

## AN ABSTRACT OF THE THESIS OF

Kaleigh Spickerman for the degree of Master of Science in Botany and Plant Pathology presented on June 11, 2015

Title: Lichen Functional Trait Variation Along an East-West Climatic Gradient in Oregon and Among Habitats in Katmai National Park, Alaska

Abstract approved: \_\_\_\_\_

Bruce McCune

Functional traits of vascular plants have been an important component of ecological studies for a number of years; however, in more recent times vascular plant ecologists have begun to formalize a set of key traits and universal system of trait measurement. Many recent studies hypothesize global generality of trait patterns, which would allow for comparison among ecosystems and biomes and provide a foundation for general rules and theories, the so-called “Holy Grail” of ecology. However, the majority of these studies focus on functional trait patterns of vascular plants, with a minority examining the patterns of cryptograms such as lichens. Lichens are an important component of many ecosystems due to their contributions to biodiversity and their key ecosystem services, such as contributions to mineral and hydrological cycles and ecosystem food webs. Lichens are also of special interest because of their reliance on atmospheric deposition for nutrients and water, which makes them particularly sensitive to air pollution. Therefore, they are often used as bioindicators of air pollution, climate change, and

general ecosystem health. This thesis examines the functional trait patterns of lichens in two contrasting regions with fundamentally different kinds of data.

To better understand the patterns of lichen functional traits, we examined reproductive, morphological, and chemical trait variation along precipitation and temperature gradients in Oregon. Specifically, we measured traits of 102 macrolichen species collected from 166 USDA Forest Service program for Forest Inventory and Analysis (FIA) plots. These plots were located in a more-or-less continuous swath across Oregon between 43°W and 45°W. Plots were grouped into seven regions (the Oregon Coast, Coast Range, Willamette Valley, Western Cascades, High Cascades, Eastern Cascades, and Eastern Oregon). Using multivariate analysis techniques we found strong linear and nonlinear trait patterns along precipitation and temperature gradients, and were able to characterize the seven main regions of Oregon by the relative abundance of lichen traits.

The literature on what lichen traits are most common in which habitats is sparse and anecdotal; understanding trait-habitat patterns could have management implications due to lichen importance as bioindicators and animal forage. Understanding how key traits are distributed among habitats could provide insight into potential air pollution impacts on certain habitats, animal movement among habitats, etc. To examine trait-habitat patterns, we measured the reproductive, morphological, and chemical traits of 429 lichen species collected haphazardly (without a formal sampling framework) from ten distinct habitats within Katmai National Park in southwest Alaska as part of a taxonomic inventory. Using multivariate analysis techniques we grouped habitats based on the expression of lichen traits and described the relative abundance of each trait in different habitats. The second goal of this study was to examine the potential

usefulness of herbarium collections in ecological studies of this type. Herbarium specimens are a large potential resource that is generally unused in ecological studies due to concerns over potential bias and noise introduced by variation in collection methods. However, recent work has suggested that herbarium specimens may yield more useful results than previously thought and could be a valid resource for ecological studies. The data for our study were collected in a haphazard manner for a floristic inventory, similar to the collection methods used for many herbarium specimens. The patterns that we observed indicates that herbarium specimens may be a good resource for future research.

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Lichen Functional Trait Variation Along an East-West Climatic Gradient in Oregon and Among  
Habitats in Katmai National Park, Alaska

by  
Kaleigh Spickerman

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

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Kaleigh Spickerman, Author

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## CONTRIBUTION OF AUTHORS

Dr. Bruce McCune assisted with the study design, data interpretation, and synthesis for both chapters of this thesis. Portions of the data used in Chapter 2 were originally published in 2007 by Dr. Linda Geiser and Dr. Peter Neitlich, and in 2015 by Dr. Heather Root, Dr. Linda Geiser, Dr. Sarah Jovan, and Dr. Peter Neitlich. Dr. Bruce McCune, Dr. Lucia Muggia, Dr. Peter Nelson, Dr. Tor Tønsberg, and James Walton assisted with data collection for Chapter 3. Elisa Alphandary compiled the chemical traits used in both Chapters 2 and 3.

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## Chapter 1: Introduction

Functional traits have been an important component of ecological and floristic studies for a long time. Since the early days of plant classification, taxonomists and ecologists have used basic traits (such as number of flower petals, leaf arrangement, etc.) to place plants into sensible groups and study their associations (Gleason 1926). In more recent years, plant ecologists have formally developed a set of key traits and a universal system of measurements, and the study of functional traits has become the focus of a large body of recent literature (Grime and Hunt 1975, Weiher *et al.* 1999, Cornelissen *et al.* 2003, Pérez-Harguindeguy *et al.* 2013).

Two of the main goals of community ecology are prediction and the establishment of general assembly and response rules; when trying to realize these goals, it is now widely recognized that classifying plants based on their functional traits has a strong advantage over classifying them based on their taxonomy (Keddy 1992, Weiher and Keddy 1995, Cornelissen *et al.* 2003, McGill *et al.* 2006, Mouillot *et al.* 2013). Although plant ecologists are still striving to form general assembly and response rules based on traits, several studies have demonstrated a global generality of trait patterns (Reich *et al.* 1997, Reich *et al.* 1999, Díaz *et al.* 2004, Wright *et al.* 2004). This global generality allows for comparison among ecosystems and biomes, and provides a foundation for ecosystem or regional models of vegetation productivity, distribution, etc. Plant functional traits can be used to understand the effects of disturbance on communities (Mouillot *et al.* 2013), links between diversity and ecosystem processes (Díaz and Cabido 2001, Lavorel and Garnier 2002), and, of increasing importance, can provide a tool for prediction of how plant communities may respond to climate change (Díaz and Cabido 1997, Soudzilovskaia *et al.* 2013).

Despite the overwhelming amount of evidence supporting the importance of functional traits to ecology, and the large body of literature regarding the functional traits of vascular plants, there is a dearth of knowledge regarding functional traits of lichens in the context of community ecology. Lichens are an important component of global ecosystems in part due to their significant contributions to nutrient cycling (Knops *et al.* 1991) and function as food sources and habitat providers for numerous vertebrate and invertebrate species (Sharnoff 1994, Brodo *et al.* 2001). Additionally, lichens are important indicators of ecosystem health (McCune 2000), climate change (Sancho *et al.* 2007, Root *et al.* 2015), and air quality (Conti and Cecchetti 2001). Although lichen diversity and species composition are widely accepted as effective indicators of environmental change, little is known about the potential effectiveness of lichen functional traits as ecological indicators (Giordani *et al.* 2012).

A first step towards understanding this is to describe how functional traits vary along environmental gradients. Some studies do support the potential for lichen functional traits to provide tools for prediction and formation of general assembly and response rules (Ellis and Coppins 2006, Johansson *et al.* 2007, Giordani *et al.* 2012, Rapai *et al.* 2012, Merinero *et al.* 2015, Matos *et al.* 2015, Nelson *et al.* 2015); however, the exploration of lichen functional traits as a tool of community ecology is still in its infancy. Additionally, much of the current lichen trait research uses binary or multistate categorical traits (e.g., presence/absence of cyanobacteria as the photobiont, growth form type, and presence/absence of various secondary substances; Giordani *et al.* 2012) or characterizes lichens by their functional groups (e.g., foliose green-algal lichens and leprose lichens; Ellis and Coppins 2006). It is generally preferable to measure continuous traits (Weiher *et al.* 1999), but only a few more recent studies have measured

continuous traits of lichens (e.g., specific thallus mass, water holding capacity, and relative growth rate; Bidussi and Gauslaa 2015, Merinero *et al.* 2015).

Chapter 2 of this thesis focuses on how functional traits vary along climatic gradients such as precipitation and temperature. This section uses epiphytic lichen data, collected as part of the US Forest Service Forest Inventory and Analysis program, to represent communities along a climatic gradient in Oregon from the coast inland to the Idaho border. Trait composition and environmental variables were compared to lichen community gradients using nonmetric multidimensional scaling and visualized using hilltop plots (Nelson *et al.* 2015). The majority of the traits measured were binary and multistate categorical; however, lichen height and average volume of reproductive propagules were measured as quantitative trait values for both Chapters 2 and 3.

Determining the distribution of functional traits (especially those with ecosystem services, such as presence of nitrogen fixing cyanobacteria) in the environment is important for both scientists and resource managers. With the goal of enhancing our knowledge of trait distributions, Chapter 3 explores how functional traits are grouped in different habitats in Katmai National Park, Alaska. Trait patterns were examined using nonmetric multidimensional scaling and two-way cluster analysis. This chapter also examines the usefulness of data collected in a haphazard manner, common to taxonomic inventories and herbarium specimens, to distinguish ecological patterns. The data used in this chapter were collected as part of a collaborative floristic inventory between Oregon State University and the National Park Service.

Chapter 4 summarizes commonalities and differences in the occurrence of lichen traits between two very different systems, the Pacific coastal and inland forests of Oregon and the

boreal forests and alpine tundra of southwest Alaska. Specifically, are relationships among traits similar between the two regions? If traits are to provide the promised universality in ecological organizing principles, then the answer should be “yes”. If not, then we need to look deeper into the problem of how the expression of lichen traits depends on environment.

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## Chapter 2: Lichen functional trait variation along environmental gradients in Oregon

### 1. INTRODUCTION:

Lichens are an important part of many ecosystems around the world, but play an especially large role in Pacific Northwest forest ecosystems where they contribute greatly to biodiversity, with over 1,000 described species (McCune and Geiser 2009). Besides their contributions to biodiversity, lichens play an important role in forest mineral cycles (Knops *et al.* 1991). For example, *Lobaria oregana* (a common Pacific Northwest lichen) can fix up to 2.6-16.5 kg N<sub>2</sub> ha<sup>-1</sup> yr<sup>-1</sup> in western Oregon forests (Antoine 2004), contributing large quantities of nitrogen to the ecosystem. Lichens also play an important part in the forest food web, providing forage material for various mollusks (Asplund and Gauslaa 2010), northern flying squirrels (*Glaucomys sabrinus*; Maser *et al.* 1986), mountain goats (*Oreamnos americanus*; Fox and Smith 1988), as well as numerous other vertebrates and invertebrates (McCune and Geiser 2009). Besides playing key roles in the forest ecosystem, lichens are also important from a management standpoint as bioindicators of air pollution (Conti and Cecchetti 2001), climate change (Sancho *et al.* 2007), and forest health (McCune 2000). Their ecosystem importance and effectiveness as bioindicators (Jovan and McCune 2004) have resulted in a great deal of knowledge about lichen species diversity and distributions. However, very little is known about lichen functional trait distributions (Giordani *et al.* 2012).

Functional trait analyses have been an important part of vascular plant ecology for a number of years, with several convincing arguments for their advantage over traditional taxonomic analyses when attempting to establish general community assembly rules and make predictions (Cornelissen *et al.* 2003, McGill *et al.* 2006, Mouillot *et al.* 2013). Despite the

evidence supporting the use of functional trait analyses in ecological studies, there is a general gap in the literature when it comes to lichen functional trait analyses. In recent years several papers have been published, highlighting the need for these types of analyses and demonstrating their potential (Giordani *et al.* 2012, Giordani *et al.* 2014, Matos *et al.* 2015, Nelson *et al.* 2015). This study will add to the literature regarding lichen functional trait patterns relating to climate; specifically by exploring lichen species and functional trait composition along environmental gradients such as annual precipitation, temperature, and continentality.

The analyses are restricted to Oregon, a state with a widely studied lichen flora for which functional trait information is widely available in the literature. Although previous lichen studies have been conducted in Oregon, the majority of these have focused on a specific area, such as the Willamette Valley or the Coast Range (e.g. Geiser and Neitlich 2007). This study will differ from previous studies by using US Forest Service Forest Inventory and Analysis plots running along a transect from the Pacific coast to the Idaho border to address the question, what are the relationships between lichen functional traits and environmental variables in Oregon?

The first step towards answering this question is choosing which traits to measure. One approach is to list the basic challenges faced by the organism, and then determine the traits that provide a solution to each challenge (Weiher *et al.* 1999). Lichens face many of the same challenges as vascular plants: need for dispersal, establishment, and persistence, which involves resource acquisition and withstanding competition, stress, and disturbance (Brodo *et al.* 2001). Lichens are also poikilohydric and therefore universally face water balance challenges. Ideally, ecologists would measure the traits that directly address these challenges, such as dispersal distance, life span, palatability, etc.; however, these “hard” traits are often difficult, time

consuming, and/or expensive to measure. Therefore, we must find a set of simple to measure “easy” traits (Table 2.1) that can serve as proxies for the more difficult traits (Weiher *et al.* 1999). After choosing a set of easy traits, I will attempt to determine the relationships between these traits and a set of precipitation, temperature, and elevation variables. It is important to note that lichens do not respond directly to elevation as a variable, but instead respond to the climatic factors that change with elevation; therefore, in this study elevation will be used as a proxy for other more complicated to measure variables such as wind speed and UV light.

**Table 2.1.** Common challenges faced by lichens and the associated easy to measure traits that address them.

<b>Challenge</b>	<b>Trait</b>
Dispersal	Reproductive method <ul style="list-style-type: none"> <li>• Sexual spores</li> <li>• Asexual isidia, soredia, and lobules</li> </ul> Reproductive propagule volume(s)
Establishment	Reproductive method <ul style="list-style-type: none"> <li>• Sexual spores</li> <li>• Asexual isidia, soredia, and lobules</li> </ul> Reproductive propagule volume(s)
Persistence: resource acquisition	Photobiont <ul style="list-style-type: none"> <li>• Bipartite: cyanobacterial</li> <li>• Bipartite: green algal</li> <li>• Tripartite: cyanobacteria and green algae</li> </ul>
Persistence: competition	Allelopathic chemicals Height/distance from substrate
Persistence: UV light stress	UV screening chemicals
Persistence: disturbance due to herbivory	Chemicals that discourage herbivory
Water balance	Height/distance from substrate Growth form <ul style="list-style-type: none"> <li>• Fruticose</li> <li>• Foliose</li> <li>• Crustose</li> <li>• Homoiomerous gelatinous</li> </ul>

*Dispersal hypotheses* – Dispersal distance is a logical trait to address the dispersal challenge. This is difficult to measure; so instead, dispersal mode (asexual or sexual reproduction) and size of the reproductive propagules can be used as proxy traits (Weiher *et al.* 1999). After they disperse, lichens must then establish themselves, which is also addressed by the type and size of their reproductive propagules. Spore discharge is restricted to periods of time when the thallus is wet (Garrett 1971); therefore, I could expect to see (Hypothesis 1: **H1**) a high relative frequency of sexually reproducing species in areas with high precipitation (e.g. western Oregon). Large propagules (such as asexually produced soredia, isidia, and lobules) have limited dispersal (Walser 2004), and are potentially less likely to be dispersed via wind, relying instead upon water trickles and animals. This could result in a (**H2**) high relative frequency of large propagules in areas with high precipitation. Small propagules are easily dispersed by wind, as well as by water and animals, (Bailey 1966, Marshall 1996, Walser 2004) and therefore disperse farther than larger propagules. I therefore expect to see (**H3**) a high relative frequency of smaller propagules in high elevation areas where high wind speed can be obtained. Larger propagules tend to be asexual, while sexual spores tend to be smaller. If I expect a high relative frequency of large propagules in wet areas and a high relative frequency of small propagules in areas with high elevation, then I must also expect to see (**H4a**) a high relative frequency of asexual propagules in wet areas and (**H4b**) a high relative frequency of sexual propagules in high elevation areas.

*Resource acquisition hypotheses* – Resource acquisition is an important part of persistence, and lichens, due to their lack of roots, face the unique challenge of having to obtain all of their nutrition and water from the atmosphere. One of the ways in which they address this

challenge is through their photobiont type (either green algal, cyanobacterial, or both). Green algae are capable of photosynthesis in the absence of liquid water (humid air is sufficient); in contrast, cyanobacteria require liquid water (in the form of rain or dew) to photosynthesize (Lange *et al.* 1986, Gauslaa 2014). Therefore, I expect to see **(H5a)** a larger proportion of cyanobacterial lichens in areas with high precipitation (such as western Oregon) and **(H5b)** a larger proportion of green algal lichens in areas with low precipitation (such as eastern Oregon). Tripartite lichens contain both photobiont types, which should theoretically allow them to inhabit both areas with high precipitation and areas with low precipitation. Therefore, I expect **(H6)** the tripartite trait to be cosmopolitan across Oregon and show no strong patterns relating to precipitation.

*Competition hypotheses* – Lichens face competition from vascular plants, bryophytes, and other lichens and can address this challenge with distance from the substrate (or height) and production of allelopathic chemicals. In this study allelopathic chemicals are defined as compounds that enhance competitive ability by negatively affecting vascular plants, bryophytes, and/or other lichens. Some classes of chemicals that are known to have allelopathic effects are depsides (Edwards *et al.* 2003), pulvinic acid, usnic acid (Lawrey 1986, Lauterwein *et al.* 1995), lichesterinic acid (aliphatic acid class), orcinol depsides, and orcinol depsidones (Rundel 1978). Both the forest floor and tree trunks of low elevation, high precipitation forests in western Oregon tend to be dominated by moss species such as *Kindbergia oregana* and *Isothecium* sp., resulting in a highly competitive environment. Therefore, I could expect to see **(H7a)** a high relative frequency of lichens that produce allelopathic chemicals and/or **(H7b)** “tall” lichens (such as fruticose or floppy foliose lichens) in these areas. On the other hand, in arid regions

lichens must compete amongst themselves and with bryophytes and vascular plants for water, so I could possibly expect to see **(H7c)** a higher relative frequency of lichens that produce allelopathic chemicals and/or **(H7d)** “tall” lichens in areas with low precipitation.

*Stress hypotheses* – UV exposure is probably an important stress for organisms, such as lichens, that often grow in well-lit environments. This challenge can be dealt with by the production of chemicals that can screen UV light. Some chemical classes that are known to protect against UV-A and UV-B, either by absorption or reradiation as longer wavelengths are usnic acid, anthraquinones (specifically parietin), xanthenes, pulvinic acid derivatives,  $\beta$ -orcinol para-depsides, atranorin (Rundel 1978, Edwards *et al.* 2003, Nybakken *et al.* 2004, Nguyen *et al.* 2013), depsides, depsidones, chromones, and dibenzofuran (Nguyen *et al.* 2013). I would expect to see a high relative frequency of lichens that produce these secondary compounds in areas that tend to have high levels of UV radiation, such as areas with high exposure and lack of canopy cover. UV radiation is not included in this study as an environmental factor so I will use elevation as a proxy, with the assumption that UV radiation levels will increase with increasing elevation. Therefore, I would expect to see **(H8)** a high relative frequency of lichens that produce UV screening secondary substances in high elevation areas.

*Disturbance hypotheses* – Herbivory is a form of chronic disturbance that lichens face and deal with through the production of a variety of discouraging chemicals. Some chemical classes that are known to discourage herbivory are usnic acid (Asplund and Gauslaa 2010), pulvinic acid (Rundel 1978, Lawrey 1986, Edwards *et al.* 2003), depsides, depsidones, terpenes, and anthraquinones (Rundel 1978). Organisms tend to invest more in protection when growing in high-stress environments (Coley 1988); therefore, I could expect to see **(H9a)** a high relative

frequency of lichens that produce secondary substances that discourage herbivory in arid areas. On the other hand, mollusks, inhabitants of wet forested areas, are known herbivores of lichens (Baur *et al.* 1994, Sharnoff 1994, Gauslaa 2005, Asplund and Gauslaa 2010), which could result in **(H9b)** a higher relative frequency of lichens that produce secondary substances that discourage herbivory in the high precipitation forests of western Oregon.

*Water balance hypotheses* – Water balance is crucial for lichens and could be measured by thallus mass and water holding capacity (Gauslaa and Coxson 2011, Merinero *et al.* 2014). However, these traits are both difficult and time consuming to measure; therefore, I will use growth form and lichen “height” (or distance from the substrate) as proxy traits to gain insight on water balance. The fruticose growth form encompasses both alectorioid (*Bryoria* sp., *Usnea* sp., etc.) and more compact, thick growth forms (*Cladonia* sp., *Ramalina* sp., etc.). Finely dissected alectorioid lichens both absorb and lose water vapor quickly, while thicker and more compact growth forms hydrate and dehydrate more slowly (Gauslaa 2014). For these reasons, “fruticose” may be too broad of a term to capture any patterns in relation to precipitation, so I do not expect to see **(H10)** any patterns in fruticose growth form relating to precipitation.

Foliose lichens tend to have high surface area and, due to increased evaporative water loss, may not be suited to dry habitats. Therefore, I expect to see **(H11)** a high relative frequency of foliose lichens in areas with high precipitation (Gauslaa 2014). Homoiomerous (gel) lichens generally contain cyanobacteria as their primary photobiont.

Because cyanobacteria require liquid water to photosynthesize (Lange *et al.* 1986), I could expect to see **(H12a)** a high relative frequency of gel lichens in areas with high precipitation. However, many gelatinous genera, such as *Collema*, form extensive soil crusts in

arid regions where the soil is calcareous. This could lead to **(H12b)** a high relative frequency of gel lichens in areas with low precipitation.

Lichen height can also affect water balance; alectorioid lichens (*Nodobryoria* sp., *Alectoria* sp., etc.) tend to be long and pendulous with a large distance from the substrate/large height. As previously discussed, these lichens are able to take up humidity quickly (Gauslaa 2014) and may be more prevalent in arid habitats where quick water uptake is a desirable trait. However, these alectorioid growth forms also dry out quickly (Gauslaa 2014), which would be a disadvantage in arid habitats. Therefore, I do not expect to see **(H13)** any patterns in lichen height relating to precipitation.

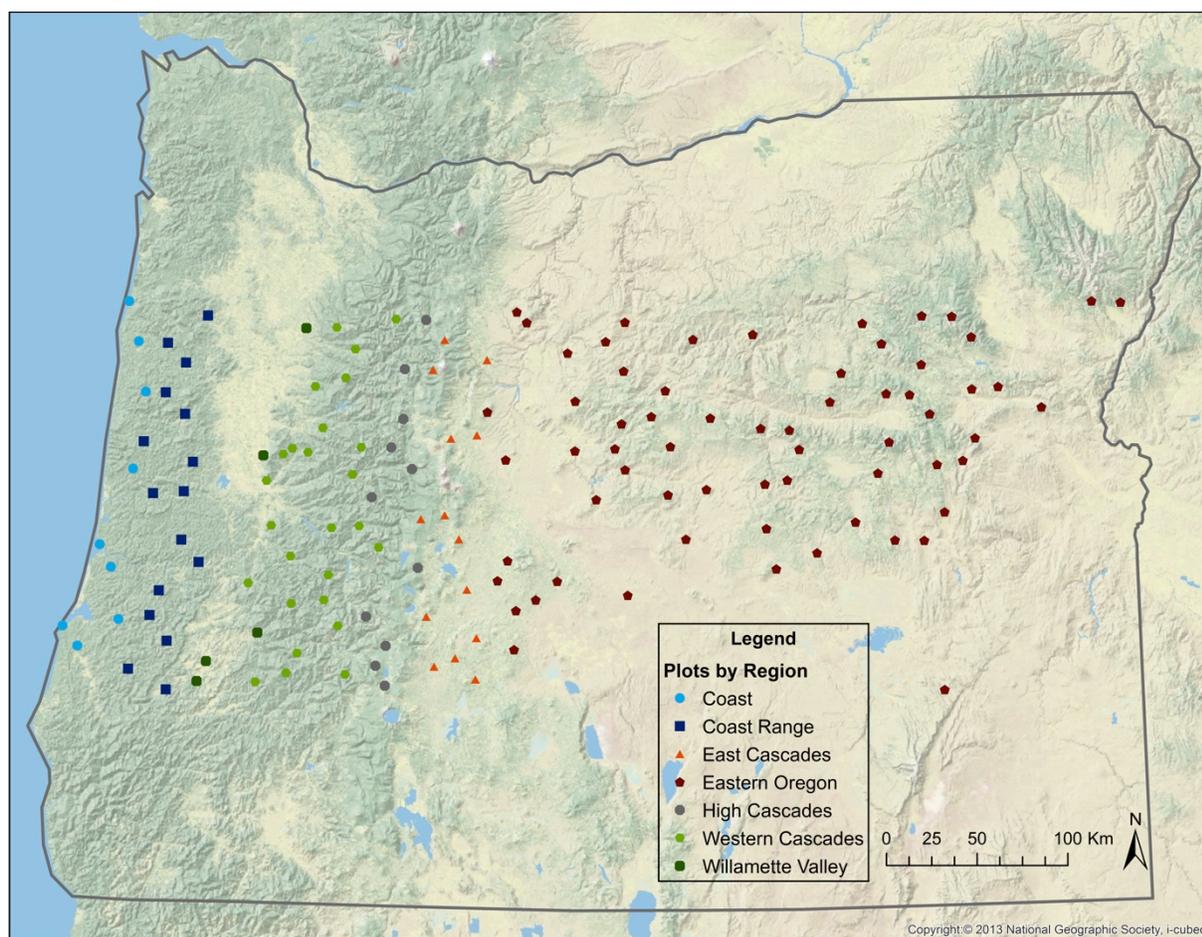
Overall, I expect to see measurable lichen trait patterns along environmental gradients in Oregon; these patterns could provide insight on how lichens address the basic challenges of dispersal, establishment, and persistence.

## 2. METHODS:

### 2.1. Study Area and Sampling Procedures:

The US Forest Service uses epiphytic lichens as forest health indicators to monitor changes in air quality, climate change, trends in biodiversity and the impacts of activities such as timber harvesting (US Forest Service 2011). This is all done as part of the Forest Inventory and Analysis (FIA) National Program, which has been collecting and analyzing data from forested plots in all land ownerships within the US for the last 80 years (O'Connell *et al.* 2014). Plots are randomly located within grid cells with approximately one plot every 38,849.8 acres, and consist of a 0.38 ha circular area with a 34.7-meter radius (McCune *et al.* 1997, US Forest Service 2011). This analysis will focus on data collected from 174 permanent FIA plots located in

Oregon between the latitudes of 43°N and 45°N (from approximately Roseburg to Salem; Figure 2.1). Plots ranged in longitude from -117.07°W to -124.32°W (from the Idaho border to the Pacific coast). All data were collected between the years of 1998 and 2003. Portions of these data were originally published in Geiser and Neitlich (2007) and Root *et al.* (2015). Plots were assigned to one of seven specific regions based on longitude and elevation, including the Coast, Coast Range, Willamette Valley, Western Cascades, High Cascades, Eastern Cascades, and Eastern Oregon. Information on how plots were assigned to region is included in Table 2.2.



