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Lichen Communities as Climate Indicators in the U.S. Pacific States

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Cover photo: Nitrogen-fixing cyanolichens (*Peltigera* spp.), Larch Mountain, western Oregon. Photo by Robert J. Smith.

Abstract

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Epiphytic lichens are bioindicators of climate, air quality, and other forest conditions and may reveal how forests will respond to global changes in the U.S. Pacific States of Alaska, Washington, Oregon, and California. We explored climate indication with lichen communities surveyed by using both the USDA Forest Service Forest Inventory and Analysis (FIA) and Alaska Region (R10) methods. Across the Pacific States, lichen indicator species and ordination "climate scores" reflected associations between lichen community composition and climate. Indicator species are appealing targets for monitoring, while climate scores at sites resurveyed in the future can indicate climate change effects. Comparing the FIA and R10 survey methods in coastal Alaska showed that plot size affected lichen-species capture but not climate scores, whereas mixing data from both methods did not improve climate scores. Remeasurements from 1989 to 2014 in south-central and southeast Alaska revealed the importance of systematically random plot designs to detect climate responses in lichen communities. We provide an appendix of lichen species with climate indicator values. Lichen indicator species and community climate scores are promising tools for meeting regional forest management objectives.

Keywords: Bioindication, climate change, coastal Pacific Northwest, forest health, gradient analysis, indicator species, niche tolerance, ordination, site scores.

Contents

Introduction

This report explores lichen communities as indicators of climatic conditions in the U.S. 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. Changes in bioindicators may precede changes in other forest vegetation or processes. Epiphytic (tree-dwelling) forest lichens are fungus-photobiont partnerships that are especially good bioindicators because their lack of any protective cuticle or active water uptake system directly exposes them to changes in temperature and atmospheric moisture (Gauslaa et al. 2014, Nimis et al. 2002). Furthermore, because they rely on atmospheric sources of nutrition, they are proportionately more sensitive to differences in climate than in soils. The U.S. Forest Service (USFS), National Park Service (NPS), and U.S. Fish and Wildlife Service (USFWS) have conducted over 8,000 lichen surveys across U.S. forests, including those considered here. This report is part of a larger effort to unite inter-agency 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. Lichen-climate relationships have been established in several regions of the continental United States (Geiser and Neitlich 2007, Jovan and McCune 2004, McMurray et al. 2015, Root et al. 2015, Will-Wolf et al. 2015), and a regional focus in northern parts of the country is now warranted owing to projections of rapid ecological change in coastal Alaska. For example, climate change is expected to affect Alaskan animal populations, tree populations, vegetation productivity, glacier and permafrost melt, microbial decomposition, wildfire patterns, and other ecosystem processes (Hennon et al. 2012, Wolken et al. 2011). There is also evidence that a changing climate will affect coastal Alaska's epiphytic lichen communities (Root et al. 2014). Surveying and monitoring lichen communities could provide an 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 that are now outside the region.

This report addresses several biological questions regarding lichen communities in the U.S. Pacific States, including southeast and south-central 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 south-central 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? How could answers to these questions inform future survey design and monitoring efforts?

Our objective was to address these questions and provide guidance on opportunities to use lichen community responses in interagency environmental monitoring programs in Alaska and other U.S. Pacific States. Knowledge of patterns and processes in lichen communities will be fundamental for environmental monitoring, and for anticipating how changing climates might affect forest ecosystems in the Western United States.

Methods

Lichens and Climate Data

Lichen data originated from two sources: Forest Inventory and Analysis (FIA) plots and USFS Alaska Region (R10) plots. The FIA plots were a subset of nationwide plots, while the R10 plots were located in coastal south-central and southeastern Alaska on the Tongass and Chugach National Forests, the Glacier Bay, Sitka, and Klondike Gold Rush units of the National Park Service, and Kodiak National Wildlife Refuge. Complete FIA protocols are described by Will-Wolf (2010: 11–14), and R10 protocols are described by 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 [0.936 vs. 0.127 ac]), number of sampling rounds (one vs. many), criteria for locating plots (random vs. targeted), geographic coverage (all Pacific coastal U.S. states vs. south-central/south-eastern Alaska only), and temporal coverage (1998 to 2014 vs. 1989 to 2014). Results of this report further quantify how each dataset performs in gradient models.

Before analyses, we translated R10 abundance values to their equivalents on the FIA scale following the crosswalk used by Geiser (2004: 18), placing all values on the same approximately logarithmic 0 to 4 scale. Values on the scale represent: 0 = not present;

1 = 1 to 3 thalli observed; 2 = 4 to 10 thalli observed; 3 = more than 10 thalli observed but on <50 percent of available branches and stems; and 4 = more than 10 thalli observed on >50 percent of available substrates. We harmonized species names per FIA analyst guidelines (Will-Wolf 2010). 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 seven climate variables: mean annual air temperature (°C), continentality (mean annual temperature difference between warmest and coldest months, °C), mean annual precipitation (mm y^{-1}), annual heat-moisture index (ratio of temperature to precipitation, unitless), frost-free period (d), percentage of precipitation as snow (%), and climatic moisture deficit (reference evaporation minus precipitation, mm). Because climate variables are commonly highly correlated, we converted them to principal components (PCs) using principal component analysis (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 9,999 randomizations. The 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 a 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 Development Core Team 2015).

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 1,118 FIA lichen plots throughout Alaska, Washington, Oregon, and California. This super-regional approach spans portions of 8 of the 17 designated FIA lichen model 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 (<three occurrences) and species-poor plots (<five species). The central gradient model for this was nonmetric multidimensional scaling (NMS) ordination (Kruskal 1964). NMS assigns scores to sites based on similarity of lichen community composition; because 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).

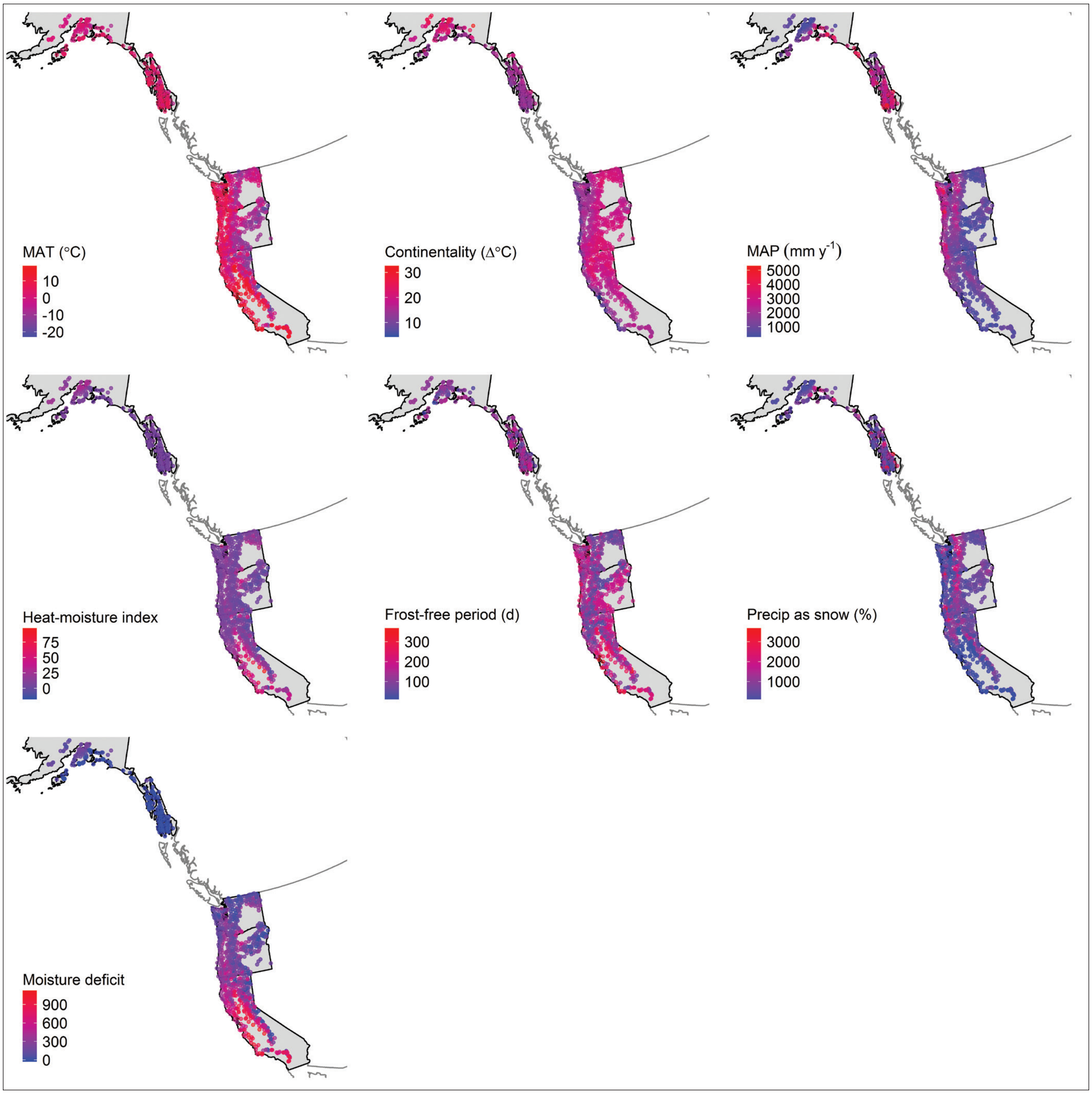

Figure 1—Raw climate values at each Forest Inventory and Analysis and Region 10 lichen plot in the Pacific States area. MAT = mean annual temperature. MAP = mean annual precipitation. Source: ClimateWNA (Wang et al. 2012).

Table 1—Summary of climate principal components (PCs)

Item	PC 1	PC 2	PC 3
Variance explained (percent)	42.3	27.6	15.5
Cumulative variance (percent)	42.3	69.9	85.4
Climate correlations:			
Mean annual air temperature	0.70	−0.55	−0.37
Continentality	−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
Precipitation as snow	−0.78	0.04	−0.37
Moisture deficit index	0.80	0.35	−0.27

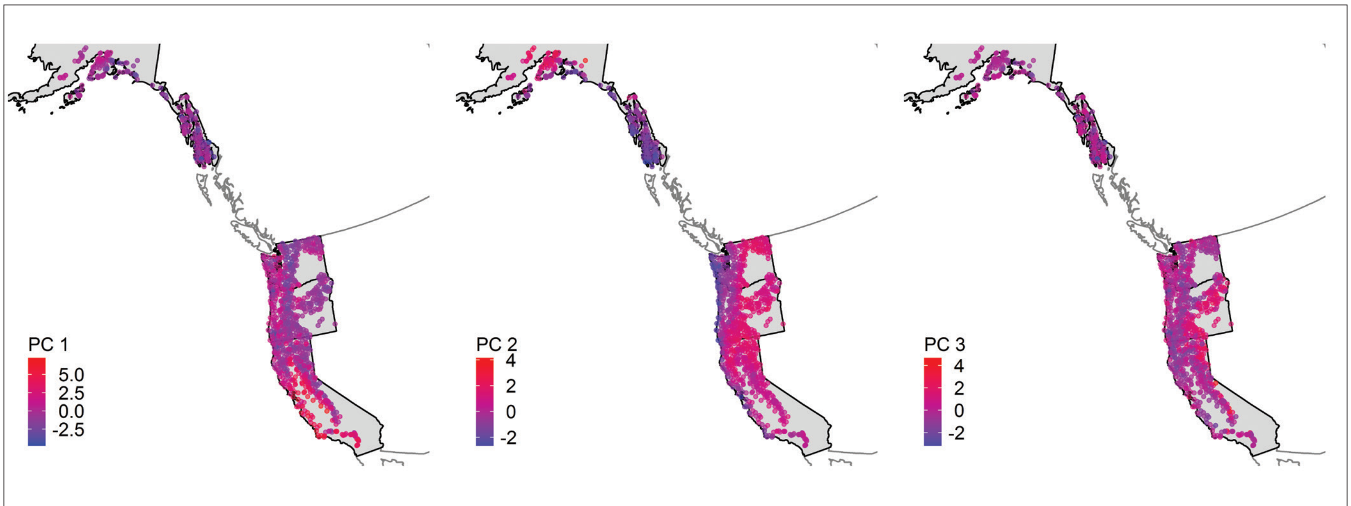

Figure 2—Principal components (PCs) climate values at each Forest Inventory and Analysis and Region 10 lichen plot in the Pacific States area. The first three (of seven possible) PCs were used in analyses. PC 1 represents a thermal gradient, PC 2 is a gradient of moisture and continentality, and PC 3 is a more complex climatic gradient.

