Lichen traits and species as indicators of vegetation and environment

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Abstract. Lichens in the Arctic play important ecological roles. They also face the threats of increasing fire and shrub and tree expansion, exacerbated or caused by climate change. These forces may lead to changes not only in lichen community composition but also in the abundance, diversity and distribution of lichen functional traits. We sought to connect landscape-scale patterns of lichen community composition and traits to environmental gradients to both monitor lichen communities and clarify community-trait-environment relationships. We measured lichens throughout one of the largest and most remote U.S. National Parks within the Arctic. We then analyzed lichen community composition and species richness within ecologically informative lichen trait groups along environmental and vascular vegetation gradients. Macrolichen species richness in 0.4 ha plots averaged 41 species with a total landscape level observed gamma diversity of 262 macrolichen species. Jackknife estimators placed the landscape level macrolichen diversity at 307 to 331 species. A gradient from low-elevation forests to high elevation rocky areas was the dominant ecological gradient as expressed by the lichen community, representing 68% of the variation in species composition. Low-elevation forests hosted more epiphytic lichens characteristic of boreal forests, whereas high-elevation lichen communities were characterized by saxicolous lichens, varying between siliceous, basic or mafic rock types. Along this gradient, species reproducing vegetatively and lichens with filamentous growth form were more frequent in forests while the diversity of traits was highest in alpine habitats. Simple cladoniiform, as opposed to erectly branched fruticose lichens in the genus *Cladonia*, were the only functional group associated with tussock tundra. Vegetation types differed significantly in lichen species composition and richness and trait richness; characteristic suites of lichen species and traits are associated with the particular vegetation types in the Arctic. We also extended the range of *Fuscopannaria abscondita* reported new to North America and *Zahlbrucknerella calcarea* new to Alaska.

Keywords. Alaska, Gates of the Arctic National Park and Preserve, growth-form, photobiont, vegetative dispersal.

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Lichens play important roles in nitrogen cycling (Crittenden 1983), providing critical winter forage for caribou (Heggberget et al. 1992) and colonizing newly exposed surfaces (Cutler 2010). Patterns in Arctic lichen community composition have received increasing attention in response to increasing fire frequency and extent (Beck et al. 2011; Kasischke & Turetsky 2006) and expanding shrub and tree populations (ACIA 2005; Cornelissen et al. 2001), both of which are linked to declines in lichen abundance (Cornelissen et al. 2001; Joly et al. 2009, 2010). Previous ecological studies in more oceanic climates of Arctic Alaska showed vascular vegetation community, fire history, elevation and soil texture were strongly correlated with community structure (Holt et al. 2006, 2007, 2008). Lichen measurements throughout the vast Arctic landscape are therefore important to disentangle background community variation from the effects of disturbance and potentially mitigate or plan for projected shifts in lichen communities.

Recently, many authors have used species traits to scale up species composition to more generalizable ecological theories rather than focusing on species-specific conclusions. Trait-based approaches can also

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point to mechanisms in determining community composition (Adler et al. 2013; Kraft et al. 2008; McGill et al. 2006; Mouillot et al. 2013). Despite these advantages, few studies have used lichen traits in community ecology. Trait patterns along environmental gradients have been interpreted as indicators of mechanisms behind lichen adaptations to the environment. For example, vegetative dispersal has been linked to recent fire (Nelson et al. 2015), lighter thallus color associated lower light conditions within the forest canopy (Färber et al. 2014) or fractal dimension of the branching morphology of some lichens correlated with increased fog deposition (Stanton & Horn 2013). Here we utilize lichen traits as well as lichen community composition in a dataset from one of the largest, most remote U.S. National Parks in the Arctic, Gates of the Arctic National Park and Preserve (hereafter "Gates"), in order to understand how lichen community composition and traits varied along environmental and vascular plant vegetation gradients.

Methods

Field sampling. Lichen community composition and abundance, vascular vegetation abundance and environmental variables were sampled on plots stratified by vegetation type using ecotype classes (Jorgenson et al. 2009) collapsed into nine coarser vegetation groups (**Table 1**). We then used the focal statistics tool in ArcGIS 9.3.1 (ESRI, Redlands, CA, U.S.A.) to remove very small patches or heterogeneous areas of vegetation to assure that plots landed in pure pixels of a given vegetation type. This approach left patches of vegetation at least nine pixels in size (30 m pixels × 9 pixels = 90 m × 90 m) available for sampling.

Sampling occurred between July and August, 2012, concentrated around float-plane accessible lakes. In Gates, there are at least 18 float-plane accessible lakes or river stretches, depending on the aircraft, weather and lake conditions. Of these lakes, those visited were selected to capture unique vegetation types (e.g., mafic rocks in the southwest corner of Gates) and maximize sampling extent across the Park (**Fig. 1**). Each lake was buffered by a 5 km radius, which delimited the sampling extent per lake, because that was considered the maximum one-way distance accessible on foot in a single day. Within each buffered lake, we generated random points (candidate plot locations) by vegetation type using the Geospatial Modeling Environment (GME, Beyer 2012) such that each point was at least 500 m apart from other points in the same vegetation type. We generated many more points than necessary so that we could later select plots for sampling based on our final base camp location. Plots within each vegetation type were also assigned random numbers to be used in selecting plots to sample. We employed this randomization in order to decrease human bias

Table 1. Ecotypes from Jørgensen et al. (2009) aggregated to form vegetation types used in stratified sampling. Symbols # and * indicate vegetation types further aggregated after MRPP of lichen community data. Vegetation types excluded from sampling include those where lichens are extremely rare or entirely absent.

