refer to Fig. 2 for geographic coverage.
[a] Mean α-diversity is lower in WA than OR (T-test, $p < 0.05$).
[b] α-diversity is lower than Wil V., Klamath, OR W. Casc. and OR Coast R. (Tukey's HSD, $\alpha = 0.05$).
[c] α-diversity is lower than all other ecoregions except OR E. Casc. and WA Coast R. (Tukey's HSD, $\alpha = 0.05$).

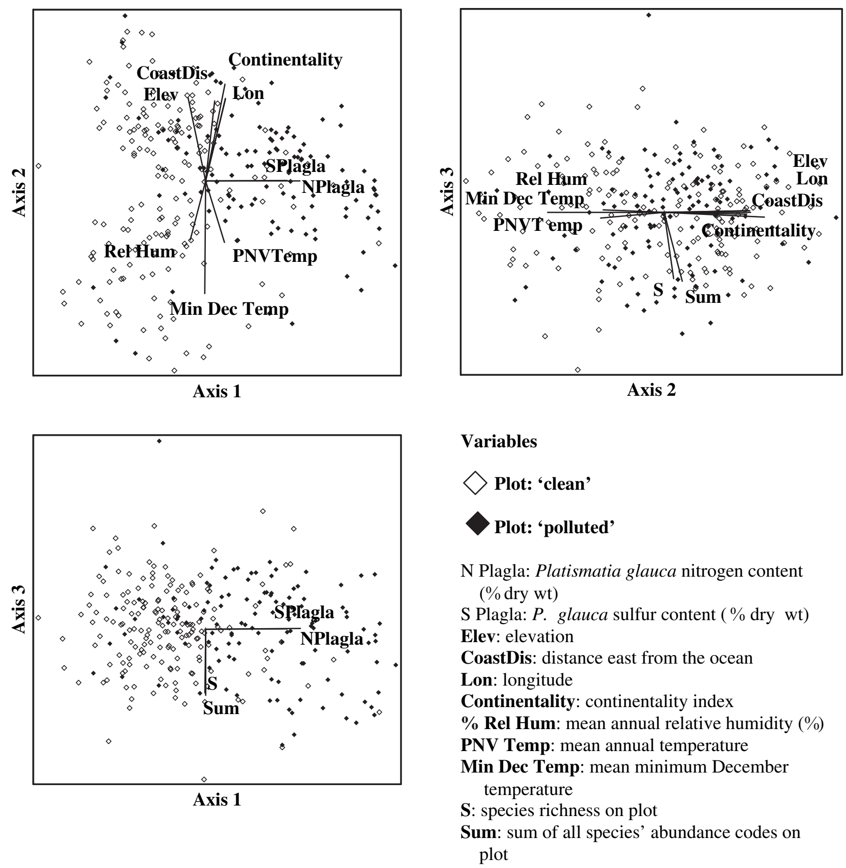

Fig. 3. Plot scores on lichen community gradients in the non-metric multidimensional scaling ordination with overlays of significant environmental variables. Axis 1 corresponds to an air quality gradient, high air scores indicate most polluted plots. Axis 2 corresponds to a climatic gradient; high climate scores correspond with coldest, most continental plots and low scores with maritime plots. The strength of the correlation of environmental variables with the ordination axes is proportional to the lengths of the vectors radiating from the centroid. Vector direction indicates the direction of increasing scores in the graph.

interpretive value (r^2 all variables <0.15) but was retained to preserve model robustness. Lichen lead concentrations, survey year, tree age, and quadratic mean diameter did not correlate well with any axis (Pearson r^2 <0.1). Pollution and climate scores are thus independent of these variables.

3.2.1. Air quality gradient

Poorest air scores occurred in urban-industrial and agricultural areas (Fig. 4a); best scores generally occurred in remote, mountainous areas. Urban plots and plots with lichen N or S content above clean site thresholds had fewer sensitive species, more nitrophilous species, and higher scores on Axis 1 than other plots. Tolerant species occurred in both polluted and non-polluted plots. Plots with <4 species had low information content and were not mapped. We used ISA-identified polluted and clean site indicator species (Table 6) with broadest geographic distributions and highest air quality indicator values to create six, biologically based divisions of the air quality gradient, i.e. divisions along Axis 1 between the lowest and highest scores (Figs. 4a, 5a). The "best air quality" division cutoff score, −0.11, is the 75% quantile of the air score distribution of the clean-air indicators; i.e., 75% of plots hosting these species had air scores <−0.11. The "good" and "fair" air quality cutoffs, <−0.02and <0.21, are the 90 and 97.5% quantiles of the clean-air indicator air score distributions. The "degraded" air quality cut-off, <0.33, was the 25% quantile of air score distributions for the polluted-air indicators (i.e., 75% of plots hosting these lichens received air scores >0.33). The "poor" air quality class was bounded by the lower cutoff for the "worst" class (<0.49) corresponding to the 100% quantile for sensitive species; the clean-air indicator lichens are thus absent where air score >0.49.