**Figure 2.1.** 174 Forest Inventory and Analysis (FIA) plots in Oregon between 43 and 45 degrees of latitude. Map created in ArcMap (ESRI) with a National Geographic Society topographic basemap, using NAD 1983 coordinate system with a Lambert Conformal Conic projection.

**Table 2.2.** Regions and descriptions of how they were assigned.

<b>Region</b>	<b>Acronym</b>	<b>Description</b>
Coast	CO	West of 123.75°W and below 200 m in elevation
Coast Range	CR	West of 123.25°W and above 200 m in elevation
Willamette Valley	WV	Between 122.75°W and 123.5°W and below 250 meters in elevation
Western Cascades	WC	Between 122°W and 123.25°W and below 1000 m in elevation
High Cascades	HC	Between 121.91°W and 122.29°W and above 1000 m in elevation
Eastern Cascades	EC	Between 121.5°W and 122°W and below 1000 m in elevation
Eastern Oregon	ES	East of 121.5°W

Forest Service field crews visited each plot during the growing season and searched for epiphytic macrolichens on all woody plants and fallen branches, with a maximum of two hours spent at each plot. Tree and shrub bases below 0.5 m were excluded from sampling to avoid terricolous species. A voucher specimen was collected from each lichen believed to be a unique species and all vouchers were sent to expert lichenologists for identification. Crews also estimated the abundance of each species using a four-step scale: 1 =  $\leq 3$  individuals per plot; 2 = 4-10 individuals per plot; 3 =  $> 10$  individuals per plot (but less than half of the woody plants have that species present); and 4 = more than half of the woody plants have that species present. 156 species were identified in the 174 plots of interest in this study. Although crewmembers were non-experts in lichen identification, they all attended an intensive methodology-training course and were all certified for their competence in collecting lichen community data (US Forest Service 2011). Additional methodological details can be found in US Forest Service (2011).

All climatic data were obtained from WorldClim (Hijmans *et al.* 2005) and ClimateWNA (Wang *et al.* 2012). Climate variables include directly calculated variables obtained from the PRISM model (Daly *et al.* 2002) as well as derived data (Table 2.3). ClimateWNA data were extracted for the specific years the plots were sampled (1998-2003). Environmental data obtained from WorldClim are long-term averages from 1971-2000.

**Table 2.3.** Summary of environmental variables and their correlation coefficients with NMS axes 1 and 2 ordinating plots in lichen species space. Also shows the cross-validated  $R^2$  ( $xR^2$ ) values for nonparametric regressions that produced the contour maps of each variable in relation to the community ordination.

Acronym	Description	Units	Source	$R^2$ Axis 1	$R^2$ Axis 2	$xR^2$
ElevM	Elevation	m	FIA	0.503	0.129	0.678
TempDiff	Difference between the mean January and July temperatures.	°C	WorldClim	0.755	0.005	0.814
TempAnnC	Mean annual temperature.	°C	WorldClim	0.413	0.190	0.664
MaxTMo	Average monthly maximum temperature.	°C	WorldClim	0.178	0.107	0.303
MinTMo	Average monthly minimum temperature.	°C	WorldClim	0.658	0.062	0.802
LogPpt	$\log_{10}$ of the total annual precipitation.	mm	WorldClim	0.773	0.048	0.869
TD	Continentality, measured as the difference between the mean warmest-month temperature and the mean coldest-month temperature.	°C	ClimateWNA	0.330	0.032	0.504
MSP	Mean May to September precipitation.	mm	ClimateWNA	0.405	0.004	0.470
AHM	Annual heat-to-moisture index.	NA	ClimateWNA	0.435	0.082	0.530
NFFD	Number of frost-free days.	days	ClimateWNA	0.404	0.045	0.620
PAS	Proportion of precipitation as snow.	mm	ClimateWNA	0.041	0.020	0.229
CMD	Climatic moisture deficit, measured as the sum of the monthly difference between the reference atmospheric evaporative demand and precipitation.	mm	ClimateWNA	0.514	0.012	0.590
RH	Annual relative humidity.	%	ClimateWNA	0.255	0.015	0.398

## 2.2. Trait Measurements:

A total of 68 traits were measured for all 156 species; traits included photobiont, growth form, distance from substrate (“height”), reproductive method, size of reproductive propagules, and chemistry. Photobiont traits were assessed as general presence/absence of cyanobacteria, cyanobacteria as the only photobiont (bipartite), and presence of both cyanobacteria and green algae (tripartite). Possible growth form traits were fruticose, foliose, or gel (growth form traits are not mutually exclusive); individual species memberships in a given growth form were determined by cortex traits, how appressed the thallus is to the substrate, and lobation of the thallus. Distance from the substrate, or height, was measured as well as modes of reproduction (production of apothecia, isidia, soredia, and lobules) and average size of reproductive propagules. Chemistry was assessed at the broad class level, with individual compounds recorded at the chemical class level. See Appendix A for detailed information on trait scoring.

Average sizes of asexual reproductive propagules were measured in the lab and gathered from the literature, and information on average sizes of sexual reproductive propagules and all other traits was gathered from the literature (see Appendix B for literature sources for individual species). Sexually produced spore volume was calculated using the formula for volume of an ellipsoid ( $volume = \frac{4}{3} * \pi * 0.5(spore\ length) * 0.5(spore\ width)^2$ ; units =  $\mu m^3$ ).

Average sizes of asexual propagules were measured for each species using the following protocol:

1. Propagule sizes were measured on specimens from Dr. Bruce McCune’s personal herbarium, the Oregon State University Herbarium, and the National Park Service Herbarium. Specimens were not necessarily collected from the study area.
2. Two separate propagules were measured on each of four different specimens, with priority given to specimens collected from the Pacific Northwest. If four specimens were not available, propagules were measured on as many specimens as possible.
3. Length and width ( $\mu m$ ) of isidia and lobules (including fibrils, spinules, and squamules) were measured on each specimen, using compound and dissecting microscopes. Two

separate propagules were measured on each specimen. Average propagule length and width were calculated for each species.

4. Diameters ( $\mu\text{m}$ ) of two separate soredia were measured on each specimen, using a compound microscope. Average diameter was calculated for each species.
5. Isidia and lobule volume were calculated using the formula for the volume of a cylinder.  $Volume = \pi * propagule\ length * 0.5(propagule\ width)^2$ . Units =  $\mu\text{m}^3$ . Final volume was expressed as  $\log_{10}(\text{volume})$ .
6. Soredia volume was calculated using the formula for the volume of a sphere.  $Volume = \frac{4}{3} * \pi * 0.5(soredia\ diameter)^3$  and expressed as  $\mu\text{m}^3$ . Final volume was calculated as  $\log_{10}(\text{volume})$ .

### 2.3. Data Preparation and Analysis:

All data manipulations and analyses were performed using Microsoft Excel and PC-ORD Version 7.0 software (McCune and Mefford 2015). A species matrix (174 plots x 156 species) of species abundance rankings in each plot was created, along with an environment matrix (174 plots x 14 environmental variables), and a trait matrix (156 species x 38 traits). A total of 6 empty plots, containing no lichens, were deleted from both the species and environment matrices. To improve comparability across traits, the trait matrix was standardized by linearly rescaling the traits from min-to-max, 0 = minimum and 1 = maximum. The species matrix was then multiplied by the trait matrix, with the resulting species x trait matrix (168 plots x 38 traits) containing abundance-weighted totals. These totals were then weighted averaged, dividing by plot totals, resulting in community-weighted means (CWM), the ranges of which are directly comparable with each other. The environment matrix was then augmented with these data to create a trait/environment matrix (168 plots x 52 traits/environmental variables). After calculating the plot x traits/environment matrix, a total of 45 rare species (defined as having 3 or fewer occurrences in all plots combined) were deleted to reduce noise in the species matrix (resulting in a matrix of 168 plots x 111 species). A total of 9 species identified only to genus were deleted to increase accuracy of trait information (resulting in a matrix of 168 plots x 102

species). Lichen abundances were measured in classes approximating a log scale, so no data transformations or relativizations were needed.

An outlier analysis was conducted by measuring the average distance (using Sørensen distance measures) from each plot to every other plot. Plots 76779 and 91907 were found to be concerning outliers, both falling 3.3 standard deviations above the mean for average distance. A closer examination of these plots revealed that they each contained only one species of lichen. These plots were deleted, resulting in a species matrix and a trait/environment matrix with 166 plots apiece.

Nonmetric Multidimensional Scaling (NMS), using Sørensen distance measures, was used to ordinate plots in lichen species space. This ordination method was chosen because of its success in recovering the nonlinear data structure common in ecological community datasets (McCune and Grace 2002). Sørensen similarity was chosen as the distance measure because it often performs better than other distance measures over the sort of large environmental distances seen in my data (McCune and Grace 2002). NMS was run on autopilot mode on the slow and thorough setting of 250 runs with both real and randomized data, with no penalization for ties, and a randomization test. This ordination was then overlaid with the traits and environmental variables to examine the relationships between lichen community composition, traits, and the environment. The final 2-dimensional solution was rotated to the principal axes, such that the axes are uncorrelated with each other. Convex hulls of the different regions were also constructed and overlaid on the ordination.

The overlay of traits and environmental variables on the ordination of plots in species space is based on linear statistics and won't capture a non-linear relationship; therefore some

information is lost. To explore possible non-linear relationships between traits and environmental variables and axes 1 and 2, I overlaid contours on the ordination. Contours were constructed using the multiplicative kernel smoother method, with contours fitting an envelope at 2.0 standard deviations, and optimizing the smoothing parameter by maximizing the cross-validated  $R^2$  ( $xR^2$ ). To visualize multiple non-linear responses simultaneously on the ordination, I constructed several hilltop plots following the methodology of Nelson *et al.* (2015). This type of plot traces the top 20% of the contour range for the overlay of each environmental variable/trait and then superimposes them on one ordination, resulting in a figure that shows the maxima of each non-linear overlay.

Multi-response Permutation Procedures (MRPP) were used to test the hypothesis of no difference between geographic regions in climate space, lichen community space, and lichen trait space. Beta diversity in each region was found by first using the `vegdist` function in the `vegan` package (Oksanen *et al.* 2015) in R version 3.1.2 (R Core Team 2014) to calculate a distance matrix, using Jaccard's dissimilarity index, for the plot by species matrix. The Jaccard dissimilarity,  $d$ , between two plots,  $i$  and  $j$ , is

$$d_{ij} = (b + c)/(a + b + c),$$

where  $a$  is the number of species shared,  $b$  is the number of species in plot 1 that do not occur in plot 2, and  $c$  is the number of species in plot 2 that do not occur in plot 1 (Anderson *et al.* 2006). The average distance of plots in each region to the region centroid is the beta diversity measure for each region. Beta diversity was compared among regions using the `betadisper` function in the `vegan` package (Anderson 2006, Anderson *et al.* 2006, Oksanen *et al.* 2015), which tests for homogeneity of multivariate dispersions in species space. This test is based on the dissimilarity

matrix, calculating the mean and variance in distance of plots in each region to its centroid in species space. I thus tested for differences among regions in mean distances to centroids with ANOVA, calculating an F-statistic with the null hypothesis of no difference in beta diversity among regions (Anderson *et al.* 2006).

### 3. RESULTS:

Geographic regions differed in climate, lichen communities and traits (MRPP; Table 2.4).

Regional and climatic gradients thus provide a basis for summarizing variation in lichen community composition and lichen traits. I will summarize the regional differences in key climatic variables, report ordination results that link lichen communities to geographic regions and climate, and discuss how lichen traits are related to the community ordination.

**Table 2.4.** Differences among geographic regions in climate, lichen community, and lichen trait space, based on MRPP.  $A$  is the effect size and  $p$  is the probability of Type I error for the hypothesis of no difference among geographic regions.

<b>Group of variables</b>	<b><math>A</math></b>	<b><math>p</math></b>
Climate	0.35	< 0.001
Lichen communities	0.24	< 0.001
Lichen traits (all)	0.19	< 0.001
Reproductive traits	0.13	< 0.001
Morphological traits	0.15	< 0.001
Chemical traits	0.31	< 0.001

### 3.1. Climatic variation:

The NMS of plots in species space resulted in a 2-dimensional solution (final stress = 11.97, randomization test,  $p = 0.004$ ; Figure 2.2) with the two axes representing a large amount of the variance in the data (cumulative  $R^2 = 0.803$ ; final stress = 12.0;  $p = 0.004$ ). The NMS showed strong environmental correlates with axis 1 (Table 2.3). Axis 1 ( $R^2 = 0.627$ ) represented a gradient in lichen community composition from low elevation plots with high precipitation and a large number of frost-free days, to continental, high elevation plots with low precipitation, a high climatic moisture deficit (CMD), and a high annual heat to moisture (AHM) index (Figure 2A). Axis 2 was the weaker axis ( $R^2 = 0.176$ ) and did not represent a single strong linear environmental gradient (Table 2.3); however, a number of traits were strongly correlated with this axis (Figure 2A; Table 2.5). Hilltop plots of environmental variables suggest that axis 2 represents a gradient in lichen communities that is related to a non-linear temperature gradient, with the top end of the axis representing plots that have a high mean annual temperature, a large difference between mean January and July temperatures, and high mean minimum monthly temperature (Figure 2.3). CMD is also related to both axis 1 and axis 2, with plots on the top right corner of the ordination having a large CMD (Figure 2.3).

The Coast region had the lowest mean elevation, highest mean annual precipitation, highest mean May to September precipitation, highest mean minimum monthly temperature, highest mean annual temperature, lowest mean difference between the mean January and July temperatures, and the lowest mean AHM (Table 2.6). The Coast Range had the lowest continentality, the highest number of frost-free days, and the highest relative humidity (Table 2.6). The Willamette Valley had the lowest mean CMD, the West Cascades had the second

highest mean annual precipitation, the High Cascades had the second lowest mean annual temperature, and the Eastern Cascades had the lowest mean relative humidity and the lowest number of frost-free days (Table 2.6). Eastern Oregon had the highest mean elevation, lowest mean annual precipitation, lowest mean May to September precipitation, lowest mean minimum monthly temperature, lowest mean annual temperature, highest mean difference between the mean January and July temperatures, highest continentality, highest mean AHM, and highest mean CMD (Table 2.6). Convex hulls of the regions overlaid on the NMS of plots in species space show a gradient from west to east along axis 1 (Figure 2.2).

**Table 2.5.** Trait descriptions and strength of relationships between lichen traits and the NMS ordination (Sørensen distance used) of plots in species space, summarized by correlation coefficients of each species with each axis and the cross-validated fits ( $xR^2$ , with an  $xR^2 > 0.2$ ) based on nonparametric regression against the pair of axes.

<b>Acronym</b>	<b>Description</b>	<b>Axis1 -R<sup>2</sup></b>	<b>Axis2 - R<sup>2</sup></b>	<b>Hilltop NPMR - xR<sup>2</sup></b>
Nfix	Containing cyanobacteria as a photobiont	0.162	0.022	0.230
tripartite	Containing both cyanobacteria and green algae as photobionts	0.194	0.022	0.242
greenalgal	Containing only green algae as a photobiont	0.162	0.022	0.230
fruticose	Fruticose growth form	0.141	0.207	0.470
foliose	Foliose growth form	0.291	0.174	0.580
gel	A homoimerous bipartite gel lichen	0.001	0.022	0.061
apothecia	Producing apothecia	0.194	0.201	0.378
lobules	Producing lobules (lobules, squamules, fibrils, schizidia, or spinules)	0.102	0.107	0.293
soredia	Producing soredia	0.180	0.552	0.739
log(height)	Log <sub>10</sub> of the height (mm)	0.001	0.487	0.675
propagule1	Reproductive propagules between 0.50-1.49, on the log scale (or with volume between 3.13 and 31.26 $\mu\text{m}^3$ )	0.018	0.000	0.288
propagule2	Reproductive propagules between 1.50-2.49, on the log scale (or with volume between 31.27 and 312 $\mu\text{m}^3$ )	0.238	0.212	0.515
propagule3	Reproductive propagules of size magnitudes 2.50-3.49, on the log scale (or with volume between 313 and 3,125 $\mu\text{m}^3$ )	0.054	0.048	0.256
propagule4	Reproductive propagules between 3.50-4.49, on the log scale (or with volume between 3,126 and 31,260 $\mu\text{m}^3$ )	0.181	0.473	0.709
propagule5	Reproductive propagules between 4.50-5.49, on the log scale (or with volume between 31,261 and 312,607 $\mu\text{m}^3$ )	0.000	0.194	0.223
propagule7	Reproductive propagules between 6.50-7.49, on the log scale (or with volume between 0.003 and 0.031 $\text{mm}^3$ )	0.265	0.019	0.265
propagule8	Reproductive propagules between 7.50-8.49, on the log scale (or with volume between 0.03 and 0.31 $\text{mm}^3$ )	0.010	0.005	0.257
propagule 9	Reproductive propagules between 8.50-9.49, on the log scale (volume from 0.31 to 3.13 $\text{mm}^3$ )	0.053	0.128	0.351

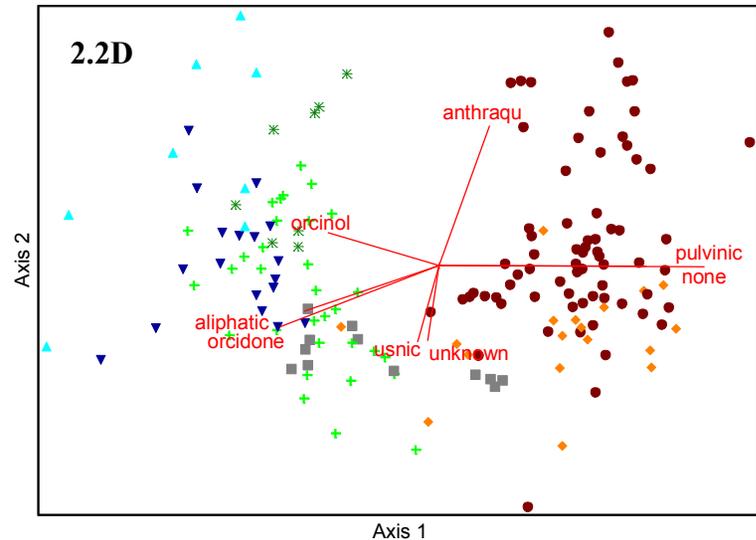
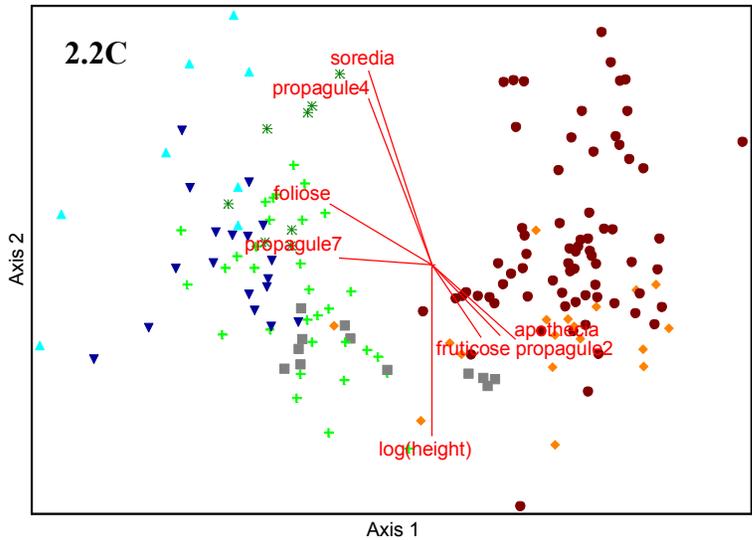
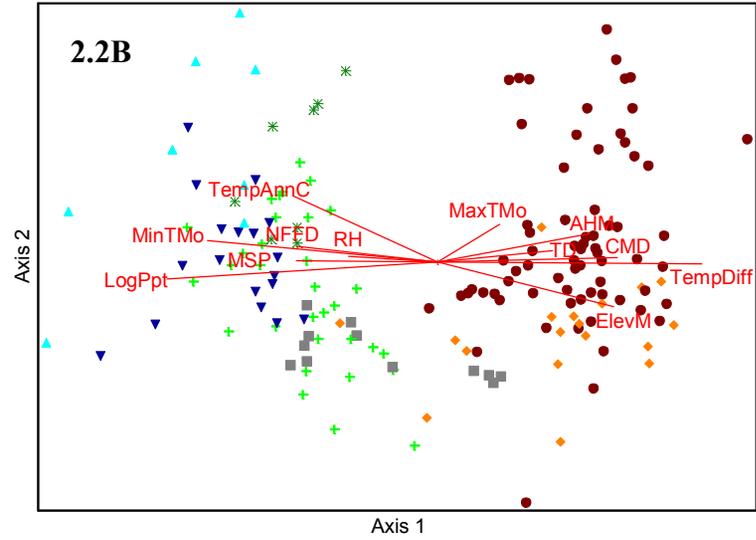
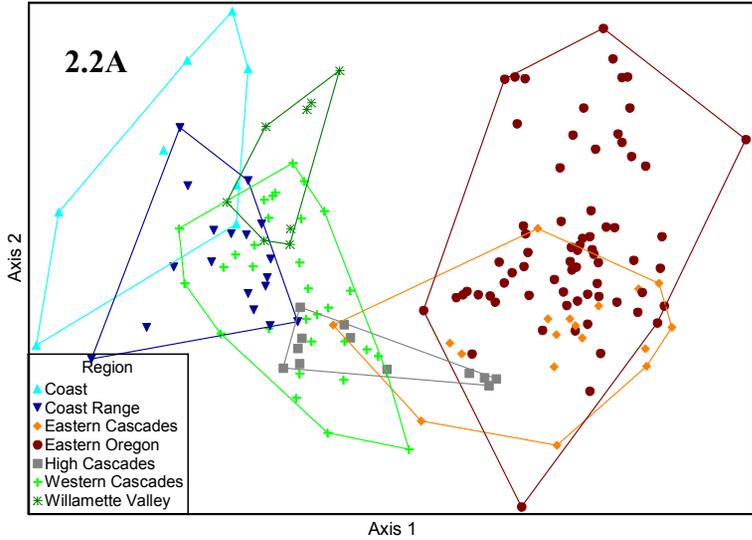
**Table 2.5 cont.**

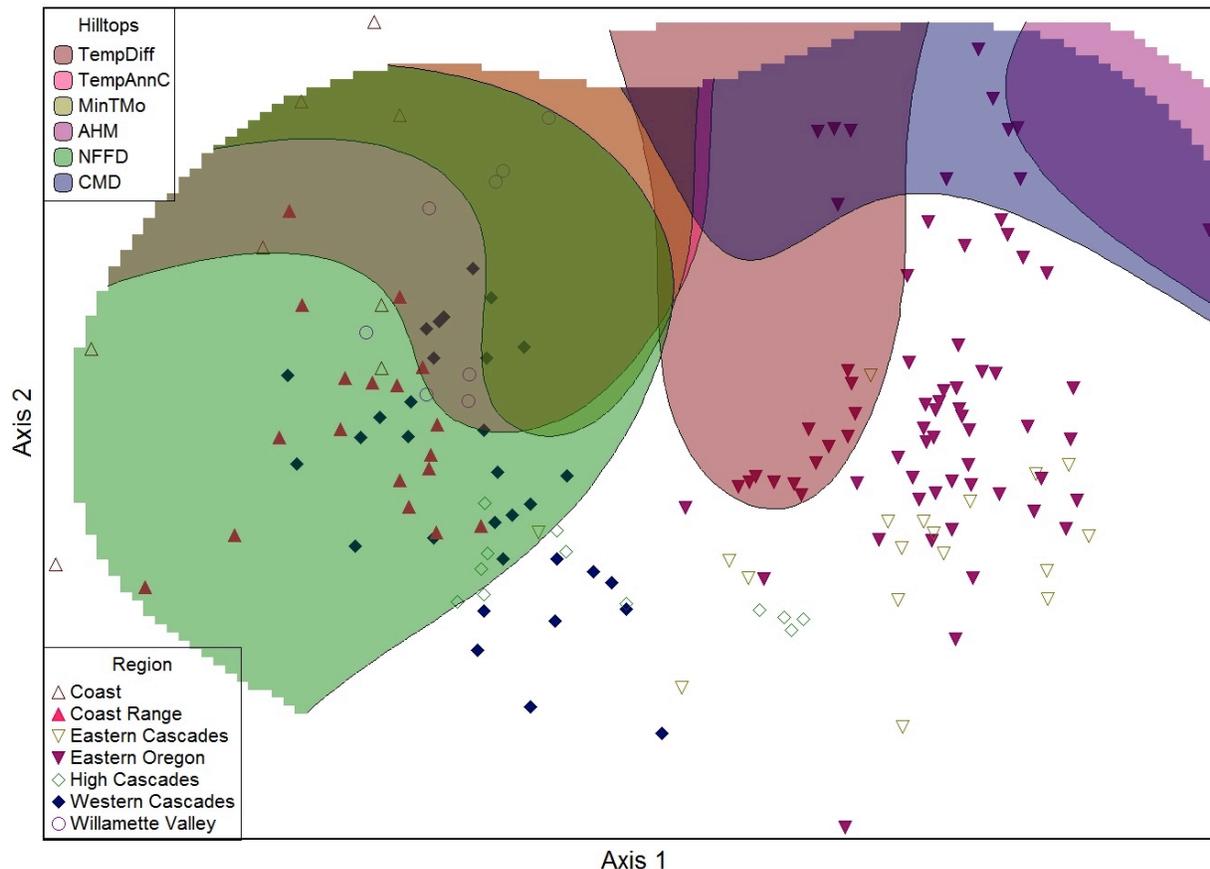
<b>Acronym</b>	<b>Description</b>	<b>Axis1 -R<sup>2</sup></b>	<b>Axis2 - R<sup>2</sup></b>	<b>Hilltop NPMR - xR<sup>2</sup></b>
propagule10	Reproductive propagules between 9.50-10.49, on the log scale (or with volume between 3.13 and 10 mm <sup>3</sup> )	0.188	0.017	0.246
aliphatic	Containing compounds in the aliphatic acid class (caperatic acid and protolichesterinic acid)	0.382	0.129	0.708
anthraqu	Containing compounds in the anthraquinone class (anthraquinone, parietin, secalonic acid, and teloschistin)	0.144	0.397	0.761
none	Containing no secondary chemistry	0.590	0.001	0.675
orcidone	Containing compounds in the orcinol depsidone class (3-hydroxyphysodic acid, 4-O-methylgrayanic acid, alectoronic acid, grayanic acid, lobaric acid, physodic acid, and $\alpha$ -collatolic acid)	0.453	0.174	0.699
orcinol	Containing compounds in the orcinol depside class (4-O-methylcryptochlorophaeic acid, divaricatic acid, evernic acid, imbricatic acid, lecanoric acid, olivetoric acid, perlatolic acid, scrobiculin, and sekikaic acid)	0.316	0.093	0.562
pulvinic	Containing compounds in the pulvinic acid class (pulvinic acid and vulpinic acid)	0.755	0.004	0.808
unknown	Containing unknown chemical compound(s)	0.032	0.214	0.376
usnic	Containing compounds in the usnic acid class (usnic acid)	0.062	0.218	0.314
$\beta$ -benzyl	Containing compounds in the $\beta$ -orcinol benzyl ester class (alectorialic acid and barbatolic acid)	0.026	0.134	0.386
$\beta$ -done	Containing compounds in the $\beta$ - orcinol depsidone class (2'-O-demethylpsoromic acid, constictic acid, cryptostictic acid, fumarprotocetraric acid, hypoprotocetraric acid, menegazziaic acid, norstictic acid, physodalic acid, protocetraric acid, psoromic acid, salazinic acid, and stictic acid)	0.157	0.013	0.328

**Table 2.6.** Mean values ( $\pm$  standard deviation), in geographic regions in west-to-east order, for all environmental variables with  $xR^2 > 0.350$ .

