Lichen communities and species indicate climate thresholds in southeast and south-central Alaska, USA

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ABSTRACT. Because of their unique physiology, lichen communities are highly sensitive to climatic conditions, making them ideal bioindicators for climate change. Southeast and south-central Alaska host diverse and abundant lichen communities and are faced with a more rapidly changing climate than many more southerly latitudes. We develop sensitive lichen-based indicators for tracking the effects of climate change in south-central and southeast Alaska. Using 196 plots, we model community composition and 12 individual species abundances in relation to synthetic climate variables. Both types of lichen indicator are closely related to the climate variable describing a transition from warm, wet oceanic climates to cooler, drier suboceanic climates. Lichen communities and individual species exhibited thresholds associated with average December minimum temperatures between -10.2 and $-7.8°C$ and annual precipitation between 106 and 172 cm, suggesting rapid turnover with relatively small changes within these ranges. These climate conditions occur close to the coast in northern portions of the region and further inland in southeast Alaska. Because lichen communities in the threshold region may be most sensitive to a changing future climate, they should be targeted for monitoring efforts.

KEYWORDS. Alaska, community analysis, climate, epiphytes, thresholds.

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Lichen communities are highly sensitive to climatic conditions (Ellis et al. 2007; Gauslaa 2014; van Herk et al. 2002). Because they lack roots to access stored water, their physiology is dependent on humidity and rainfall occurring at times when temperatures favor photosynthesis (Palmqvist et al. 2008). Lichen community surveys are commonly included in large-scale inventories for biomonitoring air quality and other facets of forest health (e.g., International Co-operative Programme, Forest Inventory and Analysis), yet applications for indicating climate change effects are not well developed.

Our objective was to develop sensitive lichen-based indicators for tracking the effects of climate change in south-central and southeast Alaska using community data collected on a systematic sampling grid (Will-Wolf 2010). Shifts in lichen distributions, as a function of climate change drivers or otherwise, potentially affect a wide range of dependent forest biota. Lichens of southeast and south-central Alaska are diverse and conspicuous. Northern latitudes are often home to hotspots of lichen diversity; for example, a comprehensive study of a national park in our study area reported 668 species in 53 km^2 (Spribille et al. 2010). In these forests comprised largely of spruce (*Picea*), pine (*Pinus*) and hemlock (*Tsuga*), we expect that the ecosystem functions of lichens are similar to comprehensively studied floras of nearby Pacific Northwest states and provinces. Alaska forests support many lichen species known to be valuable contributors of plant-available nitrogen (Antoine 2004; Holub & Lathja 2004), nesting materials for birds and rodents (Maser et al. 1986; Richardson & Young 1977), habitat and camouflage for many invertebrates (Gerson & Seaward 1977) and food for diverse animals including elk and deer (Richardson & Young 1977; Ward & Marcum 2005).

The most useful climate change indicators for land managers would detect early local shifts in climate and lichen ecological function that cannot be captured by climate models or meteorological networks. Furthermore, they would enable understanding of how individual species are responding to potentially novel climatic conditions (Williams & Jackson 2007). We conduct a multi-scale analysis to identify lichen metrics at the
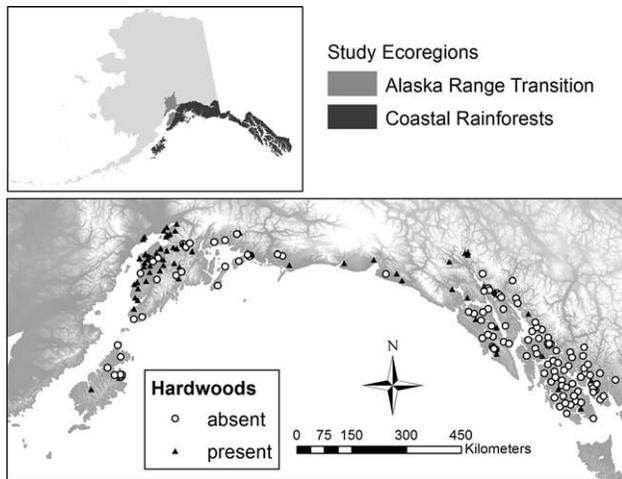
Figure 1. Location of study ecoregions in Alaska (based on the US Environmental Protection Agency's level II divisions, available at ftp://ftp. epa.gov/wed/ecoregions/ak/). Plot locations are symbolized by the presence or absence of hardwoods with elevation in the background (dark at low elevations).

community and species levels. Lichens are also sensitive to a range of other factors, including forest structure (Neitlich & McCune 1997), tree species (Campbell et al. 2010), forest continuity (Sillett et al. 2000), and air quality (Jovan et al. 2012; van Herk 1999). These factors can interact with climate-related patterns to shape lichen distributions (Ellis & Coppins 2007; Ellis et al. 2009). We incorporate a variety of environmental drivers to determine the range of conditions under which candidate metrics are sensitive to climate gradients in the study region.

The development of sensitive climate indicators is timely for southeast and south-central Alaska where clear temperature increases have been observed, estimated at between 2.69°C since 1971 (Walsh et al. 2008) and 3.4°C since 1960 (US Global Climate Change Research Program 2009) and more pronounced in winter. Concurrently, precipitation rates are increasing by about 1.4 mm per decade (Hinzman et al. 2006; SNAP 2008). The magnitude of these changes is quite variable across the state; however, their impacts are already becoming evident. Glacier melting has been documented, especially in southeast Alaska (Arendt et al. 2002). Vegetation changes associated with changing climate have been observed (Wolken et al. 2011); for example, *Callitropsis nootkatensis* and spruce forest productivity have declined (Goetz et al. 2005; Hennon et al. 2012). Continued monitoring of lichen species expected to be sensitive to small changes in climate may allow detection of trends as they are affecting forested ecosystems.