Fig. 5a interpolates air pollution gradients in western Oregon and Washington, kriging air scores in Fig. 4a. Air pollution adversely affects lichen communities in at least 24% of western Oregon and Washington (Fig. 5c). Standard error of the kriged scores was generally <8% of the gradient length (0.267). The response map is most accurate where plot density was highest (Figs. 2, 5b).

Air scores at plots around the NADP monitors were correlated with NH_4^+ concentrations (mg l^{-1}) in precipitation, but not total deposition (kg ha^{-1}), and were better correlated to N than to S concentrations in lichen thalli (Fig. 6). No significant correlations were observed between air score and mean nitrate, sulfate, or hydrogen ion concentrations in precipitation (mg l^{-1}) or total wet deposition (kg ha^{-1}) (not shown). Concentration ranges of ammonium wet deposition and nitrogen

Table 5
Pearson correlation coefficients between environmental variables and the lichen community ordination

Environmental variable	Axis 1 r^2	Axis 2 r^2	Axis 3 r^2
Mean minimum December temperature	0.004	0.629	0.000
Continentality	0.107	0.540	0.026
% Nitrogen in *Platismatia glauca*	0.529	0.000	0.004
Elevation	0.099	0.466	0.000
% Sulfur in *Platismatia glauca*	0.457	0.002	0.002
Longitude	0.111	0.456	0.009
Distance from the ocean	0.051	0.447	0.010
Mean temperature	0.106	0.344	0.029
Mean relative humidity	0.087	0.328	0.014
Mean annual precipitation	0.240	0.012	0.078
Mean days with marine fog at 100 m	0.011	0.208	0.037
Mean maximum August temperature	0.208	0.037	0.125
Mean days with measurable precipitation	0.175	0.005	0.138
Mean dew point temperature	0.168	0.017	0.031
Basal area of live trees	0.125	0.010	0.005
% Basal area in hardwoods	0.118	0.044	0.042
% Lead in lichen thalli	0.084	0.010	0.028
Survey year	0.014	0.016	0.074
Mean age of dominant trees	0.001	0.073	0.005
Quadratic mean diameter	0.008	0.001	0.002

in lichen thalli within air score divisions are summarized in Table 7.

3.2.2. Climatic gradient

We mapped lichen community response to climate (Fig. 4b) using Axis 2 scores (Fig. 3). As distance along Axis 2 increases, mean winter and annual temperatures and relative humidity decrease, while elevations, distance from the coast and continentality increase. We delineated four climate zones: maritime, lowland, montane, and high elevation. Table 6 lists ISA-identified indicator species for each zone. Maritime lichen communities occurred in the western Coast Ranges and Olympic Peninsula. Lowland communities occurred in the Medford environs, the Willamette Valley and Puget Lowlands, eastern Coast Ranges, and the northwest Olympic Peninsula. The montane zone includes the mid-elevation Cascades and the Siskiyou mountains west of Medford. The high elevation zone occupies the extreme eastern and southern borders of the study area, corresponding to the highest peaks. Artic-alpine lichens (Glew, 1998) and high mountains in the Olympic and North Cascades Ranges imply that the high elevation class should be well represented there but low sampling density limited its geospatial delineation.

Table 8 compares current climate zone temperatures to 40-year predicted changes. A dramatic change in zone boundaries can be expected by 2040. Even under the most conservative scenario (+1.5 °C), mean maritime temperatures would shift above any current climate zone range. The lowland mean would be shifted into the maritime range under the