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 three 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 in R package "optpart" (Roberts 2015). This algorithm optimizes the ratio of within-group to among-group similarity (Roberts 2015). Without requiring lichen information, it groups each plot into 1 of 10 climate zones sharing similar climatic characteristics. We identified 10 climate zones based on Euclidean distances of the three climate PCs, using 19 random starts with 99 iterations each: Zone 1 = warm mesic lowlands, Zone 2 = warm dry subcontinental, Zone 3 = hot dry lowlands, Zone 4 = cold mesic subcontinental, Zone 5 = cold dry continental, Zone 6 = cold mesic continental, Zone 7 = cool dry continental, Zone 8 = cool moist subcontinental, Zone 9 = mild moist suboceanic, and 10 = warm wet hypermaritime.

To identify the lichens that best characterized each climate zone or set of zones, we used multigroup indicator species analysis in R package "indicspecies" (de Cáceres et al. 2010). Multigroup 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. 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). A perfect indicator species would occur at all sites within a given zone and only within that zone.

Analysis 2—Alaska Regional Models: Survey Method Performance

Given that two lichen datasets existed for the same region in southeast and south-central 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 sets of species, 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 Analysis 2, 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 coregional plots for each.

Evaluating performance required a three-step process to (1) calibrate, (2) reciprocally fit, and (3) 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 to 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 PCORD 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 Development Core Team 2015).

Pairwise FIA vs. R10 comparisons were not strictly possible because plots were not exactly colocated, 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 12 sites (2 methods × 12 sites,

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

Data source	Step 1: Calibration	Step 2: Reciprocal fitting	Step 3: Evaluation
FIA model	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 model	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

FIA = Forest Inventory and Analysis, R10 = Region 10 (Alaska) of the U.S. Forest Service.

exactly colocated). 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. 2016). We repeated all these analyses for 12 plots that had both the FIA and R10 methods performed by the same observer at the exact same location (colocated).

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 because they had not 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 we used blocked perMANOVA in PCORD 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. Because 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" (Lund and Agostinelli 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. 2016). 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 PCORD (blocks = plots).

Results

Analysis 1—Super-Regional Lichen-Climate Relationships

The super-regional model was an NMS ordination of 1,118 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 percent and 37.7 percent 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, fig. 3). In geographic space, Axis 1 scores depicted a coastal-interior gradient (fig. 4), while Axis 2 scores reflected a north-south latitudinal gradient (fig. 5). Species richness ranged from 5 to 44 species per plot (fig. 6). Ten climate zones—collections of sites that shared similar climatic attributes—were based on optimal partitioning of the three climate PCs (table 4, figs. 7 and 8). Each climate zone was associated with a set of indicator species (table 5, fig. 9). Indicator values reach a maximum of 1 when a species is found only within a given climate zone at all sites of that climate zone. A complete species list and indicator values are in the appendix.

Table 3—Summary and climate correlations for Pacific States super-regional model

Item	NMS Axis 1 scores	NMS Axis 2 scores
Explained variation in community composition (percent)	30.8	37.7
Multivariate climate fit (xR^2)	0.63	0.62
Univariate climate fit (*tau*):		
Latitude	0.32	0.51
Mean annual air temperature	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
Precipitation as snow	−0.09	0.32
Moisture deficit index	−0.10	−0.49
PC 1	0.12	−0.33
PC 2	−0.46	−0.24
PC 3	−0.15	−0.05

Note: Cross-validated R^2 (xR^2) expresses fit of community axis to climate variables. Kendall's *tau* is a nonparametric correlation coefficient. NMS = nonmetric multidimensional scaling. PC = principal component.

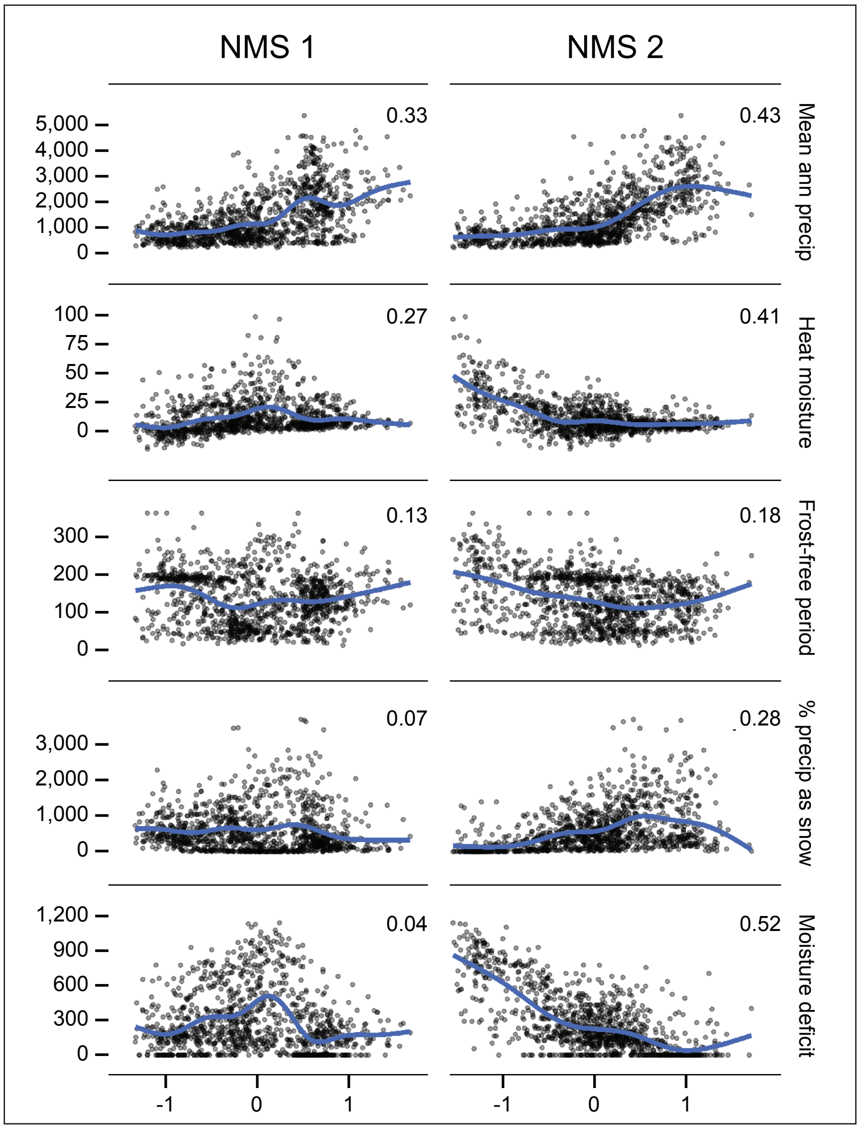

Figure 3—Nonparametric regression of lichen community nonmetric multidimensional scaling (NMS) scores against climate variables. Fit lines and 10-fold cross-validated R^2 values (from generalized additive models) reflect relationships between climate variables and community composition (NMS axes).

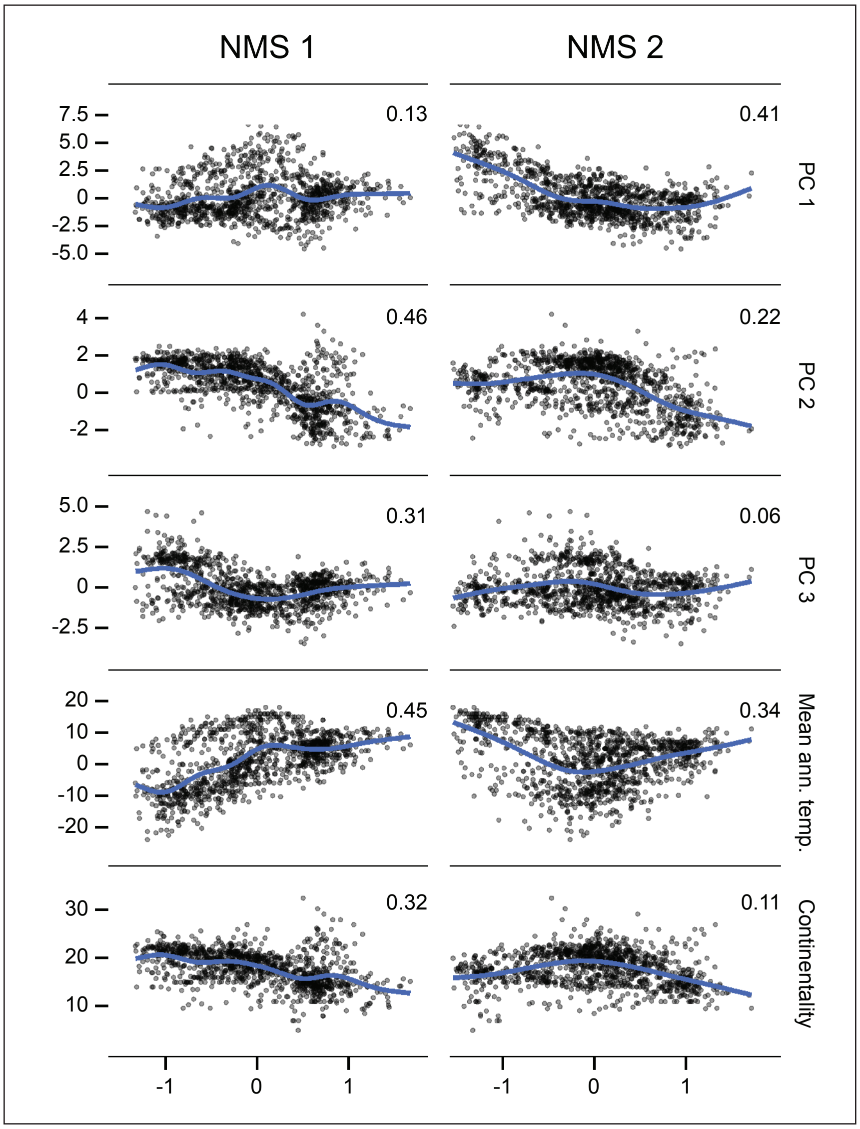

Figure 3—continued

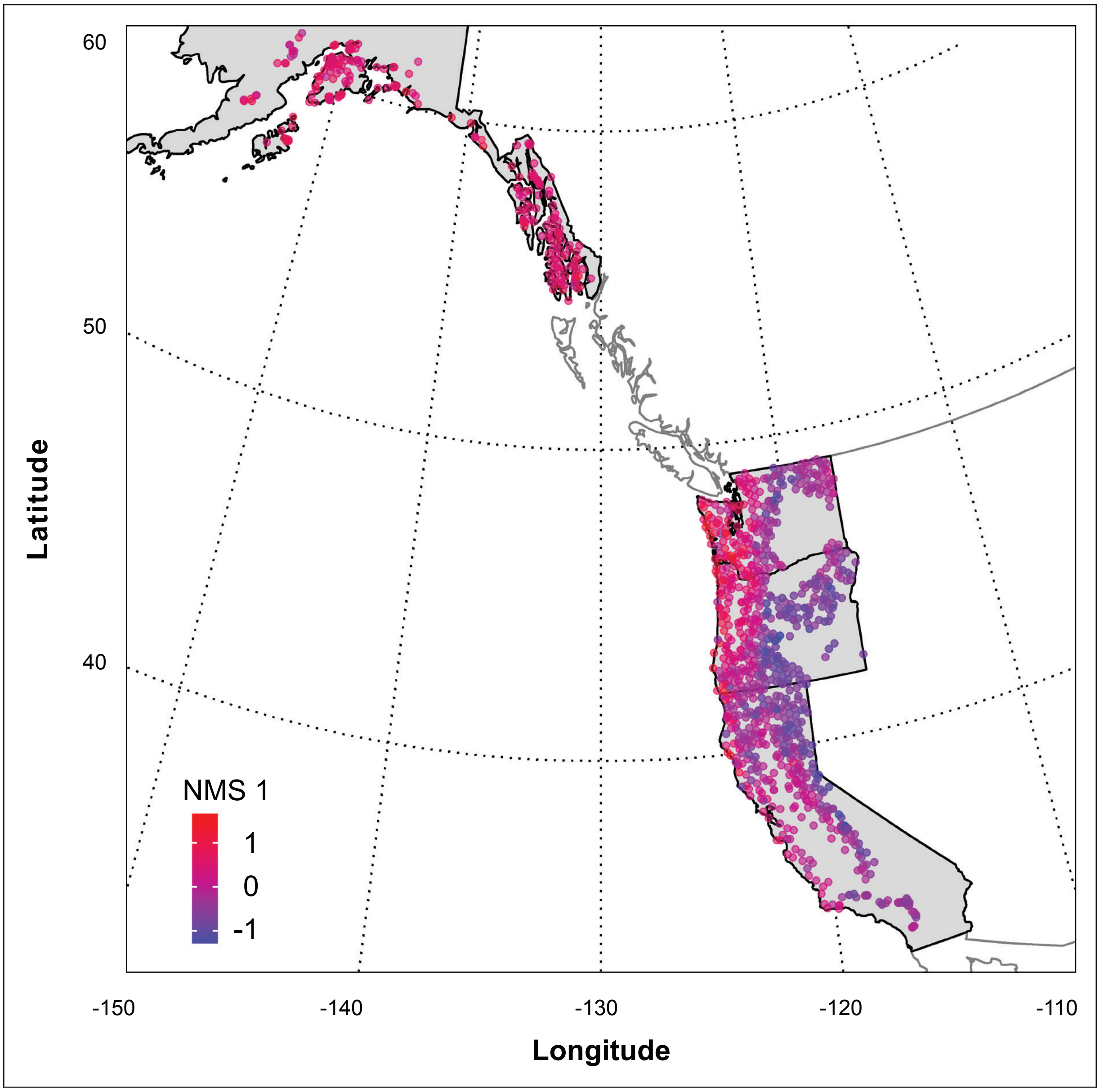

Figure 4—Lichen community nonmetric multidimensional scaling (NMS) scores (Axis 1) from the Pacific States super-regional model. Similar scores (colors) represent similar lichen species composition at each site. NMS Axis 1 reflects lichen community responses to an oceanic-continental gradient (temperature, continentality).