Our objectives were to: (1) describe lichen communities of south-central and southeast Alaska and explore their associations with climate and forest structure

gradients; (2) examine the relationships between climate variables and the distribution of individual lichen species that may exhibit climate-related thresholds.

METHODS

Study area. We focused on forested habitats of south-central and southeast Alaska (**Fig. 1**). These included temperate *Picea sitchensis* and *Pinus contorta* stands along the coast of Prince Williams Sound and the Alexander Archipelago. More suboceanic sites of the Kenai Peninsula and Cook Inlet were dominated by *Picea mariana* and *P. glauca*. Hardwood tree species in genera such as *Populus*, *Betula*, *Salix* and *Alnus* were typically minor components of our study sites except in riparian areas and beetle-killed *Picea glauca* and *P. mariana* habitats where *Populus* or *Betula* comprised a large proportion of the canopy. Elevation in our plots varied from 0 to 2700 m, annual rainfall from 34 to 536 cm. Average annual temperature ranged from −1.7 to 7.6°C, and average December minimum temperatures from −15.0 to 0.54°C.

Plot selection. Our full dataset incorporated 196 plots from two sources. Forest Inventory and Analysis (FIA; Barrett & Christensen 2011; Will-Wolf 2010) plots were established between 2004 and 2008 on a systematic grid throughout forested parts of the region (n = 125). Additional plots were installed off-grid near towns throughout the region (n = 71). We excluded five plots that hosted fewer than three species of lichens and three plots that were extreme outliers in community composition.

Lichen community. Plots were circular with an area of 0.4 ha (Will-Wolf 2010). Lichen data included the abundance of all macrolichen species from litterfall and between 0.5 and 2 m on tree boles, branches and shrubs. Lichen abundance classes followed the Forest Health Monitoring Protocol (McCune et al. 1997): 0 = not present; 1 = 1–3 thalli in the plot; 2 = 4–10 thalli in the plot; 3 = more than 10 thalli but less than 50% of all available branches and stems host the species; 4 = more than 50% of available branches and stems hosting the species. FIA plots were sampled by a well-trained field crew whereas target plots were sampled by the first author. This protocol is comparable among observers for the purposes of detecting broad-scale gradients (McCune et al. 1997).

Voucher specimens for FIA plots are on file at the FIA office in Portland, Oregon; those for target plots were curated and deposited at the Oregon State University Herbarium (OSC). Nomenclature follows Esslinger (2012) except for *Hypogymnia hultenii* and *H. lophyrea*, which were previously included in *Cavernularia* (Miadlikowska et al. 2011). *Sphaerophorus globosus* is used here in the broad sense, including both *S. tuckermanii* and *S. venerabilis*, because much of the data

Table 1. Environmental variables depicted in the ordination (shown in Fig. 2) and community and individual species models (in Table 3). R^2 (indicated by * if greater than 0.20) with non-metric multidimensional scaling (NMS) ordination axes. Synthetic climate variables are derived from the principal component analysis (PCA); the equation for PCA1 can be found in Supplementary Table S1. We interpret PCA dimensions with directionality of relationship with the strongest combination of climate variables, for example a plot scoring high on PCA1 has low precipitation and cold winters and temperature minima.

Variable	Acronym	Units	R^2 with NMS axis 1	R^2 with NMS axis 2
Conifer basal area	ConiBA	$Log_{10}(m^2/ha + 1)$	0.25*	0.02
Hardwood basal area	HdwdBA	$Log_{10}(m^2/ha + 1)$	0.40*	0.00
Betula papyrifera basal area	Betpap	$Log_{10}(m^2/ha + 1)$	0.41*	0.04
Picea glauca basal area	Picgla	$Log_{10}(m^2/ha + 1)$	0.32*	0.01
Picea mariana basal area	Picmar	$Log_{10}(m^2/ha + 1)$	0.27*	0.06
Picea sitchensis basal area	Picsit	$Log_{10}(m^2/ha + 1)$	0.06	0.24*
Populus balsamifera basal area	Popbal	$Log_{10}(m^2/ha + 1)$	0.10	0.02
Tsuga heterophylla basal area	Tsuhet	$Log_{10}(m^2/ha + 1)$	0.33*	0.01
Latitude	Lat	dd.ddd	0.51*	0.00
Longitude	Long	dd.ddd	0.60*	0.00
Synthetic climate variables (percent of climate variation represented)				
PCA1 ↓ precip. ↓ winter and min temps. (60.3)			0.71*	0.02
PCA2 ↑ precip. ↓ summer max temps. (26.1)			0.02	0.01
PCA3 ↓ summer temp. ↑ winter temp. ↓ precip. (6.4)			0.00	0.10
PCA4 ↓ summer min temp ↑ spring max temp. ↓ summer precip. (2.4)			0.01	0.01

originated before clarification of the genus by Wedin et al. (2009).

Forest and climate variables. At each plot, we visually estimated the percent of the plot covered by hardwoods, conifers and gaps in the overstory. We summarized basal area for trees exceeding 5 cm in diameter at breast height on four tree subplots for FIA plots. For target plots, we estimated basal area of trees using five variable-radius wedge prism plots positioned at the center and 23 m in each cardinal direction.

Estimates of monthly average precipitation and minimum and maximum temperatures were determined for each plot using GIS layers from the parameter-elevation regressions on individual slopes model (PRISM; Daly et al. 2008). Resolution of this interpolation was approximately 800 m and averages were taken across 30 years from 1971–2000. Because the climate variables were highly inter-correlated, we condensed these 36 variables to orthogonal synthetic variables using principal component analysis (PCA) in PC-ORD (McCune & Mefford 2010a). PCA was an appealing way to summarize climatic variation because it synthesizes the variability from several climate variables into just a few synthetic variables by taking advantage of their correlation; the algorithm for deriving PCA axes maximizes their ability to describe the variation in climate across the region. Although these synthetic PCA axes are somewhat more difficult to interpret than simpler climate summaries, they better represent how the climate variables that are currently interrelated vary across the landscape and can be simply calculated from the climatic variables for new sites. The equation for calculating the strongest gradient, PCA1, can be found in

Supplementary Table S1. Using synthetic PCA axes discouraged us from over-simplifying our interpretation of climate by emphasizing one variable despite its confounding with the others.

