Forest lichen communities and environment – How consistent are relationships across scales?

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Abstract

Question: How consistent are relationships of forest lichen community composition with environmental variables across geographic scales within region and across regions?

Location: Northwestern continental USA and east central continental USA.

Method: Four macrolichen data sets were compiled using identical plot sample protocol: species abundance estimated in 0.4-ha permanent plots on a systematic grid, as part of government (USDA-FS) forest inventory programs. One data set in each region represented a large area; the other represented part of the large area. We used global NMS ordination of plots based on species abundance to extract major axes of variation in community composition. Correlations of species, guilds, and environmental variables with ordination axes were compared between geographic scales for the two regions.

Results: Primary axes of community variation at larger scales were correlated with climate variables and related geographic variables such as latitude and elevation, and with pollution. Forest vegetation variables such as stand age and tree species composition became more important at small scales. Community variation unexplained by macro-environment variables also became more important at small scales. Of several hundred species tested, ten lichen species showed consistent behaviour between scales within region (one also across regions) and are thus potential general indicators of ecological conditions in forests. Of six lichen guilds tested, several show strong patterns not consistently related to environmental conditions

Conclusions: Interpretation of lichen species and community composition as indicating particular environmental conditions is context-dependent in most cases. Observed relationships should not be generalized beyond the geographic and ecological scale of observation.

Keywords: Climate indicator; Ecological indicator; Environmental gradient; Forest indicator; Lichen guild; Modal distribution; Pollution indicator; USA.

Abbreviations: NMS = Global Non-metric Multidimensional Scaling ordination.

Nomenclature: Esslinger (2005) for lichens; Mitchell & More (2002) for tree species.

Introduction

Plant communities and their member species are considered indicators of environmental and biotic conditions (Hawksworth & Rose 1976; Wilcox 1995) in a variety of contexts, based on two widely accepted paradigms of plant ecology: plant species and communities worldwide (1) vary by habitat (particular ranges of environmental variables), and (2) differ with disturbance (time since disturbance, nature of natural and/or anthropogenic disturbance, etc.) (e.g. Barbour & Billings 1988; Bond 2005; Ricklefs 1990; Whittaker 1975). Lichen species and communities show similar patterns (reviews by Bates & Farmer 1992; Galun 1988). Investigators have argued broadly (Gardner 1998; Hoekstra et al. 1991; Lertzman & Fall 1998; Parker & Pickett 1998; Roberts 1987; Wiens 1989; Willis & Whittaker 2002) or have shown for regional case studies (Cornell & Karlson 1996; Ingerpuu et al. 2003; Jean & Bouchard 1993; Turner et al. 2004; Weigel et al. 2003) that such relationships are dynamical and differ with context and spatial scale, so it is crucial to investigate vegetation/ environment relations at multiple spatial scales to avoid extrapolation errors. Several investigators have examined the effect of scale for lichen species and communities in particular biomes (Jovan & McCune 2004; McCune 2000; Dettki & Esseen 1998; Ojala et al. 2000; Matthes et al. 2000; Kapusta et al. 2004).

Investigating the effect of scale and context at very broad scales and across regions is more difficult, both because species turnover is high and because variation in methodology across regions can confound the investigation (Hill & Hamer 2004). Wamelink et al. (2004) and Smart & Scott (2004) recently debated problems of applying Ellenberg Indicator species and values across Europe, concluding that modification based on local context must be considered. Bergamini et al. (2005) concluded, using consistent methodology, that some indicators of lichen community composition along a land use gradient in many European countries show

promise, though confounding differences between countries were encountered. Díaz et al. (2004) found consistent patterns of plant functional traits (rather than species) across four countries worldwide, with implicit ecological scale at least somewhat comparable.

We explore variation in vegetation/environment relations between two very different USA geographic regions and two geographic scales with forest macrolichen community data. Data are collected in systematic inventories by the Forest Service of the United States of America Department of Agriculture (USDA-FS) using consistent methodology and plot selection unbiased with environment, land use, or forest type (McCune 2000). We investigate the effects of variation in environmental scale (climatic, topographic, disturbance, and vegetation variables) and ecological (biotic response) scale with spatial/geographic scale (Dungan et al. 2002) while keeping constant the scale of observation, or grain size (within-plot sample protocol). To our knowledge such a broad-scale general comparison based on consistent field methodology has not been attempted before. We can with this study address directly the questions of how consistent are organism/environment relations between scales within region, and between biomes. Our answers should lead to more effective general application of ecological indicators to assess status of ecosystems and environments, and can foster more appropriate interpretation of response to environment by lichen communities.

Methods

Study areas

Our study areas are in two widely differing temperate forest biomes in the USA (Fig. 1; Table 1). The West Large study area (the states of Washington and Oregon west of the Cascade Mountains divide, northwestern USA) has mostly conifer forest with a few broad-leaved deciduous trees; it has great topographic and climatic variation in this temperate conifer forest biome, with arid to rain forest and montane climates (Bailey 1989; Bailey et al. 1994; Omernik 1987). The West Small study area is the Willamette National Forest (Oregon) inside the eastern edge of the West Large study area. The East Large study area (the states of Delaware, Maryland, New Jersey, Pennsylvania, Virginia, and West Virginia, east central USA) has mostly broad-leaved deciduous forest and some mixed and conifer forests (Bailey 1989), with moderate topographic variation and mostly continental climate, in this temperate deciduous forest biome. The East Small study area is the Allegheny National Forest (Pennsylvania) inside the north edge of the East Large study area.

All field data were collected from permanent plots randomly located (one per grid cell) within regular geographic grids (USDA-FS Forest Inventory and Analysis Program 'Phase 3' grid nationwide with cells 19 km across, and Current Vegetation Survey Program grids in
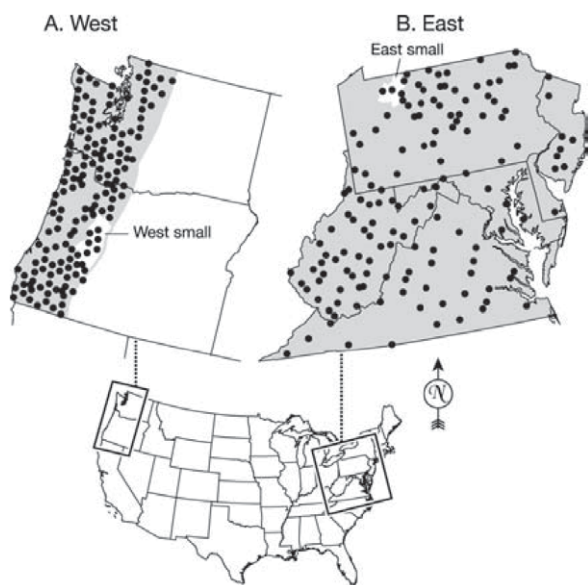

Fig. 1. Location of study areas. Black dots give approximate locations of plots in large-scale data sets. Gray shading marks the extent of the large-scale study areas. White areas inset in gray shaded areas mark the extent of the National Forests within which plots for small scale data sets are located.

