AN ABSTRACT OF THE DISSERTATION OF

Robert J. Smith for the degree of Doctor of Philosophy in Botany and Plant Pathology presented on May 1, 2017.

Title: Realized and Potential Climate Responses of Lichen and Bryophyte Communities in a National Forest Inventory

Abstract approved:

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Bruce McCune

Climate and terrestrial vegetation have had mutual feedbacks for nearly five hundred million years, yet both are now departing from recent historical norms, with uncertain implications for forest ecosystems. This dissertation outlines the current and potential future climate responses of lichen and bryophyte communities in the United States as part of a national forest inventory. The first task was to identify influences on carbon and nitrogen storage of moss and lichen "ground layers" in subarctic interior Alaska. Nutrient stores were more sensitive to local vegetation and topography than regional macroclimate. Nutrients and biomass were greatest among apparently less-disturbed stands. This suggests that climatic changes could diminish ground layer nutrient storage indirectly if they promote intensifying wildfire regimes or expansions of competitive vascular vegetation. Turning to focus on species diversity, the next task was to quantify the strength of relationship between epiphytic lichen community composition and macroclimate across the 4,000 km-long swath of the U.S. Pacific coastal states. The strongest fitting lichen response gradients involved precipitation, temperature, and a heat-moisture index. Lichen indicator species (diagnostic of ten defined climate zones) emerged as useful monitoring tools because their abundance changes could signal shifting climate zone boundaries. After establishing key present-day climatic relationships, the next task was to pinpoint nationwide locations where epiphytic lichen communities will be most vulnerable to species losses under current and future warming scenarios. Novel niche-based metrics revealed greatest vulnerability among supposedly "warm-adapted" communities in southern/lowland locations, contrary to usual assumptions centering on cooler northern/montane habitats. Vulnerability analyses can steer conservation and monitoring attention to specific locations where warming is most expected to affect

ecological communities. The final task, to anticipate how warming will impact individual lichen performance, was addressed by quantifying how experimental climate treatments (whole-ecosystem warming and CO_2 additions) affected growth of the boreal epiphytic lichen species *Evernia mesomorpha*. Over just one year, incremental warming and concurrent drying caused progressive growth declines and biomass losses among individual transplants. Such warming-induced biomass losses of epiphytic lichens could precede local population extinctions and regional range contractions. Overall, this dissertation weaves together multiple lines of evidence from nutrient, diversity and growth responses to indicate the ecological effects of climate and climatic changes on vegetation in a national forest inventory context. This work suggests a pathway for integrating lichen and bryophyte responses into nationwide climate monitoring to address emergent interactions between humans, vegetation, and the global climate commons.

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Robert J. Smith, Author

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CONTRIBUTION OF AUTHORS

Sarah Jovan contributed to study design for all chapters, contributed to all aspects of the research and writing, and helped obtain funding. Andrew Gray made contributions to analyses for Chapter Two. Peter Nelson and Paul Hanson made contributions to study design for Chapter Five. All authors reviewed the manuscripts and revisions.

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CHAPTER 1. INTRODUCTION

One of the world's most complex socioecological systems is the set of interactions among humans, vegetation and climate. Human actions have contributed to recent departures from historical climate norms, largely due to greenhouse gas emissions (IPCC 2014) and the modification or removal of natural plant communities (Dale et al. 2011). Mitigating global changes is a grand challenge that will depend, in part, on carbon-negative collective actions driven by citizens, markets and government institutions across local to global scales (Ostrom 2014; Obama 2017). Yet, grand social efforts cannot succeed without ecological evidence. If we are to sensibly manage our role in the human–vegetation–climate system, our social institutions must dialogue with evidence-based reasoning to give a deeper understanding of how and where global changes will affect communities, both human and ecological.

Understanding how global changes shape the diversity and structure of ecological communities hinges on differential species responses and the concept of the ecological niche. One classical definition of the niche is the joint set of environmental and resource conditions under which a species can persist (Hutchinson 1957). The classical perspective has recently expanded to view species' niches as the causes of relative fitness differences which govern coexistence and community structure (Chesson 2000; Kraft et al. 2015; Vellend 2016). It is axiomatic that ecological theory and methods should match the biological realities that they presume to explain (Austin 2002). Niche theory matches the realities of forest conditions to the extent that it can explain vegetation changes given new scenarios. Emergent scenarios include land cover conversion, timber harvests, wildfire regime changes, species invasions, pest and disease outbreaks, enhanced nutrient deposition, atmospheric warming, and many other local and global changes.

Among the most responsive indicators of forest conditions are lichen communities (McCune 2000). Epiphytic (tree-dwelling) lichen communities have long been used to determine air quality, calculate nutrient critical loads, and estimate heavy metal deposition (Nylander 1866;

van Haluwyn and van Herk 2002). For organisms so clearly exposed to atmospheric conditions, it is surprising that lichen communities have not been universally embraced as quantitative climate indicators. Naturalists for centuries have amassed an anecdotal record relating lichens to climate across landscapes (Lindsay 1856). By contrast, rigorous, quantitative ecological studies of lichens and macroclimate have been in short supply until the current century (but see Barkman 1958; Adams and Risser 1971; Nash et al. 1979; Bruteig 1993; McCune et al. 1997). The situation is similar for terrestrial (ground-dwelling) lichens and bryophytes, with few exceptions (Schöller 1991; Insarov and Insarova 1996; Frahm and Klaus 1997). These knowledge gaps suggest an opportunity for investigating lichen and bryophyte responses in a systematic national forest inventory to assess the effects of global changes on ecological communities.

The primary objective of this dissertation is to outline the realized and potential responses of some biological climate indicators in North America, toward anticipating the consequences of climate change on forest diversity and functioning. Sampling and analyses are based on the U.S. Forest Inventory and Analysis program for monitoring forest status and trends. The primary objective is addressed through several complementary goals: to quantify ground layer carbon storage potential and its sensitivity to environmental predictors in interior Alaska (*Chapter Two*); to quantify the strength of dependence and sensitivity of epiphytic lichen community composition to macroclimate variables across the U.S. Pacific states (*Chapter Three*); to innovate methods for assessing how and where warming-induced species losses will occur in epiphytic lichen communities nationwide (*Chapter Four*); and to quantify the effects of experimental climate changes on the growth of a boreal forest lichen species (*Chapter Five*).

Carbon is the currency of climate change – therefore, tracking status and trends in terrestrial vegetation may reveal how carbon is exchanged among atmospheric and terrestrial pools. *Chapter Two* examines carbon storage and functional diversity of moss and lichen "ground layers" in the peatlands, woodlands and forests of the Tanana River Valley of interior Alaska as part of the U.S. Forest Inventory and Analysis program. Findings from this chapter prepare the way for a landscape modeling approach of nutrients and functional diversity given local environmental conditions.

Epiphytic lichen communities are often assumed to be excellent "first responders" – sensitive bioindicators of environmental conditions like climate – but the strength of this assumption is rarely tested in a rigorous, quantitative manner. *Chapter Three* examines how strongly epiphytic macrolichen community composition is associated with climatic gradients across the U.S. Pacific states of Alaska, Washington, Oregon and California. This chapter lends credibility to the use of epiphytic macrolichen communities as robust, efficient indicators of macroclimate across large biogeographic areas.

Communities with many species approaching their climatic niche limits may be vulnerable to species losses given future climate changes. *Chapter Four* advances a novel data-driven methodological framework for measuring warming-related climate change vulnerability, and applies this to epiphytic lichen communities across the entire United States. Contrary to expectations, this chapter demonstrates that warming-induced species losses may be unexpectedly prevalent among warm-adapted communities.

Community-level climate outcomes are driven in part by the performance of individuals and single species. *Chapter Five* evaluates individual growth performance of the epiphytic, boreal forest lichen *Evernia mesomorpha* in response to experimental whole-ecosystem warming and CO_2 additions. Findings reveal how atmospheric warming and drying may cause local population declines and consequent range contraction of epiphytic species in boreal forests.

The human–vegetation–climate system is characterized by complexity, scale dependency, and emergent properties at different hierarchical levels (Levin 1999; Wimsatt 2007). A systematic, data-driven approach can capitalize on these properties to increase understanding of socioecological systems. Monitoring status and trends in a national forest inventory is one contribution to enhancing knowledge of the ways in which global changes may alter processes and diversity among ecological communities. This enterprise will facilitate dialogue towards forest management practices and policies that balance ecological integrity with economic and societal needs in the human–vegetation–climate system.

CHAPTER 2. SENSITIVITY OF CARBON STORES IN BOREAL FOREST MOSS
MATS: EFFECTS OF VEGETATION, TOPOGRAPHY AND CLIMATE

Robert J. Smith, Sarah Jovan, Andrew N. Gray, and Bruce McCune

Abstract

In northern regions, moss and lichen mats are the major carbon cycling interface between soils and the atmosphere. We aimed to quantify sensitivity of ground layer nutrient stores to environmental predictors, to better understand interactions with vegetation, topography and climatic conditions. With nondestructive forest inventory techniques, we mapped spatial distributions of biomass, carbon and nitrogen among moss/lichen ground layers in a 1.1 million ha watershed within Alaska's boreal forest region. Using nonparametric multiplicative regression, we fit response surfaces and quantified sensitivity to environmental predictors. Across 96 sites, half the ground layer biomass values were in the range 4750–18,900 kg ha^{-1} (25th to 75th percentiles). Carbon and nitrogen stores peaked in older stands and those with little forb cover (suggesting low disturbance) and low incident radiation. Most abundant among functional groups were nitrogen-fixing feather mosses, which formed extensive carpets. Nutrient stores were most sensitive to local vegetation and topography predictors, but less sensitive to regional climate. Moss and lichen mats in boreal forests are substantial carbon and nitrogen stores, with consequences for global carbon sequestration and ecosystem productivity. Their environmental sensitivity suggests that ground layer nutrient stores could decrease if global changes promote vascular vegetation expansions and intensifying wildfire regimes.

Introduction

High-latitude forests are central to understanding global changes because of robust feedbacks between vegetation, soils, and the atmosphere. Carbon exchange in boreal forests is mediated in no small part by the "ground layer", which is the three-dimensional stratum of mosses and lichens that occupy terrestrial surfaces. Ground layers (which include both living and dead organic material) are categorically neither soils nor above-ground vegetation, but instead occupy a unique transitional interface where soils and the atmosphere meet (Fig. 2.1). Terrestrial mosses and lichens have long been recognized as pivotal actors in global climate feedbacks and local nutrient budgets (e.g., Rennie 1807; Geikie 1866; Stålfelt 1937; Gorham 1953; Tamm 1953). Recent global changes have revived interest in quantifying how much carbon and nitrogen are stored in ground layers, and on the environmental conditions under which nutrients are accumulated and sequestered. If northern high-latitude climates continue to warm following recent trends (Chapin et al. 2014), melting permafrost and peat

decomposition beneath ground layers may accelerate CH_4 and CO_2 releases that could further amplify climatic warming (McGuire et al. 2009).

Moss mats account for one-fifth of all net carbon uptake and more than half of nitrogen fixation in boreal forest understories (Lindo et al. 2013; Hasselquist et al. 2016). The carbon storage capacity of ground layers is potentially huge since moss-dominated peatlands currently store about 33% of the world's terrestrial carbon (Yu 2012), most often in poorly drained tundra and boreal forests presumed to be of minor commercial value. Ecosystem engineers like peat-forming *Sphagnum* mosses simultaneously take up atmospheric carbon and inhibit decomposition by altering the pH and water content of soils (Clymo et al. 1998). Despite large carbon sequestration potential, ground layers could switch from sinks to sources under projected global changes.

Carbon storage in subarctic ground layers may face a variety of challenges. In high-latitude habitats, increased surface temperatures and CO_2 concentrations promote growth of tall shrubs that outcompete shorter-statured lichens and mosses (Cornelissen et al. 2001; Elmendorf et al. 2012; Lang et al. 2012). Of particular concern are forage lichens on which caribou and other wildlife depend, and whose decline would have socioeconomic impacts on hunting, tourism and subsistence practices (Joly et al. 2009). Another factor promoting ground layer carbon losses is the intensifying pattern of boreal forest wildfires. Large recent wildfires resulted in greater carbon emissions than at any point in the last several thousand years (Turetsky et al. 2011; Kelly et al. 2013; Hu et al. 2015). They also occurred later in the growing season when ground layers have dried, which increased both burn depth and combustive carbon losses (Kasischke and Chapin 2008).

Seeing how global changes will interact with carbon cycling at the soil–atmosphere interface (Fig. 2.1) requires an understanding of status and trends in carbon pools. Quantifying forest floor and soil carbon now takes a central role in national forest inventories of the United States, Canada, Sweden, and other nations with boreal forests (Woodall et al. 2012; Bona et al. 2013; Swedish NFI 2013). For example, the US Forest Service's Forest Inventory and Analysis (FIA) program now focuses on interior Alaska, which is the last large region of the United States without a systematic forest inventory (Mueller and Irvine 2015). Boreal forests

of interior Alaska have a great variety and abundance of ground layer mosses and lichens, although ground layers have never before been measured systematically over such large landscapes. Overlooking ground layers in forest inventory protocols would grossly underestimate carbon stores (Bona et al. 2013).

We aimed to estimate ground layer biomass, carbon, nitrogen, and ecosystem functions from a systematic forest inventory at 96 sites in the Tanana River valley of interior Alaska. Data were from a pilot for the FIA Interior Alaska Inventory, which aims to sample more than four thousand plots throughout the entirety of interior Alaska over the next decade (Mueller and Irvine 2015). Primary objectives were to identify the best environmental predictors of each ground layer attribute, to quantify their environmental sensitivity, and to estimate potentially nonlinear response surfaces. We initially expected greater sensitivity to climate predictors, relative to topography or vegetation, because of climatic control of photosynthesis and respiration that determine carbon balance. We discuss our findings in the context of global changes and carbon balances, and also explore opportunities to unify inventory data with emerging methods for predictive carbon estimation.

Materials and Methods
Study area and sampling design

Our study was part of a first-year pilot project for the FIA Interior Alaska Inventory (Mueller and Irvine 2015), a multi-year effort that combines field plot and airborne sampling to document status and trends of forest soils, trees, vegetation, fuels, downed woody materials, and other forest attributes. The study area was the Tanana River valley of interior Alaska, north of the Alaska Range and south of the Yukon-Tanana uplands. Most of the area was coniferous boreal forest dominated by black spruce and white spruce (*Picea mariana* and *P. glauca*), in addition to extensive areas of deciduous hardwoods forest including aspen, paper birch and balsam poplar (*Populus tremuloides, Betula neoalaskana, Populus balsamifera*). For the pilot study conducted June–August of 2014, FIA crews measured 96 plots at sites systematically located on 1.1 million ha of forested public lands (Tanana Valley State Forest and Tetlin National Wildlife Refuge). Plots were evenly spaced on a regular hexagonal grid to facilitate airborne surveys, with one plot per 9712-ha polygon overlaying the study area

(Pattison et al. 2017). Among other measurements described below, crews used the Ground Layer Indicator (Smith et al. 2015) to measure ground layer attributes.

Ground layer attributes

First, we estimated ground layer attributes at the 96 sites using the FIA Ground Layer Indicator (Smith et al. 2015). Briefly stated, the Ground Layer Indicator is a nondestructive method that uses prior calibrations to convert field-measured depth and cover of moss and lichen functional groups (measured in 32 microquads) into a plot-level estimate of biomass, carbon, and nitrogen for each functional group (Table 2.1). This method includes green photosynthetic material and undecomposed fibric material (live or dead), but excludes partially or fully decomposed peat that may form in deeper layers. Depth measurements are intentionally truncated at 40 cm deep, and therefore are expected to give conservative estimates. With the Ground Layer Indicator, a potentially large number of plots can be evaluated rapidly since the procedure takes less than 2 h per plot (Smith et al. 2015). A further benefit is the capacity to quantify the diversity of ecosystem functions (e.g., wildlife forage, biological N-fixation, many others) based on a predefined set of functional groups (Table 2.1). For all ground layer attributes we calculated summary statistics and generated maps of biomass distributed among plot locations.

Environmental predictors

Second, we evaluated responses of four ground layer attributes: plot mean biomass, mean total carbon content, mean total nitrogen content and the total number of functional groups (functional group richness, FGR). Candidate predictors (Table 2.2) included vegetation, climate, and topographic variables. Vegetation variables were from field measurements taken concurrently with ground layer measurements according to FIA protocols (FIA 2014a; 2014b). For example, litter depth was the average of eight point measurements per plot; seedling count was the average counts of trees < 2.54 cm diameter in four microplots of 13.5 m^2 area each; and stand age was the average of at least three tree cores per plot (FIA 2014a; 2014b). Vegetation cover was ocular estimation of vertically-projected canopy cover for each layer (trees, shrubs, forbs and grasses), which we later transformed by taking the arcsine-square-root. Climate variables were annual mean 30-year normals (1981–2010) extracted from the ClimateNA database (Wang et al. 2016). Topographic variables were

measured on site (aspect, slope), or calculated afterwards (potential direct incident radiation, heat load) following McCune and Keon (2002). Forest types were defined by dominant live tree species (FIA 2014a).

To select predictors and fit models, we used nonparametric multiplicative regression (NPMR: McCune 2006) in HyperNiche version 2.25 (McCune and Mefford 2011). NPMR is a kernel regression method that estimates mean responses as a smoothed function of all possible interactions of an optimized subset of predictors. For this, we used a local mean model with a Gaussian kernel and HyperNiche's default parsimony criteria settings (overfitting control setting = "medium", minimum average neighborhood size = 7.5, improvement criterion = 5, and minimum data-to-predictor ratio = 10), with model fit assessed by leave-one-out cross-validated R^2 (xR^2). Preliminary analyses (not reported) using log_{10}-transformations of biomass, carbon, and nitrogen did not improve predictive capacity, and were not required to meet NPMR model assumptions, therefore we used untransformed data throughout. We performed randomization tests (100 randomizations per regression model) to test the null hypothesis that the fit of each selected model was no better than obtained at random. We calculated sensitivity as a measure of the relative importance of each environmental predictor. Specifically, sensitivity was calculated as the mean absolute deviation in each response that resulted from perturbing each predictor ± 5% of its range, expressed as a proportion of the range of the response variable. Therefore, sensitivity values = 0 would indicate that perturbing a predictor has no effect on the response, while values = 1 would indicate that perturbing a predictor yields an equal magnitude change in the response variable.

Results

Ground layer attributes

At 96 plots located in the Tanana River valley of interior Alaska, ground layer biomass averaged 12,397 kg ha^{-1} (± 1345 sample standard error), including 5515 ± 583 kg ha^{-1} of carbon and 137 ± 15 kg ha^{-1} of nitrogen. The middle 50% of biomass values were in the range 4750–18,900 kg ha^{-1} (interquartile range from 25th to 75th percentiles). Geographic distributions of functional groups varied across the Tanana landscape (Fig. 2.2). For example, nitrogen-fixing mosses (with cyanobacterial associates) were most widespread, and were often the most abundant functional group in a given plot. *Sphagnum* peat-mosses

occurred in fewer plots, but often achieved highest within-plot biomass. Forage lichens were moderate in frequency but also had considerable biomass where encountered (Fig. 2.2). On average there were 6.6 ± 1.9 functional groups per plot. Black spruce forest types in the Tanana River area had the greatest mean biomass ($19,234 \pm 2062$ kg ha^{-1}) relative to other forest types. As a per-plot average, mean biomass and mean nutrient content in black spruce forest types were roughly double that of white spruce forest types, and nearly four times that of most hardwood forest types (Table 2.3).

Environmental predictors

The best predictors of biomass, carbon stores, and nitrogen stores were related to vegetation (stand age, forb cover and litter depth) and insolation (PDIR) (Table 2.4). Response surfaces and sensitivity to each of these environmental predictors were essentially identical for the three nutrient variables (biomass, carbon and nitrogen), as expected since the nutrient response variables were roughly proportional to each other. Estimated ground layer carbon and nitrogen were greatest in older stands, and were lowest in plots with high forb cover and high PDIR (Fig. 2.3). Variation in functional group richness was best explained by vegetation (seedling count and tree cover), and it was weakly sensitive to a climate proxy (percent precipitation as snow) (Table 2.4). Model fit, based on leave-one-out cross-validated R^2, ranged from $xR^2 = 0.27$–0.34 for the four models. All four regression models had better fit than expected at random (randomization *p*-values all < 0.05).

Discussion

Biomass, carbon and nitrogen stores in boreal ground layers

Mat-forming mosses and lichens in boreal forests are key actors in the accumulation and storage of carbon at the primary interface where soils and the atmosphere meet. We found that ground layers were a substantial biomass and carbon pool in boreal forests of interior Alaska, while at the same time they contributed a variety of ecosystem functions (Fig. 2.2). Our finding of 4750–18,900 kg ha^{-1} biomass is within the range of variability observed in other ground layer studies in the Tanana River area (Barney and van Cleve 1973; Mack et al. 2008), though slightly higher than other reports that excluded fibric organic matter (Mead 1995; Ruess et al. 2003). This gives a baseline estimate of the current carbon pool in the

ground layer, and suggests that plot remeasurements could indicate carbon pool trends over time in interior Alaska.

Nitrogen-fixing feather mosses are an often overlooked part of global nutrient cycles, yet they comprised the most abundant and frequent functional group in the Tanana River study area (Table 2.1 and Fig. 2.2). Because of their extensive coverage in boreal regions and ability to fix atmospheric nitrogen, cyanobacteria-harboring feather mosses have large landscape nutrient effects. Their sheer abundance makes up for comparatively modest nitrogen fixation rates (when compared per unit mass with nitrogen-fixing lichens; Gavazov et al. 2010). Nitrogen-fixing feather mosses contribute the majority of biologically available nitrogen in high-latitude tundra (Stewart et al. 2011) and in boreal forest understories (Lindo et al. 2013), an amount that can be nearly equal to the total amount of nitrogen entering via rainfall (Lagerström et al. 2007). Carbon fixation in moss mats represents about 20% of all understory net primary production (Hasselquist et al. 2016). Together, these understory nutrient cycling routes have consequences for C:N ratios, plant growth, and ecosystem productivity. Therefore, we suggest that forest inventories and dynamic vegetation models may consider including biomass of mosses, especially nitrogen-fixing feather mosses, to correctly portray nutrient budgets in boreal forests.

Environmental sensitivity and consequences

We found that biomass, carbon stores and nitrogen stores were sensitive to a topographically-derived measure of incident radiation (PDIR). This suggests that mass accumulation in ground layers is tied to physical situations (e.g., north-facing slopes) where topography limits direct insolation that may otherwise prevent establishment of mosses and lichens. Yet, at the other extreme, heavy shading from dense vascular vegetation layers (especially tall shrubs) could lead to competitive exclusion of mosses and lichens (Cornelissen et al. 2001), a concept supported by our finding of decreased biomass at high forb abundances. Aside from its direct effects, PDIR may also be an indirect indicator of waterlogging and permafrost conditions that vary according to landscape position and topography. For example, growth and accumulation in ground layers depends in part on soil and groundwater attributes that were not directly measured during this inventory (e.g., watertable height, dissolved oxygen, phenolic content). Drought and falling water levels (from warming air temperatures and

permafrost melting) can reverse the anoxic, waterlogged conditions that inhibit decomposition from peat beneath ground layers, eventually leading to net carbon emissions (Gorham 1991; Fenner and Freeman 2011; Turetsky et al. 2011). Future efforts to estimate landscape carbon could benefit from using topographic landscape position as a proxy for important hydrologic and insolation attributes.

We documented more biomass and carbon in ground layers of old stands relative to young stands. This is consistent with evidence that moss and lichen mats are carbon sinks in older boreal forests, while they may be carbon sources following recent disturbances such as wildfires (Harden et al. 1997). This emphasizes the dual challenges that wildfires pose to carbon storage, not only for acute combustion losses, but also for legacy effects that may hinder carbon uptake even decades on. Biomass and elemental content also declined at high levels of forb cover, suggesting that post-fire conditions which promote forb growth in our study area could have corresponding negative effects on ground layers. In interior Alaska, forbs like fireweeds (*Chamerion* spp.) indicate strongly disturbed sites (Dyrness and Norum 1983), and could thus indicate poor areas for ground layer accumulation. We suspect that the negative association may not imply any direct impacts of vascular vegetation, but rather that vascular forbs and nonvascular ground layers may have contrasting recovery rates following disturbances.

Our finding of modest climate sensitivity was initially surprising given that climatic temperature and moisture should be strong controls on rates of photosynthetic carbon gain and respiratory carbon losses in ground layers and organic soils (Biasi et al. 2008). However, our study area was relatively homogeneous with regards to most climate values. Greater climatic sensitivity may be expected from steeper climatic gradients; for example, the Alaska Range induces a rainshadow in cold, dry, continental interior Alaska, and separates northern areas from warmer maritime temperate forests closer to the Pacific coast.

Our findings suggest that the feedbacks between global changes, vascular vegetation, wildfire disturbances and moss/lichen ground layers will have ecosystem consequences in boreal forests. Atmospheric emissions from burned ground layers, as well as subsequent regrowth of fire-promoting vascular vegetation, could potentially amplify climate warming (Chapin et

al. 2010; Kasischke and Stocks 2012; Turetsky et al. 2015). Anticipating these changes will require continued monitoring of vascular and nonvascular vegetation, as well as predictive approaches to estimating carbon pools and fluxes.

Estimating carbon distributions

Mapping forest floor carbon (including litter, humus and fine woody debris) has been a valuable product of FIA inventories (Woodall 2012; Wilson et al. 2013). Carbon estimation in ground layers could be linked with remote sensing approaches, which have recently been used for mapping forage lichen cover for caribou habitat (Nelson et al. 2013), fire effects on moss mats (Lewis et al. 2011), peatland drought status (Harris and Bryant 2009), ecosystem productivity of moss mats (Kushida et al. 2004), and forest floor organic carbon stores (Pastick et al. 2014). Lidar, hyperspectral and thermal imaging data could be calibrated with our ground layer biomass estimates to infer regional patterns through predictive modeling and imputation. Our determination of the key predictors of ground layer attributes should aid in refining remote sensing models by accounting for topography and vegetation covariates. Accurately estimating carbon pools may also require new FIA field techniques for sampling deep organic peat increments beyond 30 cm deep (Chimner et al. 2014). The union of field measurements, remote sensing and predictive modeling will provide opportunities for ground layer carbon estimation in a part of the United States that is at the forefront of ongoing global changes.

Acknowledgements

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Tables

Table 2.1. Ground layer functional groups and their estimated abundances in the Tanana River region of interior Alaska. Each of the mutually exclusive groups integrates growth forms, potential indicator status and ecosystem effects. Estimates are from 96 forested plots.

Functional group	Functions	Biomass (kg ha^{-1})		C (kg ha^{-1})		N (kg ha^{-1})		Cover (%)	
		Mean	*SE*	Mean	*SE*	Mean	*SE*	Mean	*SE*
Biotic soil crust	Soil trapping, soil water influx, disturbance indicator	3.0	2.3	1.4	1.0	< 0.1	< 0.1	< 0.1	< 0.1
Eutrophic lichens	Indicate nutrient over-enrichment	0.4	0.3	0.2	0.2	< 0.1	< 0.1	< 0.1	< 0.1
Forage lichens	Wildlife forage (caribou, etc.)	446.4	146.7	198.1	65.1	2.7	0.9	2.7	0.8
Foliose lichens	Invertebrate habitat, bare site colonization	8.7	6.5	3.8	2.9	0.1	0.1	0.1	0.1
Fruticose lichens	Invertebrate habitat, bare site colonization	70.4	32.5	31.2	14.4	0.5	0.2	0.7	0.3
N-fixing foliose lichens	N-fixation, C:N modification	158.4	66.8	70.3	29.6	4.1	1.7	1.9	0.8
N-fixing fruticose lichens	N-fixation, increases albedo	34.1	9.9	15.1	4.4	0.9	0.3	0.3	0.1
Feather mosses	Rainfall interception, soil cooling	734	266.9	325.8	118.5	8.9	3.2	3.2	1.2
N-fixing feather mosses	Broad-area N-fixation, soil cooling	7799.2	1384.2	3461.5	614.4	88.9	15.8	25.3	4.1
Sphagnum peat-mosses	Carbon storage (peat), water regulation, soil cooling	2244.8	646.8	996.3	287.1	21.1	6.1	5.0	1.5
Turf mosses	Soil accrual, bare site colonization	1030.2	343.3	457.2	152.4	10.3	3.4	6.7	1.8
Flat liverworts	Soil/detritus binding, water infiltration	23.6	10.6	10.5	4.7	0.4	0.2	0.2	0.1
Leafy liverworts	Soil/detritus binding, water infiltration	18.9	11.5	8.4	5.1	0.3	0.2	0.1	0.1

Table 2.2. Candidate predictors for ground layer attributes. Attributes included biomass, carbon, nitrogen and functional group richness.

Symbol	Predictor	Type	Description	Units	Ref.
litt	Litter depth	Vegetation	Depth of litter overlying mosses and lichens	cm	a
seed	Seedling count	Vegetation	Number of tree seedlings occurring in subplots	count	a
age	Stand age	Vegetation	Field-estimated age of the plot trees, from 3 cores	years	a
tree	Tree cover	Vegetation	Arcsine-square-root transformed cover of trees	proportion	a
shrub	Shrub cover	Vegetation	Arcsine-square-root transformed cover of shrubs	proportion	a
forb	Forb cover	Vegetation	Arcsine-square-root transformed cover of forbs	proportion	a
grass	Grass cover	Vegetation	Arcsine-square-root transformed cover of grasses	proportion	a
slope	Slope	Topographic	Angle of slope	degrees	a
asp	Folded aspect	Topographic	Slope direction, increasing along a NE–SW axis	degrees	b
pdir	Potential direct incident radiation	Topographic	Potential annual direct incident solar radiation a slope receives, based on slope, aspect, and latitude	$MJ\ cm^{-2}\ y^{-1}$	b
htld	Heat load	Topographic	Potential heat index of a slope, accounts for both radiation and southwestness of aspect	unitless	b
mat	Mean annual temperature	Climate	Mean annual air temperature	°C	c
td	Continentality	Climate	Temp difference between warmest/coldest months	°C	c
map	Mean annual precipitation	Climate	Mean annual precipitation	mm	c
ahm	Annual heat moisture index	Climate	Ratio of temperature to precipitation	unitless	c
ffp	Frost-free period	Climate	Length of the frost-free period	d	c
pas	Percent precip as snow	Climate	Percent of annual precip in snow form	%	c
cmd	Climatic moisture deficit	Climate	Hargreaves climatic moisture deficit	mm	c

[a] FIA (2014a)
[b] McCune and Keon (2002)
[c] Wang et al. (2016)

Table 2.3. Ground layer attributes by forest type for the Tanana River region of interior Alaska.
Attributes include estimated ground layer biomass (expressed on an oven-dry basis), C and N.