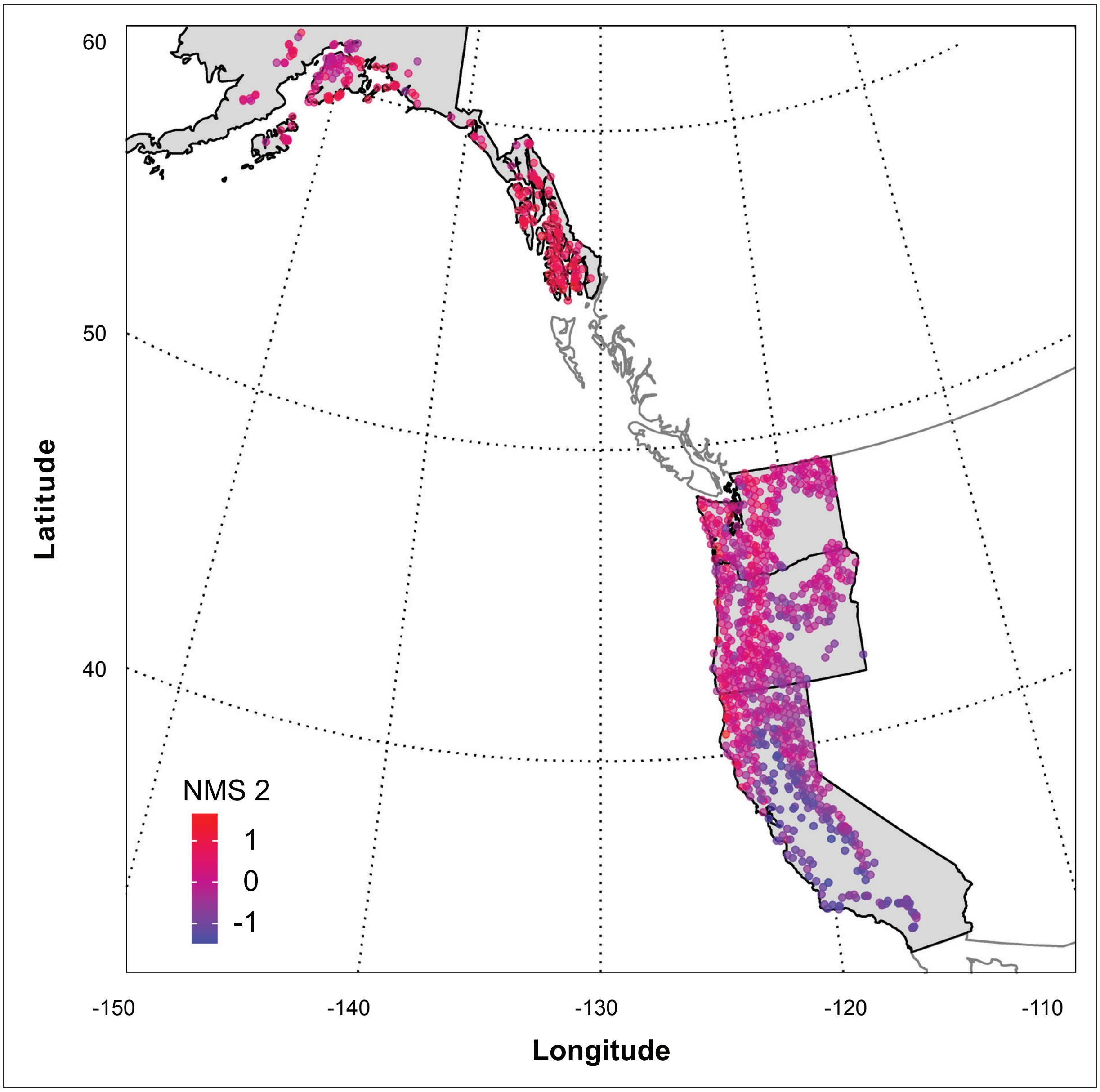

Figure 5—Lichen community nonmetric multidimensional scaling (NMS) scores (Axis 2) from the Pacific States super-regional model. Similar scores (colors) represent similar lichen species composition at each site. NMS Axis 2 reflects responses to precipitation and moisture deficit.

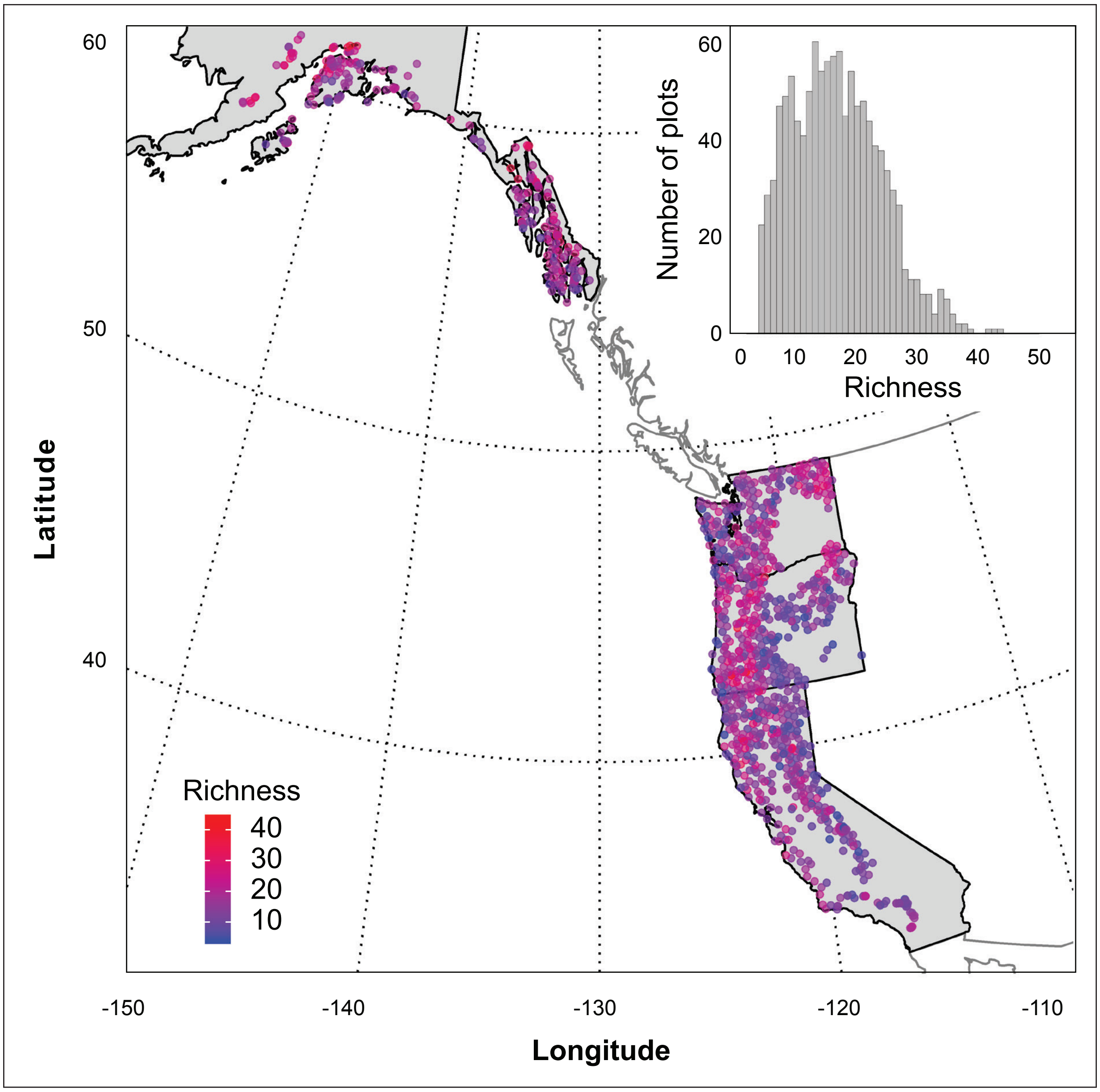

Figure 6—Lichen species richness in Forest Inventory and Analysis plots across the Pacific States area. Richness distributions shown in geographic space (main figure) and as a frequency distribution (inset). Richness ranged from 5 to 44 species per plot.

Table 4—Kendall's tau correlation with climate zones in the Pacific States super-region

Climate variables	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6	Zone 7	Zone 8	Zone 9	Zone 10
Mean annual air temperature	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
Precipitation 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

Note: Zone 1 = warm mesic lowlands, Zone 2 = warm dry subcontinental, Zone 3 = hot dry lowlands, Zone 4 = cold mesic subcontinental, Zone 5 = cold dry continental, Zone 6 = cold mesic continental, Zone 7 = cool dry continental, Zone 8 = cool moist subcontinental, Zone 9 = mild moist suboceanic, Zone 10 = warm wet hypermaritime.

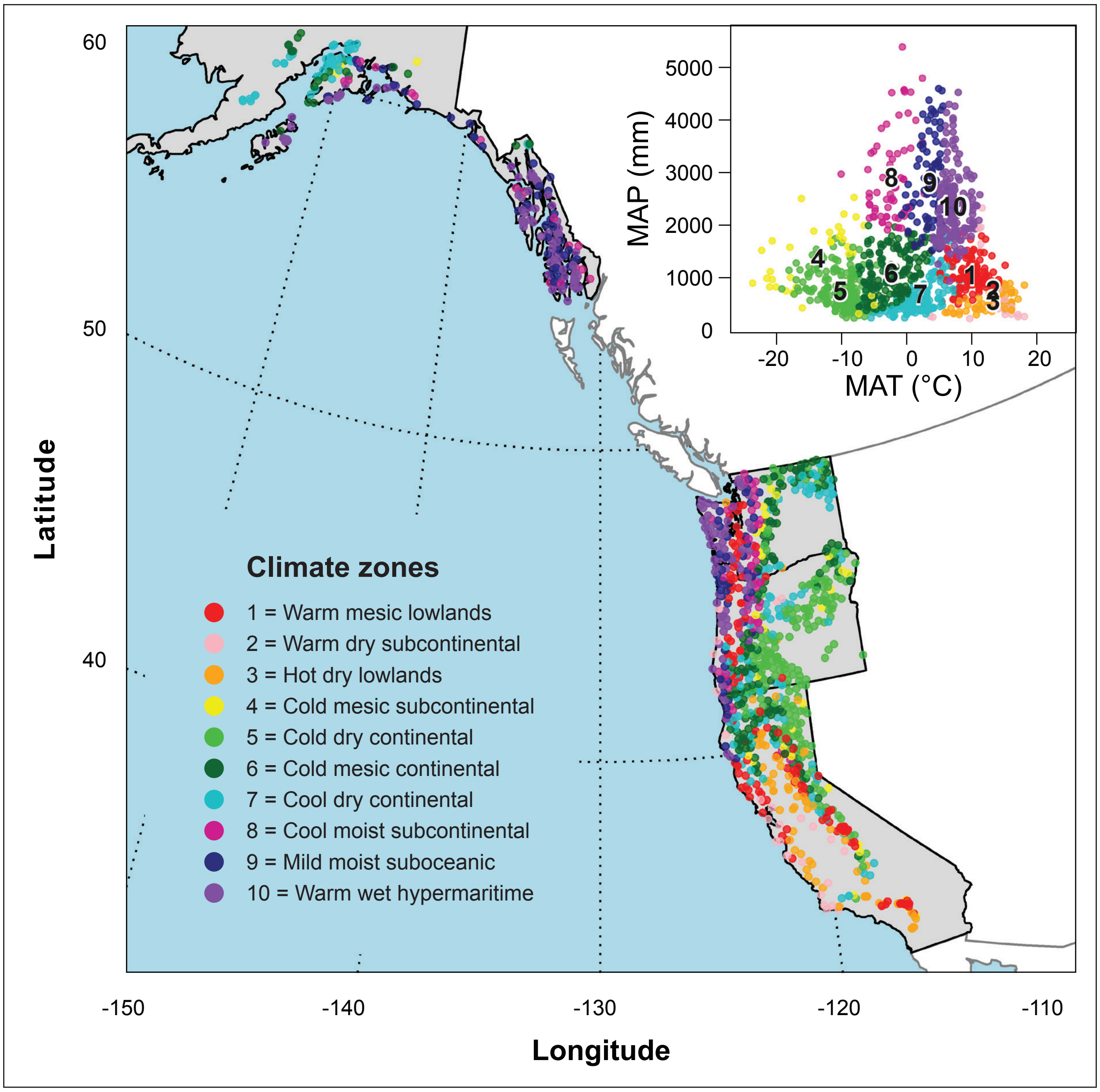

Figure 7—Climate zones for each Forest Inventory and Analysis lichen plot in the Pacific States area. Climate zones are mapped in geographic space (main figure) and climate space (inset: precipitation vs. temperature). MAP = mean annual precipitation. MAT = mean annual temperature.

