Climate and epiphytic macrolichen communities in the Four Corners region of the U.S.A.

Bruce McCune[1,4], Sunia Yang[1], Sarah Jovan[2] and Heather T. Root[3]

[1] *Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331, U.S.A.;* [2] *USDA Forest Service, PNW Research Station, Portland, OR 97205, U.S.A.;* [3] *Botany Department, Weber State University, Ogden, UT 84408, U.S.A.*

ABSTRACT. We used data on epiphytic lichen communities in 1215, 0.4-ha plots in the Southwest U.S.A. collected by the Forest Inventory and Analysis (FIA) program to analyze relationships with climate. We sought the climate variables most strongly associated with differences in epiphytic macrolichen communities and described the nature of those relationships, including diversity, community composition, and patterns in individual species. Five lichen community groups were strongly related to temperature and elevation gradients, overall moisture, and summer rain. Lichen abundance was highest in the wettest groups and lowest in the hottest and driest groups. Warm summer monsoonal climates supported the greatest number of species across all plots and within plots. The monsoonal pattern did not occupy a discrete geographic area, but instead formed a gradient, strongest in the southern part of our study area, diminishing to the north and west. In contrast, hot summer monsoonal climates had much lower within-plot richness. Hot, dry climates had the most variation in species composition among plots, but the fewest species within each plot and across all plots. Lichen community gradients had nonlinear relationships with combinations of climate variables rather than strong linear relationships with any single variable, including those derivative climate variables meant to have direct biological relevance. Relationships between air quality and community gradients were weak, potentially overwhelmed by regional climatic variation and complex topographic gradients. Richness of particular functional groups was more strongly related to climate than was overall species richness; functional groups have their own climatic tolerances, owing to the physiological consequences of growth form and photobiont. Presumably species in different functional groups have experienced their own evolutionary tradeoffs, developing peak performance in different climates. On the other hand, overall richness was driven by an even more complex combination of performances relative to climate and was in some functional groups more strongly related to geographic coordinates than to climate variables. Because climatic variables are themselves geographically structured, stronger model fit for geographic coordinates than for climate implies some influence of large-scale historical factors (i.e., factors not clearly expressed in modern climates, such as past climates, vegetation structure, or disturbance regimes).

KEYWORDS. Air quality, Arizona, climate, cluster analysis, Colorado, community composition, diversity, indicator species, monsoon, New Mexico, Nevada, nonmetric multidimensional scaling, nonparametric multiplicative regression, Utah.

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The lichen biota of southwestern U.S.A. has been well studied (Nash et al. 2002, and subsequent volumes), but the relationships between climatic drivers and lichens has been more anecdotal than quantitative. The large dataset on epiphytic lichen communities collected by the Forest Inventory and Analysis (FIA) program provides us with the opportunity to analyze their relationships with climate. Since 1994, the U.S. Forest Service has

[4] Corresponding author's e-mail:
  mccuneb@oregonstate.edu

surveyed epiphytic macrolichen abundance data in forested areas of the Southwest, both public and private. Elsewhere these lichen community data have proven to be a useful indicator of air quality and forest health in forested regions of the U.S.A. (e.g., McCune 2000; Jovan 2008; Root et al. 2014, 2015; Will-Wolf et al. 2015). Furthermore, the Southwest (here defined as the five-state region: Nevada, Utah, Colorado, New Mexico and Arizona) was identified by Smith et al. (2020) as hosting some of the most vulnerable lichen communities to climate change, finding that many ostensibly "warm-adapted" communities may be close to exceeding their climatic limits. But, to our knowledge, no one has quantitatively studied how epiphytic macrolichen communities relate to climate in this region.

The climate of the southwest U.S.A. is generally drier and hotter than the rest of the country, but both temperature and precipitation are quite variable within the region. Although regional patterns of lichen distribution in relationship to the climate have not been studied systematically, the distribution of vascular vegetation in relation to climate in the Southwest has been shown to be strongly influenced by elevation, seasonal moisture, and annual moisture (Neilson & Wullstein 1986; Peet 2000). In addition to the strong climatic gradients created by the contrast between high mountains and lower plateaus and valleys, a monsoonal precipitation pattern diminishes from southeast to northwest in western North America (Fig. 3 in Mitchell 1976) and partly controls the distribution and abundance of particular species (Neilson & Wullstein 1983, 1986). The summer monsoon season can add up to 50% of the annual rainfall in Arizona and New Mexico (Sheppard et al. 1999). This summer pulse of moisture derived from the tropical Pacific Ocean, the Gulf of California, and the Gulf of Mexico (Adams & Comrie 1997; Sheppard et al. 1999), results in a bimodal precipitation pattern in southern Arizona and New Mexico, in contrast to the dominance of winter precipitation farther west and north (Nash et al. 2002). The 'Arizona monsoon' air mass gradient postulated by Neilson & Wullstein (1983) combines both an increasing probability of summer drought stress and an increasing probability of winter and spring cold stress with increasing latitude. Although this summer precipitation pattern of southern Arizona and New Mexico has been called monsoonal, the contrast in precipitation is not nearly as pronounced as monsoonal patterns in other parts of the world, such as India.

The relationship of lichen distributions to the summer monsoonal pattern has not been explored systematically, although lichenologists have long been aware of this pattern. For example, Weber (1963) wrote:

"One peculiarity of the occurrence of corticolous lichens should be emphasized — namely, the great abundance of corticolous foliose and fruticose species on the bark of conifers at the higher altitudes throughout the high ranges of New Mexico and Arizona. This is interesting because these ranges are assumed to be arid, certainly more so than the lofty and massive Rocky Mountains of Colorado and Utah to the north. Nevertheless, the higher Rocky Mountains are notable for their paucity of corticolous lichens attributable to low humidity. Only in the easternmost foothills where there is the phenomenon of local cloud-veils on the escarpments adjacent to the plains does one encounter anything like the situation which is the rule in the southern ranges. One would suppose that despite the generally arid character of the region, moist air from the Gulf of Mexico must frequently produce low-hanging clouds on the summits of these mountains, making a suitable habitat for germination and growth of the larger corticolous lichen species."

In addition to climate, the strong influence of air quality on lichens is well known, including studies from the southwestern U.S.A. and southern Rocky Mountains (Fenn et al. 2003; McCune et al. 1998). However, two studies (Marsh & Nash 1979; Peterson & Neitlich 2001) found weak to nondetectable relationships between lichens and proximity to large coal fired power plants. Marsh & Nash (1979) postulated that the dry climate reduced air pollution impacts from a large coal-fired power plant. Peterson & Neitlich (2001) found that complex topographic and vegetation gradients had stronger relationships to lichen communities in an area in Colorado than did air quality. In studying a five-state region with strong regional and topographic gradients we anticipated that relationships of lichen communities to climate at this large scale

would be much stronger than for air quality gradients. Nevertheless, numerous air quality concerns are present in southwestern U.S.A. (e.g., Four Corners Air Quality Group 2020), so as a secondary objective we evaluated the strength of relationship between lichen communities and regional gradients in air quality.

In this study we seek the climate variables most strongly associated with the large differences in epiphytic macrolichen communities in the Southwest and describe the nature of those relationships, including diversity, community composition and patterns in individual species. For example, can lichen communities and individual species be useful indicators of climatic variations in the Southwest where forests are discontinuous, limited themselves by climatic variations, and broken by expanses of desert and shrub steppe? In particular, do lichen communities show a relationship with the summer monsoonal gradient? What factors separate the species-poor communities from the diverse communities? We approach these questions with a combination of ordination, cluster analysis, nonparametric regression and spatial analysis of the climatic and lichen community gradients. These questions are important because they provide a new, fundamental, baseline understanding of the distribution and abundance of lichens in a large region of North America. Furthermore, this builds a basis for comparison with other kinds of organisms and a basis for prioritizing management of forested regions in the Southwest. We can also use this information as a benchmark for comparison with future lichen communities as climate shifts.

METHODS

Study area. We defined our study area as the five-state region of southwestern U.S.A.: Nevada, Utah, Colorado, New Mexico and Arizona. We excluded California from the present study because its much stronger coastal influence distinguishes it from the remainder of the Southwest; furthermore, the broad scale climate relationships of epiphytes in California were revealed by Jovan & McCune (2004). Similarly, we excluded states to the Northwest to simplify the analysis by reducing the beta diversity of the data set and because lichen community relationships to climate have already

been studied in that region (Geiser & Neitlich 2007; Jovan 2008).

Lichen data. We assembled species and site data matrices from all "on-frame" FIA sites in the five-state region (total area = 1.4×10^6 km^2) of Arizona, New Mexico, Colorado, Utah and Nevada, plus two small off-frame data sets (22 plots), one from New Mexico and one from Utah, gathered in 2017 (**Table S2**) in conjunction with studies of nitrogen deposition. The combined species matrix contained 1215 sites × 162 species covering all forested areas of the southwestern U.S.A. east of California (**Fig. 1**). "On-frame sites" are those selected as part of the formal sampling scheme of FIA (Bechtold & Patterson 2005). These sites were surveyed in 1994–2010 (**Table S2**). Only forested sites were included, defined by the FIA program as >10% canopy cover (Jovan et al. 2020).

We used data from FIA standard lichen community plots that have been installed in thousands of sites in forested areas of the U.S.A., each plot circular with an area of 0.4 ha (Jovan 2008; McCune 2000; Will-Wolf 2010). Lichen data included the abundance of all macrolichen species from litterfall and between 0.5 and 2 m on tree boles, branches and shrubs. Field crews recorded macrolichen abundance on a pseudologarithmic scale following the FIA/Forest Health Monitoring Protocol (McCune et al. 1997b): 0 = not present; 1 = 1–3 thalli in the plot; 2 = 4–10 thalli in the plot; 3 = more than 10 thalli but less than 50% of all available branches and stems host the species; 4 = more than 50% of available branches and stems hosting the species. USDA Forest Service field crews with lichen training sampled FIA plots, whereas HTR and SJ sampled supplemental plots. The FIA protocol provides consistent results among observers for the purposes of detecting broad-scale gradients (McCune et al. 1997b). Voucher specimens for FIA plots were deposited in the Oregon State University Herbarium (osc). Nomenclature follows Esslinger (2019) except for cetrarioid lichens which follows Divakar et al. (2017).

