

Lichen Communities as Climate Indicators in the US Pacific States

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Abstract

Epiphytic forest lichens are bioindicators of climate, air quality and a host of other environmental conditions. Understanding variation in lichen communities reveals how forests may respond to global changes. Here we explore lichen communities as climate indicators in the US Pacific states of Alaska, Washington, Oregon, and California, summarized in four analyses.

Analysis 1 yielded a super-regional lichen–climate gradient model spanning thirty degrees of latitude in the four Pacific states. Model scores (“climate scores”) revealed correlations between lichen community composition and recent climate. Changes in climate scores at sites resurveyed in the future could indicate climatic shifts. Select lichen indicator species were associated with climate zones (sites with similar temperature, moisture, seasonality, etc.), suggesting possible monitoring targets.

Analysis 2 compared the performance of two different survey methods that had historically been implemented in the southcentral/southeast Alaska region: large-radius Forest Inventory and Analysis (FIA) and small-radius Region 10 National Forest (R10) plots. Regional climate gradient models built from either dataset had comparable if modest agreement, but the FIA dataset had consistently higher species richness, likely because the FIA plot size is seven times larger in area.

Analysis 3, a survey of historical data from R10 plots remeasured over time, detected no signal of climate change response in lichen communities of southcentral/southeast Alaska over the period 1989–2014. Species richness, climate scores, community composition, and indicator species did not change more than random expectations, possibly due to climatic buffering by the adjacent Pacific Ocean.

Analysis 4, using Alaskan R10 data, yielded lichen indicator species of six pre-defined vegetation types. These indicators may be useful focal species for regional forest management objectives.

As environmental monitoring in the western US continues, several agencies can benefit from existing data and from continued monitoring of lichens to examine how climate will shape forest communities of the Pacific coast and adjacent inland areas.

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Introduction

This report explores lichen communities as indicators of climatic conditions in the US Pacific states of Alaska, Washington, Oregon, and California. Early-responding “bioindicator” species are useful for evaluating how forests may respond to climate change because we can observe changes in species identities and abundances through time. Epiphytic (tree-dwelling) forest lichens are fungus-photobiont partnerships that are especially good bioindicators because they lack any protective cuticle or active water uptake system, which directly exposes them to changes in temperature and atmospheric moisture (Nimis et al. 2002; Gauslaa et al. 2014). Furthermore, since they rely on atmospheric sources of nutrition, they are proportionately more sensitive to differences in climate than in soils. The USFS, NPS, and USFWS have conducted over 8,000 lichen surveys across US forests, including those considered here. This project is part of a larger effort to unite interagency lichen data for the purpose of developing viable climate change indicators.

Communities of lichens have long been employed as indicators of air pollution (Geiser and Neitlich 2007; Jovan 2008; Schirokauer et al. 2014), and of forest health and function (McCune 2000; Smith et al. 2015). Recently there has been increasing focus on lichens’ role as climate indicators. While lichen–climate relationships have been determined in regions of the continental US (Geiser and Neitlich 2007; McMurray et al. 2015; Root et al. 2015; Will-Wolf et al. 2015), a regional focus in northern parts of the country is now warranted due to projections of rapid ecological change in Alaska. For example, climate change is expected to affect Alaskan animal populations, vegetation productivity, glacier and permafrost melt, microbial decomposition, wildfire patterns and other ecosystem processes (Wolken et al. 2011). There is also evidence that a changing climate will affect Alaska’s epiphytic lichen communities (Root et al. 2014). Surveying and monitoring lichen communities could provide early indication of potential ecosystem changes.

Regional approaches within ecoregions or biogeographic provinces have previously been useful in describing lichen responses to climate (Will-Wolf and Neitlich 2010). Indeed, a regional approach for Alaska is essential. However, many insights can be gained by evaluating lichen communities over large “super-regions” that span large ecological gradients and cross biogeographic boundaries. A broad scope is useful, not only because lichen–climate patterns may become more apparent over larger climatic gradients, but also because practitioners may wish to understand how Alaska’s regional findings are tied to broader trends. Furthermore, a broad scope anticipates the possibility that climate could change such that sites within the Alaska region could become more similar to sites which are now outside the region.

This report addresses several biological questions regarding lichen communities in the US Pacific states including southeast/southcentral Alaska: How are lichen communities related to current climate? What are the best indicator species of distinct climate zones? Given historical data, have lichen communities changed over time? How might lichen communities be useful for monitoring climatic changes in the future?

In addition to biological questions, workers in southeast and southcentral Alaska also had practical questions about sampling methodology: Which of two sampling methods (large- vs small-radius plots) is best for capturing lichen species and lichen community gradients? Can mixtures of data from the two methods improve the strength of lichen–climate models? Which lichen species are most indicative of Alaskan vegetation types used in a forest classification?

Here we address these questions and provide guidance on opportunities to use lichen community responses in interagency environmental monitoring programs in Alaska and other Pacific states. Knowledge of patterns and processes in lichen communities will be fundamental for environmental monitoring and for anticipating how changing climates might impact ecosystems in the western US.

Methods

Data for lichens and climate

Lichen data originated from two sources: Forest Inventory and Analysis plots (“FIA” dataset hereafter) and USFS Region 10 plots (“R10” dataset hereafter). Complete FIA protocols are described in Will-Wolf (2010:11–14), and R10 protocols in “Lichen Inventory” section of Geiser et al. (1994:22–26). Observations that were incidental or otherwise not adhering to these protocols were excluded. Both datasets were based on time-constrained surveys of a circular, fixed-area plot in which trained technicians collected and assigned abundance values for all epiphytic lichen species. However, the FIA and R10 datasets differed respectively in plot size (0.379 vs 0.051 ha), number of sampling rounds (one vs many), criteria for locating plots (random vs targeted), geographic coverage (all Pacific coastal US states vs Alaska only), and temporal coverage (1998–2014 vs 1989–2014). See summary in Table 7 of this report for further comparison.

Before analyses, we translated R10 abundance values to their equivalents on the FIA scale following the crosswalk of Geiser et al. (2004:18), placing all values on the same approximately logarithmic 0–4 scale. Values on the scale represent 0 = not present; 1 = 1–3 thalli observed; 2 = 4–10 thalli observed; 3 = more than 10 thalli observed but on < 50% of available branches and stems; and 4 = observed on > 50% of available substrates. We harmonized species names per FIA analyst guidelines (Will-Wolf 2010; FIA Lichen Indicator program list). Only epiphytic macrolichen species were included. Terrestrial or crustose species were excluded based on documented substrate and growth form.

Climate data came from the ClimateWNA database (Wang et al. 2012). For all FIA and R10 lichen plot locations (Fig. 1), we extracted mean annual air temperature, continentality, mean annual precipitation, annual heat moisture index, frost-free period, percent precipitation as snow, and climatic moisture deficit. Because climate variables are commonly highly correlated, we converted them to principal components (PCs) using PCA based on the correlation matrix in PC-ORD version 7 (McCune and Mefford 2016). The first three (of seven possible) PCs were selected for interpretation based on PC-ORD’s *Rnd-Lambda* criterion from a test with 9999 randomizations. PCs are orthogonal linear combinations interpretable in terms of the original climate variables: for example, PC 1 corresponded to a thermal gradient, PC 2 represented a gradient of increasing continentality and lower moisture, and PC 3 was a more complex climatic gradient involving frost-free period (Table 1 and Fig. 2). This and all subsequent analyses were performed in PC-ORD version 7 (McCune and Mefford 2016) and R version 3.1.2 (R Core Team 2015).

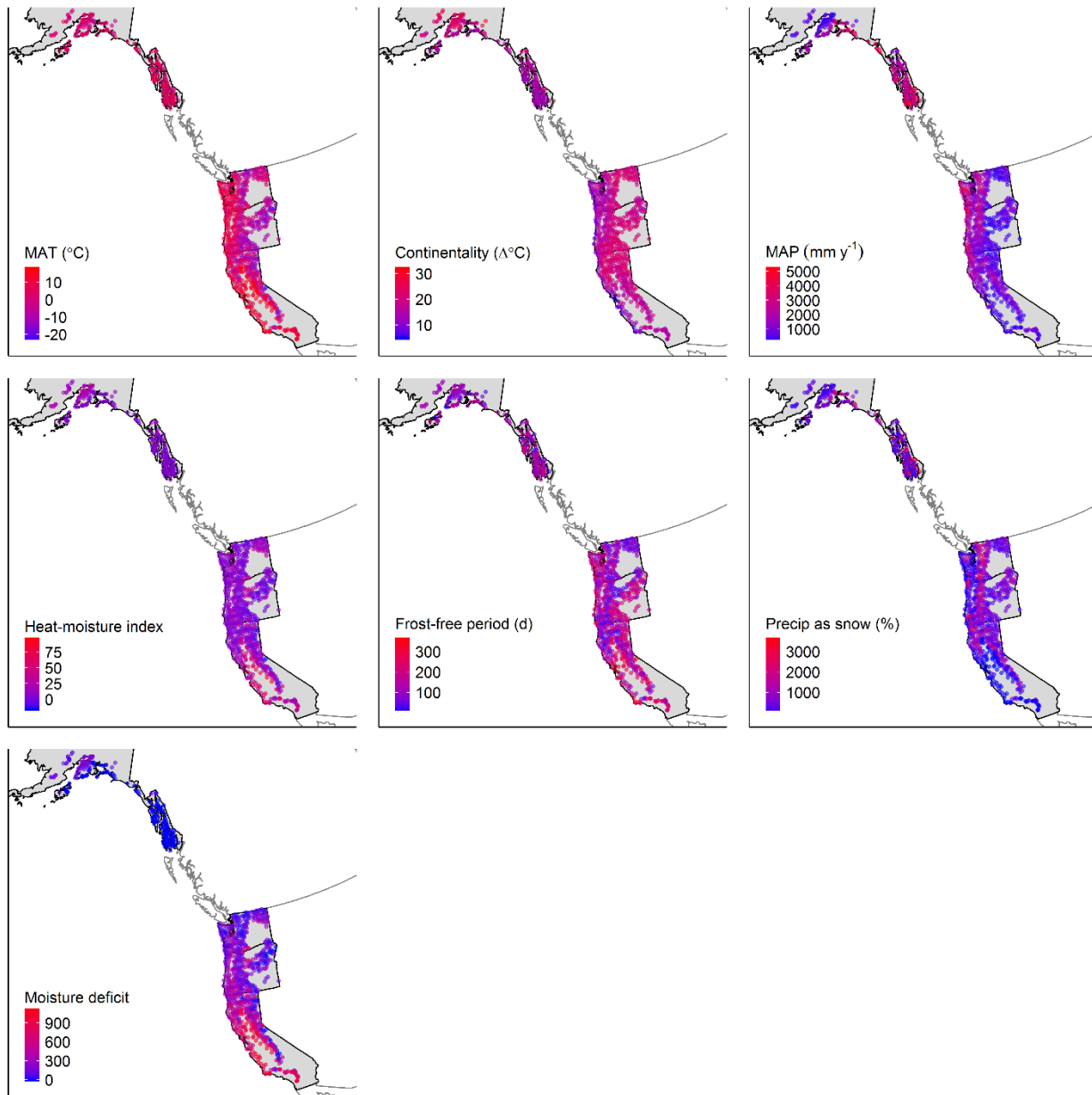


Figure 1. Raw climate values at each FIA and R10 lichen plot in the Pacific States area.

Data: ClimateWNA (Wang et al. 2012). The seven raw climate variables were also reduced to principal components (PCs).

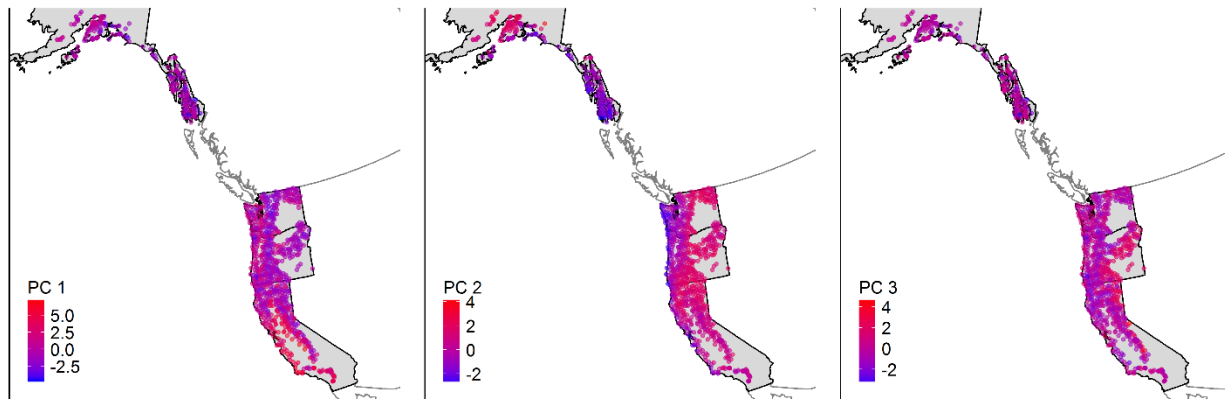


Figure 2. Principal components climate values at each FIA and R10 lichen plot in the Pacific States area. The first three (of seven possible) PCs were used in analyses. PC1 represents a thermal gradient, PC2 is a gradient of moisture and continentality, and PC3 is a more complex climatic gradient.

Table 1. Summary of climate principal components (PCs).

	PC 1	PC 2	PC 3
Variance explained (%)	42.3	27.6	15.5
Cumulative variance (%)	42.3	69.9	85.4
Climate correlations: ¹			
Mean annual air temp	0.70	-0.55	-0.37
Continentalty	-0.30	0.87	-0.04
Mean annual precipitation	-0.46	-0.80	-0.26
Annual heat moisture index	0.87	0.17	-0.29
Frost-free period	0.41	-0.28	0.76
Percent precip as snow	-0.78	0.04	-0.37
Moisture deficit index	0.80	0.35	-0.27

¹each eigenvector scaled to its standard deviation

Analysis 1 — Super-regional lichen–climate relationships

To assess how lichens were related to climate across a broad geographical scope, we created a super-regional gradient model for 1118 FIA lichen plots throughout Alaska, Washington, Oregon and California. This super-regional approach spans portions of 8 of the 17 designated FIA Lichen Regions (Will-Wolf and Neitlich 2010), and therefore incorporates both ecological and biogeographic variation.

For this we used exclusively FIA data after first removing rare species (< 3 occurrences) and species-poor plots (< 5 species). The central gradient model for this was nonmetric multidimensional scaling ordination (NMS; Kruskal 1964). NMS assigns scores to sites based on similarity of lichen community composition – since these scores implicitly reflect lichen community responses to underlying gradients like climate, we interpret NMS scores here as “climate scores”. This and all subsequent NMS models used Sørensen distances based on lichen abundance, penalized ties, and PC-ORD’s “slow-and-thorough autopilot” settings with 500 iterations, 250 runs with real data, 250 runs with randomized data, and final scores rotated to orthogonal principal axes (mutually independent axes).