Analysis. To develop a lichen community metric related to forest structure and climate variables, we used nonmetric multidimensional scaling ordination (NMS; Kruskal 1964). All tree basal areas and percent covers were log-transformed. The ordination in PC-ORD (McCune & Mefford 2010a) used Sørensen (Bray-Curtis) distance, with no penalty for tied ranks and rotation to principal axes. We used the slow-and-thorough autopilot settings in which the configuration was optimized using 250 runs with real data. We evaluated 1D to 6D solutions, selecting the dimensionality where adding a further dimension would reduce the final stress by less than 5% of the highest possible stress, and where that dimensionality passed a randomization test. The randomization test with 250 runs determined that the final stress was statistically smaller than expected by chance alone ($p < 0.05$). We interpreted environmental variables on the ordination using vectors with length and direction related to the correlation between variables and ordination axis scores. Similarly the relationship between species and the first ordination axis is interpreted using Kendall's τ, which is based on ranked correlation.

We modeled community relationships, as described by scores on NMS axes, to environmental variables using nonparametric multiplicative regression (NPMR; McCune 2006) in HyperNiche (McCune & Mefford 2010b) allowing nonlinear responses. We included all variables listed in **Table 1** as potential predictors.

Table 2. Species and number of occurrences in 196 plots (occ) and relationship (Kendall's τ) with the first non-metric multidimensional ordination axis for species with 10 or more occurrences.

Species	occ.	τ
Alectoria imshaugii	1	
Alectoria nigricans	2	
Alectoria sarmentosa	141	−0.44
Bryocaulon pseudosatoanum	12	−0.08
Bryoria bicolor	46	−0.26
Bryoria capillaris	24	0.24
Bryoria carlottae	3	
Bryoria cervinula	8	
Bryoria friabilis	5	
Bryoria fuscescens	26	0.13
Bryoria glabra	62	0.23
Bryoria implexa	3	
Bryoria lanestris	8	
Bryoria nadvornikiana	1	
Bryoria simplicior	3	
Bryoria subcana	1	
Bryoria tenuis	34	−0.21
Bryoria trichodes (includes *B. trichodes trichodes* and *B. trichodes americana*)	110	−0.14
Bryoria pseudofuscescens	20	0.35
Bunodophoron melanocarpum	4	
Candelaria concolor (includes *C. 'pacifica'*)	2	
Cetrelia cetrarioides	4	
Cladonia albonigra	17	−0.20
Cladonia amaurocraea	1	
Cladonia bellidiflora	63	−0.41
Cladonia cariosa	29	−0.12
Cladonia cenotea	17	0.17
Cladonia chlorophaea (includes *C. grayi, C. asahinae* and *C. merochlorophaea*)	26	−0.03
Cladonia coniocraea (includes *C. ochrochlora*)	100	−0.06
Cladonia cornuta	76	−0.03
Cladonia crispata	5	
Cladonia deformis	11	0.17
Cladonia digitata	1	
Cladonia ecmocyna	3	
Cladonia fimbriata	27	0.12
Cladonia furcata	2	
Cladonia gracilis (includes ssp. *turbinata*)	8	
Cladonia macilenta (includes *C. macilenta* var. *bacillaris*)	4	
Cladonia metacorallifera	3	
Cladonia multiformis	2	
Cladonia pleurota	23	0.02
Cladonia portentosa	2	
Cladonia pyxidata	8	
Cladonia rangiferina	1	
Cladonia scabriuscula	2	
Cladonia squamosa v. squamosa	107	−0.44
Cladonia squamosa v. subsquamosa	15	−0.18
Cladonia stygia	1	
Cladonia subulata	1	
Cladonia sulphurina	10	0.09
Cladonia transcendens	35	−0.37
Cladonia umbricola	59	−0.02
Cladonia verruculosa	6	

Table 2. Continued.

Species	occ.	τ
Collema furfuraceum	9	
Collema fuscovirens	3	
Collema leptaleum	1	
Erioderma sorediatum	1	
Evernia mesomorpha	6	
Fuscopannaria ahlneri (includes *F. alaskana*)	11	0.14
Fuscopannaria laceratula	7	
Fuscopannaria leucostictoides	4	
Fuscopannaria pacifica	8	
Fuscopannaria spp.	2	
Heterodermia japonica	3	
Heterodermia speciosa	2	
Hypogymnia apinnata	113	0.33
Hypogymnia austerodes	6	
Hypogymnia bitteri	25	0.41
Hypogymnia duplicata	84	−0.57
Hypogymnia enteromorpha	93	−0.32
Hypogymnia hultenii	108	−0.01
Hypogymnia inactiva	6	
Hypogymnia lophyrea	41	0.15
Hypogymnia wilfiana (includes *H. canadensis*)	18	0.15
Hypogymnia occidentalis	34	0.28
Hypogymnia oceanica	21	−0.12
Hypogymnia physodes	66	0.60
Hypogymnia pulverata	3	
Hypogymnia rugosa	1	
Hypogymnia tubulosa	16	0.22
Hypogymnia vittata	31	−0.14
Hypotrachyna sinuosa	8	
Imshaugia aleurites	9	
Leptogidium contortum	28	−0.13
Leptogium brebissonii	1	
Leptogium burnetiae	9	
Leptogium saturninum	11	0.25
Leptogium tacomae	1	
Lobaria hallii	10	0.21
Lobaria linita	89	−0.34
Lobaria oregana	70	−0.42
Lobaria pulmonaria	27	0.39
Lobaria scrobiculata	42	0.47
Melanelixia subaurifera	3	
Melanohalea exasperata	12	0.27
Melanohalea exasperatula	2	
Melanohalea multispora (includes *M. subolivacea*)	12	0.28
Melanohalea olivacea	9	
Melanohalea septentrionalis	6	
Melanohalea trabeculata	5	
Nephroma arcticum	9	
Nephroma bellum	66	0.07
Nephroma helveticum	39	−0.15
Nephroma isidiosum	10	0.15
Nephroma laevigatum	4	
Nephroma occultum	1	
Nephroma parile	34	0.34
Nephroma resupinatum	14	0.12
Nodobryoria oregana	1	
Pannaria rubiginosa	1	
Parmelia hygrophila	68	0.12