Forest type	Biomass (kg ha^{-1})		C (kg ha^{-1})		N (kg ha^{-1})	
	Mean	*SE*	Mean	*SE*	Mean	*SE*
White spruce	9370	2130	4147	942	106	24
Black spruce	19,234	2062	8541	919	210	21
Aspen	5290	1905	2354	852	58	21
Paper birch	5268	852	2331	381	58	10
Balsam poplar	247	90	112	45	3	1
Nonstocked	2735	2735	1211	1211	28	28
Overall	12,397	1345	5515	583	137	15

Table 2.4. Top predictors of ground layer attributes. Attributes were oven-dry biomass, total carbon, total nitrogen and functional group richness (FGR). Biomass and carbon were nearly identical because they are roughly proportional. Predictors were selected by nonparametric multiplicative regression, NPMR. See also the NPMR response surfaces (Fig. 2.3).

Response	xR^2	$N*$	p	Predictor 1			Predictor 2			Predictor 3			Predictor 4		
				X	Sens	Tol	X	Sens	Tol	X	Sens	Tol	X	Sens	Tol
Biomass (kg ha^{-1})	0.31	4.9	0.03	age	0.35	21.5	pdir	0.23	0.09	forb	0.21	0.09	litt	0.09	2.72
Carbon (kg ha^{-1})	0.31	4.9	0.01	age	0.35	21.5	pdir	0.23	0.09	forb	0.21	0.09	litt	0.09	2.72
Nitrogen (kg ha^{-1})	0.27	5.4	0.01	age	0.31	21.5	pdir	0.20	0.09	forb	0.15	0.10	litt	0.08	2.63
FGR (count)	0.35	8.7	0.01	seed	0.55	10.3	tree	0.51	0.06	pas	0.08	97.7	–	–	–

xR^2: Cross-validated R^2 is the proportion of variation explained by each model, based on NPMR's leave-one-out cross-validation.

$N*$: Neighborhood size is the average number of sample units used to estimate the response at a given point.

p: Randomization p-value, the proportion of 100 randomized runs with fit $\geq$ observed fit.

X: Predictor name (see Table 2.2 for symbols).

Sens: Sensitivity is a unitless measure of the relative importance of each predictor. Values = 0 indicate that perturbing a predictor has no effect on the response. Values = 1 indicate that perturbing a predictor yields an equal-magnitude change in the response variable.

Tol: Tolerance is a measure of how broadly a point estimate depends on nearby plots in predictor unit space, representing one standard deviation of the Gaussian kernel.
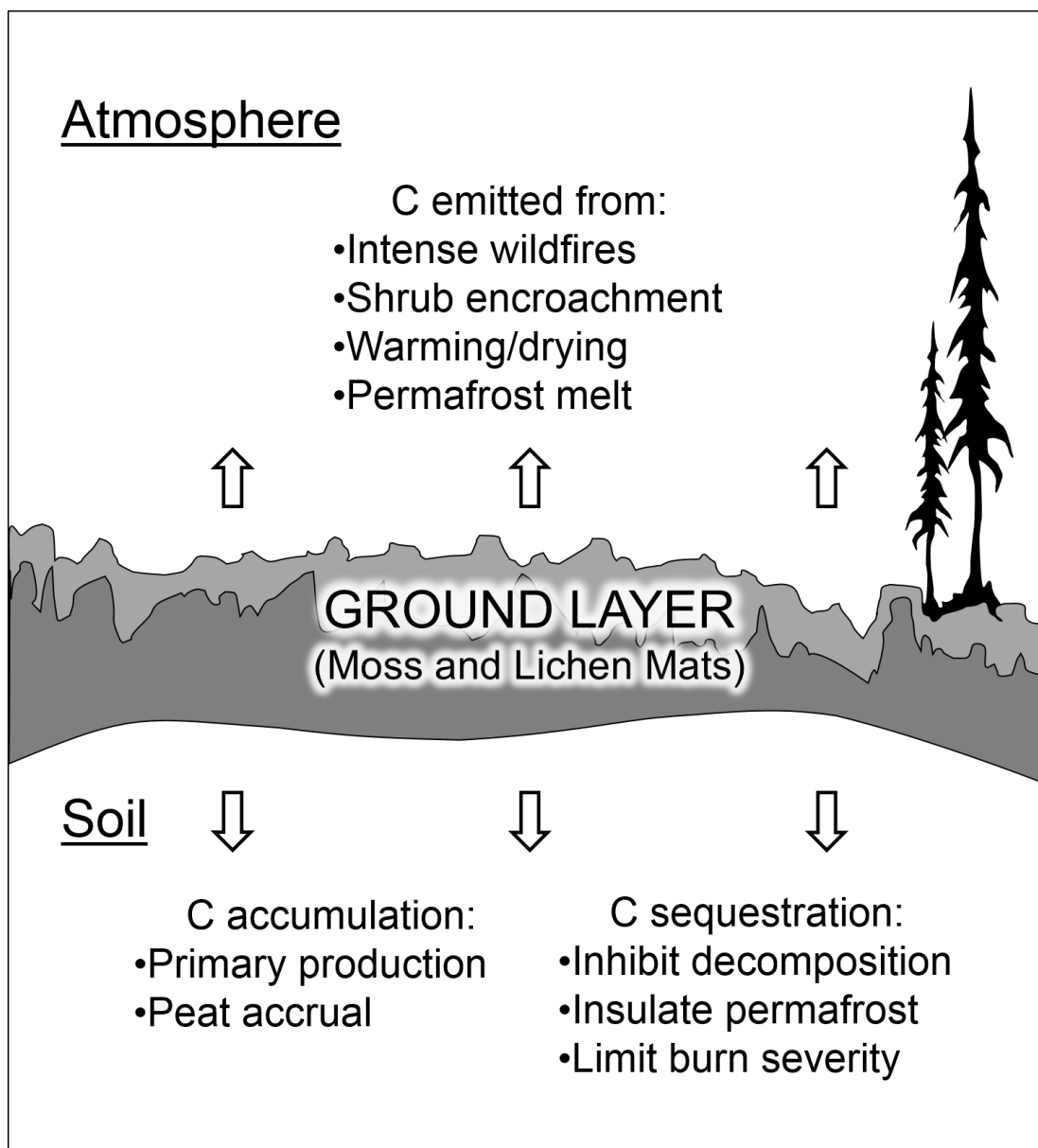
Figure 2.1. Conceptual carbon balance in moss and lichen mats at the soil–atmosphere interface. Carbon storage exists both aboveground and in organic matter transitional to soils. In addition to regulating carbon cycling, ground layer organisms have many other functions (Table 2.1).
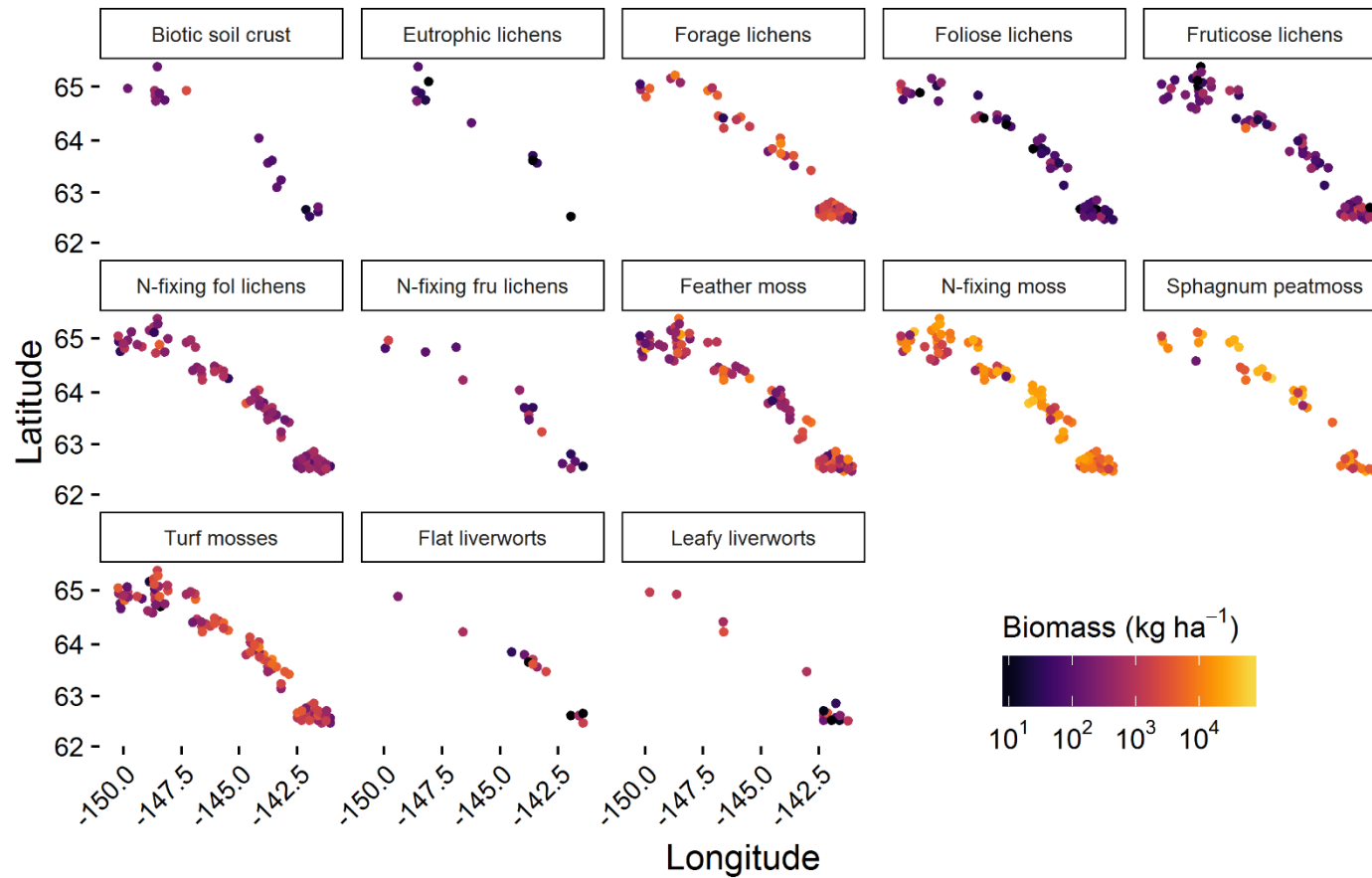
Figure 2.2. Biomass mapped across the Tanana River region of interior Alaska. Maps of biomass (on log₁₀ scale) for 13 functional groups at 96 plots (each dot). Lighter shades = greater plot biomass. Alignment of plots is roughly parallel to the Tanana River. Relative distributions and abundances of functional groups can indicate ecosystem effects across landscapes.
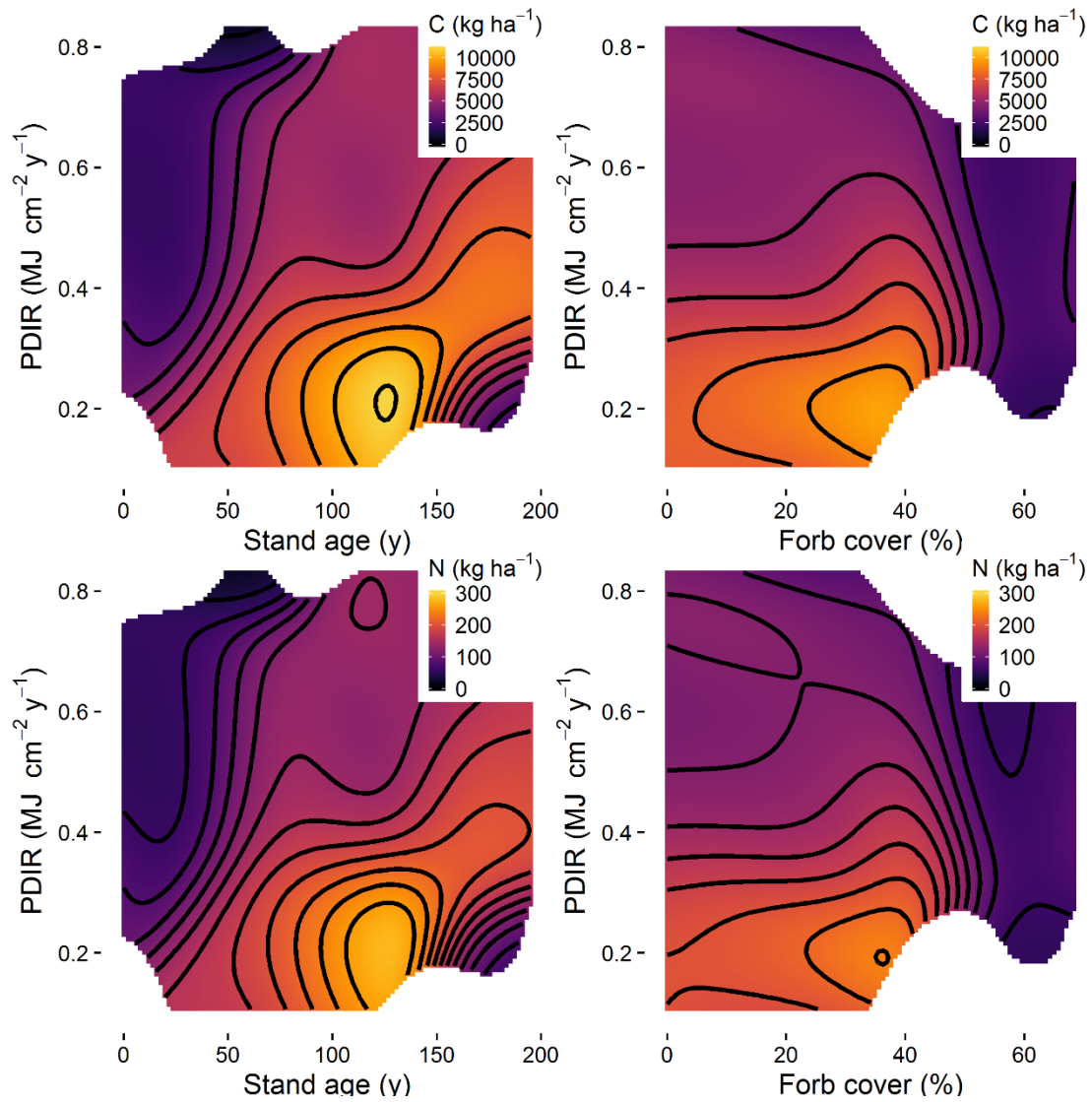
Figure 2.3. Response surfaces for ground layer nutrient stores. Estimated mean carbon (top row) and mean nitrogen stores (bottom row) in response to potential direct incident radiation (PDIR) and vegetation attributes (stand age, forb cover). Both carbon and nitrogen, which were roughly proportional to each other, reached maximal values at high-to-intermediate stand ages, at low-to-intermediate forb cover, and at low insolation (PDIR).

CHAPTER 3. SENSITIVITY OF EPIPHYTIC LICHEN COMMUNITIES TO CLIMATIC
GRADIENTS ALONG THE WEST COAST OF NORTH AMERICA

Robert J. Smith, Sarah Jovan, and Bruce McCune

Abstract

Epiphytic lichens are commonly assumed to be excellent bioindicators of climate, air quality and other forest conditions. However, these assumptions are more frequently asserted rather than tested. Our goals were to test the sensitivity and strength of relationship between climate gradients and lichen community compositions across a large super-regional extent. Based on a nationally consistent forest inventory, we analyzed 1,118 standardized lichen survey plots spanning 4,000 km and nearly 30 degrees of latitude across the U.S. Pacific states of Alaska, Washington, Oregon, and California. With dissimilarity-based methods and indicator species analyses, we determined the strength of relationship between lichen communities and macroclimate. The use of stepacross dissimilarities corrected for loss of information at large ecological distances. Scores from nonmetric multidimensional scaling ordination explained 80.4% of the variation in lichen community composition. These "lichen scores" were interpreted based on the strength of fit and sensitivity to climate variables in nonparametric multiplicative regression models. Cross-validated nonlinear fit (xR^2) was 72% and 42% for the respective ordination axes given a parsimonious subset of interacting climate variables, and 8–56% for each climate variable individually. The strongest fitting lichen-response gradients involved mean annual precipitation, temperature, and heat moisture index (temperature:precipitation ratio). Lichen scores were most sensitive to perturbations in heat moisture index, continentality, mean annual precipitation, and mean annual air temperature. Indicator species diagnostic of ten climate zones were loosely segregated into high-latitude and oceanic species, mid-latitude continental species, and species associated with hot, dry lowlands. Collectively, our results support the principle that epiphytic macrolichens are robust biological indicators of climate. Indicator species are appealing monitoring targets since their appearances or disappearances over time are visible signals of shifting climate zone boundaries. Likewise, lichen scores from sites resurveyed in the future can indicate how global changes will impact the composition and diversity of forest vegetation across large biogeographic areas.

Introduction

How strongly does their environment control the appearance and disappearance of species? Ecologists, naturalists, biogeographers and evolutionary biologists have long pondered how variation in plant species diversity relates to climatic conditions within and among continents

(Willdenow 1792; von Humboldt and Bonpland 1807). Among other ecological mechanisms, environmental selection favors or disfavors certain species, making it a major force in shaping the identity and number of species encountered in any given location (Vellend 2016). Viewing species diversity as the joint outcome of species tolerances and environmental conditions is the basis of bioindication. Among bioindicators, epiphytic lichens (autotrophic, fungus–photobiont composites) are especially sensitive to atmospheric conditions because their physiology responds closely to fluctuations in temperature, moisture and nutrient deposition (Kranner et al. 2008; Alam et al. 2015). Lichens have a long and celebrated history as air quality indicators (Nylander 1866), largely because they show impacts from the organism's perspective without relying on costly instrumentation. There is now growing awareness that air quality impacts cannot be estimated without first accounting for fundamental climate covariates (McMurray et al. 2015). Understanding how global changes will affect vegetation over a broad extent is now a primary focus shared by both researchers and forest resource managers.

The effects of global changes are now becoming apparent in the diversity of epiphytic forest vegetation. Atmospheric warming and drying over just a few decades have been associated with species turnover in epiphytic lichen floras of South America and western Europe, which have lost cold-adapted species and gained species that tolerate warmer and drier conditions (Follmann 1995; van Herk et al. 2002; Søchting 2004; Cezanne et al. 2008; Hauck 2009). The role of climate in floristic changes has been confirmed by reciprocal transplant tests (Gauslaa et al. 2006; Pirintsos et al. 2011; Song et al. 2012), experimental manipulations (Alam et al. 2015; Smith et al. 2017b) and predictive forecasts (Allen and Lendemer 2016; Nascimbene et al. 2016). However, only systematic, quantitative monitoring of community compositions over multiple regions can reveal the mark of global changes on species' distributions and relative abundances. With its cooperators, the Forest Inventory and Analysis Program of the United States Forest Service has compiled over 8,000 plot-based lichen community surveys based on a nationally consistent standard protocol (Jovan et al. 2017). The program has already yielded lichen-based gradient models for many U.S. regions (McCune et al. 1997; Jovan and McCune 2004; Geiser and Neitlich 2007; Root et al. 2014; McMurray et al. 2015; Root et al. 2015; Will-Wolf et al. 2015). We now require a way to link relationships across multiple geographic regions for the purpose of climate change

monitoring. Changes in community composition can be valuable indicators, but only if they are systematically monitored at geographic extents large enough to appropriately match the scale of expected global changes.

The biogeography of lichen species and communities is closely intertwined with climate at "super-regional" extents spanning portions of continents. Over long time spans and large areas, dispersal limitation or vicariance may be less important than climatic shifts in driving lichen diversification (Leavitt and Lumbsch 2016). Regional average macroclimate better explains the species richness of North American macrolichens than does variation in local microclimate or local stand attributes (Coyle and Hurlbert 2016). Specifically, more species occur in habitats with high precipitation and humidity, cool temperatures, and low diurnal temperature variability (Coyle and Hurlbert 2016), which indicates that lichen compositional turnover should be greatest at sharp climatic divides such as the Cascade-Sierra Nevada cordillera of western North America. General observation might suggest that influential bioclimatic variables and species should also covary with latitude. For example, the number of lichen species with oceanic affinities tends to decline southward along with summer precipitation at inland sites (Goward and Spribille 2005). However, other workers through genetic sequencing (Tripp et al. 2016) or herbarium records (Holt et al. 2015) detected only weak latitudinal richness patterns. The mixed evidence implies that any climate-driven variation in lichen community composition should be a function of nuanced and complex climate gradients operating over large geographic areas.

The purpose of this study was to test the assumption that lichens are sensitive climate indicators by determining the sensitivity and strength of relationship between epiphytic macrolichen community compositions and climate gradients at super-regional scales. We posed three questions: 1) How are lichen community compositions distributed in geographic and climate spaces? 2) What is the sensitivity and strength of relationship between lichen community compositions and climate variables? 3) What is the strength of relationship between select indicator species and defined climate zones? Together, these questions can inform the appropriate use of lichen community responses as part of interagency environmental monitoring programs in the U.S. Pacific states and elsewhere.

Materials and Methods

Lichens and climate data

Lichens data originated from the U.S. Forest Service's Forest Inventory and Analysis (FIA) program. The U.S. Forest Service, National Park Service, and Fish and Wildlife Service have conducted over 8,000 standardized lichen surveys across U.S. forests (Jovan et al. 2017), including those considered here for the U.S. states bordering on the Pacific Ocean. Unfortunately, comparable data are not available from adjacent British Columbia, leaving a gap in our study area of nearly five degrees in latitude. The FIA lichen sampling design is systematically random and geographically representative: one site is randomly located in each 39,072-ha hexagonal grid cell of a hexagonal grid covering the U.S., and a plot (sample unit) is then measured at each forested site (defined as ≥10% potential tree cover on undeveloped land ≥0.41 ha area and ≥36.6 m wide). This design is representative of many different kinds of geography, land ownerships and disturbance histories across U.S. forests.

Complete FIA lichen community survey protocols are described by Will-Wolf (2010). FIA observations were based on time-constrained surveys of a circular, fixed-area 0.379-ha plot in which trained technicians collected and assigned abundance values for all epiphytic lichen species. Sampling occurred over the period 1998–2014. Abundances were measured on an approximately logarithmic 0–4 scale where 0 = not present; 1 = 1–3 thalli observed; 2 = 4–10 thalli observed; 3 = more than 10 thalli observed but on < 50% of available branches and stems; and 4 = observed on > 50% of available substrates. To account for changes in taxonomic concepts over time, we harmonized old and new species names according to FIA analyst guidelines (Will-Wolf 2010). Only epiphytic macrolichen species were included; terrestrial species and microlichen (crustose) species were excluded. We removed rare species (< 3 occurrences) and species-poor plots (< 4 species) that could obscure the dominant species–environment relationships. Finally, we calculated average alpha diversity as species richness ($\bar{\alpha}$), gamma diversity (γ) and Whittaker's (1972) beta diversity ($\beta_W = \gamma/\bar{\alpha}-1$).

Climate data came from the ClimateNA database (Wang et al. 2016). For all FIA lichen plot locations, we extracted seven lichen-relevant variables. These were: mean annual air temperature, continentality, mean annual precipitation, annual heat moisture index (ratio of

temperature to precipitation), frost-free period, percent precipitation as snow, and climatic moisture deficit (reference evaporation minus precipitation)(Fig. 3.1). Definitions and equations follow Wang et al. (2016). Because climate variables are commonly highly correlated, we converted them to principal components (PCs) using PCA based on the correlation matrix in PC-ORD version 7 (McCune and Mefford 2016). We selected three PCs for interpretation based on the *Rnd-Lambda* criterion (Peres-Neto et al. 2005). PCs are orthogonal linear combinations interpretable in terms of the original climate variables. Subsequent analyses were performed in R version 3.3.1 (R Development Core Team 2016) unless otherwise noted.

Gradient model and climate fit

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 Regions (Will-Wolf and Neitlich 2010), and therefore integrates a wealth of ecological variation and a large species pool. The central gradient model was nonmetric multidimensional scaling ordination, NMS (Kruskal 1964). NMS assigns scores to sites based on dissimilarity of lichen community compositions. We calculated abundance-based Sørensen dissimilarities, then used flexible shortest-path stepacross adjustment (Bradfield and Kenkel 1987) to account for the fact that Sørensen dissimilarities tend to lose information at large ecological distances when beta diversity is very high (Smith 2017). Stepacross adjustments were implemented in R package 'vegan' (Oksanen et al. 2016). In preliminary screening, we evaluated five different stepacross threshold values (1.00, 0.95, 0.90, 0.85, and unmodified Sørensen dissimilarities), then selected the final threshold value that gave the largest incremental gain in NMS variance explained. All NMS models were implemented in PC-ORD version 7 using each stepacross dissimilarities matrix individually, step-down dimensionality, unpenalized ties (Kruskal strategy 2), 500 iterations, 200 runs with real data, 99 runs with randomized data, and final scores rotated to orthogonal principal axes (mutually independent axes). NMS scores reflect variation in lichen community composition attributable to underlying environmental gradients.

To interpret the strength of relationships between lichen community composition (NMS scores) and climate variables, we calculated "climate fit" by regressing NMS axes one at a time against climate variables. Specifically, the measure of fit was leave-one-out cross-validated R^2 ($= xR^2$) from nonparametric multiplicative regression (NPMR; McCune 2006) which allowed NMS scores to vary as a nonlinear function of single or potentially many interacting climate predictors. We implemented NPMR with a local mean model, Gaussian kernel, medium overfitting settings, and all other default settings in HyperNiche version 2.25 (McCune and Mefford 2011). Univariate climate fit was simply xR^2 from each single-predictor regression, and multivariate fit was xR^2 from a three-predictor model including the top three climate PCs (themselves linear combinations of all seven raw climate variables). For each NPMR model we performed a randomization test (99 randomizations each) of the null hypothesis that the model fit was no better than obtained by chance alone. We also calculated sensitivity of NMS scores to each individual climate variable as a measure of variable importance. Sensitivity, calculated by Eq. 9 in McCune (2006), is the proportion of change in the estimated NMS scores caused by perturbing each climate variable ±5% of its range. Sensitivity = 0 means that perturbing climate would have no detectable effect on NMS scores, and sensitivity = 1 means that perturbing the climate variable would result in an equal-magnitude change in the NMS scores, where both climate and NMS scores are scaled by their ranges.

Climate zones and indicator species

We grouped sites into "climate zones" based on climatic similarity. To define zones, we used optimal partitioning, a nonhierarchical algorithm that optimizes the ratio of within-group to among-group similarity, implemented in R package 'optpart' (Roberts 2015). Using only climate information (no lichen information), this assigns each plot to one of ten climate zones sharing similar climatic characteristics. This was a compromise between having a sufficient number of zones to describe climatic differences, and few enough to allow interpretation. We used Euclidean distances of the three climate PCs, with 99 random starts each with 99 iterations. To identify the lichens which best characterized each climate zone or set of zones, we used multi-group indicator species analysis in R package 'indicspecies' (de Cáceres et al. 2010). Multi-group indicator species analysis accounts for the fact that species can have broad or narrow climatic tolerances, and may therefore be indicators of multiple or single

climate zones. We specified 3rd-order groupings (indicator values calculated across one, two and three climate zones) and performed a significance test with 999 randomizations. Indicator values (*IndVal*) for each species are 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) (Dufrêne and Legendre 1997; de Cáceres et al. 2010). Therefore, *IndVal* values can range from 0 (no indicator value) to 1 (perfect indicator). A perfect indicator species, *IndVal* = 1, would occur at all sites within a given zone and only within that zone.

Results

Summary of lichens and climate

The final FIA lichens dataset contained 18,569 unique occurrences of 240 epiphytic macrolichen species in 1,118 plots. The percentage of zeros in the site-by-species community matrix was 93%. Species richness ranged from 4–44 macrolichen species per plot. Average alpha diversity was $\bar{\alpha} = 16.6$ species, gamma diversity was $\gamma = 240$ species, and beta diversity was $\beta_W = 13.5$. Very high beta diversity suggested the use of stepacross dissimilarity adjustments. Prior to flexible shortest-path stepacross adjustment, 26.1% of site pairs shared no species in common.

The first three (of seven possible) PCs were retained for further analysis based on the *Rnd-Lambda* criterion. The climate principal components (PCs) were orthogonal linear combinations interpretable in terms of the original climate variables (Table 3.1 and Fig. 3.1). PC1 corresponded to a thermal/aridity gradient commonly associated with changes in latitude and elevation: high scores on PC1 represented sites that were cool, wet, had high proportions of snow precipitation, and very low aridity (heat moisture index and climatic moisture deficit), while lower scores represented hot, dry sites with little snow precipitation and high moisture deficits. PC2 represented a gradient of moisture and continentality–oceanicity: scores higher on PC2 represented dry, continental, inland sites, while lower scores represented wet, oceanic, maritime sites. Finally, PC3 was a more complicated climatic gradient involving frost-free period: scores higher on PC3 represented sites with a short frost-free period and high proportions of snow precipitation.

Gradient analysis and climate fit

The super-regional model was an NMS ordination of 1,118 FIA plots from Alaska, Washington, Oregon, and California. We used a flexible shortest-path stepacross threshold value of 1.0 in the dissimilarities matrix for the final model. The final NMS solution was 2-dimensional, had stress = 18.7, nonmetric fit of 96.5%, and explained 80.4% of the variation in community composition: 64.0% and 16.4% for each respective axis (Table 3.2). Lichen community compositions, as represented by NMS scores on each axis, were nonlinearly related to climate. For example, first axis scores were strongly negatively related to mean annual precipitation, positively related to annual heat moisture index, positively related to climatic moisture deficit, and highest at either extreme of the mean annual temperature gradient (Fig. 3.2). Second axis scores were positively related to mean annual temperature, climatic moisture deficit and annual heat moisture index (Fig. 3.2). Climate sensitivity was generally higher on the first axis (Table 3.2). In descending order, lichen community scores (on either axis) were most sensitive to annual heat moisture index, proportion of precipitation as snow, continentality, and mean annual precipitation and temperature (Table 3.2). In geographic space, first axis scores depicted a latitudinal north–south trend (Fig. 3.3), while second axis scores were associated with an east–west divide defined by the Cascade–Sierra Nevada cordillera (Fig. 3.4).

Climate zones and indicator species

Ten climate zones, collections of sites that shared similar climatic attributes, were based on optimal partitioning of the 3 climate PCs (Table 3.3). Specifically, these ten zones were: Zone 1 = hot dry lowlands, 2 = warm dry subcontinental, 3 = warm mesic temperate, 4 = cold mesic subcontinental, 5 = cold dry continental, 6 = cold mesic continental, 7 = cool dry continental, 8 = cool moist subcontinental, 9 = mild moist suboceanic, and 10 = warm wet hypermaritime. Sites within a given zone were generally contiguous in geographic space, in climate space, and in lichen community compositional space (Fig. 3.5). Each climate zone was associated with a defined set of indicator species, many of which had significant indicator values spanning more than a single zone (Table 3.4 and Appendix A). Although species indicator values were individualistic, several groupings became apparent. Broadly defined, these groups contained species indicative of northerly and coastal sites, species indicative of interior and montane sites, and species indicative of southerly and drier lowland

sites (Fig. 3.6). Regardless of whether they indicated single or multiple climate zones, indicator species tended to occupy distinctive areas of the NMS lichen compositional space (Fig. 3.7).