<b>Region</b>	<b>ElevM (m)</b>	<b>TempDiff (°C)</b>	<b>TempAnn (°C)</b>	<b>MinTMo (°C)</b>	<b>Annual precipitation (mm)</b>	<b>TD (°C)</b>	<b>MSP (mm)</b>	<b>AHM</b>	<b>NFFD (days)</b>	<b>CMD (mm)</b>	<b>RH (%)</b>
<b>Coast</b>	76.2 $\pm$ 57.0	18.9 $\pm$ 1.7	10.7 $\pm$ 0.2	2.5 $\pm$ 0.7	1996.8 $\pm$ 216.9	16.5 $\pm$ 2.2	397.9 $\pm$ 161.9	4.9 $\pm$ 1.8	238.0 $\pm$ 61.8	262.8 $\pm$ 107.8	66.8 $\pm$ 12.3
<b>Coast Range</b>	450.4 $\pm$ 136.9	24.5 $\pm$ 1.2	9.5 $\pm$ 1.2	-0.2 $\pm$ 0.9	1811.9 $\pm$ 377.7	13.7 $\pm$ 2.1	264.7 $\pm$ 116.7	8.5 $\pm$ 4.2	312.1 $\pm$ 26.3	245.9 $\pm$ 92.2	82.9 $\pm$ 8.4
<b>Willamette Valley</b>	179.1 $\pm$ 23.8	27.5 $\pm$ 0.9	10.9 $\pm$ 1.0	0.0 $\pm$ 0.9	1274.5 $\pm$ 222.5	16.3 $\pm$ 2.9	514.1 $\pm$ 240.3	7.3 $\pm$ 5.2	256.8 $\pm$ 44.9	243.1 $\pm$ 156.2	78.3 $\pm$ 7.5
<b>Western Cascades</b>	732.5 $\pm$ 354.0	27.6 $\pm$ 1.9	8.2 $\pm$ 1.7	-2.5 $\pm$ 2.0	1660.7 $\pm$ 336.2	14.0 $\pm$ 1.8	332.4 $\pm$ 134.8	8.3 $\pm$ 2.8	251.8 $\pm$ 58.6	217.7 $\pm$ 93.7	74.7 $\pm$ 8.6
<b>High Cascades</b>	1371.5 $\pm$ $\pm$ 306.8	29.9 $\pm$ 1.7	5.4 $\pm$ 1.3	-6.4 $\pm$ 1.2	1578.4 $\pm$ 308.7	14.8 $\pm$ 2.0	339.1 $\pm$ 105.7	7.4 $\pm$ 1.7	172.2 $\pm$ 25.8	234.0 $\pm$ 88.8	65.3 $\pm$ 3.0
<b>Eastern Cascades</b>	1341.1 $\pm$ $\pm$ 292.5	33.4 $\pm$ 2.5	5.6 $\pm$ 0.9	-7.8 $\pm$ 1.2	846.3 $\pm$ 413.6	15.6 $\pm$ 1.3	160.1 $\pm$ 78.1	13.3 $\pm$ 4.7	165.1 $\pm$ 23.3	370.8 $\pm$ 101.5	63.7 $\pm$ 4.5
<b>Eastern Oregon</b>	1409.0 $\pm$ $\pm$ 393.2	36.2 $\pm$ 2.0	5.3 $\pm$ 2.0	-9.9 $\pm$ 2.6	435.5 $\pm$ 112.8	19.6 $\pm$ 2.1	128.1 $\pm$ 53.3	29.6 $\pm$ 14.6	181.3 $\pm$ 28.1	443.7 $\pm$ 76.4	65.5 $\pm$ 6.7

**Figure 2.2.** Convex hulls for region overlaid on the NMS ordination of plots in lichen species space (A). Joint plots (B-D) of plots (symbolized by the triangles) in lichen species space using Sørensen distance measures. Vectors represent environmental variables (B), morphological and reproductive traits (C) and chemical traits (D) that were strongly correlated with the axes (minimum  $R^2 = 0.2$ ), with length of the vector corresponding to  $R^2$ . Plot legend presented in ordination A pertains to all four ordinations.





**Figure 2.3.** Hilltop plot of nonlinear relationships between selected environmental variables and axes 1 and 2 of the NMS ordination of plots in lichen species space.

### 3.2. Lichen communities:

Lichen species richness peaked in the Willamette Valley, with the West Cascades and the High Cascades also having high average species richness in each plot (Table 2.7). The Willamette Valley also had a high total number of plots (30) and the highest total number of species, with 114 total species recorded in the region (Table 2.7). Eastern Oregon had the lowest plot average species richness, but had the most plots, with 71 total (Table 2.7). The Oregon Coast had the lowest number of plots (8) and the second lowest total number of species (53). Regional beta diversity was significantly different between one or more regions (ANOVA,  $F_6 = 2.86$ ,  $p =$

0.01). The Coast Range had the highest mean beta diversity and the High Cascades had the lowest mean beta diversity (Table 2.7).

A frequent species in the Cascades (Western, High, and Eastern) was *Alectoria sarmentosa*; *Parmelia sulcata* was frequently found in the Coast, the Coast Range, the Willamette Valley, and the Western Cascades (Table 2.7). *Bryoria fremontii* and *Cetraria merrillii* were frequently found in the Eastern Cascades and Eastern Oregon (Table 2.7). Species associated with low elevation, high precipitation plots with high annual temperature included *Evernia prunastri*, *Platismatia glauca*, *Ramalina farinacea*, and several species of *Hypogymnia* (Table 2.8). Species associated with high elevation plots with low precipitation, high CMD, and high AHM included *Bryoria fremontii*, *Letharia columbiana*, *L. vulpina*, and *Nodobryoria abbreviata* (Table 2.8).

**Table 2.7.** Lichen communities in geographic regions in west-to-east order. Diversity statistics are based on presence/absence of species and calculated before filtering of rare species.

<b>Region</b>	<b>Total # plots</b>	<b>Plot average species richness</b>	<b>Most frequent species (present in greater than 50% of the plots)</b>	<b>Total # species</b>	<b>Beta diversity</b>
Coast	8	13.4	<i>Cladonia coniocraea</i> , <i>Hypogymnia apinnata</i> , <i>Hypotrachyna sinuosa</i> , <i>Menegazzia terebrata</i> s.l., <i>Parmelia sulcata</i> , <i>Parmotrema perlatum</i> , <i>Ramalina farinacea</i> , <i>Usnea cornuta</i> , <i>U. filipendula</i> , and <i>U. flavocardia</i>	39	0.57
Coast Range	19	17.5	<i>Cetraria orbata</i> , <i>Evernia prunastri</i> , <i>Hypogymnia apinnata</i> , <i>Hypogymnia enteromorpha</i> , <i>Hypogymnia inactiva</i> , <i>Hypogymnia physodes</i> , <i>Parmelia hygrophila</i> , <i>Parmelia sulcata</i> , <i>Platismatia glauca</i> , <i>Platismatia herrei</i> , <i>Ramalina farinacea</i> , and <i>Sphaerophorus globosus</i> s.l.,	60	0.50
Willamette Valley	8	21.8	<i>Cetraria chlorophylla</i> , <i>Evernia prunastri</i> , <i>Hypogymnia physodes</i> , <i>Parmelia sulcata</i> , <i>Physcia aipolia</i> , <i>Platismatia glauca</i> , <i>Ramalina dilacerata</i> , <i>Ramalina farinacea</i> , and <i>Usnea filipendula</i> ,	61	0.49
Western Cascades	32	23.9	<i>Alectoria sarmentosa</i> , <i>Bryoria capillaris</i> , <i>Cetraria chlorophylla</i> , <i>Evernia prunastri</i> , <i>Hypogymnia enteromorpha</i> , <i>H. imshaugii</i> , <i>H. inactiva</i> , <i>Parmelia sulcata</i> , <i>Platismatia glauca</i> , and <i>Platismatia stenophylla</i> , and <i>Usnea filipendula</i>	88	0.51
High Cascades	12	21.5	<i>Alectoria imshaugii</i> , <i>A. sarmentosa</i> , <i>Cetraria chlorophylla</i> , <i>C. platyphylla</i> , <i>Hypogymnia enteromorpha</i> , <i>Hypogymnia inactiva</i> , <i>Nodobryoria oregana</i> , <i>Parmelia hygrophila</i> , <i>Parmeliopsis hyperopta</i> , <i>Platismatia glauca</i> , and <i>Platismatia stenophylla</i> ,	60	0.45

**Table 2.7 cont.**

<b>Region</b>	<b>Total # plots</b>	<b>Plot average species richness</b>	<b>Most frequent species (present in greater than 50% of the plots)</b>	<b>Total # species</b>	<b>Beta diversity</b>
Eastern Cascades	19	10.7	<i>Alectoria imshaugii</i> , <i>A. sarmentosa</i> , <i>Bryoria fremontii</i> , <i>B. pseudofuscescens</i> , <i>Cetraria canadensis</i> , <i>C. merrillii</i> , <i>Letharia columbiana</i> , <i>L. vulpina</i> , and <i>Nodobryoria abbreviata</i>	43	0.47
Eastern Oregon	70	10.5	<i>Bryoria fremontii</i> , <i>Cetraria merrillii</i> , <i>Hypogymnia imshaugii</i> , <i>Letharia columbiana</i> , <i>L. vulpina</i> , and <i>Nodobryoria abbreviata</i>	54	0.53

**Table 2.8.** Strength of relationships between lichen species and the NMS ordination (Sørensen distance used) of plots in species space. These are given in two ways: linear relationships with individual axes and nonlinear relationships with the pair of axes. Also shows a summary of the correlation coefficients of each species with each axis and the cross-validated fits ( $xR^2$ , with an  $xR^2 > 0.3$ ) based on nonparametric regression against the pair of axes

Lichen species	Axis 1 - $R^2$	Axis 2 - $R^2$	Hilltop NPMR $xR^2$
<i>Alectoria imshaugii</i>	0.000	0.163	0.327
<i>Bryoria capillaris</i>	0.072	0.072	0.313
<i>Alectoria sarmentosa</i>	0.050	0.312	0.651
<i>Bryoria fremontii</i>	0.217	0.085	0.522
<i>Bryoria fuscescens</i>	0.001	0.103	0.305
<i>Cetraria merrillii</i>	0.450	0.078	0.769
<i>Cetraria orbata</i>	0.159	0.019	0.303
<i>Cetraria platyphylla</i>	0.005	0.109	0.301
<i>Evernia prunastri</i>	0.279	0.071	0.548
<i>Hypotrachyna sinuosa</i>	0.176	0.089	0.406
<i>Hypogymnia apinnata</i>	0.226	0.007	0.332
<i>Hypogymnia enteromorpha</i>	0.471	0.024	0.679
<i>Hypogymnia imshaugii</i>	0.014	0.143	0.455
<i>Hypogymnia inactiva</i>	0.428	0.019	0.672
<i>Hypogymnia physodes</i>	0.399	0.000	0.568
<i>Hypogymnia tubulosa</i>	0.200	0.011	0.370
<i>Letharia columbiana</i>	0.546	0.028	0.671
<i>Letharia vulpina</i>	0.504	0.020	0.653
<i>Melanohalea elegantula</i>	0.168	0.166	0.445
<i>Nodobryoria abbreviata</i>	0.274	0.025	0.608
<i>Nodobryoria oregana</i>	0.008	0.208	0.419
<i>Parmelia hygrophila</i>	0.236	0.021	0.372
<i>Parmelia sulcata</i>	0.381	0.077	0.597
<i>Platismatia glauca</i>	0.409	0.048	0.722
<i>Platismatia herrei</i>	0.243	0.034	0.447
<i>Platismatia stenophylla</i>	0.167	0.033	0.334
<i>Parmotrema chinense</i>	0.048	0.107	0.417
<i>Parmeliopsis hyperopta</i>	0.038	0.193	0.463
<i>Ramalina farinacea</i>	0.354	0.132	0.697
<i>Sphaerophorus globosus</i> s.l.	0.287	0.026	0.423
<i>Usnea filipendula</i>	0.434	0.001	0.524

**Table 2.8 cont.**

Lichen species	Axis 1 - R <sup>2</sup>	Axis 2 - R <sup>2</sup>	Hilltop NPMR xR <sup>2</sup>
<i>Usnea flavocardia</i>	0.244	0.059	0.374
<i>Xanthomendoza oregana</i>	0.074	0.215	0.304

### 3.3. Lichen traits:

Results for lichen trait patterns along climatic gradients will be reported by their corresponding hypotheses (H1 through H13) described in the introduction and summarized in Table 2.9. For hypotheses that are supported it is important to note that only the predicted pattern is supported, not necessarily the proposed mechanism behind the pattern.

**H1/H4b** – Sexual reproduction had a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with low precipitation and a low mean annual temperature (Figure 2.4), supporting hypothesis 4b and failing to support hypothesis 1.

**H2** – Lichens with large propagules between the size magnitudes of 3.50-4.49 and 6.50-7.49 on the log scale (equivalent to about 313-3,125  $\mu\text{m}^3$  and 0.003-0.031  $\text{mm}^3$ ) peaked in relative frequency (Table 2.5) in areas with high precipitation and high mean annual temperature (Figure 2.4), supporting hypothesis 2.

**H3** – Lichens with small propagules between the size magnitudes of 1.50-2.49 on the log scale (equivalent to about 31.62-312  $\mu\text{m}^3$ ) showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with low precipitation (Figure 2.4), supporting hypothesis 3.

**H4a** – Soredia (the only asexual propagule that had a high correlation with either of the ordination axes) showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with high precipitation and high mean annual temperature (Figure 2.4). This supports the hypothesis that asexual reproduction will be most frequent in wet areas.

**H5a/H6** – Photobiont traits were not strongly correlated with axes 1 or 2 ( $R^2 < 0.2$ ); however, hilltop plots show that there is a weak nonlinear pattern of higher relative frequency of cyanobacterial lichens and tripartite lichens in areas with high precipitation (Figure 2.4), supporting hypothesis 5a and failing to support hypothesis 6.

**H5b** – Photobiont traits were not strongly correlated with axes 1 or 2 ( $R^2 < 0.2$ ), but hilltop plots showed a weak nonlinear pattern of higher relative frequency of strictly green algal lichens in areas with high precipitation (Figure 2.4), failing to support hypothesis 5b.

**H7a/H7c** – The pulvinic acid class and usnic acid showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with low precipitation and low mean annual temperature (Figure 2.4), supporting hypothesis 7c. Orcinol depsides showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with high precipitation and high mean annual temperature (Figure 2.4), supporting hypothesis 7a. Orcinol depsidones showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with high precipitation, low CMD, and low AHM (Figure 2.4), supporting hypothesis 7a.

**H7b /H7d** – Tall lichens showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with low precipitation (Figure 2.4), supporting hypothesis 7d and failing to support hypothesis 7b.

**H8** – Anthraquinones showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with low precipitation, high CMD, and high AHM (Figure 2.4), supporting hypothesis 8. As reported above, the pulvinic acid class and usnic acid showed similar patterns to anthraquinones, also supporting hypothesis 8. The aliphatic acid class showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with high precipitation, low CMD, and low

AHM (Figure 2.4), failing to support hypothesis 8. As reported above, orcinol depsides and orcinol depsidones showed similar patterns to the aliphatic acid class, also failing to support hypothesis 8.

**H9a/H9b** – The pulvinic acid class showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with low precipitation and a low mean annual temperature (Figure 2.4), supporting hypothesis 9a. Orcinol depsides showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with high precipitation and high mean annual temperature (Figure 2.4), supporting hypothesis 9b. Orcinol depsidones showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with high precipitation, low CMD, and low AHM (Figure 2.4), supporting hypothesis 9b. Anthraquinones showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with low precipitation, high CMD, and high AHM (Figure 2.4), supporting hypothesis 9a.

**H10** – Fruticose lichens showed a strong nonlinear pattern (Table 2.5) of high relative frequency in areas with high precipitation (Figure 2.4), failing to support hypothesis 10.

**H11** – Foliose lichens showed strong nonlinear patterns (Table 2.5) of high relative frequency in areas with high precipitation, and to a lesser extent in areas with low precipitation, high CMD, and high AHM (Figure 2.4), partially supporting hypothesis 11.

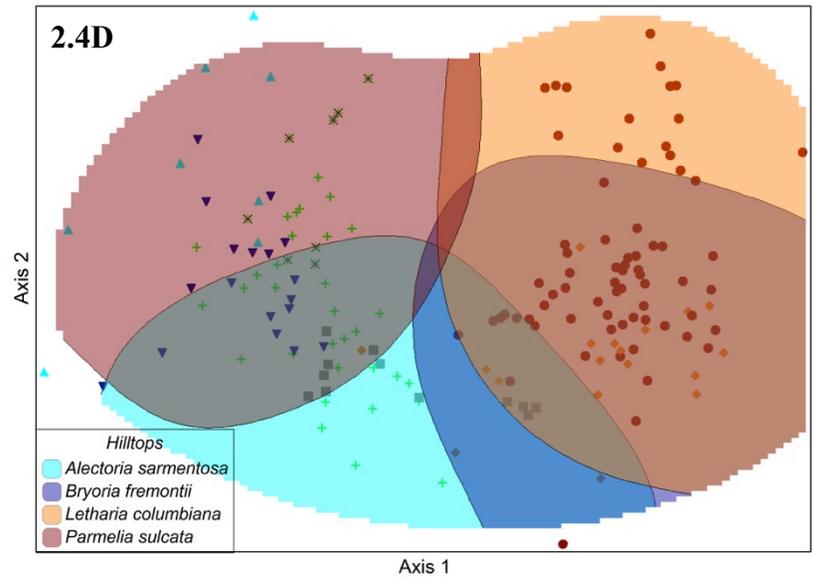
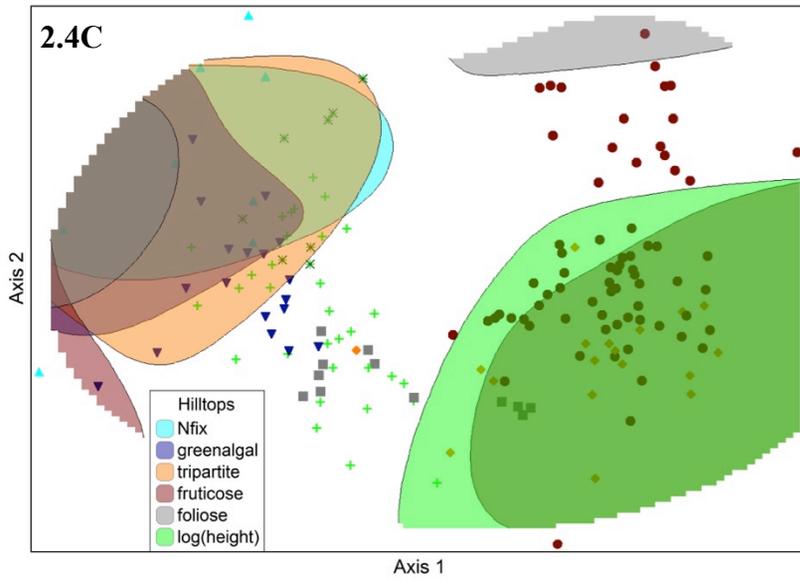
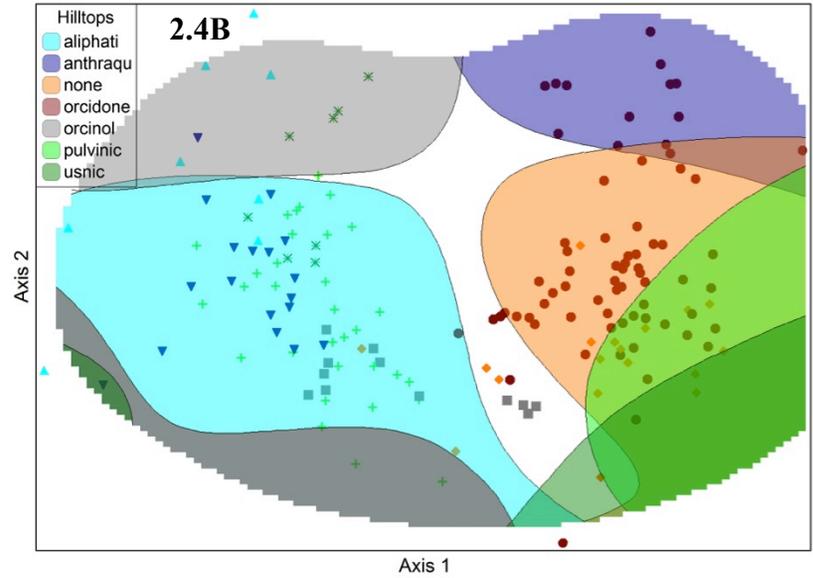
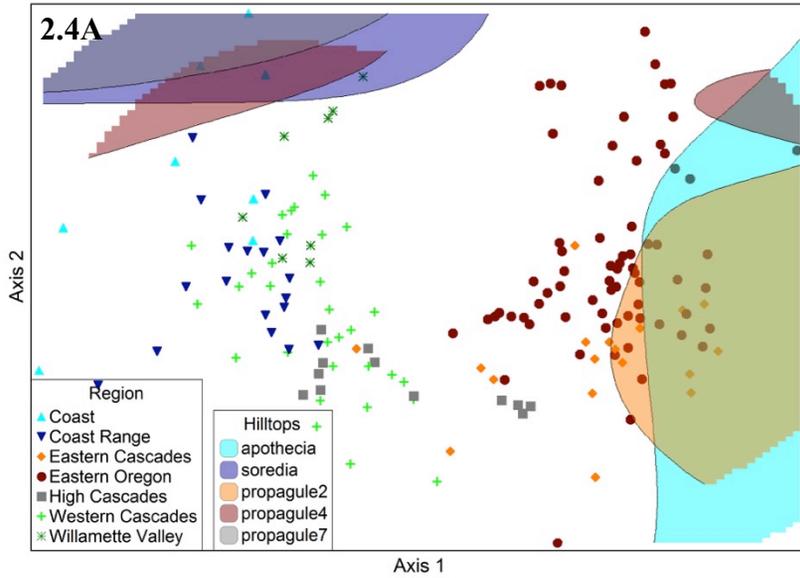
**H12a/H12b** – The gel trait was not strongly correlated with axes 1 or 2 ( $R^2 < 0.2$ ); however, hilltop plots show a weak nonlinear pattern of gel lichens peaking in frequency in areas with high precipitation (Figure 2.4), supporting hypothesis 12a and failing to support hypothesis 12b.

**H13** – As reported above, tall lichens were more frequent in areas with low precipitation (Figure 2.6), failing to support hypothesis 13.

**Table 2.9.** Hypothesis reference table.

<b>Number</b>	<b>Hypothesis</b>
H1	High relative frequency of sexually reproducing lichens in areas with high precipitation
H2	High relative frequency of large propagules in areas with high precipitation
H3	High relative frequency of small propagules in high elevation areas
H4	
a.	High relative frequency of asexual propagules in areas with high precipitation
b.	High relative frequency of sexual propagules in high elevation areas
H5	
a.	High relative frequency of cyanobacterial lichens in areas with high precipitation
b.	High relative frequency of green algal lichens in areas with low precipitation
H6	No strong patterns between the tripartite trait and precipitation
H7	
a.	High relative frequency of lichens that produce allelopathic chemicals in areas with high precipitation
b.	High relative frequency of tall lichens in areas with high precipitation
c.	High relative frequency of lichens that produce allelopathic chemicals in areas with low precipitation
d.	High relative frequency of tall lichens in areas with low precipitation
H8	High relative frequency of lichens that produce UV screening chemicals in high elevation areas
H9	
a.	High relative frequency of lichens that produce secondary substances that discourage herbivory in areas with low precipitation
b.	High relative frequency of lichens that produce secondary substances that discourage herbivory in areas with high precipitation
H10	No patterns in fruticose growth form relating to precipitation
H11	High relative frequency of foliose lichens in areas with high precipitation
H12	
a.	High relative frequency of gel lichens in areas with high precipitation
b.	High relative frequency of gel lichens in areas with high precipitation
H13	No patterns in lichen height relating to precipitation

**Figure 2.4.** Hilltop plots of nonlinear relationships between selected reproductive traits (A), selected chemical traits (B), selected morphological traits (C), and selected species (D) and axes 1 and 2 of the NMS ordination of plots in lichen species space.