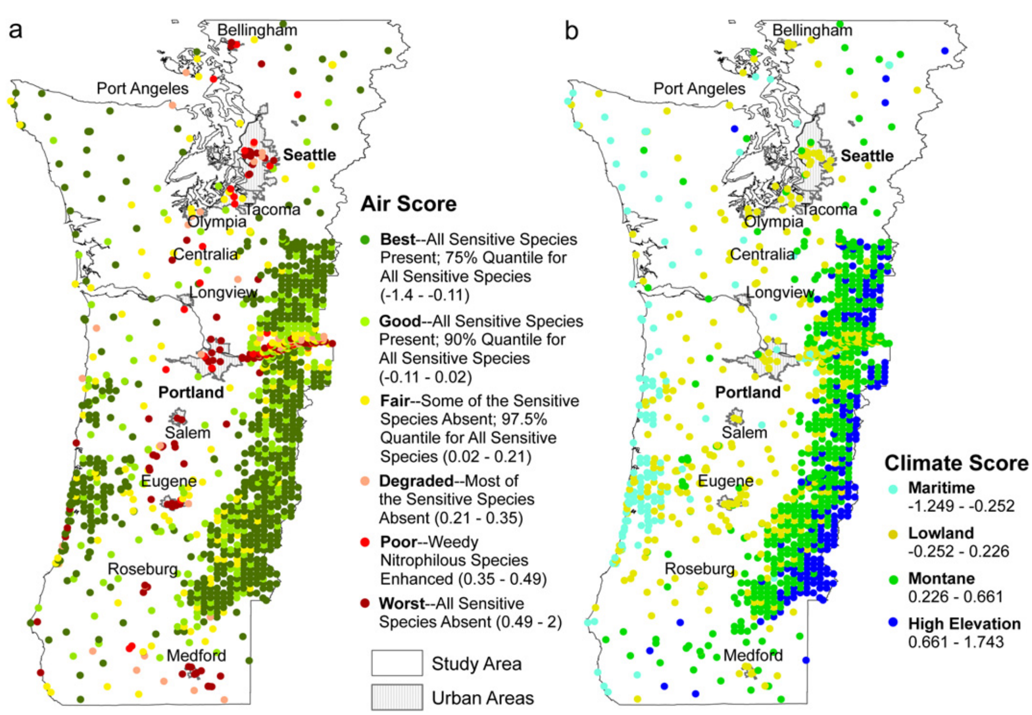

Fig. 4. Lichen-community derived maps of (a) air quality and (b) climate in western Oregon and Washington produced by the gradient model. Dots indicate scored plot locations. Scores were classed by lichen community status.

Table 6
Air quality and climate indicator lichens in western Oregon and Washington

Group	Sub-Group	Indicator Species
Clean Air	Regional distribution	***Bryoria capillaris, Lobaria oregana, Sphaerophorus globosus, Usnea filipendula, U. scabrata***
	Sub-regional distribution	***Ahtiana pallidula, Alectoria sarmentosa, Bryoria fuscescens***, *Cavernularia hultenii, Cavernularia lophyrea, Hypogymnia apinnata*, ***H. enteromorpha***, *H. metaphysodes, Menegazzia terebrata*, ***Nephroma bellum, Nodobryoria oregana***, *Platismatia herreii, P. lacunosa, P. norvegica, Pseudocyphellaria anomola, P. crocata, Usnea cornuta*
Polluted Air	Regional nitrophytes	***Candelaria concolor, Physcia adscendens, Xanthoria polycarpa***
	Sub-regional nitrophytic or tolerant species	*Evernia prunastri, Hypogymnia physodes, H. tubulosa, Leptogium saturninum, Melanelia exasperatula, M. fuliginosa, M. subaurifera, M. subelegantula, Parmelia sulcata, Physcia aipolia, P. tenella, Physconia americana, P. enteroxantha, P. isidiigera, P. perisidiosa, Platismatia glauca, Ramalina farinacea, R. subleptocarpha, Tuckermannopsis chlorophylla, Xanthoria candelaria, X. fallax*
Maritime	Acidic, low-fertility environments	*Cavernularia lophyrea, Hypotrachyna sinuosa, Menegazzia terebrata, Parmotrema chinense, Peltigera membranacea, Ramalina roeslerii, Usnea cornuta, U. wirthii*
	Additional species in moderate fertility environments	*Cetrelia cetrarioides, Cladonia ochrochlora, Hypogymnia apinnata, Lobaria oregana, Parmotrema arnoldii, Platismatia lacunosa, Pseudocyphellaria anthraspis, P. crocata, Sphaerophorus globosus*
Lowland	Acidic, low-fertility environments	*Parmelia sulcata, Ramalina farinacea, Sphaerophorus globosus, Sticta limbata, Tuckermannopsis chlorophylla, Usnea filipendula, U. glabrata, U. longissima*
	Additional species in moderate fertility environments	*Candelaria concolor, Evernia prunastri, Melanelia fuliginosa, M. subaurifera, Parmelia saxatilis, Physcia adscendens, Ramalina dilacerata, R. subleptocarpha, Xanthoria candelaria, X. fallax, X. polycarpa.*
Montane	Acidic, low-fertility environments	*Bryoria fuscescens, Fuscopannaria leucostictoides, Hypogymnia enteromorpha, H. inactiva, H. oceanica, H. physodes, H. tubulosa, Lobaria pulmonaria, Parmelia hygrophila, Peltigera collina, Platismatia herrei, P. stenophylla, Pseudocyphellaria anomola, Tuckermannopsis chlorophylla, Usnea scabrata*
	Additional species in moderate fertility environments	*Cladonia chlorophaea, Leptogium lichenoides, Nephroma helveticum, Nephroma resupinatum*
High Elevation	Acidic, low-fertility environments	*Ahtiana pallidula, Alectoria imshaugii, A. sarmentosa, Bryoria capillaris, B. fuscescens, B. glabra, Hypogymnia imshaugii, H. metaphysodes, H. rugosa, Letharia vulpina, Melanelia subelegantula, Nodobryoria oregana, Parmeliopsis ambigua, P. hyperopta, Platismatia glauca, Tuckermannopsis platyphylla*
	Additional species in moderate fertility environments	*Bryoria fremontii, Esslingeriana idahoensis, Hypogymnia occidentalis, Nodobryoria abbreviata, Parmelia hygrophila, Vulpicida canadensis*