Vegetation types	Ecotype from Jørgensen et al (2009)
Alder (& Willow) #	Lowland Alder Tall Shrub
Alder (& Willow) #	Lowland Willow Low Shrub
Alder (& Willow) #	Riverine Willow Low Shrub
Alder (& Willow) #	Riverine Alder or Willow Tall Shrub
Alder (& Willow) #	Riverine Birch-Willow Low Shrub
Alder (& Willow) #	Upland Willow Low Shrub
Alder (& Willow) #	Upland Alder-Willow Tall Shrub
Broadleaf forest #	Riverine Poplar Forest
Broadleaf forest #	Riverine White Spruce-Poplar Forest
Broadleaf forest #	Upland Birch Forest
Broadleaf forest #	Upland Spruce-Birch Forest
Dwarf Shrub	Alpine Dryas Dwarf Shrub
Dwarf Shrub	Alpine Ericaceous Dwarf Shrub
Dwarf Shrub	Riverine Dryas Dwarf Shrub
Low Birch Ericaceous *	Lowland Birch-Ericaceous-Willow Low Shrub
Low Birch Ericaceous *	Upland Birch-Ericaceous-Willow Low Shrub
Low Birch Ericaceous *	Upland Sedge-Dryas Meadow
Low Birch Ericaceous *	Lowland Sedge-Dryas Meadow
Needle Leaf	Lowland Black Spruce Forest
Needle Leaf	Riverine White Spruce-Willow Forest
Needle Leaf	Upland White Spruce Forest
Needle Leaf	Upland White Spruce-Lichen Woodland
Siliceous	Alpine Acidic Barrens
Basic	Alpine Alkaline Barrens
Mafic	Alpine Mafic Barrens
Tussock Tundra *	Upland Dwarf Birch-Tussock Shrub
Exclude	Alpine Lake
Exclude	Alpine Wet Sedge Meadow
Exclude	Lowland Ericaceous Shrub Bog
Exclude	Lowland Sedge Fen
Exclude	Lowland Lake
Exclude	Riverine Water
Exclude	Riverine Barrens
Exclude	Riverine Wet Sedge Meadow
Exclude	Snow
Exclude	Shadow/Indeterminate

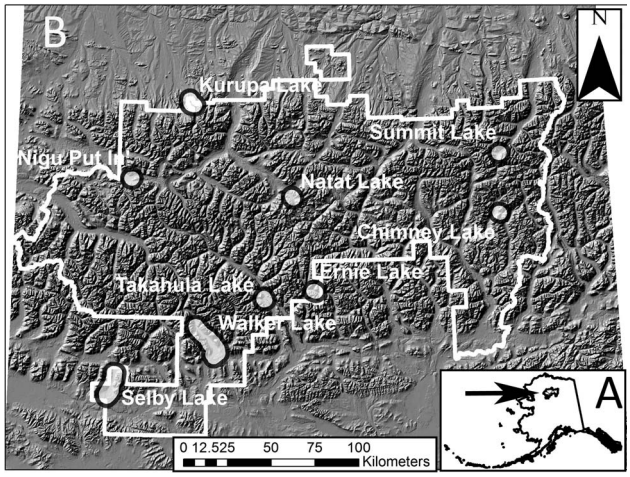

Figure 1. A. Map of Alaska and arrow indicating location of Gates of the Arctic National Park and Preserve. **B.** Map of Gates perimeter showing lakes visited during sampling.

(e.g., tendency to sample areas with easier access), primarily when many plots in the same vegetation type were spatially clustered.

Before arrival at a lake, we determined a target camp area, but occasionally we had to choose a different location based on unforeseen logistical or environmental constraints. After a camp was established, only plots within 5 km of the camp were considered available for sampling. Since the terrain could be quite rugged, it was not possible to completely randomize which plots to sample. However, we chose plots with the lowest random number within each vegetation type constrained by access and proximity to other plots of different vegetation types to reduce bias in plot selection. At each lake, we sampled plots in as many vegetation types as possible but emphasized sampling of vegetation types not found at many other lakes (e.g., mafic at Selby/Narvak Lakes). This meant that at some lakes some vegetation types were present but not sampled. We usually sampled more than one plot per vegetation type per lake.

Each plot was a 34.7 m radius circle centered on the random point. Plot measurements generally followed the Forest Inventory and Analysis (FIA) protocol (McCune et al. 1997), except that we included both ground layer and epiphytes and we modified the abundance classes slightly. Macrolichens were defined broadly as those species with large growth forms with characteristics used for identification that were observable without a compound microscope (see ***Lichen taxonomy*** for specifics). As this work was a part of the National Park Service inventory and monitoring program, only macrolichens were sampled to maximize comparability to studies in other Arctic parks (e.g., Holt et al. 2006, 2007, 2008, 2009). We conducted a time-constrained search for all macrolichens on the plot, searching for at least 30 min and continuing until either 15 min elapsed without finding a new species or 2.5 hrs since beginning the search. Each lichen species was assigned a categorical abundance; 1 = rare (< 3 thalli), 2 = uncommon (4–10 thalli), 3 = common (> 10 thalli and < 1% cover), 4 = abundant (1–5% cover), 5 = prolific (6–25% cover) and 6 = dominant (> 26% cover).

Environmental and vegetation variables (**Supplementary Table S1**) were measured on the plot by ocular estimation, and included tree, shrub, mid-tall shrub, low shrub, dwarf shrub, graminoid, forb, bryophyte, lichen, soil, duff, rock and water. The cover of these groups was estimated into the following classes: 0.5 (which means "less than 0.5"), 1, 3, 5, 10, 15, 20, …, 95 and 100%. Other environmental variables were measured in ArcGIS by intersecting each plot location with the respective layer, including snow-free date (Macander & Swingley 2012) and elevation. Some plots were misclassified in the original ecotype map and were reclassified into their correct vegetation type based on the vegetation data collected during sampling.