## 4. DISCUSSION:

### *4.1. Dispersal and establishment:*

The relative frequency of sorediate lichens peaked in low elevation plots with a high mean annual temperature and high precipitation, mostly located in the Willamette Valley. These results are similar to the findings of Nelson *et al.* (2015) who demonstrated that richness of sorediate lichens peaks in low elevation forests in Alaska. The pattern for propagules between the size magnitudes of 3.50 and 4.49 (equivalent to about 3,126-31,260  $\mu\text{m}^3$ ) mirrored this pattern, suggesting that soredia are of this size magnitude. The relative frequency of propagules between the size magnitudes of 6.50 and 7.49 (equivalent to about 0.003-0.031  $\text{mm}^3$ ) also peaked in low elevation, high precipitation habitats, potentially supporting the hypothesis that larger propagules will be more frequent in wet habitats due to water movement as a mode of dispersal. Production of sexual spores peaked in the exact opposite habitat of soredia, with the high relative frequency in Eastern Oregon and the Eastern Cascades. The pattern for propagules between the size magnitudes of 1.50 and 2.49 scale (equivalent to about 31.62-312  $\mu\text{m}^3$ ) mirrored the pattern for apothecia, because ascospores are generally of this size magnitude. These findings support the expectation of relatively large, asexual propagules in wet areas and relatively small, sexual spores in high elevation areas.

### *4.2. Resource acquisition:*

All photobiont traits showed negligible linear relationships with axes 1 and 2 ( $R^2 < 0.2$ ); however, both bipartite and tripartite cyanolichens showed similar nonlinear patterns related to axis 1. These patterns were still fairly weak, which could be due to the scale of climatic data used in this study. As previously discussed, lichens are only capable of photosynthesis when hydrated,

with green algal lichens capable of photosynthesis at lower hydration levels than cyanobacterial lichens (Lange *et al.* 1986). This leads to the hypothesis that cyanobacterial lichens will be more frequent in areas with high precipitation. However, this study uses climatic data at a regional scale and does not take into account data at finer spatial scales, such as precipitation data at the landscape, forest stand, or tree scale. Differences in water availability at these finer scales is undoubtedly important to lichen distributions (Gauslaa 2014), but is not examined in this study. A focus of future work would be to collect data on the microhabitat of each individual specimen and examine how photobiont traits are related to the microhabitat as well as climate at the broader landscape and regional spatial scales.

#### 4.3. Competition:

Some lichen secondary metabolites have been shown to have allelopathic effects that may enhance their competitive ability. Allelopathic chemical classes that were present in the dataset and had strong relationships with one or both of the ordination axes were the pulvinic acid class (vulpinic acid), usnic acid, aliphatic acid class, orcinol depsides, and orcinol depsidones. The patterns for pulvinic acid and usnic acid were similar to one another, with both chemical classes occurring more frequently in Eastern Oregon and the Eastern Cascades. However, orcinol depsides and orcinol depsidones were found in two separate habitats. Lichens containing orcinol depsides were found in almost the exact opposite habitat type of pulvinic acid and usnic acid, peaking in relative frequency in plots on the Coast and in the Coast Range, with high precipitation and high mean annual temperature. Lichens containing orcinol depsidones were also found in western Oregon, but in habitats with moderate to high precipitation, low CMD, and

low AHM. In summary, chemical classes known to have allelopathic effects peaked in relative frequency in three separate habitats.

These seemingly confusing results could be influenced by the lack of knowledge regarding the allelopathic effects of lichen secondary metabolites in nature. The majority of evidence supporting the allelopathic effects of various metabolites comes from *in vitro* studies, with minimal research conducted on their effects *in vivo* (Favero-Longo and Piervittori 2010), and even these results are disputed by other authors. The only compound with an allelopathic effect that has been positively demonstrated (on oaks, *Quercus rotundifolia*) in a natural setting is evernic acid (orcinol depside class; Legaz *et al.* 2004, Favero-Longo and Piervittori 2010). These seemingly confusing results may also be due to the fact that many lichen compounds play biological roles (Cocchietto *et al.* 2002). Therefore, interpreting the distribution of chemical classes along climatic gradients based solely on their allelopathic roles is one-sided and ignores the many interrelated biological roles that they may play.

Although very little literature examines lichen height, this trait may also enhance competitive ability. Tall lichens peaked in relative frequency in the Eastern Cascades and Eastern Oregon, suggesting that, if this trait does indeed enhance competitive ability, these regions may present a more competitive environment. However, we may have observed this pattern because overall diversity is low east of the Cascades and alectorioid lichens, such as *Alectoria sarmentosa*, *Bryoria fremontii*, *Bryoria pseudofuscescens*, and *Nodobryoria abbreviata*, make up a large fraction of the species richness. Crustose lichens were also not taken into account in this study, which undoubtedly affects our results. Height also likely plays multiple biological roles, many of which may be unknown due to the lack of literature regarding this trait. More targeted

studies should be conducted to examine the biological roles lichen height plays in nature, and the potential this trait has for enhancing competitive ability.

#### 4.4. Stress (UV light):

The chemical classes that are known to screen/absorb UV light, and were strongly related to either of the two ordination axes, were usnic acid, anthraquinones, pulvinic acid class, orcinol depsidones, and orcinol depsides. Lichens containing anthraquinones had higher relative abundance in Eastern Oregon, occupying habitats not occupied by any of the other UV screening chemical classes. In fact, besides the similar distribution patterns displayed by the usnic acid and pulvinic acid classes, all of these UV screening chemicals occupied different habitats with very little overlap.

The distributions of usnic acid, pulvinic acid class, and anthraquinones support my original hypothesis that lichens containing UV screening chemicals would have a high relative frequency in areas with high elevation (hypothesis 8). In contrast, the distribution patterns of orcinol depsides and orcinol depsidones directly contradict my hypothesis. However, the roles of pulvinic acid, usnic acid, and parietin (anthraquinone class) as UV absorbing compounds have been widely supported in the literature (e.g. Rikkinen 1995, Bjerke *et al.* 2002, Solhaug *et al.* 2003, Nybakken *et al.* 2004, McEvoy *et al.* 2006, Nybakken and Julkunen-Tiitto 2006); whereas, the UV screening properties of the orcinol depside and orcinol depsidone compounds present in this study have not been widely supported. Bjerke *et al.* (2002) found that divaricatic acid (a compound in the orcinol depside class that was present in this study), although capable of absorbing UV radiation, was of little importance for the UV-screening properties of the crustose lichen *Ophioparma ventosa*. There is some evidence supporting the UV screening abilities of

lecanoric acid (Marcano *et al.* 2012); however, there are no studies directly testing the potential UV screening properties of any of the other orcinol depside compounds present in this study (4-O-methyl cryptochlorophaeic acid, evernic acid, imbricaric acid, olivetoric acid, perlatolic acid, scrobiculin, and sekikaic acid). There are also no studies directly testing the potential UV screening properties of any of the orcinol depsidone compounds present in this study (3-hydroxyphysodic acid, 4-O-methylgrayanic acid, alectoronic acid, grayanic acid, lobaric acid, physodic acid, and  $\alpha$ -collatolic acid). In summary, my findings suggest that UV screening chemicals are most prevalent in Eastern Oregon and the Eastern Cascades and that more information is needed on UV absorbance spectra of many lichen substances.

#### 4.5. Disturbance (herbivory):

The chemical classes that are known to discourage herbivory and were strongly related to one or both of the axes were the pulvinic acid class, orcinol depsides, orcinol depsidones, and anthraquinones. All four of these chemical classes occupied different habitats, peaking in frequency in the areas previously described in the competition and stress discussion sections. Solhaug and Gauslaa (2012) recently published a review of the literature directly demonstrating anti-herbivory effects of specific lichen compounds. Of the chemical compounds present in this study, usnic acid, vulpinic acid (pulvinic acid class), physodic acid (orcinol depsidone class), and scrobiculin (orcinol depside class) were shown in the recent literature to have anti-herbivory properties (Pöykkö *et al.* 2005, Solhaug and Gauslaa 2012). Of the anthraquinones, parietin has been shown to have no effect on herbivores (Pöykkö *et al.* 2005) and the other compounds have not been directly examined for their effects on herbivores. In summary, my findings show that chemical compounds that are known to deter herbivores are present across Oregon. However,

different chemical classes show distinct patterns, suggesting that there may be complex interactions between chemicals conferring resistance to herbivory and climatic gradients. Chemical traits may also be correlated with other traits such as growth form or reproduction strategy, resulting in complex and difficult to interpret patterns.

#### 4.6. *Water balance:*

Foliose lichens had a high relative frequency in regions with high total annual precipitation, as expected. This contradicts the findings of Giordani *et al.* (2012), who found a negative association of the foliose growth form with precipitation in Italy. I did not expect to see any strong patterns of fruticose lichens; however, the fruticose growth form was related to axis 2 and was more likely to be found in the high elevation Eastern Cascades and Eastern Oregon. This could be due to the fact that fruticose species such *Alectoria sarmentosa*, *Bryoria fremontii*, and *Nodobryoria abbreviata* have high relative abundance in these regions. Tall lichens were also more likely to be found in the Eastern Cascades and Eastern Oregon. This is most likely due to the fact that the height and growth form traits are interrelated (fruticose growth forms are on average taller than foliose growth forms). These findings are similar to those of Giordani *et al.* (2012) who found a positive association between the fruticose growth form and elevation.

#### 4.7. *Conclusions:*

Some lichen functional traits showed strong, often nonlinear, patterns along climatic gradients in forested areas in Oregon from 43-45°N. These patterns allowed for characterization of geographic regions in Oregon by the relative abundance of functional traits and dominant lichen species. Western Oregon was characterized by foliose and sorediate lichens tending to have large propagules, and lichens containing the following chemical classes: aliphatic acid,

orcinol depsidone, and orcinol depside. Eastern Oregon was characterized by fruticose, tall, and sexually reproducing lichens; lichens that tended to have small propagules, and either lacked secondary chemistry or contained pulvinic acid, usnic acid, and/or anthraquinones.

Despite the presence of strong patterns, it is important to note that this dataset only includes epiphytic macrolichens; the absence of crustose lichens and terricolous lichens undoubtedly has an effect upon the patterns observed. Additionally, the traits measured for these epiphytic macrolichens were not measured directly on the specimens collected from each plot. Interspecific variability may have introduced error into this study; however, we operated under the assumption that enough trait variability was captured to show clear associations with the climatic variables. Finally, the focus on macroclimate instead of microclimate may have resulted in missed patterns due to the fact that microsite characteristics are known to be very important to lichens (Gauslaa 2014). Axis 2, which was not strongly related to any environmental gradient, but was a driver of correlation, may be explained by microsite characteristics that were not measured in this study. However, despite these caveats, the strong patterns observed in this study demonstrate the potential for the use of lichen functional traits in ecological studies.

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### **Chapter 3: Lichen functional trait distributions in habitats in Katmai National Park, Alaska**

#### 1. INTRODUCTION

Lichens contribute greatly to the biodiversity of many ecosystems (McCune and Geiser 2009) and provide a variety of ecosystem services. Lichens are also widely recognized for their importance as bioindicators and are used by various government agencies as indicator species. Historically lichens have been used as bioindicators of air pollution due to the sensitivity of many species to common atmospheric pollutants such as SO<sub>2</sub> and NH<sub>3</sub> (Ferry *et al.* 1973), and their uses have been widely reviewed in the literature (Conti and Cecchetti 2001). More recently, lichen communities have been used to monitor forest health as part of the US Forest Service Forest Health Monitoring Program (McCune 2000). Lichens have also been recognized for their potential to indicate climate change through changes in diversity, community composition, and growth rate (Geiser and Neitlich 2007, Sancho *et al.* 2007). However, the majority of the research on their use as bioindicators focuses on changes in species diversity and species composition. Over the last two decades, multiple review papers have asserted that functional diversity and community composition are equally, or even more, important than species diversity and composition (*i.e.* Lavorel and Garnier 2002, McGill *et al.* 2006, Giordani *et al.* 2012). Functional richness is crucial to ecosystem processes and is often highly sensitive to change (Díaz and Cabido 2001); species richness, despite being the focus of many studies, is not an adequate surrogate (Díaz and Cabido 2001). Despite the recognized importance of functional traits, the functional characteristics of lichens have remained largely unstudied in the context of community ecology (Ellis and Coppins 2006, Matos *et al.* 2015).

Recent work on lichen functional trait distributions has focused mainly on the variation of traits along environmental gradients at both the macro-scale (*i.e.* Matos *et al.* 2015, Nelson *et al.* 2015) and micro-scale (Giordani *et al.* 2014). Besides enhancing basic scientific knowledge, understanding trait-habitat patterns could have important management implications. Many traits provide ecosystem services; understanding the distributions of habitats with these important traits could give an idea of potential pollution impacts, animal movement, etc. For example, cyanobacterial lichens are highly sensitive to air pollution (Geiser and Neitlich 2007) and also contribute to ecosystem mineral cycles by fixing large quantities of nitrogen (Knops *et al.* 1991, Antoine 2004). If cyanobacterial lichens are highly concentrated in a certain habitat, then this habitat would be at risk for significant pollution impacts, potentially affecting the nutrient cycling in that habitat. Land managers could use this information when making management decisions, commenting on potential threats to Class I Airsheds as designated in the Clean Air Act, and forming management plans.

To describe habitats in terms of traits, we examined the morphological, reproductive, and chemical traits of over 400 macrolichen and microlichen species collected from Katmai National Park, Alaska. These trait categories were chosen based on their potential responsiveness to climate and habitat. Giordani *et al.* (2012) found that growth form was highly responsive to climatic factors, with reproductive method and photobiont responding to a lesser extent. Several other studies have also demonstrated the responsiveness of morphological, reproductive, chemical traits to climate and habitat (Rapai *et al.* 2012).

Herbarium specimens, often collected using inventory methods similar to the ones described in this study, present a large potential resource for ecological studies, especially for

locations where fieldwork may be difficult or limited. Despite the large number of herbarium specimens available to ecologists, these records are often avoided due to concerns about collection bias and variation in collection methods (Gallagher *et al.* 2009). However, recent work has suggested that herbarium specimens may have more potential uses in ecological studies and may yield more useful results than previously thought (Robbirt *et al.* 2011). Data for our study were collected as part of a lichen inventory using haphazard collecting methods similar to those used for many herbarium collections. Furthermore, quantitative lichen traits were measured using herbarium specimens. This study provided an opportunity to develop methods for contrasting lichen traits among habitats with this type of nontraditional dataset.

## 2. METHODS:

### 2.1. Study Area:

This study was carried out in Katmai National Park, located in southern Alaska at the very base of the Aleutian Peninsula (Figure 3.1). The park is divided into two physiographic provinces: the Nushagak-Bristol Bay Lowlands (a flat, low-elevation terrain with numerous kettle ponds) and the Aleutian Range, which is further divided into the Shelikof Strait seacoast, a region of lakes, and the actual Aleutian Mountains. Much of the geography of the park has been shaped by glaciation and volcanic activity. The climate of the park ranges from maritime to the east and south of the Aleutian Range, to subcontinental to the north and west of the mountains.

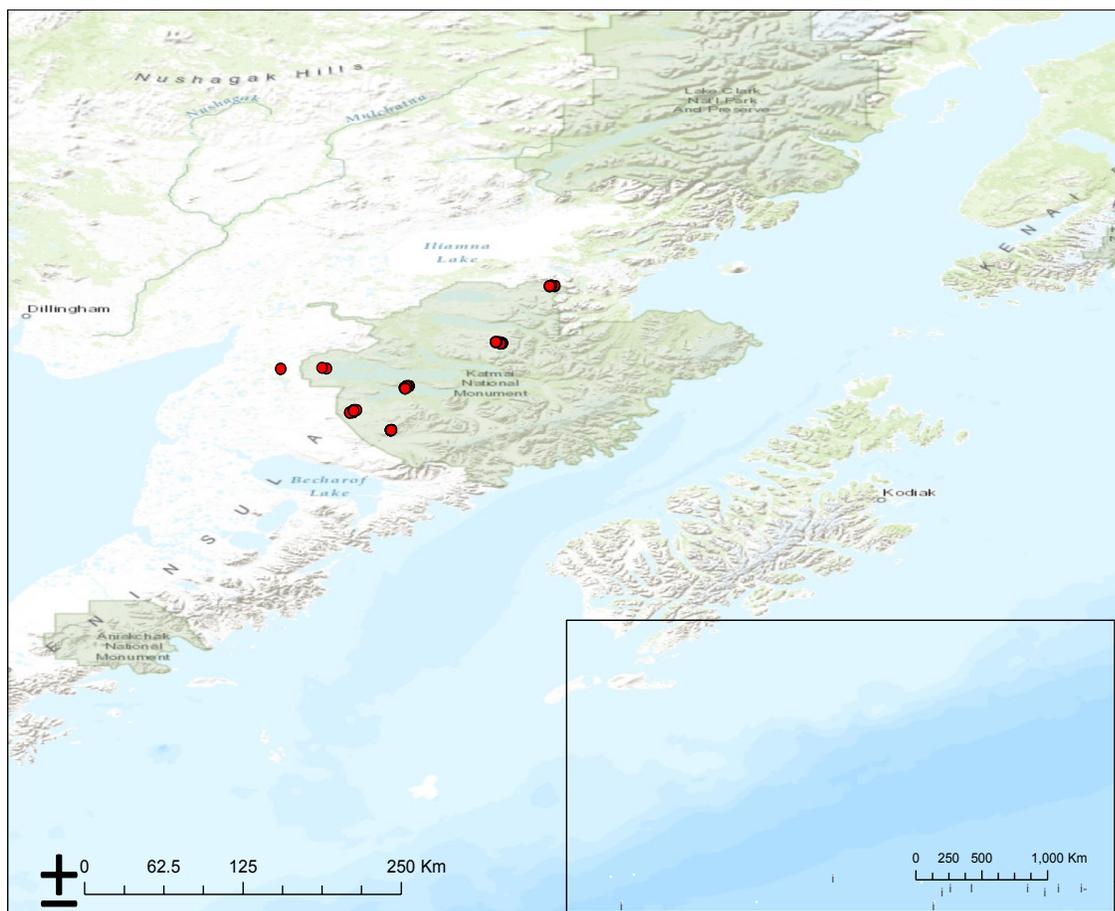
### 2.2. Data Collection:

All data for this study were collected from within Katmai National Park and from near a National Park Service (NPS) bunkhouse in King Salmon, Alaska (Figure 3.1) between July 24-August 3, 2013. Data were collected as part of a lichen species inventory of the park conducted

by the NPS Southwest Alaska Network (SWAN) in collaboration with Oregon State University. An international team of five lichenologists visited one site near the NPS bunkhouse in King Salmon and seven general sites within the park that were previously identified by the NPS as potential areas of high lichen diversity and/or contrasting vascular plant species composition. The total number of sites was limited by the remote nature of the park; all sites were accessible only by seaplane, helicopter, boat, and/or hiking. At each general site the team traveled to several general waypoints (30 total general waypoints for the park), and several specific waypoints within the general waypoints (140 total specific waypoints for the park). The research team conducted a haphazard inventory of all species present at each waypoint.

General habitat information, elevation, latitude, and longitude (NAD83 datum) were recorded for each waypoint. Collections were taken of each species for laboratory identification and measurement of traits. Substrate information was recorded for each specimen collected. All specimen collections are catalogued in the National Park Service database in Anchorage, Alaska and will be vouchered in the University of Alaska herbarium in Fairbanks (ALA).

Specimens were individually assigned *post hoc* to a habitat in two stages. First, habitat characteristics were assigned to each observation using elevation and specimen substrate information (Table 3.1). Second, habitats were defined based on all combinations of habitat characteristics. Poorly represented habitats were collapsed into a smaller number of habitats, resulting in ten total habitats each represented by 14 to 287 specimens (Table 3.2).



**Figure 3.1.** Map of waypoints (depicted as red dots) located in Katmai National Park, inset shows park location within Alaska. Map was created in ArcMap (ESRI) using Albers Equal Area Conic map projection and National Geographic Society and ESRI topographic basemaps.

**Table 3.1.** Detailed outline of the information used to assign individual specimens to primary habitat characteristics.

<b>Habitat characteristic</b>	<b>Yes</b>	<b>No</b>
High Elevation	Above 400 m	Below 400 m
Organic	Substrate is organic	Substrate is not organic
Epiphyte	Specimen is growing above 0.5 m	Specimen is growing below 0.5 m
Conifer	Specimen is growing on a coniferous tree	Specimen is not growing on a coniferous tree
Rock	Specimen is growing directly on the surface of a rock (any type/size)	Specimen is not growing directly on the surface of a rock
Sheltered	Specimen is growing in a sheltered location (on the under-hang of a rock cliff, beneath a boulder, in a rock crevice, etc.)	Specimen is not growing in a sheltered location

**Table 3.2.** Habitats derived as combinations of primary habitat characteristics. Detailed habitat information, including habitat description, total number of specimens and total number of species present in each habitat, and four example species for each habitat. Multiple specimens of the same species at a given locality were not counted as separate specimens.

Habitat	Acronym	# of specimens in habitat	# of species in habitat	Species examples
Epiphytic, unsheltered conifer at low elevation	EUCL	132	66	<i>Bryoria capillaris</i> , <i>Evernia mesomorpha</i> , <i>Hypogymnia austerodes</i> , <i>Nephroma helveticum</i>
Epiphytic, unsheltered deciduous tree at high elevation	EUDH	17	12	<i>Caloplaca sorocarpha</i> , <i>Frutidella pullata</i> , <i>Nephroma bellum</i> <i>Pertusaria carneopallida</i>
Epiphytic, unsheltered deciduous tree at low elevation	EUDL	287	121	<i>Collema furfuraceum</i> , <i>Leptogium saturninum</i> , <i>Ochrolechia szatalaensis</i> , <i>Pesudocyphellaria crocata</i>
Unsheltered on soil	GINU	27	24	<i>Baeomyces placophyllus</i> , <i>Cladonia nipponica</i> , <i>Pertusaria geminipara</i> , <i>Stereocaulon paschale</i>
Sheltered organic substrate on the ground	GOS	14	12	<i>Arthrorhaphis alpina</i> , <i>Cladonia cariosa</i> , <i>Lepraria finkii</i> , <i>Ochrolechia androgyna</i>
Unsheltered organic substrate on the ground at high elevation	GOUH	138	86	<i>Lobaria linita</i> , <i>Parmelia omphalodes</i> , <i>Rinodina conradii</i> , <i>Thamnolia vermicularis</i>
Unsheltered organic substrate on the ground at low elevation	GOUL	76	67	<i>Anaptychia bryorum</i> , <i>Cladonia albonigra</i> , <i>Massalongia carnosa</i> , <i>Lobaria pulmonaria</i>
Sheltered rock	GRS	25	19	<i>Ephebe lanata</i> , <i>Fuscidea hibernica</i> , <i>Physconia americana</i> , <i>Sporodictyon schaererianum</i>
Unsheltered rock at high elevation	GRUH	243	96	<i>Amygdalaria consentiens</i> , <i>Ephebe perspinulosa</i> , <i>Fuscidea mollis</i> , <i>Stereocaulon botryosum</i>

**Table 3.2 cont.**

<b>Habitat</b>	<b>Acronym</b>	<b># of specimens in habitat</b>	<b># of species in habitat</b>	<b>Species examples</b>
Unsheltered rock at low elevation	GRUL	111	86	<i>Flavoplaca citrina</i> , <i>Lecidella carpathica</i> , <i>Physcia caesia</i> , <i>Umbilicaria torrefacta</i>

### 2.3. Trait Measurement:

A total of 68 traits were evaluated for the 437 species collected during the lichen inventory; traits included photobiont, growth form, distance from substrate (“height”), reproductive method, size of reproductive propagules, and chemistry. Photobiont traits were assessed as general presence/absence of cyanobacteria, cyanobacteria as the only photobiont (bipartite), and presence of both cyanobacteria and green algae (tripartite). Possible growth form traits were fruticose, foliose, crustose, leprose, or gel (growth form traits are not mutually exclusive); individual species memberships in a given growth form were determined by cortex traits, how appressed the thallus is to the substrate, and how lobate the thallus was. Secondary chemistry was assessed at the chemical class level. Distance from the substrate, or height, was measured as well as modes of reproduction (production of apothecia, isidia, soredia, and lobules) and average volume of reproductive propagules. Average volumes of asexual reproductive propagules were measured in the lab and gathered from the literature (see Chapter 2 for propagule measurement protocol). I scored propagule volumes to accommodate mixed reproductive strategies (i.e. producing multiple sizes of propagules). For example, a species that produces both tiny ascospores and large vegetative propagules would be scored for both sizes. See Appendix A for detailed information on trait scoring. Information on average sizes of sexual

reproductive propagules and all other traits was gathered from the literature (see Appendix B for literature sources for individual species).

#### *2.4. Data Analysis:*

All data analyses were performed using PC-ORD Version 7.0 software (McCune and Mefford 2015). A habitat by species matrix (with presence/absence of each species in each habitat) and a species by trait matrix were constructed in two ways First, to express the representation of each trait in each habitat using the original measurement scales of the traits, I multiplied the species presence matrix by the trait matrix, followed by a weighted averaging step. The resulting habitat x trait matrix containing presence-weighted totals, where each element expresses the average value for a given trait across all species present in a given habitat.

Second, to improve comparability across traits for multivariate analysis, the trait matrix was first standardized by rescaling each trait from min-to-max, with 0 = minimum and 1 = maximum. I then multiplied the species presence matrix by the trait matrix, followed by a weighted averaging step. The resulting habitat by trait matrix containing presence-weighted means (= community-weighted means or CWM). Each element expresses the average value on a 0-1 scale for a given trait across all species present in a given habitat The ranges of various traits are thus directly comparable with each other and given equal weight in multivariate analysis.

Nonmetric Multidimensional Scaling (NMS), using Sørensen distance measures, was used to ordinate habitats in lichen trait space. This ordination method was chosen because of its success in recovering the nonlinear data structure common in ecological community datasets (McCune and Grace 2002). NMS was run on autopilot mode on the slow and thorough setting of 250 runs with both real and randomized data, with no penalization for ties, and a randomization

test. The final 2-dimensional solution was rotated to the principal axes, such that the axes are uncorrelated with each other. This ordination was then overlaid with habitat type information.

We used two-way hierarchical agglomerative cluster analyses in PC-ORD 7 (McCune and Mefford 2015) to examine groupings of habitats and traits based on lichen community composition. The data were relativized by trait standard deviates, and we used relative Euclidean distance, and Ward's method (McCune and Mefford 2015). This approach also grouped traits based on their co-occurrence in habitats.