Distributions of species with highest indicator value (in bold type) were used to define air quality zones.

minimum change scenario and above any current zone under the maximum change (+3.2 °C) scenario. Temperatures in montane and high elevation zones, with broader ranges, would likely shift to the next warmer zone.

3.3. Influences of other environmental variables

3.3.1. Stand development and composition

Because nitrophytes prefer the more alkaline, better-buffered bark of hardwood trees, the presence of hardwoods can potentially influence air score on a site. We compared air scores at 50 paired plots having different % hardwood basal areas but close physical proximity. Linear regression indicated a strong correlation between % basal area of hardwoods and air score ($r^2 = 0.84$, $p = 0.0015$), however the magnitude of the effect is small. For every 10% increase in hardwood basal area, air score increased by 0.032 units, or approximately 1% on the air quality gradient from best to poorest score in the study area. Therefore, in the unlikely situation that adjacent plots contained all hardwoods and all conifers, air scores should differ by 10% on the air quality gradient. This is not considerably greater than the mean 5% air score difference found in repeat measurements by different crews.

3.3.2. Species richness and air scores

One might hypothesize that more frequent disturbance in urban forests would affect lichen richness and air scores. Both linear and exponential regressions of species richness

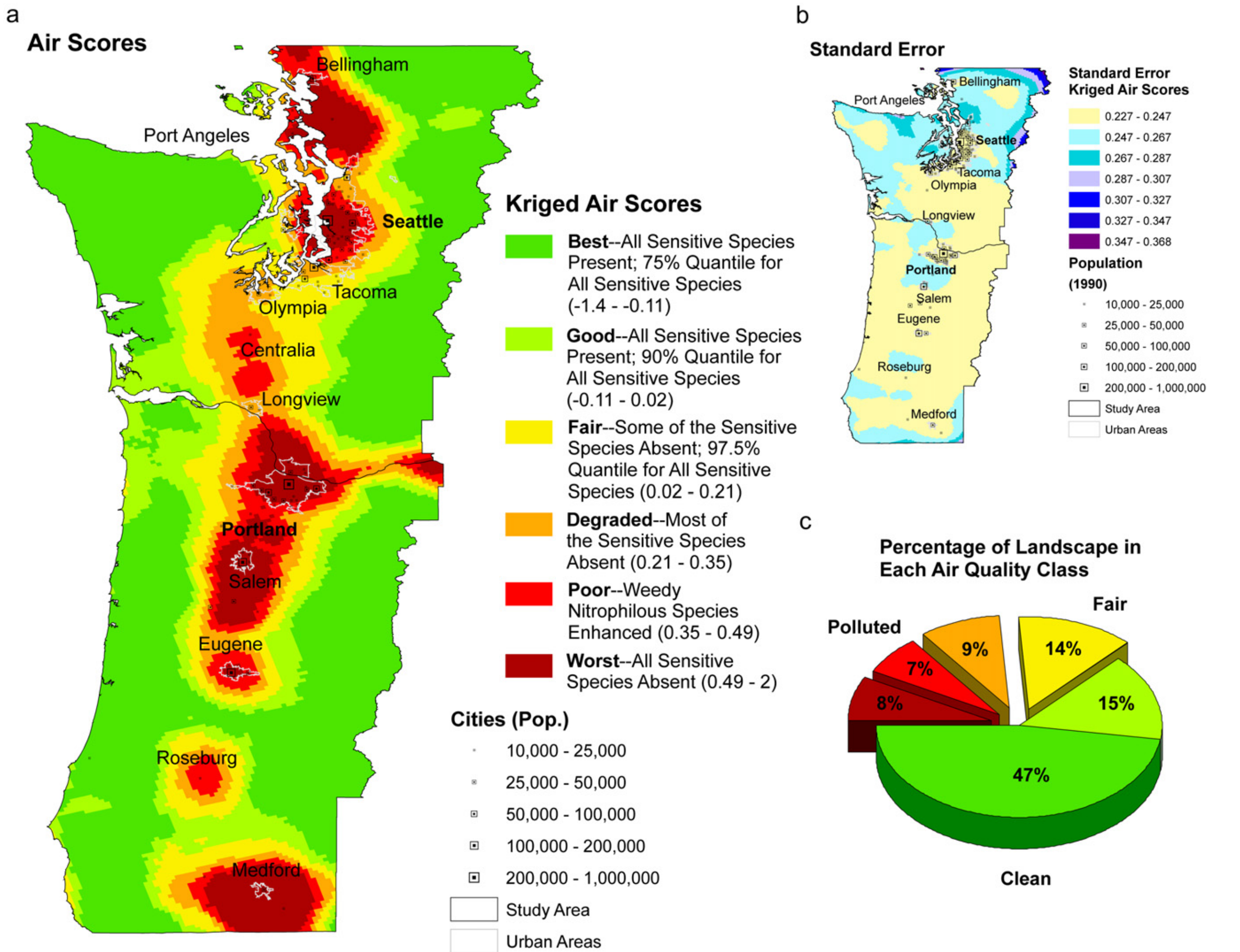

Fig. 5. 1994–2001 air quality in western Oregon and Washington indicated by lichen communities: (a) block-kriged air scores, (b) standard error of kriged air scores as percent of the air quality gradient, (c) percentage of total land area in each air quality class.