Lichen taxonomy. We defined a macrolichen based on the genera included in Thomson (1984) with the exception of the *Candelariella terrigena* group and the genera *Psora* and *Toninia*, all of which are relatively large, squamolose taxa and *Lempholemma*, which we felt were as obvious as other gelatinous macrolichen genera. We did not distinguish between *Cladonia pyxidata* and *C. pocillum* because they are conspecific (Kotelko and Piercey-Normore 2010) and lumped *C. stricta* into *C. phyllophora* because of unclear taxonomic differences. Those species of *Cladonia* and *Stereocaulon* that required identification of chemical constituents were analyzed using TLC following standard methods (Culberson et al. 1981). Nomenclature follows Esslinger (2012) except for *Cetraria*, which follows McCune & Geiser (2009).

Lichen traits. We scored the following traits for each lichen species: 1) associated photobiont, 2) mode of vegetative dispersal, 3) growth form, and 4) substrate preference. Each trait was represented

by a binary variable, where membership to a trait group was indicated by a 1 or 0. Each species could only have one state for each trait. This resulted in a total of 18 trait variables (**Supplementary Table S2**) and a matrix of 262 species × 18 traits. Photobiont trait states included green algae, cyanobacteria or both (tripartite). We categorized vegetative dispersal ability into four states; a) lacking such propagules, b) those with soredia, c) isidia or d) lobules/phyllida. We assigned species to the following three coarse growth forms: foliose (flattened), fruticose (filamentous, stalked or branched), and squamulose (small flattened granules, although some fruticose species can have basal squamules but are not classified as squamulose here). All but the squamulose growth form were divided into a second level of finer growth form categories. Within the foliose group, we further differentiated between 3-dimensional (3D) species and appressed species. We further divided the fruticose species into erect, richly branched forms (''reindeer lichen''), simple cladoniiform (Ahti 1982) (unbranched pointed or cupped stalks) and sprawling filamentous (thread-like growing bushy or tufted). We assigned each lichen species to one substrate affinity group based on our field experience: epiphytes (growing on trees or shrubs), lignicoles (wood dwelling), saxicoles (growing on rocks) or terricoles (growing on the ground).

We aggregated lichen species-level trait data to a plot by trait matrix by summing the number of species with each trait in each plot, yielding a matrix of 79 plots × 18 traits. Each element in this matrix represents the cover of species with a given trait in a given plot.

Analysis. We evaluated our lichen community dataset of 79 plots × 262 species for outliers by measuring the Sørensen distances among all pairs of plots. We defined an outlier *a priori* as a plot with a mean distance to other plots > 3 standard deviations above the grand mean of interplot distances. No plots were found to be statistical outliers. The variation among plot totals and lichen species totals in the community matrix was modest (coefficient of variation $< 125\%$), and as the abundance classes approximate a logarithmic scale, we did not apply any transformations or relativizations to the lichen abundances. However, prior to ordination, we removed lichen species that occurred only once, reducing noise in the analyses. Plot species richness and diversity measures used in overlays were, however, calculated using all species. Forty-five species were found on only one plot and were not included in the matrix used for NMS or MRPP of community composition.

We used non-metric multidimensional scaling (NMS, Kruskal 1964) in PC-ORD v.6 (McCune & Mefford 2011) to ordinate lichens using a Sørensen distance measure and ''Slow and Thorough'' autopilot settings. We assessed the relationship between community composition and environmental and vegetation variables by either linear correlation or non-parametric multiplicative regression (NPMR; McCune 2006 as implemented in HyperNiche, McCune & Mefford 2009). Linear correlations between the NMS axes and the environmental and trait richness (the count of species on a plot with a given trait) measures were calculated in PC-ORD by overlaying environmental and trait variables on the ordination. Each environmental and trait richness measure was also regressed against each NMS axis using NPMR. Non-linear relationships between environmental variables and community composition were expected (Nelson et al. 2015) so we chose NPMR because of its ability to detect non-linear relationships (McCune 2006). We used the ''Medium'' overfitting control in HyperNiche but only used the NPMR model if it improved fit over simple linear regression. We defined improvement as an increase in cross-validated fit ($\times r^2$) of at least 0.05 over the linear model. Variables where NPMR models were better than linear overlays were displayed on the side of the ordination. Only variables with either a linear fit or NPMR model with an $r^2 \geq 0.15$ were displayed. Prior to NPMR, vegetation and soil cover variables were first relativized to the column maximum so that all variables could be plotted on the same scale from zero to 1.

We tested for differences in lichen community composition and trait richness between the nine vegetation groups used in stratifying our sampling. We used Multiple Response Permutation Procedure (MRPP) because of uneven numbers of plots sampled in vegetation groups. We conducted MRPP in PC-ORD using the plot × lichen species matrix, after removing species that occurred only once, using Sørensen distance and weighting by species totals. After comparing all pairwise combinations of species composition amongst vegetation types using MRPP, we combined vegetation types that were not

significantly different ($p \geq 0.05$). Using these final vegetation types, we tested for differences among vegetation types for both the plot × species with singletons excluded and plot × trait richness matrix with singleton lichen species included.

Finally, we examined which species and traits were associated with each vegetation type using indicator species analysis (ISA; Dufrêne & Legendre 1997) in PC-ORD. We ran an ISA using the plot × species matrix without singleton species and a plot × trait matrix using all species, both of which used 4999 randomized runs.

Results

Species diversity. A total of 262 macrolichens species or subspecies were found (**Supplementary Table S3**) on the 79 plots sampled from base camps at nine different lakes (**Fig. 1**). The most frequent lichens were, in descending frequency, *Cladonia pyxidata, Cetraria cucullata, Cladonia amaurocraea, Cetraria nivalis, Peltigera leucophlebia, Thamnolia vermicularis, Cladonia rangiferina, Cladonia stygia, Cetraria laevigata* and *Cladonia arbuscula* (**Supplementary Table S3**). Macrolichen species richness in 0.4 ha plots averaged 41 species, with a beta diversity of 1.9 half changes, and a total landscape level observed gamma diversity of 262 macrolichen species. Jackknife estimators placed the landscape level macrolichen diversity at 307 to 331 species.