### 3. RESULTS:

The inventory at Katmai National Park produced 429 total lichen species representing 145 genera. We defined 10 total habitats; the epiphytic, unsheltered deciduous tree at low elevation habitat had both the largest number of specimens (287) and the highest number of species (121; Table 3.2). Trait means for each habitat are given in Appendix D. The sheltered organic substrate on the ground had the lowest number of specimens (14) and was tied with the epiphytic, unsheltered deciduous tree at high elevation habitat for the lowest number of species (12; Table 3.2).

The NMS of ten habitats in trait space, as defined by the 68 relativized traits, resulted in a 2-dimensional solution (final stress = 6.62,  $p = 0.004$ ; Table 3.3) with the two axes representing a large amount of the variance in the data (cumulative  $R^2 = 0.896$ ). Axis 1 ( $R^2 = 0.709$ ) represented a gradient in lichen trait composition from sheltered habitats and ground habitats to unsheltered habitats and epiphytic habitats (Figure 3.2). Axis 2 ( $R^2 = 0.187$ ) represented a gradient in lichen trait composition from rock to organic substrates (Figure 3.2). Many traits were highly correlated with axis 1 and/or axis 2 (Table 3.4).

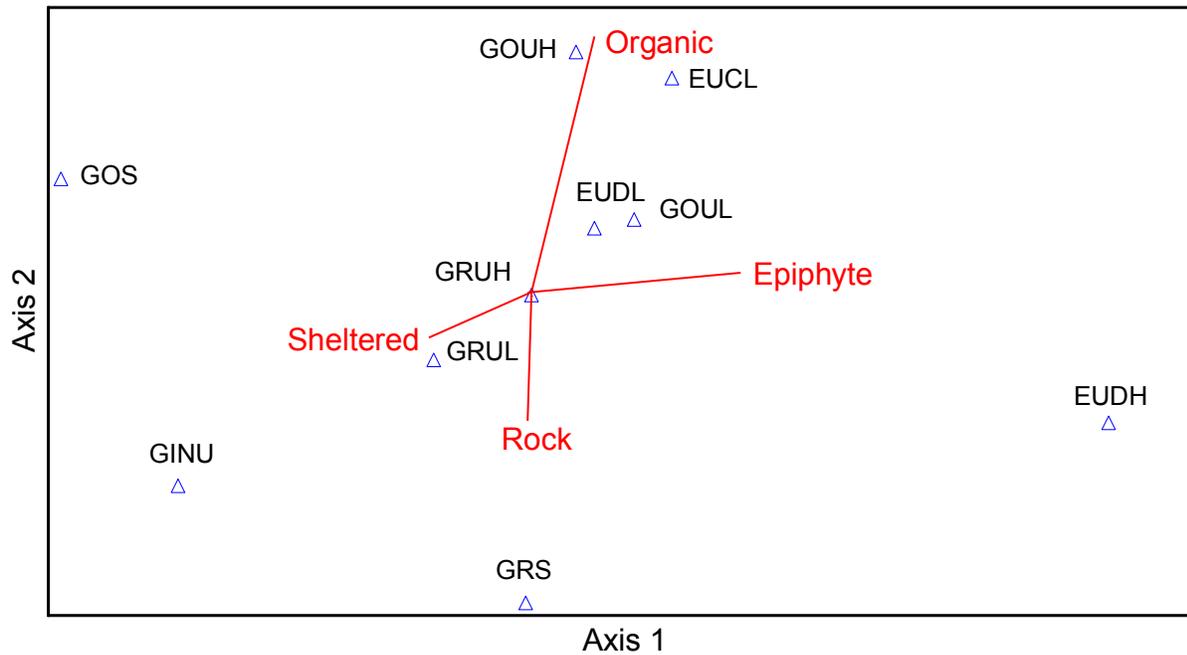
We pruned the habitat dendrogram to include four habitat clusters, a number chosen primarily for the sake of interpretability. The first habitat cluster, depicted in dark blue (Figure 3.3), contained one habitat, the only epiphytic habitat at high elevations. The second habitat cluster, depicted in light blue (Figure 3.3), contains epiphytic and ground habitats, with the common factor being an organic substrate and unsheltered location. The third habitat cluster, depicted in dark red (Figure 3.3), also contained one habitat, the only organic ground substrate that was also sheltered. The fourth habitat cluster, depicted in orange (Figure 3.3), contained all of the habitats with either rock or soil substrates.

Five primary trait clusters emerged from two-way cluster analysis. The first trait pattern was a large cluster of traits (outlined in hot pink) that were present at rather high but variable abundances in all of the habitats except the epiphytic, unsheltered deciduous tree at high elevation habitat (Figure 3.3). These traits included nine chemical traits, all of the traits related to presence of cyanobacteria as a photobiont, the foliose growth form, and several reproductive traits. The second trait cluster (outlined in purple) was smaller and only present in the second habitat cluster; this cluster included the crustose growth form, propagules with volumes from 0.03 to 0.31 mm<sup>3</sup>, xanthones, and pulvinic acid. The third trait cluster (outlined twice in orange) was present in all of the habitats except the shaded organic substrate on the ground habitat, and was composed of the fruticose growth form, triterpenes, no secondary chemistry, and several reproductive traits (Figure 3.3). The fourth trait cluster (outlined in red) was only present in unsheltered rock habitats, and was composed of the crustose growth form, propagules with volumes between 0.03 and 3.13 mm<sup>3</sup>, and several chemical traits (Figure 3.3). The last trait pattern is a cluster of traits (outlined in green) that are conspicuously absent or poorly

represented in sheltered habitats; these traits include relatively large propagules (volumes between 0.03 and 10 mm<sup>3</sup>), xanthonenes, pulvinic acid, dibenzofurans, and a number of other chemical traits (Figure 3.3).

**Table 3.3.** Correlation coefficients between habitat characteristics and axes 1 and 2 of the NMS ordination of habitats in lichen trait space, using Sørensen distance measures.

<b>Habitat</b>	<b>Axis 1 R<sup>2</sup></b>	<b>Axis 2 R<sup>2</sup></b>
Organic	0.120	0.488
Epiphytic	0.399	0.037
Rock	0.007	0.246
Conifer	0.030	0.181
Sheltered	0.195	0.086
HighElev	0.025	0.119



**Figure 3.2.** NMS joint plot of habitat characteristics superimposed on an ordination of habitats in lichen trait space using Sørensen distance measures. Habitat acronyms are defined in Table 3.2. Vectors represent habitat building blocks that were strongly correlated with the axes (minimum  $R^2 = 0.2$ ), with length of the vector corresponding to  $R^2$ .

**Table 3.4.** Summary of trait acronyms, descriptions, and trait correlation coefficients with each axis (with and  $R^2$  of at least 0.2 on at least one axis and/or with the trait present in at least 15% of all species in at least one habitat).

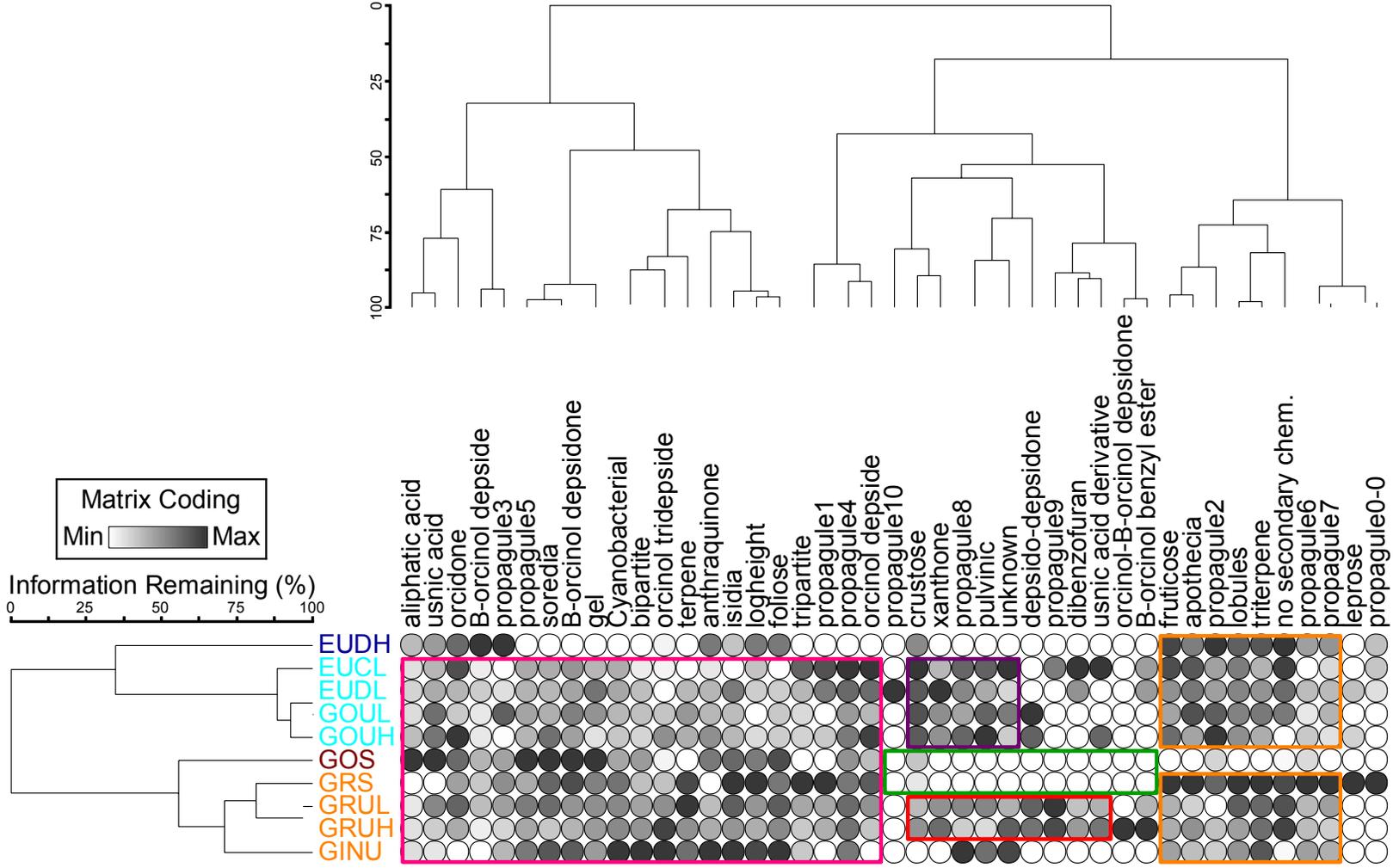
Acronym	Description	Axis 1 $R^2$	Axis 2 $R^2$
Nfix	Containing cyanobacteria as a photobiont	0.522	0.211
bipartite	Containing only cyanobacteria as a photobiont	0.623	0.12
fruticose	Fruticose growth form	0.519	0.055
foliose	Foliose growth form	0.244	0.446
leprose	Leprore growth form	0.001	0.219
crustose	Crustose growth form	0.305	0.605
gel	Homoiomerous cyanobacterial gel lichen	0.588	0.003
apothecia	Producing apothecia	0.39	0.026
isidia	Producing isidia	0.399	0.477
lobules	Producing lobules	0.362	0.265
soredia	Producing soredia	0.774	0.002
logheight	$\text{Log}_{10}$ of the height (mm)	0.085	0.645
propagule0-0.5	Reproductive propagules of size magnitudes 0-0.49, on the log scale (or with volume between 1 and $3.09 \mu\text{m}^3$ )	0.08	0.311
propagule2	Reproductive propagules of size magnitudes 1.50-2.49, on the log scale (or with volume between 31.27 and $312 \mu\text{m}^3$ )	0.473	0.003
propagule3	Reproductive propagules of size magnitudes 2.50-3.49, on the log scale (or with volume between 313 and $3,125 \mu\text{m}^3$ )	0.109	0.303
propagule4	Reproductive propagules of size magnitudes 3.50-4.49, on the log scale (or with volume between 3,126 and $31,260 \mu\text{m}^3$ )	0.207	0.093
propagule5	Reproductive propagules of size magnitudes 4.50-5.49, on the log scale (or with volume between 31,270 and $312,600 \mu\text{m}^3$ )	0.908	0.013

<b>Acronym</b>	<b>Description</b>	<b>Axis 1 R<sup>2</sup></b>	<b>Axis 2 R<sup>2</sup></b>
propagule6	Reproductive propagules of size magnitudes 5.50-6.49, on the log scale (or with volume between 312,610 and 3,126,079 $\mu\text{m}^3$ )	0.001	0.748
propagule7	Reproductive propagules of size magnitudes 6.50-7.49, on the log scale (or with volume between 0.003 and 0.031 $\text{mm}^3$ )	0.088	0.703
aliphatic	Containing compounds in the aliphatic acid class (bourgeanic acid, caperatic acid, constipatic acid, fatty acids, lichesterinic acid, murolic acid, neodihydromurolic acid, norrangiformic acid, protolichesterinic acid, rangiformic acid, and roccellic acid)	0.159	0.144
none	Containing no secondary chemistry	0.443	0.065
orcidone	Containing compounds in the orcinol depsidone class (2'-O-methylphysodic acid, 3-hydroxyphysodic acid, 4-O-methylgrayanic, alectoronic acid, diploicin, grayanic acid, lobaric acid, oxyphysodic acid, physodic acid, variolaric acid, and $\alpha$ -collatolic acid)	0.077	0.275
orcitrid	Containing compounds in the orcinol tridepside class (gyrophoric acid, hiascinic acid, methyl gyrophorate, methylgyrophoric acid, tenuiorin, and umbilicatic acid)	0.13	0.075
pulvinic	Containing compounds in the pulvinic acid class (calycin, epanorin, pinestric acid, pulvinic acid, pulvinic lactone, rhizocarpic acid, and vulpinic acid)	0.003	0.267
terpene	Containing compounds in the terpene class (diterpene, terpenoids, and triterpenes)	0.079	0.324
triterpene	Producing the chemical compound zeorin	0.143	0.645
usnic	Containing compounds in the usnic acid class (usnic acid)	0.018	0.412
usnic ac	Containing usnic acid derivative compounds (isousnic acid and placodiolic acid)	0.018	0.348
xanthone	Containing compounds in the xanthone class (2,7-dichlorolichexanthone, asemone, isoarthothelin, lichexanthone, thiophanic acid, thuringione, vinetorin, and xanthonenes)	0.023	0.227

**Table 3.4** *cont.*

<b>Acronym</b>	<b>Description</b>	<b>Axis 1 R<sup>2</sup></b>	<b>Axis 2 R<sup>2</sup></b>
β-benzyl	Containing compounds in the β-orcinol benzyl ester class (alectorialic acid and barbatolic acid)	0.005	0.039
β-done	Containing compounds in the β-orcinol depsidone class (2'-O-demethylpsoromic acid, argopsin, connorstictic acid, constictic acid, cryptostictic acid, fumarprotocetraric acid, hypoprotocetraric acid, norstictic acid, pannarin, physodalic acid, protocetraric acid, psoromic acid, salazinic acid, stictic acid, and succinprotocetraric acid)	0.733	0.015
β-orcino	Containing compounds in the β-orcinol depside class (4-O-demethylbarbatic acid, atranorin, baeomycesic acid, barbatic acid, chloratranorin, consquamatic acid, diffractaic acid, hypothamnolic acid, nephromarctin, phenarctin, squamatic acid, and thamnolic acid)	0.317	0.075

**Figure 3.3.** Two way cluster analysis (using relative Euclidean distance) dendrogram of habitats in trait space. Darker squares denote higher abundance of relative trait values (standardized from 0-1). One-way cluster analysis was used to prune habitats into four groups, denoted by color on this dendrogram. Six trait groups were also identified and outlined in color. Habitat codes can be found in Table 3.2 and trait codes can be found in Table 3.4.



### *3.1. Epiphytic, unsheltered conifer at low elevation:*

Unsheltered locations on low elevation conifers had the largest percentage of crustose lichens (over 60% of the species) of any habitat, and the average height of lichens was 1.8 mm (Table 3.5). Just over 68% of the species reproduced sexually, with propagule volume evenly spread from 31.6 to 31,260  $\mu\text{m}^3$  (Table 3.6). A large percentage (33%) of the species lacked secondary chemistry, followed by  $\beta$ -orcinol depsidones, which were produced by 24% of the species (Table 3.7). It is important to note that the crustose growth form was the dominant morphological trait in all but four of the habitats, and production of apothecia was the dominant reproductive trait in every habitat (Tables 3.5 and 3.6).

### *3.2. Epiphytic, unsheltered deciduous tree at high elevation:*

Unsheltered locations on high elevation deciduous trees also had a high percentage of crustose lichens, followed closely by a high percentage of foliose species; the average height of lichens was 2.4 mm (Table 3.5). This habitat is unique in that it was the only habitat with a complete absence of cyanobacterial species (Table 3.5), had the lowest percentage of sorediate species at 12% (Table 3.6), and the highest percentage of species lacking secondary chemistry (Table 3.7). A large percentage of propagules were between 31.6 and 3,125  $\mu\text{m}^3$  in volume (Table 3.6), and over 45% of the species produced  $\beta$ -orcinol depsides (Table 3.7).

### *3.3. Epiphytic, unsheltered deciduous tree at low elevation:*

Crustose lichens dominated unsheltered locations on low elevation deciduous trees (57% of the species), and the average height was 1.7 mm (Table 3.5). 57% of the species produced apothecia, with propagule volume evenly spread from 31.6 to 31,260  $\mu\text{m}^3$  (Table 3.6). Chemical

traits were fairly even spread between orcinol depsides, orcinol depsidones, and no secondary chemistry (Table 3.7).

#### *3.4. Unsheltered on soil:*

Unsheltered locations on bare mineral soil were unique in that the foliose growth form was dominant, comprising over 54% of the species. It also had the highest percentage of cyanobacterial lichens with over 37% of the species containing cyanobacteria (Table 3.5). The average height was 3.0 mm (Table 3.5). Although still dominated by lichens with apothecia, sorediate species made up over 33% of the lichens in this habitat and 30% of the propagules ranged in volume from 313 to 3,125  $\mu\text{m}^3$  (Table 3.6). Over 32% of the species produced  $\beta$ -orcinol depsidones, followed by 17% that lacked secondary chemistry, and 17% that produced orcinol tridepsides (Table 3.7).

#### *3.5. Sheltered organic substrate on the ground:*

Foliose lichens also dominated this habitat, making up 50% of the species; the average lichen height was 2.4 mm (Table 3.5). This habitat also had the lowest percentage of lichens producing apothecia (50%) and the highest percentage of sorediate species (37%); over 30% of the propagules ranged in volume from 313-3,125  $\mu\text{m}^3$  (Table 3.6). Over 37% of the species produced  $\beta$ -orcinol depsidones, but this habitat also had the highest percentage (25%) of species producing chemicals in the aliphatic acid class and the highest percentage (17%) of species producing usnic acid (Table 3.7).

#### *3.6. Unsheltered organic substrate on the ground at high elevation:*

Crustose lichens dominated this habitat, and fruticose and foliose species both comprised about 20% of the species apiece; average lichen height was 1.6 mm (Table 3.5). Over 60% of the

species produced apothecia and 34% of the propagules ranged in volume from 31.6-312  $\mu\text{m}^3$  (Table 3.6). Secondary chemistry production was fairly evenly spread out, with no single chemical class dominating (Table 3.7).

### *3.7. Unsheltered organic substrate on the ground at low elevation:*

Crustose lichens dominated this habitat and the average lichen height was 1.4 mm (Table 3.5). Again, apothecia were the dominant trait and a large percentage of propagules ranged in volume from 31.6 to 3,125  $\mu\text{m}^3$  (Table 3.6). Similar to the previous habitat, no single chemical class dominated this habitat (Table 3.7).

### *3.8. Sheltered rock:*

Foliose lichens dominated and, although only making up about 26% percent of the species, sheltered rocks had the highest percentage of fruticose lichens (Table 3.5). This habitat had the highest average height at 3.3 mm and the second highest percentage of cyanobacterial lichens at about 26% (Table 3.5). Over 72% of the species produced apothecia, the highest amount of any habitat, and most propagule volumes ranged from 31.6 to 3,125  $\mu\text{m}^3$  (Table 3.6). This habitat was unique due to its complete lack of any species producing usnic acid or aliphatic acids; many species either lacked secondary chemistry altogether or produced  $\beta$ -orcinol depsidones (Table 3.7).

### *3.9. Unsheltered rock at high elevation:*

Crustose lichens dominated unsheltered high elevation rocks at 49% of the species, followed closely by foliose lichens at about 38%; the average lichen height was 2.0 mm (Table 3.5). Over 62% of the species produced apothecia and the majority of propagule volumes were

evenly spread between 31.6 and 3,125  $\mu\text{m}^3$  (Table 3.6). Over 32% of the species lacked secondary chemistry (Table 3.7).

*3.10. Unsheltered rock at low elevation:*

Foliose lichens dominated unsheltered low elevation rocks and the average lichen height was 2.2 mm (Table 3.5). Apothecia were the dominant reproductive mode, but sorediate lichens made up over 30% of the species in this habitat and over 31% of the propagules ranged in volume from 313-3,125  $\mu\text{m}^3$  (Table 3.6). Chemical traits were fairly evenly spread between the production of  $\beta$ -orcinol depsidones,  $\beta$ -orcinol depsides, and a lack of secondary chemistry (Table 3.7).

**Table 3.5.** Percentage of species possessing a given **photobiont or morphological trait** in each habitat. Height values are the average heights (mm) of the species in each habitat. Traits included are photobiont and morphological traits present in greater than 20% of species in at least one habitat. See Appendix D for a summary of all traits in habitats.

<b>Habitat</b>	<b>Nfix</b>	<b>bipartite</b>	<b>fruticose</b>	<b>foliose</b>	<b>crustose</b>	<b>height (mm)</b>
Epiphytic, unsheltered conifer at low elevation	15.2	3.0	24.2	16.7	62.1	1.8
Epiphytic, unsheltered deciduous tree at high elevation	0	0	25.0	41.7	50.0	2.4
Epiphytic, unsheltered deciduous tree at low elevation	16.5	10.7	18.2	26.0	57.0	1.7
Unsheltered on soil	37.5	33.3	16.7	54.2	33.3	3.0
Sheltered organic substrate on the ground	16.7	16.7	8.3	50.0	41.7	2.4
Unsheltered organic substrate on the ground at high elevation	10.5	7.0	21.5	26.3	57.0	1.6
Unsheltered organic substrate on the ground at low elevation	13.4	10.4	16.4	26.9	58.2	1.4
Sheltered rock	26.3	10.5	26.3	42.1	36.8	3.3
Unsheltered rock at high elevation	21.9	17.7	15.6	38.5	49.0	2.0
Unsheltered rock at low elevation	22.1	15.1	15.2	47.1	43.0	2.2

**Table 3.6.** Percentage of species possessing a given **reproductive trait** in each habitat. Traits included are reproductive traits present in greater than 20% of species in at least one habitat. See Appendix D for a summary of all traits in habitats.

<b>Habitat</b>	<b>apothecia</b>	<b>soredia</b>	<b>propagule2 (31.6-312 <math>\mu\text{m}^3</math>)</b>	<b>propagule3 (313-3,125 <math>\mu\text{m}^3</math>)</b>	<b>propagule4 (3,126-31,260 <math>\mu\text{m}^3</math>)</b>
Epiphytic, unsheltered conifer at low elevation	68.3	22.9	23.5	25.2	28.9
Epiphytic, unsheltered deciduous tree at high elevation	64.2	12.5	34.2	37.5	4.2
Epiphytic, unsheltered deciduous tree at low elevation	65.0	21.5	23.6	27.1	22.7
Unsheltered on soil	57.1	33.3	19.2	30.0	20.8
Sheltered organic substrate on the ground	50.0	37.5	18.3	30.8	17.5
Unsheltered organic substrate on the ground at high elevation	60.0	30.2	34.0	25.2	20.5
Unsheltered organic substrate on the ground at low elevation	69.3	22.4	30.3	34.9	16.7
Sheltered rock	72.1	31.6	29.5	32.1	21.1
Unsheltered rock at high elevation	62.2	19.4	20.4	27.7	21.5
Unsheltered rock at low elevation	55.1	30.8	14.2	31.0	22.4

**Table 3.7.** Percentage of species possessing a given **chemical trait** in each habitat. Traits included are chemical traits present in greater than 15% of species in at least one habitat. See Appendix D for a summary of all traits in habitats.

<b>Habitat</b>	<b>aliphatic acid</b>	<b>none</b>	<b>orcinol tridepside</b>	<b>usnic acid</b>	<b><math>\beta</math>-orcinol depsidone</b>	<b><math>\beta</math>-orcinol depside</b>
Epiphytic, unsheltered conifer at low elevation	3.8	32.6	8.3	6.1	23.6	15.3
Epiphytic, unsheltered deciduous tree at high elevation	8.3	33.3	8.3	8.3	8.3	45.8
Epiphyte in an unsheltered location on a deciduous tree at low elevation	5.4	28.9	7.9	7.0	21.5	21.1
Unsheltered on soil	4.2	16.7	16.7	2.08	32.1	12.5
Sheltered organic substrate on the ground	25.0	16.7	8.3	16.7	37.5	25
Unsheltered organic substrate on the ground at high elevation	8.1	16.3	12.8	11.5	22.1	16.3
Unsheltered organic substrate on the ground at low elevation	4.3	27.6	10.4	11.9	26.9	16.3
Sheltered rock	0	31.6	10.5	0	34.2	21.6
Unsheltered rock at high elevation	3.6	32.3	16.1	4.2	19.3	15.1
Unsheltered rock at low elevation	2.9	30.9	12.8	9.9	23.8	23.3

#### 4. DISCUSSION:

Distinct patterns in lichen functional community composition were seen in different habitats. Two-way cluster analysis separated rock, non-rock ground, and epiphytic habitats into distinct clusters based on the traits present in each habitat. These findings are similar to those of Holt *et al.* (2009), who at the species level saw a partition between rock and epiphytic/shrubby communities in Noatak National Preserve, Alaska. The communities in their study were largely separated by bedrock type and dominant vegetation, the patterns of which are generally determined by soil moisture and exposure (Holt *et al.* 2009).

Some traits, such as the crustose growth form and production of apothecia, were fairly cosmopolitan across habitats, while other traits were more specific to a habitat cluster. For example, the foliose growth form was most abundant in the shaded ground and low elevation epiphytic habitat cluster. These findings are similar to those of Botting *et al.* (2008), who found that foliose lichens were much more common in epiphytic habitats than in terrestrial habitats in a sub-boreal spruce forest in British Columbia.