To interpret lichen–climate relationships, we calculated both univariate and multivariate measures of how well NMS scores fit the climate variables (both raw variables and transformed PCs). Univariate fit was Kendall’s *tau* rank correlation. Multivariate fit was leave-one-out cross-validated R^2 (xR^2) from a nonparametric multiplicative regression (NPMR; McCune 2006) of NMS scores in response to the 3 climate PCs. We implemented NPMR with a local mean model, Gaussian kernel and default settings in HyperNiche version 2.25 (McCune and Mefford 2011), which allows NMS scores to vary as a potentially nonlinear function of multiple interacting climate PCs.

Sites can be grouped by climatic similarity within “climate zones”. To do so, we used optimal partitioning, an algorithm which optimizes the ratio of within-group to among-group similarity (Roberts 2015; R package ‘optpart’). Without requiring lichen information, this groups each plot into one of 10 climate zones sharing similar climatic characteristics. For this we identified 10 climate zones based on Euclidean distances of the three climate PCs, using 19 random starts with 99 iterations each.

To identify the lichens which best characterized each climate zone or set of zones, we used multi-group indicator species analysis (de Cáceres et al. 2010; R package ‘indicspecies’). Multi-group indicator species analysis accounts for the fact that species can have broad or narrow climatic tolerances, and may therefore be indicators of multiple or single climate zones. For this we specified 3rd-order groupings (indicator values calculated across 1, 2, and 3 climate zones) and performed a significance test with 999 randomizations. Indicator values (*IndVal*) are calculated for each species as the product of its relative abundance in a given climate zone (or set of zones) multiplied by its relative frequency in that zone (or set of zones). *IndVal* scales from 0 (no indicator value) to 1 (perfect indicator).

Analysis 2 — Alaska regional models: survey method performance

Given that two lichen datasets existed for the same region in southeast and southcentral Alaska, one goal was to evaluate the respective performance of the FIA vs R10 survey data in regional gradient models. If the two methods were equivalent, then each should yield roughly identical species datasets, and each dataset should be interchangeable among regional lichen community models. More formally, we evaluated to what degree FIA-based and R10-based models were interchangeable under the null hypothesis of no difference in sampling methods. We were also interested in whether combining FIA *and* R10 datasets together could improve performance in climate response models over either dataset alone.

For this we used either FIA or R10 data from Alaska only, after first removing rare species (< 3 occurrences), species-poor plots (< 5 species), and plots that were extreme outliers in species composition

(average Sørensen distance > 3 standard deviations from the grand mean). Under these constraints there were nearly twice as many R10 plots as FIA plots (281 vs 155), so we downsampled the R10 dataset by selecting only those R10 plots that were nearest geographical neighbors to the FIA plots, yielding a balanced, equal number (155) of co-regional plots for each.

Evaluating performance required a three-step process to calibrate, reciprocally fit, and evaluate each dataset across both models (Table 2). First, for the calibration step we performed NMS ordination for each dataset (software and settings as above). Hereafter we refer to these calibration models as “FIA Model” or “R10 Model” based on their source data.

Second, the reciprocal fitting step used PC-ORD’s “NMS Scores” procedure to generate new gradient scores for each dataset when applied to its reciprocal model (scores were generated for all NMS axes simultaneously). In other words, FIA data were fit to the R10 model, and R10 data were fit to the FIA model, where new NMS scores were the outcome.

Third, for the evaluation step we used Procrustes analysis (Peres-Neto and Jackson 2001; R package ‘vegan’) and examination of ordination distances to assess agreement between models. Procrustes analysis calculates the residual differences between two configurations of NMS scores after scaling and rotating them to maximum similarity, yielding a measure of “agreement” that is roughly analogous to a correlation coefficient. Higher agreement suggests better “performance” in climate gradient models – two gradient models built with perfectly interchangeable lichen data would have Procrustes agreement approaching 1 on a scale of 0–1. We also evaluated how well NMS scores fit climate variables, using both the univariate (Kendall’s *tau*) and multivariate (xR^2) metrics described above for Analysis 1.

As a further comparison of the two datasets, we tested for differences in community composition using permutational multivariate analysis of variance (perMANOVA; Anderson 2001), implemented in PC-ORD and based on Euclidean distances of the FIA model and R10 model NMS scores. To assess differences in mean species richness between datasets, we fit a simple linear model with orthogonal *F*-tests of coefficients (base R version 3.1.2; R Core Team 2015).

Table 2. Procedure to assess between-model agreement of the two lichen datasets.

Data source	Calibration step 1		Reciprocal fitting step 2		Evaluation step 3
FIA	Use FIA data to create FIA model	→	FIA data fit to R10 model	→	Procrustes comparison of FIA plot scores between R10 model and FIA model
R10	Use R10 data to create R10 model	→	R10 data fit to FIA model	→	Procrustes comparison of R10 plot scores between R10 model and FIA model

Pairwise FIA vs R10 comparisons were not strictly possible since plots were not exactly co-located and they were measured by different observers. Therefore, to eliminate possible location and observer effects, one expert observer applied both the R10 and FIA survey methods in summer 2009 at each of twelve sites (2 methods × 12 sites, exactly co-located). We then evaluated datasets as above, except blocking by “plot” to account for the fact that values from either method were related within each plot. This included blocked perMANOVA and blocked indicator species analysis in PC-ORD; see Root et al. (2010) for a description and example of blocked indicator species analysis. We also tested for differences in mean species richness between survey methods using a separate-means linear mixed model (random block effect = plot; fixed effects = survey method; error structure correlated within plots) and orthogonal *F*-tests implemented in R package ‘nlme’ (Pinheiro and Bates 2000; Pinheiro et al. 2014).

Analysis 3 — Lichen community changes 1989–2014

To more directly test for signals of climate change responses in Alaskan lichen communities, we evaluated a subset of R10 plots that had been sampled at least twice over the 25-year period 1989–2014. There were 50 such plots, ranging from 3 to 21 years elapsed between rounds of sampling, averaging 12.9 years elapsed. Each plot was surveyed by one of four observers. Alaskan FIA data were not included in this analysis since they had not yet been remeasured as of 2014.

We used two approaches to assess changes in community composition over time. First, we calculated NMS scores for the 50 resurveyed plots (settings and software as above), then used blocked perMANOVA in PC-ORD based on Euclidean distances of the NMS scores (blocks = plots). In a second approach, we tested for directional patterning in a successional vector overlay of NMS scores. Successional vectors connect each plot's first-round and second-round NMS score with each end of a scaled and centered vector arrow. Since vectors indicate direction and magnitude of change, a consistent shift in species composition between rounds would be suggested by a directional trend of vectors in the ordination space. To formally test the null hypothesis of no change in species composition between sampling rounds, we used Kuiper's test for circular uniformity (Stephens 1970) implemented in R package 'circular' (Agostinelli and Lund 2013). Kuiper's test evaluates vector directionality but not magnitude.

To assess changes in mean species richness between sampling rounds, we fit a separate-means linear mixed model (random effect = plot, fixed effects = sampling round, observer, and their interaction; error structure correlated within observers), followed by orthogonal *F*-tests of coefficients in R package 'nlme' (Pinheiro et al. 2014). This tests the null hypothesis of no difference in mean species richness between sampling rounds (i.e., no change over time). Individual species gains and losses were evaluated with blocked indicator species analysis in PC-ORD (blocks = plots).

Analysis 4 — Indicators of Alaskan vegetation types

The goal of Analysis 4 was to identify indicator lichen species for Alaskan vegetation types. Lichen plots in the R10 dataset had previously been assigned to vegetation types for management purposes following Viereck et al. (1992). We aggregated plots by the six dominant tree species defining each vegetation type, then tested community composition differences using perMANOVA with Sørensen distances based on lichen abundances from the R10 dataset after removing rare species (< 10 occurrences). We then used first-order indicator species analysis to identify those lichens which best characterized single vegetation types (de Cáceres et al. 2010; R package 'indicpecies').

Results

Analysis 1 — Super-regional lichen–climate relationships

The super-regional model was an NMS ordination of 1118 FIA plots from Alaska, Washington, Oregon, and California. The final solution was 2-dimensional, had stress = 21.3, and included 273 species (Table 3). NMS Axis 1 and 2 scores explained 30.8% and 37.7% of the variation in community composition respectively (Table 3). Higher scores on Axis 1 were associated with lichen compositional change related to greater mean annual temperature and lower continentality (within-year temperature range), while higher scores on Axis 2 were related to greater precipitation and lower moisture deficit (Table 3, Figs. 3 and 4). Species richness ranged from 5–44 species per plot (Fig. 5). Ten “climate zones,” collections of sites that shared similar climatic attributes, were based on optimal partitioning of the 3 climate PCs (Table 4, Figs. 6 and 7). Each climate zone was associated with a set of indicator species (Table 5, Fig. 8). Complete species list and indicator values are in *Appendix 1*.

Table 3. Summary and climate correlations for Pacific states super-regional model. The cross-validated R^2 (xR^2) expresses fit of community axis to climate variables. Kendall’s τ is a nonparametric correlation coefficient.

	NMS Axis 1 scores	NMS Axis 2 scores
Explained variation in community composition (%)	30.8	37.7
Multivariate climate fit (xR^2)	0.63	0.62
Univariate climate fit (τ)		
Latitude	0.32	0.51
Mean annual air temp	0.36	−0.08
Continentality	−0.38	−0.11
Mean annual precipitation	0.36	0.46
Annual heat moisture index	0.15	−0.28
Frost-free period	−0.07	−0.18
Percent precip as snow	−0.09	0.32
Moisture deficit index	−0.10	−0.49
PC1	0.12	−0.33
PC2	−0.46	−0.24
PC3	−0.15	−0.05

Table 4. Kendall’s τ correlation with climate zones in the Pacific states super-region.

Climate variables	Climate zones									
	1	2	3	4	5	6	7	8	9	10
	warm mesic lowlands	warm dry subcontinental	hot dry lowlands	cold mesic subcontinental	cold dry continental	cold mesic continental	cool dry continental	cool moist subcontinental	mild moist suboceanic	warm wet hypermaritime
Mean annual air temp	0.36	0.18	0.33	−0.22	−0.51	−0.20	−0.01	−0.12	0.04	0.26
Continentality	−0.21	−0.15	−0.08	0.05	0.33	0.27	0.22	0.04	−0.18	−0.42
Mean annual precipitation	−0.02	−0.11	−0.23	0.03	−0.25	−0.04	−0.28	0.27	0.31	0.38
Annual heat moisture index	0.30	0.17	0.34	−0.20	−0.46	−0.05	0.31	−0.21	−0.13	−0.02
Frost-free period	0.13	0.17	0.23	0.12	0.33	−0.36	−0.28	−0.26	−0.14	0.15
Percent precip as snow	−0.34	−0.20	−0.34	0.16	0.17	0.25	−0.10	0.33	0.25	−0.17
Moisture deficit index	0.35	0.16	0.35	−0.16	−0.21	0.02	0.16	−0.15	−0.19	−0.27

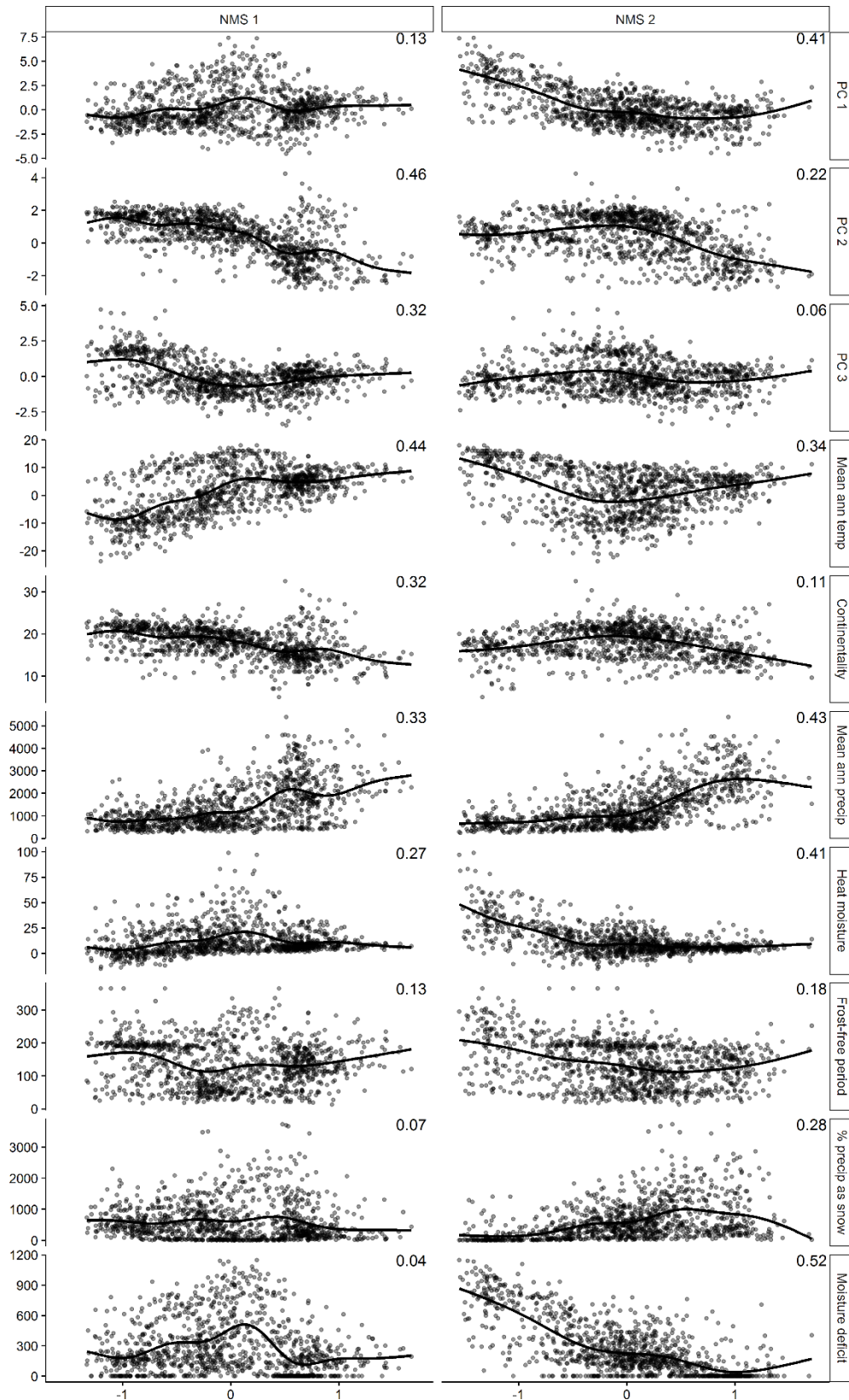


Figure 3. Nonparametric regression of lichen community NMS scores against climate variables. Fit lines and 10-fold cross-validated R^2 values are from generalized additive models.