Community and trait gradients. The NMS ordination resulted in a 2-dimensional stable (instability < 0.00001) and low stress solution (final stress = 13.7) with all axes beating the randomization test ($p = 0.004$). Axis 1 accounted for 68% of the variation and represented a gradient of high elevation, rocky plots to low elevations with taller shrubs and more trees (**Fig. 2**). The abundance of epiphytic species, such as *Vulpicida pinastri, Parmelia sulcata, Parmeliopsis hyperopta*, and lignicolous species such as *Cladonia cenotea, Cladonia coniocraea* and *Cladonia botrytes* increased to the left on Axis 1. To the right, alpine saxicolous and terricolous species were more abundant, including *Thamnolia vermicularis, Rusavskia elegans*, *Vulpicida tilesii*, *Physcia caesia* and *Blennothallia crispa.*

At low elevations, more epiphytic, lignicolous, sorediate and filamentous species occurred in the forest and tall shrub habitats (left side of axis 1; **Table 2**, **Figs. 2 & 3**). At mid elevations (middle of axis 1), graminoid and low shrub cover peaked (**Fig. 2**), broadly corresponding to peak richness of simple cladoniiform lichens (**Table 2**, **Fig. 3**). At higher elevations (right side of axis 1), many lichen trait groups, including cyanobacterial photobionts and tripartite lichens, terricolous species and fruticose, 3-D foliose, sprawling filamentous and squamulose growth forms, reached their peak richness (**Table 2**, **Fig. 3**). Axis 2 accounted for 13% of the variation and represented a gradient of low to high lichen species richness, diversity and cover and more saxicolous, erect-branched fruticose and green algal lichen species (**Fig. 3**).

NPMR models were better for all environmental and trait variables than linear models for relating ordination axes to environmental and trait variables by at least $r^2 > 0.05$.

Community differences among vegetation types. The number of plots sampled in each vegetation type ranged from three deciduous plots to 14 dwarf shrub plots, based on differing quantities of each vegetation type present in the lakes visited. The deciduous vegetation type had lichen species composition similar to alder, while low birch shared similar lichen communities to tussock. These were collapsed into alder (containing deciduous) and low birch/tussock, respectively, resulting in seven final vegetation types (**Tables 1 & 2**). These seven vegetation types differed greatly in lichen community composition ($A = 0.19$, $p \ll 0.0001$). The species composition differences are visible in the NMS ordination as separation of plots of each vegetation type (**Figs. 2 & 3**).

Trait richness differed among vegetation types overall ($A = 0.23$, $p \ll 0.0001$) although pairwise comparisons showed some vegetation types had similar trait richness patterns. Indicator Species Analysis showed some traits were good indicators of specific vegetation types while several vegetation types had no strong indicator traits (**Table 2**). The macrolichens associated with each vegetation type are described briefly here.

Siliceous.—*Allantoparmelia alpicola* was the only significant indicator species for siliceous vegetation type (Indicator Value = 20.8, $p = 0.03$). This lichen is a small, foliose species that grows tightly attached to the abundant siliceous rocks and boulders. No traits were the strongest indicator traits of siliceous rock types.

Alder.—Good indicator species of alder or willow thickets and deciduous forests included *Hypogymina*