Twenty-eight sites had no recorded lichen abundance. Using Google Earth to check each site yielded no consistent explanation for the absence of epiphytic macrolichens. Three sites likely burned not long before sampling. Three high-elevation sites were on the edge of tree line. The residual 14 sites were shrub steppe, presumably in areas close to the
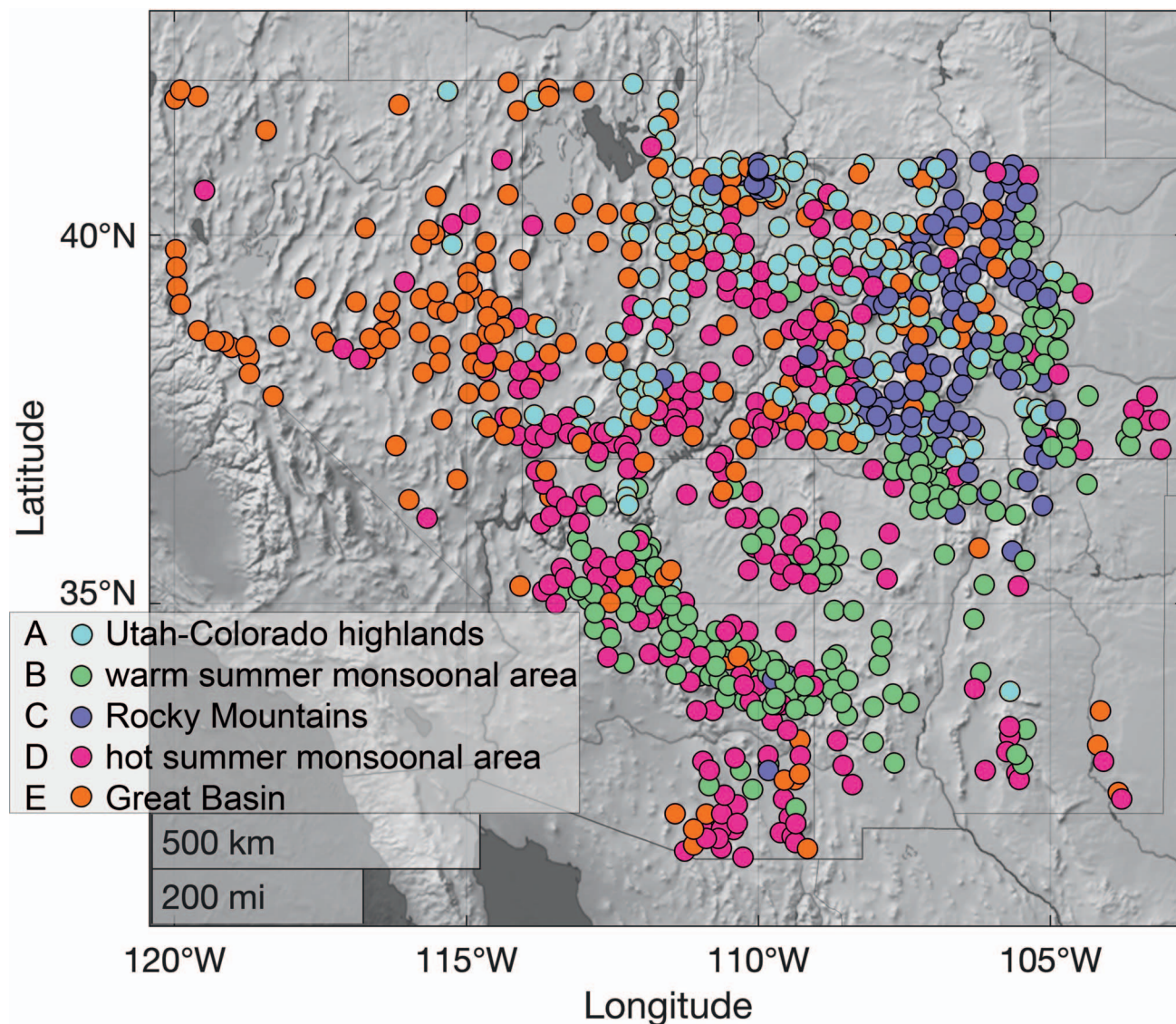
Figure 1. Lichen community plots in the five-state region (Nevada, Utah, Colorado, Arizona and New Mexico), color coded by lichen community groups as defined by cluster analysis. See Table 3 for group characteristics.

10% cover criterion for forests. No empty sites were removed because the absence or scarcity of lichens was considered an important component of lichen response to climate in the Southwest. Retaining empty sites had the consequence that we could not use proportional community distance measures (e.g., Sørensen or Jaccard), because the latter are undefined when no species are present. We preferred Euclidean distance for this data because it retains the signal of overall lichen abundance, which we regarded as informative for lichen community – climate relationships in a region where lichens vary from sparse or absent to abundant.

Site variables. The corresponding matrix of site variables (1215 sites × 21 site variables) contained geographic coordinates, elevation, slope, aspect, survey date, heat load and potential direct incident radiation (PDIR). We calculated heat load and PDIR from slope, aspect and latitude with a multidimensional kernel smoother (McCune 2007) applied to data from Buffo et al. (1972). We also added climate variables to the site matrix as described below. Maps were generated with Matlab R2019b (MathWorks 2019) and ArcMap 10.8.1.

Thirty-year averages (1981–2010) of 246 climate variables for all 1215 sites were extracted with Parameter-elevation Regressions on Independent

Table 1. Interpretation of the first six axes from principal components analysis of a matrix of 1215 sites $\times$ 114 climate variables. The interpretation of main climate gradients was based on variables correlated most strongly with each axis. Strength of relationship to lichen community gradients is given by the cross-validated R^2 ($\times R^2$) for a nonlinear response surface of PCA axis scores regressed against lichen communities as expressed by the combination of NMS axes 1 and 2, the response surface built with a kernel smoother, illustrated in Fig. 5.

PCA Axis	% Variance	Interpretation	$\times R^2$ with lichens
1	60	Hot vs. cold	0.404
2	14	Hot/dry vs. humid	0.045
3	11	Summer rain vs. continentality	0.113
4	4	Precip mostly in winter vs. year round	0.022
5	4	Rainier vs. drier/snowier	0.110
6	2	High continentality with summer rain	0.020
Total	95		

Slopes Model (PRISM) data using ClimateWNA software version 5.21 (Hamann et al. 2013). These variables included original monthly, seasonal and annual values for precipitation, temperature and radiation with some additional derived variables such as heat-moisture indices (**Supplementary Table S1**).

Air quality data. We downloaded grids of interpolated estimates (NADP 2020) for total annual nitrogen and sulphur deposition (wet+dry, kg/ha, 2000–2018), then assigned averages to each FIA plot based on these grids using ArcGIS 10.7.1. This time period corresponds with the lichen data collection period. We chose to analyze first the long-term averages because a lichen community at a given time integrates environmental conditions across multiple years. If long-term averages indicated a pattern, then we could refine the temporal signal by analyzing individual years. We then extracted point estimates for each plot as spreadsheets and combined these with the community and climate data.

Data analysis. We adopted a general strategy of nonparametric data mining and pattern recognition methods, rather than forcing the data into linear models. One exception to this was our choice of principal components analysis for creating synthetic variables to summarize a large number of climate variables. Scatterplots of climate variables relative to each other showed many relationships that could be reasonably approximated as linear. In contrast, biological community data are known to depart strongly from multivariate normality (McCune &

Root 2015) and nonlinear, interactive relationships between species performance and environment are more the rule than the exception (McCune 2006). Multivariate statistical analysis of climate and lichen data were performed with PC-ORD v. 7.07 (McCune & Mefford 2018).

Principal Components Analysis (PCA) was chosen to reduce the number of climate variables and orthogonalize them without losing appreciable information. We calculated precipitation as rain (PAR) for seasons and year by subtracting precipitation as snow (PAS) from total precipitation (MAT or PPT; **Table S1**). Two climate variables (DD_0_7, DD_0_8) were deleted because all site values were zero. Because PCA extracts a common signal from the linear relationships among variables, we checked variables for normality and linear relationships. Temperature variables had skewness <1. Because precipitation variables have somewhat higher skewness (1–2) than ideal for PCA, we also included the original annual and seasonal precipitation variables in the final environmental matrix.

After adjusting the climate matrix as described above, we performed standardized PCA on the resulting matrix of 1215 sites by 114 climate variables (**Supplementary Table S1**). We determined the number of axes with stronger covariation than expected by a randomization test with 999 randomizations, applying "Rnd-lambda" as a stopping rule (Peres-Neto et al. 2005). The stopping rule indicated six interpretable axes. We added the site scores from each of the first six PCA axes to the site matrix as six synthetic climate variables (labeled "PcaAxn" where *n* is the axis number). We based the interpretation of these axes (**Table 1**) on those climate variables with relatively strong correlation coefficients for each axis.

We then augmented the site matrix with climate variables, including the six PCA axes and 35 climate variables (various expressions of annual plus seasonal precipitation). While the PCA climate axes are redundant with the raw climate variables, we included the latter to aid interpretation and communication of climate relationships.

Large, heterogeneous ecological community data sets are often made manageable with cluster analysis. We used hierarchical agglomerative cluster analysis with Euclidean distance and Ward's linkage method (Ward 1963) to cluster sites in lichen species space, seeking groups that would be useful

for interpreting the variation in lichen communities. To decide how many groups to keep, we evaluated group separation in species space with Indicator Species Analysis (ISA; Dufrêne & Legendre 1997) and multi-response permutation procedures (MRPP; Mielke & Berry 2001), comparing results for 3–6 groups (**Supplementary Table S3**). We added variables representing group memberships to the site matrix.

In addition to classifying lichen communities into groups, we extracted continuous gradients of lichen community composition with nonmetric multidimensional scaling (NMS; Kruskal 1964). The large, heterogeneous data matrix proved challenging for ordination; we therefore provide details of how we arrived at the final ordination. We compared five NMS ordinations settings, all using Euclidean distance and no tie penalty (except setting #5 in online **Supplementary Table S4**). Because the quick and medium thoroughness ordinations (#1 and #2) were virtually identical (three-axis solution, low final stress, good final fit, high correspondence between them, based on correlations between interpoint distances with standardized Mantel statistic, $r = 0.99$), we chose the quick option for the last three ordinations, a convenience given the large sample size. We also used the standardized Mantel statistic to compare final configurations of the first ordination and each of the other four, based on all interpoint Euclidean distances in the ordination space. NMS settings 1, 2, 3 and 5 showed very little difference in final stress or fit (**Supplementary Table S4**). Setting 4 (transform abundance to presence/absence) did lower final stress but we decided to use the first ordination to retain quantitative species information.