against air score, revealed no significant correlations ($r^2 = 0.01$). Low species richness occurred in both urban and non-urban settings. Young stands in clean, remote plots differed from polluted plots in that sensitive species were usually present and nitrophilous lichens were sparse to absent.

4. Discussion

4.1. Lichen diversity

Regional frequencies of macrolichens in the western Pacific Northwest indicate a largely intact flora. Air-pollution sensitive lichens like *Alectoria, Bryoria, Usnea, Lobaria*, and *Pseudocyphellaria*, with important ecological functionality (McCune and Geiser, 1997) were abundant and widespread in the study area. We hypothesize that habitat disturbance and forest fragmentation explain the comparatively low lichen diversity, biomass, and high heterogeneity observed in densely populated ecoregions and young forests, mostly in Washington, while diverse vascular vegetation, extensive areas of undisturbed forest, and more optimal hydration regimes explain ecoregions with highest lichen diversity, mostly in Oregon.

Like Van Herk (2004), we found that under conditions of nitrogen enrichment and low sulfur dioxide, species richness had little predictive value for air quality. Rather air pollution was associated with detrimental effects on community composition: paucities of sensitive, endemic and ecologically important species and enhancements of weedy, nitrophilous and non-native species. If nitrogen pollution increases, reductions in abundance, functionality and distribution of sensitive acidophytic and cyanolichen species would be anticipated, as these species co-evolved with Pacific Northwest forests under cool, wet, nitrogen-limited conditions (Goward and Arsenault, 2000).

4.2. Climate

Climate change also threatens diversity. Lichen species distributions as summarized in our community-derived climate