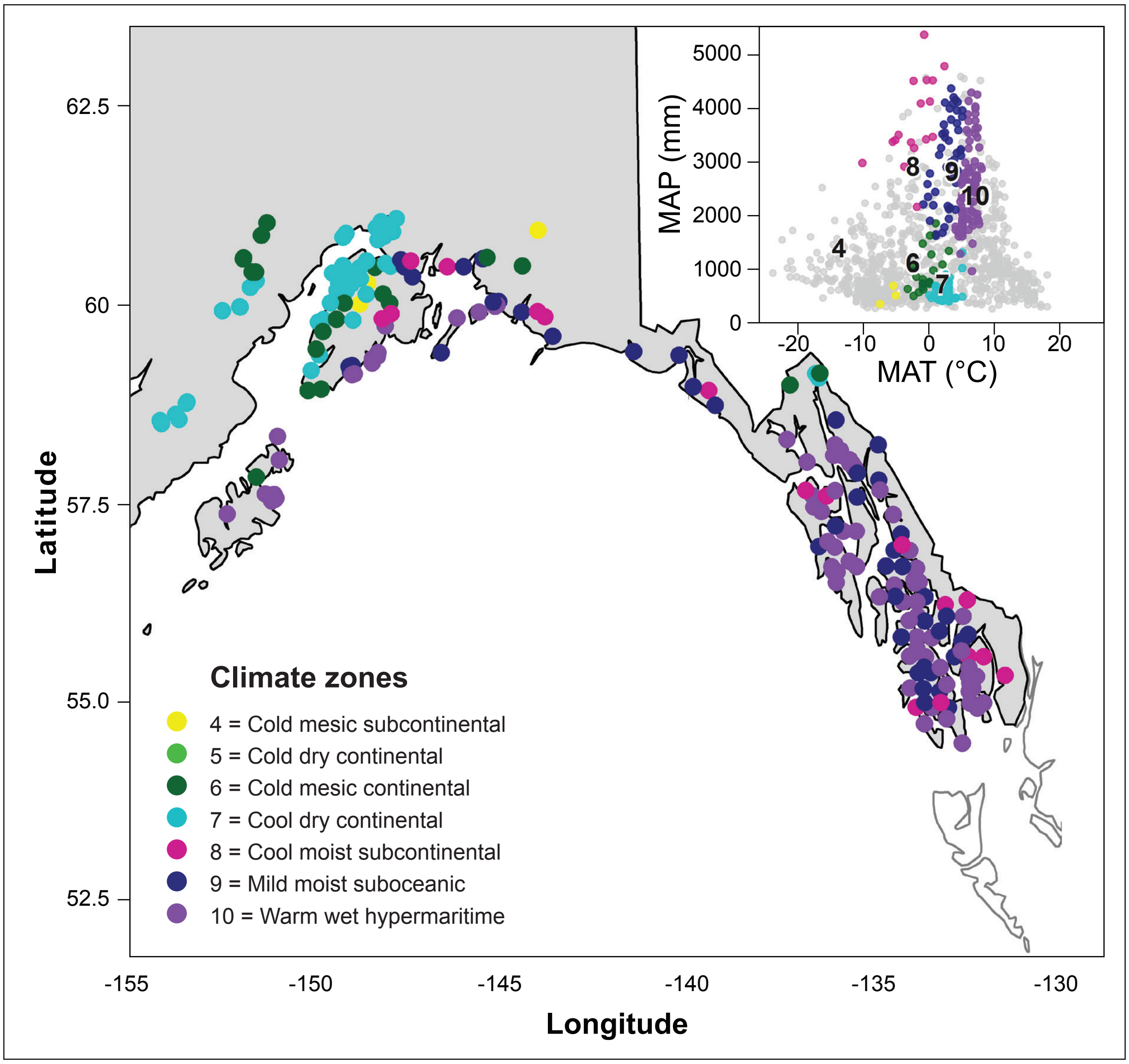

Figure 8—Climate zones for each Forest Inventory and Analysis lichen plot in the Alaska region. Climate zones are mapped in geographic space (main figure) and climate space (inset: precipitation vs. temperature). Colored symbols = Alaska plots; grey symbols = Washington, Oregon, and California plots. MAP = mean annual precipitation. MAT = mean annual temperature.

Table 5—Select indicator species for climate zone combinations of the Pacific States super-region

Indicator species	*IndVal*[a] all zones	*IndVal*[a] for single climate zones									
		1	2	3	4	5	6	7	8	9	10
Sphaerophorus aggr.[b]	0.79								0.38	0.53	0.45
Platismatia norvegica	0.61								0.22	0.40	0.40
Hypogymnia enteromorpha	0.68								0.40	0.42	0.37
Platismatia glauca	0.67						0.32		0.46	0.41	
Parmeliopsis hyperopta	0.62				0.22				0.49	0.33	
Alectoria sarmentosa	0.61						0.31		0.46	0.31	
Cetraria merrillii	0.55					0.49	0.25	0.20			
Hypogymnia imshaugii	0.65				0.29	0.39	0.41				
Letharia vulpina	0.72				0.31	0.49	0.39				
Nodobryoria abbreviata	0.69				0.30	0.49	0.35				
Bryoria fremontii	0.62				0.29	0.45	0.29				
Letharia columbiana	0.61				0.37	0.46					
Melanelixia californica	0.64			0.64							
Physconia isidiigera	0.66		0.28	0.59							
Phaeophyscia orbicularis	0.67		0.38	0.54							
Candelaria pacifica	0.70	0.32	0.39	0.53							
Physcia adscendens	0.67	0.30	0.41	0.48							
Polycauliona polycarpa	0.61	0.31	0.34	0.40							
Physcia tenella	0.61	0.32	0.39	0.38							
Parmotrema perlatum	0.61		0.61								

Note: See complete list in appendix. Blank spaces indicate species had nonsignificant indicator value (but may be present). Zone 1 = warm mesic lowlands, Zone 2 = warm dry subcontinental, Zone 3 = hot dry lowlands, Zone 4 = cold mesic subcontinental, Zone 5 = cold dry continental, Zone 6 = cold mesic continental, Zone 7 = cool dry continental, Zone 8 = cool moist subcontinental, Zone 9 = mild moist suboceanic, Zone 10 = warm wet hypermaritime.

[a] *IndVal* = (relative abundance in given climate zone or set of zones × relative frequency in given zone or set of zones) 0.5.

[b] *Sphaerophorus* species were aggregated owing to species concept changes over the sampling period.

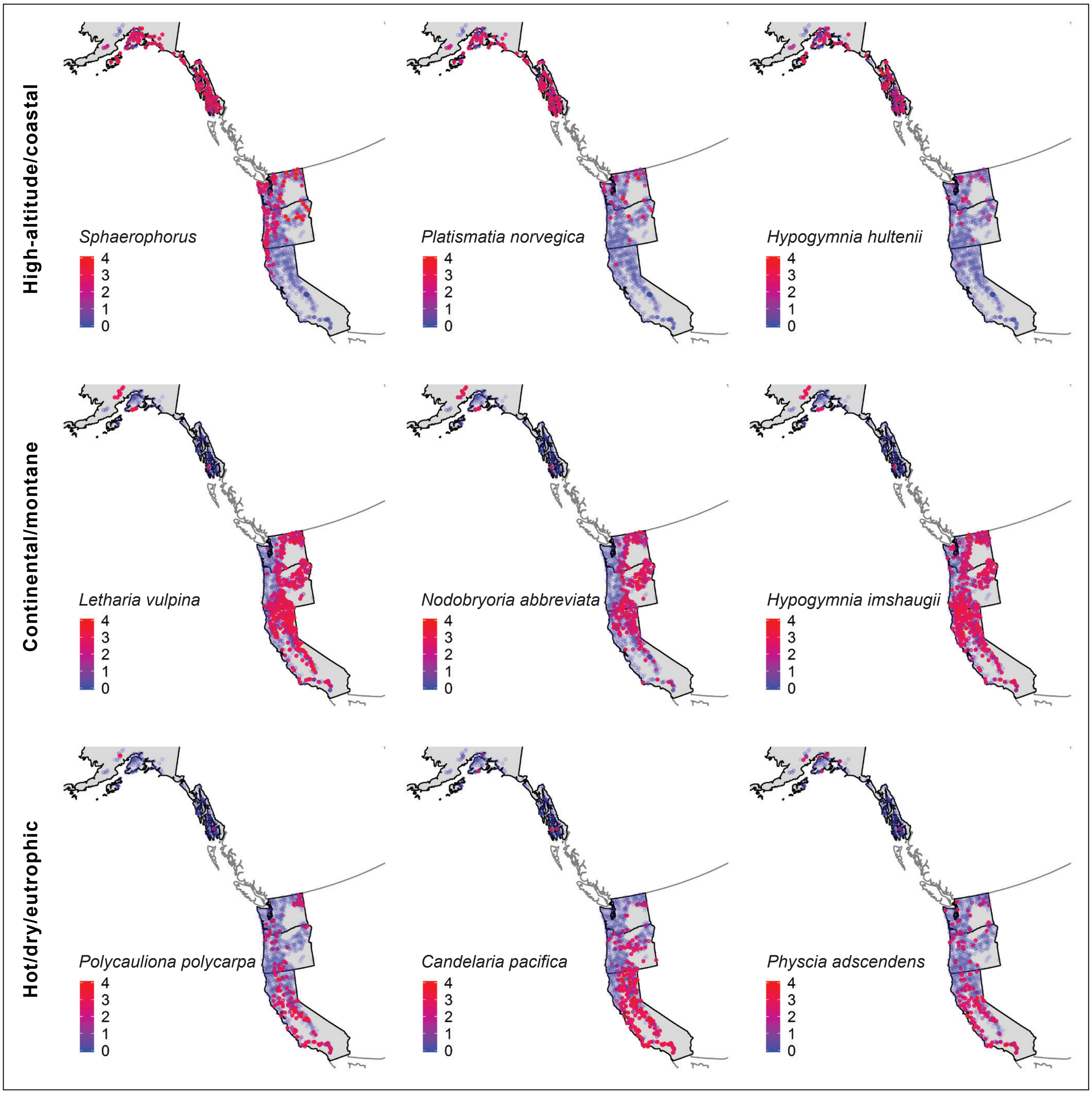

Figure 9—Indicator species' distributions across the Pacific States area. See appendix A for complete list of climate indicator values.

Analysis 2—Alaska Regional Models: Survey Method Performance

The goal of Analysis 2 was to evaluate the respective performance of the FIA vs. R10 survey data in regional gradient models to inform future choices of survey methodology. 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 to 100 (table 6 and fig. 10). Axis 1 scores explained 49 percent 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 percent 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 percent 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.

