LICHENS OF ULTRAMAFIC ROCKS: A MULTIDISCIPLINARY APPROACH TO UNDERSTANDING THE ECOLOGY OF AN UNDERSTUDIED ORGANISM IN A WELL-STUDIED SYSTEM

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ABSTRACT

Lichens of ultramafic rocks: a multidisciplinary approach to investigating the ecology of an understudied organism in a well-studied system.

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Lichens are among the most prominent and successful life forms of metal-rich habitats, including ultramafic rocks and soils; however, research on lichens of ultramafic habitats is limited, especially on the North American continent. A review of the published literature on lichens of ultramafic substrates in North America yielded a total of 437 lichen species reported from ultramafic rocks and soils. Lichen assemblages of ultramafic substrates vary in composition and are dominated by acidophytic (low pH preferring) taxa with a minor, but consistent, basiphytic (high pH preferring) component. Species lists from ultramafic habitats in different geographic regions varied widely, suggesting that factors unrelated to substrate, such as climate, have a large effect on lichen assemblage composition. However, several studies showed clear differentiation between lichen composition on nearby or adjacent ultramafic and nonultramafic habitats, suggesting that ultramafic substrates harbor regionally unique lichen assemblages.

In a regional community ecology study, we sampled lichen biotas of eight ultramafic and eight sandstone outcrops along a 70 km maritime influence gradient in order to test three hypotheses: 1) a substrate effect hypothesis that saxicolous lichen communities of ultramafic and sandstone outcrops are compositionally distinct; 2) a maritime gradient hypothesis that coastal and inland communities are compositionally distinct; and 3) a maritime moderation hypothesis that coastal ultramafic and sandstone communities are more similar than those of inland ultramafic and sandstone. Relationships between lichen communities and abiotic variables were analyzed using perMANOVA. Ultramafic communities showed significant differentiation from sandstone communities in the study area. A total of 134 taxa were recorded - 81 taxa from ultramafic outcrops and 100 taxa from sandstone, with 47 taxa found on both rock types. Ultramafic outcrops were characterized by greater similarity between samples, lower lichen cover, larger differences in cover between north and south aspects, and higher abundance and diversity of cyanolichen taxa relative to sandstone. Coastal, intermediate, and inland communities were compositionally distinct from one another, and sandstone and ultramafic assemblages were significantly differentiated in all coastal distance groups. This study is one of few to quantitatively examine lichen communities of two rock types, and is unique in that it does so at a regional scale. These results add to our understanding of the interactive roles of substrate and maritime influence in lichen community assembly.

Keywords: serpentine, ultramafic, lichen, substrate properties, community ecology

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TABLE OF CONTENTS

LIST OF TABLES ix

LIST OF FIGURES x

CHAPTER

1. Lichens of ultramafic substrates in North America: a review 1

1.1 Introduction 1

1.1.1 The lichen-substrate relationship 1

1.1.2 Definition and characteristics of ultramafic rocks/soils 2

1.1.3 Lichens of metal-rich substrates, including ultramafics, worldwide 3

1.2 Methods 7

1.2.1 Literature review and data compilation 7

1.2.2 Substrate affinity 41

1.2.3 Species distributions 42

1.3 Discussion 45

1.3.1 Substrate affinities of ultramafic lichens of North America 45

1.3.2 Species richness and diversity in ultramafic lichen assemblages 45

1.3.3 Composition of ultramafic lichen assemblages 47

1.3.4 Ultramafic affinity, distributions, and disjunct populations 49

1.3.5 Future Research Directions 51

1.4 Conclusions 53

2. The role of rock: a quantitative comparison of lichen communities of ultramafic versus sandstone outcrops across a coastal-to-inland gradient 55

2.1 Introduction 55

2.2 Methods 64

2.2.1 Study Region 64

2.2.2 Sampling Locations 64

2.2.3 Site selection criteria 64

2.2.4 Sampling 65

2.2.5 Elemental composition of rock samples 67

2.2.6 Abiotic variable measurements 67

2.2.7 Voucher specimen identification 68

2.2.8 Taxonomic Diversity 68

2.2.9 Climate parameter measurements 70

2.2.10 Data Analysis 70

2.3 Results 72

2.3.1 Substrate effects 74

2.3.2 Maritime gradient effects 84

2.3.3 Microhabitat, Microtopography, and Climate 85

2.4 Discussion 88

2.4.1 Substrate effects 88

2.4.2 Maritime influence effects......92

2.4.3 Maritime gradient effects on community differentiation across substrates 93

2.4.4 Microhabitat and Microtopography......94

2.4.5 Limitations......95

2.4.6 Future Research Directions 97

2.5 References 98

Appendix I......110

Appendix II 111

Appendix III. 113

LIST OF TABLES

Table Page

1. Published studies of ultramafic lichen communities on the North American continent as of 2021 11
2. Published floras and peer-reviewed articles including records of lichens on ultramafic substrates in North America. 12
3. Lichen species recorded from ultramafic substrates in North America in published literature. 15
4. North American ultramafic lichens categorized by substrate pH affinity 41
5. Lichen taxa apparently restricted to North America from lichens recorded on ultramafic substrates in North America in the published literature 42
6. Lichens recorded in 3+ studies of ultramafic lichens in North America 44
7. Ultramafic and sandstone outcrop sampling sites 62
8. Richness and Shannon-Wiener diversity measurements for individual sites 77
9. Strongest indicator species (index value >0.4) for sample unit groups 79
10. Results of perMANOVA for tested categorical and continuous variables 83