NMS on Sørensen distances based on a data matrix with empty sites removed yielded unusable results. With no tie penalization the final stress was very low (e.g., 3) but could not beat the randomization test, which frequently gave zero stress for randomized data sets. If tie penalization was used the final solutions were highly unstable and with high stress (e.g., 41). We believe that this resulted from the large number of sites with only one or two species present. This supported our original decision to use Euclidean distance and retain the empty and near-empty sites as ecologically meaningful. We thus chose Euclidean distance, no tie penalization, and retention of all species as the final ordination.

For multiple regression applications we used nonparametric multiplicative regression (NPMR), a method that assumes no particular functional form and automatically models interactions among predictors (McCune 2006). The method is based on a multiplicative kernel smoother, is fully nonparametric, and approximates the maximum likelihood solution, subject to penalization by leave-one-out cross validation in the model selection process. For continuous response variables (e.g., ordination axis scores) in relation to climate, we used a local linear model, Gaussian kernel and the "medium" setting for overfitting controls in the software HyperNiche v. 2.30 (McCune & Mefford 2009). Model fit was expressed with the cross-validated coefficient of determination ($\times R^2$, equivalent to a traditional R^2 but penalized with leave-one-out cross validation). For binary response variables (contrasts in climate between one community group and another), we used a local mean model, Gaussian kernel and medium setting for overfitting controls. In this case, fit was expressed as $\log B$, the log-likelihood ratio comparing a particular fitted model with a null model of equal probabilities of occurrence of a particular group at all points in the predictor space as defined by climate variables.

We regressed species richness against two separate sets of predictors with NPMR: (1) geographic coordinates (latitude, longitude, elevation) and (2) a pool of 87 climatic variables, including the first six principal components of the original climatic variables. To give equal emphasis to each lichen community group and to expedite model selection, we took a balanced stratified random sample of 60 plots from each of the 5 community groups for a total sample size of 300 plots. NPMR models were fit with a local mean and Gaussian kernel and leave-one-out cross validation during both the model fitting and evaluation phases. For model selection we used the aggressive setting for the overfitting option in HyperNiche 2.30. We express model fit as cross-validated coefficients of determination ($\times R^2$). We used a similar approach to model overall richness in relation to geographic variables, but with a larger stratified random sample of 180 on-frame plots per community group ($n = 900$), this larger sample size enhancing detail for mapping.

Because species richness of particular functional groups can be more predictable than overall species

richness, we also built models for individual functional groups against climate and geographic variables. We expressed richness within a functional group in two ways: absolute number of species present in that group and relative richness, calculated as the proportion of species assigned to a particular group. Expressing proportional richness is impossible for plots with no species, so we excluded empty plots from the regression analysis of species richness.

We originally defined six functional groups, but two groups were dropped because of no representation (tripartite cephalodiate lichens), and low numbers (0, 1, or 2 "cladonioid"), leaving four functional groups: cyanobacterial lichens (cyano), forage lichens, including pendulous hairlike species (forage), nitrophiles (affinity for high levels of nitrogen enrichment), and fruticose lichens with a shrubby growth form (shrubby).

RESULTS AND DISCUSSION

Despite the sparse species matrix and the uneven distribution of FIA sites (reflecting the uneven distribution of forests) across five large states, ordination and cluster analysis found clear patterns of lichen communities related to climatic gradients. We examine these relationships by first describing the lichen communities (clusters and diversity), then relating variation in lichen communities to climate. Because the complexity of the community-climate relationships prevented a simple one or two-dimensional summary, we then break down the problem by contrasting the climates of particular pairs of lichen community groups. We then present models relating richness within functional groups and overall species richness against climate.

Lichen community groups. From cluster analysis of plots in lichen species space we chose the 5-group level, at which 21% of information remained with 0.28% chaining. MRPP confirmed that the five community groups differed in environmental space ($A = 0.127$, $p << 0.001$; environmental variables relativized by standard deviates. The 4-group level from cluster analysis had the highest observed sum of maximum indicator values (i.e., maximizing species separation among groups), while the 5-group level had the lowest MRPP test statistic, T (lower values with stronger group differences;

Supplementary Table S3). We chose to use five groups because, from a geographical perspective, the extra group split the drier southern Arizona sites from the Nevada basin and range sites (**Fig. 1**).). The resulting five groups we name by their association with geographic regions: Utah-Colorado highlands, warm summer monsoonal area, Rocky Mountains, hot summer monsoonal area, and Great Basin (**Fig. 1**). Note that despite the geographic names, these groups are defined by lichen community similarity, not by geographic proximity, so that topographically complex areas contain more than one lichen community group.

The five lichen community groups (**Table 2**), clearly reflected the topography and climate of the Southwest region (**Figs. 1, 2**). As shown below, the groups were strongly related to the same climate gradients seen in the NMS axes: the temperature and elevation gradient, overall moisture, and summer rain. Lichen abundance was highest in the wettest groups (warm summer monsoonal area and Rocky Mountains) and lowest in the hottest and driest groups (hot summer monsoonal area and Great Basin).

Warm summer monsoonal climate provided habitat for the greatest number of lichen species across all plots ($\gamma = 120$, **Table 2**) and within plots ($\alpha = 8.9$). In contrast, hot summer monsoonal climates were less diverse across all plots ($\gamma = 109$) and had only half the within-plot richness ($\alpha = 4.9$). Hot, dry climates had the greatest variation in species composition among plots ($\beta_D = 2.8$), but the fewest species within each plot ($\alpha = 2.6$) and across all plots ($\gamma = 56$). The coldest Rocky Mountain group and cool highlands with precipitation as both rain and snow show the most consistent lichen communities ($\beta = 1.14$ and 1.0, respectively). We would expect climatic regimes with fairly consistent lichen communities to be the easiest in which to detect air quality gradients.

Indicator species contrasted the five community groups by evaluating faithfulness and exclusivity of species to particular groups. The number of significant indicator species was 66 versus 1.6 expected by chance alone, given $\alpha = 0.01$ for H_0: IVmax no higher than expected by chance, i.e. no difference in indicator value between groups, where IVmax is the largest indicator value (IV) for a given species. **Table 3** contains those species with indicator values over 15 for all groups except the

Table 2. Lichen community group characteristics for epiphytic macrolichens in the Four Corners region. See Fig. 1 for map. Diversity statistics are given for the whole data set and for plots broken down by community groups. The five groups are clusters of sites in species space resulting from hierarchical agglomerative cluster analysis. For each group we summarize climatic characteristics, geographic distribution, lichen abundance, and diversity; α is average epiphytic macrolichen species richness per plot, β_D is beta diversity measured in half changes, γ is the total number of species in that subset of the data; "Temp" is temperature, SHM is the summer heat moisture index. Beta diversity calculations were based on matrices excluding empty plots. The remaining statistics include the 28 empty plots (with no epiphytic macrolichens). Lichen functional group richness is shown for 10th percentile, median, and 90th percentile for each group (cyano = cyanolichens, forage = pendulous fruticose, shrubby = shrub form fruticose).

Group	n	α	β_D	γ	Temp	Precip	Summer rain	Main location of sites	Functional group richness (10th-median-50th %ile) all	cyano	forage	nitrophile	shrubby	other
A	230	6.8	1.00	68	cool	rain and snow	some	Utah-Colorado highlands	4-6-10	0-0-0	0-0-0	2-4-7	0-0-1	1-2-3
B	243	8.9	1.27	120	warm	summer rain	high	warm summer monsoon	6-8-13	0-0-1	0-0-1	1-4-6	1-1-3	2-3-5
C	194	9.4	1.14	109	coldest	highest; rain and snow	high lowest SHM	Rocky Mountains	5-9-15	0-0-0	0-1-2	1-3-6	1-1-3	1-3-6
D	313	4.9	1.73	91	hottest	driest	little high SHM high proportion	scattered lowlands, hot summer monsoon	2-5-7	0-0-0	0-0-0	1-3-5	0-0-1	0-1-3
E	235	2.6	2.81	56	hot	dry	lowest high SHM	Great Basin	0-2-5	0-0-0	0-0-0	0-1-3	0-0-1	0-0-2
Overall	1215	6.3	2.0	162					2-6-11	0-0-0	0-0-1	1-3-6	0-0-2	0-2-4

Great Basin, showing and the top four indicator species. To be a good indicator, according to the ISA method, a species must be both faithfully present and rather exclusive to a particular group. The Utah-Colorado highlands top indicator species was *Melanohalea elegantula,* but this widespread species was also found in all other groups (high faithfulness but rather low exclusiveness). The warm summer monsoonal area top indicator species were *Flavopunctelia soredica* and *Usnea hirta. Usnea lapponica* and *Melanohalea exasperatula* were particularly good indicator species for the Rocky Mountains, because they were found in a third of sites in this group and were infrequent in other groups. The hot summer monsoonal area had no strong indicator species because those with the highest indicator values were also common in other groups. The Great Basin had no good indicator species because it had such low lichen abundance.

Lichen diversity. The species matrix was very sparse with a small number of relatively abundant species and high heterogeneity among plots. Excluding empty plots, the community matrix was 96.0% zeros with Whittaker's beta diversity $\beta_w = 24.0$ and plots had an averaging $\beta_D = 2.0$ half changes between plots (equations in McCune &

Grace 2002, p. 31). The dust bunny index was 97%, indicating extreme departure from multivariate normality (McCune & Root 2015). Out of 162 species and 1215 sites, just 25 species were found in more than 5% of sites. In contrast, the most common species in our data, *Xanthomendoza montana,* was found at 60% of sites. Only 53% of sites had more than five lichen species and only 11% had more than 10 lichen species. Higher lichen abundance was strongly linked to relatively cool and moist sites. We address climatic factors associated with richness of particular groups after description of the climatic gradients.

Frequency distributions of number of species per plot revealed strong differences in lichen diversity among lichen community groups (**Fig. 3**). With peaks separated by approximately two additional species per plot, species richness increased in the following order: E – Great Basin, D – hot summer monsoonal area, A – Utah-Colorado highlands, B – warm summer monsoonal area, and C – Rocky Mountains.