Table 1. General characteristics of study areas (see map, Fig. 1). Ranges are given for plot level variables, with number of ecoregions included in study area. See App. 1 for more details about environmental variables.

Study area characteristics	West Large	West Small	East Large	East Small
Area (ha)	14 582 617	678 000	33 140 190	207 600
Elevation (m a.s.l.)	15-3048	305-2195	1-1200	407-679
Average temperature (°C)	1.8 - 11.8	1.3 - 11.1	6.6 - 15.1	6.6 - 8.4
Annual precipitation (mm)	44-4512	842-2828	890-1438	1080-1185
Bailey's Ecoregion Provinces[1]	3	1	5	1
Omernik's Level 3 ecoregions[2]	6	1	12	1
# Sample plots	182	210	174	160
Plots in analysis	154	178	144	140
Species in analysis	117	69	55	32
Macrolichen diversity	(all sample plots for α, γ; analytical plots only for β)			
α diversity[3]	18.9	24	11.1	7
β diversity[4]	2.12	1.21	1.95	1.52
γ diversity[5]	209	151	143	71

[1] Bailey 1989; Bailey et al. 1994. [2] Anon. 2005d; Omernik 1987. [3] Average number of species/plot.
[4] Species turnover β_D of Wilson & Schmida 1984, see text. [5] Total number of species in data set.

National Forests with cells 3.4-5.4 km across) by USDA-FS personnel 1994-2001. Plot location is strictly geographic; no *a priori* stratification by other criteria such as intensity of land use, environment, history, or vegetation classification was done. Data were collected from any plot designated forested or woodland land use without regard to actual woody cover (includes, for instance, open woodland, clear-cut or burned stands, and forestry plantations, but not orchards). Lichens are included in USDA-FS inventories as cost-effective indicators of air quality and forest ecosystem integrity (McCune 2000). Large-scale data sets include plots in any type of land ownership; small-scale data sets include only plots on government-owned land. Grids are sampled over multiple years as rotating interspersed subsets; about 70% of grids were surveyed for the large-scale data sets, while 100% of grids were surveyed for the small-scale data sets used. Adjacent plots are 19-97 km apart for large-scale data sets and 3-6 km apart for small-scale data sets, with gaps where the random plot location in a grid cell is non-forest. See Table 1 for information about study areas and plot numbers for each data set.

Lichen data

All lichen data were collected using a standard United States Forest Service field protocol (McCune et al. 1997; Anon. 2005b). In a timed (30 min minimum to 2 hr maximum) survey of a 0.4 ha permanent plot, a single trained non-specialist collects samples of each apparent macrolichen species found > 0.5 m above ground on any standing woody substrate (type not recorded), including trunks and branches of live woody plants of any diameter, dead snags, and recently fallen branches representing the canopy. Macrolichens can be separated from their substrate; they have flat and leafy, shrubby, stalked, tufted, or stringy hanging growth forms. The collector assigns an abundance code (1 = 1-3 individuals; 2 = 4-10 individuals; 3 = >10 individuals but on <1/2 of substrates; 4 = on >1/2 of substrates) for each sample in the field. Lichen specialists identify samples and calculate final abundance for each species using a standard formula. Lichen abundance by species within plot is archived in USDA-FS databases (Anon. 2005a, for West Large, East Large, East Small data sets; Anon. 2005c, for West Small data set). Vouchers are deposited in the Oregon State University Herbarium (ORS), USA, and Wisconsin State Herbarium (WIS), University of Wisconsin-Madison, USA, for data sets used here.

Estimates for three kinds of species diversity (Whittaker 1972) help characterize the macrolichen flora (Table 1). Average number of species per plot (complete data set) represents within-plot α (alpha) diversity. Our between-communities β (beta) diversity estimate

(McCune & Grace 2002) is the species turnover β_D of Wilson & Shmida (1984), which calculates half-changes in species composition (analytical data set) from average plot dissimilarity: $\beta_D = \log(1 -$ average Sørensen dissimilarity [formula below] between plots)/$\log(0.05)$). Total number of species (complete data set) is our estimate for landscape γ (gamma) diversity.

Explanatory variables

We consider explanatory variables representing environmental factors, air pollution, and forest vegetation, all previously shown to affect forest lichens in a variety of biological systems (e.g., Dettki & Esseen 1998; Kivistö & Kuusinen 2000; Peck & McCune 1997). One to several variables in each of nine categories (Table 2) were included in an environment data set for each study area; detailed description, origin, and range of values for each variable in each data set are included in App. 1. Geographic, topographic, and vegetation data were extracted from USDA-FS Forest Inventory and Analysis Program databases for the large-scale data sets, and from USDA-FS Current Vegetation Survey Program databases for the small-scale data sets. Much of this information is public (Anon. 2005a; Anon. 2005c); exact plot locations and other identifying data are private. Air quality data were either measured lichen tissue concentrations (West Small, App. 1) or were estimated from models (Coulston et al. 2004). Climate (annual averages plus temperature averages for warmest and coldest months) and elevation data were generated using the Potential Natural Vegetation model (West only: Henderson 1998) and/or the Climate Source model (Daly & Taylor 2000). Plots were fitted to a gradient model developed from an independent data set for the West Large region by Geiser & Neitlich (in press), generating scores on orthogonal gradients for lichen community response to air quality, climate, and unexplained variation in composition. All derived or modelled plot values are based on exact plot locations. Many more than the minimal set of one variable per class were available for most data sets; we included these as they were available to evaluate which of many possible forms of information seemed most useful for explaining variation in lichen communities.