Discussion

A major goal of ecologists and natural resource practitioners is the "reconciliation of local and regional perspectives" (Ricklefs 2004). We tested the strength of lichen community relationships to ecological gradients, finding broad support for the conclusion that community compositions are related to climate at super-regional geographic extents. Environmental differences are the major factors expected to regulate species diversity of lichens and other organisms over such a large and spatially heterogeneous area, along with rates of diversification and extinction (Ricklefs 2008; Leavitt and Lumbsch 2016). Although local biotic interactions among lichens may explain their diversity locally (Svensson et al. 2016), the effects of local interactions become much less important than climatic constraints when integrated across broad geographic extents (Peterson et al. 2011). Likewise, the apparent effects of ecological drift (random fluctuations in species' relative abundances) may be expected at local scales, but minimal when integrated over many species and a large extent (Vellend et al. 2014). The prominent role of environmental selection is reinforced by our finding that macroclimate alone explained more than half the variation in community composition along the first ordination axis. Testing the relative contributions of speciation, dispersal, drift and selection in shaping lichen diversity remains an active research topic.

We quantified the sensitivity and strength of relationship between epiphytic macrolichen community compositions and climate gradients. This expands on previous work establishing lichen-based climate monitoring guidelines (Smith et al. 2017a). Findings agreed with more localized studies that found high lichen compositional turnover at geographic thresholds separating warm, wet, coastal sites from cooler, drier inland sites (Root et al. 2014). Lichen scores, representing variation in community composition, had the strongest relationship with mean annual precipitation, mean annual temperature, and their ratio, annual heat moisture index. Collectively, this suggests that relatively minor warming or drying (or both) could cause proportionately large changes in lichen community compositions across the Pacific states. In principle, such trends might be offset by retention forestry that retains hospitable

microclimates (Ellis et al. 2009; Moning et al. 2009). However, western North American forests face the twin realities of changing wildfire regimes and timber harvesting that can drastically alter forest structure. While we acknowledge the pragmatic need for retention forestry, we also recognize that microclimatic refugia are likely not sufficient to prevent changes in community compositions if macroclimate changes occur across large areas.

Modeling the composition of communities over large areas is fundamentally different from modeling biogeographic signatures of single species (e.g., geographic distributions, molecular diversity) or other macroecological emergent properties (e.g., species richness, beta diversity). A primary challenge is methodological: multivariate outcomes based on pairwise dissimilarities become uncertain when high beta diversity leads to many pairs of sites sharing no species in common (Smith 2017). For this reason, Will-Wolf and Neitlich (2010) cautioned against using dissimilarity-based gradient models for large areas with high species turnover. Here, we resolve the issue by the use of stepacross dissimilarities that give realistic relative positions even for very distant sites that share no species. Another challenge regards interpreting and communicating ordination scores, which compress high-dimensional species information into a single low-dimensional score. We addressed this by an indicator species approach to distinguish which species were most indicative of specific regions of species space (lichen scores) or climate space (defined climate zones). Indicator species are intuitive markers of global change impacts that are equally informative to quantitative ecologists, natural resource managers and the general public.

Lichen indicator species are ideal candidates for monitoring because their gain or loss over time can be visible signals of climate changes (van Herk et al. 2002; Cezanne et al. 2008). Modeling indicator species over large geographic scales anticipates the possibility that communities at sites currently within a given climate zone could come to resemble communities currently outside the zone, or even those with no present analog. Our lichen indicator species of the Pacific states climate zones corresponded well with existing biogeographic concepts. One group was consistent with "oceanic-affinity" species (Goward and Spribille 2005). An intermediate group was characteristic of temperate and cool montane habitats. Yet another group had species typically associated with simultaneously warm, dry and often eutrophic lowlands (Jovan 2008). Future lichen-based climate analyses might also

explore the biological effects of atmospheric nitrogen deposition, which can be amplified in hotter, drier climates (Sheppard et al. 2011; Jovan et al. 2012). Our multi-group indicator approach allowed species to indicate potentially multiple climate zones (rather than being restricted to single zones), which reflects the biological reality that species differ in their climatic niche tolerances (breadths). It also suggests that specialists with narrow tolerances might be more responsive indicators of climate changes. For example, a hypothetical drying trend that caused local declines of a specialist indicator (e.g., *Platismatia stenophylla*: Zone 8) may or may not decrease the abundance of a co-occurring generalist (e.g., *Platismatia glauca*: Zones 3+8+9). Indicator species offer a very rapid, visible and cost-effective assessment of climate change impacts on species and communities.

The effects of climate change on community compositions are the joint outcome of changes to individual species' distributions. Continental Europe has seen rapid gains of heat-tolerant species and declines of arctic-boreal lichens over just a few decades (Aptroot and van Herk 2007, Ellis et al. 2009, van Herk et al. 2002). Climate shifts may eliminate suitable habitats in some places while simultaneously creating them elsewhere. Yet, any range expansions to new sites would depend on species' dispersal and establishment rates being sufficient to track climate. There is limited evidence of climate tracking in a few terrestrial arctic lichens (Geml et al. 2010), but epiphytic lichens often exhibit distinct colonization lags (Gjerde et al. 2012; Greenwood et al. 2016), probably due to environmental requirements during establishment stages rather than dispersal limitations (Werth et al. 2006). Climate envelope models can forecast the potential extent of suitable lichen habitats (Ellis et al. 2007), but we don't yet know enough about lichen demographic rates or expected rates of climate change to be able to predict whether lichen communities could in reality track climate shifts.

Consistent lichen–climate relationships suggest an immediate utility for monitoring how climate changes might affect other forest dwellers beyond lichens. Decreases in major forage lichen species such as *Alectoria sarmentosa* and *Bryoria fremontii* would potentially affect entire trophic networks because black-tailed deer, moose, woodland caribou, tree voles and flying squirrels variously depend on epiphytic macrolichens for forage, habitat and nesting materials (Sharnoff and Rosentreter 1998). A lichen-based monitoring program could resurvey existing plots at 5- or 10-year intervals to determine trends in community

composition. For example, will there be a trend toward communities having affinities with warmer and drier conditions, or towards communities with no current analog? Systematically tracking range shifts of a few prominent indicator species may be more efficient than resurveying entire communities. "Hot, dry" indicator species (e.g., *Candelaria, Polycauliona, Phaeophyscia, Physcia* spp.) might expand northward or upward, while "moist, coastal" indicators (e.g., *Sphaerophorus* spp., *Platismatia norvegica*, cyanolichens) could exhibit range contractions. We speculate that climate-driven changes in lichen communities could be precursors of changes in other forest vegetation, since epiphytic lichens have generally shorter life-cycles than trees and are more directly exposed to climatic fluctuations.

In conclusion, we confirmed the strength of climate relationships with lichen communities across the Pacific states super-region, using lichen-based climate scores for sites and indicator species for climate zones. A large-extent approach is effective, not only because lichen–climate affinities may become more apparent over broader gradients, but also because practitioners may wish to understand how regional findings tie into subcontinental trends. Lichen-based scores demonstrated distinctive and nonlinear relationships to precipitation, temperature, and other macroclimatic gradients. Indicator species revealed affinities to oceanic, continental or lowland habitats in a manner that will enhance monitoring of vegetation transitions under global changes. Knowledge of patterns and processes in lichen communities will be fundamental for environmental monitoring, and for anticipating how changing climates might impact forest ecosystems in the western United States.

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Tables

Table 3.1. Summary of climate principal components (PCs) in the Pacific states. PC1 corresponded to a thermal/aridity gradient commonly associated with changes in latitude and elevation; PC2 represented a gradient of moisture and continentality; PC3 was a more complicated climatic gradient involving frost-free period.

Item	Units	Abbrev	PC1	PC2	PC3
Variance explained	%	–	45.5	24.5	15.6
Cumulative variance explained	%	–	45.5	70.0	85.6
Climate correlations:					
Mean annual air temp	°C	MAT	−0.78	−0.49	0.29
Continentality	°C	TD	0.38	0.82	0.21
Mean annual precipitation	mm y^{-1}	MAP	0.42	−0.86	0.14
Annual heat moisture index	°C mm^{-1} y	AHM	−0.88	0.11	0.30
Frost-free period	d	FFP	−0.41	−0.07	−0.82
Percent precip as snow	%	PAS	0.78	−0.16	0.33
Climatic moisture deficit	mm y^{-1}	CMD	−0.84	0.17	0.29

Table 3.2. Strength of lichen-climate relationship (*xR²*) and climate sensitivity (*Sens*) from nonparametric multiplicative regression models. NMS scores are lichen-based climate scores. The final NMS solution had two dimensions, stress = 18.7, and explained 80.4% of the variation in community composition (64.0% and 16.4% on each axis respectively).

Predictor(s)	Response: NMS axis 1 scores				Response: NMS axis 2 scores			
	xR²	*Sens*	*Tol*	*N**	*xR²*	*Sens*	*Tol*	*N**
PC1, PC2, PC3	0.72	–	–	55.9	0.42	–	–	57.9
PC1	0.27	0.83	0.33	162.0	0.31	0.80	0.22	108.8
PC2	0.49	0.98	0.15	94.7	0.15	0.63	0.23	140.2
PC3	0.08	0.86	0.15	109.2	0.11	0.64	0.22	162.4
MAT	0.36	1.05	0.84	81.4	0.40	0.63	1.25	120.9
TD	0.18	1.25	0.28	63.4	0.18	0.66	0.83	183.4
MAP	0.56	1.13	51.4	60.6	*NS*	0.12	308.6	314.5
AHM	0.35	1.94	1.14	104.0	0.29	1.48	1.14	104.0
FFP	0.17	0.73	7.04	89.1	0.10	0.80	7.04	89.1
PAS	0.14	1.19	37.2	81.0	0.27	1.20	74.48	147.6
CMD	0.37	1.00	11.5	78.5	0.17	0.34	45.88	182.9

xR²: Cross-validated *R²* is the proportion of variation explained by each model, based on leave-one-out cross-validation in NPMR. Except for one model (*NS*), all models had $p < 0.05$ from a randomization test (99 randomizations) of the null hypothesis that the model fit was no better than obtained by chance alone.

Sens: Sensitivity is a unitless measure of the relative importance of each predictor; values = 0 indicate that perturbing a predictor has no effect on the response. Values = 1 indicate that perturbing a predictor yields an equal-magnitude change in the response variable, where both predictor and response are scaled by their ranges.

Tol: Tolerance is a measure of how broadly a point estimate depends on nearby plots in predictor unit space, representing one standard deviation of the Gaussian kernel, scaled by the units of each variable.

N*: Neighborhood size is the average number of sample units used to estimate the response at a given point.

Table 3.3. Climate zones in the Pacific states: species diversity and Kendall's *tau* correlation with climate variables. The ten climate zones were: Zone 1 = hot dry lowlands, 2 = warm dry subcontinental, 3 = warm mesic temperate, 4 = cold mesic subcontinental, 5 = cold dry continental, 6 = cold mesic continental, 7 = cool dry continental, 8 = cool moist subcontinental, 9 = mild moist suboceanic, and 10 = warm wet hypermaritime.

Item	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6	Zone 7	Zone 8	Zone 9	Zone 10
Gamma diversity (γ)	87	157	177	90	94	181	192	132	119	122
Alpha diversity ($\bar{\alpha}$)	15.4	17.0	17.2	11.7	12.0	18.9	19.9	18.3	18.0	15.9
Beta diversity (β_W)	4.6	8.2	9.3	6.7	6.8	8.6	8.7	6.2	5.6	6.7
N sample units	74	141	145	37	194	159	150	64	71	83
Climate correlations (*tau*)										
NMS1	0.29	0.23	−0.26	0.06	0.25	0.00	0.05	−0.17	−0.27	−0.30
NMS2	0.24	0.21	0.16	−0.15	−0.38	−0.11	0.05	−0.05	0.02	0.05
PC1	−0.35	−0.40	−0.11	0.21	0.30	0.20	−0.18	0.32	0.21	−0.10
PC2	0.01	−0.08	−0.28	0.04	0.39	0.19	0.29	−0.18	−0.29	−0.35
PC3	0.02	0.00	−0.07	−0.13	−0.47	0.28	0.26	0.30	0.10	−0.25
MAT	0.33	0.39	0.19	−0.22	−0.51	−0.19	−0.03	−0.13	0.03	0.22
TD	−0.13	−0.18	−0.27	0.05	0.33	0.26	0.24	0.04	−0.18	−0.35
MAP	−0.26	−0.08	0.24	0.03	−0.25	−0.03	−0.31	0.26	0.31	0.30
AHM	0.35	0.34	0.05	−0.21	−0.46	−0.05	0.32	−0.20	−0.15	−0.04
FFP	0.26	0.17	−0.02	0.12	0.33	−0.37	−0.28	−0.26	−0.11	0.19
PAS	−0.34	−0.38	−0.06	0.16	0.17	0.25	−0.12	0.32	0.24	−0.17
CMD	0.35	0.39	−0.07	−0.16	−0.21	0.02	0.15	−0.14	−0.23	−0.20

Table 3.4. Select indicator species for climate zone combinations of the Pacific states. See Appendix A for all remaining species. Blanks denote species had non-significant indicator value (even for zones in which the species was present). The ten climate zones were: Zone 1 = hot dry lowlands, 2 = warm dry subcontinental, 3 = warm mesic temperate, 4 = cold mesic subcontinental, 5 = cold dry continental, 6 = cold mesic continental, 7 = cool dry continental, 8 = cool moist subcontinental, 9 = mild moist suboceanic, and 10 = warm wet hypermaritime.

Indicator species	IndVal all zones	IndVal for single climate zones									
		1	2	3	4	5	6	7	8	9	10
Platismatia norvegica	0.62								0.20	0.40	0.45
Sphaerophorus aggr.	0.74								0.34	0.50	0.43
Hypogymnia enteromorpha	0.62								0.38	0.35	0.34
Alectoria sarmentosa	0.60								0.44	0.33	0.27
Parmeliopsis hyperopta	0.62				0.24				0.50	0.31	
Bryoria glabra	0.35							0.16	0.21	0.25	
Hypogymnia imshaugii	0.65				0.30	0.39	0.40				
Letharia vulpina	0.72				0.32	0.50	0.38				
Nodobryoria abbreviata	0.68				0.33	0.49	0.33				
Bryoria fremontii	0.62				0.33	0.45	0.28				
Cetraria merrillii	0.55				0.13	0.50	0.24				
Letharia columbiana	0.63				0.40	0.47					
Ramalina farinacea	0.44		0.24	0.31				0.22			
Candelaria pacifica	0.70	0.59	0.42								
Physcia adscendens	0.65	0.57	0.37								
Polycauliona polycarpa	0.61	0.50	0.37								
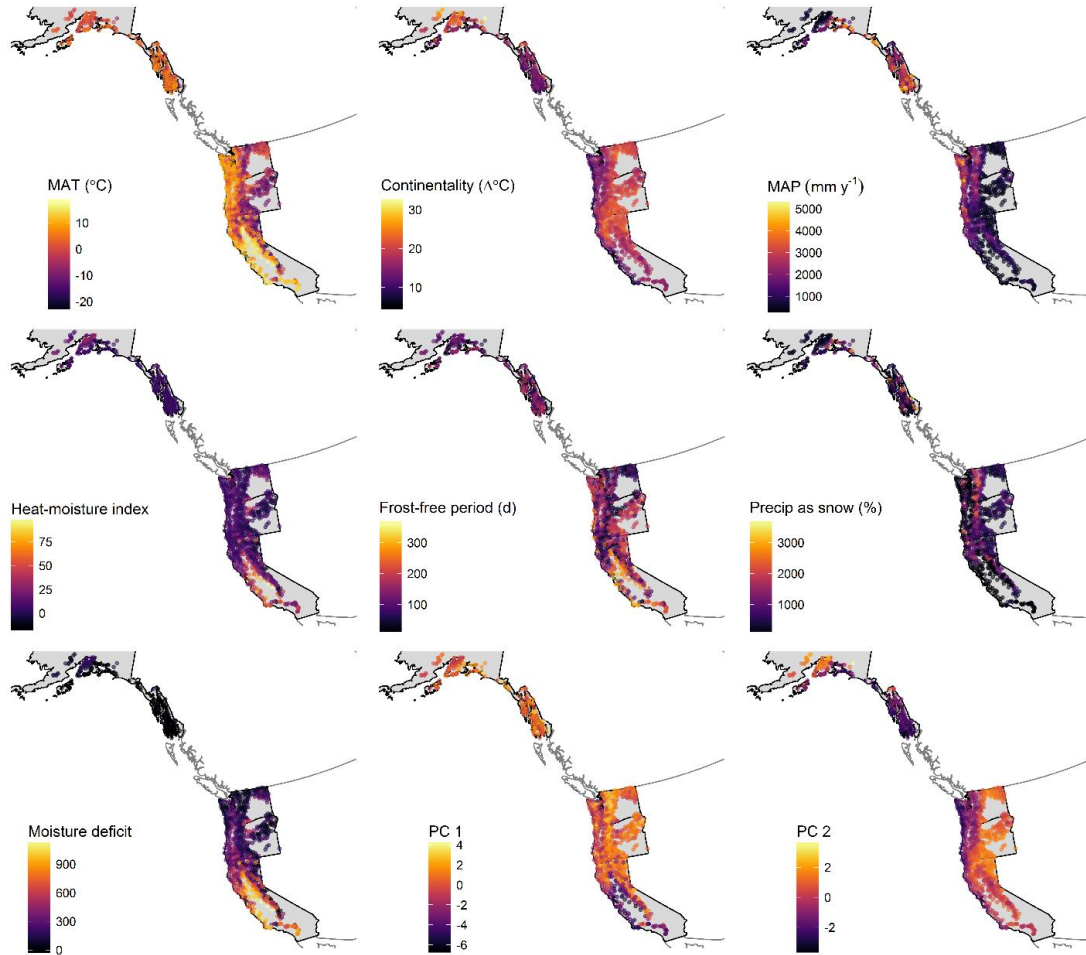
Figure 3.1. Raw and synthetic climate values at each FIA lichen plot in the Pacific states area. Climate data from ClimateNA (Wang et al. 2016). Synthetic climate variables are principal components (PCs); the first three (of seven possible) were used in analyses. PC1 represents a thermal/aridity gradient, PC2 is a gradient of moisture and continentality, and PC3 (omitted for space) is a more complicated climatic gradient involving frost-free periods.
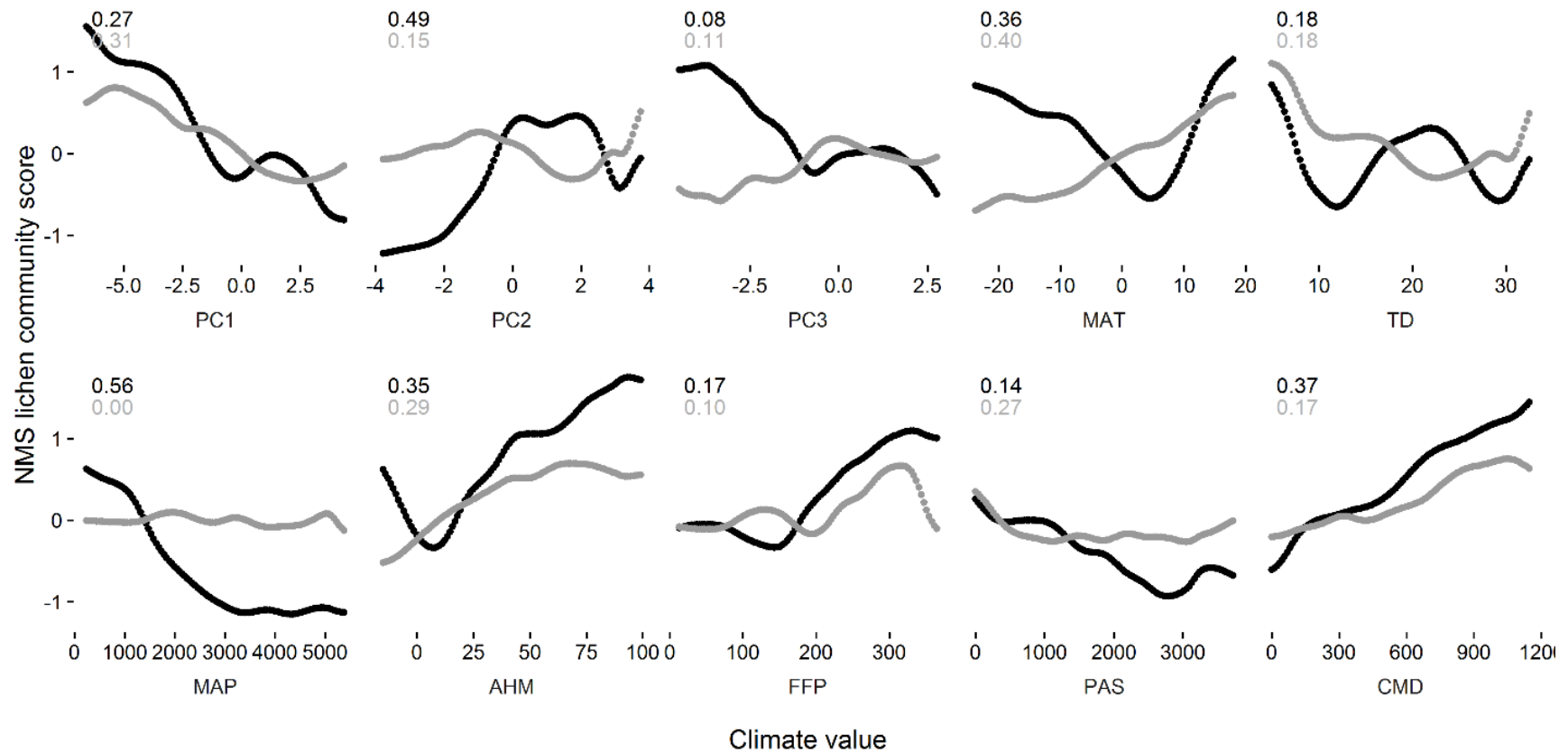
Figure 3.2. Fitted nonparametric multiplicative regression of lichen community scores in response to climate in the Pacific states. Fitted values for NMS first axis scores (black) and second axis scores (grey) scores are interpreted as climate-related variation in lichen community composition. Numerals indicate regression goodness-of-fit, cross-validated xR^2, ranging from 0–1.
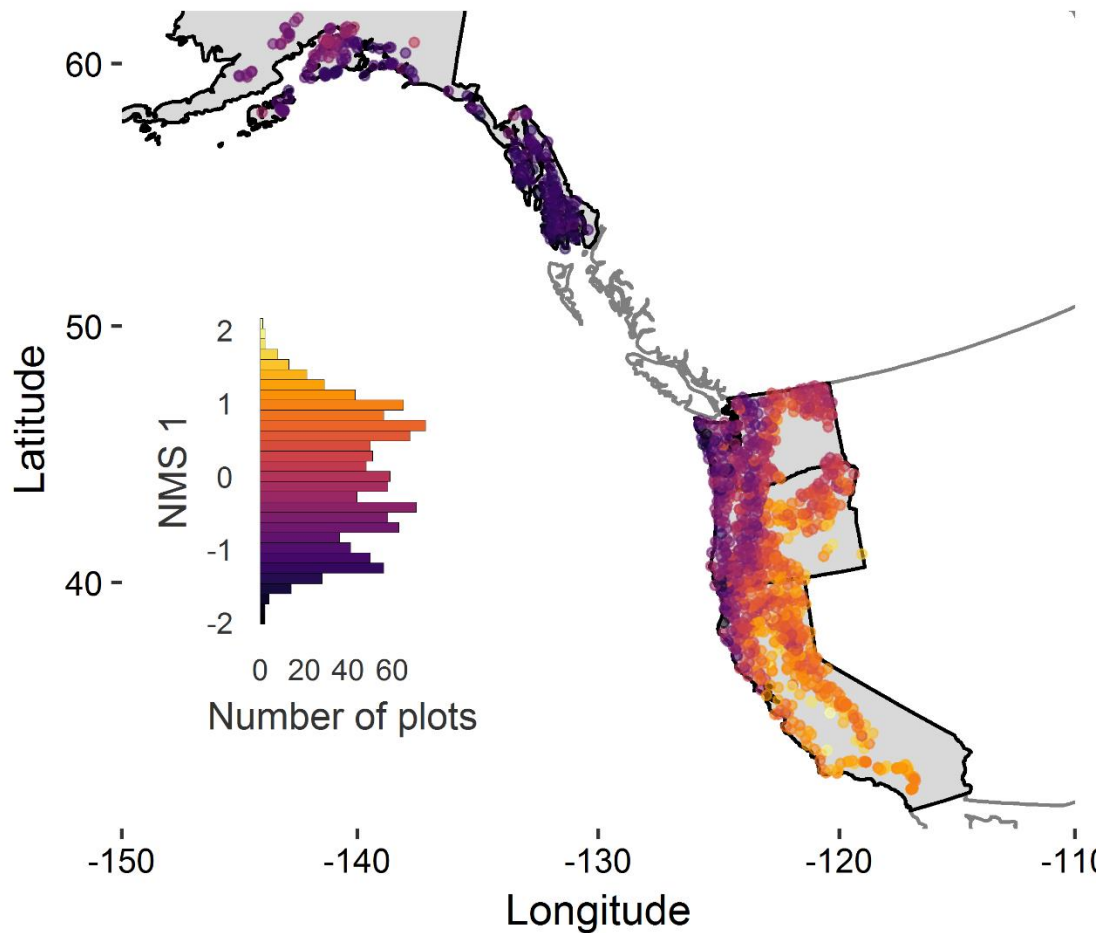
Figure 3.3. Lichen community NMS scores (Axis 1) mapped on the Pacific states area.
Similar scores (colors) represent similar lichen species compositions among sites. NMS axis 1 (explaining 64.0% of compositional variation) reflects lichen community responses to a moisture gradient involving mean annual precipitation, annual heat moisture index, and climatic moisture deficit.
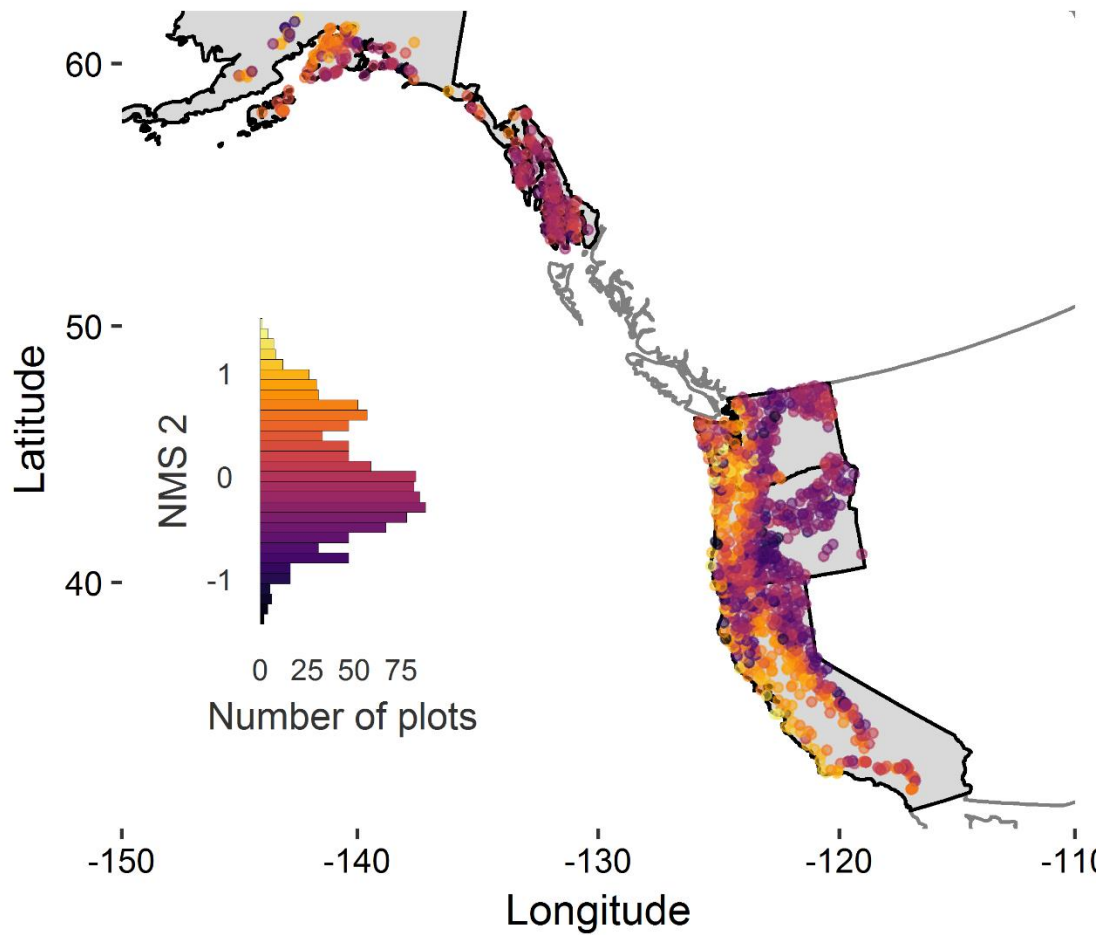
Figure 3.4. Lichen community NMS scores (Axis 2) mapped on the Pacific states area. Similar scores (colors) represent similar lichen species compositions among sites. NMS axis 2 (explaining 16.4% of compositional variation) reflects responses to a temperature gradient involving mean annual temperature and annual heat moisture index.

Figure 3.5. Climate zones for each FIA lichen plot in the Pacific states area. Climate zones, as defined by optimal partitioning, are mapped in geographic space (main figure), climate space (upper right: mean annual precipitation vs temperature), and species compositional space (lower right: NMS ordination scores). Distances between points in the NMS plot indicate dissimilarity of community compositions among sites.