Table 2. Continued.

Species	occ.	τ
Parmelia pseudosulcata	47	−0.11
Parmelia saxatilis	35	0.05
Parmelia squarrosa	21	0.19
Parmelia sulcata	84	0.63
Parmeliella triptophylla	7	
Parmeliopsis ambigua	23	0.40
Parmeliopsis hyperopta	97	−0.04
Parmotrema chinense	1	
Peltigera aphthosa	3	
Peltigera britannica	54	−0.38
Peltigera canina	1	
Peltigera collina	38	0.07
Peltigera elisabethae	2	
Peltigera leucophlebia	1	
Peltigera membranaceum	27	0.00
Peltigera neopolydactyla	59	−0.38
Peltigera pacifica	1	
Peltigera polydactylon	10	−0.03
Peltigera scabrosa	14	−0.18
Phaeophyscia ciliata	1	
Phaeophyscia kairamoi	4	
Physcia adscendens	6	
Physcia aipolia	10	0.27
Physcia caesia	2	
Physcia tenella	1	
Physconia americana	1	
Physconia detersa	2	
Physconia perisidiosa	6	
Platismatia glauca	171	−0.03
Platismatia herrei	62	−0.28
Platismatia lacunosa	70	−0.41
Platismatia norvegica	118	−0.29
Protopannaria pezizoides	1	
Pseudocyphellaria anomala	20	0.23
Pseudocyphellaria crocata	10	0.12
Pseudocyphellaria mallota	2	
Pseudocyphellaria perpetua	13	0.30
Ramalina dilacerata	27	0.46
Ramalina farinacea	39	0.50
Ramalina obtusata	4	
Ramalina pollinaria	2	
Ramalina roesleri	36	0.49
Ramalina thrausta	11	0.27
Sphaerophorus globosus s.l. (includes S. tuckermanii and S. venerabilis)	144	−0.49
Stereocaulon spp.	2	
Sticta fuliginosa	17	0.00
Sticta limbata	4	
Tuckermannopsis chlorophylla	108	0.57
Tuckermannopsis orbata	2	
Tuckermannopsis platyphylla	1	
Tuckermannopsis sepincola	14	0.28
Tuckermannopsis subalpina	3	
Usnea chaetophora	2	
Usnea cornuta	4	
Usnea diplotypus	6	
Usnea lapponica	25	0.43
Usnea longissima	25	−0.03

Table 2. Continued.

Species	occ.	τ
Usnea scabrata (includes U. filipendula)	21	0.26
Usnea spp.	1	
Vulpicida pinastri	31	0.48
Xanthoria candelaria	17	0.34

Response curves were generated using a local mean estimator and Gaussian kernel function (Bowman & Azzalini 1997) multiplied across predictors. Tolerances are smoothing parameters that reflect how broadly estimates are based on surrounding observations in predictor space and are calculated to maximize cross-validated (leave-one-out) xR^2. We selected a final model that optimized xR^2 subject to a minimum improvement of $xR^2 = 0.08$ to add predictors. Sensitivity is a measure of effect size for individual predictors; it expresses the proportion of change in the predicted response that would be caused by nudging a predictor. Minimum average neighborhood size (N^*) is the minimum average amount of data used to estimate the response variable at each point; we chose a conservative N^* of 40 to avoid overfitting. We set the minimum average neighborhood size to make an estimate at 15, meaning that responses were not estimated for sites with few potentially informative nearby data points. Using 100 randomizations, we calculated a p-value for each model. We also estimated threshold strength, T, an index ranging from 0 to 1 with increasing values indicating the abruptness of the species response to predictor variables (Lintz et al. 2011).

To identify lichen species indicators, we explored NPMR models for individual species (McCune 2006). We regressed each species abundance against environment for all common species in the dataset using HyperNiche (McCune & Mefford 2010b). We then focused on 12 species that showed strong patterns in their relationship with climate gradients. Potential predictors included the first six axes of the climate PCA and log-transformed hardwood basal area. We selected these variables because climate and substrate were the strongest explanatory variables in the community ordination. We used the same HyperNiche settings as described above for community modeling.