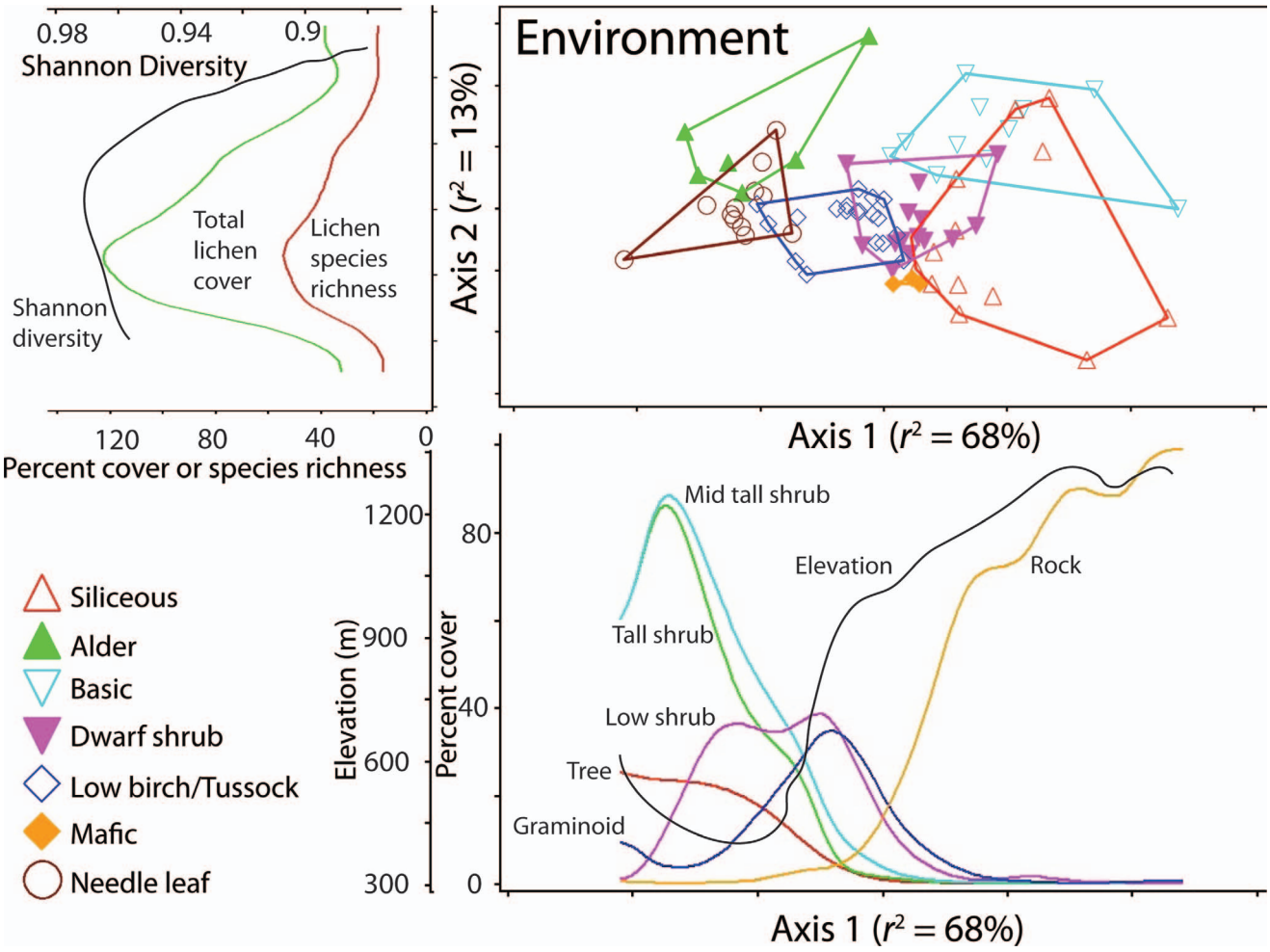

Figure 2. NMS ordination of 79 plots, shape-coded by vegetation type showing environmental relationships with community structure. Side panels show NPMR models of environmental variables regressed against NMS axes.

bitteri, Usnea *lapponica*, *Melanohalea septentrionalis* and *M. trabeculata*, all green algal epiphytic lichens common on the boles and branches. Foliose cyanolichens associated with this vegetation type included *Nephroma resupinatum* and *N. helveticum*, frequently encountered at the base of the deciduous trees and shrubs as well and *Peltigera elisabethae*, found on the soil and duff. Lichens with lobules were associated with alder and willow thickets and deciduous forests (Indicator Value = 27, p = 0.03, **Table 2**).

Basic.—All of the indicator species associated with basic rocks and soil were known calciphiles, including *Vulpicida tilesii*, *Lathagrium* cristatum, *L. undulatum*, *Psora decipiens*, *P. himalayana* and *Solorina bispora*. *Dactylina arctica* subsp. *beringica* was also associated with this vegetation type. No traits were the strong indicators of basic rock types.

Dwarf.—Several common species found in the moss/soil/plant tundra matrix were good indicators of dwarf shrub habitats, including *Cetraria cucullata*, *Lobaria linita* and *Nephroma expallidum*. Other dwarf shrub habitat indicators included lichens more specialized to thin or bare mineral soils commonly found between dwarf shrub patches, including *Bryocaulon divergens*, *Cladonia pyxidata*, *Fuscopannaria praetermissa*, *F. viridescens*, *Parmelia fraudans*, *Psoroma hypnorum* and *Anaptychia bryorum*. *Pseudephebe pubescens*, a common saxicole, was also a good indicator species, which we frequently observed on small cobbles and gravel. Indicator traits for dwarf shrubs included the foliose, squamulose, appressed and 3D-foliose growth forms, lichens of terricolous substrate and those with cyanobacterial photobionts (**Table 2**).

Low birch/tussock.—Several terricolous foliose cyanolichens (*Peltigera malacea*, *P. polydactylon* and *P. scabrosa*) or tripartite lichens (*P. aphthosa*, *Solorina crocea*) were indicator species of low birch and tussock