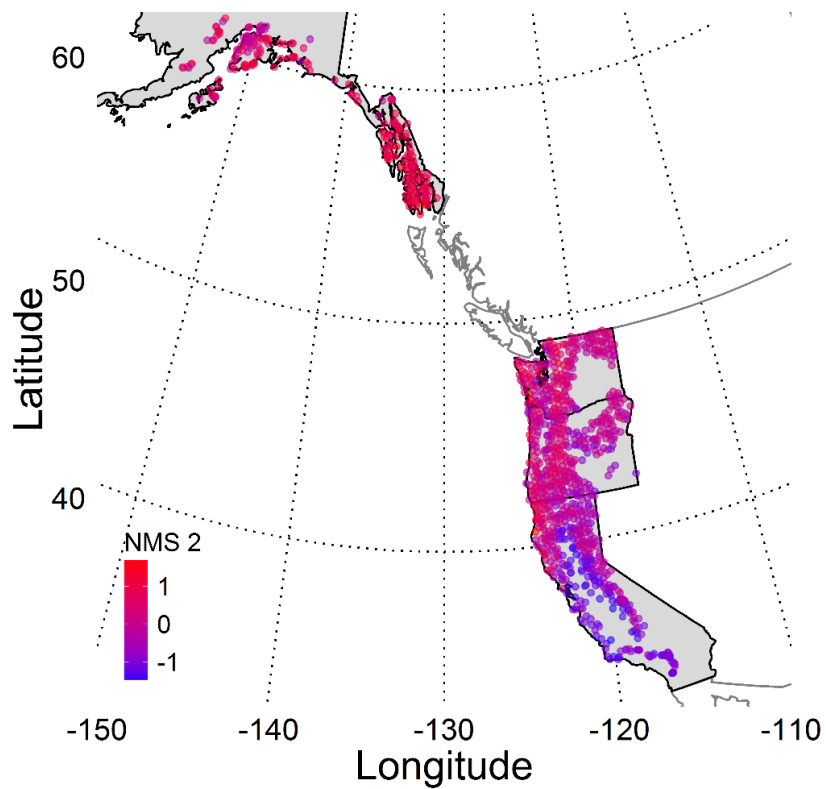
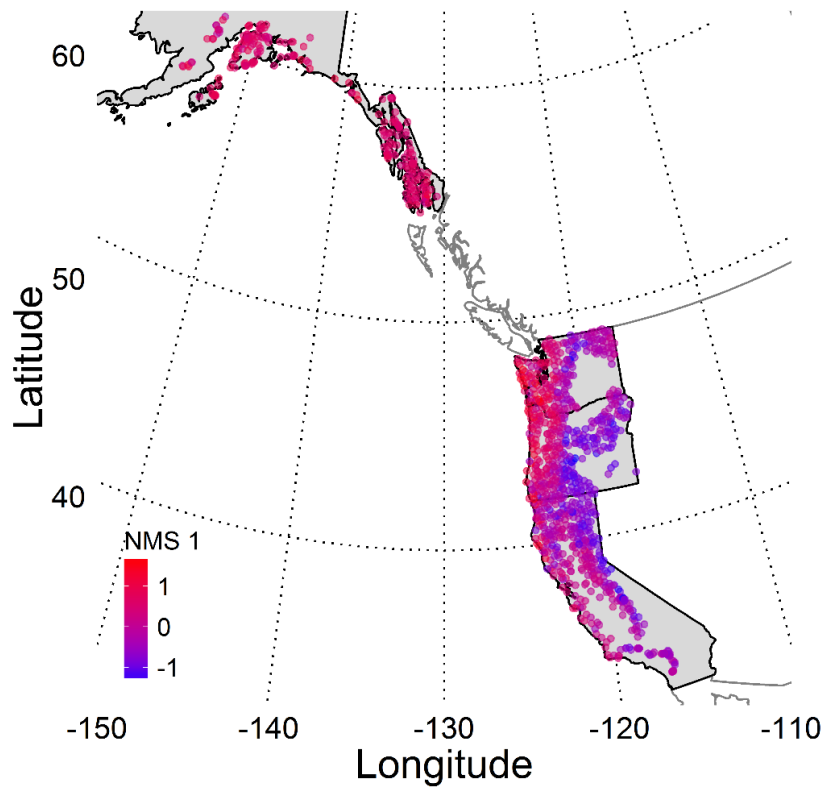


Figure 4. Lichen community NMS scores from the Pacific states super-regional model. Similar scores (colors) represent similar lichen species composition at each site. Axis 1 reflects lichen community responses to an oceanic-continental gradient (temperature, continentality). Axis 2 reflects responses to precipitation and moisture deficit.

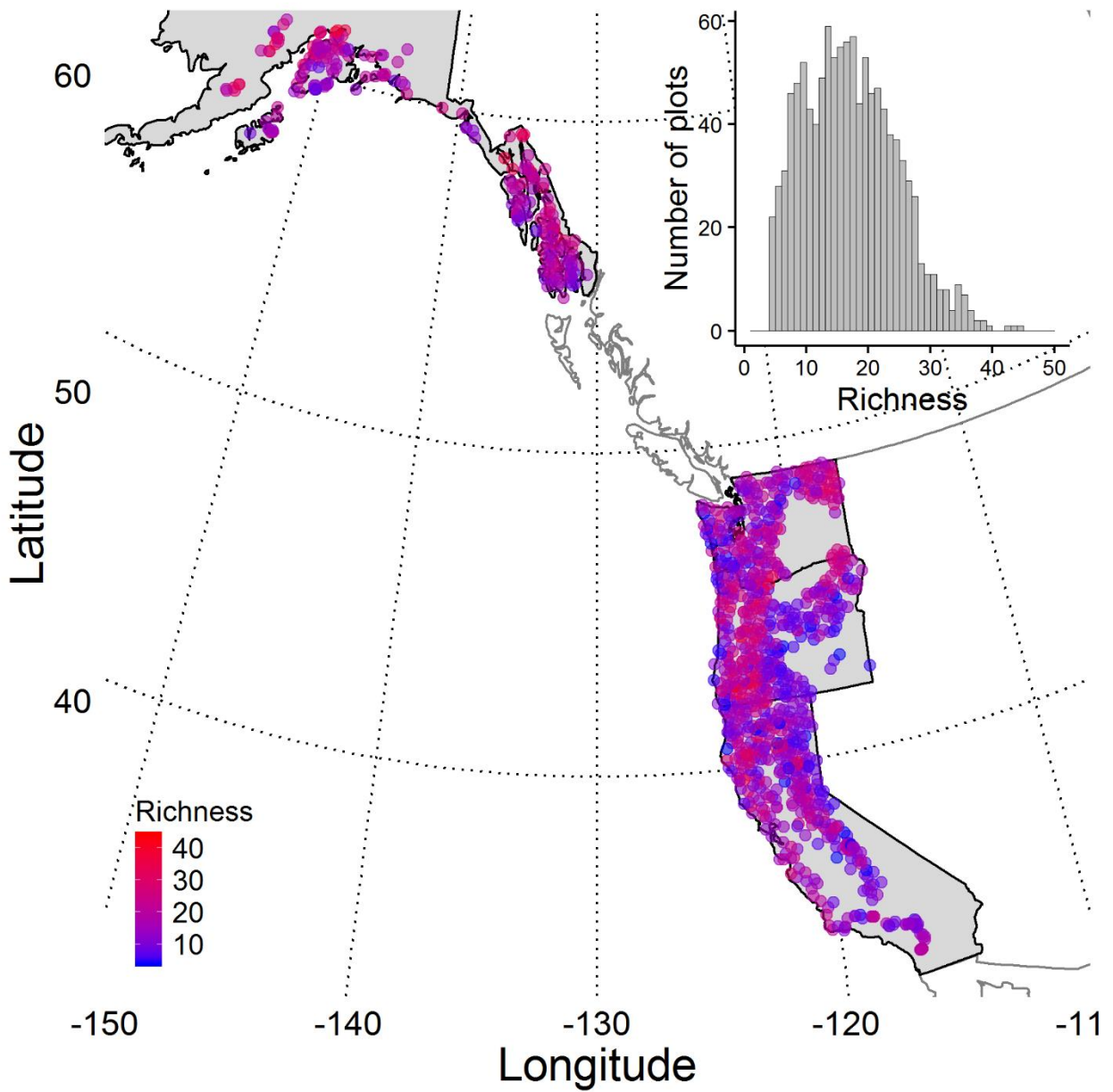


Figure 5. Lichen species richness in FIA plots across the Pacific states area. Richness distributions shown in geographic space (main figure) and as a frequency distribution (inset). Richness ranged from 5–44 species per plot.

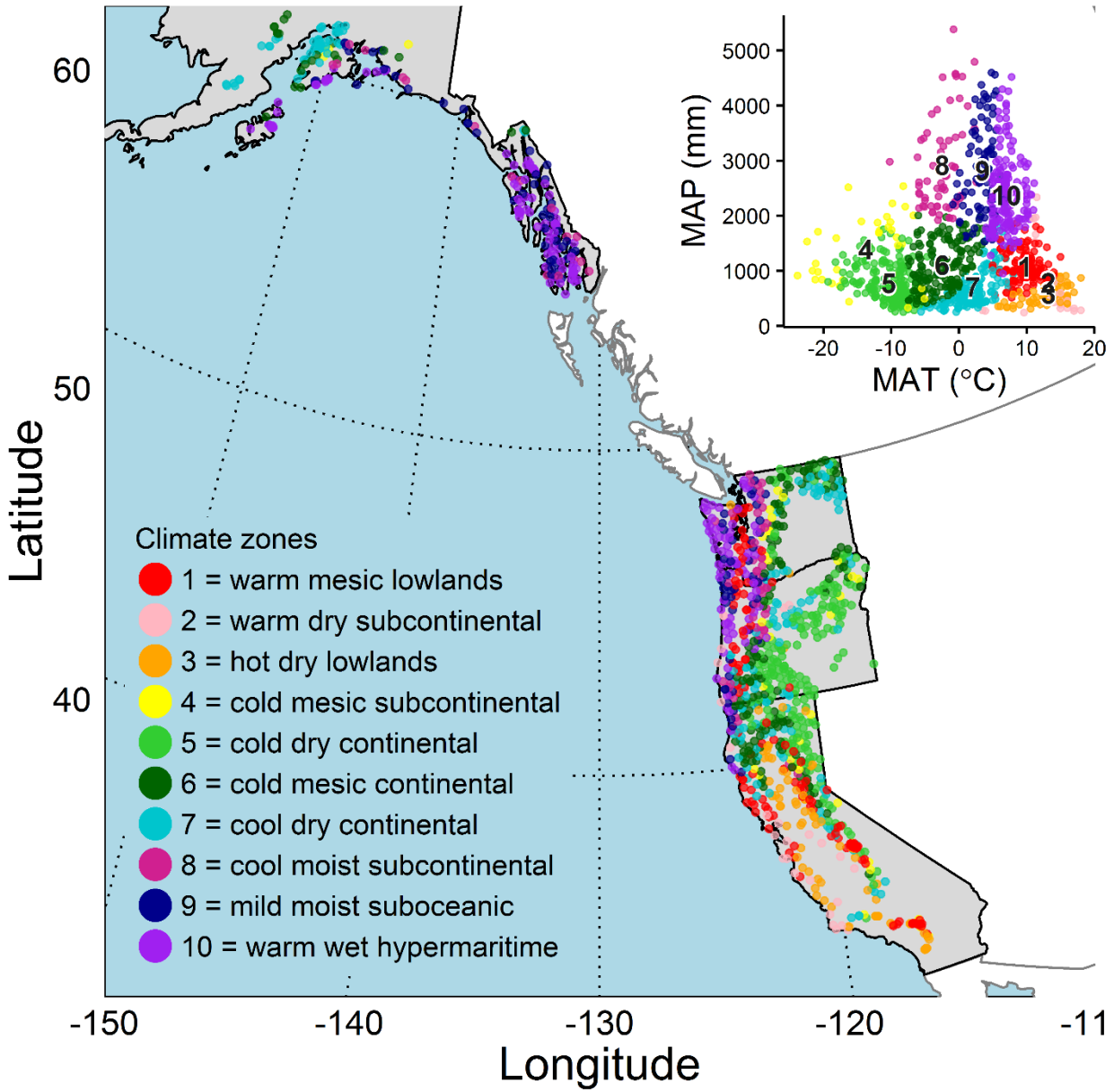


Figure 6. Climate zones for each FIA lichen plot in the Pacific states area. Climate zones are mapped in geographic space (main) and climate space (inset: precipitation vs temperature).