Presence of cyanobacteria was established in the introduction as a trait of particular interest; cyanolichens were conspicuously absent from epiphytic, unsheltered deciduous trees at high elevations, and were most abundant growing on non-rock ground substrates. These findings are similar to those of Holt *et al.* (2009), who found that cyanolichens group together in hummocky tussock tundra habitats in Noatak National Preserve, Alaska. Our findings contrast with those of Botting *et al.* (2008), who found that cyanolichens were more abundant in epiphytic habitats than terrestrial habitats. However, their study was restricted to macrolichens in

an old growth sub-boreal spruce forest, while our study examines both macro and micro lichens across a much broader array of habitats.

Due to their sensitivity to air pollution, cyanolichens can serve as important bioindicators (Geiser and Neitlich 2007); therefore, the cyanobacterial trait is interesting from a management standpoint. The nitrogen fixing capabilities of cyanolichens are also interesting from a management standpoint. Cyanobacterial lichens were most abundant in the shaded rock habitat and the organic ground habitat at low elevations, suggesting that these habitats may be at greatest risk for negative impacts from increasing air pollution. These habitats could be targeted during agency vegetation inventories to monitor any changes in cyanolichen diversity and abundance and track potential air pollution increases. In fact, cyanobacterial lichens as a functional group are already monitored by the USDA Forest Inventory and Analysis program as part of their Ground Layer Indicator (Smith *et al.* 2015).

These findings also carry implications for the potential use of historical data in future trait studies. The data used in this study were collected in a haphazard manner with no formal sampling design, similar to how many herbarium specimens are collected. Herbarium specimens collected during formal inventories and on other collecting missions are vast, largely untapped resources for measuring functional trait values. A fear of using herbarium data in ecological studies is that collection bias and the differences in collection methods between specimens may create noise masking any potential patterns (Case *et al.* 2007, Gallagher *et al.* 2009). A few fairly recent studies have used herbarium records to reconstruct the spread of invasive vascular plants in Canada (Delisle *et al.* 2003), examine the declining abundance of American ginseng (Case *et al.* 2007), and track phenological trends in alpine vascular plants in Australia (Gallagher *et al.*

2009). All of these studies successfully used herbarium specimens, but highlighted the caveats and potential errors associated with using this type of data. However, Robbirt *et al.* (2011) validated the use of herbarium specimens for phenological studies, and emphasized the need for more direct testing of the validity of herbarium specimen use in ecological research, using a wide variety of species and ecological questions. My findings suggest that herbarium specimens have the potential to be a valuable resource for future trait studies. The potential for noise and error may still be a concern; therefore, additional research should be done to see if my results are replicable.

In-situ trait measurement is challenging, if not impractical, on a wide scale for such a large number of species as included here. I was, however, able to use herbarium specimens to quantitatively measure the average volume of reproductive propagules, a trait that has been largely unexplored in lichen functional trait work, but may be of interest in future studies.

## 5. REFERENCES:

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## Chapter 4: Conclusions

For this thesis I started with the goal of examining how lichen functional traits are related to the environment, a topic in its infancy for lichens. Chapter 2 focused on how functional traits vary along macroclimatic gradients in Oregon, specifically precipitation and temperature gradients. I used plot data collected by the USDA Forest Service program for Forest Inventory and Analysis (FIA) program, spanning western to eastern Oregon between 43°W and 45°W. Chapter 3 focused on functional trait distributions among habitats in Katmai National Park, Alaska; this chapter also examined the usefulness for ecological research of floristic data collected without a formalized sampling framework. For both of these chapters I measured or scored a large number of traits for 500 total lichen species; these traits included two groups that, to the best of our knowledge, have never been quantitatively measured and studied in an ecological context for lichens. This final chapter will compare the results found in Chapters 2 and 3, summarize the new traits measured in this thesis, and emphasize topics that warrant future study.

In Oregon, the foliose growth form, production of soredia, large propagules, cyanobacteria, and lichens producing orcinol depsides were found to be most abundant in habitats with high precipitation and generally warm, stable temperatures (western Oregon). Lichens producing aliphatic acid and orcinol depsidones were also preferentially found in western Oregon, although they were more abundant in plots with a lower climatic moisture deficit (CMD) and a lower annual heat to moisture index (AHM) than the areas mentioned previously. The fruticose growth form, production of apothecia, height, small propagules, pulvinic acid, usnic acid, and a lack of secondary chemistry had the highest relative abundance

east of the Cascade Range, in habitats with low precipitation and unstable temperature (hot summers, cold winters). Relative abundance of lichens producing anthraquinones also peaked in eastern Oregon, although in plots with higher CMD and AHM than the areas mentioned previously. All other traits were only weakly to moderately related to gradients in species composition.

In Katmai National Park in southwest Alaska the foliose lichens were generally most abundant in the same habitats as cyanobacterial lichens, soredia, and large propagules. Although the habitats/climatic gradients examined in the Oregon and Alaska studies were very different, this co-occurrence of traits is similar. However, in Alaska foliose trait tended to occur with aliphatic acids, usnic acid, and anthraquinones, opposite of the pattern observed in Oregon. Fruticose lichens were relatively abundant in habitats with tall lichens, apothecia, small propagules, and a lack of secondary chemistry, similar to the patterns observed in Oregon.

Although the patterns observed in the two studies were not identical, the similarities suggest that there may be some generality to lichen trait patterns. The covariation in traits likely depends on the environmental context of the data and may also be due to different study methods (e.g. inclusion of crustose lichens in Alaska but not in Oregon) and the somewhat different questions asked in each study. Future research should be done to directly compare trait variation along environmental gradients in different regions. The patterns observed in these studies can hopefully inform such future research. Chapter 3 also provided support for the use of herbarium specimens in ecological research and demonstrates the need for more targeted studies testing this question. I found that some traits showed such distinct differences among habitats as to suggest

ecologically important patterns. The adaptive significance of these traits remains, however, largely unexplored.

One of the main contributions of this study was scoring and measuring a large number of traits for the 500 species present in the two study areas combined. These data will be useful as a starting point for future research on lichen traits. Two important groups of traits were estimated quantitatively for the first time and both groups of traits show promise for improving our understanding of lichen distribution and abundance.

One group, average reproductive volumes for each species, was measured in such a way as to allow the expression of split strategies (i.e. multiple propagule sizes) for a given species. Reproductive traits are assumed to be of key importance to all organisms, but to the best of our knowledge, this has not been studied for lichens in an ecological context. Average reproductive propagule volume was found to show marked climatic and habitat differences in both of our studies. In Oregon, several ranges of average reproductive propagule volume were strongly correlated with gradients in lichen community composition, with larger propagules preferentially associated with plots in western Oregon and smaller propagules preferentially associated with plots in eastern Oregon. Average reproductive propagule volume also showed patterns in Alaska, with smaller propagules found to be more common than larger propagules in all habitats.

The second group of quantitative traits express the height (or logarithm of height) of the organism. This was chosen as a distillation of a fundamental attribute of lichens, the degree to which they are exposed to microclimates away from the surface on which they grow. Furthermore, lichen height directly relates to the functional significance of lichens, since tall (or long) lichens are important as forage for mammals, are sensitive to air quality, and are in many

cases old-growth associated. In Oregon, height was also patterned on climatic gradients and among geographic regions, with taller (or longer) lichens found to have higher relative abundance in eastern Oregon, particularly in the eastern Cascades.

In summary, as part of this thesis we scored traits for a large number of species and examined trait patterns along environmental gradients in Oregon and among habitats in Katmai National Park, Alaska. The patterns we observed demonstrate the potential for using average propagule volume and lichen height as traits to increase our understanding of lichen distribution and abundance. Our results also demonstrate the need for future work on the usefulness of herbarium specimens in ecological research. Lastly, our findings add to an area of the literature that is still largely unexplored, enhancing our general knowledge of lichen ecology.

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## **Appendices**



## APPENDIX A

**Table A.1.** Table listing all traits measured for Chapters 2 and 3 and how they were scored. “Building block traits” were used in combination to generate other trait scores for growth forms, according to the logical statements given for each growth form.

Trait	Trait Score			
	1	0.5	0.1	0
Nfix	Cyanobacteria present	NA	NA	Cyanobacteria absent
bipartite	Bipartite	NA	NA	Not bipartite
tripartite	Tripartite	NA	NA	Not tripartite
- fruticose = (ulcortex = 1) - foliose = (lobate>0) AND (ucortex=1) AND ((lcortex=1) OR ((lcortex=0) AND (appressed<1))) - leprose = (lcortex=0) AND (ucortex=0) AND (soredia=1) - crustose = (lcortex=0) AND (ucortex=1) AND (appressed=1)	Specimens always exhibit this growth form	Specimens exhibit this growth form ~50% of the time	Specimens rarely exhibit this growth form	Specimens never exhibit this growth form
gel	Gelatinous lichen (a homoiomerous cyanobacterial bipartite lichen)	NA	NA	Not a gelatinous lichen
apothecia, isidia, lobules, soredia	Specimens commonly-always have specific reproductive propagule present	Specimens sometimes have specific reproductive propagule (~50% of the time) present	Specimens infrequently-rarely have specific reproductive propagule present	Specimens never have specific reproductive propagule present
lobate (building block trait of growth forms)	Thallus is very divided	Thallus is somewhat divided	Thallus is marginally divided	Thallus is not divided

<b>Appendix A cont.</b>				
<b>Trait</b>	<b>1</b>	<b>0.5</b>	<b>0.1</b>	<b>0</b>
ucortex (building block trait of growth forms)	Upper cortex is present	NA	NA	Upper cortex is absent
ulcortex (building block trait of growth forms)	Upper and lower cortex are identical (i.e. a fruticose lichen)	NA	NA	Upper and lower cortex are not identical (not a fruticose lichen)
lcortex (building block trait of growth forms)	Lower cortex is present	NA	NA	Lower cortex is absent
appressed (building block trait of growth forms)	Thallus is closely attached to substrate (with no space between the lower surface and the substrate) or even partially within the substrate (example: endolithic species)	Thallus is closely attached to substrate, but with some space between the lower surface and the substrate	NA	Thallus is not closely appressed to the substrate
attachment	Thallus is attached to the substrate by a single holdfast	NA	NA	Thallus is attached to the substrate by multiple holdfasts, is “painted on” to the substrate, or is not attached to the substrate at all (e.g.: <i>Thamnolia</i> sp.)
propagule0-propagule10 (Magnitudes of propagule size, units= $\mu\text{m}^3$ , log scale. For example, propagule2 refers to propagules of sizes 1.50-2.49, on the log scale)	Propagules with this magnitude of size are commonly-always present	Propagules with this magnitude of size are sometimes present	Propagules with this magnitude of size are infrequent-rarely present	Propagules with this magnitude of size are never present

<b>Appendix A cont.</b>	
<b>Trait</b>	<b>Description</b>
sporelength	Median length of spores (measured in $\mu\text{m}$ )
sporewidth	Median width of spores (measured in $\mu\text{m}$ )
sporenumber	Median number of spores per ascus
sporevolume	Volume of an ellipsoid = $(4/3) * \pi * \frac{1}{2} \text{ spore length} * (\frac{1}{2} \text{ spore width})^2$ ( $\mu\text{m}^3$ )
logsporevolume	$\log_{10}$ (spore volume)
sporeshape	$\log_{10}(\text{spore length/spore width})$
isidialength	Average length of isidia ( $\mu\text{m}$ )
isidiawidth	Average width of isidia ( $\mu\text{m}$ )
isidiavolume	Volume of an cylinder = $\pi * (\frac{1}{2} \text{ isidia width})^2 * \text{ isidia length}$ ( $\mu\text{m}^3$ )
logisidiavolume	$\log_{10}(\text{isidia volume})$
lobulelength	Average length of lobules ( $\mu\text{m}$ )
lobulewidth	Average width of lobules ( $\mu\text{m}$ )
lobulevolume	Volume of a cylinder = $\pi * \text{lobule length} * (\frac{1}{2} \text{lobule width})^2$ ( $\mu\text{m}^3$ )
loglobulevolume	$\log_{10}(\text{lobule volume})$
sorediameter	Average diameter of soredia ( $\mu\text{m}$ )
sorediavolume	Volume of a sphere = $(4/3) * \pi * (\frac{1}{2} \text{soredia diameter})^3$ ( $\mu\text{m}^3$ )
logsorediavolume	$\log_{10}(\text{soredia volume})$
aliphati through $\beta$ -orcidone	100 = present; 90 = usual; 50 = toss-up; 10 = rarely; 0 = absent Acronyms stand for the following chemical classes: aliphatic acid, anthraquinone, chromone, depsido-depsone, dibenzofuran, ester, no data, none, orcinol depside, orcinol depsidone, orcinol tridepside, orcinol $\beta$ -orcinol depsidone, pulvinic acid derivative, terpene, triterpene, unknown, usnic acid, usnic acid derivative, xanthone, $\beta$ -orcinol benzyl ester, $\beta$ -orcinol depside, $\beta$ -orcinol depsidone

## APPENDIX B

**Table B.1.** Table of all species, the literature sources used to collect trait data, and the chapter(s) each species is found in.

<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Acarospora superfusa</i>	McCune (2014) unpublished key	3
<i>Adelolecia pilati</i>	Botanische Staatssammlung München 2015b	3
<i>Alectoria imshaugii</i>	Brodo and Hawksworth 1977	2
<i>Alectoria ochroleuca</i>	Fink 1935; Botanische Staatssammlung München 2015b	3
<i>Alectoria sarmentosa</i> ssp. <i>sarmentosa</i>	Brodo and Hawksworth 1977; Nash III <i>et al.</i> 2001; McCune and Geiser 2009	2, 3
<i>Alectoria vancouverensis</i>	Brodo and Hawksworth 1977	2
<i>Alectoria vexillifera</i>	Thomson 1984	3
<i>Allantoparmelia alpicola</i>	Esslinger 1977; McCune and Geiser 2009; Botanische Staatssammlung München 2015a	3
<i>Ameliella andreaeicola</i>	Fryday and Coppins 2008	3
<i>Amygdalaria consentiens</i>	Botanische Staatssammlung München 2015b	3
<i>Amygdalaria continua</i>	Inoue 2010	3
<i>Amygdalaria panaeola</i>	Botanische Staatssammlung München 2015b	3
<i>Amygdalaria pelobotryon</i>	Botanische Staatssammlung München 2015b	3
<i>Amygdalaria subdissentiens</i>	McCune 2012	3
<i>Anaptychia bryorum</i>	Botanische Staatssammlung München 2015b	3
<i>Arctocetraria andrejevii</i>	Thomson 1997	3
<i>Arctoparmelia centrifuga</i>	Thomson 1984	3
<i>Arctoparmelia incurva</i>	Fink 1935; Botanische Staatssammlung München 2015b	3
<i>Arctoparmelia separata</i>	Botanische Staatssammlung München 2015b	3
<i>Arthrorhaphis alpina</i>	Thomson 1997; Brodo <i>et al.</i> 2001	3
<i>Asahinea chrysantha</i>	Thomson 1984	3
<i>Asahinea scholanderi</i>	Thomson 1984	3
<i>Aspicilia aquatica</i>	Nash III <i>et al.</i> 2007	3

<b>Appendix B cont.</b>		
<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Aspicilia cinerea</i>	Brodo <i>et al.</i> 2001; Nash III <i>et al.</i> 2007	3
<i>Aspicilia confusa</i>	Nash III <i>et al.</i> 2007	3
<i>Aspicilia elevata</i>	Thomson 1997	3
<i>Aspicilia subradians</i>	Thomson 1997	3
<i>Athallia holocarpa</i>	Thomson 1997	3
<i>Bacidia bagliettoana</i>	Botanische Staatssammlung München 2015b	3
<i>Bacidia circumspecta</i>	Nash III <i>et al.</i> 2004	3
<i>Baeomyces placophyllus</i>	Thomson 1984; Brodo <i>et al.</i> 2001	3
<i>Baeomyces rufus</i>	Brodo <i>et al.</i> 2001; Nash III <i>et al.</i> 2001	3
<i>Bellemeria cinereorufescens</i>	Nash III <i>et al.</i> 2007	3
<i>Bellemeria diamarta</i>	McCune 2012; Botanische Staatssammlung München 2015b	3
<i>Biatora aegrefaciens</i>	Printzen <i>et al.</i> 2002	3
<i>Biatora efflorescens</i>	McCune 2012	3
<i>Biatora flavopunctata</i>	Botanische Staatssammlung München 2015b	3
<i>Biatora kodiakensis</i>	Holien and Tønsberg 2012a	3
<i>Biatora pallens</i>	Foucard 1990; Printzen and Otte 2005	3
<i>Biatora rufidula</i>	Printzen and Tønsberg 1999	3
<i>Biatora subduplex</i>	Botanische Staatssammlung München 2015b	3
<i>Biatora vacciniicola</i>	Botanische Staatssammlung München 2015b	3
<i>Bryobilimbia diapensiae</i>	Thomson 1997; Fryday <i>et al.</i> 2014	3
<i>Bryocaulon divergens</i>	Thomson 1984	3
<i>Bryonora curvescens</i>	Botanische Staatssammlung München 2015a	3
<i>Bryoria capillaris</i>	Brodo and Hawksworth 1977; Thomson 2003; McCune and Geiser 2009	3
<i>Bryoria chalybeiformis</i>	Brodo and Hawksworth 1977; Nash III <i>et al.</i> 2001	3
<i>Bryoria fremontii</i>	Nash III <i>et al.</i> 2001	2
<i>Bryoria friabilis</i>	Brodo and Hawksworth 1977; Hinds and Hinds 2007	2
<i>Bryoria fuscescens</i>	Brodo <i>et al.</i> 2001; Nash III <i>et al.</i> 2001	2, 3

**Appendix B cont.**

<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Bryoria glabra</i>	Thell & Moberg 2011; Botanische Staatssammlung München 2015b	2
<i>Bryoria implexa</i>	Brodo and Hawksworth 1977; Botanische Staatssammlung München 2015b	3
<i>Bryoria lanestris</i>	Nash III <i>et al.</i> 2001	3
<i>Bryoria nitidula</i>	Brodo and Hawksworth 1977; Botanische Staatssammlung München 2015b	3
<i>Bryoria pseudofuscescens</i>	Brodo and Hawksworth 1977; Thomson 1984	2, 3
<i>Bryoria simplicior</i>	Brodo and Hawksworth 1977; Nash III <i>et al.</i> 2001	2, 3
<i>Bryoria tortuosa</i>	Brodo and Hawksworth 1977	2
<i>Bryoria trichodes</i>	Brodo and Hawksworth 1977; Thomson 1984; McCune and Geiser 2009	2
<i>Buellia disciformis</i>	Nash III <i>et al.</i> 2007	3
<i>Buellia erubescens</i>	Nash III <i>et al.</i> 2007	3
<i>Buellia insignis</i>	McCune 2012	3
<i>Buellia punctata</i>	Nash III <i>et al.</i> 2007	3
<i>Buellia schaeereri</i>	Nash III <i>et al.</i> 2007	3
<i>Buellia triphragmioides</i>	Nash III <i>et al.</i> 2007	3
<i>Calicium viride</i>	Nash III <i>et al.</i> 2004	3
<i>Caloplaca ahtii</i>	Søchting 1994; Wetmore 2004	3
<i>Caloplaca exsecuta</i>	Botanische Staatssammlung München 2015b	3
<i>Caloplaca nivalis</i>	Botanische Staatssammlung München 2015b	3
<i>Caloplaca sorocarpa</i>	Wetmore 2004	3
<i>Caloplaca stillicidiorum</i>	Thomson 1997	3
<i>Caloplaca tornoënsis</i>	Botanische Staatssammlung München 2015b	3
<i>Calvitimela aglaea</i>	Nash III <i>et al.</i> 2004	3
<i>Candelaria concolor</i>	Nash III <i>et al.</i> 2001	2
<i>Candelariella vitellina</i>	Nash III <i>et al.</i> 2004	3
<i>Carbonea vorticosa</i>	Nash III <i>et al.</i> 2004	3
<i>Catinarina atropurpurea</i>	Nash III <i>et al.</i> 2004	3
<i>Cetraria chlorophylla</i>	Nash III <i>et al.</i> 2004	2

<b>Appendix B cont.</b>		
<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Cetraria cucullata</i>	Botanische Staatssammlung München 2015b	3
<i>Cetraria ericetorum</i>	Nash III <i>et al.</i> 2001	3
<i>Cetraria fastigiata</i>	Thomson 1984	3
<i>Cetraria islandica</i>	Botanische Staatssammlung München 2015b; Brodo <i>et al.</i> 2001	3
<i>Cetraria islandica</i> ssp. <i>crispiformis</i>	Brodo <i>et al.</i> 2001; Botanische Staatssammlung München 2015b	3
<i>Cetraria kamczatica</i>	Thomson 1984	3
<i>Cetraria laevigata</i>	Thomson 1984	3
<i>Cetraria merrillii</i>	Nash III <i>et al.</i> 2001	2
<i>Cetraria nigricans</i>	Thomson 1984	3
<i>Cetraria nivalis</i>	Botanische Staatssammlung München 2015b	3
<i>Cetraria orbata</i>	Goward <i>et al.</i> 1994	2
<i>Cetraria pallidula</i>	Riddle 1915; McCune and Geiser 2009	2
<i>Cetraria platyphylla</i>	Fink 1935; Goward <i>et al.</i> 1994	2
<i>Cetraria sepincola</i>	Thomson 1984	3
<i>Cetrariella fastigiata</i>	Thomson 1984	3
<i>Cetrelia cetrariodes</i>	Culberson and Culberson 1968	2
<i>Chaenotheca furfuracea</i>	Nash III <i>et al.</i> 2004	3
<i>Cheiromycina petri</i>	Hawksworth and Poelt 1990	3
<i>Circinaria caesiocinerea</i>	Nash III <i>et al.</i> 2007	3
<i>Cladonia albonigra</i>	McCune and Geiser 2009; Botanische Staatssammlung München 2015b	2, 3
<i>Cladonia amaurocraea</i>	Botanische Staatssammlung München 2015a; Brodo <i>et al.</i> 2001	3
<i>Cladonia arbuscula</i>	Botanische Staatssammlung München 2015a	3
<i>Cladonia bacilliformis</i>	Nash III <i>et al.</i> 2001	3
<i>Cladonia bellidiflora</i>	Botanische Staatssammlung München 2015a; McCune and Geiser 2009	3
<i>Cladonia borealis</i>	Nash III <i>et al.</i> 2001	3
<i>Cladonia cariosa</i>	Nash III <i>et al.</i> 2001	2, 3

**Appendix B cont.**

<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Cladonia carneola</i>	Nash III <i>et al.</i> 2001	3
<i>Cladonia cenotea</i>	Nash III <i>et al.</i> 2001	3
<i>Cladonia chlorophaea</i>	Nash III <i>et al.</i> 2001	3
<i>Cladonia coccifera</i>	Nash III <i>et al.</i> 2001	3
<i>Cladonia coniocraea</i>	Nash III <i>et al.</i> 2001	3
<i>Cladonia cornuta</i>	Botanische Staatssammlung München 2015a	3
<i>Cladonia crispata</i>	Brodo <i>et al.</i> 2001; Botanische Staatssammlung München 2015a	3
<i>Cladonia crispata</i> var. <i>crispata</i>	Brodo <i>et al.</i> 2001; Botanische Staatssammlung München 2015a	3
<i>Cladonia cryptochlorophaea</i>	Botanische Staatssammlung München 2015b	3
<i>Cladonia cyanipes</i>	Botanische Staatssammlung München 2015a	3
<i>Cladonia deformis</i>	Nash III <i>et al.</i> 2001	3
<i>Cladonia ecmocyna</i>	Botanische Staatssammlung München 2015a; McCune and Geiser 2009	3
<i>Cladonia fimbriata</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009	2, 3
<i>Cladonia furcata</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009	3
<i>Cladonia gracilis</i>	Nash III <i>et al.</i> 2001	3
<i>Cladonia granulans</i>	Thomson 1984	3
<i>Cladonia kanewskii</i>	Botanische Staatssammlung München 2015a	3
<i>Cladonia luteoalba</i>	Botanische Staatssammlung München 2015b	3
<i>Cladonia macrophylla</i>	Botanische Staatssammlung München 2015b	3
<i>Cladonia nipponica</i>	Botanische Staatssammlung München 2015a	3
<i>Cladonia norvegica</i>	McCune and Geiser 2009	2
<i>Cladonia novochlorophaea</i>	Ahti 2000	3
<i>Cladonia ochrochlora</i>	Nash III <i>et al.</i> 2001	2, 3
<i>Cladonia pleurota</i>	Nash III <i>et al.</i> 2001	3
<i>Cladonia pyxidata</i>	Nash III <i>et al.</i> 2001	3
<i>Cladonia rangiferina</i>	Ahti 2000; Botanische Staatssammlung München 2015a	3
<i>Cladonia scabriuscula</i>	Nash III <i>et al.</i> 2001	3

<b>Appendix B cont.</b>		
<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Cladonia schofieldii</i>	Brodo and Ahti 1996	3
<i>Cladonia squamosa</i>	Nash III <i>et al.</i> 2001	2, 3
<i>Cladonia squamosa</i> var. <i>subsquamosa</i>	Nash III <i>et al.</i> 2001	2
<i>Cladonia straminea</i>	Ahti <i>et al.</i> 2013	3
<i>Cladonia stricta</i>	Botanische Staatssammlung München 2015a	3
<i>Cladonia subulata</i>	Nash III <i>et al.</i> 2001	3
<i>Cladonia sulphurina</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009	3
<i>Cladonia transcendens</i>	McCune and Geiser 2009	2
<i>Cladonia verruculosa</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009	3
<i>Cladonia verticillata</i>	Botanische Staatssammlung München 2015b	3
<i>Collema furfuraceum</i>	Nash III <i>et al.</i> 2004; McCune and Geiser 2009; Otálora <i>et al.</i> 2014	3
<i>Collema nigrescens</i>	Nash III <i>et al.</i> 2004; Otálora <i>et al.</i> 2014	3
<i>Dermatocarpon intestiniforme</i>	Botanische Staatssammlung München 2015b	3
<i>Dermatocarpon luridum</i>	Nash III <i>et al.</i> 2004	3
<i>Enchylium bachmanianum</i> var <i>millegranum</i>	Nash III <i>et al.</i> 2004; Otálora <i>et al.</i> 2014	3
<i>Ephebe lanata</i>	Botanische Staatssammlung München 2015b	3
<i>Ephebe perspinulosa</i>	Nash III <i>et al.</i> 2004	3
<i>Erioderma pedicellatum</i>	Jørgensen 2007d	3
<i>Esslingeriana idahoensis</i>	Esslinger 1971; Goward <i>et al.</i> 1994	2
<i>Euopsis granatina</i>	Thomson 1984	3
<i>Euopsis pulvinata</i>	Botanische Staatssammlung München 2015b	3
<i>Evernia mesomorpha</i>	Thomson 2003; Botanische Staatssammlung München 2015b	3
<i>Evernia prunastri</i>	Nash III <i>et al.</i> 2001	2
<i>Flavoplaca citrina</i>	Nash III <i>et al.</i> 2007	3
<i>Frutidella caesioatra</i>	Botanische Staatssammlung München 2015b	3