Table 6—Summary of three lichen-climate regional gradient models (FIA, R10, FIA+R10)

	FIA model			**R10 model**			**FIA+R10 model**		
Stress (%)	19.9			19.6			24.6		
Explained variation (%)	74.3			78.2			68.9		
	Axis 1	**Axis 2**	**Axis 3**	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 1**	**Axis 2**	**Axis 3**
Explained variation (%)	49.0	14.8	10.5	39.6	25.0	13.6	33.9	19.7	15.3
Multivariate climate fit (xR^2)	0.31	0.04	0.06	0.18	0.14	0.01	0.22	0.14	0.06
Univariate climate fit (*tau*):									
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 temperature	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
Precipitation 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
PC 1	-0.06	0.07	-0.18	-0.04	0.16	0.05	0.02	-0.18	-0.19
PC 2	-0.24	-0.06	0.08	-0.16	0.12	-0.08	-0.23	-0.11	0.04
PC 3	0.01	0.09	-0.20	0.01	0.12	0.06	0.07	-0.13	-0.21

Note: Climate fit statistics indicate the strength of association between nonmetric multidimensional scaling scores and climate. FIA = Forest Inventory and Analysis. R10 = Region 10 (Alaska) of the U.S. Forest Service.

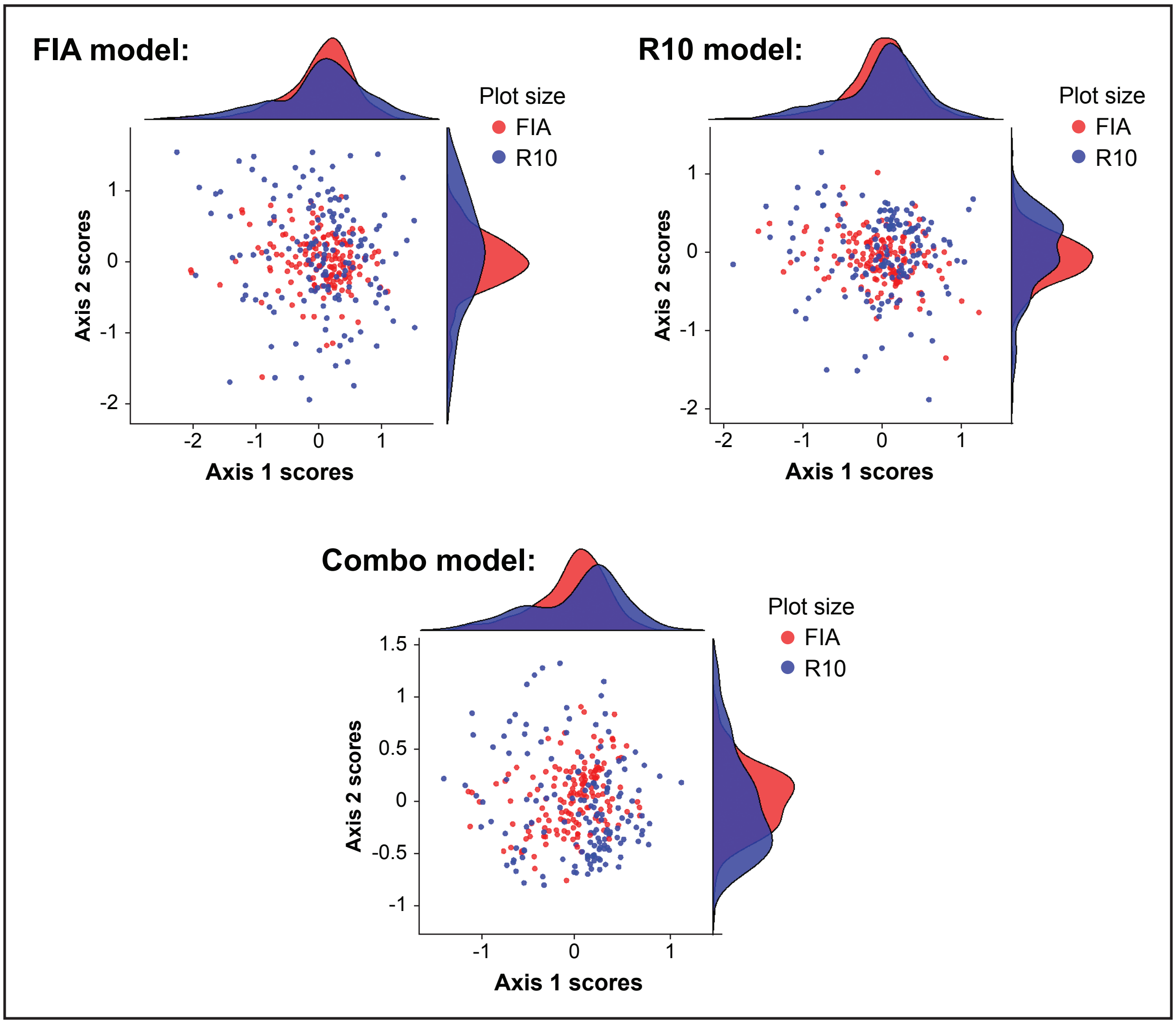

Figure 10—Ordination scores for three models: Forest Inventory and Analysis (FIA) model (left), Region 10 (R10) model (center), and combined gradient models (right). Marginal density plots are frequency distributions of scores for each dataset. Similar frequency distributions in an ordination would suggest that the two datasets have similar ranges in lichen community composition.

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. 10). Axis 1 scores explained 39.6 percent of the variation in community composition. Correlations with climate revealed that community variation along this axis represents an oceanic-inland gradient similar to the FIA model. Axis 2 scores explained 25.0 percent 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, and explained less of the variation in the species data, with a generally weaker fit to climate (table 6).

Evaluating the 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 percent on a 0- to 100-percent 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 more comparable than other axes (fig. 11).

Mean species capture in the group of large-radius FIA plots was an estimated 3.2 species (about 20 percent) greater than in the group of R10 plots (95-percent confidence interval = 1.7 to 4.6 species; $F = 18.9$, $p < 0.0001$) (fig. 12). Beta diversity (species turnover) was greater in R10 plots as a result of greater gamma diversity (observing more species regionwide) and lower alpha diversity (fewer average species per plot) (table 8). Gamma diversity differences could be due to the nonrandom placement of R10 plots, and the unintentional inclusion of nonepiphyte 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 colocated 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 (because 95 species × 0.05 assumed probability of false detection = 4.7 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

Table 7—Assessment of within-model fit and agreement between Forest Inventory and Analysis and Region 10 models

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

Note: Fit of each model is the percentage of variance explained from a nonmetric fit of ordination distances vs. original Sørensen distances. Agreement between models is the 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.

Table 8—Comparison of attributes for Forest Inventory and Analysis (FIA) and Region 10 (R10) sized plots.

Attribute	FIA plots	R10 plots	Notes
Radius	36.6 m (120 ft)	12.8 m (42 ft)	FIA 2.9 times larger
Area[a]	0.379 ha	0.051 ha	FIA 7.3 times larger
Time constraints	½ – 2 hr	½ – 2 hr	Identical
Observer skill	Trainees and experts	Experts	
Resampled?	Not yet in Alaska	At least once for 50 sites	
Temporal coverage	2004–2009 (for Alaska)	1989–2014	
Spatial coverage	all land ownerships, all U.S. regions	R10 national forests; Glacier Bay, Klondike and Sitka NPS; Kodiak National Wildlife Refuge	
Location assignment	Systematic, random	Targeted, nonrandom	
Location dispersion	Systematic, random	Clustered, nonrandom	
Transferability	Standardized across the United States	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 species
Gamma γ diversity	150	171	R10: more species overall
Beta diversity (γ/α–1)	6.6	9.6	R10: more compositional variation among plots
Procrustes agreement[b] (co-regional plots)	0.66	0.67	Similar agreement
Procrustes agreement[b] (exactly colocated plots)	0.98	0.98	Similar agreement
NMS gradient scores	Interpret freely	Caution, if related to richness	

[a] FIA lichen survey area excludes subplot areas inside the plot radius.
[b] Correlation-like statistic bounded [0–1], and approaching 1 for ordinations of identical data.
NPS = National Park Service. NMS = nonmetric multidimensional scaling.

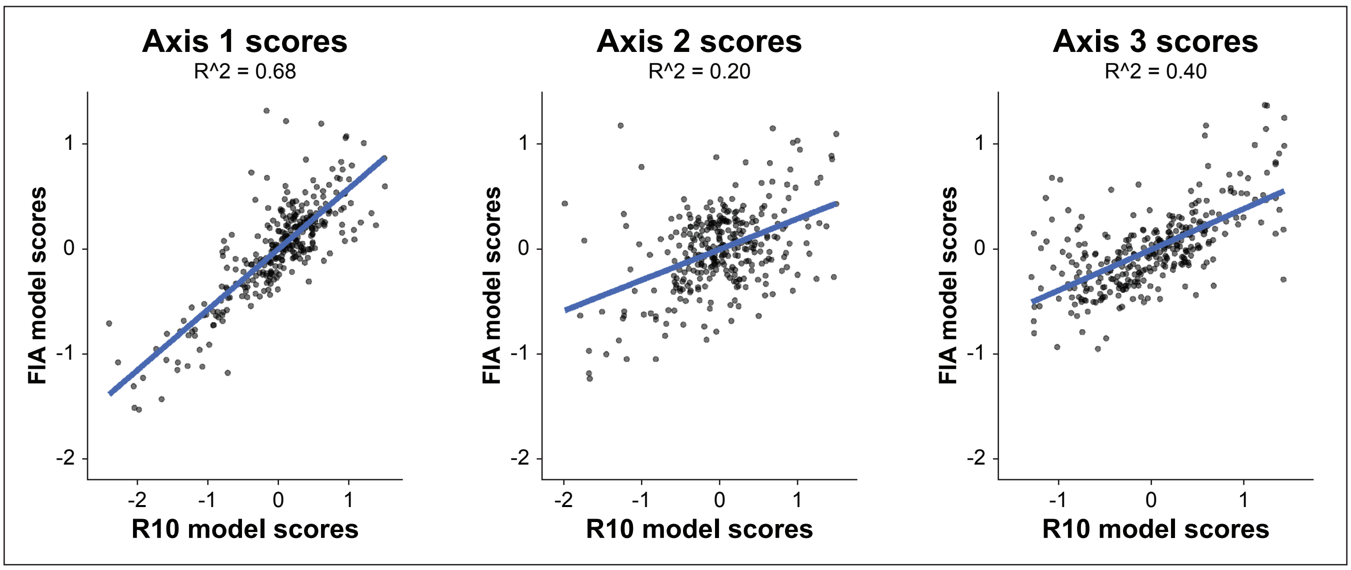

Figure 11—Direct comparison of nonmetric multidimensional scaling (NMS) scores for Forest Inventory and Analysis (FIA) and Region 10 (R10) models after Procrustes rotation to maximum similarity. Perfect agreement between models would have points fall along a straight line with $R^2 = 1$.

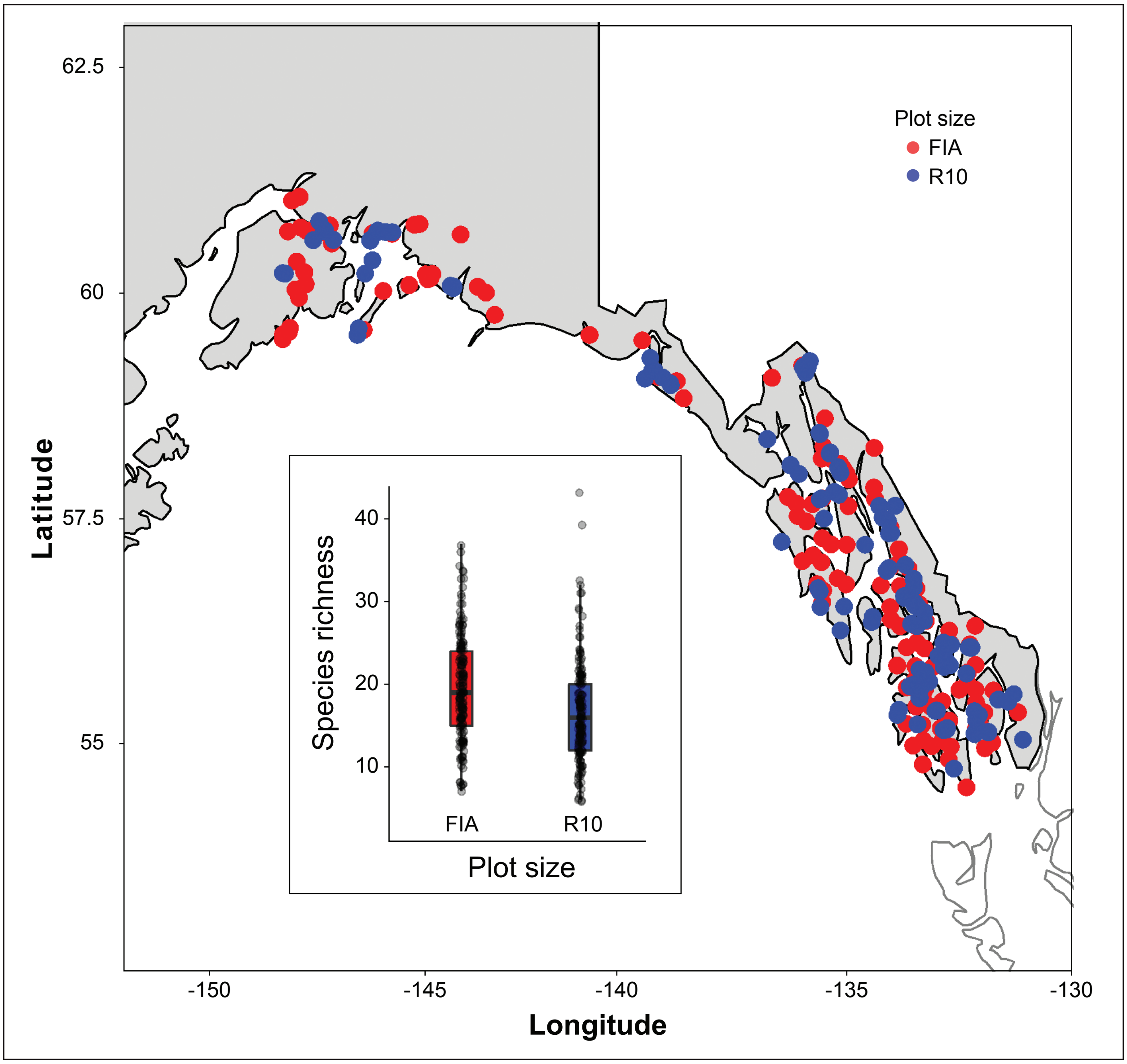

Figure 12—Locations and species richness of co-occurring Forest Inventory and Analysis (FIA) and Region 10 (R10) plots used in Analysis 2. Inset: Mean species richness in FIA plots was about three species greater than R10 plots. Boxplot center bars = median. Box ends = upper/lower quartiles. Whisker ends = 1.5 × interquartile range. Dots = each observation.