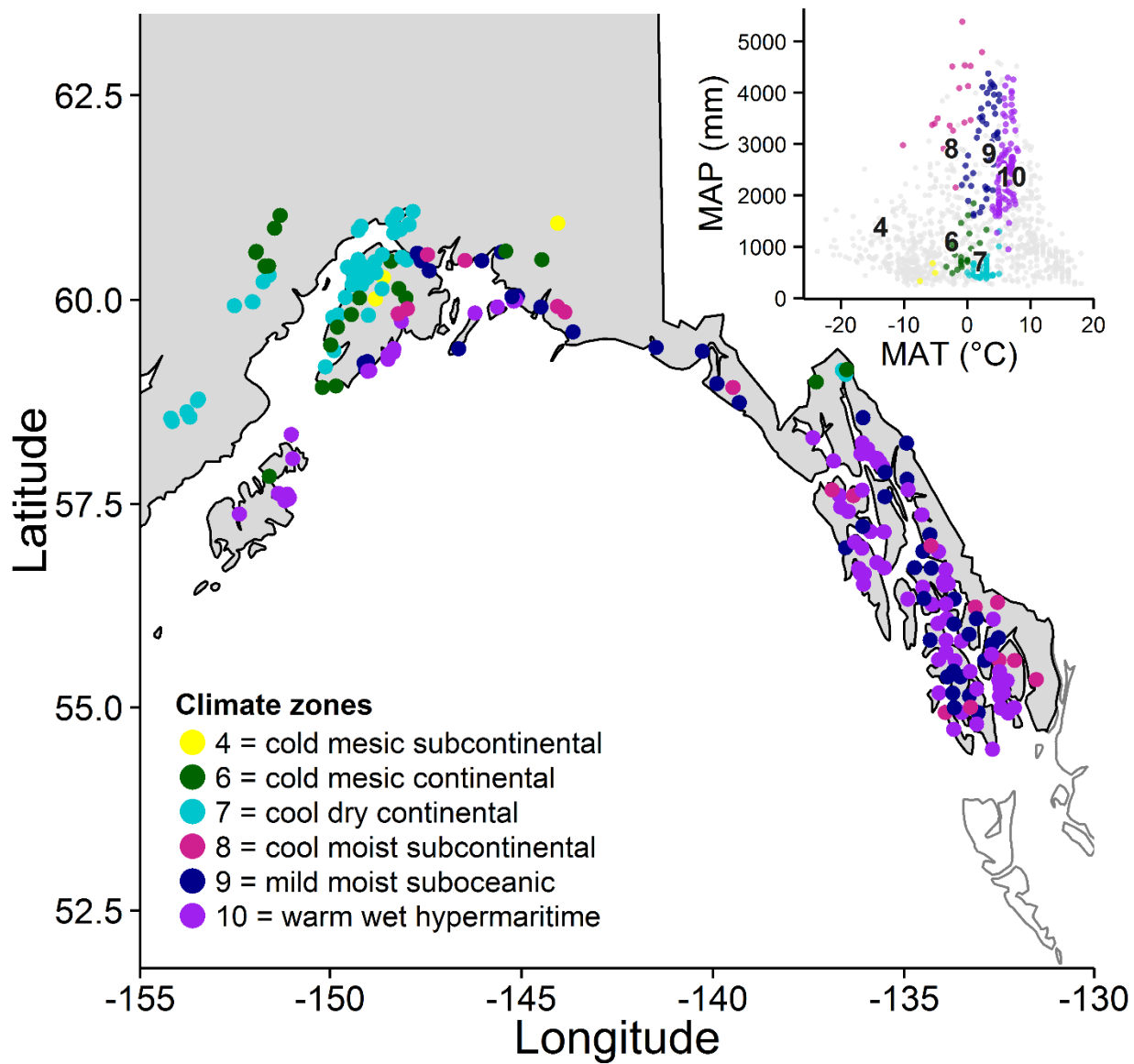


Figure 7. Climate zones for each FIA lichen plot in the Alaska region. Climate zones are mapped in geographic space (main) and climate space (inset: precipitation vs temperature). Inset colored symbols = AK plots, grey symbols = WA/OR/CA plots.

Table 5. Select indicator species for climate zone combinations of the Pacific states.

See complete list in Appendix 1. Blank spaces were substituted for species that had non-significant indicator value (but may be present).

Indicator species	Relative freq ²	Across-zone IndVal ¹	IndVal ¹ for single climate zones									
			1	2	3	4	5	6	7	8	9	10
			warm mesic lowlands	warm dry subcontinental	hot dry lowlands	cold mesic subcontinental	cold dry continental	cold mesic continental	cool dry continental	cool moist subcontinental	mild moist suboceanic	warm wet hypermaritime
<i>Sphaerophorus aggr.</i> ³	0.27	0.79								0.38	0.53	0.45
<i>Platismatia norvegica</i>	0.15	0.61								0.22	0.40	0.40
<i>Hypogymnia enteromorpha</i>	0.26	0.68								0.40	0.42	0.37
<i>Platismatia glauca</i>	0.51	0.67						0.32		0.46	0.41	
<i>Parmeliopsis hyperopta</i>	0.25	0.62				0.22				0.49	0.33	
<i>Alectoria sarmentosa</i>	0.39	0.61						0.31		0.46	0.31	
<i>Cetraria merrillii</i>	0.25	0.55					0.49	0.25	0.20			
<i>Hypogymnia imshaugii</i>	0.46	0.65				0.29	0.39	0.41				
<i>Letharia vulpina</i>	0.43	0.72				0.31	0.49	0.39				
<i>Nodobryoria abbreviata</i>	0.28	0.69				0.30	0.49	0.35				
<i>Bryoria fremontii</i>	0.20	0.62				0.29	0.45	0.29				
<i>Letharia columbiana</i>	0.26	0.61				0.37	0.46					
<i>Melanelixia californica</i>	0.11	0.64			0.64							
<i>Physconia isidiigera</i>	0.12	0.66		0.28	0.59							
<i>Phaeophyscia orbicularis</i>	0.08	0.67		0.38	0.54							
<i>Candelaria pacifica</i>	0.27	0.70	0.32	0.39	0.53							
<i>Physcia adscendens</i>	0.18	0.67	0.30	0.41	0.48							
<i>Polycauliona polycarpa</i>	0.17	0.61	0.31	0.34	0.40							
<i>Physcia tenella</i>	0.13	0.61	0.32	0.39	0.38							
<i>Parmotrema perlatum</i>	0.02	0.61		0.61								

¹ IndVal = (relative abundance in given climate zone or set of zones × relative frequency in given zone or set of zones)^{0.5}

² Relative frequency, the proportion of 1118 plots in which the species occurred.

³ *Sphaerophorus* species were aggregated due to species concept changes over the sampling period.

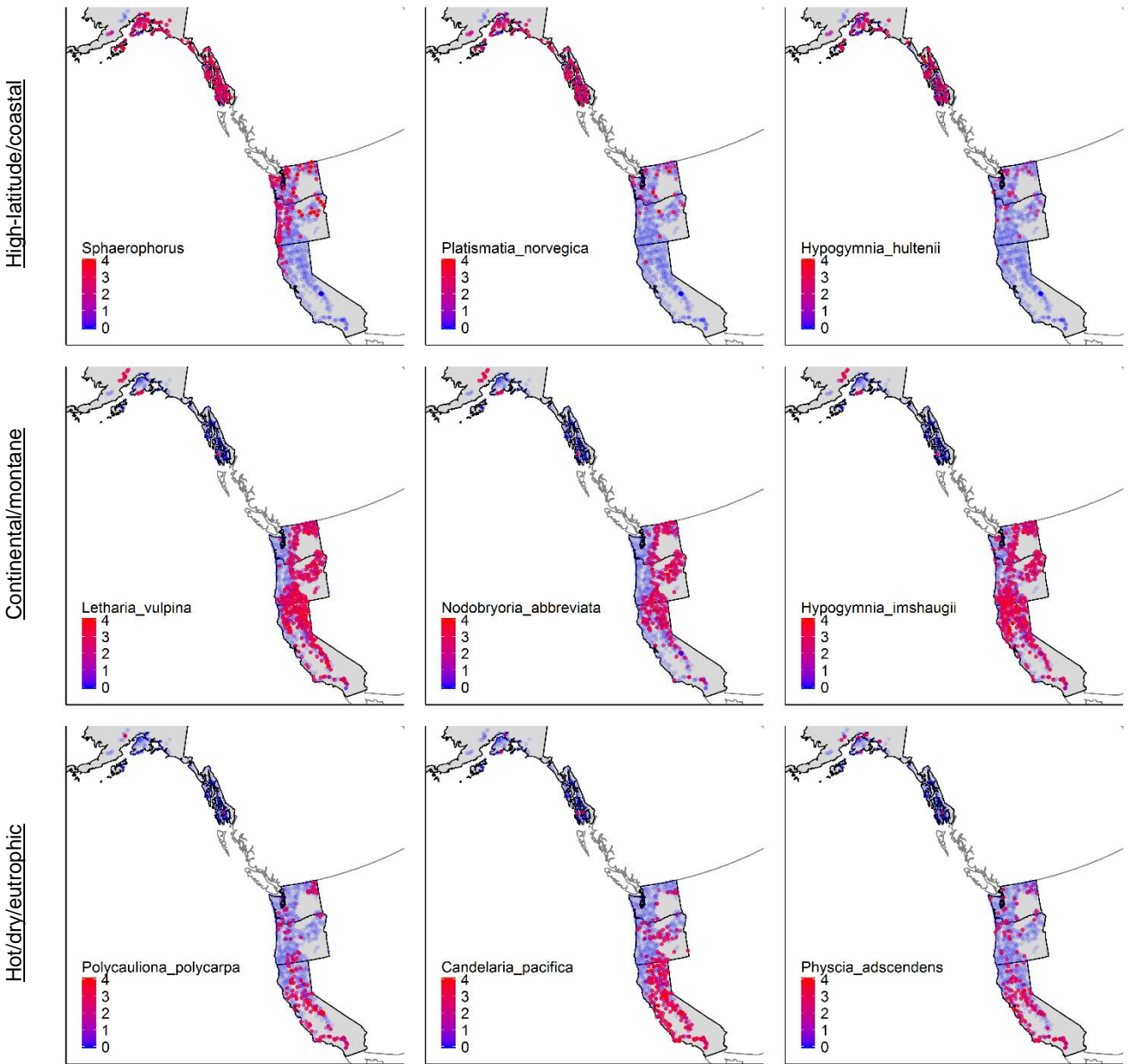


Figure 8. Indicator species' distributions across the Pacific states area. Shown are high-latitude and coastal lichens (top row), continental-montane species (middle row), and species that tolerate hot, dry, or eutrophic conditions (bottom row). See Appendix 1 for all climate indicator values.

Analysis 2 — Alaska regional models: survey method performance

Based on 135 species, the FIA calibration model ordinated 155 “large-radius” plots in a 3-dimensional solution with final stress = 19.9 on a scale of 0–100 (Table 6 and Fig. 9). Axis 1 scores explained 49% of the variation in community composition, and were correlated with decreasing continentality, decreasing moisture deficit and increasing precipitation, suggesting that community change along this axis reflects an oceanic–inland gradient. Axis 2 scores explained 14.8% of the variation in community composition and were correlated with decreasing temperature and shorter frost-free period, suggesting that community change along this axis reflects temperature tolerances. Axis 3 explained 10.5% of the variation in community composition and was correlated with decreasing temperature, shorter frost-free period, and increasing precipitation as snow. Axis 1 scores increased toward lower latitudes.

Based on 156 lichen species, the R10 calibration model ordinated 155 “small-radius” plots in a 3-dimensional solution with final stress = 19.6 (Table 6 and Fig. 9). Axis 1 scores explained 39.6% of the variation in community composition and correlated revealed that community variation along this axis represents an oceanic–inland gradient similar to the FIA model. Axis 2 scores explained 25.0% of the variation in community composition and were correlated with variables that suggested tolerances to the timing and availability of moisture. Axis 3 scores were not strongly related to climate (Table 6). As with the FIA model, NMS scores on the R10 model’s first axis showed weak geographical structuring.

A combined model including both FIA+R10 data had higher stress (24.6) than either model alone, explained less of the variation in the species data, and had generally weaker fit to climate (Table 6).

Table 6. Summary of three lichen–climate regional gradient models (FIA, R10 and FIA+R10). Climate fit statistics indicate the strength of association between NMS scores and climate.

	FIA model			R10 model			FIA+R10 model		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Stress	19.9			19.6			24.6		
Explained variation in community composition (%)	74.3			78.2			68.9		
Explained variation in community composition (%)	49.0	14.8	10.5	39.6	25.0	13.6	33.9	19.7	15.3
Multivariate climate fit (χR^2):	0.31	0.04	0.06	0.18	0.14	0.01	0.22	0.14	0.06
Univariate climate fit (τ):									
Latitude	-0.27	0.03	0.03	-0.20	0.09	-0.09	-0.27	-0.13	0.03
Longitude	0.23	-0.01	0.02	0.17	-0.10	0.06	0.23	0.15	-0.04
Mean annual air temp	0.10	0.11	-0.19	0.07	0.06	0.08	0.16	-0.06	-0.21
Continentality	-0.24	-0.04	0.12	-0.17	0.07	-0.07	-0.25	-0.09	0.07
Mean annual precipitation	0.22	0.01	0.08	0.17	-0.22	0.04	0.16	0.23	0.09
Annual heat moisture index	-0.17	0.05	-0.15	-0.14	0.23	-0.01	-0.10	-0.25	-0.16
Frost-free period	0.07	0.11	-0.21	0.05	0.08	0.08	0.12	-0.08	-0.21
Percent precip as snow	0.02	-0.07	0.19	0.02	-0.14	-0.06	-0.04	0.16	0.20
Moisture deficit index	-0.29	-0.03	-0.04	-0.22	0.21	-0.04	-0.26	-0.25	-0.08
PC1	-0.06	0.07	-0.18	-0.04	0.16	0.05	0.02	-0.18	-0.19
PC2	-0.24	-0.06	0.08	-0.16	0.12	-0.08	-0.23	-0.11	0.04
PC3	0.01	0.09	-0.20	0.01	0.12	0.06	0.07	-0.13	-0.21

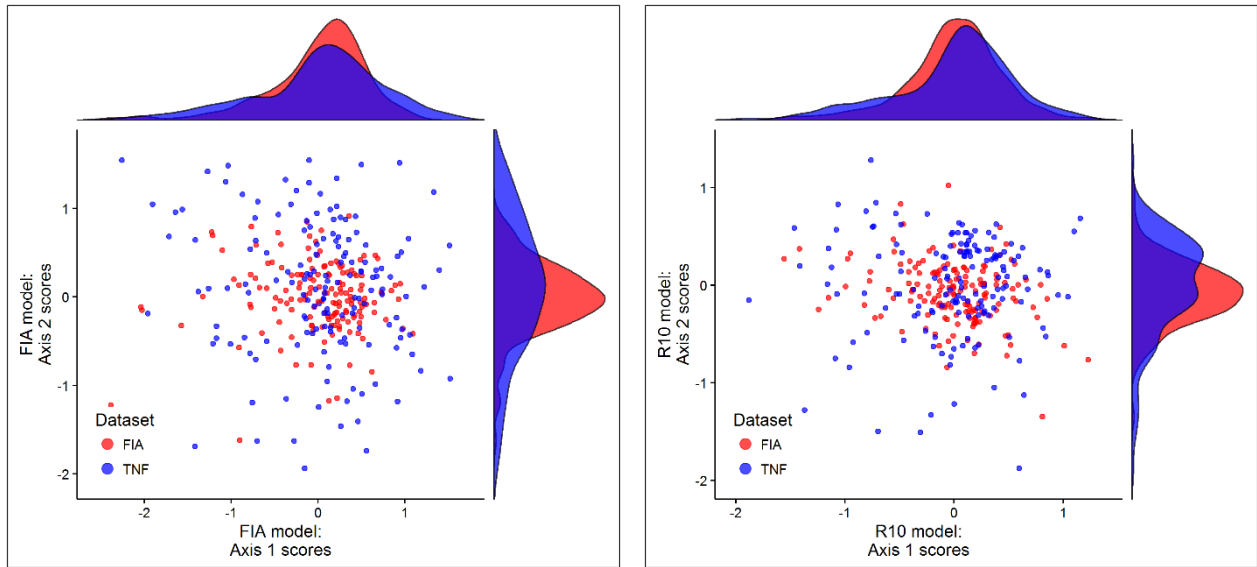


Figure 9. Ordination scores for the FIA and R10 gradient models.