Data analysis

All data analysis protocols were selected to maximize comparability of analyses for our four data sets. Our primary data analysis tool was unconstrained ordination; the investigator extracts major axes of variation in macrolichen community composition, then compares these community gradients *a posteriori* with individual

environmental variables. Unconstrained ordination is preferred for exploratory analysis; it avoids distortion of community gradients from *a priori* selection of environmental variables and bias from inclusion of correlated environmental variables. The two latter effects are intrinsic to constrained ordination techniques such as Canonical Correspondence Analysis that combine community and environmental data for analysis, rendering these techniques more suitable for testing of specific hypotheses than for comparison and hypothesis generation (McCune 1997; Økland 1996).

We selected global Non-metric Multidimensional Scaling (NMS) ordination with Sørensen dissimilarity $(1 - \sum(\min |a_{ij}, a_{ik}|)$, where a_{ij} is the relative abundance of species i in plot j and a_{ik} is the relative abundance of species i in plot k, for all species $1 - n$ in either plot) as the pairwise plot distance measure; we used PC-ORD v. 4.37 software (McCune & Mefford 1999). NMS ordination is one of the most robust and effective unconstrained methods for multivariate data reduction (especially with species × sample data and city-block distance measures like Sørensen distance) to extract important variation in composition and to facilitate exploration of relationships with environmental variables (Legendre & Legendre 1998; McCune & Grace 2002). We used one ordination technique to facilitate unbiased comparison; this is not necessarily the optimal analysis for any one data set.

We modified the four complete data sets before analysis. Species found at fewer than three plots were excluded, to reduce noise from rare and inadequately sampled taxa. Plots with tree basal area $\leq 5 m^2.ha^{-1}$ were excluded from East data sets because in this region shrubs are not important macrolichen substrates and very young stands have limited colonization. In the western USA, hardwood shrubs and small trees are important macrolichen substrates, and some older stands in arid areas have small trees, so basal area was not a criterion for exclusion of plots. Outlier plots (those with average Sørensen distance from other plots >2.5 standard deviations higher than average distance for all pairs of plots) were excluded from all data sets. Abundance of the remaining species at these plots (Table 1) constituted the primary lichen analytical data sets. All further analyses were conducted on these four data sets. Four α (within-plot) diversity indices (App. 1) calculated for analytical data sets were included in environmental data sets as lichen community response variables. Before further analysis, lichen data were relativized by dividing each species' abundance by total plot abundance to remove unwanted signal from variation in total abundance and to enhance expression of variation due to species composition of plots. For East data sets this signal (coefficient of variation for raw plot abundance:

65% Large and 49% Small) was strong enough to affect ordination pattern (McCune & Grace 2002).

Final ordinations are three-dimensional solutions (for each set the most different from random of one- to six-dimensional solutions), the best (lowest final stress 17.5-20.6, final instability ≤ 0.04) of multiple 3-d solutions (>280 runs for each data set) from random starts (each final solution non-random, $p < 0.03$, compared with 100-200 Monte Carlo runs). Ordination axes were rigid-rotated for each analysis (PC-ORD routine Graph) to have Axis 1 express the highest proportion of variation among plots (Pearson squared correlation r^2 of between-plot distances on axis with original distances), with axes 2 and 3 following in descending order (orthogonality > 95% in all cases). We calculated Pearson and Kendall correlations with ordination axes for all quantitative variables (App. 2) and species (App. 3). Pearson r^2 can be interpreted as the proportion of total variation in species abundance or variable values expressed as correlation with that axis (Sokal & Rohlf 1995).

Designation of lichen guilds

We assigned each lichen species in the analytical data set to a unique morphological/functional guild (group of species with similar structure and/or function). Flat leafy lichens were divided into three guilds: Small Leafy (lobes < 2 mm wide, mature individual thallus usually < 5 cm wide), Medium Leafy (lobes > 2 and < 6-8 mm wide, thallus usually 3-15 cm wide), and Large Leafy (lobes > 6-8 mm wide, thallus usually 5 to > 20 cm wide). The Tufted/Hanging guild includes all tufted, shrubby, or hanging species, and the *Cladonia*-like guild includes species with fruiting stalks on a base thallus. The five morphological guilds have loose links to function in that size, shape, and surface/volume ratio of a thallus may be related to water and mineral balance and sensitivity to atmospheric conditions (Nash 1996). Nitrogen-fixing lichens with cyanobacteria as symbionts are a true functional guild, including here a broad size range of flat, leafy growth forms. Nitrogen-fixing species are not included in the three Leafy guilds; all guild designations are mutually exclusive.

Relation of guild membership to lichen community pattern was investigated in two ways, first by evaluating patterns shown by individual species grouped by guild and second by calculating correlations of summed relative abundance of all guild species with ordination axes. Pearson r^2 and Kendall's τ values for all guilds are reported as lichen community response variables (Apps. 1 and 2).

Assigning importance to species and environmental variables

Species having a Pearson $r^2 \geq 0.10$ of abundance with plot scores on at least one ordination axis are considered important contributors to ordination pattern. If $0.20 > r^2 \geq 0.10$, pattern is described as minor; if $r^2 \geq 0.20$, pattern is described as major. Although a relationship that explains 10% of variation seems modest biologically, that correlation strength was highly significant for all ordination axes ($p < 0.000$ for $r^2 = 0.10$, smallest $N = 140$ for East Small, see Apps. 2 and 3). Linear correlation of species abundance with axis scores is sensitive primarily to strength of monotonic distribution along an axis, while many instances of unimodal species distribution along long environmental gradients are known. To test for modal species distribution along axes, we calculated deviation of plot score from the species weighted average axis score, then calculated Pearson and Kendall correlation of the plot deviation with species abundance. A unimodal pyramidal species distribution would give correlation near –1.0, generally unimodal distribution would give negative correlation, and bimodal distribution would give positive correlation with plot scores for deviation. We calculated this modal correlation for all species found at ten or more plots. If the modal r^2 was higher than the linear r^2 or modal $r^2 \geq 0.10$ we included the modal Pearson r^2 and Kendall τ in App. 3 and based assessment of pattern strength on the higher r^2. Sign on the linear Kendall τ indicates location on the axis of the centre of species distribution. Interpretation of species relations to environmental variables is based on linear correlations with ordination axes.