LIST OF FIGURES

Figure Page

1. Sampling locations for five published studies focusing on ultramafic lichen communities in North America . . 7
2. Examples of ultramafic rocks and soils in North America 9
3. Lichens on ultramafic substrates in North America 10
4. Map of lichen sampling sites 61
5. NMDS ordination of samples with overlaid vectors for selected environmental variables and ellipses representing 95% confidence intervals of the centroids for both ultramafic and sandstone quadrats. 76
6. Microhabitat and mesohabitat differences in richness 81
7. Shannon-Wiener diversity for microhabitat and mesohabitat 82
8. NMDS ordination of samples with overlaid vectors for selected environmental variables and ellipses represent 95% confidence intervals of the centroids for coastal, intermediate, and inland samples 85
9. Lichen cover relationships with aspect 87

Chapter 1: Lichens of ultramafic substrates in North America: a review.

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Introduction

The lichen-substrate relationship

Lichens are among the most successful and prominent life forms in extreme habitats. They occur in almost all biomes on Earth, including latitudinal and altitudinal extremes, as well as the hottest and driest deserts in the world (Alpert 2000; Grube 2010; Armstrong 2017). Lichens have traditionally been defined as a symbiotic association between a fungus (mycobiont) and a photosynthetic partner (photobiont; an alga or cyanobacterium), but the presence of a diversity of micro-organisms that inhabit lichen thalli (e.g., Bates et al. 2012, Spribille et al. 2016) has led some to argue that lichens are better thought of as micro-ecosystems or microbiomes (Hawksworth and Grube 2020). While there are differing views on lichens as a concept, it remains true that a primary mycobiont provides the bulk of a lichen's structure, anchors the lichen in place, and is the source of a lichen's nomenclature and systematic position.

The importance of substrate characteristics to lichen ecology is apparent when comparing lichen biotas on different substrates. Common substrates for lichens include rocks (i.e., saxicolous lichens), tree bark (corticolous), exposed wood (lignicolous), and soil (terricolous), although a much wider range of both natural and anthropogenic substrates are also utilized (Brodo et al. 2001). The lichen-substrate relationship is often described as intimate, with many lichen growth forms maintaining close surface contact along much of their lower surface. Unsurprisingly, then, most lichen species have affinities for certain substrate properties (Brodo 1973). Important substrate properties for lichens include surface texture (Brodo 1973), water retention capacity (Garty and Galun 1974), and elemental composition (Purvis and Halls 1996; Rajakaruna et al. 2012). The latter is of particular importance because it largely dictates the pH level at the lichen-substrate interface, and pH plays a paramount role in determining lichen community assembly (Gilbert and James 1987). For this reason, acidophytic (silicicolous) and basiphytic (calcicolous) lichen biotas are widely recognized as distinct (Brodo 1973; Gilbert 1984, 2000).

For saxicolous lichens, the relationship between lichen assemblages and their rock substrates has been well-studied. At the local level, research and inventories of lichen biotas of specific rock types (i.e., lithology-specific) are fairly common (e.g., Gilbert 1996; Paukov 2009); however, larger-scale studies at regional, continental, and global scales are rare. To date, the only global-scale, lithology-specific studies of lichens are for ultramafic rocks and soils (Favero-Longo et al. 2004, 2018). To the author's knowledge, no analogous reviews of lichens of other lithologies have been carried out.

Definition and characteristics of ultramafic rocks/soils

Ultramafic rocks are named for their high concentrations of iron and magnesium relative to other rocks typical of terrestrial environments. Technically, they are defined as igneous and metamorphic rocks composed of >90% of the mafic minerals olivine and pyroxene, and/or the alteration products of these minerals, e.g., serpentine (Le Maitre et al. 2002). Ultramafic lithologies are widespread on continental landforms, where they make up ~1% of global land surfaces (Oze et al. 2007). Most continental ultramafic exposures are ophiolites (oceanic crust and mantle that has been uplifted onto land). Less common types of terrestrial ultramafic lithologies include mélanges, stratiform mafic-ultramafic complexes, and exposed areas of subcontinental mantle (Moores 2011). Essentially all of the world's exposed ultramafic rocks have undergone some degree of serpentinization, a process by which ultramafic parent material is hydrothermally altered into serpentinite, a metamorphic rock (Malpas 1992). Serpentinite is composed of the serpentine group minerals antigorite, chrysotile, and lizardite (Coleman and Jove 1992).