Red symbols = FIA data, blue symbols = R10 data. Marginal density plots depict frequency distributions of scores for each dataset. Similar frequency distributions within an ordination would suggest that the two data sets have similar ranges in lichen community composition.

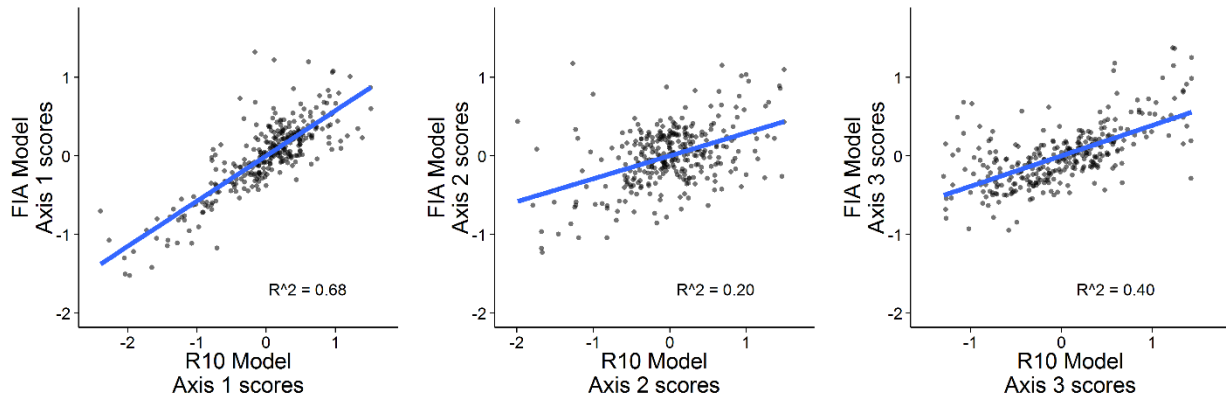


Figure 10. Direct comparison of NMS scores for FIA model and R10 models after Procrustes rotation to maximum similarity. Perfect agreement between models would have points fall along a straight line with $R^2 = 1$.

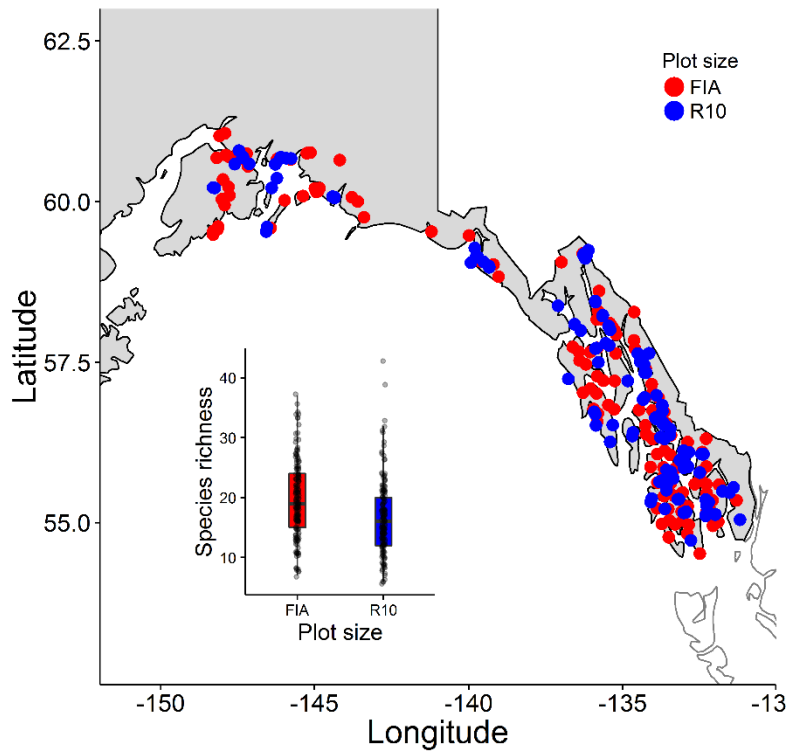


Figure 11. Locations and species richness of co-occurring FIA and R10 plots used in Analysis 2. Inset: Mean species richness in FIA plots was about 3 species greater than R10 plots (boxplot center bars = median, box ends = upper/lower quartiles, whisker ends = $1.5 \times$ inter-quartile range, dots = each observation).

Evaluating cross-model performance of each dataset (to assess the null hypothesis of no difference in sampling methods), we found that each dataset had comparable measures of fit within its own calibration model as well as when reciprocally fit to the evaluation model (Table 7). Between-model agreement, based on ordination distances compared among calibration and evaluation models, approached 89% on a 0-100 scale of variance explained. The Procrustes analysis of each model likewise found comparable residual error and between-model agreement (Table 8). This suggests that each dataset performed similarly when fit to opposing gradient models (Procrustes agreement, which is analogous to a correlation coefficient, was = 0.67 vs. 0.66). Following Procrustes rotation, Axis 1 scores for each model were most comparable (Fig. 10).

Table 7. Assessment of within-model fit and agreement between FIA and R10 models.

“Fit of model to data” is the percentage of variance explained from a nonmetric fit of ordination distances vs original Sørensen distances. “Agreement between models” is percentage variance explained from an orthogonal least-squares regression of evaluation vs calibration model distances when each dataset was fit to the other model in the evaluation step.

	Fit of model to data		Agreement between models
	FIA model	R10 model	
FIA data	78.4	55.8	88.9
R10 data	61.6	81.9	89.5

Mean species capture in the group of large-radius FIA plots was an estimated 3.2 species (about 20%) greater than in the group of R10 plots (95% confidence interval = 1.7 to 4.6 species; $F = 18.9$, $p < 0.0001$; Fig. 11). Beta diversity (species turnover) was greater in R10 plots as a result of greater gamma diversity (observing more species region-wide) and lower alpha diversity (fewer average species per plot; Table 8). Gamma diversity differences could be due to the non-random placement of R10 plots, and the unintentional inclusion of non-epiphyte species in the R10 dataset (we attempted to manually remove these based on knowledge of species’ requirements and recorded substrate, but substrate was not always recorded).

For the 12 exactly co-located plots surveyed by the single expert observer, community composition differed significantly between the R10 vs. FIA methods (blocked perMANOVA, pseudo- $F = 20.3$, $p = 0.0006$). From the 95 recorded lichen species, there were 3 significant indicator species for the large-radius FIA method and zero for the small-radius R10 method; these 3 indicator species are fewer than the number that might be expected at random (since $95 \text{ species} \times 0.05$ assumed probability of false detection = 4.6 species). Despite differences in community composition, models agreed strongly between the methods (Procrustes agreement: FIA = 98.8 and R10 = 98.9). After accounting for observer and site effects, mean species capture using the large-radius FIA method was an estimated 3.7 species (about 15%) greater than when using the R10 method (95% confidence interval = 1.9 to 5.4 species; $F = 22.0$, $p = 0.0007$). The FIA method had higher within-plot diversity (alpha diversity: 23.5 vs 19.8 species) and collected a greater number of species across the 12 plots (gamma diversity: 95 vs 79 species), but had similar beta diversity (beta diversity: 3.0 vs 2.9). The FIA method did not miss any of the 95 species observed collectively in the 12-plot subset, while the R10 method omitted 16 species.

Table 8. Comparison of attributes for FIA- and R10-sized plots.

Attribute	FIA	R10	Notes
Radius	36.6 m (120 ft)	12.8 m (42 ft)	FIA larger by $\times 2.9$
Area ¹	0.379 ha	0.051 ha	FIA larger by $\times 7.3$
Time constraints	½ – 2 hr	½ – 2 hr	Identical
Observer skill	Trainees	Experts	
Resampled?	Not yet in Alaska	At least once for 50 sites	
Temporal coverage	2004–2009 (for AK)	1989–2014	
Spatial coverage	all land ownerships, all US regions	R10 National Forests (Alaska), Glacier Bay, Klondike and Sitka NPS sites, and Kodiak NWR	
Location assignment	Systematic, random	Targeted, nonrandom	
Location dispersion	Systematic, random	Clustered, nonrandom	
Transferability	Standardized across US	Require unknown correction factors for scaling	
Terrestrial species	Never included	Must manually exclude	
Alpha α diversity	19.8	16.1	FIA: average 3.7 more spp.
Gamma γ diversity	150	171	R10: more species recorded overall
Beta diversity ($\gamma/\alpha-1$)	6.6	9.6	R10: more compositional variation among plots
Procrustes agreement, ² (co-regional plots)	0.66	0.67	Similar agreement
Procrustes agreement, ² (exactly co-located plots)	0.98	0.98	Similar agreement
NMS gradient scores	Interpret freely	Caution if related to richness	

¹FIA lichen survey area excludes subplot areas inside the plot radius.

²Correlation-like statistic = $(1 - \text{sum-of-squared-error})^{0.5}$; ranges 0–1 and approaches 1 for ordinations from identical data.

Analysis 3 — Lichen community changes 1989–2014

A suite of analyses revealed no signal of climate change in lichen communities of coastal Alaska over the 25-year period 1989–2014. The 50 remeasured plots ranged from 3 to 21 years elapsed between rounds of sampling, averaging 12.9 years elapsed. Change in lichen species composition over time was indistinguishable from random. Successional vectors from the NMS ordination (3-dimensional solution, stress = 22.0) exhibited no directional patterning in species space, suggesting no consistent pattern of species replacement over time (null hypothesis not rejected by Kuiper’s test, Fig. 12). Using another method, there were no changes in community composition between sampling rounds (blocked perMANOVA pseudo- $F = 0.49$, $p = 0.16$).

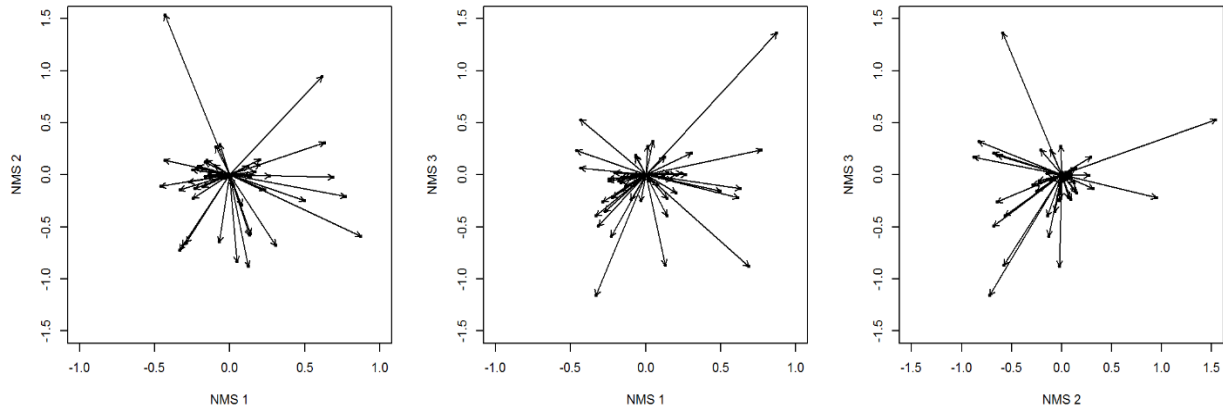


Figure 12. Centered successional vectors from NMS ordination of 50 resampled plots in Alaska. Vector tails = lichen plot 1st-round NMS scores, vector heads = 2nd-round scores. Vectors radiate uniformly, indicating that the pattern of species replacement over time was not significantly different from random.

Species richness in the resampled plots exhibited roughly as many gains as losses over time (24 plots had increases, 5 remained equal, 21 saw decreases; Fig. 13). There was an estimated mean of 18.8 species (± 6.5 SD) across all 100 plot rounds. Minor changes in mean species richness among sampling rounds were attributable to observer effects rather than time effects (Table 9). From the blocked indicator species analysis there were 4 significant “increaser” species and 4 significant “decreasers”. Yet, these 8 observed indicators (from the observed pool of 166 species) did not differ from the number that might be expected at random (since $166 \text{ species} \times 0.05 \text{ assumed probability of false detection} = 8.3 \text{ species}$).

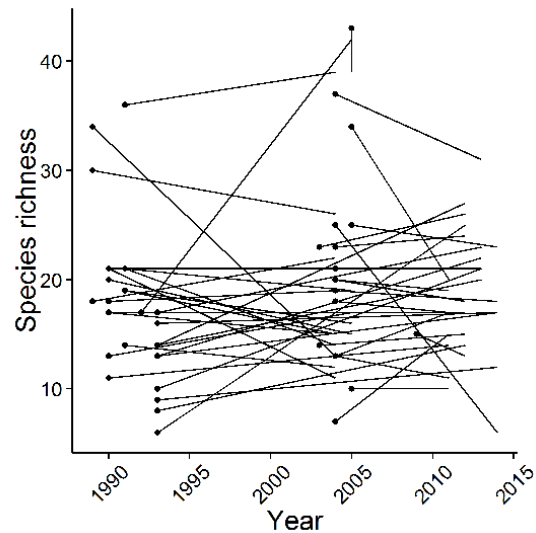
Table 9. Evaluation of species richness differences between sampling rounds and observers.

From linear mixed-effects model *F*-test.

	Num df	Den df.	<i>F</i> -value	<i>p</i> -value
Model intercept	1	49	446.24	<0.0001
Sampling round	1	43	0.53	0.4696
Observer	3	43	10.48	<0.0001
Round \times Observer	3	43	0.31	0.8143

Figure 13. Change in species richness, 1989–2014.

There were just as many gains as losses over time (24 increases, 5 equal, 21 decreases). →



Analysis 4 — Indicators of Alaskan vegetation types

There were 366 R10 plots (Fig. 14) that had previously been designated as one of six Region 10 vegetation types equivalent to Level IV of Viereck et al. (1992). Epiphytic lichen species composition differed significantly among all vegetation types (perMANOVA pseudo- $F = 13.2$, $p < 0.001$) and among all pairwise comparisons (all pairwise $p < 0.001$). From the pool of 273 lichen species, we identified 51 indicator lichen species for the six vegetation types (Table 10).

Lichen indicators of mixed conifer vegetation types included two *Hypogymnia* species. Foliose cyanolichens (e.g., species of *Nephroma*, *Peltigera*, *Lobaria*, *Sticta*) dominated indicators of riparian hardwood types. Foliose chlorolichens and several *Hypogymnia* species were indicators of *Pinus contorta* (shore pine) types. Cyanolichens, particularly species of *Pseudocyphellaria* and its recent *Lobaria* segregates, were indicators of *Picea sitchensis* (Sitka spruce) types. *Lobaria oregana* was the sole indicator of *Tsuga heterophylla* (western hemlock) types. Fruticose forage lichens of genus *Bryoria* characterized *Tsuga mertensiana* (mountain hemlock) types.