Figure 3.6. Climate zone indicator species' distributions across the Pacific states area.
Top row = high-latitude and coastal species. Middle row = continental-montane species.
Bottom row = species that tolerate hot, dry, or eutrophic conditions. See Appendix A for
complete list of all species climate indicator values.
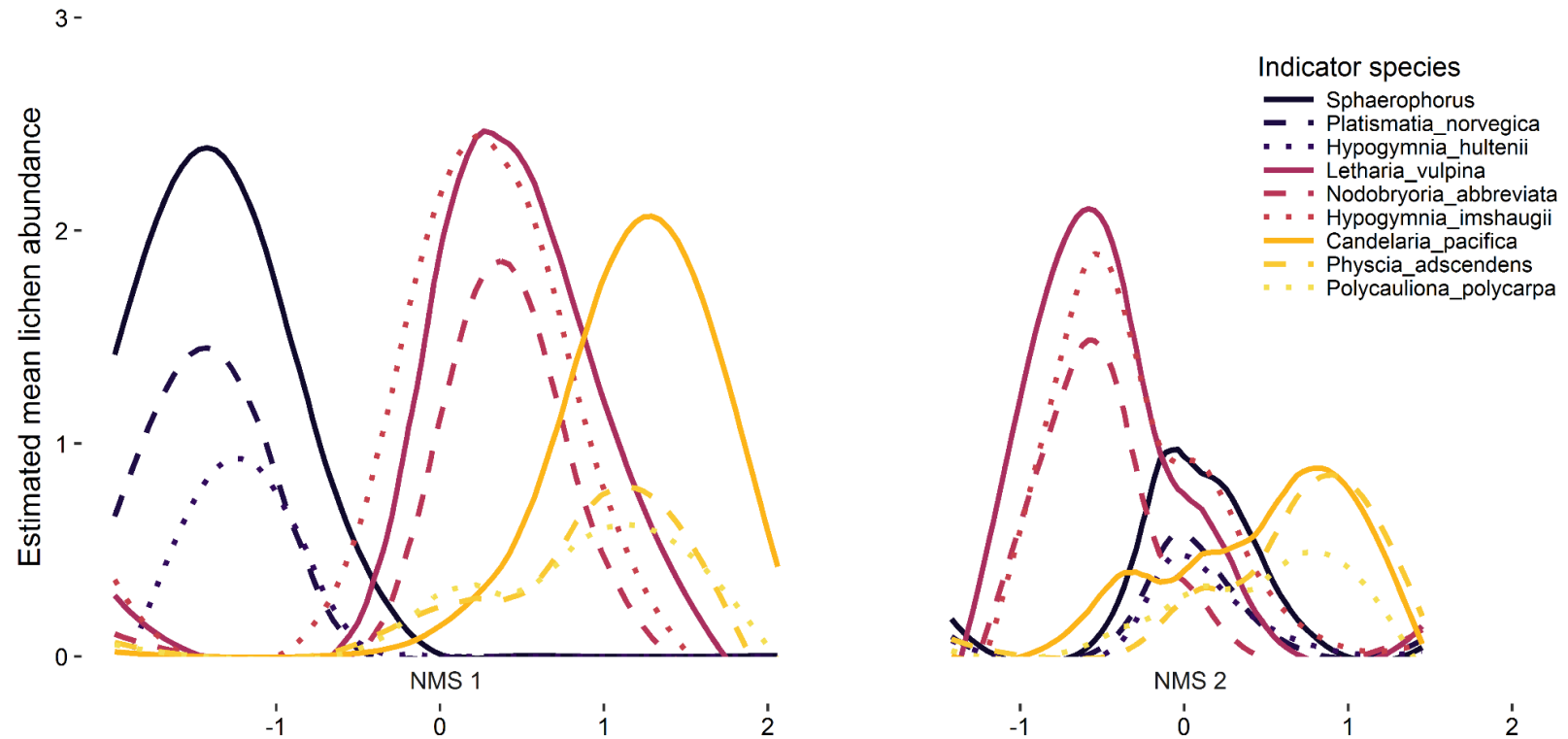
Figure 3.7. Climate indicator species' estimated mean abundances across NMS lichen scores. Estimated abundances are from locally-weighted regressions. Three groups of indicator species represented high-latitude and coastal sites (purples), continental-montane sites (reds) and hot, dry, or eutrophic sites (yellows). Abundances range from 0 to 4 on an approximately logarithmic scale. See Appendix A for complete list of all species climate indicator values.

CHAPTER 4. VULNERABILITY OF FOREST LICHEN COMMUNITIES TO SPECIES
LOSS UNDER CLIMATIC WARMING

Robert J. Smith, Sarah Jovan, and Bruce McCune

Abstract

Resolving how species differ in their tolerances to climatic constraints can help anticipate how global changes will cause range shifts. Communities with many species at or near their niche limits may be vulnerable to species losses, suggesting that niche-based measures can inform vulnerability assessments. In a two-stage process, we first estimated realized niches as empirical cumulative distribution functions for 443 epiphytic macrolichen species across fifteen climate gradients based on rasterized herbarium records (46,343 sites in Mexico, Canada and the U.S.). We then estimated thermal vulnerability based on systematic, whole-community epiphytic macrolichen surveys from the U.S. Forest Inventory and Analysis (FIA) program (6,474 U.S. sites). Herbarium data addressed possible niche truncation, while systematic FIA data resolved sampling representativity concerns. Three niche-based thermal vulnerability indices (TVIs) respectively showed *i*) percentage of vulnerable species at their upper thermal limits, *ii*) community-mean thermal percentile rank, and *iii*) thermal deviation measuring deviation of local temperatures from average upper thermal limits. Sensitivity of these indices to uncertainty in climate variables was minor (1.9–6.2% change in noise-added TVI values as a percentage of original TVI range). Present-day thermal vulnerability was greatest in north-central California, in the Southwest along the western Colorado Plateau, and on the Southeastern coastal plain, suggesting that warming-induced species losses will become most evident in these areas. Under proposed warming scenarios (increases of +0.5 to +3.6 °C), the percentage of U.S. epiphytic macrolichen communities exceeding thermal safety margins grew from about 2% to 20%. In all scenarios the most vulnerable communities were concentrated in low-elevation and southerly locations, which suggests that lichens otherwise assumed to be "warm-adapted" may nevertheless be commonly on the verge of exceeding their upper thermal limits. Our findings indicate that warming will modify community compositions through the loss of warming-intolerant species pushed beyond their niche limits. Assessing vulnerability of bioindicators such as lichens will help prioritize locations where the greatest climate-induced changes in species distributions and forest diversity will occur.

Introduction

Emerging global changes are sparking the need to discriminate how and where basic ecosystem properties like species diversity will change. This need underpins climate

adaptation in fields as diverse as agriculture, forestry and commercial fisheries. Climate is one of many selective pressures on ecological communities as it favors some species and eliminates others (Vellend 2016). Therefore, characterizing climatic limits to species distributions will help to identify which taxa are most at risk of local extinctions, and can identify locations where communities are most vulnerable to species losses. Climate change vulnerability assessments incorporate exposure, sensitivity and adaptability to determine species-level extinction risks (Ellis 2013; Foden et al. 2013; Pacifici et al. 2015), but there is now also a need to understand responses to global changes at the community-level. For example, warming climates may force the local extinction of cold-tolerant species while warm-tolerant species thrive, a process termed thermophilization (Gottfried et al. 2012). The need to quantify how communities will respond to warming is now critical for identifying where biological responses will be greatest, given that warming air temperatures are expected in virtually all United States (U.S.) locations over the next century (Melillo et al. 2014).

Warm-season temperatures impose a critical upper thermal boundary on epiphytic organisms such as lichens because they are directly exposed to atmospheric fluctuations. Epiphytic lichens are fungus–photobiont symbioses with an aerial lifestyle defined by nutritional and metabolic dependency on atmospheric conditions. This lifestyle makes them excellent bioindicators of climate. For example, atmospheric warming and drying alter lichen reproductive allocation (Martinez et al. 2012) and cause rapid growth declines and mortality (Song et al. 2012; Smith et al. 2017b), which can lead to local exclusion of species. At regional scales, the greatest changes in lichen community composition are expected where colder/drier areas transition to warmer/wetter conditions (Root et al. 2014), or where climatic warming expands tree distributions faster than epiphytes can track (Greenwood et al. 2016). At subcontinental scales, variation in lichen community diversity is highly correlated with mean annual air temperature, continentality, precipitation and moisture deficits (Coyle and Hurlbert 2016; Smith et al. 2017a), suggesting that national monitoring of lichens will be effective for detecting the biological effects of global changes on forests. Given lichens' multiscale relationships with climate, we employed niche-based vulnerability analyses to determine how and where lichen community diversity is expected to change under contemporary climates and future warming scenarios.

Climate change vulnerability assessments are predicated on sufficient knowledge of species' realized climate niches. Early 20th-century Russian and European vegetation workers developed semi-quantitative "ecological indicator values" to rank plant species' optimum positions along environmental gradients (Ramensky et al. 1956; Ellenberg 1974), an approach later extended to lichens and other fungi (Barkman 1958; Wirth 2010). More recently, workers have combined gridded climate data with species occurrences to yield fully quantitative niche centrality measures based on the center of a temperature niche for single species (Species Temperature Index), or else the community-weighted average of species' niche centers (Community Temperature Index) (e.g., Elmendorf et al. 2015). Evaluating changes in niche centrality measures can reveal whether shifts in organisms' distributions might keep pace with observed rates of warming (Devictor et al. 2008; Feeley et al. 2013; Savage and Vellend 2015). However, niche centrality measures ignore information about the remainder of realized niches, such as the upper and lower bounds that describe species' climatic constraints. It is these constraints, and the climate changes that violate them, that determine how species losses will occur.

Our overall goal was to advance a simple approach to determine niche-based climate change vulnerability for any set of ecological communities. We had five specific objectives with respect to epiphytic forest macrolichen communities across the United States. These objectives were: 1) to quantitatively delineate the realized climatic niche of all U.S. epiphytic macrolichen species; 2) to test the effects of geographical extent on niche coverage and apparent "truncation" (niche underestimation); 3) to define and implement a set of vulnerability indices showing warming effects on species losses; 4) to evaluate the sensitivity of the indices to uncertainty in climate variables; and 5) to apply the vulnerability indices to expected future climates across the United States. We further discussed extensions of this approach for comparative assessments to identify the relative sensitivity of different organism groups to global changes.

Methods and Materials
Data for U.S. lichens and climate

All analyses were performed in R version 3.3.1 (R Development Core Team 2016). Inferences apply to epiphytic macrolichen communities on forested lands in the United States

sampled as part of the U.S. Forest Service's Forest Inventory and Analysis (FIA) lichen program. The National FIA Lichen Database (Jovan et al. 2017) gives abundances of all epiphytic macrolichen species recorded over the period 1989–2012 at 8,344 plots across the United States. We first excluded 1,870 externally contributed plots that did not adhere to the systematically random FIA sampling design, yielding a final FIA lichen dataset with 75,740 unique occurrences of 443 species at 6,474 sites (plots). The FIA lichen sampling design is systematically random and geographically representative: one site is randomly located in each 39,072-ha hexagonal grid cell of a hexagonal grid covering the U.S., and a plot (sample unit) is then measured at each forested site (defined as ≥10% potential tree cover on undeveloped land ≥0.41 ha area and ≥36.6 m wide). This design is representative of many different kinds of geography, land ownerships and disturbance histories across U.S. forests. Field sampling consisted of a 2-h, time-constrained, exhaustive inventory of a circular, 0.379-ha fixed area plot in which technicians collected and assigned logarithmic abundance values (0–4) for all epiphytic macrolichen species growing on trees above 0.5 m. Abundance values were: $0 =$ not present; $1 = 1$–3 thalli observed; $2 = 4$–10 thalli observed; $3 =$ more than 10 thalli observed but on $< 50\%$ of available branches and stems; and $4 =$ observed on $> 50\%$ of available substrates. Because its goal is complete inventory of all species present (within measurement time constraints), the FIA method provides informative absences that facilitate predictive species modeling. All climate data originated from the ClimateNA database (Wang et al. 2016). For all FIA lichen plot locations, we extracted fifteen lichen-relevant climate variables as 30-y annual normals covering the period 1980–2010 (Table 4.1); these included Mean Warmest Month Temperature (MWMT hereafter) used for thermal vulnerability analyses.

Species' climatic niche measures

For each of the 443 lichen species and fifteen climate variables (Table 4.1), we calculated realized niche space as an empirical cumulative distribution function (ECDF). We can describe the probability of encountering a given species at any point along a continuous environmental gradient as a probability density function shown as a 'solid' curve (Fig. 4.1); the ECDF is simply the area under this curve. For any given niche value, the ECDF gives the fraction of observations that are less than or equal to that value (Fig. 4.1), and is useful to describe sample quantiles. This data-driven, nonparametric approach makes no assumptions

about any statistical distribution, and allows species niche responses to be nonlinear, polymodal or asymmetrical in a way that realistically portrays the rich and individualistic climate responses of many species (Whittaker 1967). From each species' ECDF for each of the fifteen climate variables (Table 4.1), we determined sample quantiles, including each species' climatic median (= center), interquartile range (= spread), and 5th and 95th percentiles (= lower and upper limits). Interquartile range (75th percentile minus 25th percentile) is a measure of niche spread indicating where a species falls on a specialist–generalist spectrum; it is analogous to a standard deviation but is more robust to outliers, non-normal distributions, and skewed distributions (Zwillinger 2012). Hereafter, the "thermal niche" and "thermal vulnerability" analyses refer specifically to Mean Warmest Month Temperature (MWMT), which is calculated as the 30-year mean air temperature of each year's warmest month, typically July or August in the Northern Hemisphere (Wang et al. 2016). MWMT therefore reflects average warm-season temperatures and is a measure of the upper thermal conditions to which lichens are commonly exposed. We also calculated species relative frequencies to show geographical rarity in the U.S. study area.

Niche coverage: truncated versus extended climate niches

Realized niches may appear "truncated" if the full range of climate conditions do not exist, are incompletely sampled, or if a species' geographic center of mass is outside the study area (Feeley and Silman 2010; Peterson et al. 2011). Because the FIA dataset is restricted to the United States, it may underestimate ("truncate") thermal niches for southern-centered species, and overestimate thermal niches for northern-centered species. Therefore, we "extended" the coverage of species climate niches by introducing lichen herbarium records for the entirety of North America (U.S., Mexico and Canada), sourced from the Consortium of North American Lichen Herbaria database (CNALH 2017). We retained only georeferenced herbarium observations, and harmonized species names with the FIA dataset. The final herbarium dataset had 172,127 unique occurrences of 443 species at 46,343 North American sites (plots). Herbarium observations are not systematically sampled, therefore some species and locations are under- or over-represented given collector biases, and any absences are ambiguous (uninformative). For example, an absence could mean that no lichens existed at a site thoroughly searched (true negative), or that many lichens truly existed but the site was never visited (false negative). To reconcile these issues, we rasterized (binned) all point

occurrences into grid cells (approximately 50×50 km) projected over North America, and from climate data extracted at each point occurrence, we calculated the mean climate value in each grid cell for each species. Rasterizing retains information otherwise lost by thinning, filtering or subsetting observations. We then recalculated species niche measures as above in parallel with the FIA dataset, giving two sets of niche measures calibrated either with the "truncated" FIA data or "extended" herbarium data. We compared outcomes using range-standardized MAD (mean absolute deviation expressed as a proportion of each range of "extended" values) to evaluate the effects of niche coverage on several vulnerability indices.

Thermal vulnerability indices

TVIA: VULNERABLE SPECIES PERCENTAGE

The first Thermal Vulnerability Index (*TVIa*) is defined here as the percentage of all co-occurring species that locally approached their upper thermal limits. Upper thermal limits are defined by local MWMT values exceeding the 95th percentile of each species' empirical cumulative distribution function. On a 0–100% scale, *TVIa* can be interpreted as the potential community-level effect of incrementally raising warm-season temperatures, where higher values indicate greater thermal vulnerability and 100% indicates that all species are vulnerable. The numerator describes the number of vulnerable species approaching their upper thermal limits at a site, and the denominator describes the total number of species present.

$$TVIa_i = \left(\frac{\sum_{j=1}^{n} a_{ij} \, I_{ij}\left[T_i \geq \left(T \middle| P_{95j}\right)\right]}{\sum_{j=1}^{n} a_{ij}} \right) \times 100$$

where a_{ij} is the presence (0 or 1) of species j in site i, I_{ij} is an indicator function taking the value 1 when true and 0 when false, T/P_{95j} is the 95th percentile MWMT value from the set of all MWMT values T in which species j occurs (upper thermal tolerance of species j), T_i is the MWMT value of site i, and n is the total number of species we observed over all sites.

TVIB: COMMUNITY-MEAN THERMAL PERCENTILE

Rather than a measure based on discrete cutoffs, a measure based on averaging percentile ranks of all species at a given temperature would provide insight about the *degree* of vulnerability, applicable even to relatively less-vulnerable communities. By this logic, we defined a second Thermal Vulnerability Index (*TVIb*) as the community-mean of all species percentile ranks at a given temperature, where higher values indicate greater average vulnerability.

$$TVIb_i = \left(\frac{\sum_{j=1}^{n} a_{ij}\left(P_{Xj}|T_i\right)}{\sum_{j=1}^{n} a_{ij}}\right) \times 100$$

where a_{ij} is the presence (0 or 1) of species j in site i, P_{Xj}/T_i is the Xth percentile rank of species j given site MWMT value T_i, T_i is the MWMT value of site i, and n is the total number of species we observed over all sites.

TVIC: THERMAL DEVIATION

Finally, a third Thermal Vulnerability Index (*TVIc*) was "thermal deviation", defined as the deviation of local MWMT (°C) from community-mean upper thermal tolerances (95th percentile MWMT values). Positive *TVIc* values indicate that local warm-season temperatures exceed average community upper thermal tolerances ("vulnerable" communities), while negative values indicate that local warm-season temperatures are less than average tolerances (communities with a margin of safety). The magnitude of *TVIc* indicates how far the average community upper thermal tolerances depart from local warm-season temperatures.

$$TVIc_i = T_i - \left(\frac{\sum_{j=1}^{n} a_{ij}\left(T|P_{95j}\right)}{\sum_{j=1}^{n} a_{ij}}\right)$$

where a_{ij} is the presence (0 or 1) of species j in site i, T/P_{95j} is the 95th percentile MWMT value from the set of all MWMT values T in which species j occurs (upper thermal tolerance of species j), T_i is the MWMT value of site i, and n is the total number of species we observed over all sites. Stuart-Smith et al. (2015) used a nearly identical "thermal bias" measure,

except they reversed the order of terms. Blonder et al. (2017) refer to a similar measure as "community climate lag" when integrating change over time.

Sensitivity of thermal vulnerability

Measurement and model error can propagate to uncertainty in climate variables and thermal vulnerability indices (TVIs). We evaluated uncertainty using sensitivity analyses in which we added noise to the original climate data, then measured corresponding effects on thermal vulnerability. Added noise was uniformly-distributed with bounds ± 5% the range of the original climate values. Sensitivity, Q, was the range-standardized mean absolute deviation of original vs noise-added TVI values, expressed as a proportion of the range of original TVI values.

$$Q = \left(\frac{\sum_{i=1}^{N} \left| TVI_{noise_i} - TVI_{orig_i} \right|}{N \left| \max TVI_{orig_i} - \min TVI_{orig_i} \right|} \right) \times 100$$

where TVI_{noise} and TVI_{orig} are TVI values for site i respectively resulting from noise-added and original data, and N is the total number of sites. Sensitivity, Q, is interpreted as the proportion of change in the TVI response caused by a corresponding change in the MWMT variable. $Q = 0\%$ would mean that climate uncertainty has no effect on the response, while $Q = 100\%$ would mean that a change in climate variables results in an average TVI change of equal magnitude. For each TVI, we calculated the average sensitivity of 100 noise-added datasets.

Future climate change scenarios

We evaluated changes in thermal vulnerability under four future climate change scenarios. For consistency, we refer to each of the four alternative warming scenarios by their mean warming increment (+0.5, +1.0, +2.5, +3.6 °C). First, we incrementally added +0.5, and +1.0 °C to contemporary MWMT to mimic small amounts of uniform warming across sites. Second, since real warming is not likely to be uniform, we also used MWMT values for the 30-year period spanning 2041–2070 from two realistic ensemble model projections based on optimistic (CMIP5-RCP4.5) and pessimistic (CMIP5-RCP8.5) greenhouse gas emissions

scenarios (IPCC 2014). Ensemble model projections were obtained from ClimateNA (Wang et al. 2016). Finally, for each warming scenario we then estimated the percentage of "very vulnerable" communities where vulnerability exceeded subjective critical values ($TVIa \geq$ 50%, $TVIb \geq$ 95%, $TVIc \geq 0$ °C).

Results

Species' climatic niche measures

The major macrolichen species of the United States exhibited an array of realized climate niches for fifteen different climatic variables, which we collected into one central database. Beyond the present application to vulnerability, these realized niche values should prove useful for researchers hoping to conduct climatic trait analyses and climate-based distributional mapping in future studies. We focus hereafter on thermal upper tolerance niches (Appendix B) defined by mean warmest month temperature, MWMT.

Niche coverage: truncated versus extended climate niches

Disagreement of thermal vulnerability between truncated vs extended niches was 3.4% (range-standardized MAD for *TVIa*), 6.4% (*TVIb*) and 3.6% (*TVIc*), suggesting minor but important effects of niche coverage. Robustness to niche coverage differed among TVIs (*TVIb* had slightly greater disagreement than *TVIa* or *TVIc*). Truncated niches gave apparently higher vulnerability relative to extended niches, with greatest differences at Southeastern U.S. sites (Fig. 4.2). By contrast, niche coverage had little effect on thermal vulnerability at Western U.S. sites, where species' niches were almost equally captured by either niche coverage method. Extended niches had the greatest effect on warm-tolerant lichen genera (*Heterodermia, Sticta, Teloschistes*) whose geographical distributions extended well south of the FIA study area. By contrast, extremely common species exhibited very little difference in niche coverage between the truncated vs extended methods, where "extremely common" species refer to those occurring in $\geq$20% of all plots: *Flavoparmelia caperata, Punctelia rudecta, Phaeophyscia rubropulchra* in the East; *Melanohalea subolivacea, Hypogymnia imshaugii, Letharia vulpina* in the West; and *Parmelia sulcata, Physcia adscendens, Hypogymnia physodes* throughout. Based on niche breadths, specialist and generalist species were similarly dispersed across the MWMT gradient (Figs. 4.3 and 4.4). However, lichens of the eastern U.S. tended to occupy generally warmer areas of niche

space relative to western species, and many eastern species tended to reach apparent upper thermal boundaries near approximately 28 °C, even after accounting for niche truncation (Fig. 4.4).

Thermal vulnerability indices

Hereafter, all inferences refer to the FIA lichen survey sites based on "extended" niches. All three TVI measures agreed: thermal vulnerability by any measure was consistently greatest in northern and central California, in the Southwest along the Sonoran–Colorado Plateau interface, and to a lesser degree on the Southeastern coastal plain (Fig. 4.2). All three TVIs were greatest at low elevations and low latitudes (Fig. 4.5). For example, lichen communities below 2000 m elevation and south of 49° latitude had the greatest thermal vulnerability.

Sensitivity of thermal vulnerability

Sensitivity, Q, is interpreted as the proportion of change in the TVI response caused by a corresponding change in the MWMT variable, where lower values are more desirable ($Q = 0\%$ means no effect of climate uncertainty, while $Q = 100\%$ means equal-magnitude change in TVI resulting from uncertainty in climate variables). After adding $\pm 5\%$ noise to the original climate data to mimic uncertainty, the sensitivity of *TVIa*, *TVIb* and *TVIc* was respectively 1.9%, 6.2% and 2.5%. After adding $\pm 10\%$ noise, sensitivity was 4.5%, 11.9% and 4.9%, respectively.

Future climate change scenarios

Thermal vulnerability increased under future climate warming scenarios (+0.5, +1.0, +2.5, +3.6 °C), with the greatest changes in lichen communities expected for the U.S. Southeast, Southwest, California and the Intermountain West (Fig. 4.6). The percentage of "very vulnerable" sites exceeding critical values also increased with warming (Fig. 4.7). For example, the percentage of U.S. communities with more than half of all species vulnerable (*TVIa* $\geq 50\%$) increased from 1.9 to 32.4%. The percentage of communities at excessive community-mean thermal percentiles (*TVIb* $\geq 95\%$) increased from 1.3 to 20.4%. The percentage of communities with positive thermal deviation (*TVIc* ≥ 0 °C) increased from 1.8 to 28.7% (Fig. 4.7). Collectively, the three TVIs indicated that at least one-fifth of all U.S.

lichen communities would meet the criteria for severe loss of species within the 30-year period 2041–2070 given pessimistic emissions scenarios.

<p align="center">Discussion</p>

Overall, our findings suggest that lichen communities with the greatest vulnerability of warming-related species losses are those at low-elevation and southerly locations in the United States. This finding contradicts a commonly accepted view that thermal vulnerability should be greatest among high-elevation and high-latitude communities. High-elevation lichens have long been a conservation focus because of high endemism and rarity (Allen and Lendemer 2016), and because of assumptions that communities dominated by cold-tolerant species should be more sensitive than warm-tolerant communities to increasing temperatures (van Herk et al. 2002; Aptroot and van Herk 2007; Hauck 2009). By contrast, we found that warm-tolerant communities are nevertheless quite commonly very near to exceeding their upper thermal limits.

The climate change vulnerability of warm-tolerant vegetation communities requires critical re-thinking. For example, tropical lowland macrolichens are at risk from global changes because they often occur in physiologically marginal locations that would become too warm to support species if exposed to even minor amounts of warming (Zotz and Bader 2009). Experiments (Zotz et al. 2003) confirm that the negative impacts of minor warming are not merely an artifact of underestimating fundamental niches in the absence of hotter current conditions (Feeley and Silman 2010). Others have invoked greater vulnerability of tropical/subtropical vegetation because of dominance by thermal specialists (Perez et al. 2016), though we found inconclusive support because both generalists and specialists occurred at warmer temperatures in this study. Aside from direct physiological impacts, atmospheric warming may also have indirect effects on lowland lichen communities due to rising sea levels (Lendemer and Allen 2014) or shifts in moisture regimes (Follmann 1995). Similar to cold-tolerant and temperate species, the only recourse for warm-tolerant lichen species would be upward or northward range expansion, as seems to be recently underway in western Europe (Wolfskeel and van Herk 2000; van Herk et al. 2002; Søchting 2004; Aptroot and van Herk 2007; van den Broeck 2010). Maintaining populations via range expansion assumes that species' dispersal rates can track suitable climates. Yet, for at least some

species, dispersal and establishment rates necessary to maintain populations may lag behind rates of climate change (Greenwood et al. 2016).

Warming scenarios revealed that the local consequences of climate changes will not be restricted to warm areas. High-elevation montane areas and high-latitude areas also became increasingly vulnerable with progressive warming. Suitable montane and alpine habitats may become increasingly limited in some locations such as the Appalachian Mountains of the U.S. Southeast (Allen and Lendemer 2016). To the extent that dispersal allows, climate migration in the mountainous U.S. West could involve both poleward and upward shifts, but poleward shifts may be the only feasible route in the U.S. East where mountains are much lower. The loss of some epiphytic macrolichen species from boreal and montane forests would likely have repercussions on forest functions such as water retention, cycling of carbon, nitrogen and phosphorous, and the provision of wildlife habitat (Berryman and McCune [2006], and sources therein). Therefore, the potential for lichen species decline implies direct consequences for other forest processes.

Under future emissions scenarios leading to warming (+0.5, +1.0, +2.5, +3.6 °C), the greatest increases in thermal vulnerability were concentrated in lichen communities of the U.S. Southeast, Southwest, California and the Intermountain West. Under pessimistic emissions scenarios (+3.6 °C), we found that a large fraction (nearly one-fifth) of all U.S. lichen communities could lose half their current lichen species by the late-21st century, based on exceedances of upper thermal tolerances. A similar proportion of lichen communities had positive thermal deviation, meaning that local warm-season temperatures are expected to exceed the average upper thermal tolerances of these communities by the end of the century. Taken together, these findings suggest that multiple strategies for stabilizing greenhouse gas concentrations (e.g., emissions reductions, afforestation, shifts to renewable energy; Pacala and Socolow 2004) could, in part, help address the warming-related decline of forest diversity over broad areas of the United States.

Resource managers and policy makers need a rapid way to score sites according to climate change extinction risks. Ideally, such a method would avoid the burden of specifying each species' demography or assumed climate response traits (Pacifici et al. 2015). Our approach

was to model species responses individualistically (as nonparametric cumulative distribution functions of niches) and simultaneously (as collective thermal vulnerability indices for each site). This approach differs from most other ecological response approaches by modeling species occurrence probabilities via cumulative distribution functions, rather than regression functions. Cumulative distribution functions realistically portray 'solid' response curves where many zero or low-abundance values can occur even at a species' optimum on one niche axis due to constraints on other, possibly unobserved niche axes (Whittaker 1967; McCune and Grace 2002). In the process of estimating species niches this way, we found subtle but important effects of extending niche coverage to avoid truncation. Correcting for niche truncation lowered the perceived degree of vulnerability in this study and others (Feeley and Silman 2010), leading to more realistic vulnerability estimates. An ongoing challenge remains to account for novel climate combinations not yet observed in realized ranges.

Thermal vulnerability indices show the degree to which climate changes will impinge on species tolerances to affect community-level outcomes. Sensitivity analysis found that our thermal vulnerability indices were largely robust to moderate uncertainty in climate data, which could otherwise lead to spurious conclusions about community climate-change responses (Rodríguez-Sánchez et al. 2012). Like other niche-based methods, our approach assumes that species' realized niches are indicative of potentially habitable climate space (Peterson et al. 2011). We explored the effects of climatic warming in removing species from local populations, but future modifications might also incorporate other ecological processes that may remove species, such as competitive selection or ecological drift, or processes that can introduce species, like immigration or speciation (Vellend 2016). These modifications would permit more precise forecasting of future forest conditions.

The consensus view is that epiphytic lichen communities are excellent bioindicators of both air quality and climate in forests (McMurray et al. 2015). Yet the question remains whether lichens will be more sensitive to climate change than other kinds of vegetation. Rapid population turnover in lichens (Larsson and Gauslaa 2011) suggests that climate-related responses could manifest in lichen communities before longer-lived vegetation such as trees. Our TVI approach could be used for relative comparisons of climate change vulnerability

among different groups of organisms with contrasting life histories (e.g., trees vs understory vs epiphytic vegetation) that could respond at different rates over time. We speculate that forest trees, understory plants, and epiphytic lichens (in that order) would be increasingly vulnerable because of different population growth-rates and life histories.

In conclusion, niche-based climate change vulnerability indices are useful tools for scoring whole communities (sites), specific habitats, and geographic regions according to the joint vulnerability of all species present. Environmental constraints limit species membership in ecological communities, and are central to predicting diversity changes. Among epiphytic forest macrolichen communities of the United States, thermal constraints in current and future climate scenarios appear to limit species membership in low-elevation and southern locations, though high-elevation and northern locations are anything but exempt. Vulnerability analyses are one avenue toward helping anticipate how the strength of climate selection may change over time.

Acknowledgements

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Tables

Table 4.1. Summaries of fifteen climate variables used to construct "extended" niches for North American macrolichen species. Also included are latitude and longitude. Climate data (from ClimateNA database) was extracted for each location in the herbarium data (from the Consortium of North American Lichen Herbaria). Locations included the entirety of Canada, United States and Mexico.