large-radius FIA method was an estimated 3.7 species (about 15 percent) greater than when using the R10 method (95 percent 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.

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 that had elapsed between rounds of sampling, averaging 12.9 elapsed years. 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. 13). Using another method, there were no changes in community composition between sampling rounds (blocked perMANOVA pseudo-$F = 0.49$, $p = 0.16$).

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. 14). 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 four significant "increaser" species and four 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 (because 166 species × 0.05 assumed probability of false detection = 8.3 species).

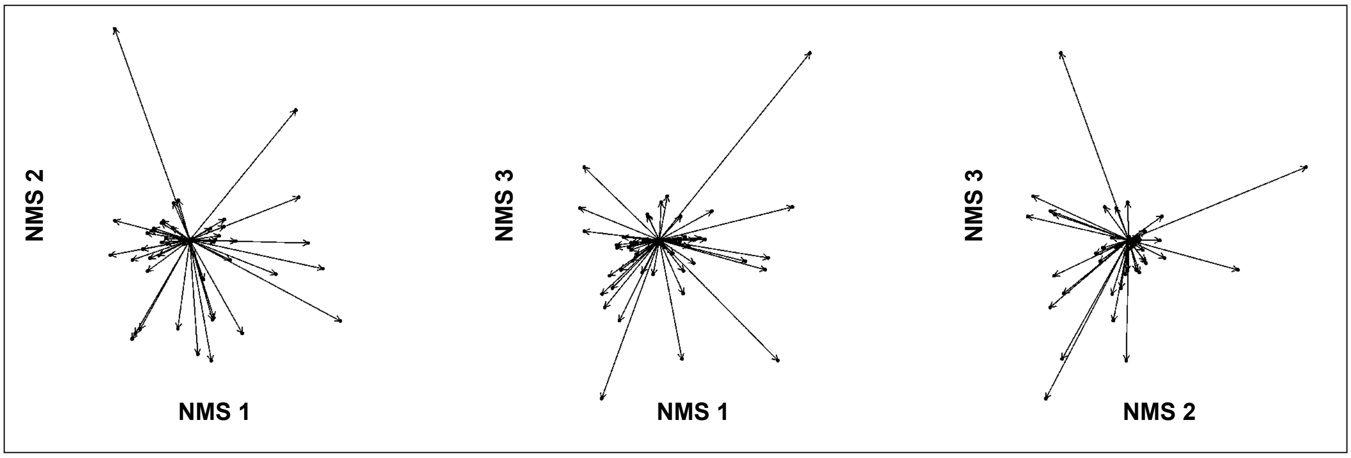

Figure 13—Centered successional vectors from nonmetric multidimensional scaling (NMS) ordination of 50 resampled plots in Alaska. Vector tails = lichen plot 1st-round NMS scores, vector heads = 2nd-round scores. Vectors radiate uniformly, indicating that the pattern of species replacement over time was not significantly different from random.

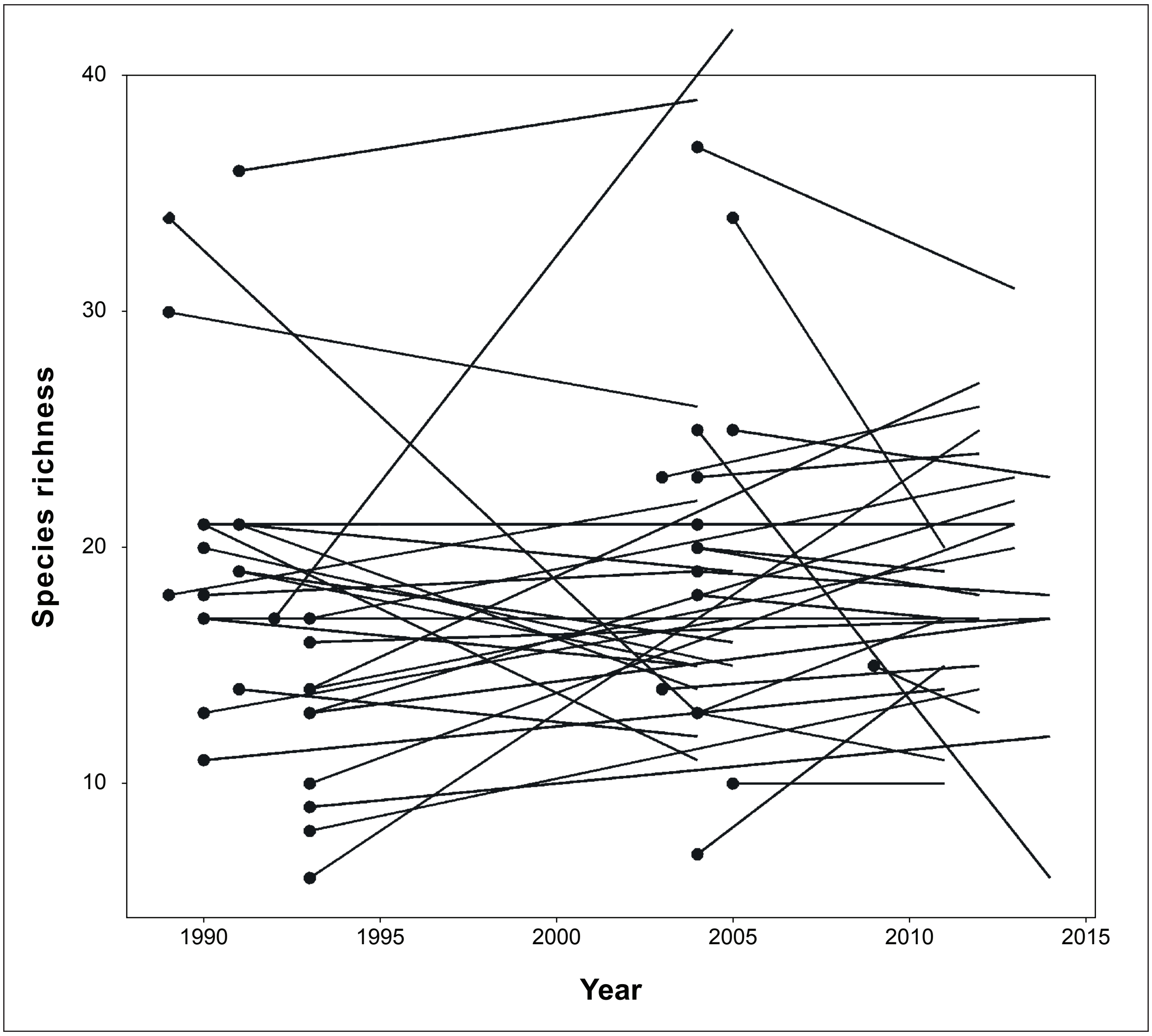

Figure 14—Change in species richness, 1989–2014. Each line = one resampled plot. There were just as many gains as losses over time (24 increases, 5 equal, 21 decreases).

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

Coefficient	Num d.f.	Den d.f.	*F*-value	*p*-value
Model intercept	1	49	446.24	<0.0001
Sampling round	1	43	0.53	0.4696
Observer	3	43	10.48	<0.0001
Sampling round × observer	3	43	0.31	0.8143

Note: Values are from orthogonal F-tests of linear mixed-effects model coefficients, blocking by site. Statistical degrees of freedom = “d.f.” for numerator (Num) and denominator (Den).

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 subcontinental 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 because 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 such a case, we might expect a decline in single-zone indicators, but perhaps not as much change in multizone indicators like *Platismatia glauca* (Zone 6 + 8 + 9 indicator).

Survey Method Performance

Evaluating how data perform in regional gradient models can help inform which survey methodology to use for regional forest assessments and inventories. 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, for example, in simple inventories. Because richness indirectly affects lichen-climate gradient scores, the R10 plots may also warrant caution when attempting to interpret any environmental gradients that are related to species richness. Aside from the obvious species-area relationship, larger plots can also better include microhabitat diversity in patchy landscapes. Although 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 south-central/southeast Alaska. This may be due to at least two reasons. The first is that biological responses could lag climate change over time spans greater than the 25-year period we studied (interval between sampling rounds averaged 12.9 years). 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 do not 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 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 farther 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 (Aptroot and van Herk 2007, Ellis et al. 2009, van Herk et al. 2002). Our findings suggest possible ways detection of climate change with lichens might be improved by expanding both the habitat window and the time window of observation. For example, systematically random plot locations would encompass a broader range of habitats and cover inland climatic thresholds where change in lichen communities is expected.

Future Monitoring Targets

Climate-driven changes in lichen communities could be precursors of larger changes in forests because 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 could be used individually 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? Could there be a trend toward more "continental" and less "coastal" conditions? Could there be a trend toward 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 because 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 because the biological effects of atmospheric nitrogen deposition can be amplified in hotter, drier climates (Jovan et al. 2012, Sheppard et al. 2011). Much of Alaska currently has good air quality relative to the continental United States, 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 lichen 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 south-central/southeast Alaska, and (3) evaluated community change from 1989 to 2014 in south-central/southeast Alaska. We found that lichen-based climate scores demonstrated clear relationships to temperature, moisture, and other factors 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. Large- and small-radius survey plots each had comparable performance in regional lichen-climate models, but there was a tradeoff 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 because of demographic response lags 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 affect forests of the U.S. Pacific States.