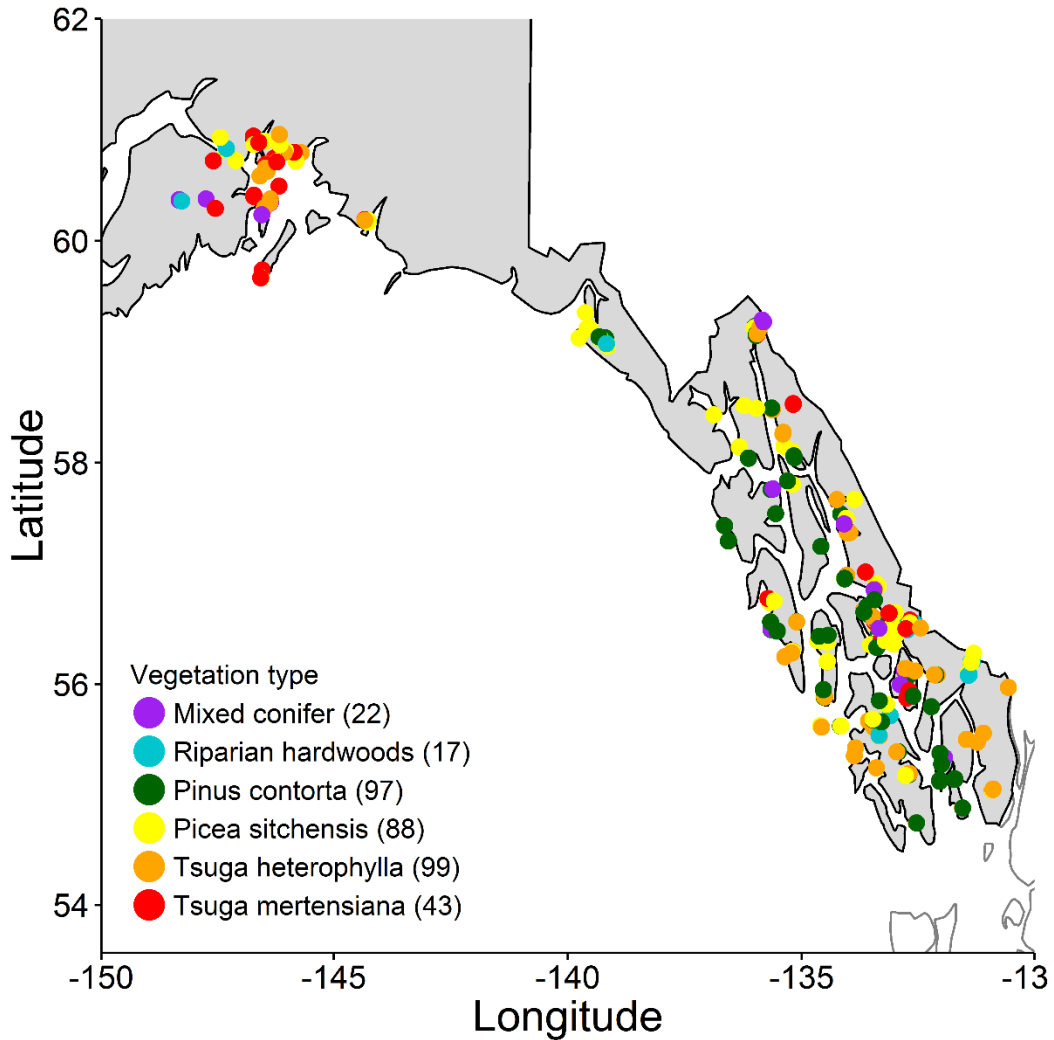


Figure 14. Vegetation types (and number of plots) as defined by Region 10 National Forests. Lichen indicators of these vegetation types are in Table 10. Numbers of plots are given in parentheses.

Table 10. Indicator species of vegetation types of coastal Alaska.

From a pool of 273 spp. in 366 R10 plots. Maximum indicator value bold text. All $p < 0.05$ from 9999 randomizations.

Indicator species	Rel. freq.	<i>IndVal</i> ¹ in vegetation types					
		Mixed conifer	Riparian hardwood	Pinus contorta	Picea sitchensis	Tsuga heterophylla	Tsuga mertensiana
		22 plots, 4 ind spp	17 plots, 19 ind spp	97 plots, 15 ind spp	88 plots, 11 ind spp	99 plots, 1 ind spp	43 plots, 3 ind spp
<i>Cladonia bellidiflora</i>	0.26	0.39	0.00	0.21	0.10	0.24	0.30
<i>Hypogymnia physodes</i>	0.11	0.34	0.07	0.12	0.14	0.10	0.07
<i>Hypogymnia occidentalis</i>	0.04	0.26	0.09	0.08	0.02	0.03	0.11
<i>Bryoria lanestris</i>	0.03	0.25	0.00	0.13	0.02	0.00	0.10
<i>Nephroma parile</i>	0.10	0.12	0.52	0.01	0.16	0.03	0.13
<i>Nephroma bellum</i>	0.24	0.12	0.50	0.03	0.28	0.12	0.30
<i>Peltigera collina</i>	0.16	0.11	0.62	0.05	0.27	0.07	0.05
<i>Nephroma resupinatum</i>	0.08	0.06	0.49	0.00	0.19	0.02	0.10
<i>Hypotrachyna sinuosa</i>	0.08	0.06	0.41	0.01	0.29	0.03	0.00
<i>Lobaria scrobiculata</i>	0.10	0.06	0.36	0.05	0.25	0.05	0.06
<i>Cladonia fimbriata</i>	0.11	0.06	0.35	0.06	0.18	0.06	0.22
<i>Lobaria pulmonaria</i>	0.14	0.02	0.68	0.04	0.28	0.03	0.02
<i>Nephroma isidiosum</i>	0.07	0.00	0.64	0.01	0.18	0.01	0.00
<i>Leptogium saturninum</i>	0.03	0.00	0.61	0.00	0.07	0.00	0.00
<i>Leptogium</i> spp.	0.03	0.00	0.61	0.00	0.06	0.00	0.00
<i>Parmeliella triptophylla</i>	0.04	0.00	0.47	0.02	0.10	0.03	0.00
<i>Peltigera polydactylon</i>	0.05	0.00	0.46	0.00	0.05	0.06	0.14
<i>Menegazzia subsimilis</i>	0.03	0.00	0.42	0.00	0.14	0.00	0.00
<i>Sticta fuliginosa</i>	0.13	0.00	0.35	0.03	0.29	0.16	0.07
<i>Cetrelia cetrarioides</i>	0.05	0.00	0.35	0.00	0.21	0.06	0.00
<i>Lobaria hallii</i>	0.05	0.00	0.32	0.00	0.25	0.00	0.00
<i>Fuscopannaria leucostictoides</i>	0.05	0.00	0.32	0.00	0.24	0.03	0.00
<i>Cladonia chlorophaea</i>	0.08	0.00	0.31	0.08	0.14	0.08	0.14
<i>Alectoria sarmentosa</i>	0.79	0.34	0.09	0.51	0.26	0.41	0.43
<i>Hypogymnia duplicata</i>	0.43	0.34	0.00	0.48	0.09	0.34	0.22
<i>Sphaerophorus aggr.</i>	0.79	0.33	0.05	0.47	0.34	0.43	0.41
<i>Hypogymnia enteromorpha</i>	0.58	0.32	0.10	0.43	0.29	0.32	0.31
<i>Platismatia glauca</i>	0.77	0.32	0.09	0.45	0.38	0.41	0.35
<i>Platismatia norvegica</i>	0.71	0.28	0.09	0.48	0.33	0.40	0.35
<i>Bryoria trichodes</i>	0.51	0.28	0.00	0.52	0.24	0.24	0.33
<i>Platismatia herrei</i>	0.41	0.22	0.00	0.52	0.16	0.33	0.17
<i>Bryocaulon pseudosatoanum</i>	0.12	0.17	0.00	0.39	0.01	0.01	0.23
<i>Bryoria carlotae</i>	0.06	0.17	0.00	0.30	0.01	0.00	0.07
<i>Hypogymnia inactiva</i>	0.17	0.16	0.00	0.62	0.04	0.02	0.02
<i>Hypogymnia oceanica</i>	0.21	0.09	0.16	0.57	0.09	0.08	0.03
<i>Bryoria cervinula</i>	0.08	0.09	0.00	0.32	0.08	0.03	0.07
<i>Cetraria californica</i>	0.04	0.07	0.00	0.31	0.05	0.00	0.00
<i>Cladonia rangiferina</i>	0.03	0.00	0.00	0.26	0.00	0.00	0.11
<i>Lobaria anomala</i>	0.14	0.00	0.34	0.02	0.44	0.06	0.06
<i>Pseudocyphellaria crocata</i>	0.12	0.00	0.25	0.01	0.41	0.09	0.04
<i>Nephroma helveticum</i>	0.15	0.09	0.17	0.00	0.40	0.15	0.13
<i>Hypogymnia lophyrea</i>	0.21	0.09	0.00	0.19	0.39	0.21	0.07
<i>Hypogymnia apinnata</i>	0.26	0.17	0.06	0.10	0.39	0.18	0.28
<i>Cetraria chlorophylla</i>	0.27	0.29	0.10	0.13	0.39	0.17	0.17
<i>Sticta beauvoisii</i>	0.06	0.00	0.00	0.00	0.36	0.08	0.08
<i>Ramalina farinacea</i>	0.07	0.07	0.20	0.00	0.36	0.02	0.00
<i>Fuscopannaria laceratula</i>	0.05	0.00	0.00	0.05	0.35	0.05	0.00
<i>Usnea filipendula</i>	0.05	0.00	0.00	0.00	0.31	0.12	0.00
<i>Lobaria anthraspis</i>	0.03	0.00	0.15	0.00	0.26	0.02	0.00
<i>Lobaria oregana</i>	0.40	0.19	0.20	0.01	0.40	0.45	0.24
<i>Parmeliopsis hyperopta</i>	0.27	0.27	0.09	0.33	0.06	0.08	0.52
<i>Bryoria fuscescens</i>	0.10	0.16	0.00	0.13	0.10	0.03	0.37
<i>Bryoria bicolor</i>	0.25	0.12	0.03	0.38	0.10	0.14	0.39

¹ *IndVal* = (relative abundance in given vegetation type × relative frequency in given vegetation type)^{0.5}

Discussion

Super-regional lichen–climate relationships

A major goal of ecologists and resource managers is the “reconciliation of local and regional perspectives” (Ricklefs 2004). Our super-regional approach integrated lichen responses to large ecological gradients at a sub-continental scale with regional implications for climate monitoring. A broad approach avoids idiosyncratic effects of local interactions among lichens (competition, facilitation), as these interactions become less important than climatic niche constraints across broad spatial areas (Peterson et al. 2011:40). Though other factors like evolutionary history (diversification, extinction) should also affect single species’ patterns, the fact that lichen communities had clear and consistent climate relationships suggests their immediate utility for climate indication.

We identified lichen indicators of potentially multiple climate zones, rather than restricting indicator values to only single zones. Such an approach acknowledges that lichen species could have different climatic niche tolerances. This has real consequences for climate monitoring since species with narrow tolerances might be more visible as climate change indicators. Consider a hypothetical example: what if (say) Alaska’s eastern Kenai Peninsula were to experience a drying transition from moist Zone 8 to mesic Zone 6? In this case we might expect a decline in single-zone indicators, but perhaps not as much change in multi-zone indicators like *Platismatia glauca* (Zone 6+8+9 indicator).

Survey method performance

Data from the FIA and R10 survey methods performed similarly in lichen–climate models, implying no clear superiority for climate modeling purposes. However, mixing the two datasets made models worse. For this reason, we do not recommend mixing data from the two survey methods in community analyses. Species capture (richness) was higher in the FIA plots, which had a physical area more than seven times larger than the R10 plots, suggesting that large-radius FIA plots may be advantageous if capturing locally rare species is the goal. Since richness indirectly affects lichen–climate gradient scores, the R10 plots may also warrant caution when attempting to interpret environmental gradients related to species richness. Aside from the obvious species–area relationship, larger plots can also better include microhabitat diversity in patchy landscapes. While smaller plot sizes are more convenient in difficult terrain or dense understories, users might consider how plot size ultimately affects diversity estimates, rare species capture, and transferability beyond focal regions.

Climate change in lichen communities

Given no substantial change in lichen community composition, species richness, or indicator species, we could not confirm a signal of climate change response for lichens in southcentral/southeast Alaska. This may be due to at least two reasons. The first is that biological responses could lag climate change over timespans greater than the 25 y period we studied (interval between sampling rounds averaged 12.9 y). Delayed climate response is inherently tied to species’ demographic rates: any climate-driven population declines would not become evident until persistent, long-lived individuals die without replacement. Likewise, any range expansions to new sites would depend on lichen species’ dispersal capacity and colonization rates (Gjerde et al. 2012). Despite “climate envelope” forecasts (Ellis et al. 2007), we don’t yet know enough about lichen demographic rates or about the expected rate of climate change to be able to predict whether lichen communities could “track” climate shifts.

The second, more likely reason we did not observe strong lichen community changes is the close proximity of the Alaskan plots to the Pacific Ocean, with weak representation of high-elevation alpine habitats where change is most expected. The Pacific has a moderating influence on coastal climate, and

reduces year-to-year variation in temperature, moisture availability and moisture seasonality. Lichen responses to climate are likely to be most visible at climatic “threshold” sites further inland and away from the coast (Root et al. 2014). Inland sites of continental Europe, for example, have seen rapid gains of heat-tolerant species and declines of arctic-boreal lichens over just two decades (van Herk et al. 2002; Aptroot and van Herk 2007; Ellis et al. 2009). Our findings suggest possible ways in which the detection of climate change with lichens might be improved by expanding both the habitat window and the time window of observation.

Future monitoring targets

Climate-driven changes in lichen communities could be precursors of larger changes in forests since epiphytic lichens have generally shorter life-cycles than trees and are more directly exposed to climatic fluctuations. What options are available to resource managers and practitioners who wish to capitalize on lichen responses as part of environmental monitoring programs? Several options that could be used alone or in combination:

Option 1: Resurvey entire communities at existing sites. A program could resurvey existing plots at 5- or 10-year intervals, determine new climate scores with the “NMS Scores” procedure, then assess whether lichen composition has changed and in which “direction.” For example, in southeast Alaska will there be a collective trend toward gradient extremes representing warmer and drier conditions? Towards more “continental” and less “coastal” conditions? Towards lichen assemblages with no current analogue?

Option 2: Resurvey select indicator species at existing sites. Systematically tracking abundance changes and range shifts of a few prominent indicator species may be more efficient than resurveying entire communities. For example, will “hot, dry” indicator species (e.g., *Candelaria*, *Polycauliona*, *Phaeophyscia*, *Physcia* spp.) expand northward or upward in elevation? Will there be range contractions for “moist, coastal” indicators (e.g., *Sphaerophorus* spp., *Platismatia norvegica*, coastal cyanolichens)? How far from existing sites will novel populations occur?