Climatic gradients. Gradients in lichen community composition were clearly related to climate (**Fig. 4**). The final NMS ordination explained 83% of the variation in the community data with three
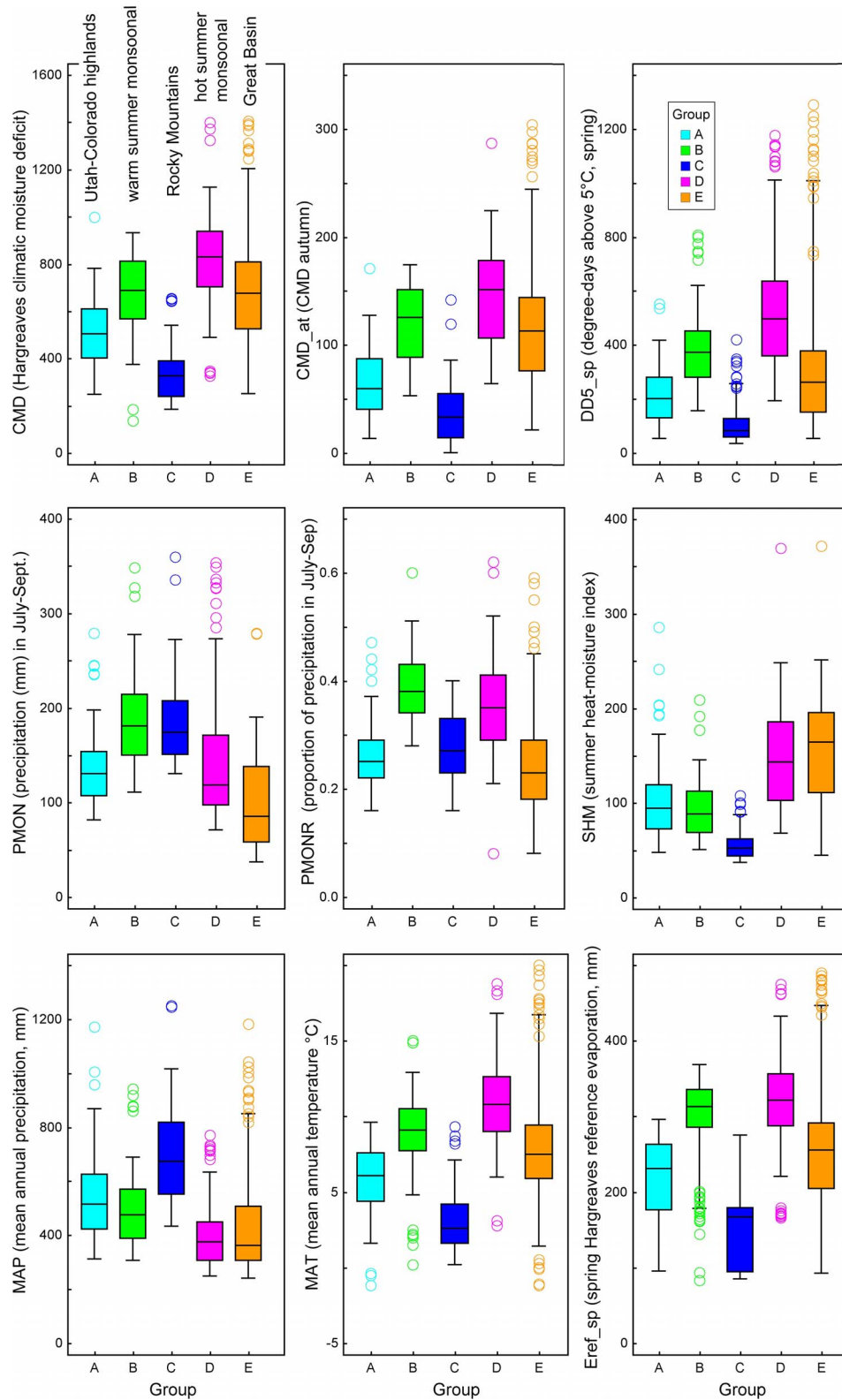
Figure 2. Boxplots of key climate variables vs. lichen community groups. See **Table 3** for summary of group characteristics. Boxes show interquartile range with median; whiskers show 5th and 95th percentiles, and circles are outliers falling more than 1.5× the interquartile range beyond the boxes.

Table 3. Top indicator species for each group of plots, in descending order of IVmax within groups. For groups A–D, indicator values (IV) over 15 are in boldface. For group E, the top four indicator values are in boldface. "IVavg" is the average indicator across the five groups; "IVmax" is the maximum indicator value of the species across the five groups; "Group" specifies the group with IVmax; "Abund" is the summation of each species' abundance classes (0–4) across all sites.

Acronym	Species	# Plots	IV avg	IV max	Group	IV by Group					Abund
						A	B	C	D	E	
Melele	*Melanohalea elegantula*	354	9	34	A	**34**	2	5	1	5	999
Xanmon	*Xanthomendoza montana*	730	15	31	A	**31**	10	**23**	6	2	2080
Phybiz	*Physcia biziana*	516	11	20	A	**20**	**18**	8	8	0	1454
Xanful	*Xanthomendoza fulva*	142	4	11	A	**11**	0	1	0	**8**	404
Xangal	*Xanthomendoza galericulata*	112	4	15	A	**15**	0	0	1	4	308
Usnhir	*Usnea hirta*	339	12	53	B	1	**53**	7	1	0	895
Fpusor	*Flavopunctelia soredica*	363	10	40	B	1	**40**	3	9	0	948
Xanfal	*Xanthomendoza fallax*	464	11	27	B	3	**27**	1	**23**	0	1202
Melsol	*Melanohalea subolivacea*	713	14	26	B	**22**	**26**	14	9	0	2063
Cetfen	*Nephromopsis fendleri*	96	5	21	B	0	**21**	2	0	0	276
Usnlap	*Usnea lapponica*	235	13	64	C	1	2	**64**	0	0	658
Melexl	*Melanohalea exasperatula*	296	14	62	C	7	0	**62**	0	0	873
Bryfus	*Bryoria fuscescens*	109	8	38	C	0	1	**38**	0	0	252
Phyads	*Physcia adscendens*	427	13	34	C	**29**	2	**34**	0	0	1177
Popamb	*Parmeliopsis ambigua*	66	4	21	C	0	0	**21**	0	0	168
Phacil	*Phaeophyscia ciliata*	71	4	18	C	0	1	**18**	0	0	195
Phyaip	*Physcia aipolia*	129	4	15	C	0	7	**15**	0	0	348
Phydim	*Physcia dimidiata*	416	8	20	D	6	7	0	**20**	**8**	1068
Letcol	*Letharia columbiana*	23	2	9	E	0	0	0	0	**9**	54
Letvul	*Letharia vulpina*	32	2	8	E	0	0	0	0	**8**	64

axes and a final stress of 14.5 (**Table 4**). Removing rare species or using presence/absence transformations made little difference in the results. In general, linear combinations of the climate variables extracted by PCA had nonlinear relationships with lichen community gradients as expressed by NMS ordination (**Fig. 5**). The first NMS axis was strongly related to PCA axis 1 (temperature, cross-validated coefficient of determination $\times R^2 = 0.404$); two of the remaining five climate PCA axes had moderate relationships with NMS axes (**Tables 1, 4, Figs. 4–5**). All of the relationships between PCA axes and NMS axes were strongly nonlinear (**Fig. 5**). Many temperature-related climate variables, the components of PCA axis 1, were strongly related to the first NMS community axis, with more than 10 variables having a correlation coefficient stronger than ±0.6 with axis 1.

Groups from cluster analysis of lichen communities were strongly structured in the NMS ordination space (**Fig. 4**). Axis 1 clearly separated the Rocky Mountains as the lichen communities associated with the coolest climates, then the

Utah-Colorado highlands as the next coolest, followed by the remaining groups all falling on the warm extreme of axis 1. Although the linear fits between NMS axis 1 and temperature variables were reasonably strong, a nonlinear response surface had an even stronger relationship between temperature variables and NMS axis 1, in addition to revealing
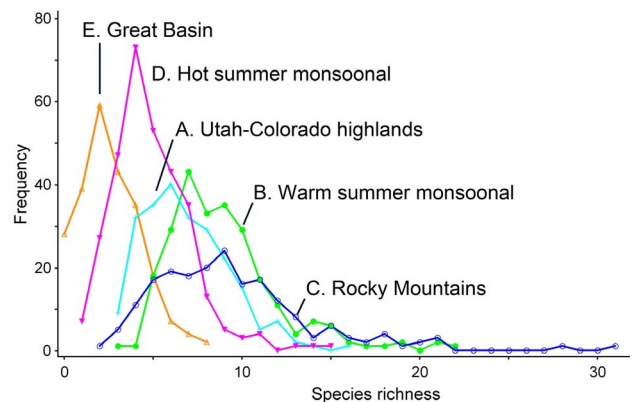