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English Equivalents

When you know:	Multiply by:	To get:
Millimeters (mm)	0.394	Inches
Centimeters (cm)	0.394	Inches
Meters (m)	3.28	Feet
Kilometers (km)	0.621	Miles
Hectares (ha)	2.47	Acres
Square kilometers (km^2)	0.386	Square miles
Degrees Celsius (°C)	1.8°C + 32	Degrees Fahrenheit

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Appendix: Species List

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

Species	Relative frequency[b]	Mean abundance (0–4)	*IndVal*[a] all zones	*IndVal*[a] for single climate zones 1	2	3	4	5	6	7	8	9	10
Ahtiana sphaerosporella	0.05	0.11	0.31	0.13	—	—	0.18	0.21	—	—	—	—	—
Alectoria imshaugii	0.10	0.22	0.37	—	—	—	—	0.20	0.26	—	0.15	—	—
Alectoria sarmentosa	0.39	1.05	0.61	—	—	—	—	—	0.31	—	0.46	0.31	—
Alectoria vancouverensis	0.02	0.04	—	—	—	—	—	—	—	—	—	—	—
Bryocaulon pseudosatoanum	0.01	0.03	—	—	—	—	—	—	—	—	—	—	—
Bryoria	0.05	0.12	0.36	—	—	—	0.16	—	—	—	0.32	—	—
Bryoria bicolor	0.05	0.13	0.40	—	—	—	—	—	—	—	—	0.30	0.27
Bryoria capillaris	0.17	0.44	0.48	—	—	—	0.22	—	0.32	—	0.26	—	—
Bryoria carlottae	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Bryoria cervinula	0.01	0.02	0.20	—	—	—	—	—	—	—	—	0.20	—
Bryoria fremontii	0.20	0.56	0.62	—	—	—	0.29	0.45	0.29	—	—	—	—
Bryoria friabilis	0.03	0.07	0.24	—	—	—	0.09	—	—	—	0.23	—	—
Bryoria fuscescens	0.17	0.44	0.42	—	—	—	0.22	—	0.26	—	0.23	—	—
Bryoria glabra	0.07	0.19	0.36	—	—	—	—	—	—	0.17	0.22	0.26	—
Bryoria implexa	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Bryoria lanestris	0.01	0.03	0.18	—	—	—	—	—	—	0.18	—	—	—
Bryoria nadvornikiana	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Bryoria pseudofuscescens	0.12	0.33	0.40	—	—	—	—	0.24	0.22	0.22	—	—	—
Bryoria simplicior	0.04	0.09	0.29	—	—	—	0.16	0.20	—	0.12	—	—	—
Bryoria subcana	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Bryoria tenuis	0.04	0.10	0.34	—	—	—	—	—	—	—	—	0.31	0.19
Bryoria trichodes	0.14	0.36	0.49	—	—	—	—	—	—	—	0.17	0.32	0.33
Bunodophoron melanocarpum	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Candelaria pacifica	0.27	0.75	0.70	0.32	0.39	0.53	—	—	—	—	—	—	—
Cetraria	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Cetraria californica	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Cetraria canadensis	0.12	0.27	0.45	—	—	—	—	0.22	0.26	0.30	—	—	—
Cetraria chlorophylla	0.34	0.81	0.53	—	—	—	—	—	0.32	0.33	0.26	—	—

Summary of species from the Forestry Inventory and Analysis dataset: relative frequency, mean abundance, and significant indicator values (across all climate zones, and for single climate zones)—continued

Species	Relative frequency[b]	Mean abundance (0–4)	*IndVal*[a] all zones	*IndVal*[a] for single climate zones 1	2	3	4	5	6	7	8	9	10
Cetraria merrillii	0.25	0.64	0.55	—	—	—	—	0.49	0.25	0.20	—	—	—
Cetraria orbata	0.24	0.58	0.43	—	—	—	0.14	—	0.33	—	0.20	—	—
Cetraria pallidula	0.04	0.07	0.24	—	—	—	0.12	—	0.19	—	—	—	—
Cetraria pinastri	0.02	0.04	0.23	—	—	—	0.16	—	0.08	0.15	—	—	—
Cetraria platyphylla	0.25	0.66	0.55	—	—	—	0.17	0.32	0.41	—	—	—	—
Cetraria sepincola	0.01	0.04	0.30	—	—	—	—	—	—	0.30	—	—	—
Cetraria subalpina	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Cetrelia cetrarioides	0.02	0.04	—	—	—	—	—	—	—	—	—	—	—
Cladonia	0.03	0.07	0.21	0.11	—	—	—	—	—	—	0.16	0.10	—
Cladonia albonigra	0.02	0.04	0.24	—	0.09	—	—	—	—	—	0.09	0.20	—
Cladonia amaurocraea	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Cladonia arbuscula	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Cladonia bacillaris	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Cladonia bellidiflora	0.07	0.19	0.46	—	—	—	—	—	—	—	0.14	0.34	0.29
Cladonia borealis	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Cladonia carneola	0.04	0.09	0.27	—	—	—	—	—	—	—	0.23	0.15	—
Cladonia cenotea	0.02	0.03	—	—	—	—	—	—	—	—	—	—	—
Cladonia chlorophaea	0.03	0.07	0.22	—	—	—	—	—	—	—	0.09	0.17	0.12
Cladonia coniocraea	0.21	0.50	0.53	—	—	—	—	—	—	—	0.20	0.34	0.35
Cladonia cornuta	0.07	0.18	0.38	—	—	—	—	—	—	—	0.15	0.32	0.19
Cladonia deformis	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Cladonia fimbriata	0.08	0.17	0.31	—	—	—	—	—	—	0.17	—	0.23	0.14
Cladonia furcata	0.01	0.03	—	—	—	—	—	—	—	—	—	—	—
Cladonia macilenta	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Cladonia maxima	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Cladonia merochlorophaea	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Cladonia multiformis	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Cladonia norvegica	0.02	0.05	—	—	—	—	—	—	—	—	—	—	—
Cladonia pyxidata	0.01	0.03	0.24	—	—	—	—	—	—	—	0.13	0.20	—

Summary of species from the Forestry Inventory and Analysis dataset: relative frequency, mean abundance, and significant indicator values (across all climate zones, and for single climate zones)—continued

Species	Relative frequency[b]	Mean abundance (0–4)	*IndVal*[a] all zones	*IndVal*[a] for single climate zones 1	2	3	4	5	6	7	8	9	10
Cladonia rangiferina	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Cladonia scabriuscula	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Cladonia squamosa	0.13	0.32	0.57	—	—	—	—	—	—	—	0.22	0.39	0.35
Cladonia squamosa var. *subsquamosa*	0.05	0.12	0.30	—	—	—	—	—	—	—	0.11	0.14	0.24
Cladonia straminea	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Cladonia subfurcata	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Cladonia sulphurina	0.01	0.03	0.19	—	—	—	0.09	—	—	—	0.17	—	—
Cladonia transcendens	0.14	0.38	0.42	—	—	—	—	—	—	—	0.21	0.21	0.28
Cladonia umbricola	0.08	0.18	0.37	—	—	—	0.08	—	—	—	—	0.21	0.28
Cladonia uncialis	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Cladonia verruculosa	0.01	0.03	—	—	—	—	—	—	—	—	—	—	—
Collema	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Collema curtisporum	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Collema furfuraceum	0.05	0.12	0.37	—	0.20	0.30	—	—	—	—	—	—	—
Collema nigrescens	0.03	0.08	0.30	—	0.23	0.20	—	—	—	—	—	—	—
Dendriscocaulon intricatulum	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Dendrosticta wrightii	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Erioderma sorediatum	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Esslingeriana idahoensis	0.12	0.29	0.46	—	—	—	—	—	0.38	0.22	0.17	—	—
Evernia mesomorpha	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Evernia prunastri	0.28	0.65	0.54	0.37	0.19	0.32	—	—	—	—	—	—	—
Flavoparmelia caperata	0.01	0.04	0.44	—	0.44	—	—	—	—	—	—	—	—
Flavopunctelia flaventior	0.06	0.17	0.59	—	0.43	0.41	—	—	—	—	—	—	—
Fuscopannaria	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Fuscopannaria ahlneri	0.01	0.02	0.18	—	—	—	—	—	—	0.17	—	—	0.08
Fuscopannaria alaskana	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Fuscopannaria confusa	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Fuscopannaria laceratula	0.01	0.02	0.17	—	—	—	—	—	—	—	—	0.14	0.10
Fuscopannaria leucostictoides	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—

Summary of species from the Forestry Inventory and Analysis dataset: relative frequency, mean abundance, and significant indicator values (across all climate zones, and for single climate zones)—continued

Species	Relative frequency[b]	Mean abundance (0–4)	*IndVal*[a] all zones	*IndVal*[a] for single climate zones 1	2	3	4	5	6	7	8	9	10
Fuscopannaria mediterranea	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Fuscopannaria pacifica	0.02	0.04	—	—	—	—	—	—	—	—	—	—	—
Heterodermia	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Heterodermia japonica	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Heterodermia leucomela	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Heterodermia speciosa	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Hypogymnia	0.03	0.06	—	—	—	—	—	—	—	—	—	—	—
Hypogymnia apinnata	0.20	0.52	0.51	—	—	—	—	—	—	—	0.32	0.23	0.32
Hypogymnia austerodes	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Hypogymnia bitteri	0.02	0.06	0.35	—	—	—	0.07	—	—	0.34	—	—	—
Hypogymnia canadensis	0.02	0.03	0.18	—	—	—	—	—	—	0.12	—	0.10	0.08
Hypogymnia duplicata	0.09	0.25	0.54	—	—	—	—	—	—	—	0.20	0.35	0.35
Hypogymnia enteromorpha	0.26	0.67	0.68	—	—	—	—	—	—	—	0.40	0.42	0.37
Hypogymnia heterophylla	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Hypogymnia hultenii	0.14	0.34	0.56	—	—	—	—	—	—	—	0.22	0.32	0.40
Hypogymnia imshaugii	0.46	1.26	0.65	—	—	—	0.29	0.39	0.41	—	—	—	—
Hypogymnia inactiva	0.16	0.43	0.47	0.18	—	—	—	—	—	—	0.38	0.30	—
Hypogymnia lophyrea	0.05	0.11	0.36	—	0.06	—	—	—	—	—	—	0.16	0.32
Hypogymnia occidentalis	0.17	0.42	0.41	—	—	—	0.15	—	0.27	0.26	—	—	—
Hypogymnia oceanica	0.02	0.04	0.25	—	—	—	—	—	—	—	0.06	0.15	0.19
Hypogymnia physodes	0.27	0.70	0.50	—	—	—	—	—	—	0.33	0.28	0.24	—
Hypogymnia pulverata	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Hypogymnia rugosa	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Hypogymnia tubulosa	0.17	0.37	0.41	0.22	—	—	—	—	—	0.24	0.26	—	—
Hypogymnia vittata	0.04	0.08	0.31	—	—	—	—	—	—	—	0.11	0.23	0.19
Hypogymnia wilfiana	0.13	0.30	0.43	—	—	—	0.20	—	0.30	—	0.19	—	—
Hypotrachyna sinuosa	0.07	0.16	0.36	—	0.16	—	—	—	—	—	—	0.19	0.24
Imshaugia aleurites	0.01	0.02	0.23	—	—	—	—	—	—	0.23	—	—	—
Lathagrium fuscovirens	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—

Summary of species from the Forestry Inventory and Analysis dataset: relative frequency, mean abundance, and significant indicator values (across all climate zones, and for single climate zones)—continued

Species	Relative frequency[b]	Mean abundance (0–4)	*IndVal*[a] all zones	*IndVal*[a] for single climate zones 1	2	3	4	5	6	7	8	9	10
Leptochidium albociliatum	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Leptogidium contortum	0.03	0.06	0.30	—	—	—	—	—	—	—	0.07	0.11	0.29
Leptogidium dendriscum	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Leptogium	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Leptogium burnetiae	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Leptogium cyanescens	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Leptogium insigne	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Leptogium pseudofurfuraceum	0.01	0.04	0.25	—	—	0.25	—	—	—	—	—	—	—
Leptogium saturninum	0.02	0.05	0.20	—	—	—	0.12	—	—	0.14	0.09	—	—
Letharia columbiana	0.26	0.72	0.61	—	—	—	0.37	0.46	—	—	—	—	—
Letharia vulpina	0.43	1.24	0.72	—	—	—	0.31	0.49	0.39	—	—	—	—
Lobaria anomala	0.07	0.16	0.28	0.15	—	—	—	—	0.17	0.17	—	—	—
Lobaria anthraspis	0.06	0.16	0.27	0.15	—	—	—	—	0.16	0.16	—	—	—
Lobaria hallii	0.02	0.03	—	—	—	—	—	—	—	—	—	—	—
Lobaria linita	0.09	0.24	0.49	—	—	—	—	—	—	—	0.23	0.32	0.29
Lobaria oregana	0.10	0.25	0.53	—	—	—	—	—	—	—	0.19	0.34	0.36
Lobaria pulmonaria	0.10	0.24	0.33	0.16	—	—	—	—	—	0.25	—	0.15	—
Lobaria retigera	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Lobaria scrobiculata	0.05	0.12	0.29	—	—	—	0.10	—	—	0.23	—	0.12	—
Melanelia	0.05	0.11	—	—	—	—	—	—	—	—	—	—	—
Melanelixia californica	0.11	0.30	0.64	—	—	0.64	—	—	—	—	—	—	—
Melanelixia fuliginosa	0.06	0.15	0.33	0.28	0.14	—	—	—	—	—	—	—	—
Melanelixia subargentifera	0.02	0.05	0.42	—	—	0.42	—	—	—	—	—	—	—
Melanelixia subaurifera	0.03	0.05	0.23	—	0.23	—	—	—	—	—	—	—	—
Melanohalea elegantula	0.14	0.39	0.44	0.25	—	0.18	—	0.31	—	—	—	—	—
Melanohalea exasperatula	0.18	0.47	0.44	—	—	—	0.22	—	0.25	0.26	—	—	—
Melanohalea olivacea	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Melanohalea septentrionalis	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Melanohalea subelegantula	0.06	0.16	0.34	—	—	—	0.24	0.20	0.16	—	—	—	—

Summary of species from the Forestry Inventory and Analysis dataset: relative frequency, mean abundance, and significant indicator values (across all climate zones, and for single climate zones)—continued