For three of the data sets, an environmental variable is considered important only if it has a Pearson $r^2 \geq 0.20$ with at least one ordination axis. For the East Small data set, a lower threshold, $r^2 \geq 0.10$, is accepted, since all correlations of quantitative explanatory variables with axes were low here. Only linear correlations were calculated for explanatory and community response variables. Variable categories are rated for importance based on individual correlations and on the number of relatively independent variables in that class which meet the threshold for importance.

Results and Discussion

General macrolichen diversity patterns

The two West areas have steeper environmental gradients (greater range for a given geographic area, for example elevation and precipitation, Table 1) than do the East areas; the wide geographic scale difference between East Large and East Small is offset somewhat by the shallower environmental gradients there. West study areas have higher lichen α- and γ-diversity (from complete data sets) than do East areas (Table 1), and both large-scale data sets have higher γ-diversity and β-diversity (from analytical data sets) than do small-scale data sets, as expected from general knowledge of lichen diversity in the two regions. Comparisons of numbers of Bailey & Omernik ecoregions (Table 1) suggest more ecological variation for vascular plant communities in East Large and greater ecological scale difference between East Large and East Small, assuming equivalent ecological range for ecoregions at the same level nationwide.

In contrast, lichen β-diversity values (Table 1) suggest that for lichen communities ecological scale is similar for East Large and West Large, and that ecological scale difference between geographic scales is similar for the two regions. For West Small 23% of species show unimodal pattern (modal Pearson $r^2 \geq 0.10$, Kendall τ negative) while about 16% of species in the other three data sets show unimodal pattern (App. 3), an indication that ecological range is slightly larger for West Small but equivalent for the rest. β-diversity and frequency of modal pattern thus suggest that ecological scales are fairly similar between East and West. Lichen species tend to respond to microhabitat distinctions differently from vascular plants, with widely varying dispersal limitations and moderate to severe establishment limitations related to substrate and other factors at small scales (Nash 1996); this may relate to the apparent difference in how lichens and vascular plants register ecological scale (Will-Wolf et al. 2002).

As is usual in biotic community data sets, most species are rare. Over half the species in each complete data set were excluded for rarity. A total of 181 taxa were included in analytical data sets. For three of the areas about 45% of included species occur at <10% of plots in the analytical data set and no more than one species occurs at > 80% of plots, while for West Small 25% of included species occur at <10% of plots and six species occur at > 80% of plots. The more frequent the lichen species, the more likely it is to contribute pattern to its ordination; 57-88% of species with > 20% frequency in a data set show pattern, and all eight species with frequency > 80% show pattern (App. 3). Apparently ecological gradients related to each data set are long enough that no lichen species was too common to show pattern. Grain size (including sample time limits) of our lichen sample protocol was selected to maximize comparability with forest vegetation data and to meet cost and time constraints; a possible reason no
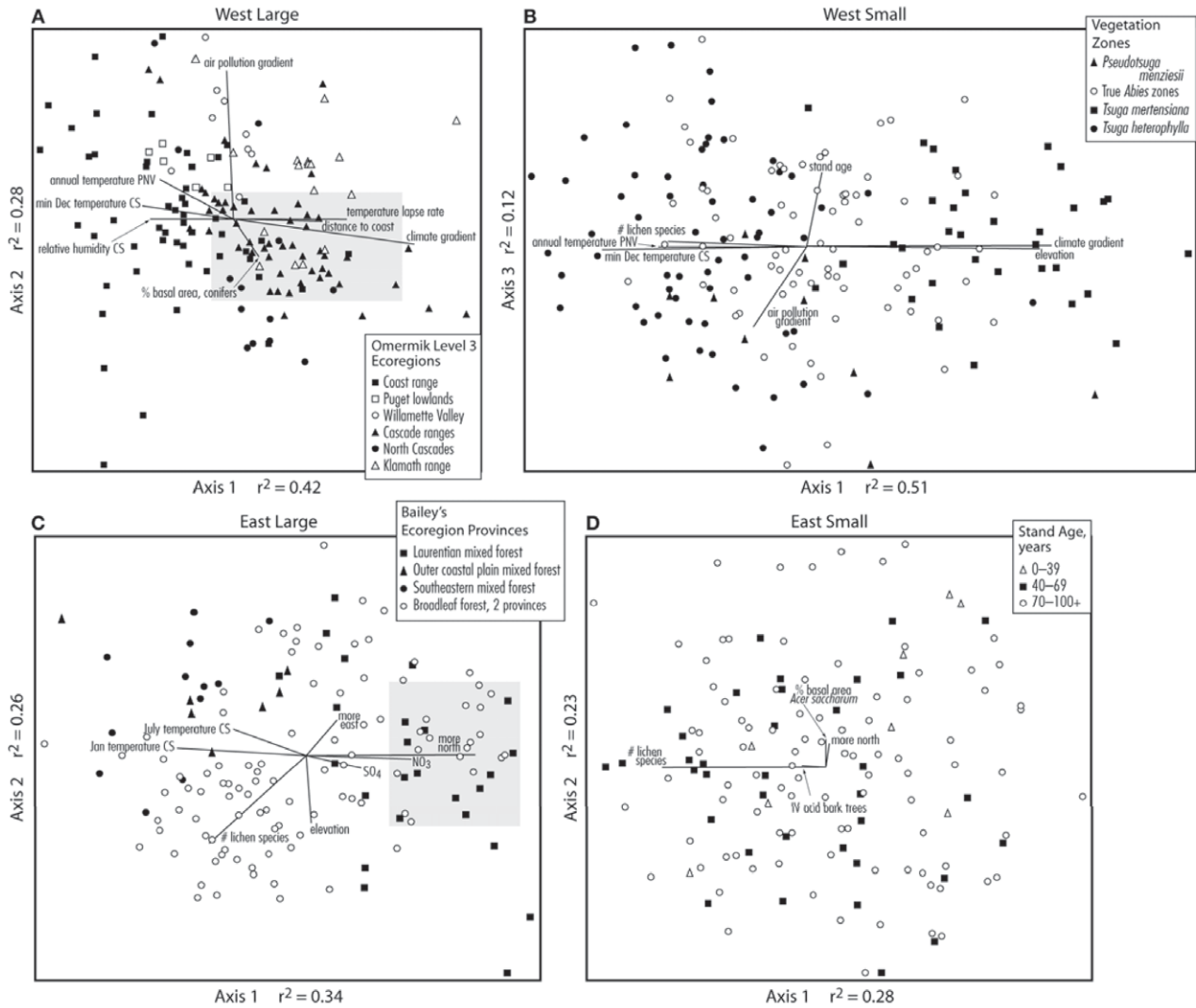
Fig. 2. Ordinations of the four data sets displaying explanatory variables. Gray box in Large ordinations (**A** and **C**) indicates area where plots also in Small (**B** and **D**) data sets are placed. Pearson r^2 value for an axis gives proportion of variation expressed on that axis. Length of overlaid vectors is proportional to Pearson r^2 of variables with axes. The variable in each class (Table 2, App. 2) with the highest $r^2 > 0.20$ (> 0.10 for D. East Small) for an axis is displayed; additional variables are included if they provide additional information. Number of lichen species is displayed here as well as on Fig. 3 if $r^2 > 0.20$, for reference. One categorical variable is portrayed on each ordination; see symbol key next to each diagram. For all but West Large, the axis not displayed here is displayed in Fig. 3. **A.** West Large total $r^2 = 0.79$, Axis 3 (not displayed) $r^2 = 0.09$; **B.** West Small total $r^2 = 0.83$ – note Axis 1 and Axis 3 are displayed; **C.** East Large total $r^2 = 0.78$; **D.** East Small total $r^2 = 0.72$.