Figure 3. Frequency distribution of number of species per plot for each of the five lichen community groups. See Figure 1 for map and Table 2 for sample sizes and interpretation.
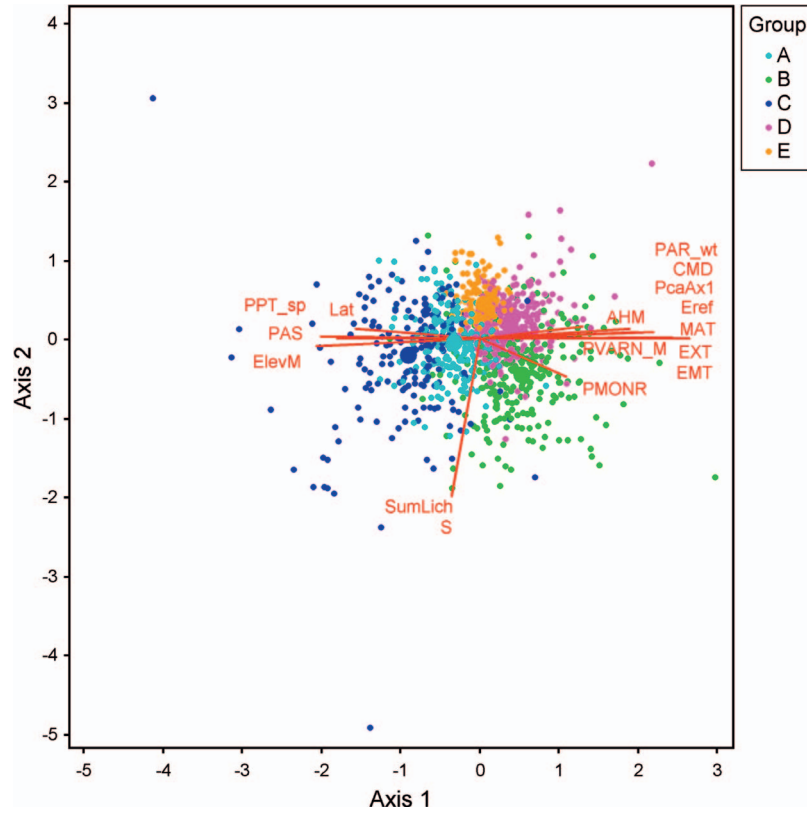
Figure 4. Ordination of plots in epiphytic macrolichen species space with nonmetric multidimensional scaling (NMS) axes 1 and 2. Each point represents a site color coded by lichen community group (Table 3). Geographic, climatic, and diversity variables are overlaid with a joint plot. AHM = annual heat-moisture index, CMD = Hargreaves climatic moisture deficit, ElevM = elevation, EMT = ,Eref = , EXT = extreme maximum temperature, Lat = latitude, MAT = mean annual temperature, PAR_wt = precipitation as rain in winter, PAS = precipitation as snow, PcaAx1 = climate PCA axis 1, PMONR = proportion of precipitation in July through September, PPT_sp = spring precipitation; PVARN_M = (see more details in **Table S1**). S = lichen species richness; SumLich = sum of lichen abundance classes. This traditional linear overlay of environmental variables on community ordinations has shortcomings because strong nonlinear relationships (Fig. 6, 7) are not captured well, particularly for axis 2. We show it here to help make that point.
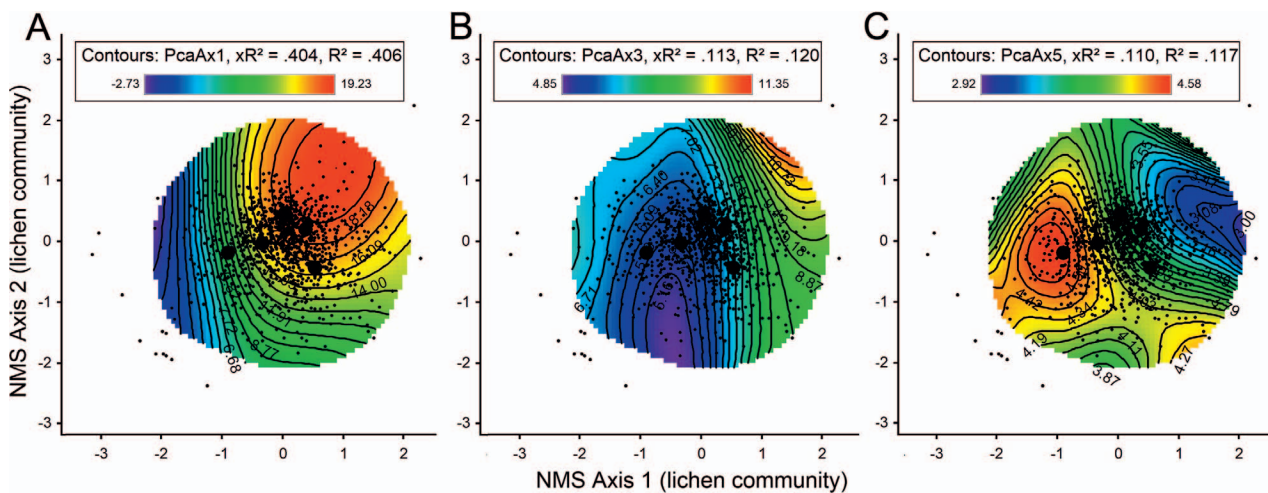

Figure 5. Nonlinear relationships of lichen communities to climate variables as shown by surface fitting of PCA climate scores on axes 1 and 2 from nonmetric multidimensional scaling (NMS) of lichen community gradients. Surfaces were fit with a multiplicative kernel smoother with bandwidth optimized by cross-validation. Areas beyond the central, roughly circular fitted surface had too few points to meet our criteria for the minimum amount of data needed to make an estimate. Only the three PCA axes having the strongest relationship with the lichen communities are shown. **A.** PCA climate axis 1 contours overlaid on NMS community axes 1 and 2. Points are plots in lichen community space. **B.** Same for PCA axis 3. **C.** Same for PCA axis 5.

Table 4. Nonmetric multidimensional scaling (NMS) axis summary with interpretation. The ordination was based on Euclidean distances among sites in species space, no tie penalty; final stress = 14.5, final instability = 0.00048, nonmetric fit $R^2n = 0.98$ for three axes combined. See Table 1 for interpretation of PCA axes.

NMS Axis	Lichen community variance represented (metric R^2m)	Strongest correlated PCA climate axis	Description
1	0.46	PcaAx1	Temperature/elevation gradient
2	0.22	PcaAx5	Lichen abundance/diversity, overall moisture throughout year
3	0.15	PcaAx3	Continentality versus summer rain
Total	0.83		

an interaction with NMS axis 2 (see PCA axis 1 overlay in **Fig. 5**). In any case, the relationship of lichen communities with temperature successfully separated two of the five groups from the remaining groups.

The remaining three groups separate from each other on NMS axis 2, but strikingly, none of the many climate variables showed a strong linear relationship to axis 2. The only variables strongly related to axis 2 were those describing the abundance and diversity of lichens, with species richness and sum of abundance classes both decreasing strongly with axis 2. This piqued our interest in NMS axis 2 even more: what factors drive the strongest gradient in lichen diversity and abundance in southwestern U.S.A.? Remarkably, none of the 96 climate variables provided a strong relationship with the lichen community gradient represented by NMS axis 2.

Several explanations for the lack of apparent climate relationships to this major regional lichen community gradient are possible: (1) The differences among the warm community groups (B, D and E) are not related to current climatic differences, but instead are driven by other factors such as bedrock, historical climates, air quality, or disturbance history; (2) the measured climatic variables inadequately characterize climate as perceived by lichens, and (3) the community gradients have nonlinear relationships with combinations of climate variables, rather than having strong linear relationships with any single variable, including those derivative climate variables meant to have direct biological relevance. Although the three explanations are not mutually exclusive, the third seemed most promising and relatively easy to address.

Contrasts among warm community groups. To explore the third explanation, we sought models for specific contrasts among the three groups that

separated on axis 2: warm summer monsoonal, hot summer monsoonal, and Great Basin (groups B, D and E). This is the main axis for lichen abundance and richness, so understanding this axis is the key to explaining why more lichens are found in some places than others. We chose a modeling framework that automatically detects interactions and nonlinear relationships, nonparametric multiplicative regression (NPMR). We built models for three specific contrasts: (1) NMS axis 2 scores for only the warmer climate groups B, D and E in relationship to climate; (2) warm vs. hot summer monsoonal groups, because both of these appear in regions thought to have a summer monsoonal climate, with hot summer group D more restricted to southern Arizona and New Mexico and the warm summer group B overlapping with Group D, but wrapping across the southern Rocky Mountains and up the east front of the Rockies; and (3) hot summer monsoonal (group D) vs. Great Basin (group E), hypothesizing that this contrast separates hot summer monsoonal climates from areas with hot but proportionately drier summers toward the western border of the study area. This contrast is a fundamental concept in characterizations of the climate of Arizona and New Mexico (Adams & Comrie 1997). Each of these specific contrasts is presented below.

1. Warmer climate groups. NMS axis two separated the lichen community groups associated with warmer climates but no climate variables had a strong, simple linear relationship to that axis ($r < 0.2$ for each of 97 climate variables). Much stronger relationships (cross validated fit, $\times R^2 = 0.427$) were revealed with nonparametric regression of NMS axis 2 scores against climate for only the warmer climate groups (B, D, and E; 791 plots). PMON (July–September precipitation) and DD5_sp (growing degree days in spring) were the strongest predictors
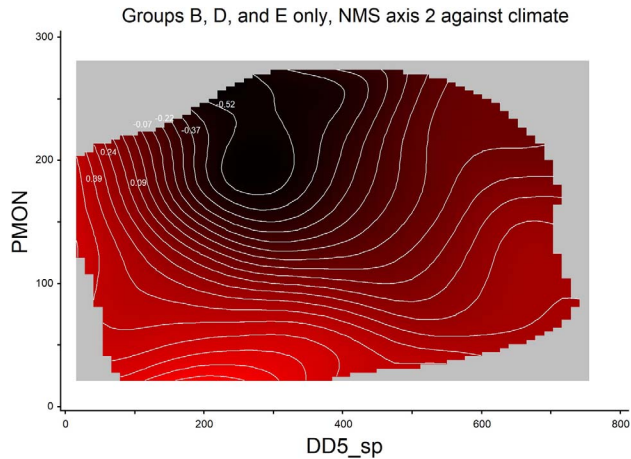
Figure 6. Nonparametric regression response surface of lichen community NMS axis 2 scores against climate for only groups: warm summer monsoonal area (B), hot summer monsoonal area (D), and Great Basin (E). PMON (July–September precipitation, mm) and DD5_sp (growing degree days in spring); cross-validated fit $\times R^2 = 0.427$, N = 791 plots. Darker shading (negative values on contours) indicates lower NMS axis 2 scores, while brighter red shading and positive contours indicate plots falling above the centroid of the community gradient. Gray shaded areas did not meet the criterion for minimum data to make an estimate.

with Axis 2 scores highest with low summer precipitation but only with intermediate values of DD5_sp (**Fig. 6**). Plots with low summer precipitation but either high or low growing degree days in spring had axis 2 scores near the centroid (i.e., neither low nor high). This two-predictor model provided substantially stronger results than the best single-predictor model ($\times R^2 = .195$ for PMON). Adding a third predictor provided only slightly better fit ($\times R^2 = 0.454$ vs. 0.427 for the 2-predictor model).