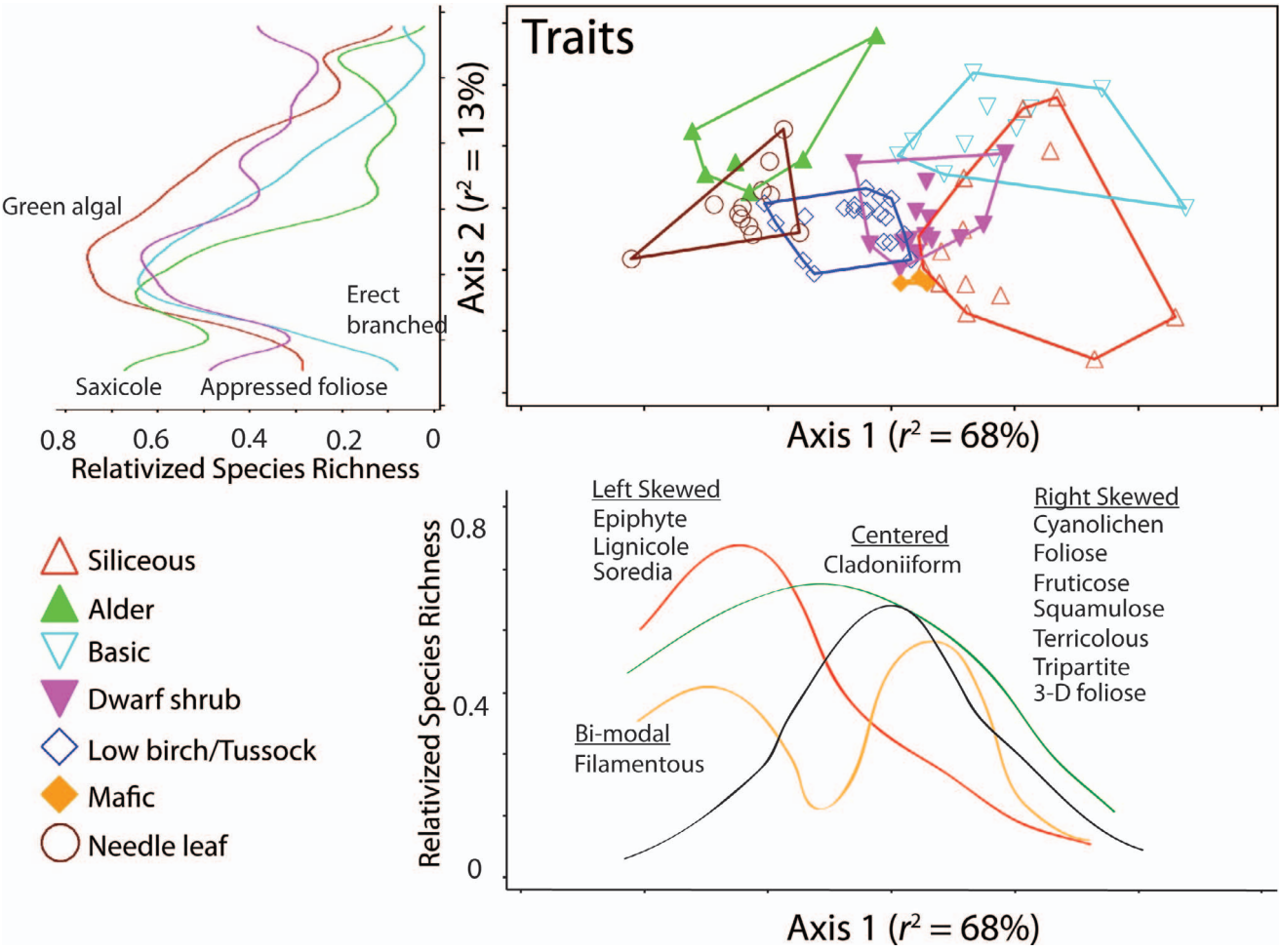

Figure 3. NMS ordination of 79 plots, shape-coded by vegetation type showing trait relationships with community structure. Side panels show NPMR models of trait variables regressed against NMS axes. Due to the high number of related traits, the Axis 1 side panel NPMR models were aggregated to four categories; centered, left or right skewed or bi-modal shaped curves.

tundra. Fruticose green algal species associated with this vegetation type included *Cladonia cyanipes* and *Dactylina arctica subsp. arctica*. The vagrant macrolichen, *Masonhalea richardsonii*, was also a good indicator. No traits were robust indicators of the Low birch/tussock vegetation type, although simple cladoniiform lichens had a weak association with this vegetation type (Indicator Value = 18.9, p = 0.07).

Mafic.—Only three plots were in truly mafic rocks, all of which were around Lake Selby and Narvak Lake. Twenty-six species were good indicators of mafic areas. *Stereocaulon apocalypticum* (Indicator Value = 93.4, p = 0.0002) and *Massalongia carnosa* (Indicator Value = 88.3, p = 0.0002) were found almost exclusively in this vegetation type. Five species had indicator values between 50–70, including *Sphaerophorus fragilis, Polychidium muscicola, Arctoparmelia centrifuga, Umbilicaria caroliniana* and *Stereocaulon subcoralloides*. The remaining twenty-six indicator species for mafic areas included other saxicolous and terricolous species. Indicator traits of mafic areas were green photobiont, saxicolous substrate specificity and fruticose, erect-branched and filamentous growth forms.

Needle.—Twenty-four species, mostly epiphytes or lignicoles, were indicator species of coniferous forests. Epiphytic indicators included *Bryoria simplicior, B. lanestris, Cetraria halei, C. pinastri, Evernia mesomorpha, Hypogymnia austerodes, H. physodes, Melanohalea exasperatula, Parmelia hygrophila, P. sulcata, Parmeliopsis ambigua, Ramalina dilacerata, R. roesleri* and *Usnea scabrata*. Lignicolous indicators included *Cladonia botrytes, C. cenotea, C. coniocraea, C. cornuta, C. crispata C. gracilis* subsp. *turbinata* and *C. sulphurina*. A few terricolous species were also coniferous indicator species,

Table 2. Average trait cover and environmental variable values by vegetation type. Trait cover is the average cover of all the species with a trait. Bolded values indicate that trait had the maximum indicator value that was statistically significant ($p \leq 0.05$) for that vegetation group except for "*", which was $p = 0.07$. Siliceous = sparsely vegetated areas with non-calcareous rock with low heavy metal content; Alder = alder, willow or deciduous tree dominated vegetation; Basic = sparsely vegetated areas with calcareous rock; Dwarf = dwarf shrub dominated vegetation, Low Birch/Tussock = Dwarf birch (*Betula nana* group) or tussock (primarily *Eriophorum* sp.) dominated vegetation; Mafic = sparsely vegetated areas with non-calcareous rock with high heavy metal content; Needle = conifer dominated vegetation (*Picea glauca* or *P. mariana*).