RESULTS

Lichen community composition. We observed 172 macrolichen taxa in the dataset (**Table 2**). Lichen community composition was strongly related to climate, geographic, and substrate variables in the two-dimensional NMS of the entire dataset (2-dimensional solution, stress = 18.3; **Fig. 2**, **Table 1**). The strongest gradient was associated with climate PCA1 ($R^2 = 0.71$), a
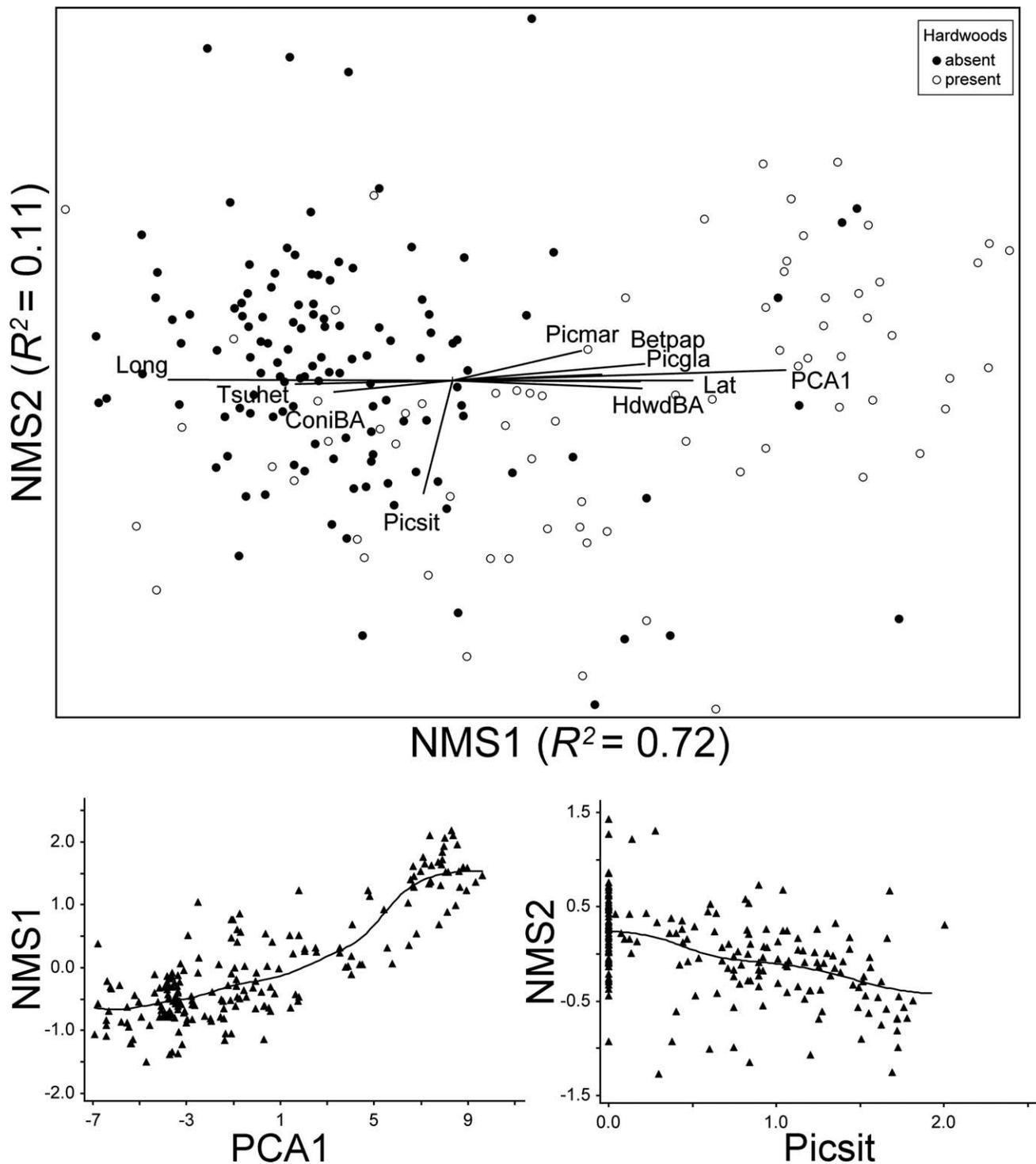
Figure 2. Non-metric multidimensional scaling (NMS) ordination of plots in lichen species space for entire region coded by ecoregion. Vectors are overlays of environmental variables with length proportional to their correlation with each axis; they are only shown when their R^2 with the NMS axes exceeds 0.20. Variable names in Table 1. Lower panels depict nonparametric multiplicative regression (NPMR) models (Table 3) relating NMS community axes to the strongest environmental variable for each axis.

gradient from wet areas with warm winters and maximum temperatures to dry places with cold winters and minimum temperatures; we interpret this change in temperature variability as a shift from oceanic to suboceanic climate regimes. The first ordination axis, NMS1, was best predicted by PCA1 using NPMR

(**Table 1, Fig. 2**) and showed a moderate threshold ($T = 0.71$) with the greatest change in community composition corresponding to PCA1 between approximately 3 and 6. Associated with this pattern was a geographic relationship with latitude and longitude. Tree species composition was associated with this gradient in

Table 3. Nonparametric multiplicative regression (NPMR) model summary for community composition (non-metric multidimensional scaling; NMS1 and NMS2) and each of 12 focal species. Potential predictors (Pred) for NMS1 and NMS2 included all variables in Table 1; for individual species, we restricted predictors to climate and hardwood basal area. The cross-validated R^2 (xR^2) represents the percent of the variation in species' abundance represented by the model using a leave-one-out jackknife approach. T represents the threshold strength (Lintz et al. 2011). N^* represents the average number of plots nearby in environmental space used to estimate the response. The p-value (p) is generated separately for each model by examining the number of models with equal or higher xR^2 in 100 randomizations. The tolerance (Tol) represents how broadly response estimates draw on abundances in plots nearby in environmental space. The sensitivity (Sens) represents a measure of effect size for each predictor.