2. Warm vs. hot monsoonal. Nonparametric regression contrasting membership in warm vs. hot monsoonal lichen community groups (B vs. D) revealed a strong nonlinear pattern (**Fig. 7**) with hot monsoonal lichen communities much more likely to occur in areas with either high levels of autumn climatic moisture deficit (CMD_at) or high summer heat moisture index (SHM), with strong fit (cross-validated log likelihood ratio, log$B = 50.3$). Both groups have relatively high summer precipitation and are thus considered monsoonal, but we interpret group D as having the relatively hot monsoonal pattern, with moisture at least partly derived from the Pacific Ocean and Gulf of California, while group B has a cooler monsoonal
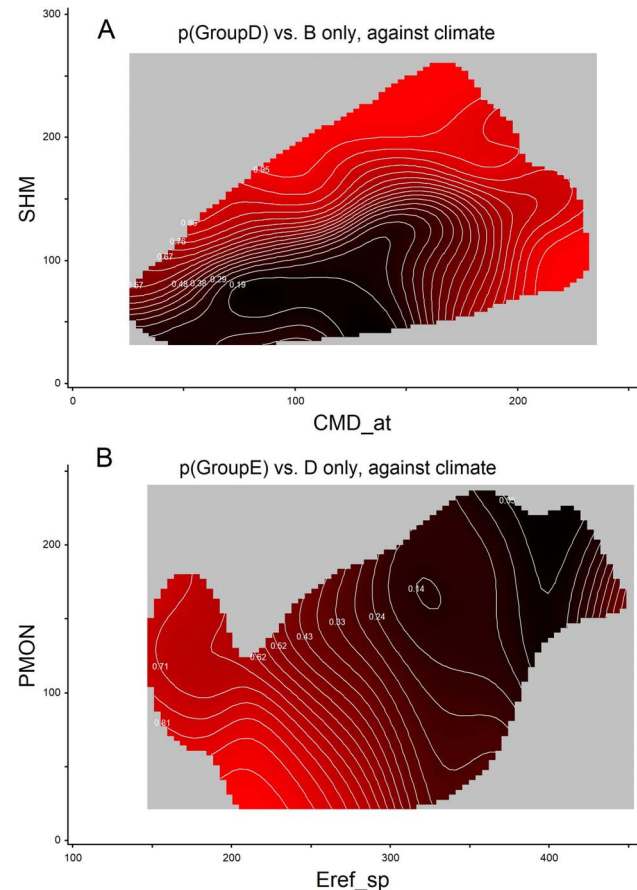

Figure 7. Pairwise contrasts between specific lichen community groups. Response surfaces are based on nonparametric regression of probability of group membership against climate variables. **A.** Contours of probability of membership in lichen community group D (hot monsoonal) versus group B (warm monsoonal). Darker shading indicates lower probability of group membership while redder shading indicates higher probability of group membership. The strongest predictors were SHM (summer heat moisture index) and CMD_at (autumn climatic moisture deficit); cross-validated log likelihood ratio, log$B = 50.3$. **B.** Contours of probability of membership in lichen community group E (Great Basin) versus group D (hot monsoonal). The strongest predictors were PMON (July–September precipitation, mm) and Eref_sp (spring Hargreaves reference evaporation, mm); cross-validated log likelihood ratio, log$B = 45.0$.

pattern with moisture derived more from the Gulf of Mexico.

Spatially, the monsoonal precipitation pattern is best expressed in lichen communities as an arc from the east front of the Rocky Mountains extending south through New Mexico to southwestern Arizona (**Fig. 1**, groups B and D). *Flavopunctelia soredica* and *Usnea hirta* may be good indicators of an area with summer monsoons caused by incursions of moisture from the Gulf of Mexico. However, many of the

most interesting species groups associated with this monsoonal pattern, such as *Sticta* species, were too rare to be detected in our data, despite the large number of plots. For example, although Weber (1963) did not explicitly define a monsoonal element to the biota, he listed the following species as "pansubtropical", which we interpret as monsoonal associates. For each we have added parenthetically our reassignment in the current taxonomy and the number of occurrences in our data:

Anaptychia diademata (Heterodermia rugulosa, 21, hot monsoonal, group D)
Anaptychia neoleucomelaena (Heterodermia leucomela ssp. *boryi*, 0)
Coccocarpia cronia (C. palmicola, 0, mainly saxicolous)
Leptogium hildenbrandii var. furfuraceum (L. pseudofurfuraceum?, 54, warm monsoonal, group B)
Physcia setosa (Phaeophyscia hispidula, 28, warm monsoonal, group B)
Ramalina sinensis (43, Rocky Mountain, group C)
Sticta weigelii (0)

Although three of these species were identified as statistically significant indicators, none was frequent enough to be among the best indicators, when filtered by strict criteria (**Table 3**). Indicator species analysis considers the best indicators to be both faithful (always occurring in a particular group), and exclusive (occurrences concentrated in a particular group). Because infrequent species are never faithful, the method does not highlight them as strong indicators.

A more revealing result was obtained by plotting group fidelity against exclusivity, the two components of Dufrêne & Legendre (1997) indicator values (**Fig. 8**). Many of the characteristic monsoonal species showed rather low frequency but high exclusiveness. In other words, these species seldom occurred in other groups, but they are relatively infrequent even in their preferred group, perhaps because of microhabitat restrictions or historical disturbance events. In the warm monsoonal group B, this included *Cetraria fendleri, Enchylium conglomeratum, Leptogium pseudofurfuraceum, Leptogium milligranum, Parmelia barrenoae, Usnea intermedia*, and *Usnea parvula*. In the hotter, drier monsoonal group D, this included *Flavopunctelia darrowii, Heterodermia rugulosa, Heterodermia trop-*

ica, Physciella nepalensis, and *Punctelia hypoleucites* (**Fig. 8**). The presence of numerous species with high exclusivity but low fidelity in the monsoonal groups is also expressed in the high beta diversity of those groups (**Table 2**).

The monsoonal pattern does not occupy a discrete geographic area, but instead forms a gradient, strongest in the southern part of our study area, diminishing to the north and west (see groups B and D in **Fig. 1**). Even as far north as Utah the pattern persists, albeit in weakened form, and this is expressed in various components of the biota, including vascular plants. For example, Neilson & Wullstein (1983, 1986) found that the loss of sexual reproductive capacity *Quercus gambelii* in northern Utah results from the transition out of the monsoonal precipitation pattern, the existing populations being relicts from earlier climates. Similar subtle examples can be expected for lichens in mesic microsites in the mountains of Utah, but at present our data are insufficient to show that. The Uinta Mountains of northeastern Utah host plots in four of the five community groups, supporting the hypothesis that the Uinta Mountains are a key transitional area for monsoons (Shaw & Long 2007).

From the perspective of lichen distribution, the Arizona monsoonal pattern smoothly transitions from the mountains of southern Arizona and New Mexico, up the east front of the Rocky Mountains as far north as Montana and out onto the Great Plains. Climatically this transition is from moisture deriving from the Pacific Ocean and Gulf of California (the Arizona-Mexican monsoon) to moisture from the Gulf of Mexico. This transition appears to cross the Continental Divide seamlessly. Thus, many of the monsoonal lichen associates also occur up the East Front of the Rockies, including several of the species highlighted as indicators of the warm monsoonal group B, such as *Flavopunctelia soredica, Imshaugia placorodia, Usnea hirta*, and *Xanthoria fallax*. All of those species are rather common through eastern Colorado, Wyoming, and eastern Montana.

3. Hot monsoonal vs. Great Basin. A nonparametric regression contrasting membership in Great Basin and hot monsoonal lichen community groups revealed a strong nonlinear pattern (**Fig. 7**, lower panel) with Great Basin lichen communities much more likely to occur in areas with *both* low levels of summer moisture (PMON, Jul–Sept) and low spring
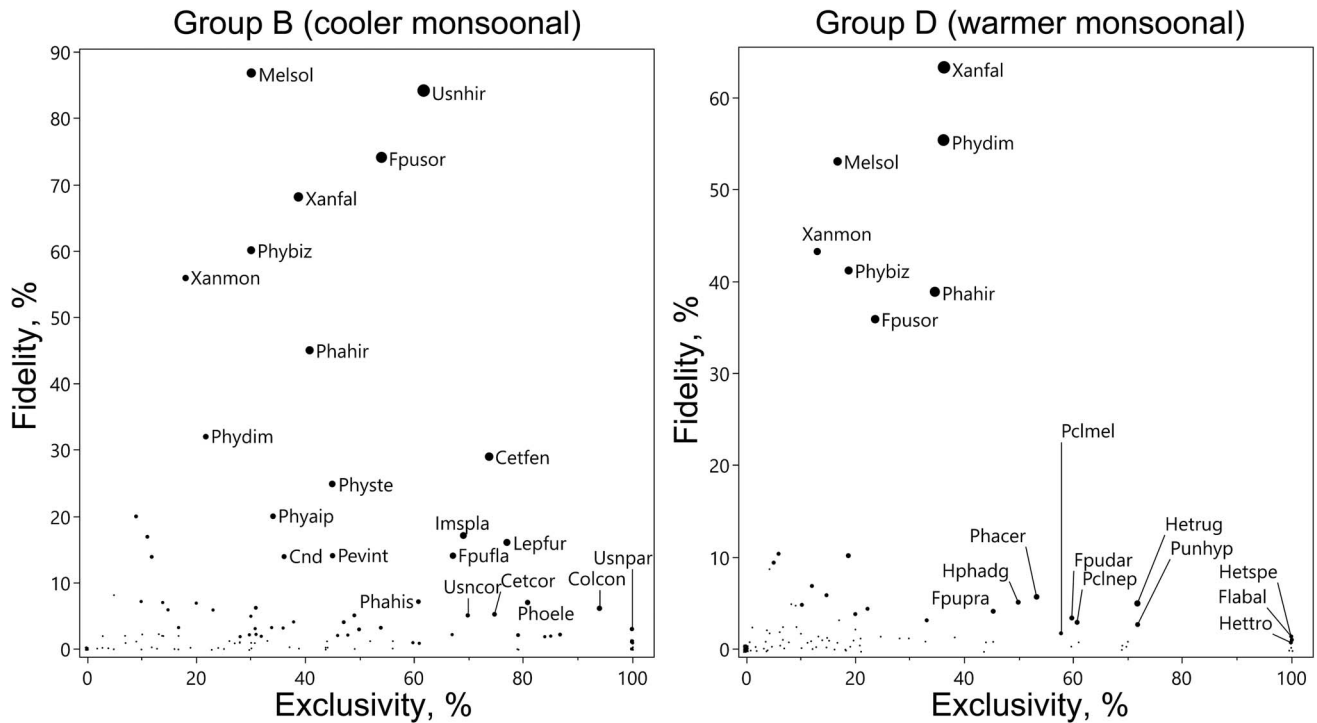
Figure 8. Epiphytic macrolichen indicator species of Arizona monsoonal lichen community groups B (warm monsoonal) and D (hot monsoonal) based on components of Indicator Species Analysis. Each species is a point; species acronyms are in Supplementary Table S5. Diameter of the symbol is proportional to the combined indicator value, which is based on the product of fidelity and exclusivity. Fidelity is the percentage frequency of a given species in a particular group of plots. If a species occurs in all plots in a group then fidelity = 100%. Exclusivity is the percentage concentration of abundance within a particular group. If all of a species' occurrences were in only one group, then exclusivity = 100%.

evaporation (Eref_sp), with strong fit (cross-validated log likelihood ratio, log$B$ = 45.0). In contrast, hot monsoonal lichen communities, contrast with Great Basin communities in having high spring evaporation and high July–Sept precipitation.