Option 3: Survey new sites. Establishing new plots can fill in gaps in “environmental space” that are unique combinations of climate not currently represented, which could help anticipate shifts into novel climate spaces. Priority locations should include climatic thresholds where rapid biological changes are expected. Another priority is to establish plots at sites with contrasting disturbance and harvest histories since stand attributes can mediate the effects of climate (Ellis et al. 2009).

Option 4: Include air quality gradients. Interactions between climate and air quality suggest that models could be improved by accounting for both. This is especially relevant since the biological effects of atmospheric nitrogen deposition can be amplified in hotter, drier climates (Sheppard et al. 2011; Jovan et al. 2012). Much of Alaska currently has good air quality relative to the continental US, but there are local exceptions related to ore processing and cruise ship emissions (Derr 2010; Schirokauer et al. 2014). Comprehensive environmental monitoring in Alaska and elsewhere would integrate lichens responses to both climate and air quality.

Conclusion

In summary, we 1) identified climate indicator species and climate scores across the Pacific states super-region, 2) evaluated two lichen survey methods in southcentral/southeast Alaska, 3) evaluated community change from 1989–2014 in southcentral/southeast Alaska, and 4) demonstrated lichen indicator species of vegetation types in southcentral/southeast Alaska. We found that lichen-based climate scores demonstrated clear responses to temperature, moisture, and other drivers over large areas and within specific regions. Indicator species revealed affinities to high-latitude/coastal, continental/montane,

and low-latitude/hot/dry habitats across the Pacific states super-region, as well as to specific vegetation types in the Alaska region. Large-radius and small-radius survey plots each had comparable performance in regional lichen–climate models, but there was a trade-off between plot size and species capture. Plot-sizes should not be mixed in lichen–climate models. Climate change responses were not evident in lichen communities of coastal Alaska over a 25-year period, probably due to demographic response lags and/or oceanic climate buffering. From continued surveys of lichen climate scores and indicator species, interagency environmental monitoring programs can begin to anticipate how climate change will impact forests of the US Pacific states.

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Appendix 1

Summary of species from the FIA dataset: relative frequency, mean abundance, and significant indicator values (across all climate zones, and for single climate zones).

Species	Relative freq	Mean abund (0-4)	Across-zone IndVal ¹	IndVal ¹ for single climate zones									
				1	2	3	4	5	6	7	8	9	10
<i>Ahtiana sphaerosporella</i>	0.05	0.11	0.31	0.13	--	--	0.18	0.21	--	--	--	--	--
<i>Alectoria imshaugii</i>	0.10	0.22	0.37	--	--	--	--	0.20	0.26	--	0.15	--	--
<i>Alectoria sarmentosa</i>	0.39	1.05	0.61	--	--	--	--	--	0.31	--	0.46	0.31	--
<i>Alectoria vancouverensis</i>	0.02	0.04	--	--	--	--	--	--	--	--	--	--	--
<i>Bryocaulon pseudosatoanum</i>	0.01	0.03	--	--	--	--	--	--	--	--	--	--	--
<i>Bryoria</i>	0.05	0.12	0.36	--	--	--	0.16	--	--	--	0.32	--	--
<i>Bryoria bicolor</i>	0.05	0.13	0.40	--	--	--	--	--	--	--	--	0.30	0.27
<i>Bryoria capillaris</i>	0.17	0.44	0.48	--	--	--	0.22	--	0.32	--	0.26	--	--
<i>Bryoria carlottae</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Bryoria cervinula</i>	0.01	0.02	0.20	--	--	--	--	--	--	--	--	0.20	--
<i>Bryoria fremontii</i>	0.20	0.56	0.62	--	--	--	0.29	0.45	0.29	--	--	--	--
<i>Bryoria friabilis</i>	0.03	0.07	0.24	--	--	--	0.09	--	--	--	0.23	--	--
<i>Bryoria fuscescens</i>	0.17	0.44	0.42	--	--	--	0.22	--	0.26	--	0.23	--	--
<i>Bryoria glabra</i>	0.07	0.19	0.36	--	--	--	--	--	--	0.17	0.22	0.26	--
<i>Bryoria implexa</i>	0.01	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Bryoria lanestris</i>	0.01	0.03	0.18	--	--	--	--	--	--	0.18	--	--	--
<i>Bryoria nadvornikiana</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Bryoria pseudofuscescens</i>	0.12	0.33	0.40	--	--	--	--	0.24	0.22	0.22	--	--	--
<i>Bryoria simplicior</i>	0.04	0.09	0.29	--	--	--	0.16	0.20	--	0.12	--	--	--
<i>Bryoria subcana</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Bryoria tenuis</i>	0.04	0.10	0.34	--	--	--	--	--	--	--	--	0.31	0.19
<i>Bryoria trichodes</i>	0.14	0.36	0.49	--	--	--	--	--	--	--	0.17	0.32	0.33
<i>Bunodophoron melanocarpum</i>	0.01	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Candelaria pacifica</i>	0.27	0.75	0.70	0.32	0.39	0.53	--	--	--	--	--	--	--
<i>Cetraria</i>	0.01	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Cetraria californica</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Cetraria canadensis</i>	0.12	0.27	0.45	--	--	--	--	0.22	0.26	0.30	--	--	--
<i>Cetraria chlorophylla</i>	0.34	0.81	0.53	--	--	--	--	--	0.32	0.33	0.26	--	--
<i>Cetraria merrillii</i>	0.25	0.64	0.55	--	--	--	--	0.49	0.25	0.20	--	--	--
<i>Cetraria orbata</i>	0.24	0.58	0.43	--	--	--	0.14	--	0.33	--	0.20	--	--
<i>Cetraria pallidula</i>	0.04	0.07	0.24	--	--	--	0.12	--	0.19	--	--	--	--
<i>Cetraria pinastri</i>	0.02	0.04	0.23	--	--	--	0.16	--	0.08	0.15	--	--	--
<i>Cetraria platyphylla</i>	0.25	0.66	0.55	--	--	--	0.17	0.32	0.41	--	--	--	--
<i>Cetraria sepincola</i>	0.01	0.04	0.30	--	--	--	--	--	--	0.30	--	--	--

Appendix 1 (con't). Summary of species.

Species	Relative freq	Mean abund (0-4)	Across-zone IndVal ¹	IndVal ¹ for single climate zones									
				1	2	3	4	5	6	7	8	9	10
<i>Cetraria subalpina</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Cetrelia cetrarioides</i>	0.02	0.04	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia</i>	0.03	0.07	0.21	0.11	--	--	--	--	--	--	0.16	0.10	--
<i>Cladonia albonigra</i>	0.02	0.04	0.24	--	0.09	--	--	--	--	--	0.09	0.20	--
<i>Cladonia amaurocraea</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia arbuscula</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia bacillaris</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia bellidiflora</i>	0.07	0.19	0.46	--	--	--	--	--	--	--	0.14	0.34	0.29
<i>Cladonia borealis</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia carneola</i>	0.04	0.09	0.27	--	--	--	--	--	--	--	0.23	0.15	--
<i>Cladonia cenotea</i>	0.02	0.03	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia chlorophaea</i>	0.03	0.07	0.22	--	--	--	--	--	--	--	0.09	0.17	0.12
<i>Cladonia coniocraea</i>	0.21	0.50	0.53	--	--	--	--	--	--	--	0.20	0.34	0.35
<i>Cladonia cornuta</i>	0.07	0.18	0.38	--	--	--	--	--	--	--	0.15	0.32	0.19
<i>Cladonia deformis</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia fimbriata</i>	0.08	0.17	0.31	--	--	--	--	--	--	0.17	--	0.23	0.14
<i>Cladonia furcata</i>	0.01	0.03	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia macilenta</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia maxima</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia merochlorophaea</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia multiformis</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia norvegica</i>	0.02	0.05	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia pyxidata</i>	0.01	0.03	0.24	--	--	--	--	--	--	--	0.13	0.20	--
<i>Cladonia rangiferina</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia scabriuscula</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia squamosa</i>	0.13	0.32	0.57	--	--	--	--	--	--	--	0.22	0.39	0.35
<i>Cladonia squamosa var subsquamosa</i>	0.05	0.12	0.30	--	--	--	--	--	--	--	0.11	0.14	0.24
<i>Cladonia straminea</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia subfurcata</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia sulphurina</i>	0.01	0.03	0.19	--	--	--	0.09	--	--	--	0.17	--	--
<i>Cladonia transcendens</i>	0.14	0.38	0.42	--	--	--	--	--	--	--	0.21	0.21	0.28
<i>Cladonia umbricola</i>	0.08	0.18	0.37	--	--	--	0.08	--	--	--	--	0.21	0.28
<i>Cladonia uncialis</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Cladonia verruculosa</i>	0.01	0.03	--	--	--	--	--	--	--	--	--	--	--
<i>Collema</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Collema curtisporum</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Collema furfuraceum</i>	0.05	0.12	0.37	--	0.20	0.30	--	--	--	--	--	--	--
<i>Collema nigrescens</i>	0.03	0.08	0.30	--	0.23	0.20	--	--	--	--	--	--	--

Appendix 1 (con't). Summary of species.

Species	Relative freq	Mean abund (0-4)	Across-zone IndVal ¹	IndVal ¹ for single climate zones									
				1	2	3	4	5	6	7	8	9	10
<i>Dendriscoaulon intricatum</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Dendrosticta wrightii</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Erioderma solediatum</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Esslingeriana idahoensis</i>	0.12	0.29	0.46	--	--	--	--	--	0.38	0.22	0.17	--	--
<i>Evernia mesomorpha</i>	0.01	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Evernia prunastri</i>	0.28	0.65	0.54	0.37	0.19	0.32	--	--	--	--	--	--	--
<i>Flavoparmelia caperata</i>	0.01	0.04	0.44	--	0.44	--	--	--	--	--	--	--	--
<i>Flavopunctelia flaventior</i>	0.06	0.17	0.59	--	0.43	0.41	--	--	--	--	--	--	--
<i>Fuscopannaria</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Fuscopannaria ahlneri</i>	0.01	0.02	0.18	--	--	--	--	--	--	0.17	--	--	0.08
<i>Fuscopannaria alaskana</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Fuscopannaria confusa</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Fuscopannaria laceratula</i>	0.01	0.02	0.17	--	--	--	--	--	--	--	--	0.14	0.10
<i>Fuscopannaria leucostictoides</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Fuscopannaria mediterranea</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Fuscopannaria pacifica</i>	0.02	0.04	--	--	--	--	--	--	--	--	--	--	--
<i>Heterodermia</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Heterodermia japonica</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Heterodermia leucomela</i>	0.01	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Heterodermia speciosa</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Hypogymnia</i>	0.03	0.06	--	--	--	--	--	--	--	--	--	--	--
<i>Hypogymnia apinnata</i>	0.20	0.52	0.51	--	--	--	--	--	--	--	0.32	0.23	0.32
<i>Hypogymnia austerodes</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Hypogymnia bitteri</i>	0.02	0.06	0.35	--	--	--	0.07	--	--	0.34	--	--	--
<i>Hypogymnia canadensis</i>	0.02	0.03	0.18	--	--	--	--	--	--	0.12	--	0.10	0.08
<i>Hypogymnia duplicata</i>	0.09	0.25	0.54	--	--	--	--	--	--	--	0.20	0.35	0.35
<i>Hypogymnia enteromorpha</i>	0.26	0.67	0.68	--	--	--	--	--	--	--	0.40	0.42	0.37
<i>Hypogymnia heterophylla</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Hypogymnia hultenii</i>	0.14	0.34	0.56	--	--	--	--	--	--	--	0.22	0.32	0.40
<i>Hypogymnia imshaugii</i>	0.46	1.26	0.65	--	--	--	0.29	0.39	0.41	--	--	--	--
<i>Hypogymnia inactiva</i>	0.16	0.43	0.47	0.18	--	--	--	--	--	--	0.38	0.30	--
<i>Hypogymnia lophyrea</i>	0.05	0.11	0.36	--	0.06	--	--	--	--	--	--	0.16	0.32
<i>Hypogymnia occidentalis</i>	0.17	0.42	0.41	--	--	--	0.15	--	0.27	0.26	--	--	--
<i>Hypogymnia oceanica</i>	0.02	0.04	0.25	--	--	--	--	--	--	--	0.06	0.15	0.19
<i>Hypogymnia physodes</i>	0.27	0.70	0.50	--	--	--	--	--	--	0.33	0.28	0.24	--
<i>Hypogymnia pulverata</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Hypogymnia rugosa</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Hypogymnia tubulosa</i>	0.17	0.37	0.41	0.22	--	--	--	--	--	0.24	0.26	--	--

Appendix 1 (con't). Summary of species.