Abbreviation	Variable	Lower	Upper	Mean	*SD*	*CV* (%)	Skewness	Kurtosis
lat	Latitude (°)	15.4	82.4	42.9	8.5	19.8	0.30	0.86
lon	Longitude (°)	−177.9	−52.6	−99.0	21.0	21.2	−0.62	0.19
mat	Mean annual temperature (°C)	−20.6	29.4	8.5	6.2	73.0	0.1	0.4
mwmt	Mean warmest-month temperature (°C)	0.5	35.7	19.8	4.6	23.0	0.1	−0.5
mcmt	Mean coldest-month temperature (°C)	−37.7	28.1	−3.1	9.0	289.9	−0.1	−0.1
td	Continentality (°C)	1.2	47.1	22.9	7.3	31.9	−0.1	−0.3
map	Mean annual precipitation (mm)	50.0	7823.0	1075.5	612.0	56.9	2.3	9.3
msp	Mean summer precipitation (mm)	3.0	2895.0	438.6	209.8	47.8	1.1	7.3
ahm	Annual heat moisture index (unitless)	−119.9	642.0	21.7	21.6	99.5	10.2	165.6
shm	Summer heat moisture index (unitless)	2.6	9389.6	88.8	228.4	257.2	11.1	203.1
ffp	Frost-free period (d)	0.0	365.0	163.7	68.1	41.6	1.0	0.6
pas	Precipitation as snow (mm)	0.0	5052.0	156.5	207.9	132.9	4.4	43.9
emt	30-y extreme minimum temperature (°C)	−64.2	21.8	−29.0	11.2	38.8	0.5	−0.2
ext	30-y extreme maximum temperature (°C)	16.0	51.3	36.5	3.9	10.7	−0.6	0.6
eref	Reference evaporation (mm)	29.0	2249.0	851.6	338.0	39.7	0.6	−0.3
cmd	Climatic moisture deficit (mm)	0.0	1827.0	253.8	250.6	98.7	2.1	5.2
rh	Mean annual relative humidity (%)	39.0	87.0	61.8	6.5	10.5	0.4	0.7
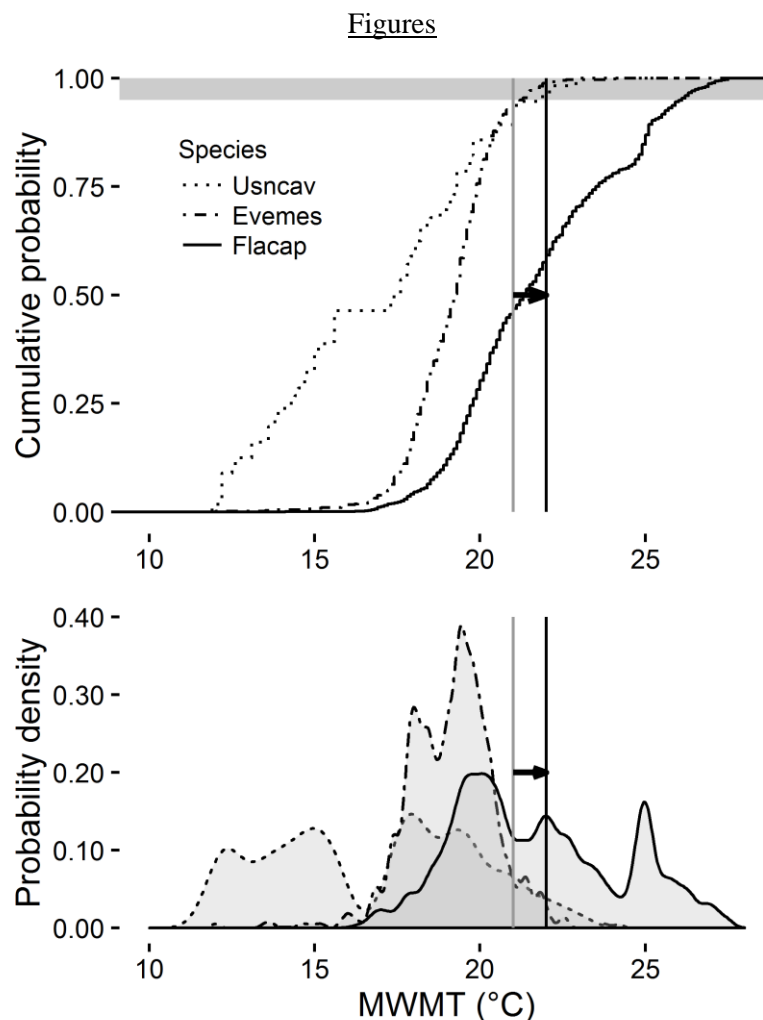
Figures

Figure 4.1. Hypothetical example of species niches and community thermal vulnerability. Imagine an example lichen community at MWMT = 21 °C containing species *Usnea cavernosa*, *Evernia mesomorpha* and *Flavoparmelia caperata*. Curves give each species' realized niche as an empirical cumulative distribution function (ECDF, top panel) or a 'solid' probability density function (PDF, bottom panel). The PDF here is the observed proportion of plots with the species present across the temperature gradient, while the ECDF is the area under the PDF curve. A single species is "vulnerable" wherever it occurs at the limits of upper thermal tolerance beyond its 95th percentile (grey band in top panel). For example, the site with MWMT = 21 °C (grey vertical line) is just below the 95th percentile of two of these three species. Therefore, incremental warming to a new temperature (22 °C, black line) could either lead to local extinctions of cold-tolerant species (*Usnea* and *Evernia*), or no change for warm-tolerant species (*Flavoparmelia*). Thermal vulnerability indices (TVIs) are community-level measures that account for such potential species losses under warming climates.

Truncated **Extended**
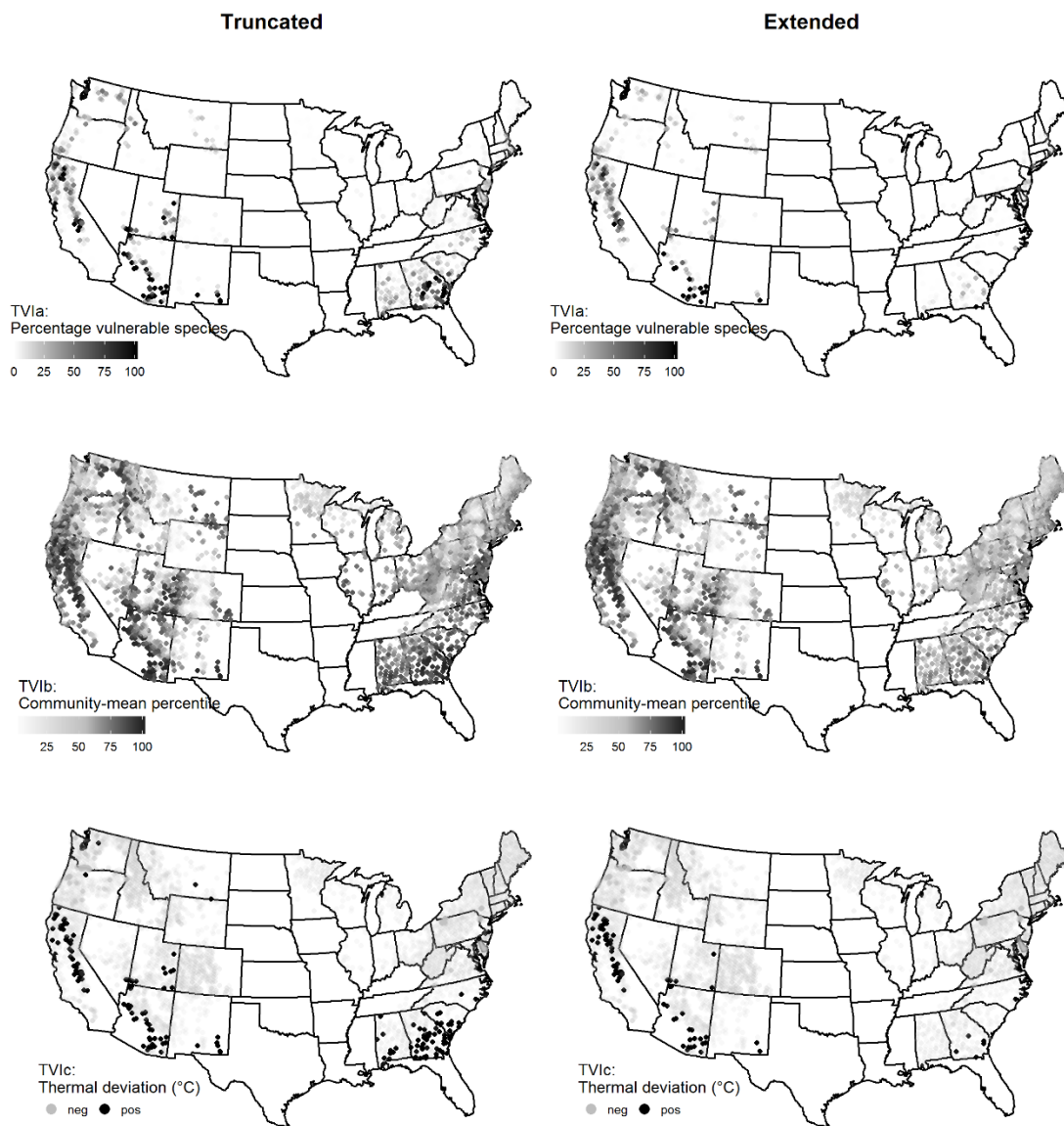
Figure 4.2. Niche coverage effects on thermal vulnerability of U.S. lichen communities.
Truncated niches (left column) and extended niches (right column) were used to estimate TVI values at 6,474 FIA lichen community sites. Extended niches more completely characterized the true realized niche, particularly of warm-tolerant species, leading to apparently lower thermal vulnerability in some locations like the Southeast. Thermal vulnerability by any TVI measure was consistently greatest in northern and central California, in the Southwest along the western Colorado Plateau, and to a lesser degree on the Southeastern coastal plain. Alaska not shown for brevity. Each point is a lichen plot from the Forest Inventory and Analysis program.

Figure 4.3. Thermal niche breadths of epiphytic macrolichen species in the western United States. Each species' thermal niche (each line segment) depicted across mean warmest month temperature (MWMT, °C). These are "extended" niches based on herbarium data from Canada, United States and Mexico. Generalists have wider segments, specialists more narrow.
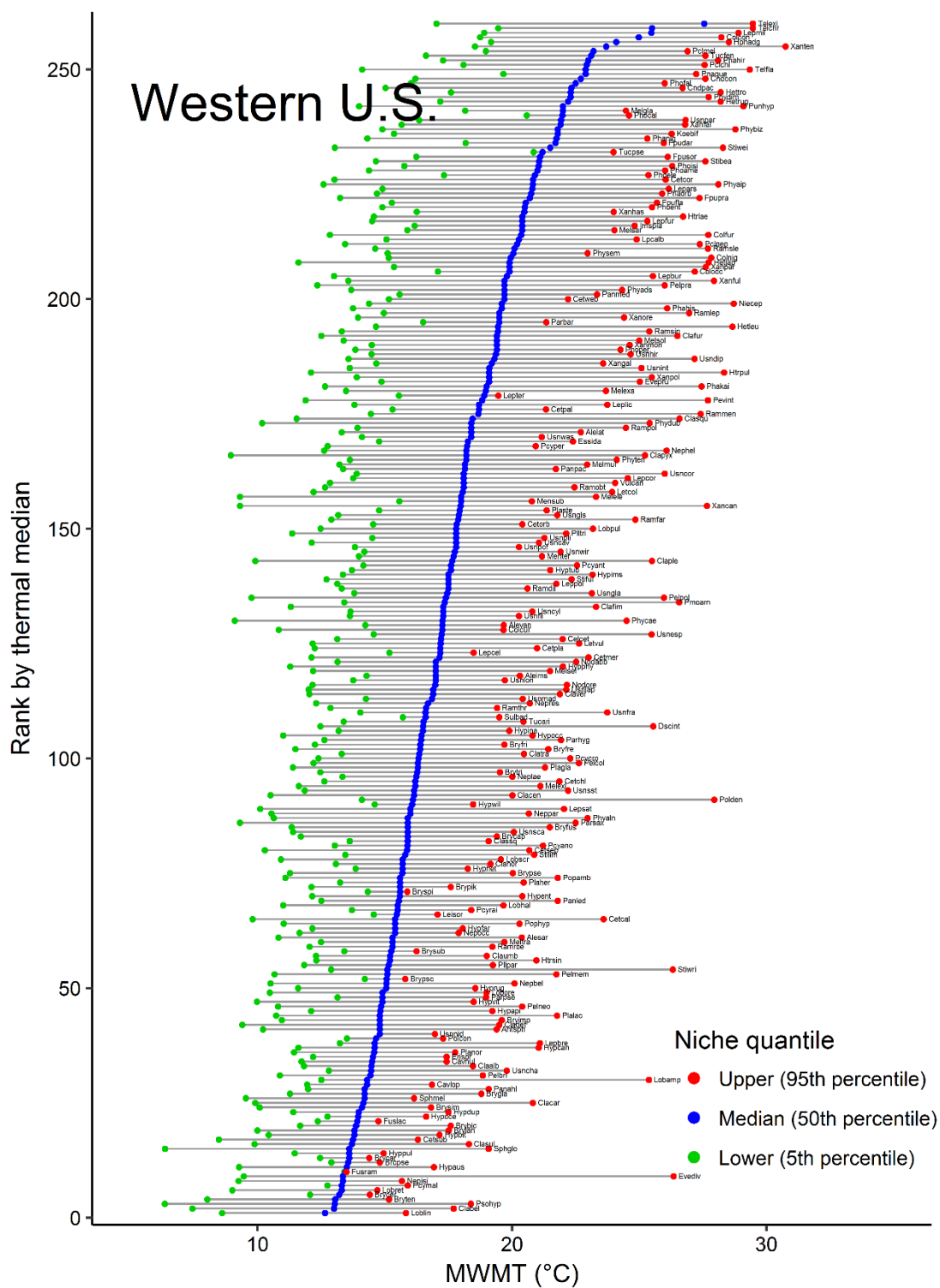
Figure 4.3. Thermal niche breadths of epiphytic macrolichen species in the western United States.

Figure 4.4. Thermal niche breadths of epiphytic macrolichen species in the eastern United States. Each species' thermal niche (each line segment) depicted across mean warmest month temperature (MWMT, °C). These are "extended" niches based on herbarium data from Canada, United States and Mexico. Generalists have wider segments, specialists more narrow.

Figure 4.4. Thermal niche breadths of epiphytic macrolichen species in the eastern United States.
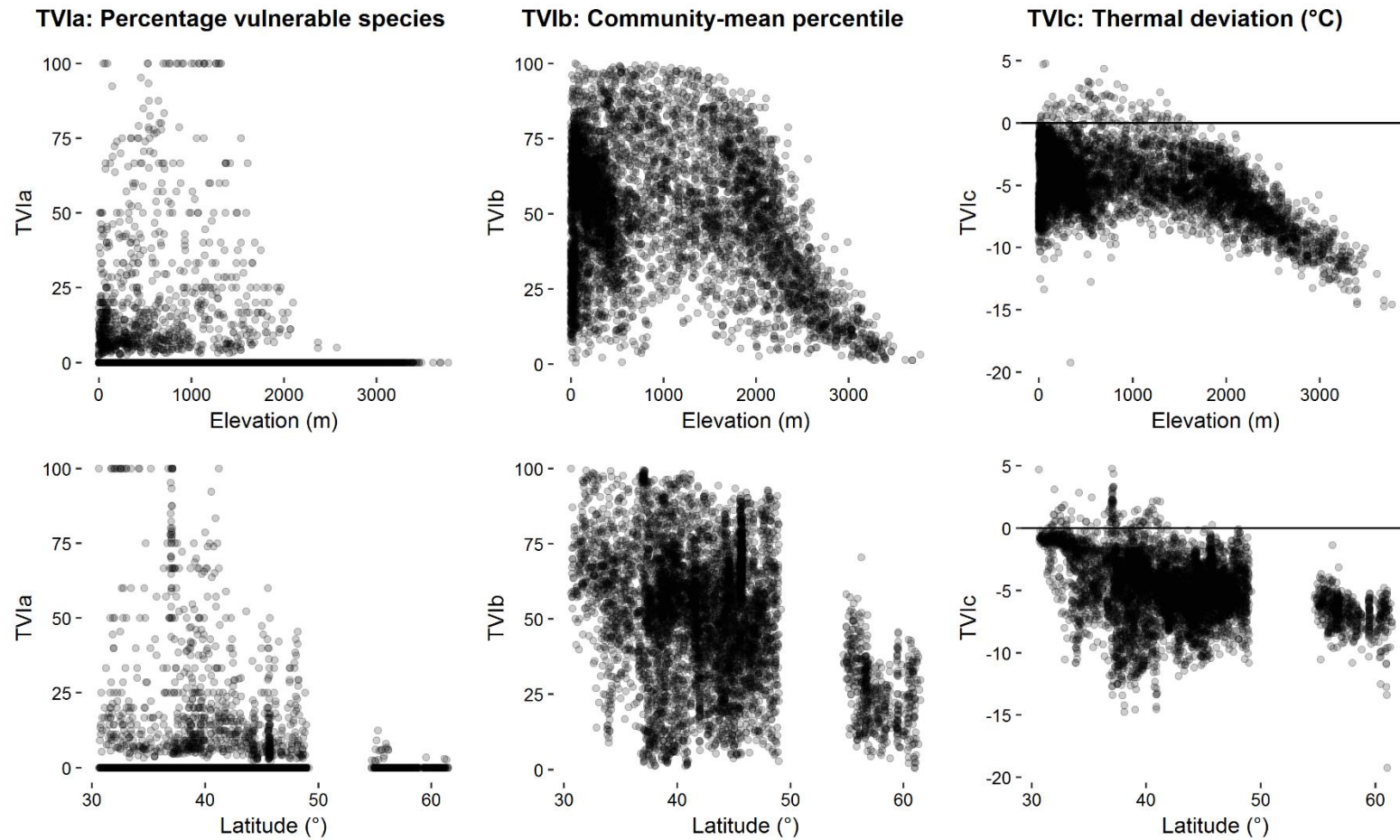
Figure 4.5. Thermal vulnerability of U.S. lichen communities across elevations and latitudes. All TVIs were greatest at low-elevation sites (top row) and southerly latitudes (bottom row). The latitude gap is Canada between continental U.S. and Alaska. Each point is a lichen plot from the Forest Inventory and Analysis program.
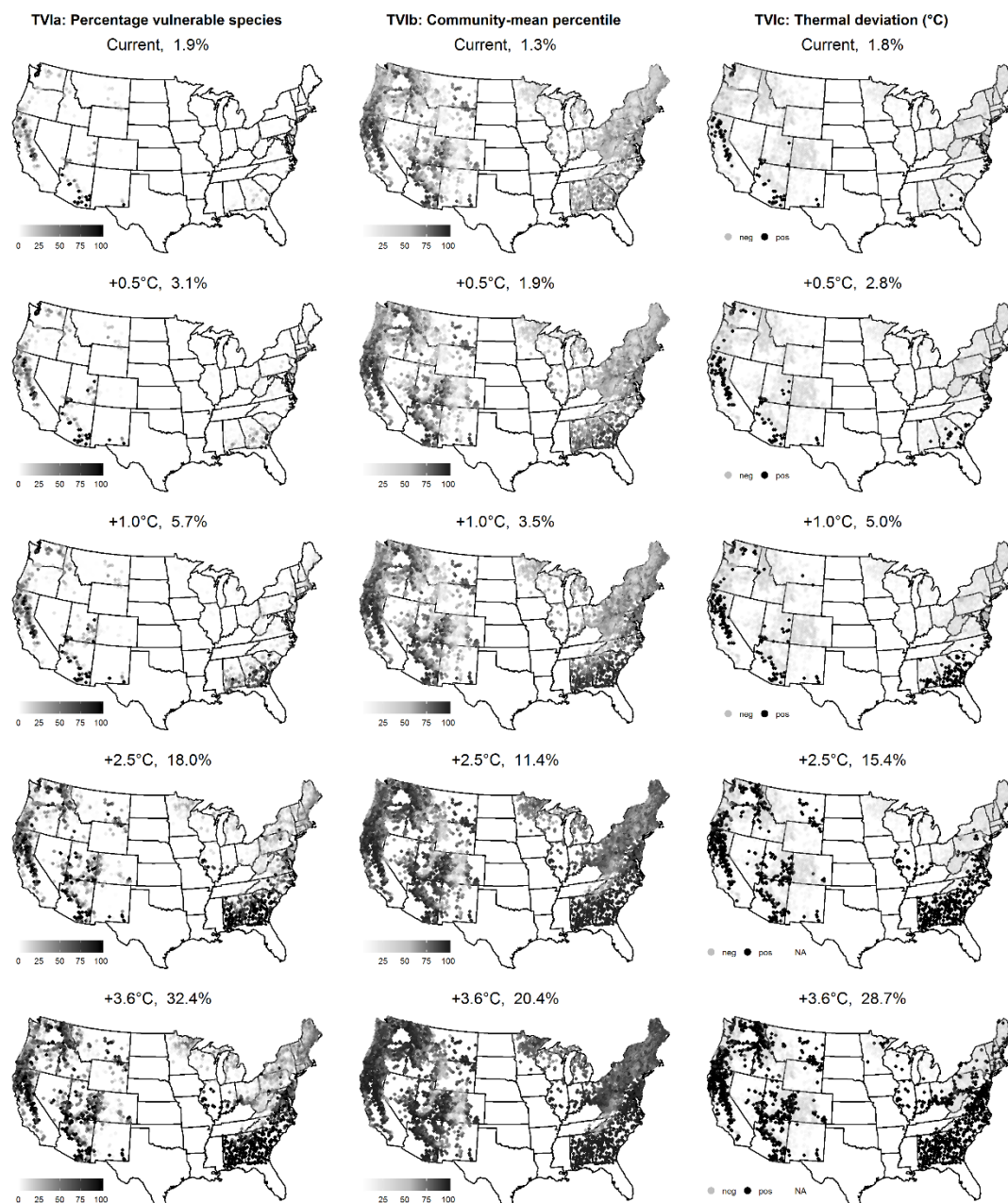
Figure 4.6. Warming effects on thermal vulnerability of U.S. lichen communities. Four warming scenarios (+0.5, +1.0, +2.5, +3.6 °C) were compared to the contemporary baseline. Percentages are the number of 6,474 sites identified as "very vulnerable" communities exceeding critical values (more than half of all species vulnerable = *TVIa* ≥ 50%; community-mean thermal percentile extremely high = *TVIb* ≥ 95%; positive thermal deviation = *TVIc* ≥ 0 °C). Alaska not shown for brevity. Each point is a lichen plot from the Forest Inventory and Analysis program.
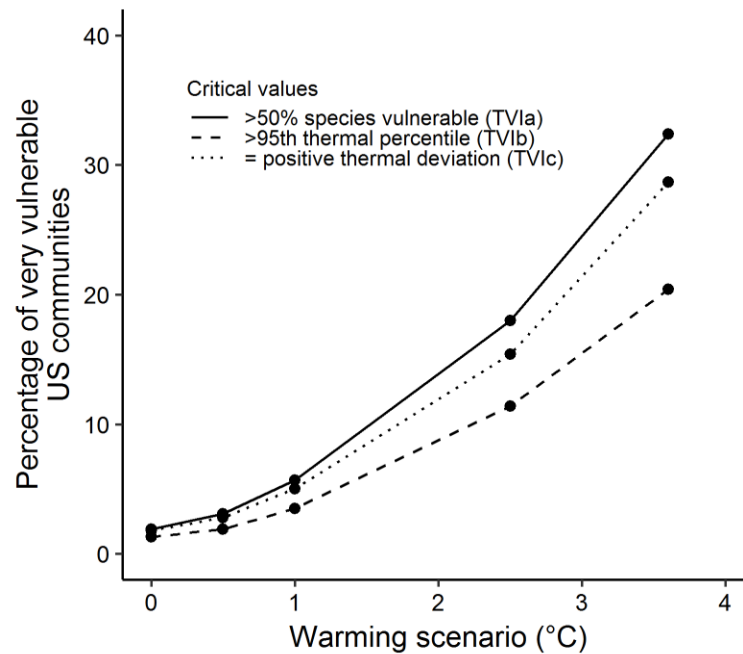
Figure 4.7. Percentage of very vulnerable U.S. lichen communities exceeding thermal safety margins. Percentages are the number of 6,474 sites identified as very vulnerable communities exceeding critical values. Critical values were defined as: more than half of all species vulnerable = *TVIa* ≥ 50%; community-mean thermal percentile extremely high = *TVIb* ≥ 95%; positive thermal deviation = *TVIc* ≥ 0 °C. Warming scenario data originated from ClimateNA (Wang et al. 2016) based on IPCC (2014) emissions scenarios.

CHAPTER 5. DECLINE OF THE BOREAL LICHEN *EVERNIA MESOMORPHA* OVER
ONE YEAR OF WHOLE-ECOSYSTEM CLIMATE CHANGES

Robert J. Smith, Peter R. Nelson, Sarah Jovan, Paul J. Hanson, and Bruce McCune

Abstract

Climatic changes promise to affect the abundance and distribution of global vegetation. Boreal forests are of particular interest because of biophysical feedbacks to global climate, and because changes in diversity will have consequences for the conservation and utilization of forest resources. Bioindicators such as lichens could provide early warning of biological responses to climate changes. We evaluated individual growth performance of the epiphytic lichen *Evernia mesomorpha* in the first year of a decade-long experiment featuring whole-ecosystem warming, drying and CO_2 addition. Field experimental enclosures were located near the southern edge of that species' range. Mean annual biomass growth of *Evernia* significantly declined 4 percentage points for every $+1°C$ of experimental warming. Mean annual biomass growth was 14% in ambient treatments, 2% in unheated control treatments, and -9% to -19% (decreases) in energy-added treatments ranging from $+2.25$ to $+9.00°C$ above ambient. Contrary to expectations, CO_2 addition did not initially boost lichen growth rates. There may be a lag between performance decreases and eventual population declines because moribund individuals observed in energy-added treatments remained structurally intact, at least temporarily. Experimental treatments induced lower relative humidity than ambient conditions, creating climatic conditions similar to the U.S. Great Plains. Our findings suggest that future warming and drying would decrease or eliminate *Evernia* biomass accumulation at its southern range margins, with consequences for the maintenance of local and regional populations. Local extinctions of epiphytes would have broader implications not only for biodiversity but also for net carbon accumulation and nutrient mobilization.

Introduction

A growing consensus is illuminating the effects of future climatic changes on the world's northern forests. Rising temperatures, moisture changes and increasing CO_2 concentrations will alter processes that determine the growth and composition of forest vegetation (Hyvönen et al. 2007). Climate-driven shifts in vegetation composition are well illustrated by epiphytic lichens, which are fungus–photobiont composite organisms that are directly exposed to fluctuations in atmospheric conditions. In recent decades, temperate and subtropical lichen species have invaded warming habitats, while cold-adapted arctic and boreal species receded to local extinction (Aptroot and van Herk 2007; Hauck 2009; Evju and Bruteig 2013).

Likewise, lichen species not adapted to drying climates can also disappear over just a few decades (Follmann 1995). The apparent climatic dependency of epiphytic lichens stems from their direct physiological reliance on atmospheric temperatures, moisture and nutrients without recourse to soil reserves. Therefore, changes in climate could impact the growth performance and population dynamics of epiphytic lichen species, especially those adapted to cool, boreal forest habitats.

Global changes in boreal forests are expected as a mixture of factors (including warming, drying and increased CO_2 concentrations) which may have interacting or counteracting effects on vegetation growth and carbon exchange. Warming and drying are hypothesized to cause performance declines of lichens through multiple mechanisms, which include photorespiratory carbon losses (Palmqvist 2000), chlorophyll degradation (Pisani et al. 2007), oxidative membrane damage (Kranner et al. 2008), and increased heterotrophic decomposition (Caldiz et al. 2007). These can kill individuals and eventually lead to demographic collapses and changes in species relative abundances, favoring drought-tolerant and temperate species at the expense of cold-adapted boreal species. Alternatively, increasing CO_2 concentrations could promote lichen growth (Huebert et al. 1985) or not (Balaguer et al. 1999), depending on the supply of sufficient light and moisture. Knowing the magnitude of changes required to elicit such responses requires an integrated experimental approach.

Here we focus on the climate responses of one species of epiphytic lichenized fungi in the initial year of a 10-year, whole-ecosystem climate change experiment. The purpose of the SPRUCE experiment ("Spruce and Peatland Responses Under Climatic and Environmental change") is to evaluate responses of northern peatland ecosystems to whole-ecosystem warming, drying and atmospheric CO_2 addition (ORNL 2017). Peatlands at the SPRUCE site are important to ecosystem climate science because large stocks of terrestrial carbon could mobilize as greenhouse gases CO_2 and CH_4. Its location at the southern edge of the Western Hemisphere's boreal forest provides potential insight into drivers of ecosystem transitions. While our inferences are site-specific, the experiment also opens the door to understanding how local responses of indicator species might scale to entire landscapes across the Midwest region.

Our objective was to determine how growth of an epiphytic lichen species would respond to experimental whole-ecosystem warming, drying and CO_2 addition at the local level. We measured responses from in-situ lichen communities and transplants of a boreal lichen species, *Evernia mesomorpha* ("*Evernia*" hereafter), at the southern edge of its range. This is a fruticose (shrubby) lichen species that has a single point of attachment to the substrate, making it conducive for use as a transplant to assess growth. Its geographic distribution is very similar to the iconic boreal forest tree *Picea mariana* (black spruce), and it can be interpreted as indicative of North American boreal forests. Here we report on the growth measurements while a follow-up article will report on whole-community effects. For our target species *Evernia*, we hypothesized that concurrent warming and drying would reduce lichen growth rates (due to departure from photosynthetically optimal combinations of temperature and moisture), while CO_2 additions would increase lichen growth (due to greater photosynthetic efficiency at high CO_2 concentrations). This work provides the basis for ecological forecasting of climate-related effects on the focal species.

Materials and methods

Experimental site description

The SPRUCE experimental site is an 8.1-ha ombrotrophic *Picea-Sphagnum* peat bog located at Marcell Experimental Forest in northern Minnesota (47.5057, −93.4534; 418 m a.s.l.). Organic peat deposits averaging 2.5 m lay atop postglacial ancient lakebed sediments (Sebestyen et al. 2011) in a landscape of rolling uplands, lakes and low-lying peatlands. The climate is subhumid continental. At Marcell Experimental Forest over the period 1961–2005, mean annual air temperature was 3.3°C (daily mean extremes −38°C and 30°C), with 768 mm of mean annual precipitation falling mostly as warm-season rain. Mean annual air temperatures have increased about 0.4°C per decade over the last 40 years, mostly due to winter increases of about 0.6°C per decade (Sebestyen et al. 2011). Trees in the bog are *Picea mariana* and *Larix laricina* about 5–8 m tall, which have begun to regenerate nearly 50 years after two strip-cut harvests in 1969 and 1974 (Verry and Elling 1978). Hardwoods, *Populus tremuloides* and *Betula papyrifera,* circle the bog margins. Understory vegetation includes *Sphagnum* mosses (*Sphagnum angustifolium, S. capillifolium, S. magellanicum*), true mosses (*Aulacomnium palustre, Pleurozium schreberi, Polytrichum juniperinum*),

ericaceous shrubs (*Rhododendron groenlandicum, Chamaedaphne calyculata, Andromeda polifolia* var. *glaucophylla*) and graminoids (*Carex trisperma, Eriophorum spissum*) (Hanson et al. 2012).