Geographically, toward the western side of our study area, approaching California, the monsoonal pattern weakens and very dry summers predominate, even in the mountains. It was this contrast between summer precipitation in southern California versus southern Arizona and northern Mexico that led to the recognition of the North American monsoon, also known as the Arizona monsoon or Mexican monsoon (Adams & Comrie 1997). The areas with drier summers generally have lower lichen abundance and diversity (Great Basin, group E, **Table 2**); indeed, the forests of the east slope of the southern Sierra Nevada have perhaps the lowest epiphytic macrolichen diversity and abundance of anywhere in the U.S.A.; "empty" plots are common (McCune pers. obs.; underlying data in Jovan et al. (2020)).

Air quality. The strongest linear relationships between air quality variables and the NMS ordination axes were negligible. We found very weak positive relationships between NMS Axis 3 and average annual sulfur and nitrogen deposition (r^2 = 0.05, r^2 = 0.04 respectively). Nonlinear fits for total N and total S in relationship to the ordination axes were similarly weak with cross-validated $\times R^2$ = 0.06 and 0.05, respectively (NPMR, local mean, smoothing parameters optimized to maximize $\times R^2$). Given these weak relationships we focused on the much stronger climatic gradients.

Although the FIA lichen community method was originally designed to detect regional air quality gradients, even the earliest results from this method showed that regional climatic gradients were expressed as strong or more strongly than air quality gradients (McCune et al. 1997a; McCune 2000). Our results for the southwestern U.S.A. accord with previous findings of weak community relationships to air quality in the region (Marsh & Nash 1979; Peterson and Neitlich 2001) and support our hypothesis that, at the scale of our study,

Table 5. Model fit expressed as cross-validated coefficient of determination ($\times R^2$) for species richness regressed against climatic predictors and geographic predictors (latitude, longitude, elevation). Columns for "abs" and "rel" indicate absolute species richness and relative species richness (proportion of richness in a particular functional group). Strongest predictors are listed in order of entry during stepwise variable selection. Variables are explained in text and Supplementary Table S1. The strongest response surfaces are in Fig. 10.

	overall	cyanobacterial lichen species richness		forage lichen species richness		nitrophile species richness		shrubby lichen species richness	
		abs	rel	abs	rel	abs	rel	abs	rel
Climatic predictors									
1	0.169	0.119	0.176	0.252	0.361	0.097	0.258	0.235	0.210
2	0.235	0.201	0.261	0.316	0.457	0.169	0.314	0.345	0.303
3	0.282	0.275	0.296	0.373	0.476	0.183	0.355	0.386	0.333
4	0.301	0.281	0.309	0.402	0.486	0.189	0.375	0.390	0.335
Strongest predictors	SHM	PAR	PAR	NFFD_sm	NFFD_sm	DD_0_wt	NFFD_sm	PAR_sm	PAR_sm
	PAR_sm	PAR_sp	PcaAx6	PcaAx3	CMD_sp	Tmax_sp	TD	MWMT	PcaAx6
	PAS	PAR_at	NFFD_wt	DD_18_sm	Eref_sp	PAR_at	CMD_sm	PPT_sp	DD_0_wt
							EMT		
Geographic predictors									
1	0.187	0.211	0.231	0.174	0.179	0.030	0.231	0.234	0.290
2	0.309	0.303	0.323	0.264	0.250	0.070	0.335	0.378	0.359
3	0.322	0.325	0.340	0.291	0.275	0.108	0.418	0.412	0.392

relationships of lichen communities to climate would be much stronger than those for air quality gradients. That lichen communities depend on air quality is very well established but detecting a relationship to air quality gradients depends on the relative strength of the air quality effects versus other factors. In the present case, the large amount of regional climatic variation amplified by complex topographic gradients apparently overwhelmed community differences related to air quality. In addition, we cannot rule out the possibility that air pollution effects are reduced in drier climates, as suggested by Marsh & Nash (1979).

Species richness predicted by climate vs. geography. Overall species richness had modest relationships to climatic variables, based on non-parametric regression with automatic interactions among predictors, with cross-validated coefficient of determination ($\times R^2$) of 0.28 for a 3-predictor model (**Fig. 9**, **Table 5**). Climate predictors were selected to maximize $\times R^2$, drawing from the pool of 87 climatic variables, including principal components of climate variables. Adding more than three predictors yielded only small improvements in $\times R^2$. The best predictors of epiphytic macrolichen richness were summer heat moisture index (SHM), precipitation as snow (PAS), and summer precipitation as rain (PAR_sm).

Species richness peaked in areas with medium to high summer precipitation as rain and low summer heat moisture index (**Fig. 9**). Although summer heat moisture index tends to increase as summer precipitation decreases, the response surface of richness was complex, nonlinear and interactive. The interaction is clearly illustrated by slicing the response surface and observing the qualitatively different responses to one variable, depending on the value of the other variable (**Fig. 9B**).

Species richness was slightly more predictable from geographic location than climate, with $\times R^2 = 0.32$ for latitude and longitude alone versus $\times R^2 = 0.23$ for the best two-predictor climate model. Including elevation as a third predictor increased $\times R^2$ only to 0.35.

Species richness within functional groups. Relative richness of a functional group was more predictable than absolute richness, based on climate, for three of the four functional groups, with improvements in $\times R^2$ of 0.06 to 0.15 for two-predictor climate models (**Table 5**). The sole exception was fruticose lichens with a shrubby growth form, for which relativizing richness dropped $\times R^2$ by 0.05 for 2- and 3-predictor models.

On the other hand, relative and absolute richness had similar $\times R^2$ values for two-predictor geographic models, except for nitrophiles (**Table 5**). Relative richness of nitrophiles predicted from geographic coordinates plus elevation was the among the strongest of all models that we examined,
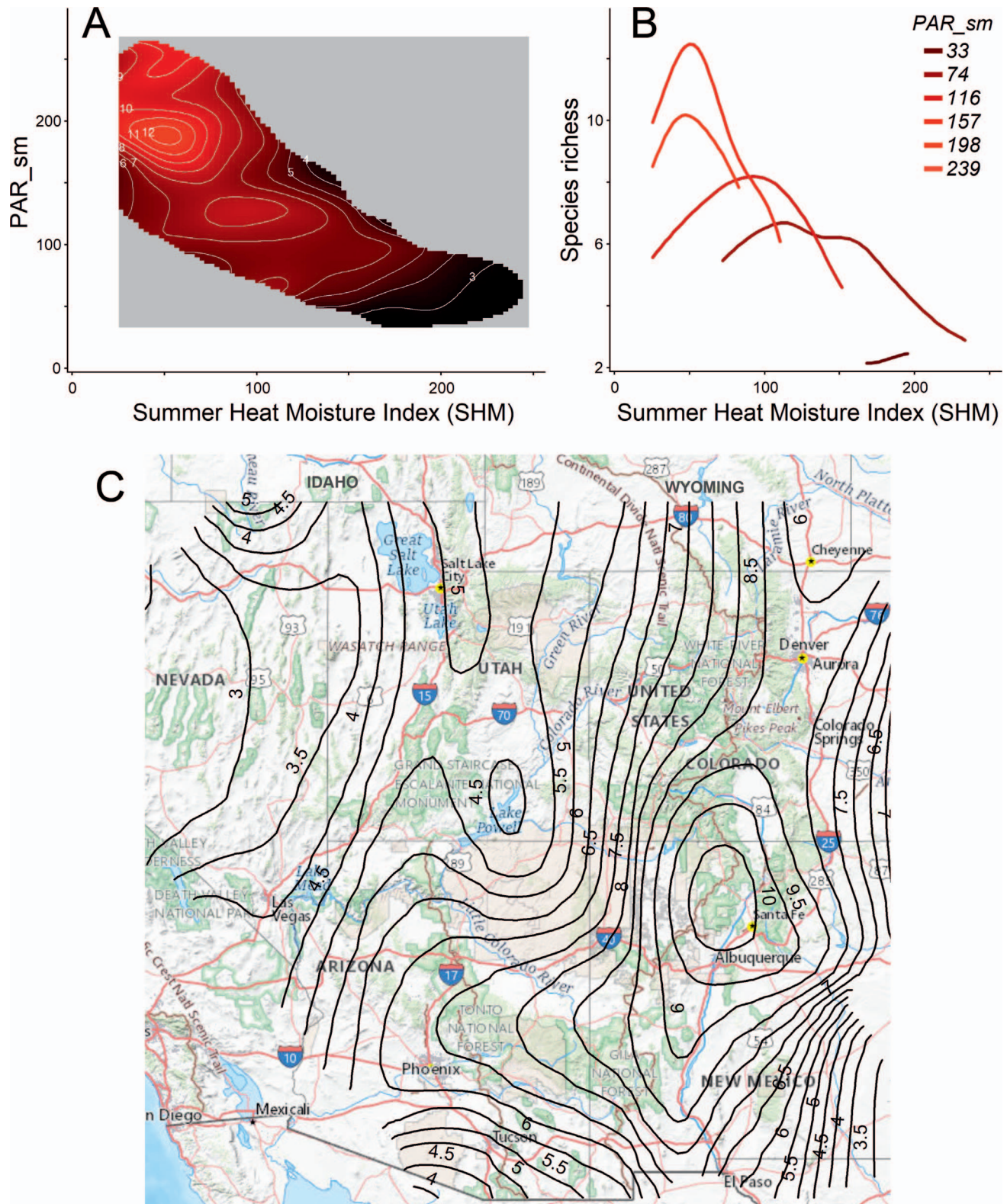
Figure 9. Response surfaces for overall epiphytic macrolichen richness against climate and geography. **A, B**. The top two predictors based on nonparametric multiplicative regression ($\times R^2 = 0.23$). The graph on the right slices the response surface in six parallel planes, each at a different level of summer precipitation. Gray areas indicate insufficient data to make estimates because those combinations of the predictors were not present in the data. **C.** Richness in relationship to latitude and longitude ($\times R^2 = 0.32$). Including elevation as well increased $\times R^2$ by only 0.03. Contours represent average epiphytic macrolichen species richness across all forest conditions; interval: 0.5 species. Basemap: USGS National Map, 2021.

with $\times R^2 = 0.42$. In contrast, absolute richness of nitrophiles was only weakly related to geography, with $\times R^2 = 0.11$ for latitude, longitude, and elevation combined.

Cyanolichens were very few in this data set (**Table 2**) but were concentrated in group B (summer monsoonal). These areas have relatively high continentality but with high summer precipitation. This is further illustrated by the response surface of relative richness of cyanolichens against precipitation as rain (PAR) and PCA axis 6, interpreted as increasing continentality with summer rain (PcaAx6; **Fig. 10B**; $\times R^2 = 0.26$; **Table 5**;).