Response	xR^2	T	N^*	p	Pred	Tol	Sens	Pred	Tol	Sens
NMS1	0.73	0.71	41	0.01	PCA1	1.157	0.46			
NMS2	0.22	0.61	62	0.01	Picsit	0.260	0.19			
Hypogymnia bitteri	0.60	0.59	54	0.01	PCA1	2.479	0.29	PCA3	2.065	0.14
Hypogymnia duplicata	0.35	0.69	53	0.01	PCA1	2.809	0.34	PCA4	1.099	0.25
Hypogymnia physodes	0.69	0.75	41	0.01	PCA1	1.157	0.51			
Parmelia sulcata	0.46	0.65	54	0.01	PCA1	2.479	0.39	PCA3	2.065	0.19
Parmeliopsis ambigua	0.44	0.72	41	0.01	PCA1	1.157	0.27			
Ramalina dilacerata	0.56	0.70	41	0.01	PCA1	1.157	0.44			
Ramalina farinacea	0.45	0.65	71	0.01	HdwdBA	0.553	0.10	PCA1	3.140	0.20
Ramalina roesleri	0.45	0.70	41	0.01	PCA1	1.157	0.57			
Sphaerophorus globosus	0.47	0.74	68	0.01	PCA1	2.148	0.37			
Tuckermannopsis sepincola	0.28	0.53	62	0.01	PCA1	3.140	0.12	PCA3	1.979	0.78
Vulpicida pinastri	0.70	0.73	41	0.01	PCA1	1.157	0.32			
Xanthoria candelaria	0.41	0.50	42	0.01	PCA1	1.818	0.15	PCA4	1.290	0.09

lichen communities from forests with high conifer basal area and *Tsuga heterophylla* in more oceanic climates to those with greater hardwood basal area and *Picea mariana* and *P. glauca* in suboceanic climates. The strongest environmental variable along the second axis of the ordination was *Picea sitchensis* basal area (**Table 1**, **Fig. 2**).

A suite of species was associated with oceanic and suboceanic climates as described by the first ordination axis (**Table 2**). Several genera showed differential associations; for example, *Hypogymnia apinnata, H. bitteri, H. occidentalis* and *H. physodes* were associated with suboceanic climates whereas *H. duplicata* and *H. enteromorpha* were found in more oceanic climates (**Table 2**). Similarly, *Lobaria pulmonaria, L. scobiculata* and *L. hallii* were associated with suboceanic habitats whereas *L. linita* and *L. oregana* were more associated with oceanic climates. Some genera, such as *Ramalina*, were fairly consistently associated with suboceanic habitats, although many of these species occur on hardwoods along beach fringes in more oceanic southeast Alaska (Karen Dillman, personal comm.).

Individual species models. The twelve species that we focused on for modeling were strongly related to climate variables and showed moderate thresholds (**Table 3**). *Hypogymnia physodes, Parmeliopsis ambigua, Ramalina dilacerata, R. roesleri* and *Vulpicida pinastri* showed similar patterns with greater abundance in suboceanic climates (high PCA1, **Fig. 3**). *Sphaerophorus globosus* had the opposite pattern and was more abundant in oceanic climates. *Hypogymnia bitteri, Parmelia sulcata* and *Tuckermannopsis sepincola* were most abundant in dry climates

with cold winters and warm summers (high on PCA1 and low on PCA3; **Fig. 3**). *Hypogymnia duplicata* and *Xanthoria candelaria* were both sensitive to PCA1 and PCA4, but with opposite patterns. *Hypogymnia duplicata* was associated with oceanic climates with warm summer days and low summer precipitation, whereas *X. candelaria* was associated with suboceanic climates with cool summer days and more summer precipitation (**Fig. 3**). *Ramalina farinacea* was most abundant in more suboceanic climates with high hardwood basal area (**Fig. 3**).

Like the community composition metric, several individual species models exhibited threshold strengths exceeding 0.70 (**Table 2**, T statistics), which can be interpreted as a moderate threshold (Lintz et al. 2011). Lichen community and species metrics changed most abruptly between PCA1 values of three and six (**Table 3**, **Fig. 3**). This corresponds to inland locations in southeast Alaska and Prince Williams Sound and along the Gulf of Alaska coastline on the Kenai Peninsula and mainland and interior Kodiak Island (**Fig. 4**). Although our synthetic climate variable integrated 36 monthly variables to describe the gradient from oceanic to suboceanic climates, it was strongly related to simpler variables, December minimum temperature ($R^2 = 0.90$) and annual precipitation ($R^2 = 0.67$). PCA1 values between 3 and 6 correspond to average December minimum temperatures between -10.2 and $-7.8°C$ and annual precipitation between 106 and 172 cm.