Experimental treatments

The SPRUCE experiment consisted of twelve experimental plots distributed along a permanent boardwalk, including ten 8-m tall, open-topped enclosures (Fig. 5.1a). Each plot was an unreplicated treatment unit randomly assigned to one of twelve different treatments. Treatments consisted of six levels of warming via energy addition (ambient, enclosed controls, +2.25, +4.50, +6.75, and +9.00°C) factorially crossed with two CO_2 levels (ambient at 450 ppm vs enriched at ~900 ppm). All treatments were maintained year-round. Ambient plots had no enclosures and no energy added. Control plots also had no energy added, but had full enclosures (structural walls, transparent sheathing, ductwork) installed to assess infrastructure effects. Remaining enclosures had energy added relative to the control plots, with heated air circulated by fans and by underground heaters embedded in the peat layer (Hanson et al. 2017). Construction of the whole-ecosystem experiment was incremental. In summer of 2013, boardwalks, plumbing and hydrologic skirts were installed for underground deep peat heating, which began in summer 2014 but did not immediately affect air temperatures (Hanson et al. 2017). Enclosure panels were installed in April 2015, and circulating fans began 24-h operation in July 2015. On 12 Aug 2015, air warming treatments began – this date is the initiation point ('time zero') for determining warming and drying treatment effects resulting from energy addition. On 16 June 2016, CO_2 addition began. We recorded responses of epiphytic lichens by measuring single-species biomass over each of the two years preceding climate treatments (2013–14 and 2014–2015 periods), as well as one year after treatments (2015–2016 period). Lichen measurements took place each mid-August from 2013 through 2016.

Lichen measurements

In 2013, we installed 320 *Evernia* lichen transplants on *Picea mariana* branches in the plots, 27 per plot (Figs. 5.1a and 5.1b). In a separate forthcoming study to be reported elsewhere, we also monitored all lichen species in permanent community transects for assessing community changes. After gathering healthy *Evernia* thalli from the same bog (but outside

the boundary of the experiment), we attached them to monofilament line with silicone caulk (McCune et al. 1996). These apparatus materials were inert and did not change over time in preliminary trials. We fixed transplants with removable nylon cable ties to living *Picea* branches 1.5–2.2 m above boardwalks (Fig. 5.1b), while avoiding dense foliage on younger twigs, avoiding other experimental equipment, and randomizing locations each year among multiple trees within each plot. Every August 2013–2016, we temporarily removed transplants, transported them within 2 h to a controlled-environment laboratory, and equilibrated them for 24 h at 20°C and ambient relative humidity before weighing with an analytical balance (precision $\pm$ 0.0001 g). To account for potential bias caused by relative humidity fluctuations during weighing, we used the sacrificial method (McCune et al. 1996) in which out-of-sample *Evernia* thalli were collected from nearby, maintained at identical humidity side-by-side with in-sample thalli, and weighed both before and immediately after oven-drying for 1.5 h at 60°C. The air-dried masses of in-sample thalli (minus the mass of the inert apparatus) were multiplied by the ratio of oven-dried to air-dried sacrificial thalli to yield corrected mass. Sacrificial masses remained steady throughout each weighing period, within 0.0005 g of the mean, indicating only minor fluctuations. Annual biomass growth was calculated as percentage change in dry mass following Eq. 4 in McCune et al. (1996).

Statistical models

All analyses were performed in R version 3.3.1 (R Development Core Team 2016). For the temperature variable in all analyses, we used the actual observed annual mean temperature differentials in each plot (relative to ambient) because actual temperature increases differed slightly from targets. We determined the proportion of transplants that were lost, visibly fragmented or not recorded in all four annual sampling events, and excluded these from further analyses. We also excluded any individuals with annual biomass losses greater than 2.5 standard deviations below each treatment mean because such drastic changes were likely due to unseen fragmentation rather than climate-related growth declines (only seven individuals met this criterion). For each of the three sampling periods (two pre-treatment and one post-treatment), we then used a fixed-effects linear model to test the null hypothesis of no difference in mean annual biomass growth among climate treatments:

$$Y_i = \beta_0 + \beta_1 T_i + \beta_2 C_i + \beta_3 (T*C)_i + \varepsilon_i$$

where:

Y_i is the average annual biomass growth rate of transplants in plot i over a one-year

         sampling period,

β_0 is the mean annual biomass growth rate at ambient temperatures and $[CO_2] = 0$ ppm,

β_1 is the incremental effect of a 1°C increase in warming on the mean annual biomass

         growth rate,

β_2 is the incremental effect of a 1 ppm increase in $[CO_2]$ on the mean annual biomass

         growth rate,

β_3 is the further incremental effect of both a 1°C increase in warming and a 1 ppm

         increase in $[CO_2]$ on the mean annual biomass growth rate,

T_i is the amount of warming (°C) in plot i,

C_i is the amount of $[CO_2]$ (ppm) in plot i,

ε_i is the random error term for the ith plot and $\varepsilon_i \sim N(0,\sigma^2)$ and ε_i and $\varepsilon_{i'}$ are independent.

Each of the three models were fit using the base function 'lm' in R version 3.3.1 (R Development Core Team 2016). After model fitting, we checked the assumptions that errors were symmetrically distributed by inspecting a QQ plot and a plot of the model residuals vs. fitted values. Upon verifying that assumptions were reasonably met, we performed an *F*-test of the null hypothesis that the interaction and main-effect coefficients did not differ from zero.

Representativeness of climate treatments

We examined how actual conditions in the SPRUCE experiment corresponded to current and potential future climates across the central U.S. and Canada. First, we quantified actual conditions in each SPRUCE plot as the annual mean differentials of relative humidity and temperature (relative to ambient) based on half-hourly measurements taken at 2 m above the bog surface. This effectively gave the climate conditions that lichens actually experienced, rather than assuming target values. We compared these with values extracted from the ClimateNA database (Wang et al. 2016) for central U.S. and Canada sites. Current-day values from the database were 30-year normals (1981–2010). Potential future values were from a pessimistic ensemble model scenario (CMIP5-RCP8.5) that assumed emissions would

increase through the 21st century until 2085 (IPCC 2014). We selected the pessimistic scenario only for illustration purposes, without making claims about the chances of its actually occurring. We then determined which geographic locations were similar to the unique combinations of temperature and relative humidity that lichens actually experienced in each SPRUCE plot.

<div align="center">Results</div>

Overall, we found that one year of experimental whole-ecosystem warming and drying caused significant biomass losses of a boreal epiphytic lichen species, but two months of CO_2 addition had no significant effect. Of 322 original *Evernia* transplants, 280 remained three years later (13% loss). Transplants in ambient treatments (Fig. 5.1c) were green and healthy as before treatments, but transplants in all energy-added plots were visibly tan and chlorotic (Fig. 5.1d). For each pre-treatment period *prior to* experimental energy additions, mean annual biomass growth did not significantly differ among treatment plots (Table 5.1; Fig. 5.2a,b). Specifically, growth declined (mean −31.5%, sample standard deviation ± 15.8%; Fig. 5.2a) in the first annual period pre-treatment across all plots, which corresponded to very harsh winter conditions (ORNL 2017). Moderate positive growth in the second annual period pre-treatment (15.3% ± 17.8%; Fig. 5.2b) corresponded to milder winter conditions.

After one year of applied warming and drying, mean annual biomass growth significantly decreased 4.1 percentage points (95% CI: −6.4 to −1.9 percentage points) for every 1°C increase after accounting for CO_2 concentration (Table 5.1; Fig. 5.2c). Specifically, mean annual growth rates progressively declined from 14% in ambient treatments, to 2% in control treatments with no energy added, to a range of −9% to −19% (decreases) across energy-added treatments (Table 5.2). There was no significant effect of CO_2 addition on mean annual biomass growth (Table 5.1). Actual temperature differentials differed slightly from targets (Table 5.2).

Based on local measurements, ambient plots and enclosed control plots had temperatures, precipitation inputs, and relative humidity conditions that were quantitatively similar to other locations along the southern edge of the North American boreal coniferous forest. As expected, the energy-added treatments had warmer temperatures and reduced relative

humidity when compared to ambient conditions. The representativeness analysis revealed that these treatments represented current modern conditions at semi-arid locations trending southwesterly across the western Great Plains toward the Rocky Mountain Front (Fig. 5.3). Such trends were similar for projected future climates given IPCC (2014) emissions scenarios. Energy-added treatments represented realistic potential future warming (projected 5.9 °C increase) expected for the SPRUCE site in the year 2085. The treatments had a less distinct match to potential changes in average relative humidity (projected 3 percentage-point increase), although average moisture changes are also expected to be accompanied by a larger range of variability at the northern Minnesota SPRUCE site based on comparison to forecast data (IPCC 2014; Dunn et al. 2017).

<div align="center">Discussion</div>

Anticipating future ecological changes requires knowing the magnitude of climatic changes required to affect individual growth, population demographics and species membership in local communities. Here, we identified the short-term effects of warming, drying and CO_2 addition on growth of the boreal lichen species *Evernia mesomorpha* at a northern Minnesota peat bog, finding significant growth decreases as warming increased. Observed annual biomass growth (+14%) in ambient treatments corresponded very well with *Evernia* growth in unharvested boreal forests in western Quebec, Canada (Boudreault et al. 2013). Significant observed biomass decreases (−9% to −19%) in our energy-added treatments suggest that future warming and drying beyond the historical range of variability could pose a challenge to the maintenance of populations at this location.

Our finding of no CO_2 effect on growth was initially surprising, given prior evidence that net photosynthesis of *Evernia mesomorpha* increases monotonically with CO_2 concentrations in the range of 100–460 ppm when moisture and light are not limiting (Huebert et al. 1985). However, no CO_2 fertilization effect would be expected if atmospheric carbon were not the most limiting resource in lichen photosynthesis. For example, moisture limitation could decrease photosynthetic efficiency (Huebert et al. 1985). It is also possible that CO_2 fertilization effects would require more time to develop. In any case, increasing CO_2 concentrations in the future may not be enough to offset biomass losses caused by warmer and drier climates.

The amount and timing of moisture availability should have strong effects on *Evernia* metabolism. Pearson (1969) considered *Evernia mesomorpha* a moisture indicator species requiring alternating wet–dry cycles, implying that prolonged dry (or prolonged wet) periods are detrimental. Warming in the SPRUCE experiment was accompanied by proportional decreases in relative humidity as a product of the experimental design, which precluded dew formation by limiting energy loss to the sky (Fig. 5.4; Hanson et al. 2017). Protracted lack of dew in future climates would be a challenge to lichen populations because it could severely impact photosynthesis and biomass accumulation of poikilohydric organisms that rely explicitly on dew and humid air as sources of moisture instead of liquid rain (Gauslaa 2014).

Identifying whether warming or drying had the greater unique effect on lichen growth was not easy to determine since we applied both simultaneously. While this may hinder forecasts based on either atmospheric warming or moisture reductions alone, it nevertheless increases our predictive ability to account for the joint influence of these two factors. Moisture reductions ranging from mild to drastic are projected for the U.S. Midwest region given plausible carbon emissions scenarios (Dunn et al. 2017). Our energy-added treatments were representative of existing thermal and moisture combinations currently found in semi-arid portions of the U.S., which are indicative of the kinds of future climates that lichens might realistically experience. If moisture is regarded as the sole factor of interest, future experiments could explicitly isolate its effects by misting or humidifying enclosures.

Could lichens in nature acclimate to warming air temperatures? Some species demonstrate seasonal acclimation of photosynthesis (Lange and Green 2005), but until now we have possessed scant information on how lichen growth may respond to extended periods at high temperatures well beyond photosynthetic optima. For *Evernia mesomorpha*, the estimated photosynthetic optimum is near 15°C, above which net photosynthesis quickly declines (Huebert et al. 1985). Summer daily means at SPRUCE rarely exceeded 20°C in ambient treatments, but summer daily means in energy-added treatments rarely ever fell *below* 20°C (Hanson et al. 2017). The rapid onset of energy additions in our experiment could prohibit any acclimation responses that might be possible with more gradual rates. Even given gradual rates of warming, lichen species similar to *Evernia mesomorpha* may not possess the

upper thermal tolerance necessary to maintain positive carbon balance, and could therefore become locally extinct.

Local extinctions at southern margins would shrink the range sizes of boreal lichens unless compensated by expansion elsewhere. Yet we do not know enough about dispersal and colonization probabilities to accurately predict how fast migration could happen. For *Evernia mesomorpha*, rates of colonization may be limited by dispersal and by the ecophysiological tolerances of the algal photobiont partner (Piercey-Normore 2006). Average colonization rate of the closely-related congener *Evernia prunastri* was approximately 30 m y^{-1}, with fewer than 1% of diaspores dispersing over 100 m y^{-1} (Tapper 1976), although rare long-distance dispersal events could permit range expansion. Considering rates of dispersal, colonization, and extinction across environmental gradients will help in building process-based species distribution models (Evans et al. 2016) and for accurately forecasting future range shifts due to any climatic changes.

The apparent population- and community-level effects of warming and drying may lag well behind their proximal causes. Our observation that individual thalli persisted on *Picea* branches despite clearly negative growth rates suggests that individuals may remain structurally intact (at least temporarily) even while they are functionally moribund. The lag between the physiological decline of individuals and their eventual disappearance suggests the possibility of an extinction debt, wherein some species may be committed to local extinction even as individuals persist (Öckinger and Nilsson 2010). Lichen thalli may die yet remain intact on tree branches for several months to years if decomposition and mechanical disturbances are slow. Aside from direct climate effects, future interactions with host trees and other lichens may change lichen communities in non-intuitive ways. For example, foliage loss (from drought-stressed host trees) or foliage gains (from increased tree vigor) would alter sub-canopy light availability that could differentially affect lichen species based on differing light tolerances. Therefore, outcomes depend not only on abiotic conditions, but also on biotic processes mediated by light-tolerance and other evolved traits. Continued monitoring of single species and communities over the next decade will reveal outcomes of biotic interactions as the SPRUCE experiment proceeds.

The next challenge will be to model expectations for focal species and for many species together across large landscapes. Regional gradient analyses and correlative niche modeling will be an initial step, but could go farther. First, distribution models and forecast models could include the effects of disturbances and climate-related amplification of Midwest fire regimes (Clark 1990) that could eliminate habitat. Second, we need to quantify performance across experimental and natural gradients in terms of physiological responses (e.g., photosynthesis, secondary metabolite production) and demographic measures (change in establishment, growth, survival, fecundity). Using these performance measures as inputs to process-based models for multiple species (Evans et al. 2016) will improve upon existing correlative niche models. Novel combinations of experimentation and modeling will help link local responses to landscape levels, and will allow forecasts of range shifts in forest species vulnerable to warming and drying trends.

Acknowledgements

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Tables

Table 5.1. Summary of statistical tests for mean annual biomass growth rates of *Evernia mesomorpha* at the SPRUCE experiment in Minnesota. Models involve *F*-tests of coefficients in three linear models testing effects of whole-ecosystem warming/drying and CO_2 addition on mean annual biomass growth rates of *Evernia mesomorpha*. *SS* = Type III Sums-of-squares; *MSE* = Mean Square Error; *df* = degrees of freedom. Bold face = significant ($\alpha = 0.01$).

Model	Coefficient	*SS*	*MSE*	*Num df*	*Den df*	*F*	*p*
2013-14, pre-treatment	**Model intercept**	**563**	**563**	**1**	**8**	**24.84**	**0.001**
	Warming/drying	8	8	1	8	0.37	0.55
	CO_2	14	14	1	8	0.63	0.45
	Warming/drying $\times$ CO_2	8	8	1	8	0.37	0.56
2014-15, pre-treatment	**Model intercept**	**76**	**76**	**1**	**8**	**10.82**	**0.01**
	Warming/drying	10	10	1	8	1.39	0.27
	CO_2	1	1	1	8	0.15	0.71
	Warming/drying $\times$ CO_2	6	6	1	8	0.80	0.40
2015-16, post-treatment	**Model intercept**	**137**	**137**	**1**	**8**	**9.04**	**0.01**
	Warming/drying	**272**	**272**	**1**	**8**	**17.96**	**0.003**
	CO_2	35	35	1	8	2.27	0.17
	Warming/drying $\times$ CO_2	23	23	1	8	1.52	0.25

Table 5.2. Mean annual biomass growth of *Evernia mesomorpha* transplants at the SPRUCE experiment in Minnesota. Measurements were in twelve experimental plots at the SPRUCE experiment over the first year of whole-ecosystem warming, drying, and CO_2 addition. Transplant numbers are unbalanced because of incomplete measurements or losses over time. Rows sorted by actual temperature differentials as measured at 2 m above the bog surface.

Target differential (°C)	Actual differential (°C)	CO_2 treatment (ppm)	N transplants	Annual growth (mean ± SD, %)	Net effect 2015–2016
ambient	0.0	450	25	17.4 ± 11.8	+
ambient	0.2	450	25	11.3 ± 8.7	+
control	1.9	900	21	3.0 ± 8.3	+
control	2.2	450	22	0.4 ± 14.6	+
2.25	4.4	900	24	−9.5 ± 8.5	−
2.25	4.4	450	25	−7.6 ± 5.9	−
4.50	6.6	900	25	−12.4 ± 6.3	−
4.50	6.7	450	8	−12.8 ± 7.6	−
6.75	8.4	450	27	−13.4 ± 4.7	−
6.75	8.4	900	26	−17.2 ± 8.1	−
9.00	10.2	900	23	−17.3 ± 8.6	−
9.00	10.6	450	22	−20.5 ± 7.2	−

Figures
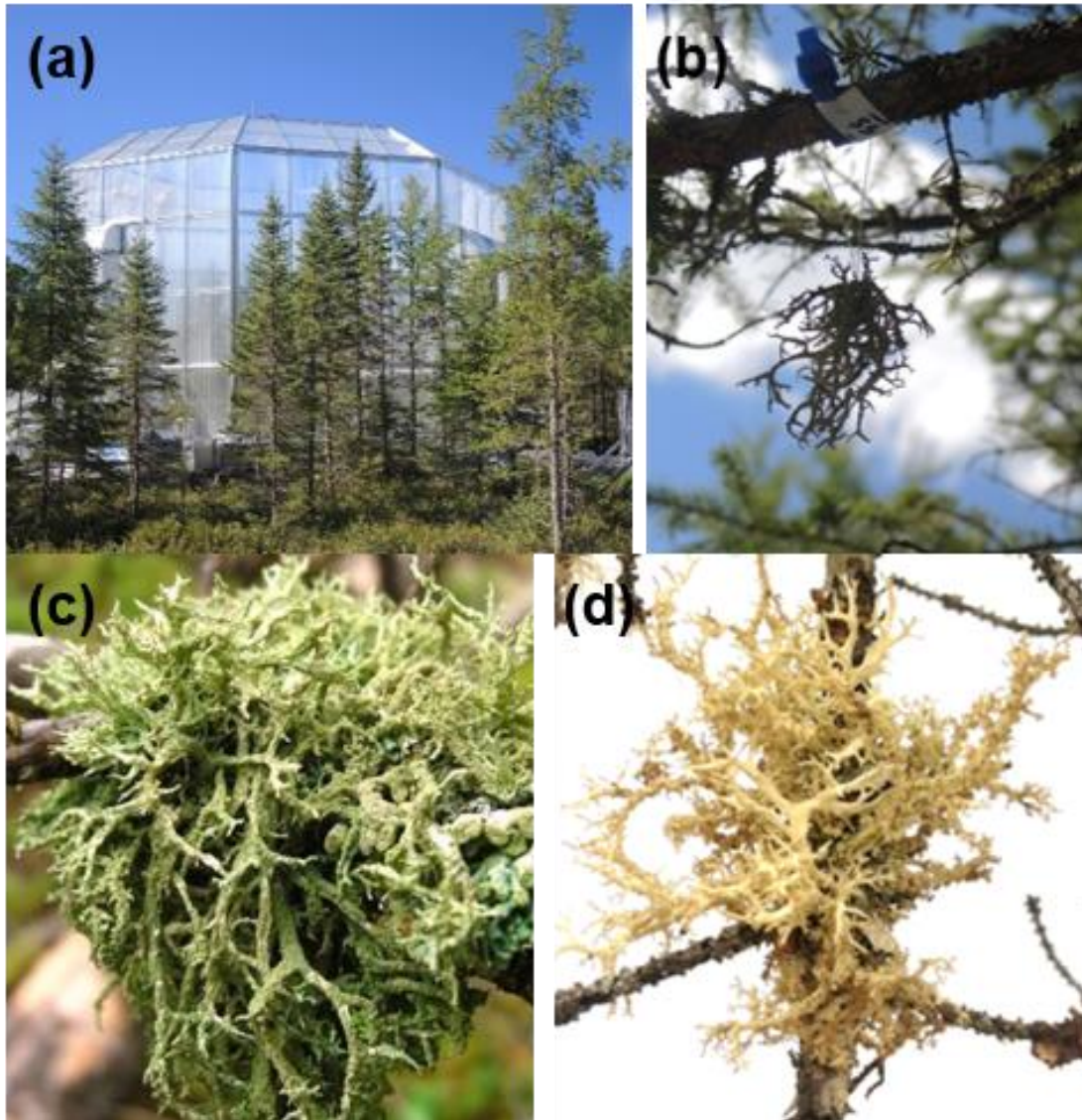
Figure 5.1. Overview of the SPRUCE experiment. (a) Twelve plots installed at the SPRUCE experiment site in a northern Minnesota peat bog. Each 8-m tall, open-topped enclosure is dynamically maintained in reference to ambient temperatures and CO_2 concentrations. **(b)** A single *Evernia mesomorpha* transplant hung with monofilament from *Picea mariana*. **(c)** Healthy *Evernia mesomorpha* in ambient conditions. **(d)** Bleached or failing *Evernia mesomorpha* tended to persist on *Picea* branches in the energy-added treatments.
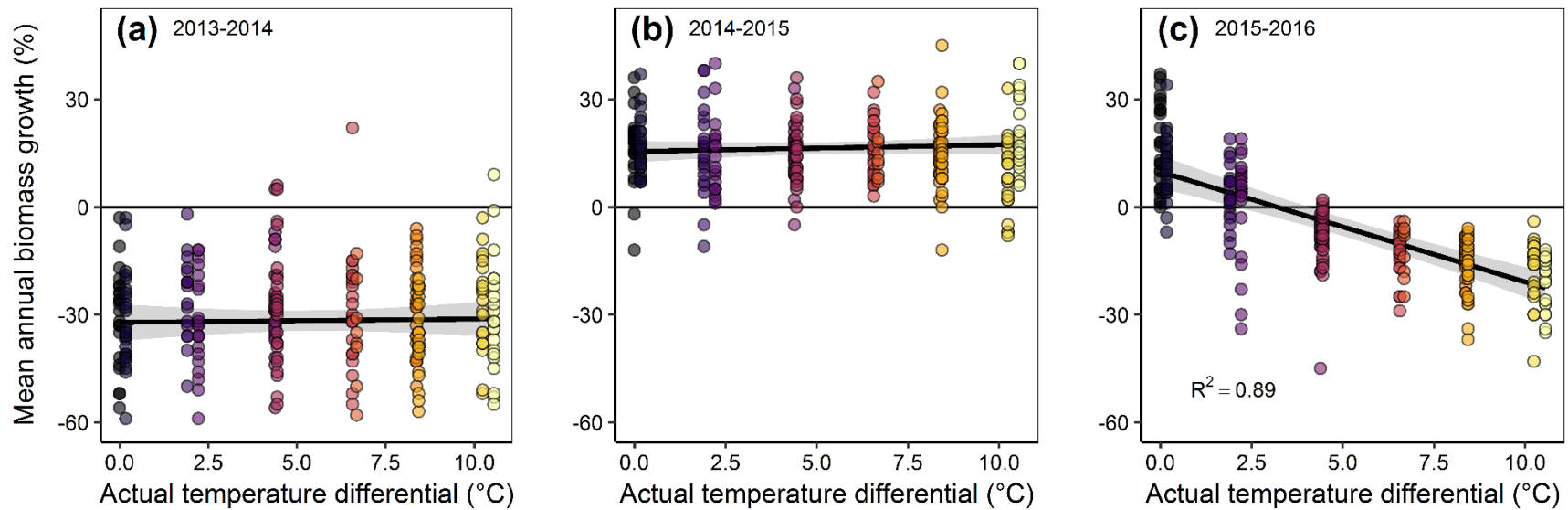
Figure 5.2. Annual biomass growth rates of *Evernia mesomorpha* transplants at the SPRUCE experimental site in northern Minnesota. Each symbol is the annual biomass growth rate for one transplanted lichen thallus. Growth rates are for each pre-treatment year **(a,b)** and in the first year of whole-ecosystem warming and drying **(c)**. Slope of regression lines are the estimated incremental effect of a 1°C increase in warming on the mean annual biomass growth rate, and shaded area around lines are 95% confidence intervals of the estimated mean. In the first year of whole-ecosystem warming and drying, mean growth significantly decreased 4.1 percentage points for every 1°C increase in warming (95% CI: −6.4 to −1.9 percentage points).
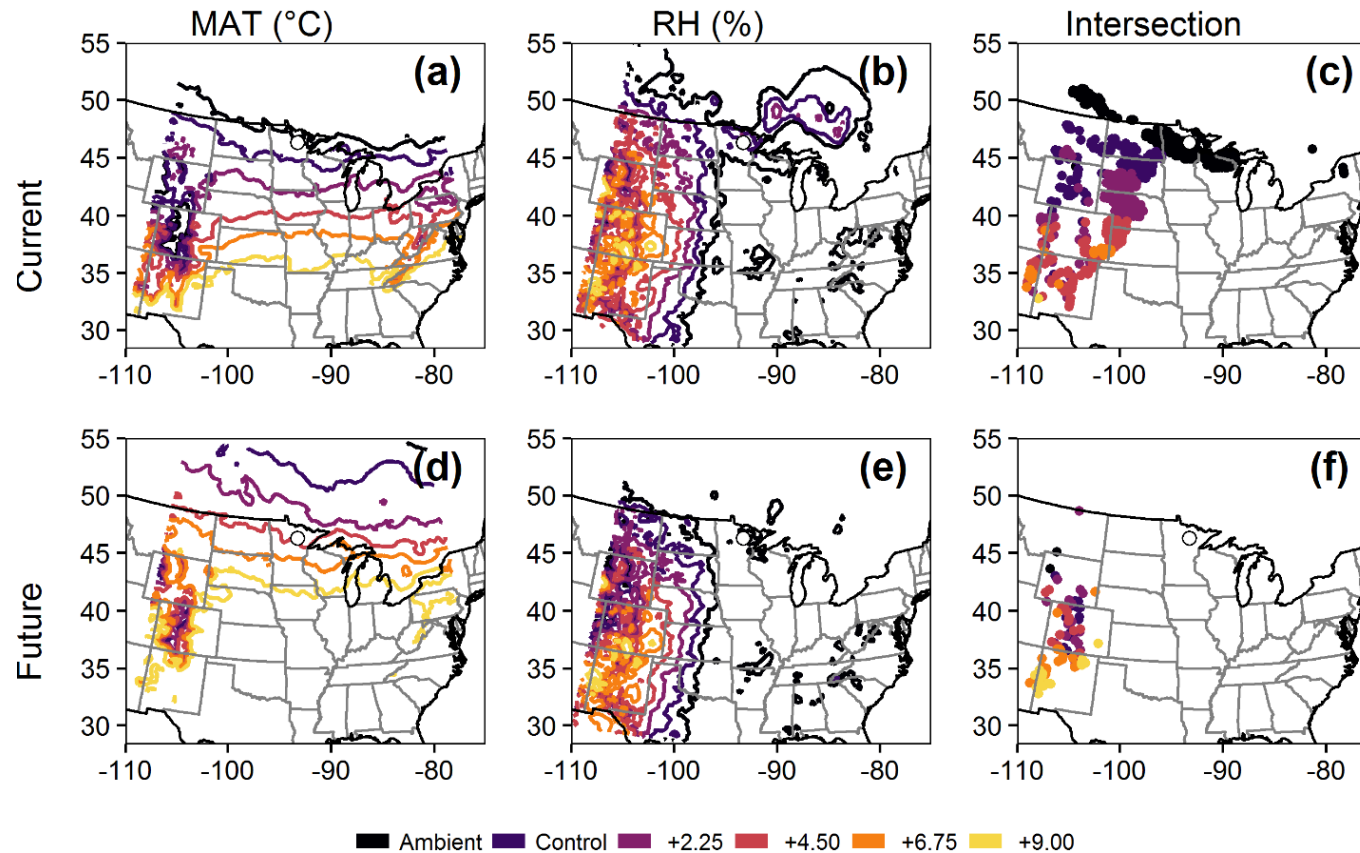
Figure 5.3. Representativeness of SPRUCE experimental treatment conditions. Representativeness is measured relative to current-day climate **(a,b,c)** and potential future climate **(d,e,f)** across the central United States and Canada. Each isoline corresponds to conditions in experimental treatments. Mean annual temperature **(a,d)** increases under the potential future scenario, with little change in mean annual relative humidity **(b,e)**. Combinations of temperature and humidity in treatments were similar to current-day conditions at locations along the western Great Plains and Rocky Mountain Front **(c,f)**, primarily due to low relative humidity. Data for current climate: Wang et al. (2016). Data for future climate: IPCC (2014).

Ambient Plot with Dew
Early AM, 18 Oct 2016

Control Plot without Dew
Early AM, 18 Oct 2016

Figure 5.4. Dew formation in SPRUCE experimental plots. Increased temperatures and decreased relative humidity co-occurred as a product of the experimental design. Enclosure walls limited energy loss to the sky, which precluded dew formation in enclosures. Photos: Paul J. Hanson.

CHAPTER 6. CONCLUSIONS AND PROSPECTS

Conclusions

The unifying theme of this dissertation is the detection and prediction of climate signals among communities of lichens and bryophytes surveyed in a national forest inventory. The U.S. Forest Service's Forest Inventory and Analysis (FIA) program provides nationally consistent reporting of forest status and trends based on a statistically defensible sampling design and reproducible measurements (Bechtold and Peterson 2005). Within this context, the chapters respectively: elucidated the biogeochemical consequences of climate and local factors (*Chapter Two*), revealed biogeographic climate affinities (*Chapter Three*), reported prospects for climate-related diversity changes (*Chapter Four*), and explained how single-species growth rates may scale to regions given climatic changes (*Chapter Five*). This improves our understanding of the ways in which climate can structure ecological properties of vegetation across large landscapes, and reduces the uncertainty in our expectations of future climate change effects. This concluding chapter summarizes key outcomes, describes their broader importance, and proposes a future research arc.