Species	Relative freq	Mean abund (0-4)	Across-zone IndVal ¹	IndVal ¹ for single climate zones									
				1	2	3	4	5	6	7	8	9	10
<i>Hypogymnia vittata</i>	0.04	0.08	0.31	--	--	--	--	--	--	--	0.11	0.23	0.19
<i>Hypogymnia wilfiana</i>	0.13	0.30	0.43	--	--	--	0.20	--	0.30	--	0.19	--	--
<i>Hypotrachyna sinuosa</i>	0.07	0.16	0.36	--	0.16	--	--	--	--	--	--	0.19	0.24
<i>Imshaugia aleurites</i>	0.01	0.02	0.23	--	--	--	--	--	--	0.23	--	--	--
<i>Lathagrium fuscovirens</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Leptochidium albociliatum</i>	0.01	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Leptogidium contortum</i>	0.03	0.06	0.30	--	--	--	--	--	--	--	0.07	0.11	0.29
<i>Leptogidium dendriscum</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Leptogium</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Leptogium burnetiae</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Leptogium cyanescens</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Leptogium insigne</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Leptogium pseudofurfuraceum</i>	0.01	0.04	0.25	--	--	0.25	--	--	--	--	--	--	--
<i>Leptogium saturninum</i>	0.02	0.05	0.20	--	--	--	0.12	--	--	0.14	0.09	--	--
<i>Letharia columbiana</i>	0.26	0.72	0.61	--	--	--	0.37	0.46	--	--	--	--	--
<i>Letharia vulpina</i>	0.43	1.24	0.72	--	--	--	0.31	0.49	0.39	--	--	--	--
<i>Lobaria anomala</i>	0.07	0.16	0.28	0.15	--	--	--	--	0.17	0.17	--	--	--
<i>Lobaria anthraspis</i>	0.06	0.16	0.27	0.15	--	--	--	--	0.16	0.16	--	--	--
<i>Lobaria hallii</i>	0.02	0.03	--	--	--	--	--	--	--	--	--	--	--
<i>Lobaria linita</i>	0.09	0.24	0.49	--	--	--	--	--	--	--	0.23	0.32	0.29
<i>Lobaria oregana</i>	0.10	0.25	0.53	--	--	--	--	--	--	--	0.19	0.34	0.36
<i>Lobaria pulmonaria</i>	0.10	0.24	0.33	0.16	--	--	--	--	--	0.25	--	0.15	--
<i>Lobaria retigera</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Lobaria scrobiculata</i>	0.05	0.12	0.29	--	--	--	0.10	--	--	0.23	--	0.12	--
<i>Melanelia</i>	0.05	0.11	--	--	--	--	--	--	--	--	--	--	--
<i>Melanelixia californica</i>	0.11	0.30	0.64	--	--	0.64	--	--	--	--	--	--	--
<i>Melanelixia fuliginosa</i>	0.06	0.15	0.33	0.28	0.14	--	--	--	--	--	--	--	--
<i>Melanelixia subargentifera</i>	0.02	0.05	0.42	--	--	0.42	--	--	--	--	--	--	--
<i>Melanelixia subaurifera</i>	0.03	0.05	0.23	--	0.23	--	--	--	--	--	--	--	--
<i>Melanohalea elegantula</i>	0.14	0.39	0.44	0.25	--	0.18	--	0.31	--	--	--	--	--
<i>Melanohalea exasperatula</i>	0.18	0.47	0.44	--	--	--	0.22	--	0.25	0.26	--	--	--
<i>Melanohalea olivacea</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Melanohalea septentrionalis</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Melanohalea subelegantula</i>	0.06	0.16	0.34	--	--	--	0.24	0.20	0.16	--	--	--	--
<i>Melanohalea subolivacea</i>	0.29	0.82	0.49	--	--	0.30	0.24	0.30	--	--	--	--	--
<i>Melanohalea trabeculata</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Menegazzia subsimilis</i>	0.04	0.10	0.33	--	0.14	--	--	--	--	--	--	0.12	0.26
<i>Nephroma</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--

Appendix 1 (con't). Summary of species.

Species	Relative freq	Mean abund (0-4)	Across-zone IndVal ¹	IndVal ¹ for single climate zones									
				1	2	3	4	5	6	7	8	9	10
<i>Nephroma arcticum</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Nephroma bellum</i>	0.07	0.18	0.38	--	--	--	--	--	--	--	0.23	0.23	0.21
<i>Nephroma helveticum</i>	0.08	0.19	0.34	--	--	--	--	--	0.19	--	--	0.21	0.20
<i>Nephroma isidiosum</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Nephroma laevigatum</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Nephroma occultum</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Nephroma parile</i>	0.04	0.09	0.24	--	--	--	--	--	0.10	0.21	0.10	--	--
<i>Nephroma resupinatum</i>	0.04	0.10	0.25	--	--	--	--	--	0.17	0.13	--	0.13	--
<i>Niebla cephalota</i>	0.01	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Nodobryoria</i>	0.01	0.03	--	--	--	--	--	--	--	--	--	--	--
<i>Nodobryoria abbreviata</i>	0.28	0.79	0.69	--	--	--	0.30	0.49	0.35	--	--	--	--
<i>Nodobryoria oregana</i>	0.16	0.43	0.54	--	--	--	0.31	--	0.26	--	0.39	--	--
<i>Pannaria</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Parmelia</i>	0.05	0.11	--	--	--	--	--	--	--	--	--	--	--
<i>Parmelia hygrophila</i>	0.22	0.54	0.43	--	--	--	--	--	0.23	--	0.27	0.26	--
<i>Parmelia pseudosulcata</i>	0.06	0.13	0.40	--	--	--	--	--	--	--	0.17	0.35	0.18
<i>Parmelia saxatilis</i>	0.06	0.15	0.33	--	--	--	--	--	--	--	--	0.19	0.26
<i>Parmelia squarrosa</i>	0.03	0.06	0.27	--	--	--	--	--	--	0.14	--	--	0.24
<i>Parmelia sulcata</i>	0.42	1.09	0.51	0.28	--	--	--	--	0.29	0.32	--	--	--
<i>Parmeliella parvula</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Parmeliella triptophylla</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Parmelina coleae</i>	0.08	0.20	0.51	--	--	0.51	--	--	--	--	--	--	--
<i>Parmeliopsis</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Parmeliopsis ambigua</i>	0.14	0.34	0.45	--	--	--	0.20	--	0.27	0.29	--	--	--
<i>Parmeliopsis hyperopta</i>	0.25	0.64	0.62	--	--	--	0.22	--	--	--	0.49	0.33	--
<i>Parmotrema</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Parmotrema arnoldii</i>	0.02	0.04	0.24	0.16	0.19	--	--	--	--	--	--	--	--
<i>Parmotrema austrosinense</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Parmotrema perlatum</i>	0.02	0.05	0.61	--	0.61	--	--	--	--	--	--	--	--
<i>Peltigera</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Peltigera aphthosa</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Peltigera britannica</i>	0.06	0.14	0.42	--	--	--	--	--	--	--	--	0.34	0.26
<i>Peltigera collina</i>	0.11	0.25	0.30	0.19	--	--	--	--	0.15	--	--	0.19	--
<i>Peltigera degenii</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Peltigera elisabethae</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Peltigera horizontalis</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Peltigera leucophlebia</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Peltigera membranacea</i>	0.03	0.07	0.28	--	--	--	--	--	--	--	0.07	0.11	0.25

Appendix 1 (con't). Summary of species.

Species	Relative freq	Mean abund (0-4)	Across-zone IndVal ¹	IndVal ¹ for single climate zones									
				1	2	3	4	5	6	7	8	9	10
<i>Peltigera neopolydactyla</i>	0.06	0.15	0.42	--	--	--	--	--	--	--	0.18	0.32	0.23
<i>Peltigera pacifica</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Peltigera polydactylon</i>	0.01	0.01	0.18	--	--	--	--	--	--	--	0.05	0.09	0.15
<i>Peltigera praetextata</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Peltigera scabrosa</i>	0.02	0.04	0.22	--	--	--	--	--	--	--	--	0.11	0.18
<i>Phaeophyscia ciliata</i>	0.01	0.02	0.23	--	--	0.23	--	--	--	--	--	--	--
<i>Phaeophyscia hirsuta</i>	0.01	0.03	0.34	--	0.30	0.21	--	--	--	--	--	--	--
<i>Phaeophyscia kairamoi</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Phaeophyscia orbicularis</i>	0.08	0.21	0.67	--	0.38	0.54	--	--	--	--	--	--	--
<i>Physcia</i>	0.02	0.05	0.22	--	--	0.22	--	--	--	--	--	--	--
<i>Physcia adscendens</i>	0.18	0.47	0.67	0.30	0.41	0.48	--	--	--	--	--	--	--
<i>Physcia alnophila</i>	0.11	0.28	0.40	0.24	--	0.31	--	--	0.17	--	--	--	--
<i>Physcia biziana</i>	0.07	0.19	0.56	--	--	0.56	--	--	--	--	--	--	--
<i>Physcia caesia</i>	0.01	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Physcia dimidiata</i>	0.04	0.11	0.29	--	0.28	0.16	--	--	--	0.13	--	--	--
<i>Physcia dubia</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Physcia leptalea</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Physcia stellaris</i>	0.05	0.12	0.38	0.21	--	0.34	--	--	--	--	--	--	--
<i>Physcia tenella</i>	0.13	0.35	0.61	0.32	0.39	0.38	--	--	--	--	--	--	--
<i>Physcia tribacia</i>	0.02	0.04	0.33	0.33	--	--	--	--	--	--	--	--	--
<i>Physciella melanchra</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Physconia</i>	0.02	0.04	--	--	--	--	--	--	--	--	--	--	--
<i>Physconia americana</i>	0.11	0.28	0.49	--	--	0.49	--	--	--	--	--	--	--
<i>Physconia enteroxantha</i>	0.10	0.28	0.50	0.25	--	0.49	--	--	--	--	--	--	--
<i>Physconia fallax</i>	0.02	0.06	0.42	--	--	0.42	--	--	--	--	--	--	--
<i>Physconia isidiigera</i>	0.12	0.32	0.66	--	0.28	0.59	--	--	--	--	--	--	--
<i>Physconia leucoleiptes</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Physconia perisidiosa</i>	0.16	0.41	0.57	--	--	0.57	--	--	--	--	--	--	--
<i>Platismatia glauca</i>	0.51	1.40	0.67	--	--	--	--	--	0.32	--	0.46	0.41	--
<i>Platismatia herrei</i>	0.19	0.45	0.53	--	--	--	--	--	--	--	0.28	0.36	0.28
<i>Platismatia lacunosa</i>	0.08	0.19	0.48	--	--	--	--	--	--	--	--	0.33	0.35
<i>Platismatia norvegica</i>	0.15	0.39	0.61	--	--	--	--	--	--	--	0.22	0.40	0.40
<i>Platismatia stenophylla</i>	0.10	0.23	0.44	--	--	--	--	--	--	--	0.44	--	--
<i>Polycauliona candelaria</i>	0.06	0.14	0.27	--	--	0.19	--	0.13	--	0.15	--	--	--
<i>Polycauliona polycarpa</i>	0.16	0.43	0.61	0.31	0.34	0.40	--	--	--	--	--	--	--
<i>Polycauliona tenax</i>	0.02	0.05	0.46	--	0.46	--	--	--	--	--	--	--	--
<i>Polychidium muscicola</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Protopannaria pezizoides</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--

Appendix 1 (con't). Summary of species.

Species	Relative freq	Mean abund (0-4)	Across-zone IndVal ¹	IndVal ¹ for single climate zones									
				1	2	3	4	5	6	7	8	9	10
<i>Pseudocyphellaria crocata</i>	0.03	0.06	0.22	--	--	--	--	--	--	0.17	--	0.11	0.09
<i>Pseudocyphellaria mallota</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Pseudocyphellaria rainierensis</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Punctelia jeckeri</i>	0.03	0.08	0.40	--	0.28	0.29	--	--	--	--	--	--	--
<i>Ramalina</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Ramalina dilacerata</i>	0.06	0.14	0.29	0.14	--	--	--	--	--	0.25	0.11	--	--
<i>Ramalina farinacea</i>	0.20	0.48	0.47	0.27	0.41	--	--	--	--	0.19	--	--	--
<i>Ramalina leptocarpha</i>	0.02	0.04	0.60	--	0.60	--	--	--	--	--	--	--	--
<i>Ramalina menziesii</i>	0.01	0.03	0.42	--	0.42	--	--	--	--	--	--	--	--
<i>Ramalina obtusata</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Ramalina pollinaria</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Ramalina roesleri</i>	0.04	0.11	0.33	--	--	--	0.15	--	--	0.28	--	--	--
<i>Ramalina subleptocarpha</i>	0.03	0.08	0.44	--	0.41	0.25	--	--	--	--	--	--	--
<i>Ramalina thrausta</i>	0.02	0.04	0.19	0.08	--	--	--	--	--	0.19	--	--	--
<i>Scytinium cellulorum</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Scytinium lichenoides</i>	0.03	0.06	0.22	0.10	--	0.17	--	--	0.12	--	--	--	--
<i>Scytinium palmatum</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Scytinium polycarpum</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Scytinium teretiussculum</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Sphaerophorus aggr.</i> ³	0.27	0.74	0.79	--	--	--	--	--	--	--	0.38	0.53	0.45
<i>Sticta</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Sticta beauvoisii</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Sticta fuliginosa</i>	0.03	0.06	0.25	0.12	--	--	--	--	--	--	--	0.15	0.16
<i>Sticta limbata</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Sulcaria badia</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Teloschistes chrysophthalmus</i>	0.01	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Usnea</i>	0.14	0.33	0.31	0.17	--	--	--	--	--	0.19	--	0.17	--
<i>Usnea cavernosa</i>	0.01	0.03	--	--	--	--	--	--	--	--	--	--	--
<i>Usnea cornuta</i>	0.04	0.10	0.46	--	0.46	--	--	--	--	--	--	--	--
<i>Usnea cylindrica</i>	0.00	0.00	--	--	--	--	--	--	--	--	--	--	--
<i>Usnea filipendula</i>	0.21	0.55	0.40	--	--	--	--	--	0.24	--	0.23	0.22	--
<i>Usnea flavocardia</i>	0.08	0.23	0.40	0.24	--	--	--	--	--	--	--	0.19	0.26
<i>Usnea glabrata</i>	0.05	0.12	0.32	0.24	0.21	--	--	--	--	--	--	--	--
<i>Usnea glabrescens</i>	0.00	0.01	--	--	--	--	--	--	--	--	--	--	--
<i>Usnea hirta</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Usnea intermedia</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Usnea lapponica</i>	0.09	0.23	0.33	0.16	0.14	--	--	--	--	0.25	--	--	--
<i>Usnea longissima</i>	0.04	0.09	0.36	--	0.09	--	--	--	--	--	--	--	0.33

Appendix 1 (con't). Summary of species.

Species	Relative freq	Mean abund (0-4)	Across-zone <i>IndVal</i> ¹	<i>IndVal</i> ¹ for single climate zones									
				1	2	3	4	5	6	7	8	9	10
<i>Usnea pacificana</i>	0.02	0.05	--	--	--	--	--	--	--	--	--	--	--
<i>Usnea scabrata</i>	0.08	0.19	0.28	--	--	--	--	--	0.15	0.18	--	0.16	--
<i>Usnea subfloridana</i>	0.06	0.16	0.26	0.16	--	--	--	--	--	--	0.12	0.16	--
<i>Usnea substerilis</i>	0.02	0.04	--	--	--	--	--	--	--	--	--	--	--
<i>Xanthomendoza fallax</i>	0.06	0.18	0.45	--	0.17	0.41	--	--	--	--	--	--	--
<i>Xanthomendoza fulva</i>	0.11	0.29	0.42	0.22	0.14	0.34	--	--	--	--	--	--	--
<i>Xanthomendoza galericulata</i>	0.01	0.02	--	--	--	--	--	--	--	--	--	--	--
<i>Xanthomendoza hasseana</i>	0.11	0.29	0.41	--	0.27	0.28	--	--	0.18	--	--	--	--
<i>Xanthomendoza oregana</i>	0.13	0.36	0.55	--	0.51	0.33	--	--	--	--	--	--	--
<i>Xanthoria</i>	0.02	0.04	--	--	--	--	--	--	--	--	--	--	--
<i>Xanthoria parietina</i>	0.01	0.02	0.27	--	0.27	--	--	--	--	--	--	--	--

¹ *IndVal* = (relative abundance in given climate zone or set of zones × relative frequency in given zone or set of zones)^{0.5}

² proportion of 1118 plots in which the species occurred.

³ *Sphaerophorus* species were aggregated due to species concept changes over the sampling period.