Species	Relative frequency[b]	Mean abundance (0–4)	*IndVal*[a] all zones	*IndVal*[a] for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Melanohalea subolivacea	0.29	0.82	0.49	—	—	0.30	0.24	0.30	—	—	—	—	—
Melanohalea trabeculata	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Menegazzia subsimilis	0.04	0.10	0.33	—	0.14	—	—	—	—	—	—	0.12	0.26
Nephroma	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Nephroma arcticum	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Nephroma bellum	0.07	0.18	0.38	—	—	—	—	—	—	—	0.23	0.23	0.21
Nephroma helveticum	0.08	0.19	0.34	—	—	—	—	—	0.19	—	—	0.21	0.20
Nephroma isidiosum	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Nephroma laevigatum	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Nephroma occultum	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Nephroma parile	0.04	0.09	0.24	—	—	—	—	—	0.10	0.21	0.10	—	—
Nephroma resupinatum	0.04	0.10	0.25	—	—	—	—	—	0.17	0.13	—	0.13	—
Niebla cephalota	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Nodobryoria	0.01	0.03	—	—	—	—	—	—	—	—	—	—	—
Nodobryoria abbreviata	0.28	0.79	0.69	—	—	—	0.30	0.49	0.35	—	—	—	—
Nodobryoria oregana	0.16	0.43	0.54	—	—	—	0.31	—	0.26	—	0.39	—	—
Pannaria	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Parmelia	0.05	0.11	—	—	—	—	—	—	—	—	—	—	—
Parmelia hygrophila	0.22	0.54	0.43	—	—	—	—	—	0.23	—	0.27	0.26	—
Parmelia pseudosulcata	0.06	0.13	0.40	—	—	—	—	—	—	—	0.17	0.35	0.18
Parmelia saxatilis	0.06	0.15	0.33	—	—	—	—	—	—	—	—	0.19	0.26
Parmelia squarrosa	0.03	0.06	0.27	—	—	—	—	—	—	0.14	—	—	0.24
Parmelia sulcata	0.42	1.09	0.51	0.28	—	—	—	—	0.29	0.32	—	—	—
Parmeliella parvula	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Parmeliella triptophylla	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Parmelina coleae	0.08	0.20	0.51	—	—	0.51	—	—	—	—	—	—	—
Parmeliopsis	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Parmeliopsis ambigua	0.14	0.34	0.45	—	—	—	0.20	—	0.27	0.29	—	—	—
Parmeliopsis hyperopta	0.25	0.64	0.62	—	—	—	0.22	—	—	—	0.49	0.33	—

Summary of species from the Forestry Inventory and Analysis dataset: relative frequency, mean abundance, and significant indicator values (across all climate zones, and for single climate zones)—continued

Species	Relative frequency[b]	Mean abundance (0–4)	*IndVal*[a] all zones	*IndVal*[a] for single climate zones 1	2	3	4	5	6	7	8	9	10
Parmotrema	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Parmotrema arnoldii	0.02	0.04	0.24	0.16	0.19	—	—	—	—	—	—	—	—
Parmotrema austrosinense	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Parmotrema perlatum	0.02	0.05	0.61	—	0.61	—	—	—	—	—	—	—	—
Peltigera	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Peltigera aphthosa	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Peltigera britannica	0.06	0.14	0.42	—	—	—	—	—	—	—	—	0.34	0.26
Peltigera collina	0.11	0.25	0.30	0.19	—	—	—	—	0.15	—	—	0.19	—
Peltigera degenii	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Peltigera elisabethae	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Peltigera horizontalis	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Peltigera leucophlebia	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Peltigera membranacea	0.03	0.07	0.28	—	—	—	—	—	—	—	0.07	0.11	0.25
Peltigera neopolydactyla	0.06	0.15	0.42	—	—	—	—	—	—	—	0.18	0.32	0.23
Peltigera pacifica	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Peltigera polydactylon	0.01	0.01	0.18	—	—	—	—	—	—	—	0.05	0.09	0.15
Peltigera praetextata	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Peltigera scabrosa	0.02	0.04	0.22	—	—	—	—	—	—	—	—	0.11	0.18
Phaeophyscia ciliata	0.01	0.02	0.23	—	—	0.23	—	—	—	—	—	—	—
Phaeophyscia hirsuta	0.01	0.03	0.34	—	0.30	0.21	—	—	—	—	—	—	—
Phaeophyscia kairamoi	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Phaeophyscia orbicularis	0.08	0.21	0.67	—	0.38	0.54	—	—	—	—	—	—	—
Physcia	0.02	0.05	0.22	—	—	0.22	—	—	—	—	—	—	—
Physcia adscendens	0.18	0.47	0.67	0.30	0.41	0.48	—	—	—	—	—	—	—
Physcia alnophila	0.11	0.28	0.40	0.24	—	0.31	—	—	0.17	—	—	—	—
Physcia biziana	0.07	0.19	0.56	—	—	0.56	—	—	—	—	—	—	—
Physcia caesia	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Physcia dimidiata	0.04	0.11	0.29	—	0.28	0.16	—	—	—	0.13	—	—	—
Physcia dubia	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—

Summary of species from the Forestry Inventory and Analysis dataset: relative frequency, mean abundance, and significant indicator values (across all climate zones, and for single climate zones)—continued

Species	Relative frequency[b]	Mean abundance (0–4)	*IndVal*[a] all zones	*IndVal*[a] for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Physcia leptalea	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Physcia stellaris	0.05	0.12	0.38	0.21	—	0.34	—	—	—	—	—	—	—
Physcia tenella	0.13	0.35	0.61	0.32	0.39	0.38	—	—	—	—	—	—	—
Physcia tribacia	0.02	0.04	0.33	0.33	—	—	—	—	—	—	—	—	—
Physciella melanchra	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Physconia	0.02	0.04	—	—	—	—	—	—	—	—	—	—	—
Physconia americana	0.11	0.28	0.49	—	—	0.49	—	—	—	—	—	—	—
Physconia enteroxantha	0.10	0.28	0.50	0.25	—	0.49	—	—	—	—	—	—	—
Physconia fallax	0.02	0.06	0.42	—	—	0.42	—	—	—	—	—	—	—
Physconia isidiigera	0.12	0.32	0.66	—	0.28	0.59	—	—	—	—	—	—	—
Physconia leucoleiptes	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Physconia perisidiosa	0.16	0.41	0.57	—	—	0.57	—	—	—	—	—	—	—
Platismatia glauca	0.51	1.40	0.67	—	—	—	—	—	0.32	—	0.46	0.41	—
Platismatia herrei	0.19	0.45	0.53	—	—	—	—	—	—	—	0.28	0.36	0.28
Platismatia lacunosa	0.08	0.19	0.48	—	—	—	—	—	—	—	—	0.33	0.35
Platismatia norvegica	0.15	0.39	0.61	—	—	—	—	—	—	—	0.22	0.40	0.40
Platismatia stenophylla	0.10	0.23	0.44	—	—	—	—	—	—	—	0.44	—	—
Polycauliona candelaria	0.06	0.14	0.27	—	—	0.19	—	0.13	—	0.15	—	—	—
Polycauliona polycarpa	0.16	0.43	0.61	0.31	0.34	0.40	—	—	—	—	—	—	—
Polycauliona tenax	0.02	0.05	0.46	—	0.46	—	—	—	—	—	—	—	—
Polychidium muscicola	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Protopannaria pezizoides	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Pseudocyphellaria crocata	0.03	0.06	0.22	—	—	—	—	—	—	0.17	—	0.11	0.09
Pseudocyphellaria mallota	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Pseudocyphellaria rainierensis	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Punctelia jeckeri	0.03	0.08	0.40	—	0.28	0.29	—	—	—	—	—	—	—
Ramalina	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Ramalina dilacerata	0.06	0.14	0.29	0.14	—	—	—	—	—	0.25	0.11	—	—
Ramalina farinacea	0.20	0.48	0.47	0.27	0.41	—	—	—	—	0.19	—	—	—

Summary of species from the Forestry Inventory and Analysis dataset: relative frequency, mean abundance, and significant indicator values (across all climate zones, and for single climate zones)—continued

Species	Relative frequency[b]	Mean abundance (0–4)	*IndVal*[a] all zones	*IndVal*[a] for single climate zones 1	2	3	4	5	6	7	8	9	10
Ramalina leptocarpha	0.02	0.04	0.60	—	0.60	—	—	—	—	—	—	—	—
Ramalina menziesii	0.01	0.03	0.42	—	0.42	—	—	—	—	—	—	—	—
Ramalina obtusata	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Ramalina pollinaria	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Ramalina roesleri	0.04	0.11	0.33	—	—	—	0.15	—	—	0.28	—	—	—
Ramalina subleptocarpha	0.03	0.08	0.44	—	0.41	0.25	—	—	—	—	—	—	—
Ramalina thrausta	0.02	0.04	0.19	0.08	—	—	—	—	—	0.19	—	—	—
Scytinium cellulosum	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Scytinium lichenoides	0.03	0.06	0.22	0.10	—	0.17	—	—	0.12	—	—	—	—
Scytinium palmatum	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Scytinium polycarpum	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Scytinium teretiusculum	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Sphaerophorus aggr.[c]	0.27	0.74	0.79	—	—	—	—	—	—	—	0.38	0.53	0.45
Sticta	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Sticta beauvoisii	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Sticta fuliginosa	0.03	0.06	0.25	0.12	—	—	—	—	—	—	—	0.15	0.16
Sticta limbata	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Sulcaria badia	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Teloschistes chrysophthalmus	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Usnea	0.14	0.33	0.31	0.17	—	—	—	—	—	0.19	—	0.17	—
Usnea cavernosa	0.01	0.03	—	—	—	—	—	—	—	—	—	—	—
Usnea cornuta	0.04	0.10	0.46	—	0.46	—	—	—	—	—	—	—	—
Usnea cylindrica	0.00	0.00	—	—	—	—	—	—	—	—	—	—	—
Usnea filipendula	0.21	0.55	0.40	—	—	—	—	—	0.24	—	0.23	0.22	—
Usnea flavocardia	0.08	0.23	0.40	0.24	—	—	—	—	—	—	—	0.19	0.26
Usnea glabrata	0.05	0.12	0.32	0.24	0.21	—	—	—	—	—	—	—	—
Usnea glabrescens	0.00	0.01	—	—	—	—	—	—	—	—	—	—	—
Usnea hirta	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Usnea intermedia	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—

Summary of species from the Forestry Inventory and Analysis dataset: relative frequency, mean abundance, and significant indicator values (across all climate zones, and for single climate zones)—continued

Species	Relative frequency[b]	Mean abundance (0–4)	*IndVal*[a] all zones	*IndVal*[a] for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Usnea lapponica	0.09	0.23	0.33	0.16	0.14	—	—	—	—	0.25	—	—	—
Usnea longissima	0.04	0.09	0.36	—	0.09	—	—	—	—	—	—	—	0.33
Usnea pacificana	0.02	0.05	—	—	—	—	—	—	—	—	—	—	—
Usnea scabrata	0.08	0.19	0.28	—	—	—	—	—	0.15	0.18	—	0.16	—
Usnea subfloridana	0.06	0.16	0.26	0.16	—	—	—	—	—	—	0.12	0.16	—
Usnea substerilis	0.02	0.04	—	—	—	—	—	—	—	—	—	—	—
Xanthomendoza fallax	0.06	0.18	0.45	—	0.17	0.41	—	—	—	—	—	—	—
Xanthomendoza fulva	0.11	0.29	0.42	0.22	0.14	0.34	—	—	—	—	—	—	—
Xanthomendoza galericulata	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Xanthomendoza hasseana	0.11	0.29	0.41	—	0.27	0.28	—	—	0.18	—	—	—	—
Xanthomendoza oregana	0.13	0.36	0.55	—	0.51	0.33	—	—	—	—	—	—	—
Xanthoria	0.02	0.04	—	—	—	—	—	—	—	—	—	—	—
Xanthoria parietina	0.01	0.02	0.27	—	0.27	—	—	—	—	—	—	—	—

Note: Zone 1 = warm mesic lowlands, Zone 2 = warm dry subcontinental, Zone 3 = hot dry lowlands, Zone 4 = cold mesic subcontinental, Zone 5 = cold dry continental, Zone 6 = cold mesic continental, Zone 7 = cool dry continental, Zone 8 = cool moist subcontinental, Zone 9 = mild moist suboceanic, and Zone 10 = warm wet hypermaritime.

[a] IndVal = (relative abundance in given climate zone or set of zones × relative frequency in given zone or set of zones) 0.5.

[b] proportion of 1,118 plots in which the species occurred.

[c] *Sphaerophorus* species were aggregated owing to species concept changes over the sampling period.

Pacific Northwest Research Station

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