Chapter Two examined carbon storage and functional diversity of moss and lichen "ground layers" as part of the FIA program in interior Alaska. The inventory used novel nondestructive techniques (Smith et al. 2015). Findings helped to determine the sensitivity of ground layer nutrient stores with respect to interactions among local vegetation, topography and climatic conditions. These conditions are informative because carbon-rich mosses and lichens could be persistently excluded by advances of competitive vascular vegetation and by growing wildfire regimes (Cornelissen et al. 2001; Gibson et al. 2016), both of which are expected to accompany climatic warming in subarctic regions over the next several decades. Monitoring status and trends in terrestrial vegetation is critical for tracking carbon exchange among atmospheric and terrestrial pools (Bachelet et al. 2001; McKinley et al. 2011). A natural extension of this chapter would be scaling carbon estimates to landscapes while accounting for the increasingly important roles of wildfires and the seasonal hydration status of ground layers.

Chapter Three identified which macroclimatic variables most contributed to lichen community composition across a large super-regional extent encompassing multiple ecoregions, and quantified the strength of the lichen–climate relationship. Lichen species richness has been seen as a mixed or weak predictor of macroclimate (Holt et al. 2015; Tripp et al. 2016), suggesting the need for community approaches that account for community composition and species identities. This is critically important in the context of global changes because lichen identity directly affects ecosystem functioning (Cornelissen et al. 2007). For example, losses of cyanobacterial "nitrogen-fixing" lichen species (e.g., *Lobaria oregana*) would not be functionally equivalent to identical changes in "wildlife forage" species (e.g., *Alectoria sarmentosa*). A focus on species composition also permits direct comparison to historical floristic surveys of lichens (Nelsen et al. 2007; Will-Wolf and Nelsen 2008). Indeed, comparing historical and modern surveys is one prospective path to hindcasting the effects of global changes over recent decades.

Chapter Four identified the location and magnitude of expected species losses given atmospheric warming in current and future scenarios. Findings challenged the default assumption that warming-induced species losses should be most prevalent among "cold-adapted" lichen communities in montane or northern habitats (Ellis et al. 2007; Allen and Lendemer 2016). To the contrary, "warm-adapted" low-elevation and southern communities tended to have many species very near to exceeding upper thermal limits. This is a compelling outcome, because such locations in coming decades are expected to attain climates that have no existing analogue (Williams and Jackson 2007). The novel vulnerability indices developed in this chapter are concise, intuitive metrics of climate change impacts that are readily accessible to policy makers, natural resource managers and the general public. Pinpointing locations where biological changes are expected will help direct conservation resources and public attention to areas where intensified monitoring may be most efficient.

Chapter Five identified growth and biomass losses of a boreal epiphyte species (*Evernia mesomorpha*) under experimental climate changes. Findings confirmed the strong moisture and temperature dependence of lichen growth (Song et al. 2012; Alam et al. 2015). Progressive warming and drying caused clear monotonic decreases in mean annual biomass

growth of target species transplants. This pattern is strikingly similar to warming-induced growth declines of *Evernia mesomorpha*'s major host tree *Picea mariana* (Subedi and Sharma 2012; Walker and Johnstone 2014). Convergent environmental responses between similarly adapted species raise the intriguing possibility that climate-related variation in epiphytic lichen growth could be a useful predictor of tree growth, although intensive evaluation will be needed to confirm. We observed that lichen thalli remained intact despite biomass losses, which could indicate a possible extinction debt. Overall, observed growth declines suggest that atmospheric warming could shrink the southern range boundary of the target species, with consequent losses of local diversity.

<div align="center">Prospects</div>

What are the prospects for a future research agenda involving climate responses among lichens? A wealth of questions still await answer. For example, will changes in lichen communities precede changes among other forest organisms (e.g., trees, understory vegetation, arthropods, vertebrates, fungi)? What is the generality of climate effects among these different organisms, and which ones are the "best" bioindicators of climate? How do the lichen community effects of climate interact with the effects of nitrogen deposition (McMurray et al. 2015) and with land use/disturbances (Ellis et al. 2009)? What are the effects of multiple interacting climate variables, and of novel, no-analog climates (Williams and Jackson 2007)? How may lagged climate responses contribute to extinction debts? And how can these questions best address forest management? Effectively answering these questions requires that a research agenda seeks agreement from multiple angles.

A first step is defining species climatic responses and limits within a causal framework. Forest inventories permit description of ecological patterns, but they could also be complemented by experimental approaches to move from descriptive mode to predictive mode. For epiphytic lichens, options include reciprocal transplants, natural experiments, whole-ecosystem experiments, and no-analog climates simulated in controlled growth chamber assays. Performance metrics typically include photosynthetic response curves, biomass accumulation rates, or secondary metabolite production, all of which reflect intrinsic carbon metabolism of lichens (Palmqvist et al. 2000). Since experimental approaches can establish physiological limits along key climatic gradients, they can illuminate how

fundamental niches may constrain geographic distributions. Screening for climatic constraints across an array of common and rare species could then inform process-based predictive models for lichen communities.

Second, approaches could explicitly consider how spatial and historical processes across large regions (Ricklefs 2004) shape lichen communities in the context of global changes past and present. Spatial processes (e.g., dispersal, dispersal limitations) determine whether lichens can track suitable climate spaces (Belinchón et al. 2015). Spatial processes could be inferred by combining molecular and geospatial methods to test (for example) the prediction that compositional dissimilarity among sites should decrease with increasing dispersal (Vellend 2016). Historical processes (e.g., speciation, historical climate shifts) likewise shape lichen community patterns across large landscapes. These could be inferred by probing phylogenies of large lichen species pools (e.g., Miadlikowska et al. 2014) to test (for example) the predictions that diversification rates correlate with climatic boundaries in space (Schluter and Ricklefs 1993) and with climatic shift events over time (Divakar et al. 2012; Leavitt et al. 2012). Together, spatial and historical processes could inform expectations of future changes.

Third, modeling global change responses through time (hindcasting and forecasting) would promote greater understanding of vegetation changes. Hindcasting to retrospectively detect climate change signals can capitalize on historical and modern surveys for lichens (van Herk et al. 2002) and other vegetation (Vellend et al. 2013). Forecasting future effects can take either a process-based or correlative approach. Process-based forecasting uses existing knowledge of biotic interactions, and physiological, demographic, and dispersal rates to predict future species distributions and community structures (Evans et al. 2016). When such knowledge is lacking, correlative forecasting remains a pragmatic option, especially given the ready availability of species occurrence data in many Western nations. All approaches can benefit from modeling species jointly to retain realistic mixtures of co-occurring species in communities (D'Amen et al. 2017).

Finally, bridging technical and social approaches can reinforce forest management and societal outcomes. The scope of the FIA program is ideal for climate-aware, evidence-based

management that helps managers and the public understand how global changes impact forests now and in the near future (e.g., Zhu et al. 2012; Woodall et al. 2013). For land managers, the prospect of global changes evokes much uncertainty about the location, scale and nature of ecological changes, and their implications for human livelihoods. Ecologists could identify immediate forest management needs in direct collaboration with practitioners and policy makers, which tends to improve socioecological outcomes (DeFries et al. 2012). Identifying influences on the distributions of organisms (and resulting impacts on the human communities that depend on them) will be critical for crafting policies and actions that account for carbon storage, diversity maintenance and other key ecosystem functions. Interdisciplinary dialogue and evidence-based reasoning both promise to foster a more complete understanding of the complex set of interactions among humans, vegetation, and the global climate commons.

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APPENDICES

Appendix A. Species summaries and climate zone indicator values for macrolichens of the U.S. Pacific states

Table A.1. Summary for 1,118 FIA lichen survey plots includes each species' relative frequency, mean abundance, and significant indicator value(s) across all significant climate zones, and for single climate zones. Non-significant *IndVal* ($p > 0.05$ from test with 999 randomization) not reported.

Species	Rel. freq	Mean abund (0–4)	*IndVal* all zones	*IndVal* for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Ahtiana sphaerosporella	0.05	0.11	0.31	—	0.12	—	0.22	0.21	—	—	—	—	—
Alectoria imshaugii	0.10	0.22	0.35	—	—	—	—	0.20	0.24	—	0.15	—	—
Alectoria sarmentosa	0.37	1.02	0.60	—	—	—	—	—	—	—	0.44	0.33	0.27
Alectoria vancouverensis	0.02	0.04	—	—	—	—	—	—	—	—	—	—	—
Bryocaulon pseudosatoanum	0.01	0.03	0.17	—	—	—	—	—	—	—	0.09	0.07	0.11
Bryoria sp.	0.05	0.11	0.35	—	—	—	0.15	—	—	—	0.32	—	—
Bryoria bicolor	0.05	0.12	0.41	—	—	—	—	—	—	—	—	0.30	0.28
Bryoria capillaris	0.17	0.43	0.49	—	—	—	0.25	—	0.31	—	0.26	—	—
Bryoria carlottae	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Bryoria cervinula	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Bryoria fremontii	0.20	0.57	0.62	—	—	—	0.33	0.45	0.28	—	—	—	—
Bryoria friabilis	0.03	0.07	0.24	—	—	—	0.08	—	—	—	0.23	—	—
Bryoria fuscescens	0.17	0.44	0.42	—	—	—	0.24	—	0.25	—	0.23	—	—
Bryoria glabra	0.07	0.19	0.35	—	—	—	—	—	—	0.16	0.21	0.25	—
Bryoria implexa	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Bryoria lanestris	0.02	0.06	0.26	—	—	—	—	—	—	0.26	—	—	—
Bryoria pseudofuscescens	0.13	0.37	0.41	—	—	—	—	0.23	0.22	0.26	—	—	—
Bryoria simplicior	0.05	0.14	0.31	—	—	—	0.17	0.17	—	0.19	—	—	—
Bryoria tenuis	0.03	0.09	0.37	—	—	—	—	—	—	—	—	0.33	0.20
Bryoria trichodes	0.14	0.39	0.45	—	—	0.21	—	—	—	—	—	0.34	0.26

Species	Rel. freq	Mean abund (0–4)	*IndVal* all zones	*IndVal* for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Bunodophoron melanocarpum	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Candelaria pacifica	0.27	0.77	0.70	0.59	0.42	—	—	—	—	—	—	—	—
Cetraria sp.	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Cetraria canadensis	0.12	0.27	0.44	—	—	—	—	0.23	0.24	0.29	—	—	—
Cetraria chlorophylla	0.34	0.83	0.54	—	—	—	—	—	0.31	0.35	0.27	—	—
Cetraria merrillii	0.25	0.65	0.55	—	—	—	0.13	0.50	0.24	—	—	—	—
Cetraria orbata	0.23	0.57	0.43	—	—	—	0.15	—	0.32	—	0.22	—	—
Cetraria pallidula	0.04	0.07	0.25	—	—	—	0.15	—	0.19	—	—	—	—
Cetraria pinastri	0.03	0.08	0.29	—	—	—	0.11	—	0.14	0.22	—	—	—
Cetraria platyphylla	0.25	0.66	0.55	—	—	—	0.18	0.33	0.39	—	—	—	—
Cetraria sepincola	0.02	0.06	0.34	—	—	—	—	—	—	0.34	—	—	—
Cetraria subalpina	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Cetrelia cetrarioides	0.02	0.03	0.20	—	—	0.20	—	—	—	—	—	—	—
Cladonia sp.	0.03	0.07	0.23	—	—	0.15	0.05	—	—	—	0.17	—	—
Cladonia albonigra	0.02	0.04	0.21	—	—	—	—	—	—	—	0.10	0.19	0.09
Cladonia bacillaris	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Cladonia bellidiflora	0.07	0.18	0.50	—	—	—	—	—	—	—	—	0.35	0.35
Cladonia carneola	0.04	0.10	0.27	—	—	—	—	—	—	—	0.21	0.12	0.15
Cladonia cenotea	0.02	0.04	—	—	—	—	—	—	—	—	—	—	—
Cladonia chlorophaea	0.04	0.10	—	—	—	—	—	—	—	—	—	—	—
Cladonia coniocraea	0.21	0.53	0.56	—	—	0.34	—	—	—	—	—	0.31	0.31
Cladonia cornuta	0.07	0.18	0.37	—	—	—	—	—	—	—	0.14	0.33	0.17
Cladonia deformis	0.01	0.03	—	—	—	—	—	—	—	—	—	—	—
Cladonia fimbriata	0.08	0.17	0.32	—	—	0.17	—	—	—	0.16	—	0.22	—
Cladonia furcata	0.01	0.03	—	—	—	—	—	—	—	—	—	—	—

Species	Rel. freq	Mean abund (0–4)	IndVal all zones	IndVal for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Cladonia macilenta	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Cladonia norvegica	0.01	0.03	0.18	—	—	0.08	—	—	—	—	0.16	—	0.09
Cladonia pyxidata	0.01	0.03	0.22	—	—	—	—	—	—	—	0.12	0.20	—
Cladonia rangiferina	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Cladonia squamosa	0.12	0.30	0.55	—	—	—	—	—	—	—	0.19	0.40	0.36
Cladonia squamosa var subsquamosa	0.05	0.12	0.32	—	—	0.13	—	—	—	—	—	0.13	0.31
Cladonia straminea	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Cladonia sulphurina	0.02	0.04	0.17	—	—	—	0.07	—	0.09	—	0.14	—	—
Cladonia transcendens	0.14	0.37	0.43	—	—	0.24	—	—	—	—	—	0.22	0.28
Cladonia umbricola	0.07	0.15	0.34	—	—	0.20	—	—	—	—	—	0.15	0.22
Cladonia verruculosa	0.01	0.03	0.18	—	—	—	0.07	—	—	—	—	0.16	0.07
Collema curtisporum	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Collema furfuraceum	0.05	0.14	0.33	0.29	0.18	—	—	—	—	0.14	—	—	—
Collema nigrescens	0.03	0.08	0.28	0.26	0.14	—	—	—	0.10	—	—	—	—
Dendriscocaulon intricatulum	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Esslingeriana idahoensis	0.12	0.29	0.44	—	—	—	—	—	0.36	0.19	0.19	—	—
Evernia mesomorpha	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Evernia prunastri	0.28	0.66	0.52	0.28	0.39	—	—	—	—	0.23	—	—	—
Flavoparmelia caperata	0.01	0.04	0.26	0.25	0.13	—	—	—	—	—	—	—	—
Flavopunctelia flaventior	0.06	0.17	0.54	0.54	—	—	—	—	—	—	—	—	—
Fuscopannaria ahlneri	0.01	0.02	0.16	—	—	0.10	—	—	—	0.13	—	—	—
Fuscopannaria confusa	0.01	0.03	—	—	—	—	—	—	—	—	—	—	—
Fuscopannaria laceratula	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Fuscopannaria leucostictoides	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Fuscopannaria mediterranea	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—

Species	Rel. freq	Mean abund (0–4)	IndVal all zones	IndVal for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Fuscopannaria pacifica	0.01	0.03	—	—	—	—	—	—	—	—	—	—	—
Heterodermia japonica	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Heterodermia leucomela	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Heterodermia speciosa	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Hypogymnia sp.	0.03	0.06	—	—	—	—	—	—	—	—	—	—	—
Hypogymnia apinnata	0.21	0.56	0.49	—	—	0.26	—	—	—	—	0.30	—	0.30
Hypogymnia austerodes	0.01	0.04	0.21	—	—	—	0.08	—	—	0.19	—	—	—
Hypogymnia bitteri	0.04	0.13	0.41	—	—	—	—	—	—	0.41	—	—	—
Hypogymnia canadensis	0.01	0.03	0.18	—	—	0.15	—	—	—	0.10	—	—	—
Hypogymnia duplicata	0.08	0.23	0.56	—	—	—	—	—	—	—	0.17	0.40	0.38
Hypogymnia enteromorpha	0.25	0.64	0.62	—	—	—	—	—	—	—	0.38	0.35	0.34
Hypogymnia heterophylla	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Hypogymnia hultenii	0.12	0.32	0.54	—	—	0.28	—	—	—	—	—	0.37	0.31
Hypogymnia imshaugii	0.46	1.27	0.65	—	—	—	0.30	0.39	0.40	—	—	—	—
Hypogymnia inactiva	0.16	0.43	0.48	—	—	0.28	—	—	—	—	0.38	0.19	—
Hypogymnia lophyrea	0.05	0.11	0.37	—	—	0.22	—	—	—	—	—	0.15	0.28
Hypogymnia occidentalis	0.16	0.42	0.39	—	—	—	0.14	—	0.26	0.24	—	—	—
Hypogymnia oceanica	0.02	0.04	0.23	—	—	0.10	—	—	—	—	—	0.14	0.18
Hypogymnia physodes	0.28	0.77	0.51	—	—	0.27	—	—	—	0.35	0.26	—	—
Hypogymnia pulverata	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Hypogymnia rugosa	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Hypogymnia tubulosa	0.17	0.37	0.38	—	—	0.19	—	—	—	0.22	0.26	—	—
Hypogymnia vittata	0.03	0.07	0.28	—	—	0.12	—	—	—	—	—	0.27	0.11
Hypogymnia wilfiana	0.13	0.30	0.43	—	—	—	0.21	—	0.31	—	0.19	—	—
Hypotrachyna sinuosa	0.06	0.15	0.41	—	—	0.26	—	—	—	—	—	0.17	0.27

Species	Rel. freq	Mean abund (0–4)	IndVal all zones	IndVal for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Imshaugia aleurites	0.02	0.07	0.31	—	—	—	—	—	—	0.31	—	—	—
Lathagrium fuscovirens	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Leptochidium albociliatum	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Leptogidium contortum	0.03	0.05	0.33	—	—	—	—	—	—	—	—	—	0.33
Leptogium sp.	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Leptogium burnetiae	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Leptogium pseudofurfuraceum	0.01	0.04	0.23	0.23	—	—	—	—	—	—	—	—	—
Leptogium saturninum	0.03	0.08	0.25	—	—	—	0.10	—	—	0.23	—	—	—
Letharia columbiana	0.27	0.74	0.63	—	—	—	0.40	0.47	—	—	—	—	—
Letharia vulpina	0.43	1.25	0.72	—	—	—	0.32	0.50	0.38	—	—	—	—
Lobaria anomala	0.07	0.16	0.26	—	—	0.13	—	—	0.18	0.14	—	—	—
Lobaria anthraspis	0.06	0.15	0.25	—	0.14	—	—	—	0.17	0.13	—	—	—
Lobaria hallii	0.02	0.05	0.21	—	—	—	—	—	0.10	0.20	—	—	—
Lobaria linita	0.08	0.21	0.50	—	—	—	—	—	—	—	0.17	0.42	0.27
Lobaria oregana	0.08	0.23	0.51	—	—	—	—	—	—	—	0.15	0.38	0.34
Lobaria pulmonaria	0.11	0.28	0.38	—	—	0.22	—	—	0.16	0.27	—	—	—
Lobaria scrobiculata	0.07	0.17	0.33	—	—	—	0.08	—	—	0.32	—	—	—
Melanelia sp.	0.05	0.11	—	—	—	—	—	—	—	—	—	—	—
Melanelixia californica	0.11	0.31	0.57	0.47	0.36	—	—	—	—	—	—	—	—
Melanelixia fuliginosa	0.06	0.15	0.32	—	0.23	0.22	—	—	—	—	—	—	—
Melanelixia subargentifera	0.02	0.05	0.39	0.39	—	—	—	—	—	—	—	—	—
Melanelixia subaurifera	0.03	0.05	0.18	0.07	0.15	0.09	—	—	—	—	—	—	—
Melanohalea elegantula	0.15	0.39	0.46	0.19	0.27	—	—	0.32	—	—	—	—	—
Melanohalea exasperatula	0.18	0.47	0.42	—	—	—	0.23	0.24	—	0.25	—	—	—
Melanohalea olivacea	0.01	0.05	0.28	—	—	—	—	—	—	0.28	—	—	—

Species	Rel. freq	Mean abund (0–4)	*IndVal* all zones	*IndVal* for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Melanohalea septentrionalis	0.01	0.02	0.21	—	—	—	—	—	—	0.21	—	—	—
Melanohalea subelegantula	0.06	0.16	0.33	—	—	—	0.23	0.20	0.16	—	—	—	—
Melanohalea subolivacea	0.29	0.83	0.49	0.25	0.29	—	—	0.30	—	—	—	—	—
Melanohalea trabeculata	0.01	0.03	0.20	—	—	—	—	—	—	0.20	—	—	—
Menegazzia subsimilis	0.04	0.09	0.33	—	—	0.15	—	—	—	—	—	0.12	0.32
Nephroma sp.	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Nephroma arcticum	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Nephroma bellum	0.07	0.17	0.36	—	—	—	—	—	—	—	0.18	0.29	0.15
Nephroma helveticum	0.07	0.18	0.33	—	—	—	—	—	0.17	—	—	0.19	0.22
Nephroma isidiosum	0.01	0.03	0.21	—	—	—	—	—	—	—	—	0.21	—
Nephroma laevigatum	0.01	0.02	0.21	—	—	0.21	—	—	—	—	—	—	—
Nephroma occultum	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Nephroma parile	0.05	0.13	0.28	—	—	—	—	—	—	0.28	—	—	—
Nephroma resupinatum	0.04	0.10	0.24	—	—	0.12	—	—	0.15	0.13	—	—	—
Niebla cephalota	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Nodobryoria sp.	0.01	0.03	—	—	—	—	—	—	—	—	—	—	—
Nodobryoria abbreviata	0.29	0.79	0.68	—	—	—	0.33	0.49	0.33	—	—	—	—
Nodobryoria oregana	0.17	0.43	0.53	—	—	—	0.31	—	0.25	—	0.39	—	—
Pannaria sp.	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Parmelia sp.	0.04	0.09	—	—	—	—	—	—	—	—	—	—	—
Parmelia hygrophila	0.21	0.53	0.44	—	—	0.24	—	—	—	—	0.26	0.26	—
Parmelia pseudosulcata	0.05	0.13	0.38	—	—	—	—	—	—	—	—	0.38	—
Parmelia saxatilis	0.06	0.15	0.34	—	—	0.21	—	—	—	—	—	0.14	0.24
Parmelia squarrosa	0.02	0.06	0.23	—	—	0.12	—	—	—	0.12	—	—	0.17
Parmelia sulcata	0.43	1.15	0.54	—	—	0.30	—	—	0.29	0.34	—	—	—

Species	Rel. freq	Mean abund (0–4)	*IndVal* all zones	*IndVal* for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Parmeliella triptophylla	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Parmelina coleae	0.08	0.20	0.47	0.34	0.33	—	—	—	—	—	—	—	—
Parmeliopsis ambigua	0.15	0.37	0.47	—	—	—	0.22	—	0.28	0.30	—	—	—
Parmeliopsis hyperopta	0.25	0.64	0.62	—	—	—	0.24	—	—	—	0.50	0.31	—
Parmotrema sp.	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Parmotrema arnoldii	0.02	0.04	0.24	—	0.17	—	—	—	—	—	—	0.09	0.14
Parmotrema austrosinense	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Parmotrema perlatum	0.02	0.05	0.30	0.20	—	—	—	—	—	—	—	—	0.22
Peltigera sp.	<0.01	—	—	—	—	—	—	—	—	—	—	—	—
Peltigera aphthosa	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Peltigera britannica	0.06	0.13	0.46	—	—	—	—	—	—	—	—	0.39	0.26
Peltigera collina	0.11	0.27	0.31	—	—	0.17	—	—	—	0.16	—	0.21	—
Peltigera elisabethae	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Peltigera membranacea	0.03	0.07	0.27	—	—	—	—	—	—	—	—	0.14	0.23
Peltigera neopolydactyla	0.06	0.16	0.47	—	—	—	—	—	—	—	0.14	0.39	0.27
Peltigera pacifica	<0.01	—	—	—	—	—	—	—	—	—	—	—	—
Peltigera polydactylon	0.01	0.01	0.16	—	—	0.08	—	—	—	—	—	0.05	0.15
Peltigera praetextata	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Peltigera scabrosa	0.01	0.03	0.23	—	—	—	—	—	—	—	—	0.10	0.22
Phaeophyscia ciliata	0.01	0.02	0.17	0.17	0.09	—	—	—	—	—	—	—	—
Phaeophyscia hirsuta	0.01	0.04	0.34	0.34	—	—	—	—	—	—	—	—	—
Phaeophyscia kairamoi	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Phaeophyscia orbicularis	0.08	0.21	0.69	0.69	—	—	—	—	—	—	—	—	—
Physcia sp.	0.02	0.05	0.23	0.23	—	—	—	—	—	—	—	—	—
Physcia adscendens	0.18	0.47	0.65	0.57	0.37	—	—	—	—	—	—	—	—

Species	Rel. freq	Mean abund (0–4)	IndVal all zones	IndVal for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Physcia alnophila	0.12	0.29	0.40	0.31	0.23	—	—	—	—	0.18	—	—	—
Physcia biziana	0.08	0.19	0.49	0.45	0.27	—	—	—	—	—	—	—	—
Physcia caesia	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Physcia dimidiata	0.04	0.11	0.30	0.28	—	—	0.08	—	—	0.15	—	—	—
Physcia dubia	<0.01	—	—	—	—	—	—	—	—	—	—	—	—
Physcia leptalea	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Physcia stellaris	0.05	0.13	0.39	0.24	0.30	—	—	—	—	—	—	—	—
Physcia tenella	0.13	0.36	0.62	0.49	0.40	—	—	—	—	—	—	—	—
Physcia tribacia	0.02	0.04	0.36	—	0.36	—	—	—	—	—	—	—	—
Physciella melanchra	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Physconia sp.	0.02	0.04	—	—	—	—	—	—	—	—	—	—	—
Physconia americana	0.11	0.29	0.46	0.40	0.27	—	—	—	0.17	—	—	—	—
Physconia enteroxantha	0.11	0.29	0.51	0.39	0.34	—	—	—	—	—	—	—	—
Physconia fallax	0.02	0.06	0.41	0.41	—	—	—	—	—	—	—	—	—
Physconia isidiigera	0.12	0.33	0.63	0.62	0.32	—	—	—	—	—	—	—	—
Physconia leucoleiptes	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Physconia perisidiosa	0.16	0.42	0.58	0.48	0.36	—	—	—	—	—	—	—	—
Platismatia glauca	0.50	1.37	0.65	—	—	0.33	—	—	—	—	0.44	0.38	—
Platismatia herrei	0.19	0.45	0.52	—	—	—	—	—	—	—	0.27	0.34	0.29
Platismatia lacunosa	0.07	0.18	0.50	—	—	—	—	—	—	—	—	0.35	0.36
Platismatia norvegica	0.14	0.37	0.62	—	—	—	—	—	—	—	0.20	0.40	0.45
Platismatia stenophylla	0.10	0.23	0.46	—	—	—	—	—	—	—	0.46	—	—
Polycauliona candelaria	0.07	0.15	0.29	0.17	—	—	—	0.15	—	0.18	—	—	—
Polycauliona polycarpa	0.17	0.44	0.61	0.50	0.37	—	—	—	—	—	—	—	—
Polycauliona tenax	0.02	0.05	0.50	0.50	—	—	—	—	—	—	—	—	—

Species	Rel. freq	Mean abund (0–4)	IndVal all zones	IndVal for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Polychidium muscicola	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Pseudocyphellaria crocata	0.03	0.07	0.24	—	—	—	—	—	—	0.23	—	0.08	—
Punctelia jeckeri	0.03	0.08	0.38	0.30	0.25	—	—	—	—	—	—	—	—
Ramalina sp.	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Ramalina dilacerata	0.07	0.16	0.33	—	—	0.15	—	—	—	0.30	0.10	—	—
Ramalina farinacea	0.20	0.48	0.44	—	0.24	0.31	—	—	—	0.22	—	—	—
Ramalina leptocarpha	0.02	0.04	0.48	0.48	—	—	—	—	—	—	—	—	—
Ramalina menziesii	0.01	0.03	0.35	0.35	—	—	—	—	—	—	—	—	—
Ramalina obtusata	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Ramalina pollinaria	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Ramalina roesleri	0.05	0.14	0.36	—	—	—	0.12	—	—	0.33	—	—	—
Ramalina subleptocarpha	0.03	0.08	0.43	0.43	—	—	—	—	—	—	—	—	—
Ramalina thrausta	0.01	0.04	0.20	—	—	—	—	—	—	0.20	—	—	—
Scytinium cellulosum	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Scytinium lichenoides	0.03	0.06	0.22	—	0.17	—	—	—	0.12	—	0.07	—	—
Scytinium palmatum	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Scytinium polycarpum	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Scytinium teretiusculum	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Sphaerophorus aggr.	0.25	0.69	0.74	—	—	—	—	—	—	—	0.34	0.50	0.43
Sticta fuliginosa	0.03	0.06	0.24	—	—	0.12	—	—	—	—	—	0.19	0.10
Sticta limbata	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Sulcaria badia	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Teloschistes chrysophthalmus	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Usnea sp.	0.14	0.33	0.30	—	—	0.19	—	—	0.16	0.16	—	—	—
Usnea cavernosa	0.01	0.03	—	—	—	—	—	—	—	—	—	—	—

Species	Rel. freq	Mean abund (0–4)	*IndVal* all zones	*IndVal* for single climate zones									
				1	2	3	4	5	6	7	8	9	10
Usnea cornuta	0.04	0.10	0.32	0.11	—	—	—	—	—	—	—	0.12	0.32
Usnea filipendula	0.20	0.54	0.40	—	—	0.23	—	—	0.24	—	0.24	—	—
Usnea flavocardia	0.08	0.23	0.41	—	—	0.29	—	—	—	—	—	0.12	0.27
Usnea glabrata	0.05	0.12	0.29	—	0.19	0.18	—	—	—	—	—	—	0.13
Usnea glabrescens	<0.01	0.01	—	—	—	—	—	—	—	—	—	—	—
Usnea hirta	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Usnea intermedia	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Usnea lapponica	0.11	0.27	0.37	—	0.16	—	—	—	0.17	0.31	—	—	—
Usnea longissima	0.03	0.07	0.37	—	—	—	—	—	—	—	—	—	0.37
Usnea pacificana	0.02	0.05	—	—	—	—	—	—	—	—	—	—	—
Usnea scabrata	0.08	0.19	0.28	—	—	0.20	—	—	0.14	0.14	—	—	—
Usnea subfloridana	0.06	0.16	0.24	—	0.13	0.14	—	—	—	—	0.14	—	—
Usnea substerilis	0.02	0.04	—	—	—	—	—	—	—	—	—	—	—
Xanthomendoza fallax	0.06	0.18	0.40	0.39	0.20	—	—	—	—	—	—	—	—
Xanthomendoza fulva	0.11	0.29	0.43	0.34	0.27	—	—	—	—	—	—	—	—
Xanthomendoza galericulata	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—
Xanthomendoza hasseana	0.11	0.29	0.45	0.36	0.25	—	—	—	0.20	—	—	—	—
Xanthomendoza oregana	0.13	0.37	0.48	0.48	—	—	—	—	—	—	—	—	—
Xanthoria sp.	0.02	0.04	—	—	—	—	—	—	—	—	—	—	—
Xanthoria parietina	0.01	0.02	0.17	0.17	—	—	—	—	—	—	—	—	—

Appendix B. Descriptive measures of macrolichen thermal niches based on mean warmest month air temperature (°C)

Table B.1. Descriptive measures of macrolichen thermal niches based on mean warmest month air temperature (°C). Rel freq gives relative frequencies in 6,474 FIA lichen survey plots nationwide. Other measures (*p05, p50, p95, IQR*) respectively describe the 5th, 50th, and 95th percentiles and the interquartile range of each species' "extended" thermal niche. "Extended" niches were from rasterized lichen herbarium data at 46,343 North American sites (Mexico, Canada and the U.S.), which were used for final calculations of thermal vulnerability. Abbreviations follow the FIA lichen communities indicator program, where first three letters generally apply to genus and next three to specific epithet.