lichen species appear too common to show pattern.

While it is much larger than grain size (individual trees or quadrats on tree trunks, rocks, or ground) often used for studies of lichen communities (e.g. Bergamini et al. 2005; Ketner-Oostra et al. 2006), our grain size is fine enough to detect broad patterns in lichen community composition (Fig. 2, Fig. 3). For three of the data sets within-plot lichen diversity measures are strongly correlated ($r^2 > 0.30$) with one or both of the two ordination axes correlated with environment (Fig. 2, App. 2); for West Large, they are weakly correlated with Axis 1 ($r^2 = 0.15$-0.17, App. 2, Table 2.1).

Comparisons between regions and between scales

Proportion of variation expressed in ordinations is similar for the four data sets (r^2 for all three axes was 0.72-0.84, Fig. 2). Small data sets designed to be geographic and environmental subsets of the Large data sets in their region can also be considered floristic subsets; each Small data set has a much lower percentage of species found only at that scale than does the respective Large data set (unique species, Table 3). Proportion of species contributing to pattern (Table 3) for East data sets is similar (ca. 38%), while for West data sets there is
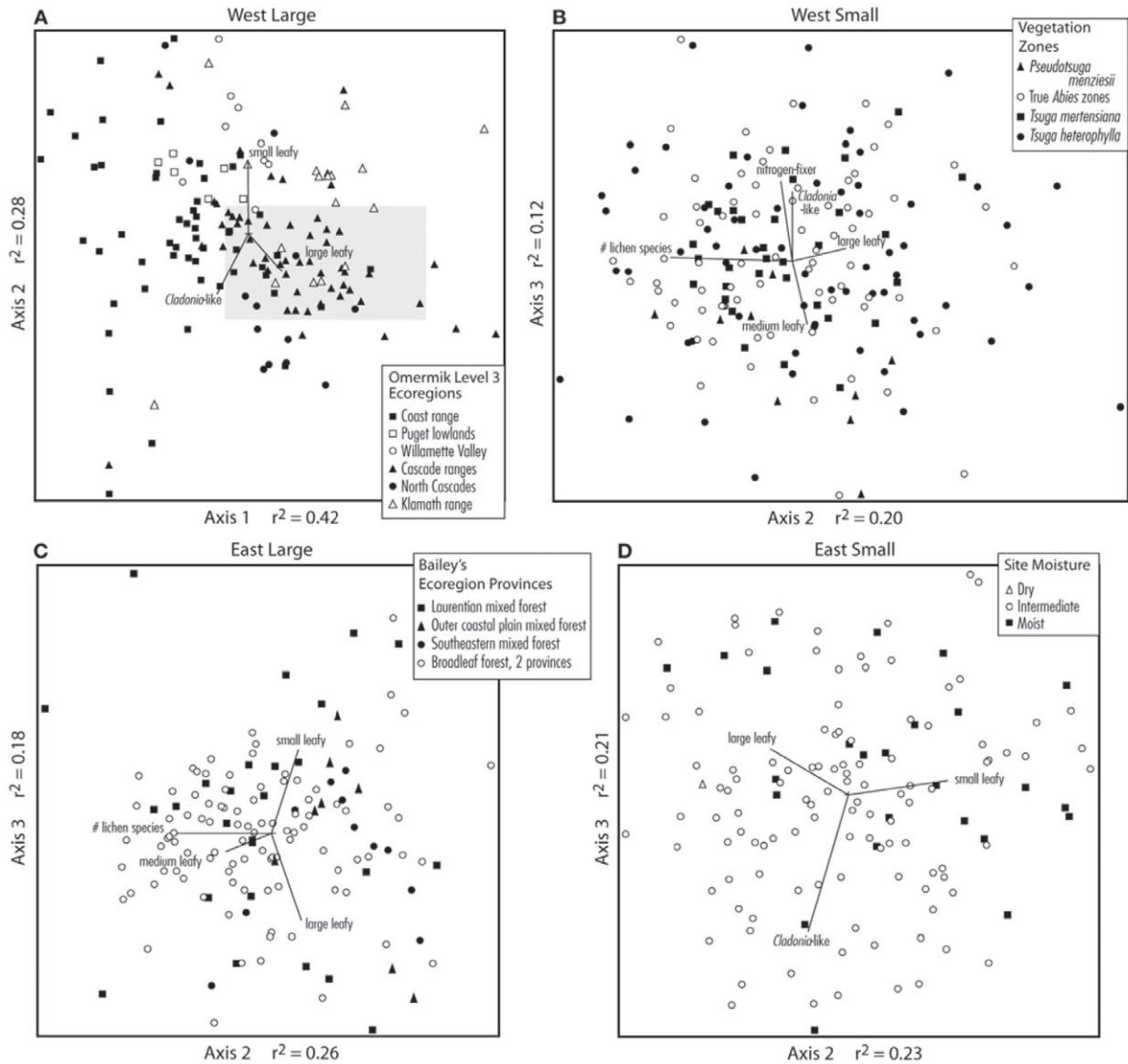
Fig. 3. Ordinations of the four data sets showing lichen community response variables. Pearson r^2 value for an axis gives proportion of variation expressed on that axis. Length of overlaid vectors is proportional to Pearson r^2. One categorical variable is portrayed on each ordination; see symbol key next to each diagram. **A.** West Large – note axes and categorical variable are the same as for Fig. 2A; **B.** West Small – note axes are different but categorical variable is the same as for Fig. 2B; **C.** East Large – note axes are different but categorical variable is the same as for Fig. 2C; **D.** East Small – note axes and categorical variable are different from Fig. 2D.