<b>Appendix B cont.</b>		
<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Frutidella pullata</i>	Purvis <i>et al.</i> 1992	3
<i>Fuscidea aleutica</i>	Fryday 2008	3
<i>Fuscidea hibernica</i>	Purvis <i>et al.</i> 1992	3
<i>Fuscidea intercincta</i>	Fryday 2008	3
<i>Fuscidea mollis</i>	Fryday 2008; Botanische Staatssammlung München 2015b	3
<i>Fuscidea pusilla</i>	Lendemer 2011; Fryday 2008	3
<i>Fuscopannaria ahlneri</i>	Jørgensen 2007d; Botanische Staatssammlung München 2015b	3
<i>Fuscopannaria confusa</i>	Jørgensen 2000; Jørgensen 2007d; Carlsen <i>et al.</i> 2012	3
<i>Fuscopannaria mediterranea</i>	Jørgensen 2000; Nash III <i>et al.</i> 2001; Jørgensen 2007d	3
<i>Fuscopannaria pacifica</i>	Jørgensen 2000	2
<i>Fuscopannaria ramulina</i>	Jørgensen 2000; McCune and Geiser 2009	3
<i>Fuscopannaria viridescens</i>	Jørgensen and Zhurbenko 2002	3
<i>Gowardia nigricans</i>	Brodo and Hawksworth 1977	3
<i>Gyalolechia flavovirescens</i>	Nash III <i>et al.</i> 2007	3
<i>Gyalolechia xanthostigmoidea</i>	Botanische Staatssammlung München 2015b	3
<i>Heterodermia galactophylla</i>	Lendemer 2009	3
<i>Hydropunctaria rheitrophila</i>	Krzewicka 2012	3
<i>Hydropunctaria scabra</i>	McCune 2012; Krzewicka 2012	3
<i>Hypogymnia apinnata</i>	Goward and McCune 1993; McCune and Geiser 2009	2, 3
<i>Hypogymnia austerodes</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009; Goward <i>et al.</i> 2012	3
<i>Hypogymnia bitteri</i>	Nash III <i>et al.</i> 2001	3
<i>Hypogymnia enteromorpha</i>	Goward <i>et al.</i> 1994	2
<i>Hypogymnia hultenii</i>	Purvis <i>et al.</i> 1992	2, 3
<i>Hypogymnia imshaugii</i>	Nash III <i>et al.</i> 2001	2
<i>Hypogymnia inactiva</i>	Goward <i>et al.</i> 1994; McCune and Geiser 2009	2
<i>Hypogymnia metaphysodes</i>	Goward <i>et al.</i> 1994; Botanische Staatssammlung München 2015b	2
<i>Hypogymnia occidentalis</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009	2, 3

**Appendix B cont.**

<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Hypogymnia physodes</i>	Nash III <i>et al.</i> 2001	2, 3
<i>Hypogymnia pulverata</i>	McCune and Geiser 2009	3
<i>Hypogymnia rugosa</i>	Goward <i>et al.</i> 1994; McCune and Geiser 2009	2
<i>Hypogymnia tubulosa</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009	2
<i>Hypotrachyna sinuosa</i>	Purvis <i>et al.</i> 1992	2
<i>Immersaria athroocarpa</i>	Nash III <i>et al.</i> 2004	3
<i>Imshaugia aleurites</i>	Nash III <i>et al.</i> 2001	3
<i>Ionaspis lacustris</i>	Botanische Staatssammlung München 2015b	3
<i>Japewia subaurifera</i>	Tønnsberg 1990	3
<i>Japewia tornoënsis</i>	Nash III <i>et al.</i> 2004	3
<i>Koerberiella wimmeriana</i>	Rambold <i>et al.</i> 1990; Botanische Staatssammlung München 2015b	3
<i>Lecanora allophana</i>	Nash III <i>et al.</i> 2004	3
<i>Lecanora anopta</i>	Botanische Staatssammlung München 2015b	3
<i>Lecanora bicincta</i>	Nash III <i>et al.</i> 2004	3
<i>Lecanora boligera</i>	Nash III <i>et al.</i> 2004	3
<i>Lecanora circumborealis</i>	Nash III <i>et al.</i> 2004	3
<i>Lecanora dispersa</i>	Nash III <i>et al.</i> 2004	3
<i>Lecanora expallens</i>	Nash III <i>et al.</i> 2004	3
<i>Lecanora intricata</i>	Nash III <i>et al.</i> 2004	3
<i>Lecanora invadens</i>	Sliwa 2007	3
<i>Lecanora leptacina</i>	Botanische Staatssammlung München 2015b	3
<i>Lecanora muralis</i>	Nash III <i>et al.</i> 2004	3
<i>Lecanora polytropa</i>	Nash III <i>et al.</i> 2004	3
<i>Lecanora rupicola</i>	Nash III <i>et al.</i> 2004	3
<i>Lecanora symmicta</i>	Nash III <i>et al.</i> 2004	3
<i>Lecanora zosteræ</i> var. <i>palanderi</i>	Nash III <i>et al.</i> 2004	3
<i>Lecidea alpestris</i>	Brodo 1981; Thomson 1997	3

<b>Appendix B cont.</b>		
<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Lecidea erythrophaea</i>	Nash III <i>et al.</i> 2004	3
<i>Lecidea lactea</i>	Thomson 1997	3
<i>Lecidea leucothallina</i>	Botanische Staatssammlung München 2015a	3
<i>Lecidea lithophila</i>	Botanische Staatssammlung München 2015a	3
<i>Lecidea praenubila</i>	Botanische Staatssammlung München 2015b	3
<i>Lecidea sphaerella</i>	Thomson 1997	3
<i>Lecidella bullata</i>	Thomson 1997	3
<i>Lecidella carpathica</i>	Nash III <i>et al.</i> 2004	3
<i>Lecidella euphorea</i>	Nash III <i>et al.</i> 2004	3
<i>Lecidella scabra</i>	Nash III <i>et al.</i> 2004	3
<i>Lecidella stigmathea</i>	Nash III <i>et al.</i> 2004	3
<i>Lecidoma demissum</i>	Botanische Staatssammlung München 2015b	3
<i>Lepraria finkii</i>	Nash III <i>et al.</i> 2001b	3
<i>Lepraria jackii</i>	Tønsberg 1992	3
<i>Lepraria neglecta</i>	Nash III <i>et al.</i> 2004	3
<i>Lepraria vouauxii</i>	Nash III <i>et al.</i> 2004	3
<i>Leptogidium contortum</i>	Galloway 1985	3
<i>Leptogium polycarpum</i>	Goward <i>et al.</i> 1994; Otálora <i>et al.</i> 2014	2
<i>Leptogium saturninum</i>	Nash III <i>et al.</i> 2004	3
<i>Letharia columbiana</i>	Nash III <i>et al.</i> 2001	2
<i>Letharia vulpina</i>	Nash III <i>et al.</i> 2001	2
<i>Lichinodium canadense</i>	Henssen 1968	3
<i>Lichinodium sirosiphoideum</i>	Henssen 1968; Arvidsson 1979	3
<i>Lobaria hallii</i>	Jordan 1973; McCune and Geiser 2009; Botanische Staatssammlung München 2015b	3
<i>Lobaria linita</i>	Jordan 1973; Thomson 1984; McCune and Geiser 2009	3
<i>Lobaria oregana</i>	Jordan 1973	2

<b>Appendix B cont.</b>		
<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Lobaria pulmonaria</i>	Jordan 1973	2, 3
<i>Lobaria scrobiculata</i>	Jordan 1973	2, 3
<i>Lobothallia melanaspis</i>	Botanische Staatssammlung München 2015b	3
<i>Lopadium coralloideum</i>	Thomson 1997	3
<i>Massalongia carnosa</i>	Nash III <i>et al.</i> 2001a; Jørgensen 2007c	3
<i>Melanelia hepatizon</i>	Botanische Staatssammlung München 2015b	3
<i>Melanelia stygia</i>	Esslinger 1977; Botanische Staatssammlung München 2015b	3
<i>Melanelixia fuliginosa</i>	Nash III <i>et al.</i> 2001	2
<i>Melanelixia subargentifera</i>	Esslinger 1977; Nash III <i>et al.</i> 2001	3
<i>Melanohalea elegantula</i>	Esslinger 1977; Nash III <i>et al.</i> 2001	2
<i>Melanohalea exasperatula</i>	Esslinger 1977; Nash III <i>et al.</i> 2001	2, 3
<i>Melanohalea multispora</i>	Esslinger 1977; Nash III <i>et al.</i> 2001	2, 3
<i>Melanohalea olivacea</i>	Esslinger 1977; Botanische Staatssammlung München 2015b	3
<i>Melanohalea septentrionalis</i>	Esslinger 1977; Botanische Staatssammlung München 2015b	3
<i>Melanohalea subaurifera</i>	Thomson 1984	2
<i>Melanohalea subelegantula</i>	Blanco <i>et al.</i> 2004; McCune and Geiser 2009	2
<i>Melanohalea subolivacea</i>	Esslinger 1977; Nash III <i>et al.</i> 2001	2
<i>Melanohalea trabeculata</i>	Esslinger 1977	3
<i>Menegazzia terebrata</i>	Thell & Moberg 2011	2
<i>Micarea incrassata</i>	Botanische Staatssammlung München 2015b	3
<i>Micarea misella</i>	Nash III <i>et al.</i> 2007	3
<i>Miriquidica deusta</i>	Botanische Staatssammlung München 2015b	3
<i>Miriquidica deusta</i> var. <i>picea</i>	Botanische Staatssammlung München 2015b	3
<i>Miriquidica nigroleprosa</i>	Purvis <i>et al.</i> 1992	3
<i>Montanelia disjuncta</i>	Nash III <i>et al.</i> 2001	3
<i>Montanelia soredata</i>	Botanische Staatssammlung München 2015b	3
<i>Mycoblastus affinis</i>	Purvis <i>et al.</i> 1992; Botanische Staatssammlung München 2015b	3

<b>Appendix B cont.</b>		
<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Mycoblastus alpinus</i>	Tønsberg 1992; Botanische Staatssammlung München 2015b	3
<i>Mycoblastus sanguinarius</i>	Tønsberg 1992; Botanische Staatssammlung München 2015b	3
<i>Myrionora albidula</i>	Palice <i>et al.</i> 2013	3
<i>Nephroma arcticum</i>	Botanische Staatssammlung München 2015b	3
<i>Nephroma bellum</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009	3
<i>Nephroma helveticum</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009	2, 3
<i>Nephroma isidiosum</i>	Botanische Staatssammlung München 2015b	3
<i>Nephroma laevigatum</i>	Botanische Staatssammlung München 2015b	2
<i>Nephroma parile</i>	Nash III <i>et al.</i> 2001	3
<i>Nodobryoria abbreviata</i>	Nash III <i>et al.</i> 2001	2
<i>Nodobryoria oregana</i>	Nash III <i>et al.</i> 2001	2
<i>Ochrolechia alaskana</i>	McCune 2012	3
<i>Ochrolechia androgyna</i>	Nash III <i>et al.</i> 2004	3
<i>Ochrolechia arborea</i>	Nash III <i>et al.</i> 2004	3
<i>Ochrolechia farinacea</i>	Howard 1970; McCune 2012	3
<i>Ochrolechia frigida</i>	Botanische Staatssammlung München 2015b	3
<i>Ochrolechia juvenalis</i>	Brodo 1991; McCune 2012	3
<i>Ochrolechia mahluensis</i>	Brodo 1991	3
<i>Ochrolechia oregonensis</i>	McCune 2012	3
<i>Ochrolechia subplicans</i> ssp. <i>hultenii</i>	Thomson 1997	3
<i>Ochrolechia szatalaensis</i>	Brodo 1991; McCune 2012	3
<i>Ophioparma lapponica</i>	Thomson 1997	3
<i>Orphniospora moriopsis</i>	Botanische Staatssammlung München 2015b	3
<i>Palicella filamentosa</i>	Rodriguez Flakus and Printzen 2014	3
<i>Parmelia hygrophila</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009	2, 3
<i>Parmelia omphalodes</i>	Botanische Staatssammlung München 2015b	3

<b>Appendix B cont.</b>		
<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Parmelia pseudosulcata</i>	McCune and Geiser 2009	2
<i>Parmelia saxatilis</i>	Nash III <i>et al.</i> 2001	2, 3
<i>Parmelia squarrosa</i>	Thomson 2003; McCune and Geiser 2009; Botanische Staatssammlung München 2015b	3
<i>Parmelia sulcata</i>	Nash III <i>et al.</i> 2001a; Thomson 2003	2, 3
<i>Parmeliella parvula</i>	Jørgensen 2000; Jørgensen 2007d	3
<i>Parmeliella triptophylla</i>	Jørgensen 2000; Nash III <i>et al.</i> 2001; Jørgensen 2007d	3
<i>Parmeliopsis ambigua</i>	Nash III <i>et al.</i> 2001	2, 3
<i>Parmeliopsis hyperopta</i>	Nash III <i>et al.</i> 2001	2, 3
<i>Parmotrema arnoldii</i>	Nash III <i>et al.</i> 2001	2
<i>Parmotrema perlatum</i>	Nash III <i>et al.</i> 2001	2
<i>Parvoplaca jemtlandica</i>	Foucard 2001	3
<i>Peltigera aphthosa</i>	Vitikainen 1985; McCune and Geiser 2009; Botanische Staatssammlung München 2015b	3
<i>Peltigera canina</i>	Vitikainen 1985; McCune and Geiser 2009; Botanische Staatssammlung München 2015b	3
<i>Peltigera collina</i>	Vitikainen 1985; Nash III <i>et al.</i> 2001b	2, 3
<i>Peltigera degenii</i>	Vitikainen 1985; Botanische Staatssammlung München 2015b	3
<i>Peltigera didactyla</i>	Vitikainen 1985; Nash III <i>et al.</i> 2004	3
<i>Peltigera extenuata</i>	Nash III <i>et al.</i> 2004; Vitikainen 2007	3
<i>Peltigera lepidophora</i>	Vitikainen 1985; Nash III <i>et al.</i> 2004	3
<i>Peltigera leucophlebia</i>	Vitikainen 1985; Nash III <i>et al.</i> 2004; McCune and Geiser 2009	3
<i>Peltigera malacea</i>	Vitikainen 1985; Nash III <i>et al.</i> 2004; McCune and Geiser 2009	3
<i>Peltigera membranacea</i>	Vitikainen 1985; Nash III <i>et al.</i> 2004; McCune and Geiser 2009	3
<i>Peltigera neckeri</i>	Vitikainen 1985; Nash III <i>et al.</i> 2004; McCune and Geiser 2009	3
<i>Peltigera neopolydactyla</i>	Vitikainen 1985; Nash III <i>et al.</i> 2004; McCune and Geiser 2009	3
<i>Peltigera polydactylon</i>	Nash III <i>et al.</i> 2001b; Thomson 2003; Vitikainen 1985	3

**Appendix B cont.**

<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Peltigera scabrosa</i>	Vitikainen 1985; Botanische Staatssammlung München 2015b	3
<i>Peltigera scabrosella</i>	Vitikainen 1985; Botanische Staatssammlung München 2015b	3
<i>Pertusaria alaskensis</i>	Thomson 1997; McCune 2012	3
<i>Pertusaria borealis</i>	Tønsberg 1992	3
<i>Pertusaria carneopallida</i>	Thomson 1997	3
<i>Pertusaria dactylina</i>	Botanische Staatssammlung München 2015b	3
<i>Pertusaria geminipara</i>	Botanische Staatssammlung München 2015b	3
<i>Pertusaria glaucomela</i>	McCune 2012	3
<i>Pertusaria glomerata</i>	Botanische Staatssammlung München 2015b	3
<i>Pertusaria oculata</i>	Botanische Staatssammlung München 2015b	3
<i>Pertusaria panyrga</i>	Botanische Staatssammlung München 2015b	3
<i>Pertusaria pupillaris</i>	Purvis <i>et al.</i> 1992; Tønsberg 1992	3
<i>Pertusaria sommerfeltii</i>	Nash III <i>et al.</i> 2001	3
<i>Pertusaria subobducens</i>	Thomson 1997	3
<i>Phaeocalicium populneum</i>	Nash III <i>et al.</i> 2004	3
<i>Phaeophyscia ciliata</i>	Nash III <i>et al.</i> 2004	3
<i>Phaeophyscia decolor</i>	Nash III <i>et al.</i> 2004	3
<i>Phaeophyscia hirsuta</i>	Nash III <i>et al.</i> 2004	3
<i>Phaeophyscia kairamoi</i>	Nash III <i>et al.</i> 2004	3
<i>Phaeophyscia orbicularis</i>	Nash III <i>et al.</i> 2004	3
<i>Phaeophyscia sciastra</i>	Nash III <i>et al.</i> 2004	3
<i>Physcia adscendens</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009	2, 3
<i>Physcia aipolia</i>	Nash III <i>et al.</i> 2001	2, 3
<i>Physcia alnophila</i>	Nash III <i>et al.</i> 2001	3
<i>Physcia caesia</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009	3
<i>Physcia dimidiata</i>	Nash III <i>et al.</i> 2001	2
<i>Physcia phaea</i>	Nash III <i>et al.</i> 2001	3

<b>Appendix B cont.</b>		
<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Physcia stellaris</i>	Nash III <i>et al.</i> 2001	3
<i>Physcia tenella</i>	Purvis <i>et al.</i> 1992; Thomson 2003; McCune and Geiser 2009	2, 3
<i>Physconia americana</i>	Nash III <i>et al.</i> 2001	2, 3
<i>Physconia detersa</i>	Nash III <i>et al.</i> 2001	3
<i>Physconia grumosa</i>	Esslinger and Dillman 2010	3
<i>Physconia isidiigera</i>	Nash III <i>et al.</i> 2001	2, 3
<i>Physconia labrata</i>	T. L. Esslinger personal communication	3
<i>Physconia muscigena</i>	Nash III <i>et al.</i> 2001; McCune and Geiser 2009	3
<i>Physconia perisidiosa</i>	Nash III <i>et al.</i> 2001	3
<i>Pilophorus nigricaulis</i>	Jahns 1981; McCune and Geiser 2009	3
<i>Placopsis argillacea</i>	Galloway 2007	3
<i>Placopsis cribellans</i>	Thomson 1997	3
<i>Placopsis gelida</i>	Purvis <i>et al.</i> 1992; Botanische Staatssammlung München 2015b	3
<i>Placynthium rosulans</i>	Jørgensen 2007 e.; Botanische Staatssammlung München 2015b	3
<i>Platismatia glauca</i>	Nash III <i>et al.</i> 2001	2, 3
<i>Platismatia herrei</i>	Culberson and Culberson 1968	2
<i>Platismatia stenophylla</i>	Culberson and Culberson 1968	2
<i>Polycauliona candelaria</i>	Nash III <i>et al.</i> 2001b	3
<i>Porpidia albocaerulescens</i>	Purvis <i>et al.</i> 1992	3
<i>Porpidia flavocaerulescens</i>	Purvis <i>et al.</i> 1992; Botanische Staatssammlung München 2015b	3
<i>Porpidia melinodes</i>	Botanische Staatssammlung München 2015b	3
<i>Porpidia thomsonii</i>	Thomson 1997	3
<i>Porpidia tuberculosa</i>	Botanische Staatssammlung München 2015b	3
<i>Protomicarea limosa</i>	Botanische Staatssammlung München 2015b	3
<i>Protopannaria pezizoides</i>	Nash III <i>et al.</i> 2001a; Jørgensen 2007d	3
<i>Protoparmelia badia</i>	Nash III <i>et al.</i> 2004	3
<i>Protoparmelia memnonia</i>	Nash III <i>et al.</i> 2004	3

**Appendix B cont.**

<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Pseudephebe minuscula</i>	Nash III <i>et al.</i> 2001	3
<i>Pseudephebe pubescens</i>	Nash III <i>et al.</i> 2001	3
<i>Pseudocyphellaria anomala</i>	Nash III <i>et al.</i> 2001	2
<i>Pseudocyphellaria anthraspis</i>	Nash III <i>et al.</i> 2001	2
<i>Pseudocyphellaria crocata</i>	Jørgensen 2007b; McCune and Geiser 2009	2, 3
<i>Pseudocyphellaria epiflavoides</i>	Jørgensen 2007b; McCune and Geiser 2009	3
<i>Pseudocyphellaria perpetua</i>	Miadlikowska <i>et al.</i> 2002; McCune and Geiser 2009	3
<i>Psora globifera</i>	Nash III <i>et al.</i> 2001	3
<i>Psoroma hypnorum</i>	Jørgensen 2000; Nash III <i>et al.</i> 2001; Jørgensen 2007d	3
<i>Pycnothelia papillaria</i>	Botanische Staatssammlung München 2015b	3
<i>Pyrenopsis sanguinea</i>	Thus and Schultz 2009	3
<i>Pyrrhospora cinnabarina</i>	Thomson 1997	3
<i>Ramalina dilacerata</i>	McCune and Geiser 2009; Botanische Staatssammlung München 2015b	2, 3
<i>Ramalina farinacea</i>	Nash III <i>et al.</i> 2004; McCune and Geiser 2009	2, 3
<i>Ramalina roesleri</i>	McCune and Geiser 2009; Botanische Staatssammlung München 2015b	3
<i>Ramalina thrausta</i>	McCune and Geiser 2009; Botanische Staatssammlung München 2015b	2
<i>Ramboldia subcinnabarina</i>	Holien and Tønsberg 2012b	3
<i>Rhizocarpon badioatrum</i>	Nash III <i>et al.</i> 2004	3
<i>Rhizocarpon bolanderi</i>	Nash III <i>et al.</i> 2004	3
<i>Rhizocarpon cinereovirens</i>	Purvis <i>et al.</i> 1992; Botanische Staatssammlung München 2015b	3
<i>Rhizocarpon copelandii</i>	Thomson 1997	3
<i>Rhizocarpon ferax</i>	Thomson 1997	3
<i>Rhizocarpon geminatum</i>	Nash III <i>et al.</i> 2004	3
<i>Rhizocarpon geographicum</i>	Nash III <i>et al.</i> 2004	3
<i>Rhizocarpon infernulum</i> var. <i>infernulum</i>	Fryday 2002	3
<i>Rhizocarpon jemtlandicum</i>	Purvis <i>et al.</i> 1992; Botanische Staatssammlung München 2015b	3

**Appendix B cont.**

<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Rhizocarpon lavatum</i>	Purvis <i>et al.</i> 1992; Botanische Staatssammlung München 2015b	3
<i>Rhizocarpon oederi</i>	Botanische Staatssammlung München 2015b	3
<i>Rhizocarpon polycarpum</i>	Nash III <i>et al.</i> 2004	3
<i>Rhizocarpon submodestum</i>	McCune 2012	3
<i>Rhizocarpon superficiale</i>	Purvis <i>et al.</i> 1992; Botanische Staatssammlung München 2015b	3
<i>Rimularia furvella</i>	Bota Botanische Staatssammlung München 2015b	3
<i>Rimularia limborina</i>	Purvis <i>et al.</i> 1992	3
<i>Rinodina athallina</i>	Na Nash III <i>et al.</i> 2004	3
<i>Rinodina buckii</i>	Sheard <i>et al.</i> 2012	3
<i>Rinodina conradii</i>	Purvis <i>et al.</i> 1992; Botanische Staatssammlung München 2015b	3
<i>Rinodina degeliana</i>	Coppins 1983; Tønsberg 1992; Giralt 1995; Sheard 2010	3
<i>Rinodina efflorescens</i>	Giralt 1995; Nash III <i>et al.</i> 2004; Sheard 2010	3
<i>Rinodina griseosoralifera</i>	Nash III <i>et al.</i> 2004; Sheard 2010	3
<i>Rinodina metaboliza</i>	Nash III <i>et al.</i> 2004; Sheard 2010	3
<i>Rinodina oregana</i>	Nash III <i>et al.</i> 2004; Sheard 2010	3
<i>Rinodina pallidescens</i>	Sheard <i>et al.</i> 2014	3
<i>Rinodina septentrionalis</i>	Sheard 2010; Botanische Staatssammlung München 2015b	3
<i>Rinodina turfacea</i>	Thomson 1997; Sheard 2010	3
<i>Rostania occultata</i> var. <i>populneum</i>	Otálora <i>et al.</i> 2014	3
<i>Rusavskia elegans</i>	Nash III <i>et al.</i> 2004	3
<i>Rusavskia sorediata</i>	Nash III <i>et al.</i> 2004	3
<i>Sagedia mastrucata</i>	McCune 2012; Nordin <i>et al.</i> 2010	3
<i>Santessoniella arctophila</i>	Jørgensen 2000; Jørgensen 2007d	3
<i>Schaereria corticola</i>	Tønsberg 1992	3
<i>Schaereria dolodes</i>	Nash III <i>et al.</i> 2007	3
<i>Schaereria fuscocinerea</i>	Nash III <i>et al.</i> 2004	3