Trait/Env Variable	Siliceous	Alder	Basic	Dwarf	Low birch/ tussock	Mafic	Needle
	14	6	11	14	19	3	12
			Traits				
Green	27.1	23.5	17.5	39.4	32.9	**41.7**	33.5
Cyano	5.4	6.8	4.5	**9.6**	5.7	8.3	3.3
Tripartite	3.9	2.7	3.2	6.4	6.2	6	1.5
Saxicole	10.3	1.2	2.9	11.2	3.2	**14.7**	0.9
Terricole	26.3	19.2	22.1	**43.4**	38.3	40.3	21.9
Epiphyte	0.6	10.7	0.3	1.3	3.4	0.7	**13.3**
Lignicole	0	3.5	0.3	0.7	1.5	1	**4**
Foliose	21.6	20	16.2	**33.3**	22.2	28.7	16.8
Fruticose	14.9	13	9	21.7	22.4	**27.3**	20.4
Simple cladoniiform	7.6	8.2	6.1	11.3	**13.4***	12	12.3
Squamolose	1.4	1	1.4	**2.9**	1.1	0.7	0
Erect branched	5.1	2.8	2.1	7.2	7.2	**11**	6.4
Appressed	13.8	13.5	8.4	**19.6**	11.4	19	9.8
Filamentous	2.1	2	0.8	3.2	1.8	**4.3**	2.8
3D foliose	6.3	5.5	6.5	**10.8**	9.6	9	7
Sorediate	3.6	13	2.1	6.4	8.2	8.3	**16.5**
Isidiate	1.5	**2.2**	0.8	1.6	1.5	1.7	2.1
Lobulate	0.3	0.8	0	0.4	0	0.3	0
			Environmental Variables				
Species Richness	36.4	33	25.2	55.4	44.9	56	38.3
Cover	80.5	70.8	52.2	122.6	100.9	121.3	93.8
Evenness	1	1	1	1	1	1	1
Simpson	1	1	0.9	1	1	1	1
Shannon	3.4	3.3	3.1	3.9	3.7	3.9	3.6
Elevation (ft)	4171.4	2182.5	3481.5	3818.6	2670.4	2922.3	1140
Snow-Free Date (Julian)	139.4	139	138.3	141.2	139.2	129.3	138.5
Tall Shrub cover	0.3	80.3	0.5	0.1	0.8	0.3	44.2
Tree cover	0	3.3	0.1	0	1.1	0.3	35.4
Low Shrub cover	1.6	5.7	0.2	1	37.6	5.3	39.6
Mid Tall Shrub cover	0.3	82	0.6	0.5	8	0.3	54.2
Dwarf Shrub cover	6.3	4.5	23	55	16.2	10.5	21.7
Forb cover	2.3	23.1	0.6	1.5	5.9	0.5	10.1
Graminoid cover	0.3	12.7	1.2	10.3	39.3	0.3	3.5
Bryophyte cover	3.9	1.2	0.6	11	21.6	20.3	30.7
Lichen cover	7.8	0.5	3.8	5.7	2.8	0.4	6.1
Duff cover	0.2	4.1	0.4	2.1	1.3	0.3	0.9
Soil cover	0.2	0.9	5.8	2.9	0.7	0	0.2
Rock cover	85.2	1.7	65.7	14.2	1.3	80	0.3
Water cover	0	0.1	0	0.2	0.4	0	0.1

including *C. gracilis* subsp. *vulnerata, C. scabriuscula* and *C. stellaris*. Epiphytic, lignicolous and sorediate lichens were all indicator traits of conifer forests (**Table 2**).

Floristic discoveries. We report *Fuscopannaria abscondita* as new to North America and *Zahlbruc knerella calcarea* as new to Alaska. *F. abscondita*, a very distinctive species with a large, coralloid thallus, was

previously known only from Svalbard (Kristinsson et al. 2010). Our single specimen was found in a frost boil in a dwarf shrub vegetation zone. *Z. calcarea* is a saxicolous calciophile found across North American arctic and alpine zones but has likely been overlooked in Alaska. We found it in several alpine basic rock outcrops.

Discussion

Species diversity. Gamma diversity in Gates (262 species on 79 plots) was higher than adjacent Noatak National Preserve (201 species on 88 plots, Holt et al. 2009) and nearby Bering Land Bridge National Preserve (140 species on 78 plots, Holt et al. 2007). Jackknife estimates of diversity for all three parks/preserves support the same pattern (McCune et al. 2009), with Gates having the highest estimated gamma diversity. Both Noatak and Bering Land Bridge were recently sampled with the same protocol used here with nearly the same sample sizes and similar stratified sampling approach. The similarity of these studies implies diversity increases with continentality, moving from west to east in northern Alaska. This is counterintuitive at first, as more oceanic climates are generally more diverse for lichens. However, as McCune et al. (2009) point out, Noatak has much more topographic and geologic diversity than Bering Land Bridge. Like Noatak, Gates has a diversity of rock types, including extensive limestone, as well as forests, which present many more habitats for lichens to inhabit than the rolling tundra of Bering Land Bridge. More detailed comparisons between Noatak and Gates are not explored here but one explanation of the higher gamma diversity in Gates versus Noatak could be the more extensive limestone areas and the presence of mafic rocks, which hosted many species rarely found elsewhere in Gates.

Previous lichen work in Gates focused primarily on lichen inventory which cumulatively documented 248 macrolichen species (Neitlich & Hasselbach 1998). Our work provides the first, park-wide inquiry into lichen community composition over many vegetation types. Our inventory efforts also yielded many new taxa to Gates (**Supplementary Table S4**), although a full floristic inventory is pending identification of crustose lichen specimens collected by collaborators and the first author during fieldwork.

Community and trait gradients. Lichen community composition across interior and northern Alaska is strongly related to elevation, soil texture and substrate diversity (Holt et al. 2007; McCune et al. 2009; Nelson et al. 2015). Low elevation lichen communities are frequently dominated by epiphytes on conifers and shrubs whereas middle elevations are primarily wet tundra communities. Higher elevations are dominated by saxicolous or terricolous species. Our findings add to literature describing this general pattern but provide new perspective by viewing community composition through lichen traits.

Photobiont, dispersal and growth-form traits displayed a variety of richness maxima, some of which clearly corresponded to environmental or vegetation variables or vegetation types. We interpreted this as environmental filtering favoring lichens with different combinations of traits. Lichen composition and traits differed among vegetation types, implying the suite of biotic and abiotic variables characteristic of that vegetation type favored a unique suite of lichen traits and species.

Sorediate and filamentous lichens and species specialized to grow on trees or wood peaked at lower elevation forests and shrublands, visible as peaks far left side of axis 1 (**Figs. 2 & 3**). Soredia enable lichens to quickly colonize available substrate at shorter dispersal distances (Bailey 1966; Werth et al. 2006) relative to sexual diaspores. Soredia are also effective at long-distance dispersal because they carry both partners in the lichen symbiosis. Indeed, within a number of genera (e.g., *Hypogymnia*, Miadlikowska et al. 2011), sorediate species tend to be widespread across continents, while species without specialized asexual propagules tend to be regional or continental endemics. In our case, the frequency of sorediate lichens in forests was twice that of any other vegetation type (**Table 2**), yet it is unclear how this pattern is related to dispersal ability. Others have also found sorediate lichens peak in forests in Denali National Park (Nelson et al. 2015), approximately 500 km south of our study area as did researchers working in southwestern Canada (Rapai et al. 2012). While this emerging pattern is compelling, the question remains open as to why sorediate lichens are more frequent in forests.