Richness of **forage lichens**, including pendulous species of *Usnea* and *Bryoria*, was high only in areas with low climatic moisture deficit in spring (CMD_sp) and a small number of frost-free days in summer (NFFD_sm; **Fig. 10B**; $\times R^2 = 0.46$). A large portion of the predictor space (gray in figure) does not exist in this region: the only places with relatively few frost-free days in summer are higher elevation areas that also have low moisture deficits in spring. Models were slightly stronger for relative richness than for absolute richness of forage lichens.

Relative **nitrophile** richness as a function of geography was complex and strongly bimodal, with highest values in the Great Basin, lower values in the Rocky Mountains and the east front of the Sierra Nevada in western Nevada, and high values on the east front of the Rocky Mountains.

Relative richness of nitrophiles had a generally sigmoidal relationship to the combination of continentality (TD) and climatic moisture deficit in summer (CMD_sm; **Fig. 10C**; $\times R^2 = 0.31$). Proportion of nitrophiles was highest in continental climates with strong moisture deficits in summer. Absolute number of nitrophiles was less strongly related to climate and the best predictors were quite different than for proportional richness, showing a bivariate unimodal relationship to the combination of (degree days below 0°C in winter, DD_0_wt and spring mean maximum temperature (Tmax_sp; $\times R^2 = 0.17$; response surface not shown).

Richness of **shrubby lichens** had relatively strong relationships to climate and geography, whether expressed as absolute or relative richness. Of those four models, two of the strongest were absolute richness of shrubby fruticose lichens predicted from geographic coordinates ($\times R^2 = 0.38$) and from mean warmest month temperature

(MWMT) and summer precipitation as rain (PAR_sm; **Fig. 10D**, $\times R^2 = 0.35$). As with overall species richness, richness of shrubby lichens displayed a bimodal relationship to summer precipitation in rather cool climates, peaking at 150–280 mm of summer rainfall. Richness of shrubby lichens was low in the both the coldest and warmest climates, peaking with a mean warmest month temperature of 13–16°C.

Drivers of diversity. Species richness of epiphytic macrolichens, both as an overall total and for selected functional groups, was only modestly predictable from climatic variables ($0.28 < \times R^2 < 0.48$ for the best 3-predictor models; **Table 5**), despite a very large pool of potential predictors that expressed climate in a variety of ways, ranging from basic totals and means (precipitation, temperature), seasonal totals and means, composite variables designed to express climate in biologically relevant ways (e.g., climatic moisture deficits), and synthetic variable represent the dominant patterns of covariance among climatic variables (PCA axis scores). We expected this limited success because of the large number of local factors that are known to affect diversity of lichen communities, such as disturbance, microtopography, woody plant species composition, and air quality. On the other hand, given the large number of partially redundant variables, the repeated emergence of certain climatic predictors was noteworthy: precipitation as rain (PAR, particularly in summer, PAR_sm), number of frost-free days in summer (NFFD_sm), climatic moisture deficit in spring and summer (CMD_sp and CMD_sm), and PCA axis 6, which we interpret as indicating high continentality combined with summer rain. Not surprisingly, these variables or largely redundant variants of them were also found to be strongly related to species composition.

Richness of particular functional groups was more strongly related to climate ($0.30 < \times R^2 < 0.48$ for the best 3-predictor models) than was overall macrolichen species richness ($\times R^2 = 0.28$). This result would be expected if functional groups have their own climatic controls, owing to the physiological consequences of growth form and photobiont. Overall species richness then becomes driven by an even more complex combination of performances in relation to climate. Presumably each functional group has experienced its own evolutionary tradeoffs, developing peak performance in
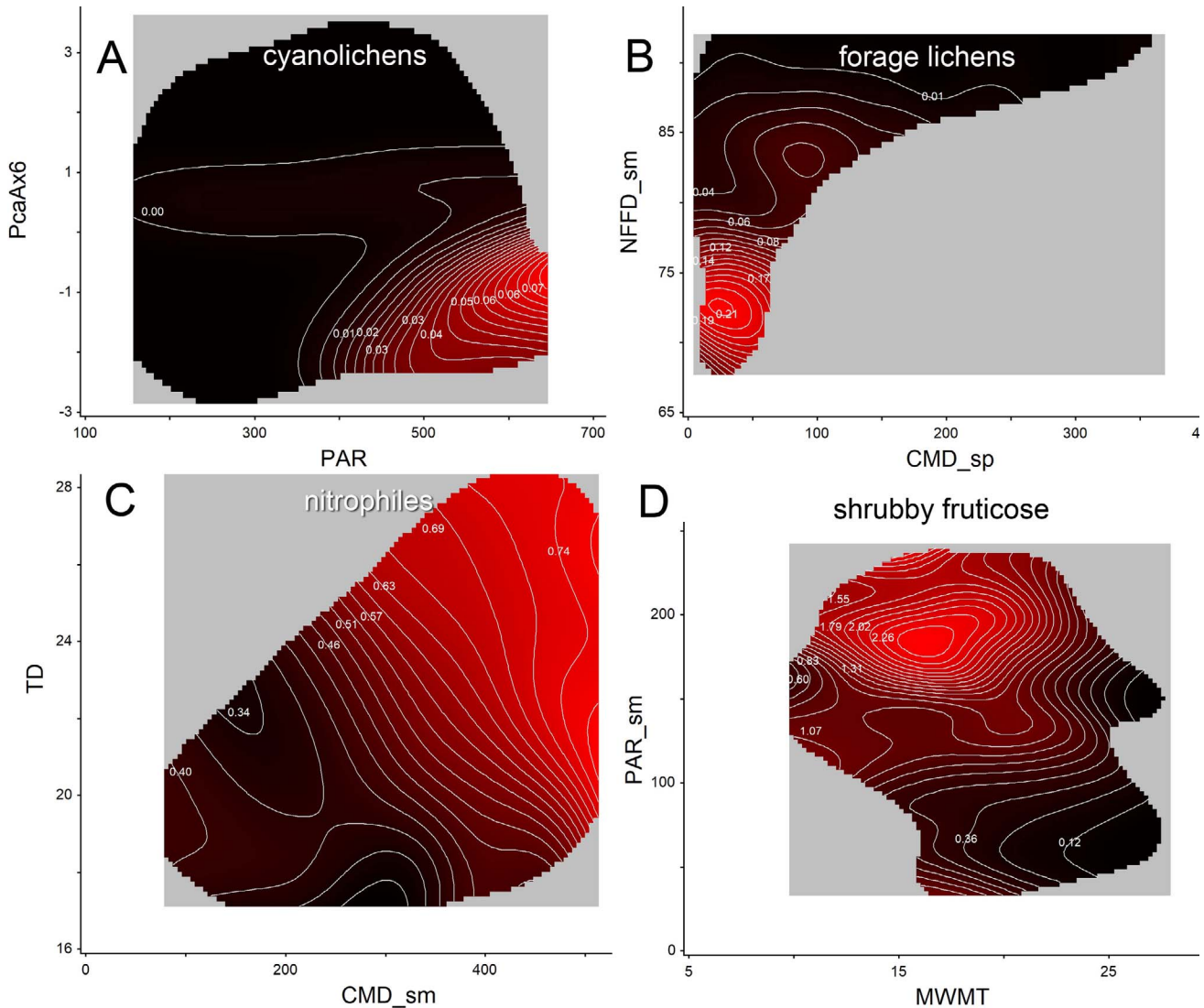
Figure 10. Species richness within functional groups in relationship to climate, based on nonparametric regression. Gray areas indicate insufficient data to make estimates because those combinations of the predictors were not present in the data. Contours represent the response variable in relation to the strongest pair of climatic predictors. **A.** Relative richness of cyanolichens against precipitation as rain (PAR) and PCA axis 6, interpreted as increasing continentality but with summer rain (PcaAx6; $\times R^2 = 0.26$). **B.** Relative richness of forage lichens against climatic moisture deficit in spring (CMD_sp) and number of frost-free days in summer (NFFD_sm; $\times R^2 = 0.46$). **C.** Relative richness of nitrophiles against continentality (TD) and climatic moisture deficit in summer (CMD_sm; $\times R^2=0.31$). **D.** Absolute richness of shrubby fruticose lichens against summer precipitation as rain (PAR_sm) and mean warmest month temperature (MWMT; $\times R^2 = 0.35$).

different climates, so that if one analyzes overall species richness, in effect one combines response surfaces, the richness pattern from one group partially cancelling out others, weakening the fit between richness and climate.

In some cases species richness was more strongly related to geographic coordinates than to climate variables, based on comparisons of model fits with equal numbers of predictors. Because climatic variables are themselves geographically structured,

stronger model fit for geographic coordinates implies an influence of large-scale historical factors that are not clearly expressed in modern climates, such as past climates, vegetation, or disturbance regimes. We observed this pattern for overall epiphytic macrolichen richness, cyanolichen richness and shrubby lichen richness, with $\times R^2$ showing geographic coordinates providing an additional 5 to 10% of the total variance in richness represented by the best two-predictor models.

Conversely, we would expect climate variables to more efficiently predict species richness if richness is controlled by smaller scaled topographic factors that are well expressed in climate grids but show a complex large-scale geographic pattern. For example, the basin-and-range topographic structure in large areas of the southwestern U.S.A. is expressed in climate grids but makes a wrinkled smaller-scaled pattern on top of the smoother large-scaled climatic pattern. Forage lichen richness and nitrophile richness both showed this pattern, of somewhat stronger fits (6–20% of the total variance) for climate models than geographic models.

Conclusions. Considering our results more broadly, in the context of modeling ecological community relationships to climate, we found nonlinear responses and interacting predictors everywhere we looked. Commonly these are not perceived or reported, simply because tools assuming a linear relationship are chosen uncritically, without examining the underlying relationships with more detail. The most conspicuous example of this is the typical representation of environmental gradients, including climatic factors, to ecological communities as biplots or joint plot vectors showing linear relationships to community ordinations. Had we restricted ourselves to that method, then we would have missed many strong, but nonlinear and interactive relationships of lichen communities to climate.

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Supplementary documents online:

Supplementary Table S1. List of climate variables.

Supplementary Table S2. Number of plots sampled in each year by state, 1994 to 2017.

Supplementary Table S3. MRPP and indicator species analyses to determine optimum number of groups from cluster analysis of lichen communities in species space.

Supplementary Table S4. Influence of nonmetric multidimensional scaling (NMS) ordination settings on final stress, fit, and instability.

Supplementary Table S5. Frequency of each species within each community group.