**Appendix B cont.**

<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Scoliciosporum chlorococcum</i>	Purvis <i>et al.</i> 1992	3
<i>Scoliciosporum umbrinum</i>	Nash III <i>et al.</i> 2004	3
<i>Scytinium cellulorum</i>	Otálora <i>et al.</i> 2014	3
<i>Scytinium gelatinosum</i>	Otálora <i>et al.</i> 2014	3
<i>Scytinium intermedium</i>	Otálora <i>et al.</i> 2014	3
<i>Scytinium lichenoides</i>	Otálora <i>et al.</i> 2014	3
<i>Scytinium rivale</i>	Sierk 1964; Otálora <i>et al.</i> 2014	3
<i>Scytinium subtile</i>	Otálora <i>et al.</i> 2014	3
<i>Siphula ceratites</i>	Purvis <i>et al.</i> 1992; Botanische Staatssammlung München 2015b	3
<i>Solorina crocea</i>	Jørgensen 2007a; Botanische Staatssammlung München 2015b	3
<i>Sphaerophorus fragilis</i>	Botanische Staatssammlung München 2015b	3
<i>Sphaerophorus globosus</i> s.l.	Nash III <i>et al.</i> 2004	2, 3
<i>Spilonema americana</i>	Henssen and Tønsberg 2000	3
<i>Sporastatia polyspora</i>	Thomson 1984	3
<i>Sporodictyon cruentum</i>	Thomson 1997; Savić and Tibell 2009	3
<i>Sporodictyon schaeererianum</i>	Savić and Tibell 2009	3
<i>Staurothele areolata</i>	Thomson 1991; Nash III <i>et al.</i> 2001	3
<i>Staurothele clopima</i>	Thomson 1991	3
<i>Staurothele fissa</i>	Thomson 1991; Botanische Staatssammlung München 2015b	3
<i>Stereocaulon alpinum</i>	Thomson 1984	3
<i>Stereocaulon arcticum</i>	Thomson 1984	3
<i>Stereocaulon botryosum</i>	Thomson 1997	3
<i>Stereocaulon condensatum</i>	Thomson 2003; Botanische Staatssammlung München 2015b	3
<i>Stereocaulon groenlandicum</i>	Thomson 1984	3
<i>Stereocaulon klondikense</i>	Spribille <i>et al.</i> 2010	3
<i>Stereocaulon paschale</i>	Thomson 2003; Botanische Staatssammlung München 2015b	3
<i>Stereocaulon rivulorum</i>	Thomson 1984	3

<b>Appendix B cont.</b>		
<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Stereocaulon spathuliferum</i>	Purvis <i>et al.</i> 1992; McCune and Geiser 2009; Botanische Staatssammlung München 2015b	3
<i>Stereocaulon symphycheilum</i>	Purvis <i>et al.</i> 1992; Botanische Staatssammlung München 2015b	3
<i>Stereocaulon tornense</i>	Fryday and Coppins 1996; Fryday and Coppins 1997	3
<i>Stereocaulon vesuvianum</i>	Purvis <i>et al.</i> 1992; Botanische Staatssammlung München 2015b	3
<i>Sticta fuliginosa</i>	Nash III <i>et al.</i> 2004; Jørgensen 2007b	2
<i>Sticta limbata</i>	Nash III <i>et al.</i> 2004	2
<i>Tephromela atra</i>	Nash III <i>et al.</i> 2004	3
<i>Thamnozia subuliformis</i>	Thomson 1984	3
<i>Thamnozia vermicularis</i>	Thomson 1984	3
<i>Thelenella modesta</i>	Nash III <i>et al.</i> 2001	3
<i>Toensbergia leucococca</i>	Bendiksby and Timdal 2013	3
<i>Trapeliopsis flexuosa</i>	Nash III <i>et al.</i> 2004	3
<i>Trapeliopsis granulosa</i>	Nash III <i>et al.</i> 2004	3
<i>Tremolecia atrata</i>	Nash III <i>et al.</i> 2004	3
<i>Umbilicaria arctica</i>	Botanische Staatssammlung München 2015b	3
<i>Umbilicaria cinereorufescens</i>	Nash III <i>et al.</i> 2004	3
<i>Umbilicaria cylindrica</i>	Nash III <i>et al.</i> 2004	3
<i>Umbilicaria hyperborea</i>	Nash III <i>et al.</i> 2004	3
<i>Umbilicaria proboscidea</i>	Botanische Staatssammlung München 2015b	3
<i>Umbilicaria torrefacta</i>	Nash III <i>et al.</i> 2004	3
<i>Usnea cavernosa</i>	Fink 1935; Nash III <i>et al.</i> 2007	2
<i>Usnea cornuta</i>	Nash III <i>et al.</i> 2007	2
<i>Usnea filipendula</i>	Botanische Staatssammlung München 2015b	2
<i>Usnea flavocardia</i>	Nash III <i>et al.</i> 2007	2
<i>Usnea glabrata</i>	Nash III <i>et al.</i> 2007	2
<i>Usnea lapponica</i>	Nash III <i>et al.</i> 2007; McCune and Geiser 2009	2, 3

**Appendix B cont.**

<b>Species</b>	<b>Literature Sources</b>	<b>Chapter</b>
<i>Usnea pacificana</i>	Halonen 2000	2
<i>Usnea scabrata</i>	Nash III <i>et al.</i> 2007; McCune and Geiser 2009	2
<i>Usnea subfloridana</i>	Nash III <i>et al.</i> 2007	2
<i>Variolaria ophthalmiza</i>	Nash III <i>et al.</i> 2001	3
<i>Verrucaria aethiobola</i>	Nash III <i>et al.</i> 2007	3
<i>Verrucaria fuscoatroides</i>	Nash III <i>et al.</i> 2007	3
<i>Verrucaria margacea</i>	Nash III <i>et al.</i> 2007; Krzewicka 2012	3
<i>Verrucaria nigrescens</i>	Nash III <i>et al.</i> 2007; Krzewicka 2012	3
<i>Verrucaria praetermissa</i>	Purvis <i>et al.</i> 1992; Krzewicka 2012; Botanische Staatssammlung München 2015b	3
<i>Vestergrenopsis elaeina</i>	Purvis <i>et al.</i> 1992; Botanische Staatssammlung München 2015b	3
<i>Vestergrenopsis isidiata</i>	Thomson 1984	3
<i>Violella fucata</i>	Purvis <i>et al.</i> 1992; Tønsberg 1992	3
<i>Vulpicida canadensis</i>	Nash III <i>et al.</i> 2001	2
<i>Vulpicida pinastri</i>	Nash III <i>et al.</i> 2001	3
<i>Xanthomendoza fallax</i>	Nash III <i>et al.</i> 2004	2
<i>Xanthomendoza fulva</i>	Nash III <i>et al.</i> 2004	2
<i>Xanthomendoza hasseana</i>	Nash III <i>et al.</i> 2004	2, 3
<i>Xanthomendoza oregana</i>	Nash III <i>et al.</i> 2004	2
<i>Xanthoparmelia coloradoënsis</i>	Botanische Staatssammlung München 2015b	3
<i>Xanthoria candelaria</i>	Kondratyuk 1997; Nash III <i>et al.</i> 2004	2, 3
<i>Xanthoria elegans</i>	Nash III <i>et al.</i> 2004	3
<i>Xanthoria polycarpa</i>	Nash III <i>et al.</i> 2004	2
<i>Xylographa trunciseda</i>	Purvis <i>et al.</i> 1992	3
<i>Xylographa vermicularis</i>	Spribille <i>et al.</i> 2014	3
<i>Xylographa vitiligo</i>	Purvis <i>et al.</i> 1992; Nash III <i>et al.</i> 2004	3

## APPENDIX C.

**Table C.1.** Table summarizing species by geographic regions in west-to-east order. Values are the percent of plots in each region that contain the given species. Note: this table only pertains to Chapter 2.

<b>Species</b>	<b>Coast</b>	<b>Coast Range</b>	<b>Willamette Valley</b>	<b>Western Cascades</b>	<b>High Cascades</b>	<b>Eastern Cascades</b>	<b>Eastern Oregon</b>
<i>Alectoria imshaugii</i>	0	0	0	28.1	75	50	15.7
<i>Alectoria sarmentosa</i>	0	33.3	25	56.3	100	66.7	18.6
<i>Alectoria vancouverensis</i>	0	27.8	12.5	9.4	8.3	0	0
<i>Bryoria capillaris</i>	0	16.7	12.5	53.1	50	11.1	1.4
<i>Bryoria fremontii</i>	0	0	0	3.1	41.7	61.1	60
<i>Bryoria friabilis</i>	0	11.1	12.5	21.9	41.7	0	0
<i>Bryoria fuscescens</i>	12.5	5.6	12.5	25	75	33.3	28.6
<i>Bryoria glabra</i>	0	0	0	9.4	8.3	5.6	0
<i>Bryoria pseudofuscescens</i>	0	22.2	0	12.5	50	50	18.6
<i>Bryoria simplicior</i>	0	0	0	0	0	22.2	20
<i>Bryoria tortuosa</i>	0	0	0	0	0	11.1	7.1
<i>Bryoria trichodes</i>	0	0	0	3.1	0	5.6	1.4
<i>Candelaria concolor</i>	0	0	25	12.5	0	5.6	34.3
<i>Cetraria canadensis</i>	0	5.6	0	0	8.3	77.8	24.3
<i>Cetraria chlorophylla</i>	25	50	62.5	71.9	66.7	22.2	10
<i>Cetraria merrillii</i>	0	0	0	3.1	33.3	100	70
<i>Cetraria orbata</i>	25	72.2	37.5	62.5	50	16.7	22.9
<i>Cetraria pallidula</i>	0	5.6	0	9.4	16.7	5.6	0
<i>Cetraria platyphylla</i>	0	0	0	28.1	66.7	27.8	34.3
<i>Cetrelia cetrarioides</i>	12.5	0	25	0	0	0	0
<i>Cladonia albonigra</i>	12.5	5.6	12.5	6.3	0	0	0
<i>Cladonia carneola</i>	0	5.6	0	3.1	8.3	0	0

<b>Appendix C cont.</b>							
<b>Species</b>	<b>Coast</b>	<b>Coast Range</b>	<b>Willamette Valley</b>	<b>Western Cascades</b>	<b>High Cascades</b>	<b>Eastern Cascades</b>	<b>Eastern Oregon</b>
<i>Cladonia coniocraea</i>	50	44.4	12.5	34.4	8.3	5.6	0
<i>Cladonia fimbriata</i>	12.5	16.7	0	25	8.3	0	2.9
<i>Cladonia norvegica</i>	0	11.1	0	0	8.3	0	0
<i>Cladonia squamosa</i>	0	0	12.5	6.3	0	0	0
<i>Cladonia squamosa</i> var. <i>subsquamosa</i>	12.5	5.6	0	12.5	25	0	0
<i>Cladonia transcendens</i>	25	27.8	12.5	50	50	0	0
<i>Esslingeriana idahoensis</i>	0	0	12.5	12.5	25	5.6	2.9
<i>Evernia prunastri</i>	25	61.1	100	53.1	0	0	10
<i>Fuscopannaria pacifica</i>	0	0	12.5	6.3	0	0	0
<i>Hypogymnia apinnata</i>	50	55.6	37.5	37.5	16.7	5.6	0
<i>Hypogymnia enteromorpha</i>	12.5	83.3	50	84.4	66.7	5.6	1.4
<i>Hypogymnia hultenii</i>	0	5.6	0	3.1	8.3	0	0
<i>Hypogymnia imshaugii</i>	0	22.2	12.5	56.3	75	33.3	58.6
<i>Hypogymnia inactiva</i>	25	83.3	50	84.4	66.7	5.6	1.4
<i>Hypogymnia metaphysodes</i>	0	0	0	18.8	33.3	22.2	12.9
<i>Hypogymnia occidentalis</i>	25	11.1	12.5	25	41.7	11.1	5.7
<i>Hypogymnia physodes</i>	37.5	72.2	75	75	33.3	5.6	0
<i>Hypogymnia rugosa</i>	0	0	0	0	8.3	11.1	1.4
<i>Hypogymnia tubulosa</i>	25	50	50	46.9	41.7	16.7	7.1
<i>Hypotrachyna sinuosa</i>	50	38.9	25	25	8.3	0	0
<i>Leptogium polycarpum</i>	0	0	0	12.5	8.3	0	0
<i>Letharia columbiana</i>	0	0	0	0	0	61.1	82.9
<i>Letharia vulpina</i>	0	0	12.5	28.1	41.7	83.3	82.9
<i>Lobaria oregana</i>	0	11.1	0	15.6	8.3	0	0
<i>Lobaria pulmonaria</i>	12.5	44.4	50	37.5	33.3	0	0

<b>Appendix C cont.</b>							
<b>Species</b>	<b>Coast</b>	<b>Coast Range</b>	<b>Willamette Valley</b>	<b>Western Cascades</b>	<b>High Cascades</b>	<b>Eastern Cascades</b>	<b>Eastern Oregon</b>
<i>Lobaria scrobiculata</i>	0	11.1	25	18.8	0	0	0
<i>Melanelixia fuliginosa</i>	12.5	5.6	50	28.1	8.3	0	0
<i>Melanohalea elegantula</i>	0	0	12.5	0	0	0	42.9
<i>Melanohalea exasperatula</i>	0	16.7	37.5	28.1	8.3	5.6	18.6
<i>Melanohalea multisporea</i>	0	0	0	0	0	0	5.7
<i>Melanohalea subaurifera</i>	12.5	5.6	37.5	9.4	0	0	1.4
<i>Melanohalea subelegantula</i>	0	0	12.5	3.1	0	5.6	17.1
<i>Melanohalea subolivacea</i>	0	0	0	12.5	8.3	5.6	44.3
<i>Menegazzia terebrata</i>	50	11.1	12.5	6.3	0	0	0
<i>Nephroma helveticum</i>	0	5.6	0	9.4	8.3	0	0
<i>Nephroma laevigatum</i>	0	0	0	21.9	0	0	0
<i>Nodobryoria abbreviata</i>	0	0	0	6.3	0	55.6	68.6
<i>Nodobryoria oregana</i>	0	0	0	43.8	100	16.7	12.9
<i>Parmelia hygrophila</i>	25	61.1	12.5	62.5	66.7	0	4.3
<i>Parmelia pseudosulcata</i>	0	16.7	0	6.3	0	0	0
<i>Parmelia saxatilis</i>	0	5.6	0	9.4	0	0	0
<i>Parmelia sulcata</i>	75	77.8	100	56.3	41.7	11.1	20
<i>Parmeliopsis ambigua</i>	0	0	0	15.6	25	0	12.9
<i>Parmeliopsis hyperopta</i>	0	5.6	0	40.6	91.7	27.8	7.1
<i>Parmotrema arnoldii</i>	25	0	0	3.1	0	0	0
<i>Parmotrema perlatum</i>	50	0	0	3.1	0	0	0
<i>Peltigera collina</i>	0	0	50	21.9	8.3	0	0
<i>Physcia adscendens</i>	0	11.1	50	9.4	0	0	7.1
<i>Physcia aipolia</i>	0	0	62.5	12.5	8.3	0	0
<i>Physcia dimidiata</i>	0	0	12.5	0	0	0	10
<i>Physcia tenella</i>	0	5.6	25	18.8	0	0	5.7

<b>Appendix C cont.</b>							
<b>Species</b>	<b>Coast</b>	<b>Coast Range</b>	<b>Willamette Valley</b>	<b>Western Cascades</b>	<b>High Cascades</b>	<b>Eastern Cascades</b>	<b>Eastern Oregon</b>
<i>Physconia enteroxantha</i>	0	0	25	3.1	0	0	8.6
<i>Physconia isidiigera</i>	0	0	25	0	0	0	2.9
<i>Platismatia glauca</i>	25	72.2	75	100	83.3	22.2	5.7
<i>Platismatia herrei</i>	37.5	66.7	25	62.5	50	0	0
<i>Platismatia stenophylla</i>	0	27.8	25	59.4	58.3	11.1	0
<i>Pseudocyphellaria anomala</i>	0	5.6	25	15.6	16.7	5.6	0
<i>Pseudocyphellaria anthraspis</i>	12.5	5.6	12.5	15.6	0	0	0
<i>Pseudocyphellaria crocata</i>	0	5.6	0	21.9	8.3	0	0
<i>Ramalina dilacerata</i>	12.5	22.2	62.5	25	8.3	0	0
<i>Ramalina farinacea</i>	62.5	72.2	100	46.9	8.3	0	5.7
<i>Ramalina thrausta</i>	0	11.1	0	6.3	0	0	0
<i>Sphaerophorus globosus</i> s.l.	25	77.8	0	46.9	50	0	0
<i>Sticta fuliginosa</i>	0	11.1	12.5	12.5	8.3	0	0
<i>Sticta limbata</i>	0	11.1	0	15.6	0	0	0
<i>Usnea cavernosa</i>	0	0	25	9.4	0	0	0
<i>Usnea cornuta</i>	62.5	11.1	0	3.1	0	0	0
<i>Usnea filipendula</i>	50	72.2	100	71.9	25	16.7	11.4
<i>Usnea flavocardia</i>	62.5	50	12.5	25	0	0	0
<i>Usnea glabrata</i>	12.5	0	37.5	15.6	0	0	0
<i>Usnea lapponica</i>	12.5	0	25	18.8	0	0	2.9
<i>Usnea pacificana</i>	12.5	11.1	0	3.1	0	0	0
<i>Usnea scabrata</i>	25	33.3	12.5	28.1	16.7	5.6	0
<i>Usnea subfloridana</i>	25	22.2	12.5	21.9	16.7	0	0
<i>Xanthomendoza fallax</i>	0	0	0	0	0	0	10
<i>Xanthomendoza fulva</i> *	0	0	0	0	0	0	27.1
<i>Xanthomendoza hasseana</i>	0	0	25	12.5	0	0	1.4

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**Appendix C cont.**


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<b>Species</b>	<b>Coast</b>	<b>Coast Range</b>	<b>Willamette Valley</b>	<b>Western Cascades</b>	<b>High Cascades</b>	<b>Eastern Cascades</b>	<b>Eastern Oregon</b>
<i>Xanthomendoza oregana</i> *	0	0	25	3.1	0	5.6	28.6
<i>Xanthoria candelaria</i>	0	0	12.5	0	0	0	11.4
<i>Xanthoria polycarpa</i>	0	0	12.5	15.6	0	0	1.4

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\*Note that *Xanthomendoza fulva* may have been incorrectly identified as *X. oregana*

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## APPENDIX D.

**Table D.1.** Table showing the proportion of species present in each habitat (Chapter 3) that contain each trait. All values are proportions except the values for height, which are the average height (mm) of all species in the given habitat. See Appendix A for full trait descriptions.

<b>Trait</b>	<b>Epiphytic unsheltered conifer at low elevation</b>	<b>Epiphytic unsheltered deciduous tree at high elevation</b>	<b>Epiphytic unsheltered deciduous tree at low elevation</b>	<b>Unsheltered on soil</b>	<b>Sheltered organic substrate on the ground</b>	<b>Unsheltered organic substrate on the ground at high elevation</b>	<b>Unsheltered organic substrate on the ground at low elevation</b>	<b>Sheltered rock</b>	<b>Unsheltered rock at high elevation</b>	<b>Unsheltered rock at low elevation</b>
Nfix	0.15	0.00	0.17	0.38	0.17	0.10	0.13	0.26	0.22	0.22
bipartite	0.03	0.00	0.11	0.33	0.17	0.07	0.10	0.11	0.18	0.15
tripartite	0.12	0.00	0.06	0.04	0.00	0.03	0.03	0.16	0.04	0.07
fruticose	0.24	0.25	0.18	0.17	0.08	0.22	0.16	0.26	0.16	0.15
foliose	0.17	0.42	0.26	0.54	0.50	0.26	0.27	0.42	0.39	0.47
leprose	0.00	0.00	0.02	0.00	0.00	0.01	0.00	0.05	0.00	0.00
crustose	0.62	0.50	0.57	0.33	0.42	0.57	0.58	0.37	0.49	0.43
gel	0.03	0.00	0.06	0.04	0.08	0.01	0.04	0.05	0.04	0.05
apothecia	0.68	0.64	0.65	0.57	0.50	0.60	0.69	0.72	0.62	0.55
isidia	0.02	0.04	0.07	0.10	0.08	0.05	0.04	0.11	0.06	0.09
lobules	0.10	0.13	0.10	0.08	0.00	0.09	0.10	0.16	0.08	0.13
soredia	0.23	0.13	0.21	0.33	0.38	0.30	0.22	0.32	0.19	0.31
height	1.80	2.45	1.72	3.02	2.43	1.63	1.39	3.26	1.96	2.18
propagule0-0.5	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00

Appendix D *cont.*

Trait	Epiphytic unsheltered conifer at low elevation	Epiphytic unsheltered deciduous tree at high elevation	Epiphytic unsheltered deciduous tree at low elevation	Unsheltered on soil	Sheltered organic substrate on the ground	Unsheltered organic substrate on the ground at high elevation	Unsheltered organic substrate on the ground at low elevation	Sheltered rock	Unsheltered rock at high elevation	Unsheltered rock at low elevation
propagule1	0.02	0.00	0.02	0.00	0.00	0.01	0.00	0.03	0.01	0.01
propagule2	0.23	0.34	0.24	0.19	0.18	0.34	0.30	0.29	0.20	0.14
propagule3	0.25	0.38	0.27	0.30	0.31	0.25	0.35	0.32	0.28	0.31
propagule4	0.29	0.04	0.23	0.21	0.18	0.20	0.17	0.21	0.21	0.22
propagule5	0.11	0.00	0.10	0.17	0.25	0.09	0.11	0.11	0.11	0.16
propagule6	0.02	0.08	0.06	0.08	0.04	0.05	0.03	0.16	0.06	0.07
propagule7	0.03	0.08	0.05	0.06	0.00	0.02	0.06	0.16	0.04	0.08
propagule8	0.06	0.00	0.05	0.08	0.00	0.06	0.04	0.00	0.02	0.05
propagule9	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
propagule10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
aliphatic acid	0.04	0.08	0.05	0.04	0.25	0.08	0.04	0.00	0.04	0.03
anthraquinone	0.02	0.08	0.05	0.13	0.08	0.07	0.04	0.00	0.05	0.04
depso-depsidone	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.01	0.01
dibenzofuran	0.02	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.01
none	0.33	0.33	0.29	0.17	0.17	0.16	0.28	0.32	0.32	0.3
orcinol depsidone	0.10	0.08	0.04	0.00	0.08	0.11	0.03	0.05	0.05	0.09

Appendix D *cont.*

Trait	Epiphytic unsheltered conifer at low elevation	Epiphytic unsheltered deciduous tree at high elevation	Epiphytic unsheltered deciduous tree at low elevation	Unsheltered on soil	Sheltered organic substrate on the ground	Unsheltered organic substrate on the ground at high elevation	Unsheltered organic substrate on the ground at low elevation	Sheltered rock	Unsheltered rock at high elevation	Unsheltered rock at low elevation
orcinol depside	0.13	0.00	0.09	0.00	0.04	0.12	0.04	0.11	0.34	0.07
orcinol tridepside	0.08	0.08	0.08	0.17	0.08	0.13	0.10	0.11	0.17	0.13
orcinol- $\beta$ -depsidone	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
pulvinic acid	0.05	0.00	0.02	0.04	0.00	0.06	0.04	0.00	0.01	0.03
terpene	0.00	0.00	0.02	0.04	0.00	0.02	0.03	0.05	0.03	0.06
triterpene	0.04	0.08	0.05	0.08	0.00	0.04	0.07	0.10	0.07	0.08
unknown	0.05	0.00	0.01	0.04	0.00	0.01	0.03	0.00	0.04	0.02
usnic acid	0.06	0.08	0.07	0.02	0.17	0.12	0.12	0.00	0.04	0.10
usnic acid derivative	0.02	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.01
xanthone	0.02	0.00	0.04	0.00	0.00	0.02	0.02	0.00	0.03	0.02
$\beta$ -orcinol benzyl ester	0.02	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.03	0.01
$\beta$ -orcinol depsidone	0.24	0.08	0.21	0.32	0.38	0.22	0.27	0.34	0.19	0.24
$\beta$ -orcinol depside	0.25	0.46	0.21	0.13	0.25	0.16	0.16	0.22	0.15	0.23

## APPENDIX E.

**Table E.1.** Archived data files for Chapter 2: FIA plots in Oregon between 43°W and 45°W. The following data files have been saved to a CD-ROM and archived with the National Park Service, Southwest Area Network, Anchorage, and the US Forest Service FIA program, Portland, Oregon.

<b>File name</b>	<b>File type</b>	<b>Contents</b>
SppFIAMFiltered2.csv	Comma separated values	Species abundances following the FIA four-step scale: 1 = ≤ 3 individuals per plot; 2 = 4-10 individuals per plot; 3 = > 10 individuals per plot (but less than half of the woody plants have that species present); and 4 = more than half of the woody plants have that species present. Matrix = 166 plots x 102 species.
ORFIAenv6_43to45.csv	Comma separated values	Raw environmental variables and region data. Matrix = 166 plots x 14 environmental variables.
FIA_Trait_43to45_4.csv	Comma separated values	Raw trait data. Matrix = 102 species x 70 traits.
FIA_TraitEnv_9.csv	Comma separated values	Habitat by weighted trait averages, standardized from 0 to 1. Also includes environmental variables. Matrix = 166 plots x 52 variables (traits and environmental variables).
FIA_acrodic_1.csv	Comma separated values	Species acronyms.
FIA_env_metadata.csv	Comma separated values	Descriptions of all environmental data (including data sources). The contents of this file are displayed in Table 2.3.
FIA_trait_metadata.csv	Comma separated values	Descriptions of trait scoring. The contents of this file are displayed in Appendix A.

**Table E.2.** Archived data files for Chapter 3: Katmai National Park, Alaska. The following data files have been saved to a CD-ROM and archived with the National Park Service, Southwest Area Network, Anchorage, and the US Forest Service FIA program, Portland, Oregon.

<b>File name</b>	<b>File type</b>	<b>Contents</b>
habitat_by_species.csv	Comma separated values	Presence/absence of species in habitats. Matrix = 10 habitats x 429 species.
Trait_specimens_v5.csv	Comma separated values	Raw trait data. Matrix = 437 species x 70 traits
Habitat_types_2.csv	Comma separated values	Habitat descriptions. Matrix = 10 habitats x 6 habitat building blocks used to place specimens into a habitat.
Habitat_by_trait_3.csv	Comma separated values	Unstandardized traits in habitats. Values for all traits scaled from 0-1 are the proportion of species in the given habitat with the trait. Height trait values are the average height (on the log scale) of species in the given habitat. Values for all chemical traits (scaled from 0 to 100) are the percentage of species in the given habitat that contain each chemical. Matrix = 10 habitats x 43 traits.
Habitat_by_trait_4.csv	Comma separated values	Product of the multiplication of habitat_by_species.csv and Trait_specimens_v8.csv (with traits standardized from 0 to 1). Matrix = 10 habitats x 43 traits.