Lobulate lichens were also associated with tall shrub thickets. Large vegetative propagules have been shown to be associated with old-growth forests, where they may be more effective dispersal propagules because of the more stable habitats found

there. Old forest may also have more lobulate lichens because larger propagules take longer to get there (Sillett et al. 2000). Investing in a larger propagule that needs to travel shorter distances likely results in a higher colonization success rate, since larger propagules are thought to be more robust to desiccation, physical damage, etc. Like the observed patterns in sorediate lichens, lobulate lichen distribution needs further study to find a compelling explanation for this pattern.

Filamentous lichens also peaked in richness in forests, perhaps due to their higher surface area/mass ratio, which generally gives lichens a greater capacity to quickly absorb moisture (Larson & Kershaw 1976). However, filamentous lichen richness also peaked in higher elevations. This bi-modal distribution is unique among the lichen traits we analyzed, suggesting some conditions shared by epiphytic and alpine habitats. The ability of filamentous lichens to quickly hydrate during relatively short periods of atmospheric humidity (fog) in forests or ephemeral precipitation (dew, light snow) in the alpine may explain the bimodal distribution of this trait. However, we do not have precipitation data at sufficiently fine grain to test this explanation.

Many lichen traits peaked in richness in the alpine vegetation types of mafic, siliceous, basic and dwarf shrub (right side of axis 1). Traits peaking in these alpine areas include cyanobacterial and tripartite photobionts, foliose, fruticose, squamulose, 3-D foliose and filamentous growth forms and lichens specialized to terricolous substrates. We interpret this diversity in photobiont and growth-form richness maxima as further support of the hypothesis that most lichen life strategies are designed to escape competition with faster growing, larger vascular plants by specializing in harsher environments, such as the alpine (Grime 1977). Others working in Alaska have also supported the stress-tolerant lichen life history theory by finding elevation and rockiness (e.g., environmental harshness) being strongly related to lichen community composition (Holt et al. 2007). However, our plots extended beyond the elevation richness maximum of all the trait groups we measured (far right of axis 1), indicating the environment is too harsh for macrolichens beyond that elevation, and suggesting that macrolichen diversity peaks, then declines along a gradient of increasing stress. Since we did not measure microlichens (crustose species) in our plots, it is possible that species with that growth form are still abundant and diverse at the highest elevations.

While low elevations are rich in fruticose and sorediate lignicolous and epiphytic species and alpine areas host lichens with many traits, middle elevation areas, mainly tussock tundra and low birch-ericaceous vegetation types, appear to be unfavorable for most lichens except simple cladoniiform form species. The correspondence of simple cladoniiform lichens with graminoids in Gates differs from another study using the same trait categories on a similar species pool in Denali National Park and Preserve (Nelson et al. 2015). They found that simple cladoniiform lichens reached a richness peak in low elevation forests and after fires. In areas of high graminoid cover in Gates, simple cladoniiform lichens occur between tussocks, on leaf litter on the sides of the tussocks and on dead tussocks. In Denali, Nelson et al. (2015) sampled many more plots in the boreal forest than graminoid-rich tussock tundra, which could have emphasized the association of simple cladoniiform lichens with forests. In contrast, there is far more tussock tundra than forest in Gates. Simple cladoniiform lichens are possibly switching their central substrate tendency from one organic substrate (wood in Denali) to another (tussock leaf litter in Gates).

The few lichen trait variables most strongly related to axis 2, including green algal, erect-branched fruticose (''reindeer lichen''), saxicole and appressed foliose lichens, were not easily interpreted in the context of environmental gradients because no environmental variables were strongly related to axis 2. All these traits had hump-shaped relationships with axis 2, peaking low along this axis. There were also hump-shaped relationships between axis 2 and total lichen cover and species richness peaking low on axis 2, below which species richness and cover plummeted (**Fig. 2**). The few plots pulling species richness and cover down low on axis 2 were all unstable siliceous scree and talus (lower right in ordination, **Figs. 2 & 3**). On a subset of these plots, saxicolous and appressed foliose lichen richness increased but overall richness was low. Axis 2 could represent a competition/stress gradient, where high on axis 2, vascular vegetation is more abundant and overall lichen trait and species richness is low. Higher axis 2 values associated with greater disturbance and/or stress may be associated with decreased vascular plant vigor (e.g., cold, alpine habitats or exposed, wind-swept ridges),

where lichens can persist with lower vascular plant competition.

Conclusions

Lichen communities are known to be largely controlled by water, light and substrate (Giordani et al. 2012). Our results show nuances within this framework unique to the Arctic, including vegetative dispersal and filamentous growth form traits being associated with lowland forests while the bulk of lichen trait diversity is concentrated at higher elevation, rocky areas. We unexpectedly found tussock tundra to be relatively depauperate of lichen trait variation where simple cladoniiform form lichens were the only group to reach their peak richness. All of these environment/trait relationships point to broad morphological and physiological adaptations that lichens have developed in response to the extreme climate of the Arctic. Future studies should focus on refining trait and environment measurement while focusing on specific environmental gradients, especially spatiotemporal variation in precipitation and light, to better understand lichen community assembly.

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Supplementary documents online

Supplementary Table S1. List of lichen species traits and environmental variables.

Supplementary Table S2. Trait matrix (alphabetical by species). ''1'' indicates a species possesses that trait.

Supplementary Table S3. Lichen species mean abundance and frequency over 79 plots sorted from increasing to decreasing frequency.

Supplementary Table S4. Trait matrix (alphabetical by species). ''1'' indicates a species possesses that trait.