a strong contrast, with almost twice as many West Small species contributing to pattern. Variation in lichen community composition not strongly linked with any of our explanatory variables is more important in both regions at small scales; Axis 3 of both West Large and East Large displays unexplained variation, while Axis 2 of West Small displays mostly unexplained variation, and much variation on all three East Small axes remains unexplained (Table 2, Fig. 2, App. 2).

The relation of the Small data set to the Large data set is somewhat different East versus West. West Small is located in a part of the West Large region with relatively lower air pollution; pollution-sensitive species are not at a disadvantage, and average frequency of species across plots is the highest of the four data sets. This may explain both the lower γ-diversity and the very high percentage of species showing pattern in West Small. The higher percentage of unimodal species also

suggests species associations are more strongly defined here. In contrast, East Small is in a part of its Large region that has experienced high regional air pollution for many years (Coulston et al. 2004; Showman & Long 1992), resulting in loss of sensitive lichen species (1982 survey by J. Thomson, I. Brodo & T. Nash, pers. comm.) since the 1940s (Thomson 1944; Mozingo 1948). East Small also has the narrowest range of variation of the four data sets for most of the explanatory variables, and the combination of reduced lichen flora and short environmental gradients probably explains weak correlations of explanatory variables with East Small ordination axes. This difference does not seem to have affected the validity of comparisons between scales; East Small has a higher percentage of unique species (Table 3) than does West Small and a similar percentage of unimodal species to East Large, when the opposite would be expected for both patterns if East Small had lost ecological signal because only very common pollution-tolerant species remain in its flora.

Explanatory variables

For all but East Small, a variety of explanatory environmental variables show strong correlations with ordination pattern (Fig. 2, Table 2, App. 2). Geographic location, climate/temperature, and air quality are major correlates of lichen community variation at large scales in both regions. The major climatic and geographic gradients in West data sets vary strongly E to W (distance to coast) with little to no variation expressed N to S. The reverse is true for East Large, where most expressed variation is N to S, and only secondarily E to W. Variation in moisture is moderately important for West areas but not East Large. Geographic location in East Small shows weak correlation with lichen community composition, and is unrelated to macroclimate variables, which themselves vary little for East Small. For

West analyses, macroclimate variables from the very detailed regional Potential Natural Vegetation model are mostly more strongly correlated with lichen composition gradients (ordination axes) than are environmental variables from the national Climate Source model (Apps. 1 and 2), supporting the value of regional modelling of climate. In both regions variables representing temperature extremes give stronger correlations than annual averages. Strong correlations of the Geiser & Neitlich (In press) composite climate response scores with both of our West climate axes (Axis 1, Fig. 2A, B) and strong correlation of their composite air quality scores with another axes independent of climate (West Large Axis 2, Fig. 2A; West Small Axis 3, Fig. 2B) confirm that they achieved their goal to develop independent lichen community response indicators for climate and air quality that are generally applicable in the West region. Directly measured air quality variables were not correlated with any of our West axes, so the Geiser & Neitlich (In press) composite air quality response variable is our estimate of air pollution for both West data sets. Air quality is more strongly correlated with lichen community composition at large scales: in West Small most plots have relatively clean air and in East Small plots have uniformly dirty air (as compared with the range of values for pollution variables in the Large data sets for each region, App. 2).

Elevation, a topographic variable widely considered a useful surrogate for climate, shows an interesting pattern. For West Small (Fig. 2B) and East Large (Fig. 2C), which each include a single mountain range, elevation is strongly correlated with lichen community composition. For West Large, which includes distinct coastal and inland mountain ranges, elevation is weakly correlated (App. 2, Table A2.1) and instead temperature lapse rate (Fig. 2A), which expresses the effect of elevation on climate, is strongly correlated with lichen community composition. The elevation range for East

Table 2. Importance of classes of explanatory and response variables for data sets, based on correlation with ordination axes (App. 2, Tables A2.1 - A2.4). Number of plus signs indicates the relative importance of that variable class; '—' means not important. Relative importance is based both on strength of individual correlations and on the number of relatively independent variables in that class showing important correlations. See App. 1 for detailed descriptions of all variables.

Variable class	Importance of variables			
	West Large	West Small	East Large	East Small
Geography/location	+++ax1	++ax1	+++ax1 +ax2	—
Geography/topography	+ax1	+++ax1	++ax2	+ax2 +ax3
Climate/temperature	+++ax1 +ax2	+++ax1	+++ax1 +ax2	—
Climate/moisture	++ax1 +ax2	+ax1	—	—
Pollution	++ax2	+ax1 ++ax3	++ax1	—
Vegetation structure (stand biomass, age)	+ax2	++ax3	—	+ax1
Vegetation composition (regions, zones)	++ax1 ++ax2	++ax1 +ax2	+++ax1 ++ax2	—
Vegetation composition (local diversity, composition)	+ax1 +ax2	++ax1 +ax2 +ax3	—	+ax1 +ax2 (+)ax3
Macrolichen composition (local diversity, composition)	+ax1 ++ax2	+++ax1 ++ax2 ++ax3	+ax1 +++ax2 ++ax3	+++ax1 ++ax2 ++ax3

Table 3. Percentage by guild within analytical data set of all lichen species, of unique species, and of species contributing to pattern (Pearson $r^2 \geq 0.10$ with at least one ordination axis). 'Unique' species are species found only at that scale within that region. Numbers summarized from App. 3.