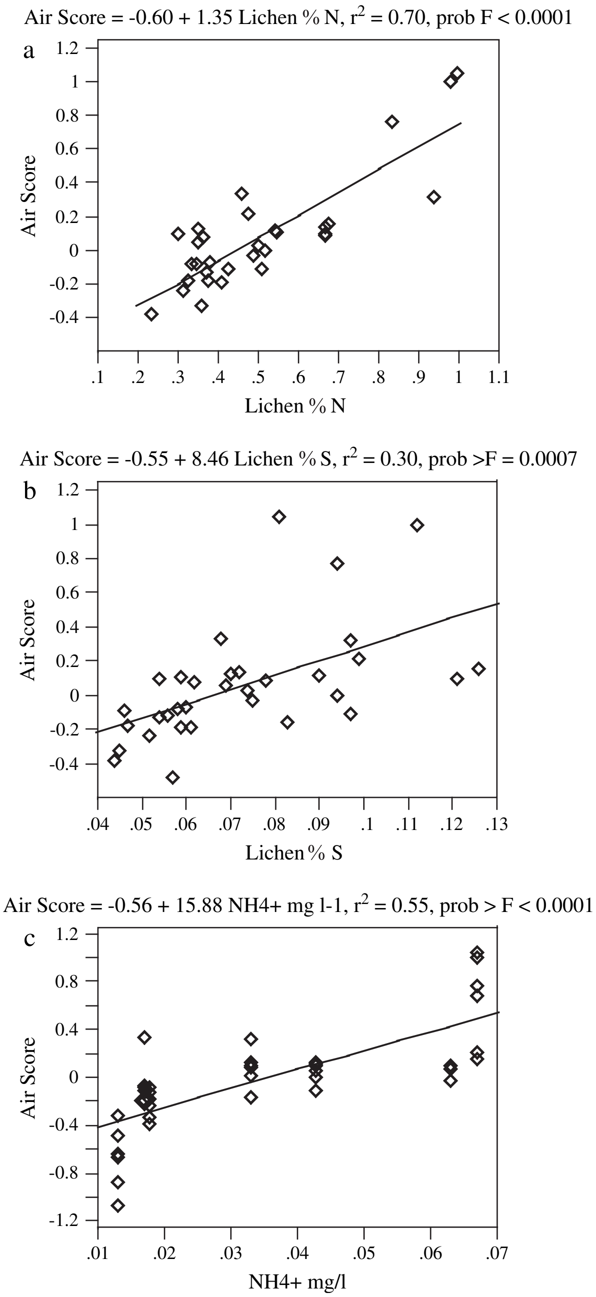

Fig. 6. Correlations between lichen-community based air scores and pollution parameters at lichen plots adjacent to NADP monitors in western Oregon and Washington: (a) air scores and dry weight nitrogen concentrations in the lichen *Platismatia glauca*. (b) air scores and dry weight sulfur concentrations in *Platismatia glauca*, (c) air scores and mean concentrations of NH_4^+ in wet deposition at the closest NADP monitor.

map, generally followed regional topographic and eco zones. Predicted 2040 regional temperatures increases of 1.5–3.2 °C can be expected to dramatically alter lichen community composition. Climate-driven changes to other coastal lichen floras are already being noted (Follmann, 1995; Van Herk et al., 2002). As climate zones shift geographically, species survival can be roughly predicted by remaining habitat size and species dispersal rates (Thomas et al., 2004). As the coolest climate zones shrink, species in their southernmost ranges could be lost or greatly restricted, particularly in the Olympic Peninsula and North Cascades where many arctic-alpine species already occur in isolated patches (Glew, 1998). Maritime dunes and headlands support habitat-limited species distributed along relatively small temperature and fog ranges (Glavich et al., 2005). Unprecedented mean temperatures predicted for maritime and lowland communities would create climates with no current regional analogue and could drive regional extinctions. Predicted fire frequency increases (Mote et al., 2003), especially in species-rich old-growth stands where many dispersal-limited species occur (Sillett et al., 2000), would exacerbate threats from warming and pollution. Cyanolichens, most of which are rare and sensitive to both air pollution and heat stress (Richardson and Cameron, 2004), face especially uncertain prospects. Although regional climate change models predict winter precipitation changes from −2 to 22% (Mote et al., 2003) that could well affect lichen community composition by 2040, unfortunately our gradient model is rather insensitive to precipitation (see low correlation coefficients in Table 5).

4.3. Air pollution

Modeling a data subset containing equal numbers of polluted and clean plots across regional precipitation, elevation, and hardwood ranges was key to isolating lichen pollution response from potentially confounding environmental variables; our large dataset permitted this. Mapping lichen response over the study area, like Ferretti et al. (2004), we found that increased plot density did not linearly reduce interpolation error (compare Figs. 4a and 5b). Yet the extra effort would have more accurately delineated gradients in the topographically variable Olympic Peninsula and North Cascades. The areas with poorest air scores were:

1. The Puget Sound. Poor air scores occurred in a wide swath from the highly populated and industrialized Seattle metropolitan area north to Canada. Tacoma supported more sensitive species than expected for a large city. Surface winds bring clean air from the Olympic peninsula to Tacoma before urban areas farther north (Jackson, 1993).
2. The central valleys. Poor scores occurred in a continuous zone from Centralia—a coal-fired power plant there is the largest stationary source of SO_2 in the bi-state area (US EPA, 2005)—through the Willamette Valley to Eugene-Springfield and eastward from Portland through the Columbia River Gorge, where diurnal winds funnel pollutants. Agriculture and urban sprawl dominate land use in the Willamette Valley. The southeast end of the Willamette Valley is particularly susceptible to air stagnation and inversions in summer and autumn (Jackson, 1993).
3. Roseburg and Medford vicinities. These areas supported few sensitive lichens. Although Medford emissions are lower than Portland and Seattle (US EPA, 2005), air pollution has an equally strong effect on lichen communities. Pollution effects are likely intensified by extended air stagnation periods, greater heat and drought stress, and fewer

Table 7
Summary of air score relationships to lichen community condition, wet deposition of ammonium ions, and lichen element concentrations