Species	Rel freq	*p05*	*p50*	*p95*	*IQR*	Species	Rel freq	*p05*	*p50*	*p95*	*IQR*	Species	Rel freq	*p05*	*p50*	*p95*	*IQR*
Ahtsph	0.01	10.21	14.80	19.39	4.25	*Brypik*	<0.01	12.11	15.60	17.59	2.00	*Cavlop*	0.02	11.95	14.30	16.85	1.97
Aleims	0.04	14.28	17.00	20.31	2.80	*Brypsc*	<0.01	14.21	15.07	15.80	0.88	*Celcet*	0.01	13.13	17.20	21.99	3.95
Alelat	<0.01	13.30	18.40	22.70	4.25	*Brypse*	0.05	11.27	15.69	20.03	4.47	*Celchi*	<0.01	15.69	18.90	22.55	2.45
Alesar	0.16	10.82	15.30	20.38	3.97	*Brysim*	0.01	10.08	14.10	16.82	2.90	*Celoli*	0.01	16.71	19.00	22.08	1.85
Alevan	<0.01	14.23	17.26	19.67	2.40	*Bryspi*	<0.01	14.33	15.60	15.88	0.40	*Cetaur*	0.01	16.89	18.95	22.11	0.98
Anapal	0.01	17.50	21.89	27.33	5.17	*Brysub*	<0.01	13.41	15.25	16.24	1.75	*Cetcal*	<0.01	9.80	15.40	23.60	4.65
Anzcol	<0.01	17.95	23.50	27.47	5.02	*Bryten*	0.02	8.02	13.05	15.16	2.98	*Cetchl*	0.15	12.62	16.20	21.86	3.65
Brcpse	0.01	12.90	13.55	14.80	0.85	*Brytri*	0.05	12.46	16.27	19.52	4.00	*Cetcil*	0.03	15.84	20.68	24.95	4.29
Brybic	0.02	11.67	13.87	17.59	2.06	*Bulcon*	<0.01	26.58	27.50	27.92	0.37	*Cetcor*	<0.01	13.02	20.83	26.04	3.37
Brycap	0.08	11.70	15.90	19.40	3.60	*Bulgoe*	0.01	25.95	27.50	28.03	0.68	*Cetmer*	0.07	12.11	17.15	23.01	5.49
Brycar	0.01	12.45	13.60	14.39	0.65	*Bulisi*	<0.01	25.96	27.45	27.80	0.70	*Cetoak*	0.08	15.94	19.00	22.29	2.44
Brycer	0.01	12.06	13.20	14.40	1.20	*Bullae*	<0.01	25.94	27.58	28.00	0.37	*Cetorb*	0.14	14.54	17.82	20.40	2.48
Bryfre	0.08	11.48	16.39	21.43	4.58	*Canama*	<0.01	23.49	27.60	27.96	0.40	*Cetpal*	0.01	15.30	18.70	21.33	3.25
Bryfri	0.01	12.25	16.40	19.70	5.23	*Canamb*	<0.01	21.57	26.90	27.67	1.65	*Cetpla*	0.09	12.24	17.18	20.98	3.60
Bryfur	0.03	14.68	18.47	21.61	2.80	*Cancar*	0.04	21.38	27.31	28.20	1.82	*Cetsep*	<0.01	10.28	15.87	20.68	5.33
Bryfus	0.15	11.34	15.90	21.48	3.82	*Cancro*	0.01	21.06	25.50	26.50	3.90	*Cetsub*	<0.01	8.47	13.75	16.30	2.79
Brygla	0.03	11.27	14.20	18.79	3.13	*Cancry*	<0.01	26.70	27.56	28.28	0.40	*Cetvir*	<0.01	21.04	25.40	27.38	2.02
Bryimp	<0.01	10.95	14.80	19.60	4.01	*Cansal*	<0.01	22.61	27.60	28.23	0.47	*Cetweb*	<0.01	15.16	19.70	22.20	3.48
Brylan	0.01	9.99	13.80	17.51	3.04	*Cantex*	0.01	19.10	25.90	27.70	2.25	*Claalb*	<0.01	11.82	14.47	18.46	1.62
Brynad	0.01	12.63	16.76	19.79	2.93	*Cavhul*	0.05	11.72	14.50	17.43	2.20	*Clabac*	0.03	14.43	21.55	27.30	5.56

Species	Rel freq	*p05*	*p50*	*p95*	*IQR*	Species	Rel freq	*p05*	*p50*	*p95*	*IQR*	Species	Rel freq	*p05*	*p50*	*p95*	*IQR*
Clabel	0.02	7.44	13.00	17.70	3.50	*Cndcon*	0.16	16.20	22.70	27.60	5.30	*Fuslac*	0.01	12.36	13.91	14.75	1.10
Clacae	0.02	17.50	21.33	27.40	5.67	*Cndfib*	<0.01	18.96	23.70	27.80	4.88	*Fusram*	<0.01	13.41	13.45	13.49	0.05
Clacar	0.01	9.90	14.15	20.82	3.50	*Cndpac*	0.02	15.02	22.33	26.70	3.45	*Hetalb*	0.01	20.80	27.30	29.16	1.53
Clacen	<0.01	10.50	16.15	20.01	4.59	*Cocery*	<0.01	15.55	27.40	28.30	2.33	*Hetapp*	<0.01	19.62	21.25	27.29	3.07
Clachl	0.05	10.65	17.90	24.95	5.74	*Cocpal*	<0.01	17.38	26.40	28.30	2.95	*Hetbar*	<0.01	19.75	28.75	29.74	7.47
Clacon	0.17	12.90	18.82	26.03	5.40	*Colcon*	<0.01	18.75	24.98	28.23	6.04	*Hetcas*	<0.01	18.91	27.30	28.05	3.15
Clacri	0.01	15.20	20.60	27.23	5.71	*Colcur*	<0.01	10.83	17.26	19.66	4.16	*Hetech*	<0.01	24.57	27.40	28.53	1.40
Clacyl	0.01	18.78	23.00	27.90	4.72	*Colfur*	0.02	12.84	20.36	27.72	8.61	*Hetgal*	<0.01	13.43	21.23	27.73	7.90
Cladef	<0.01	9.40	14.80	19.50	4.03	*Colnig*	0.01	15.15	19.95	27.83	5.45	*Hetgra*	<0.01	18.23	24.75	28.12	5.37
Cladid	<0.01	19.21	26.00	28.10	5.07	*Colocc*	<0.01	17.08	19.90	27.18	5.40	*Hethyp*	<0.01	17.69	22.00	26.70	4.60
Clafim	0.03	11.30	17.30	23.30	5.14	*Colsub*	0.01	15.19	20.25	27.80	6.40	*Hetjap*	<0.01	11.60	19.90	27.73	7.18
Clafur	<0.01	12.50	19.40	26.50	6.60	*Dirapp*	<0.01	27.30	28.05	30.46	1.30	*Hetleu*	<0.01	14.64	19.45	28.66	6.20
Clagra	0.01	14.02	21.80	27.28	6.00	*Dircon*	<0.01	26.17	27.85	30.15	0.80	*Hetobs*	0.04	18.39	26.20	28.01	2.97
Clamac	0.02	14.24	19.65	27.50	4.50	*Dirpic*	<0.01	24.84	27.80	29.59	0.80	*Hetrug*	<0.01	17.18	22.20	28.20	4.30
Clanor	<0.01	13.07	15.70	19.15	2.90	*Dscint*	<0.01	12.46	16.50	25.55	7.27	*Hetspe*	0.02	15.30	21.80	27.60	6.25
Clapar	0.01	18.16	23.38	27.80	5.80	*Erisor*	<0.01	12.18	14.53	17.43	1.28	*Hetsqu*	<0.01	17.13	20.96	27.44	3.75
Clapex	<0.01	20.18	25.56	28.00	3.90	*Essida*	0.04	14.77	18.27	22.40	3.09	*Hettro*	<0.01	17.60	22.30	28.20	6.10
Claple	<0.01	9.90	17.65	25.50	7.48	*Evediv*	<0.01	9.45	13.35	26.35	6.02	*Hphadg*	0.01	19.17	24.10	28.52	3.60
Clapyx	0.01	8.94	18.20	25.22	7.10	*Evemes*	0.09	13.07	18.40	21.80	3.67	*Hphsyn*	<0.01	20.69	25.20	29.10	4.03
Claram	<0.01	16.92	22.07	27.70	5.50	*Evepru*	0.13	14.87	19.10	25.02	3.54	*Htrafr*	<0.01	17.24	19.23	22.93	1.77
Clarei	<0.01	15.10	20.20	24.36	3.40	*Evscat*	<0.01	16.90	17.82	19.78	0.84	*Htrcro*	<0.01	16.84	20.40	27.20	5.57
Clasqu	0.05	11.53	18.45	26.58	6.37	*Flabal*	<0.01	19.18	23.02	27.47	4.63	*Htrimb*	<0.01	14.84	20.00	26.91	4.52
Classq	0.01	13.62	15.90	19.08	2.90	*Flacap*	0.24	16.70	21.34	26.97	5.12	*Htrlae*	<0.01	14.57	20.40	26.72	4.48
Clasul	0.01	9.88	13.70	18.30	3.30	*Fpudar*	<0.01	18.17	21.70	25.96	2.47	*Htrliv*	0.04	21.37	26.62	28.20	2.34
Clatra	0.03	13.30	16.35	20.47	3.46	*Fpufla*	0.04	15.27	20.54	25.70	3.24	*Htross*	<0.01	21.33	27.22	28.00	1.82
Claumb	0.02	12.29	15.21	19.01	3.49	*Fpupra*	<0.01	13.24	20.70	27.37	5.59	*Htrpse*	<0.01	15.01	17.20	21.81	3.90
Claver	<0.01	12.03	16.90	21.88	4.32	*Fpusor*	0.07	16.23	21.10	26.12	3.60	*Htrpul*	<0.01	12.09	19.10	28.34	6.06

Species	Rel freq	p05	p50	p95	IQR	Species	Rel freq	p05	p50	p95	IQR	Species	Rel freq	p05	p50	p95	IQR
Htrpus	<0.01	21.40	26.20	27.70	2.22	*Koebif*	<0.01	15.36	21.80	26.28	5.70	*Lobscr*	0.03	10.91	15.70	19.56	4.15
Htrrev	<0.01	14.14	18.30	22.65	3.51	*Leisor*	<0.01	14.56	15.47	17.07	0.78	*Lpcalb*	<0.01	15.06	20.27	24.90	4.55
Htrroc	<0.01	16.55	20.85	23.11	3.86	*Lepars*	<0.01	14.90	20.80	26.16	3.30	*Melalb*	<0.01	13.15	19.18	21.76	3.33
Htrsho	0.01	19.05	21.84	27.57	4.51	*Lepaus*	<0.01	21.52	27.10	28.50	2.20	*Melele*	0.13	9.30	18.00	23.30	5.50
Htrsin	0.03	12.31	15.20	20.96	3.20	*Lepbre*	<0.01	13.23	14.60	21.09	1.53	*Melexa*	0.01	13.47	18.97	23.69	3.32
Htrvir	<0.01	18.78	20.30	23.27	2.03	*Lepbur*	<0.01	13.00	19.80	25.54	7.65	*Melexl*	0.18	11.61	16.20	21.11	4.70
Hypapi	0.07	12.10	14.82	19.23	3.34	*Lepcel*	<0.01	15.18	17.18	18.49	1.99	*Melgla*	0.05	18.16	22.00	24.48	4.50
Hypaus	0.01	9.27	13.50	16.93	3.05	*Lepcor*	<0.01	13.76	18.10	24.55	4.74	*Melhal*	0.01	16.69	18.30	20.70	1.51
Hypbit	0.01	10.43	13.80	17.15	2.60	*Lepcrt*	<0.01	16.98	24.40	27.82	5.65	*Melmul*	0.01	13.21	18.15	22.95	4.17
Hypcan	<0.01	11.60	14.60	21.05	4.25	*Lepcya*	0.02	16.34	23.30	28.00	7.57	*Meloli*	0.01	11.68	17.70	20.66	4.07
Hypdup	0.04	11.40	13.97	17.50	1.79	*Lepfur*	0.01	14.50	20.40	25.32	4.30	*Melsar*	0.01	15.88	20.40	24.02	2.80
Hypent	0.11	12.14	15.59	20.40	3.60	*Leplac*	<0.01	15.58	18.40	22.27	1.90	*Melsel*	0.04	12.18	17.00	21.49	3.62
Hypfar	<0.01	12.15	15.40	18.06	3.10	*Leplic*	0.01	13.80	18.70	23.75	3.18	*Melsep*	0.02	10.70	16.80	20.34	5.40
Hyphet	<0.01	13.85	15.70	18.26	1.22	*Lepmil*	<0.01	18.90	25.47	28.90	4.60	*Melsol*	0.2	13.38	19.40	25.00	5.32
Hypims	0.18	13.35	17.50	23.16	4.24	*Leppol*	0.01	13.13	17.50	21.74	3.73	*Melsub*	0.13	14.87	19.18	22.70	2.80
Hypina	0.08	13.18	16.49	19.89	3.51	*Lepsat*	0.01	10.10	16.00	22.05	5.67	*Meltra*	<0.01	12.49	15.30	19.70	3.25
Hypkro	0.01	16.85	18.65	21.46	1.55	*Lepter*	<0.01	15.55	18.90	19.46	1.08	*Mensub*	<0.01	15.57	18.00	20.78	1.85
Hypocc	0.06	11.00	16.44	20.81	4.15	*Letcol*	0.1	12.20	18.06	23.93	5.30	*Menter*	0.02	13.98	17.70	21.18	2.48
Hypoce	0.02	12.74	13.95	16.62	2.10	*Letvul*	0.21	12.16	17.19	22.64	4.90	*Myeaur*	0.11	18.30	23.50	27.79	5.65
Hypphy	0.27	11.28	17.00	22.00	4.80	*Lobamp*	<0.01	12.50	14.30	25.38	5.75	*Myegal*	0.06	17.64	21.80	27.16	6.10
Hyppul	<0.01	11.46	13.60	14.95	0.81	*Lobhal*	0.01	11.00	15.50	19.66	4.70	*Myemet*	<0.01	17.07	20.25	23.69	0.78
Hyprug	0.01	11.59	15.05	18.55	2.77	*Loblin*	0.03	8.60	12.65	15.83	3.01	*Nepbel*	0.03	10.50	15.06	20.10	4.72
Hyptub	0.13	13.70	17.60	21.50	3.45	*Lobore*	0.04	10.48	14.90	19.00	2.92	*Nephel*	0.03	12.61	18.20	26.07	4.90
Hypvit	0.02	9.97	14.90	18.49	3.97	*Lobpul*	0.08	12.47	17.80	23.18	4.30	*Nepisi*	0.01	9.25	13.35	15.67	2.46
Hypwil	0.05	14.60	16.08	18.47	1.64	*Lobque*	0.02	16.87	19.42	24.98	2.59	*Neplae*	0.01	13.33	16.23	20.01	3.02
Imsale	0.03	13.66	19.07	25.07	4.26	*Lobrav*	<0.01	22.12	27.51	28.19	1.02	*Nepocc*	<0.01	11.64	15.40	17.90	2.70
Imspla	0.01	16.17	20.40	24.82	3.24	*Lobret*	<0.01	9.00	13.30	14.70	2.10	*Neppar*	0.02	10.54	16.00	20.66	5.19

Species	Rel freq	p05	p50	p95	IQR	Species	Rel freq	p05	p50	p95	IQR	Species	Rel freq	p05	p50	p95	IQR
Nepres	0.03	12.30	16.70	20.70	4.00	*Pcyper*	<0.01	12.75	18.23	20.93	2.61	*Phoele*	<0.01	17.32	20.90	25.36	3.35
Niecep	<0.01	14.38	19.60	28.72	9.80	*Pcyrai*	<0.01	13.70	15.50	18.40	2.27	*Phoent*	0.04	14.90	20.50	25.50	4.40
Nodabb	0.11	13.14	17.00	22.52	3.95	*Pelbri*	0.02	10.87	14.43	18.85	2.59	*Phofal*	<0.01	16.02	22.50	26.00	3.70
Nodore	0.05	12.16	16.98	22.16	4.18	*Pelcol*	0.06	12.20	16.30	22.63	4.42	*Phoisi*	0.03	15.76	21.05	26.30	4.24
Panahl	<0.01	11.98	14.20	19.08	3.75	*Peleli*	<0.01	12.20	18.30	22.54	3.10	*Pholeu*	0.01	18.41	22.23	26.20	4.54
Pancon	<0.01	12.47	18.20	23.88	3.61	*Pelmem*	0.01	10.66	15.10	21.74	4.50	*Phoper*	0.04	13.84	19.40	24.26	4.33
Panled	0.01	12.50	15.55	21.80	4.86	*Pelneo*	0.01	10.80	14.85	20.40	3.75	*Phyads*	0.19	13.67	19.70	24.33	4.41
Panleu	<0.01	14.85	22.22	27.50	7.44	*Pelpol*	<0.01	9.76	17.40	25.97	5.92	*Phyaip*	0.12	12.58	20.82	28.11	5.82
Panmed	<0.01	15.58	19.70	23.34	4.65	*Pelpra*	<0.01	12.34	19.70	26.00	4.83	*Phyaln*	<0.01	10.63	15.90	22.97	6.00
Panpac	0.01	13.36	18.15	21.72	4.03	*Pevcla*	<0.01	15.19	18.40	21.06	2.00	*Phyame*	0.04	20.46	25.80	28.53	3.84
Panrub	<0.01	14.38	19.10	27.51	4.73	*Pevcon*	0.01	14.49	19.10	22.76	2.59	*Phybiz*	0.09	14.90	21.80	28.78	5.56
Pantav	<0.01	14.64	20.52	27.81	7.79	*Pevint*	0.01	11.88	18.82	27.70	5.84	*Phycae*	0.01	9.10	17.27	24.50	7.00
Parbar	<0.01	16.50	19.50	21.34	2.10	*Phaadi*	0.01	17.56	22.20	26.67	4.63	*Phycri*	<0.01	21.95	27.65	28.64	0.73
Parfer	<0.01	16.38	18.34	18.98	0.67	*Phacil*	0.03	15.06	22.77	27.61	5.50	*Phydim*	0.08	15.50	22.30	27.73	4.88
Parhyg	0.1	12.62	16.43	21.93	4.10	*Phaery*	<0.01	17.70	20.05	22.20	2.65	*Phydub*	0.01	10.17	18.40	25.41	6.51
Parpse	0.02	13.14	14.90	18.98	2.40	*Phahir*	0.06	17.29	23.00	28.10	4.40	*Phymil*	0.18	18.40	22.43	27.30	4.66
Parsax	0.04	9.30	15.90	22.50	5.90	*Phahis*	0.01	13.75	19.60	26.10	4.80	*Phyneo*	0.01	21.80	27.70	28.76	1.00
Parsqu	0.08	13.19	18.80	23.41	3.57	*Phahrt*	<0.01	17.70	23.30	27.80	5.35	*Physem*	<0.01	15.11	20.05	22.97	3.15
Parsul	0.32	10.80	17.72	23.10	5.70	*Phains*	<0.01	20.96	24.90	27.45	2.40	*Physor*	<0.01	21.56	27.70	29.34	0.80
Pclchl	0.03	18.09	22.93	27.57	4.68	*Phakai*	<0.01	12.65	19.00	27.45	7.20	*Physte*	0.13	15.55	21.80	27.60	5.00
Pclmel	0.01	18.97	23.20	26.90	3.10	*Phanig*	0.01	14.31	21.75	25.32	4.40	*Phyten*	0.04	13.63	18.20	24.12	4.36
Pclnep	<0.01	13.43	20.20	27.38	5.10	*Phaorb*	0.03	14.69	20.75	25.90	4.47	*Phyund*	<0.01	18.53	28.60	32.61	7.38
Pcyano	0.04	13.03	15.89	21.21	4.66	*Phapus*	0.1	17.00	21.50	26.70	5.70	*Plagla*	0.15	11.38	16.30	21.30	4.36
Pcyant	0.02	14.15	17.60	22.55	4.74	*Pharub*	0.21	17.65	21.90	27.40	5.66	*Plaher*	0.08	13.24	15.60	20.46	2.90
Pcyaur	<0.01	14.97	26.45	28.16	6.74	*Phoame*	0.03	14.38	21.00	26.02	4.23	*Plalac*	0.03	10.73	14.80	21.77	5.88
Pcycro	0.02	12.39	16.33	22.29	4.42	*Phocal*	<0.01	20.58	21.98	24.60	2.75	*Planor*	0.06	11.43	14.58	17.77	2.30
Pcymal	<0.01	12.74	13.30	15.90	2.20	*Phodet*	0.02	13.79	19.40	24.70	3.22	*Plaste*	0.05	14.77	17.94	21.36	3.31

Species	Rel freq	*p05*	*p50*	*p95*	*IQR*	Species	Rel freq	*p05*	*p50*	*p95*	*IQR*	Species	Rel freq	*p05*	*p50*	*p95*	*IQR*
Platuc	0.03	15.96	19.20	24.03	2.28	*Pmotin*	0.01	20.81	27.43	28.55	1.35	*Pyxber*	<0.01	20.98	27.70	28.72	0.80
Pllpar	<0.01	11.83	15.15	19.25	3.03	*Pmoult*	<0.01	22.49	27.20	28.11	1.27	*Pyxcae*	0.01	23.40	27.40	28.21	1.64
Plltri	0.01	11.35	17.80	22.13	3.42	*Pmoxan*	<0.01	20.90	26.70	27.77	2.81	*Pyxesc*	<0.01	27.07	27.70	28.66	0.50
Pmoarn	0.02	13.41	17.35	26.57	4.91	*Pmozol*	<0.01	18.85	26.45	27.64	2.30	*Pyxsor*	0.06	17.43	21.96	27.80	6.00
Pmoaus	<0.01	17.50	26.20	29.17	2.50	*Pnaque*	0.01	19.66	22.90	27.24	3.57	*Pyxsub*	0.01	23.96	26.60	28.20	2.00
Pmocet	<0.01	19.86	24.66	28.01	4.77	*Polcon*	0.01	13.51	14.65	17.29	1.97	*Ramame*	0.05	16.99	20.78	27.90	5.49
Pmochi	0.02	15.15	20.10	27.80	6.73	*Polden*	<0.01	14.10	16.10	27.95	12.02	*Ramcom*	<0.01	26.00	28.20	30.04	1.40
Pmocri	0.01	14.87	20.83	28.00	7.96	*Popamb*	0.13	11.09	15.60	21.80	4.80	*Ramden*	<0.01	27.40	28.20	29.66	1.20
Pmocrs	<0.01	17.48	27.66	28.73	0.78	*Popcap*	0.01	15.62	18.66	20.29	1.60	*Ramdil*	0.04	13.30	17.50	20.60	3.13
Pmodil	0.01	19.88	27.50	28.62	1.50	*Pophyp*	0.11	11.02	15.40	20.29	4.52	*Ramfar*	0.1	12.90	17.88	24.85	4.08
Pmoend	<0.01	22.92	27.90	28.57	0.60	*Popsub*	<0.01	24.64	27.33	27.90	1.21	*Ramlep*	<0.01	14.96	19.50	26.96	6.23
Pmoeur	0.01	16.00	24.70	29.32	6.50	*Ppasph*	<0.01	16.78	27.70	28.34	0.50	*Rammen*	0.01	14.45	18.67	27.41	6.64
Pmogar	<0.01	23.95	27.40	28.16	2.20	*Ppshor*	0.02	19.02	26.60	27.88	3.80	*Ramobt*	<0.01	12.65	18.10	22.45	4.65
Pmohai	<0.01	16.50	24.80	27.70	4.80	*Ppsmin*	0.04	19.12	26.60	28.00	3.65	*Rampol*	<0.01	13.92	18.40	24.48	4.10
Pmohyl	<0.01	18.61	27.30	28.86	1.93	*Ppsspu*	<0.01	20.50	27.50	28.17	0.82	*Ramroe*	0.02	12.04	15.30	19.23	3.85
Pmohyp	0.07	20.80	25.80	29.00	3.00	*Psohyp*	<0.01	6.35	13.03	18.38	3.50	*Ramsin*	0.01	13.30	19.45	25.40	4.80
Pmolou	<0.01	18.32	27.90	28.68	0.60	*Punapp*	<0.01	16.91	20.00	24.89	2.98	*Ramsle*	0.01	14.62	20.10	27.70	7.20
Pmomad	<0.01	20.57	26.15	27.66	3.05	*Punbol*	0.01	19.37	23.25	28.43	3.88	*Ramste*	<0.01	26.58	27.90	29.93	1.16
Pmomar	0.02	19.40	23.10	26.79	3.85	*Punbor*	<0.01	16.02	20.60	28.32	4.23	*Ramthr*	0.01	12.86	16.62	19.41	3.20
Pmomel	<0.01	16.70	26.60	27.90	5.90	*Puncas*	<0.01	17.11	20.43	25.53	4.21	*Ramwil*	<0.01	25.39	27.83	29.49	0.91
Pmomic	0.02	24.53	27.20	28.40	1.64	*Punhyp*	<0.01	13.99	22.00	29.10	5.30	*Rimcet*	0.01	16.62	25.38	28.86	5.80
Pmoper	0.02	16.43	26.70	29.02	3.90	*Punmis*	0.02	20.53	25.31	26.90	1.80	*Rimdif*	<0.01	24.31	24.45	24.59	0.15
Pmoram	0.01	19.56	27.50	28.14	1.00	*Punper*	0.03	14.82	19.99	27.31	5.55	*Rimret*	0.05	17.94	25.75	28.21	4.15
Pmorig	0.01	26.75	27.80	29.19	0.65	*Punred*	<0.01	19.24	20.60	21.32	1.20	*Rimsub*	0.01	19.23	26.50	28.02	2.44
Pmostu	0.01	13.02	20.80	27.46	5.11	*Punrud*	0.22	17.60	22.90	28.00	6.27	*Sphglo*	0.11	6.36	13.60	19.08	5.08
Pmosub	<0.01	18.08	25.55	27.87	4.29	*Punsem*	0.01	18.41	25.33	28.62	4.56	*Sphmel*	<0.01	9.53	14.20	16.15	0.64
Pmosul	<0.01	27.30	27.81	28.88	0.46	*Punsub*	0.07	17.96	19.80	24.34	1.80	*Stibea*	<0.01	14.64	21.07	27.60	5.32

Species	Rel freq	p05	p50	p95	IQR	Species	Rel freq	p05	p50	p95	IQR	Species	Rel freq	p05	p50	p95	IQR
Stiful	0.03	12.70	17.50	22.34	3.75	*Usnlon*	0.03	13.76	17.00	19.72	3.20	*Xanore*	0.04	13.94	19.50	24.40	4.15
Stilim	0.02	13.44	15.80	20.87	3.04	*Usnmad*	<0.01	14.26	16.85	20.42	2.85	*Xanpar*	<0.01	15.36	19.90	27.62	4.10
Stiwei	0.01	13.03	21.50	28.29	9.38	*Usnmer*	<0.01	14.62	19.01	24.10	3.07	*Xanpol*	0.07	13.90	19.10	25.49	4.20
Stiwri	<0.01	12.89	15.10	26.32	5.50	*Usnmut*	0.01	18.65	26.23	28.10	5.38	*Xanten*	<0.01	18.54	23.70	30.75	4.42
Sulbad	<0.01	15.71	16.60	19.50	2.00	*Usnnid*	<0.01	14.80	14.80	16.96	1.20	*Xanulo*	0.01	17.20	21.30	24.18	2.60
Telchr	<0.01	19.46	25.50	29.47	4.75	*Usnocc*	<0.01	13.86	14.60	15.98	1.40						
Telexi	<0.01	17.03	27.55	29.47	3.54	*Usnpar*	<0.01	16.34	21.93	26.82	2.90						
Telfla	<0.01	14.11	22.90	29.35	9.92	*Usnpcf*	0.01	13.82	17.80	20.27	2.90						
Tucari	<0.01	13.38	16.52	20.45	4.45	*Usnpli*	<0.01	14.51	17.80	21.27	2.71						
Tucfen	0.02	16.61	23.11	27.60	6.46	*Usnrub*	0.01	15.40	24.88	27.74	6.61						
Tucpse	<0.01	20.84	21.20	23.99	1.75	*Usnsca*	0.03	11.39	15.90	20.07	3.48						
Usncad	<0.01	16.00	20.50	27.30	7.10	*Usnsfu*	<0.01	16.43	19.20	25.80	2.05						
Usncav	0.01	12.12	17.80	21.06	2.80	*Usnssc*	<0.01	17.20	25.30	27.70	6.10						
Usncer	0.01	14.93	19.28	27.55	4.00	*Usnsst*	0.02	11.84	16.15	22.20	4.33						
Usncha	<0.01	12.80	14.46	19.79	3.15	*Usnstr*	0.05	18.65	26.70	28.60	4.63						
Usncor	0.02	13.90	18.10	26.00	5.25	*Usnsub*	0.05	13.82	18.10	22.18	3.40						
Usncyl	<0.01	13.65	17.30	20.80	2.85	*Usntri*	<0.01	15.95	22.27	29.12	8.40						
Usndip	<0.01	13.57	19.30	27.17	3.57	*Usnwas*	<0.01	14.10	18.40	21.17	3.23						
Usnesp	<0.01	14.56	17.23	25.48	3.88	*Usnwir*	0.03	14.19	17.75	21.91	3.10						
Usnfil	0.07	13.63	17.30	20.27	2.75	*Vulcan*	0.05	12.84	18.10	24.05	4.04						
Usnfra	0.01	14.03	16.60	23.75	2.93	*Vulpin*	0.03	10.81	16.15	20.55	4.99						
Usngla	0.01	13.79	17.45	23.14	3.93	*Xancan*	0.03	9.30	17.98	27.66	8.47						
Usngls	<0.01	13.17	17.91	21.78	3.49	*Xanfal*	0.1	15.66	21.91	26.80	4.44						
Usnhes	<0.01	15.50	18.70	21.80	2.55	*Xanful*	0.06	13.56	19.70	27.94	5.70						
Usnhir	0.11	14.48	19.37	24.66	3.56	*Xangal*	0.02	14.66	19.20	23.58	5.30						
Usnint	<0.01	13.62	19.11	25.09	5.10	*Xanhas*	0.04	16.25	20.48	24.00	3.21						
Usnlap	0.12	12.00	16.90	22.13	5.13	*Xanmon*	0.11	14.49	19.40	24.62	4.63						