Discussion

We found exceptionally diverse, abundant epiphytic lichen communities in southeast and south-central
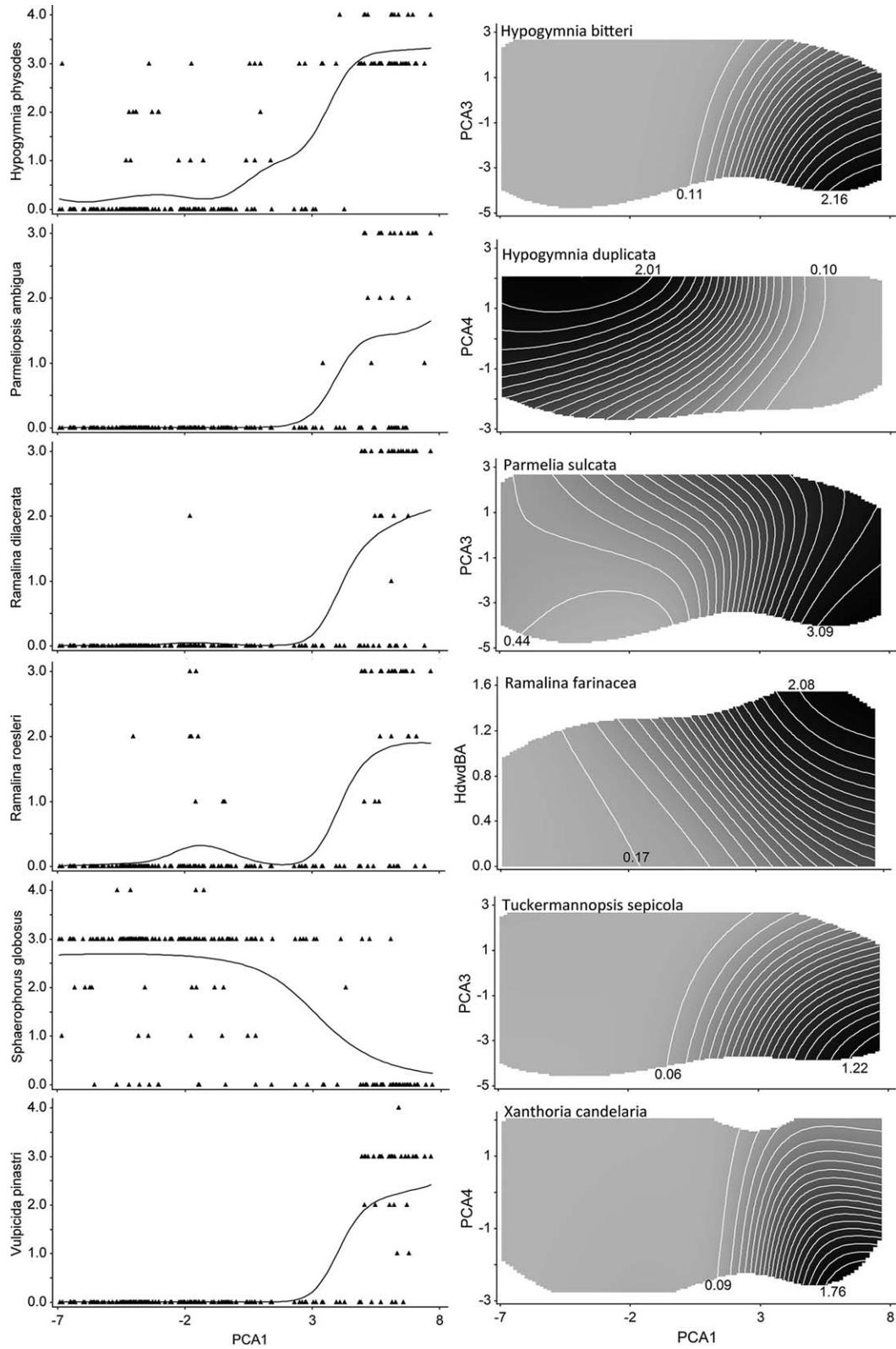
Figure 3. Models for 12 selected lichen species in relation to synthetic climate variables and hardwood basal area (Table 3). For one-predictor models, both modeled surface and observed abundances are shown. For two-predictor models, contour lines and labels indicate modeled abundance, which is greatest in the darker portions of graphs. The white areas represent portions of environmental space without enough data to model.
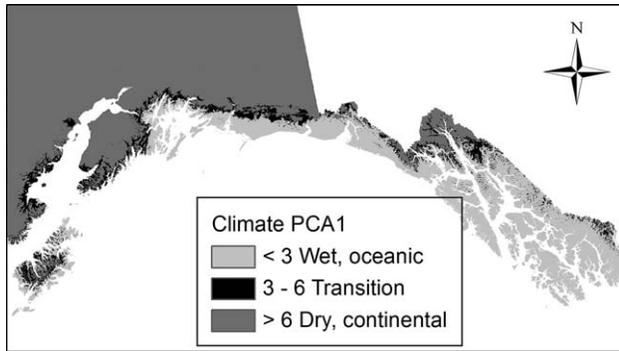
Figure 4. Map of climate synthetic variable PCA1 in our study region of Alaska. PCA1 values between 3 and 6 corresponded to threshold responses in community composition (Fig. 2) and the abundance of several epiphytic lichens species (Fig. 3).

Alaska. In particular, these communities were rich in cyanolichens and alectorioids often considered sensitive to air quality and forest continuity (Geiser & Neitlich 2007; Root et al. 2010). Some species in each group were associated with both ends of the community ordination. Prominence of these groups throughout the region is likely due in part to low N deposition throughout most of the region (NADP 2012), except for localized emissions near point sources (Dillman et al. 2007).

Lichen metrics including community composition and individual species abundances were strongly related to a gradient from wet, oceanic forests of southeastern coastal areas to relatively dry, suboceanic climates further inland. Our observational study was unable to examine the mechanism for the climate thresholds observed. However, the pattern is likely driven by lichen sensitivity to the combination of favorable temperature and moisture availability (Muir et al. 1997). Species show differing physiological responses to the combination of light, temperature and moisture (Palmqvist et al. 2008). A strong association between lichen community composition and temperature, precipitation or humidity has been observed in several other regions (Ellis et al. 2007; Geiser & Neitlich 2007; Giordani & Incerti 2008; Jovan & McCune 2005; van Herk et al. 2002). As in Britain (Ellis et al. 2007), precipitation and temperature covaried in this study and together were the strongest predictors of community composition.

Lichen ecology theory (Gauslaa 2014; McCune 1993) suggests that comparable climate gradients can be observed in lichen communities at multiple scales. For example, moisture is comprised largely of rainfall and humidity in oceanic habitats, with lichens in shaded canopies experiencing more humidity and those in the treetops being exposed to rainfall (Gauslaa 2014). In comparison, suboceanic communities experience more dew and less precipitation; at the stand scale, dew as a moisture source may be more pronounced in forest gaps

(Gauslaa 2014). Because of the diversity of microhabitats within stands and the degree to which they can modify important climate drivers of lichen communities, we expect that lichens with different climatic optima already co-occur within forest stands, particularly in forests with substantial structural heterogeneity. Maintenance of forest structural heterogeneity and continuity may be a valuable tool to ensure that lichen diversity is maintained under changing climates (Ellis & Coppins 2007; Ellis et al. 2009).