Zone		1 (best and good)	2 (fair and degraded)	3 (poor and worst)
Lichen community condition		Sensitive lichens abundant, no nitrophytes	Fewer sensitive lichens, some nitrophytes	Nitrophytes abundant, few to no sensitive species
% of study area		62	14	24
Air score	Number of lichen surveys	1067	207	258
	Minimum air score	−1.37	0.023	0.209
	Maximum air score	0.018	0.204	1.743
	Median air score	−0.28	0.09	0.53
Wet deposition of NH_4^+ (mg l^{-1})	Number of NADP monitors[a]	3	3	1
	Minimum deposition	0.013	0.033	0.067
	Maximum deposition	0.018	0.063	0.067
	Mean deposition	0.016	0.046	0.067
	SD	0.0026	0.0153	NA
% N in *Platismatia glauca*	Number of lichen samples	675	91	120
	2.5% quantile	0.26	0.32	0.42
	99.75% quantile	0.69	1.15	1.20
	Mean	0.42	0.57	0.86
	SD	0.094	0.217	0.205
% S in *Platismatia glauca*	Number of lichen samples	716	88	117
	2.5% quantile	0.036	0.037	0.057
	99.75% quantile	0.079	0.149	0.163
	Mean	0.054	0.073	0.108
	SD	0.0107	0.0276	0.0260

[a] Each NADP monitor was assigned to the air zone corresponding to the mean air score of the 3–7 lichen plots within 2 km of it.

rainy days in Medford's Rogue River Valley compared to lowlands further north (Jackson, 1993). Higher dry deposition might create acute effects upon rehydration.

4. The immediate coast. Localized poor pollution scores occurred in close proximity to pulp mills and dairylands but also on the remote southern coast and isolated promontories. Higher nutrient deposition and substrate alkalinization by sea-salt laden marine aerosols enhances the growth of nitrophilous lichens, resulting in artificially high air pollution scores at these locations.

4.4. Relationship between air scores and regional pollutants

4.4.1. SO_2

Direct SO_2 damage to lichens was probably confined to major urban areas. Our plots were not co-located with state SO_2 monitors but 1990s mean ambient SO_2 levels in the Portland and Seattle-Bellingham environs ('poor' and 'worst' zones) were 11–96 μg m^{-3} (Estus, 2000), in compliance with human health standards but harmful to sensitive lichens (De Wit, 1976; Hawksworth and Rose, 1970; LeBlanc et al., 1972). Tacoma SO_2 was in the lowest range harmful to lichens, 13–15 μg m^{-3}, and air scores were better ('somewhat degraded'). Johnson (1979) and Taylor and Bell (1983) observed similar regional effects.

4.4.2. Deposition

The positive correlation between wet deposition of $NH4^+$ and nitrophyte-dominated lichen communities is consistent with observations in Europe (Van Dobben et al., 2001, 1998; Van Herk, 2004; Wolseley et al., 2004) and California (Jovan and McCune, 2005). Van Herk et al. (2003) reported a decrease in sensitive species, including *Bryoria capillaris* and *B. fuscescens*, among 25 European monitoring stations in precipitation with NH_4^+ concentrations as low as 0.33 mg l^{-1} N. We observed incipient community changes at NH_4^+ concentrations between 0.04 and 0.08 mg l^{-1} N (Table 7: 0.03–0.06 mg l^{-1} NH_4^+ for zone 2), a substantially lower concentration.

Table 8
Current and predicted annual temperatures in lichen community-defined climate zones based on minimum and maximum mean annual temperature increases of 1.5–3.2 °C predicted for the Pacific Northwest by 2040

Climate zone	Year 2000 (°C)				Year 2040 (°C)			
	Mean	SE	2.5% quantile	97.5% quantile	Predicted minimum mean	Predicted maximum mean	Predicted minimum 2.5% quantile	Predicted maximum 97.5% quantile
Maritime	10.2	0.1	8.4	11.4	11.7	13.4	9.9	14.6
Lowland	9.6	0.1	6.7	11.8	11.1	12.8	8.2	15
Montane	7.2	0.1	3.5	11	8.7	10.4	5	14.2
High elevation	4.9	0.1	1.5	8.1	6.4	8.1	3	11.3