Guild	West Large (N = 117 species)				West Small (N = 69 species)			
	% all spp.	% spp. with pattern	% unique spp.	% unique spp. with pattern	% all spp.	% spp with pattern	% unique spp.	% unique spp. with pattern
Small Leafy	17.9	7.7	12.8	5.1	8.7	4.3	0.0	0.0
Medium Leafy	24.8	9.4	7.7	0.9	30.4	13.0	1.4	0.0
Large Leafy	6.8	3.4	3.4	0.0	5.8	5.8	0.0	0.0
Tufted/Hanging	28.2	10.3	10.3	1.7	30.4	18.8	0.0	0.0
Cladonia-like	12.0	1.7	9.4	0.9	4.3	1.4	0.0	0.0
Nitrogen-fixing	10.3	0.9	1.7	0.0	20.3	13.0	5.8	1.4
Total	100.0	33.3	45.3	8.5	100.0	56.5	7.2	1.4
	East Large (N = 55 species)				East Small (N = 32 species)			
Small Leafy	29.1	12.7	18.2	9.1	18.8	9.4	0.0	0.0
Medium Leafy	23.6	10.9	12.7	7.3	25.0	12.5	6.3	6.3
Large Leafy	25.5	10.9	18.2	7.3	12.5	6.3	0.0	0.0
Tufted/Hanging	10.9	1.8	7.3	1.8	9.4	0.0	3.1	0.0
Cladonia-like	10.9	1.8	1.8	0.0	34.4	9.4	18.8	9.4
Nitrogen-fixing	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	100.0	38.2	58.2	25.5	100.0	37.5	28.1	15.6

Small is apparently too narrow for this variable to be a useful surrogate for habitat conditions there (App. 2, Table A2.4).

Vegetation structure variables are more strongly correlated with lichen community composition at small scales (Stand Age, Axis 3, West Small, Fig. 2B; Stand Age Class, Axis 1, East Small, Fig. 2D; Stand Basal Area not strongly correlated anywhere), but even there they are relatively weak explanatory variables. This is possibly because the study was not stratified to ensure adequate representation of the full range of stand structure across the full range of environment and vegetation composition.

Vegetation composition variables are relatively strong explanatory variables at both scales in both regions. Variables from models and vegetation classifications seemed as good as those from plot data at both scales, but this may be because quantitative data for tree species composition were obtained only for East Small. In the latter instance, quantitative tree species composition was generally consistent with assignment to vegetation classes. Lichens are known to be strongly linked to substrate conditions (Nash 1996); the relatively weak and inconsistent correlations of plot substrate variables (% conifers for West Large, Fig. 2A; importance of trees with acid bark for East Small, Fig. 2D; no variables for other data sets, App. 2) with lichen composition axes in this study occur because lichen composition is averaged across all woody substrates on a plot.

Species

About one-third of the lichen species found at both scales within a region contribute to ordination pattern at both scales (Table 4). Of these, eight western species and four eastern species have similar pattern strengths and relate to similar variables between scales based on correlations with ordination axes (App. 3). Most of

Table 4. Comparison by guild of number of species that occur in analytical data sets at both scales within region. Species contributing to pattern have Pearson $r^2 \geq 0.10$ with at least one ordination axis. Similar species respond to similar variables (in the same variable class, Table 2), and have similar pattern strength, based on correlations with ordination axes (App. 3).

Region	Guild	# species in common	# species with pattern at both scales	# species similar, both pattern strength and variables
West	Small Leafy	6	2	0
	Medium Leafy	20	5	2
	Large Leafy	4	4	1
	Tufted/Hanging	21	9	5
	Cladonia-like	3	1	0
	Nitrogen-fixing	10	1	0
	Total	64	22	8
East	Small Leafy	6	1	1
	Medium Leafy	6	3	2
	Large Leafy	4	2	0
	Tufted/Hanging	2	0	0
	Cladonia-like	5	1	1
	Nitrogen-fixing	0	0	0
	Total	23	7	4

these species show responses between scales consistent with generally similar habitat preference, even though they show varied responses to surrogate habitat variables such as elevation, latitude, and distance from coast. West *Alectoria imshaugii, A. sarmentosa, Hypogymnia imshaugii, Letharia vulpina*, and *Nodobryoria oregana* are found in cooler habitats. West *Platismatia stenophylla* occurs in habitats with temperature and moisture intermediate for the region. East *Hypogymnia physodes* occurs in habitats with at least some conifers and other trees with acid bark. East *Punctelia perreticulata* occurs in broad-leaved forest not dominated by *Acer saccharum*. West *Evernia prunastri* and East *Flavoparmelia caperata* show consistent correlations between scales with higher air pollution, lower lichen diversity, or young plots, all related to disturbed habitats. These ten species are good candidates for cross-scale indicator species within their region.

Five lichen species are found in all four data sets; two of them are quite common in all. *Parmelia sulcata* and *H. physodes* (discussed above) each have worldwide (especially northern hemisphere) distributions. *H. physodes* is ubiquitous with no pattern in West Large. Its association in both East data sets with conifers is consistent with its West Small association with warmer, lower elevation conifer forests. *P. sulcata*, the only species to contribute pattern in both regions at both scales, shows consistent correlations with higher air pollution, lower lichen diversity, or young plots, all related to disturbed habitats. It is the only good candidate for an indicator species (for disturbed habitats) across both regions and scales.

Guilds

Distribution of species among guilds is consistent between scales within region ($p > 0.05$, likelihood ratio tests on species frequency by guild), but is significantly different between West and East (smallest likelihood ratio 26.2, $df = 5$, $p < 0.000$), with higher percentages of Nitrogen-fixing and Tufted/Hanging species in West and higher percentages of Small and Large Leafy species in East. Within each data set percentage of species in a guild is generally a good predictor of the percentage of species in that guild that show pattern (Table 3), with a few exceptions. In West data sets the Large Foliose guild is poorly represented, but many of its species show pattern. In all four data sets the *Cladonia*-like guild has a lower percentage of species with pattern than expected from its representation in the flora.