Lichen communities in our study area showed strong differences in composition and individual species occurrences within a fairly narrow climatic window; this can allow targeted monitoring efforts in the areas where rapid change is most likely (**Fig. 4**). Threshold values in the oceanic to suboceanic gradient corresponded to average December minimum temperatures between -10.2 and $-7.8°C$ and annual precipitation between 106 and 172 cm. We were able to define 12 indicator species that exhibit clear responses to climate and exhibit a range of temperature and moisture optima. We recommend that future monitoring efforts track these indicator species as well as species flux in the transition zone for sensitive detection of community shifts including the possible development of novel species assemblages. We were also able to detect a geographic 'transition' zone where local conditions encompass climate thresholds (**Fig. 4**). Twelve of our plots fell within this transition zone; these exhibited a community with a mixture of species associated with oceanic and suboceanic habitats. Many contained *Hypogymnia apinnata* and *Bryoria glabra*, typically suboceanic indicators as well as *Alectoria sarmentosa*, *Platismatia norvegica* or *Sphaerophorus globosus*, typically associates of oceanic climates in our study area. Interestingly, several of the transitional plots included *Hypogymnia lophyrea* and *H. hultenii*, which did not show strong patterns in their overall association with the climate gradient.

Lichen responses to climate vary by geographic region such that, at least initially, indicator species and community metrics must be evaluated on a region-to-region basis. Many individual species associations observed in this study corresponded with habitat associations observed in the Pacific Northwest (PNW), but others differed (Geiser & Neitlich 2007). *Sphaerophorus globosus* s.l. was a maritime and lowland species in the PNW; in our analysis it was also found in warm, wet sites characteristic of maritime areas. *Ramalina roesleri* was strongly associated with cold, dry sites with warm summer temperatures, which were overall drier and colder than the maritime habitats it was associated with in the PNW (Geiser & Neitlich 2007). These differences may suggest that in colder regions such as Alaska, hygrophytic lichens can be successful inland by

obtaining needed moisture from dew whereas in warmer regions such as the PNW they require coastal fog. Lichen ecologists focused on regional studies have developed strong models for community habitat associations within several regions (e.g., Geiser & Neitlich 2007; Jovan & McCune 2005); however, to understand why habitat associations differ for species among regions, broader habitat analyses spanning species ranges may be necessary.

In addition to direct climate effects, lichen communities are indirectly affected by climate through its effects on forest composition and disturbance regimes (Barkman 1958; Ellis et al. 2009; Neitlich & McCune 1997; Peterson & McCune 2003). Indirect climate effects on lichen communities are likely if forest extent expands, disturbances become more frequent, or stands shift from conifer to hardwood dominance. Maritime and temperate conifer forests in southeast and south-central Alaska are predicted to expand their altitudinal extent (Bachelet et al. 2005; Ettinger et al. 2011), although some tree species have declined in the region (Hennon et al. 2012). Expansion of forest extent would allow epiphytic macrolichens to expand into habitat that currently lacks suitable substrates. Increased wildfires and insect outbreaks predicted with climate change (Waring et al. 2011; Wolken et al. 2011) may negatively affect species that are associated with late seral habitat (Ellis et al. 2009) or limited by dispersal (Sillett et al. 2000). While climate appeared to be the strongest driver of community composition and the individual species modeled, several species, such as *Ramalina farinacea*, were favored by hardwood substrates (**Fig. 3**). Hardwoods were more abundant in suboceanic climates, particularly on the Kenai Peninsula, which was strongly affected by bark beetle outbreaks in the 1990s (Boucher & Mead. 2006). In heavily affected stands, we observed a large birch component. Differing lichen communities on hardwoods have long been observed (Barkman 1958) and these substrates are known hotspots of diversity in the Pacific Northwest (Neitlich & McCune 1997; Peterson & McCune 2003).

Using lichens to monitor biological responses to a changing climate is potentially a sensitive tool for detecting trends before major changes in tree communities can be observed. Many tree species require disturbances to become established—in these cases, the effects of a changing climate on tree composition may not be seen until a disturbance initiates a new cohort. Although some forests in southeast Alaska are undergoing rapid canopy turnover in response to insects, disease and fire (e.g., Boucher & Mead 2006), many other forests are relatively stable (Barrett & Christensen 2011). Lichens may serve as early indicators of changes in such forests because they can become established relatively

quickly following changed microhabitat conditions without requiring disturbance for community turnover (within 10 years; Root et al. 2010).

Conclusions. Lichen communities are rich and diverse in southeast and south-central Alaska. Community composition is strongly patterned by a gradient from warm, wet *Picea sitchensis* forests of southeast Alaska to cool, dry *Picea mariana* and *Picea glauca* forests of the Kenai Peninsula and Cook Inlet. The lichen community and several lichen species show climate-related thresholds and are likely to be useful for targeting monitoring efforts. Our study is unusual in that we consider lichen indicators including both community composition and individual species. We describe the strength of climate thresholds for each type of indicator and bracket the range of values across several species that show the same broad transitional region. Other synthetic climate gradients were selected as important predictors for several individual species, suggesting that different lichen species can be useful for monitoring different trends in climate.

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Supplementary documents online:

Supplementary Table S1. Equation for calculating scores for plots on Principal Components Analysis axis 1 (PCA1) from PRISM climate data. We included 36 monthly climate variables based on the 1971–2000 normals: precipitation for each month as ppt01–ppt12 (mm * 100); average maximum temperature tmax01-tmax12 ($^{\circ}$C * 100); and average minimum temperature as tmin01-tmin12 ($^{\circ}$C * 100). The PCA equation includes coefficients for each of the 36 variables, which are standardized by the mean and standard deviation for the dataset from which the PCA was derived.