Although the 10-fold difference in incipient community response levels between the two studies seems at first inconsistent, wet deposition of ammonium ions and total (wet, dry and gaseous) deposition of inorganic N have been calculated to be about 10-fold higher throughout most of western Europe compared to western Oregon and Washington (Holland et al., 2005). The median 1978–1998 $NH4^+$ wet deposition concentration at the 15 remote sites in the Van Herk et al. (2003) study was 0.62 mg l^{-1} (range 0.13–0.99) compared to 0.03 mg l^{-1} (range 0.01–0.08) at western Oregon and Washington NADP monitors (1980–2005 site averages, NADP 2006). We would argue that these higher background levels of nitrogen deposition have already altered European lichen community composition. For example, of the four clean air indicator species in Table 7 that also occurred in the Netherlands in 1900 (*Bryoria capillaris, B. fuscescens, Usnea cornuta, U. filipendula*), three are now extinct and *B. fuscescens* is in critical condition according to the Netherlands red list for lichens (Aptroot et al., 1998). These same species are abundant and widespread in the US Pacific Northwest. The US and European studies are therefore detecting changes along opposing ends of the combined air pollution gradient.

While lichen sulfur concentrations have predictive power for air score, lichen nitrogen was the best predictor. Because epiphytic lichen element content is influenced by wet and dry deposition (from particulates, precipitation, cloud water, ambient gases, stem flow) and meteorological conditions (Levia, 2002), they provide a more integrated measure of nitrogen availability than wet deposition alone.

Wet deposition sulfate and nitrate, and total inorganic N (i.e. $N\text{-}NH4^+ + N\text{-}NO_3^-$) concentrations at regional NADP monitors were not correlated with air score. This result was somewhat surprising given that we did see a correlation with wet deposition of ammonium. A recent study indicates that epiphytic lichens take up ammonium ions about three times faster than nitrate ions when these ions are available at the same concentrations (Dahlman et al., 2004). It is possible that neither nitrate nor sulfate was absorbed in quantities sufficient to detect an influence on lichen community composition. Mean $N\text{-}NH_4^+$:$N\text{-}NO_3^-$ concentrations in wet deposition at our NADP sites varied greatly from 0.3 to 1.2 (median 0.6). This variability, together with differential uptake of the two types of nitrogen could have masked air score correlations to total inorganic N. Finally, we did we not demonstrate a relationship between acidity and air score; mean pH at NADP monitors was 5.1–5.4, apparently tolerable to nitrophytic and sensitive lichens. Acidic pollutants may be harming urban lichens, but urban pH measurements were unavailable.

4.4.3. Ozone and NO_x

Ozone is potentially adversely affecting Pacific Northwest lichens. Peak ozone concentrations at 24 state-run continuous ozone monitors in the "poor" and "worst" air score zones, ranged from 118 to 280 μg m^{-3} (mean 204, SD 49) (ORDEQ, 2001; Estus, 2000). Ozone at 20–60 μg m^{-3} may harm some lichens (Egger et al., 1994; Eversman and Sigal, 1987) but repeated peak concentrations of 180–240 μg m^{-3} are more often the harmful threshold (Ross and Nash, 1983; Scheidegger and Schroeter, 1995; Sigal and Nash, 1983), or not (Ruoss and Vonarburg, 1995). Without knowing whether lichens are hydrated during peak periods, it is difficult to estimate the ozone threat in our study area. Presumably lichens in urban areas are most often dry and relatively insensitive to ozone during hot sunny days when peak ozone production occurs. Lichens in downwind rural areas such as the Columbia River Gorge may be more vulnerable than urban lichens if transported ozone peaks later in the day (e.g. Böhm et al., 1995) when lichens have re-hydrated.

Whether NO_x directly impacts Pacific Northwest lichen communities is unknown. Mean ambient NO_x concentrations in "poor" and "worst" air score zones during the 1990s were <120 μg m^{-3}. Ambient concentrations of NO_x often correlate with SO_2, making it difficult to separate SO_2 effects on lichen communities from NO_x effects (Van Dobben et al., 2001). We join Jovan and McCune (2005) in calling for studies of NO_x effects on lichens at urban ambient concentrations.

5. Conclusions

Increasing regional and global human activities threaten air quality and climate in western Oregon and Washington. Lichen-based air pollution and climate maps delineate gradients based on ecological response, while re-measurements can be used to track changes. Plots with poor air scores, 24% of the study area, were characterized by: a paucity of regionally endemic, ecologically important, air-pollution sensitive lichens; an enhancement of weedy, nitrophilous species; lichen nitrogen concentrations >0.8%; mean annual wet deposition of ammonium >0.06 mg l^{-1}; and levels of SO_2 and ozone legally safe for humans but harmful to lichens. Remaining plots supported a nearly pristine, ecologically functional lichen diversity. Even conservative climate change scenarios imply a dramatic alteration of lichen diversity, frequency, and community composition by 2040. Better energy efficiency and emission controls, lower per capita consumption, and better population planning would slow climate change, improve air quality and aid human and ecosystem health.

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