In addition to patterns of individual species by guild, summed abundance within guild shows relatively strong correlations with ordination axes for all data sets (App. 2), providing additional insights into how communities

vary on ordination axes weakly correlated with explanatory variables (Fig. 3B axis 2; Fig. 3C axis 3; Fig. 3D axis 3). The Leafy guilds showed strong patterns in all four areas; for all but West Small, Large and Small Leafy guilds segregated on a single axis. This pattern was not consistently correlated with any class of explanatory variable. The Tufted/Hanging and Nitrogen-fixing guilds showed little or no pattern for West Large but very strong segregation along elevation (Fig. 2B axis 1) for West Small, with the Nitrogen-fixers at lower elevations. Success of Nitrogen-fixing lichens has been correlated with pollution status and forest age/continuity (old-growth status) in multiple studies of forests worldwide (Antoine & McCune 2004; Sillett & Antoine 2004; review in Will-Wolf et al. 2004), so it is surprising to find that in our study abundance of this guild was independent of pollution status and forest age. A possible explanation is that such a pattern would be expected primarily at habitats equivalent to lower elevation West Small sites where the guild is most common, and is not distinguishable in analyses of either West data set from the stronger, more widespread patterns. The *Cladonia*-like guild showed relatively strong pattern in each area, often segregating from one or more Leafy guilds but showing no consistent association with explanatory variables. This is an excellent example of a growth form showing strong pattern even when few of the individual species having that growth form contribute pattern to the ordination. Most *Cladonia*-like species were found at fewer than 20% of plots in all four analytical data sets; low frequency probably accounts for their lack of pattern.

For both East and West, guild correlations with ordinations are stronger for Small data sets (correlated with more important axes and/or stronger correlations with similar axes; Fig. 3, App. 2) than with Large data sets. This suggests that a specific relation of growth form to conditions is moderately local, rather than linked to macroclimate or macro-environment characteristics reliably partitioned along region-wide gradients. Guilds, in contrast to species, are not consistently associated with the same, sometimes not with any, climate or habitat conditions across scales. Responses consistent by lichen growth form may relate to conditions not adequately captured by our explanatory macrohabitat variables, or they may be linked to local context and thus not expressed consistently on our environmental gradients. Lichens identified by guild alone thus may have little potential as indicators of forest condition generally, though they may have potential as indicators of forest condition locally or possibly forest microhabitat conditions broadly relevant to lichens in a manner somewhat analogous to Díaz et al. (2004).

Conclusions

Comparability of data sets

East and West analytical data sets, despite coming from quite different biomes and having mostly different lichen floras, have enough similarities in lichen community structure and relationships to environmental variables that comparisons give valuable insights into the generality of relations between community patterns and environmental variables across scales and regions. All four ordinations display similar proportions of lichen community variation, and correlations of environmental variables with axes are comparable for most. Within-plot lichen diversity correlates with major ordination axes at both scales in both regions (weak correlation for West Large), another indication that variation in lichen communities is of about the same order in all four data sets. Comparisons of patterns between scales within region are minimally affected by the different environmental context of West Small and East Small with respect to their Large regions.

Species patterns across scales

Species that consistently contribute patterns to composition gradients relating to similar explanatory variables across scales are potentially helpful indicators of ecological conditions for a variety of purposes. Of the 181 species examined and 28 species that contributed pattern at both scales within region, only ten contribute consistent pattern even with our deliberately weak criteria. The consistent patterns relate to explicit habitat characteristics such as temperature, air quality, or vegetation type; not to widely used surrogate environmental variables such as elevation or latitude. These ten species could perhaps be used as indicators of ecological conditions across scales within their region. One species, *Parmelia sulcata*, is associated with variables indicating disturbed plots in all four analytical data sets, and so is a potentially useful indicator between regions as well. The inescapable conclusion is that most lichen species are likely to be useful indicators of ecological conditions only within narrow environmental contexts and scale ranges.

Usefulness of macrolichen guilds

Ecologists have found that species guilds – groups of species that use the same environmental resources in the same manner – are useful as ecological and environmental indicators (Simberloff & Dayan 1991). Several investigators have adopted related approaches for lichens (reviewed in Will-Wolf et al. 2004). Here we found three potentially useful patterns relating to lichen guilds; (1) distribution of species among guilds is consistent between scales within region but different between regions, probably related to climate and macrohabitat differences between regions, (2) guilds that are represented by more species in a region are likely to include a higher percentage of species that contribute pattern to defining composition gradients in that region, and (3) abundance of lichens summed by guild shows some pattern correlated with species composition gradients independent of patterns for individual species.

For West, relatively more species in Medium Leafy, Tufted/Hanging, and Nitrogen-fixing guilds contribute strong pattern at one or both scales. For East, relatively more species in the three Leafy guilds contribute strong pattern at one or both scales. Many of these patterns are related to our explanatory variables, and as such are potentially valuable ecological indicators at the scale where the pattern is displayed.

Abundance by guild shows fairly strong pattern in all four data sets, but in contrast to species we have little evidence to describe particular environmental conditions to which guilds respond with any consistency. With such strong patterns the possibility that more detailed studies will identify variables relevant for lichen ecology seems good, but our study offers no support to suggest that factors correlated with lichen guild responses are broadly consistent. Distinctions among lichen guilds may relate to particular sets of conditions only across narrow scale ranges. This does highlight the danger of assuming that general patterns found for one taxonomic group in forest ecosystems, such as vascular plants, will hold for other taxonomic groups such as lichens or arthropods.

Applications to ecological indicator studies

Macrolichen species and guilds for the most part do not consistently indicate similar forest condition at widely different scales, and are not equally suitable as indicators of any sort across wide scales; we have demonstrated this in two different forest biomes at two different geographic scales with scale of observation (grain size) held constant, and with relatively relaxed criteria for consistency. The circumstances of our study in combination with previous studies support a general statement that in most cases ecological indicator species and groups are reliable only over finite, often relatively narrow geographic and ecological scales. Composite lichen community response indicators such as those developed by Geiser & Neitlich (In press) and McCune et al. (1997) appear more reliable than individual species or groups (McCune 2000) for large regions.

Assumptions about vegetation/environment relations

Our study supports and extends the growing body of evidence that suitability of particular species or groups of species as indicators of ecological condition is almost always context-dependent. Our finding that relative abundance of one species, *Parmelia sulcata*, is an indicator across both of the biological systems and geographic scales we investigated is for one particular context: disturbed forest. We suggest that in future literature, all statements about vegetation/environment relations should include explicit description of the ecological context and spatial scales across which they have been investigated, so the limits inherent in these statements are also made explicit.

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