In addition to iron and magnesium, ultramafic rocks and soils are characteristically high in metals such as nickel, chromium, and cobalt. They are also typically low in nutrients essential to plants and other life forms, including nitrogen, phosphorus, potassium, and calcium (Kruckeberg 1992; Rajakaruna and Boyd 2014). The low molar ratio of calcium to magnesium ions (<1:1) in ultramafic soils (Burt et al. 2001) has also been hypothesized as a stressor (Ghasemi et al. 2020), and there is evidence that this may inhibit root growth and cell wall integrity in vascular plants (O'Dell and Claassen 2006; O'Dell and Rajakaruna 2011). This combination of stressors creates a very harsh environment for vascular plants, leading to high rates of ultramafic endemism (Kruckeberg 2002; Galey et al. 2017). To deal with the multiple stressors of ultramafic substrates, plants have evolved a remarkable suite of adaptations, including metal hyperaccumulation and growth forms suited toward tolerance of water stress, soil elemental imbalances, and microhabitat bareness (Brady et al. 2005; O'Dell and Rajakaruna 2011; Sianta and Kay 2019).

Lichens of metal-rich substrates, including ultramafics, worldwide

Lichens of metal-rich rocks and soils and other metal-rich substrates, such as mine tailings, have received considerably less attention than vascular plants occurring on such substrates. However, there is a long and consistent history of work on lichens of metal-rich substrates (Purvis and Halls 1996; Favero-Longo 2014). Although ecotypic differentiation and geoedaphic endemism are common in vascular plants of metal-rich substrates (O'Dell and Rajakaruna 2011), this trend is not as consistently observed in lichens, particularly in ultramafic substrates (Favero-Longo et al. 2018). However, lichen assemblages of metal-rich substrates are often compositionally unique, and narrow endemism to metal-rich rocks has been thoroughly documented for several lichen species occurring on high-elevation metal-rich sedimentary rocks of the Anakeesta Formation in the southern Appalachians (Lendemer and Harris 2013a; Lendemer and Harris 2013b; Lendemer and Tripp 2015). These same habitats support unique lichen communities that include disjunct populations as well as known heavy-metal-tolerant lichen taxa (Lendemer and Harris 2013b). In Great Britain, Purvis and Halls (1996) describe lichen species associations characteristic of metal-rich mine tailings and spoil heaps. Additionally, comparative studies of adjacent ultramafic and non-ultramafic substrates often show marked differences in lichen species composition (e.g., Favero-Longo and Piervittori 2009; Paukov 2009; Sirois et al. 1988), suggesting a substrate effect. At the same time, lichen communities of ultramafic substrates display high degrees of species turnover at regional and global scales (Favero-Longo et al. 2004), indicating that factors other than substrate are more important in determining species composition.

Most of the available research on lichens of ultramafic substrates has been carried out in Europe (Wirth 1972; Favero-Longo and Piervittori 2009; Favero-Longo et al. 2018). In a worldwide review of studies investigating lichens of ultramafic rocks, Favero-Longo et al. (2004) found evidence for several ecological trends in lichen communities of ultramafic substrates. Perhaps most interestingly, their review indicated that ultramafic substrates harbor a mix of silicicolous and calcicolous lichen species, a finding that has often been noted in studies and observations of lichen biotas on ultramafic substrates (Gilbert 2000; Paukov 2009). Their review also highlighted studies reporting instances of lichens reaching their known latitudinal limits on ultramafic substrates (Wirth 1972; Gilbert 2000). Other reported characteristics, such as low species richness, low percent cover, and the occurrence of lichen ecotypes, do not appear to be consistent features of ultramafic lichen assemblages (Favero-Longo et al. 2004). Similarly, ultramafic endemism in lichens appears to be very rare, with just eight species currently known only from ultramafic substrates, including five that are known only from their type localities (Favero-Longo et al. 2018). Of these, just one, *Porpidia nadvornikiana* (Vězda) Hertel, has a disjunct distribution (Fryday 2005) that provides strong support for its classification as an ultramafic endemic.

The broad goal of this review is to examine the published literature on lichens of ultramafic substrates, specifically from North America, in order to better understand patterns of lichen assemblages of ultramafic rocks and soils on the North American continent (see Figures 1-3). Studies of lichens of mafic substrates, such as gabbro and basalt, are not considered here, although these substrates share some compositional similarities to ultramafic substrates (e.g., relatively high metal content), and often support distinctive vascular plant communities. In eastern North America, lichens of diabase, a type of mafic rock, have received some attention (Lendemer 2005; Waters and Lendemer 2019).

The first step of this review was to compile an updated list of lichen taxa reported on ultramafic substrates within North American from the published literature. To the extent possible, we then compared the attributes of ultramafic lichen assemblages with those of non-ultramafic substrates. We were interested in exploring **1)** attributes of lichen taxa on ultramafic substrates; **2)** similarities and differences of ultramafic and non-ultramafic lichen assemblages under similar abiotic conditions; **3)** patterns of lichen richness and diversity within and among ultramafic habitats, as well as compared to that of non-ultramafic habitats; **4)** geographic distributions of lichens of ultramafic substrates (i.e., prevalence of widespread/cosmopolitan taxa vs. taxa with restricted ranges); and **5)** spatial variation in ultramafic lichen assemblages, including an assessment of the relative importance of abiotic factors on assemblage composition. Lastly, we sought to identify gaps in the knowledge of ultramafic lichens in North America to help focus future research and surveys.

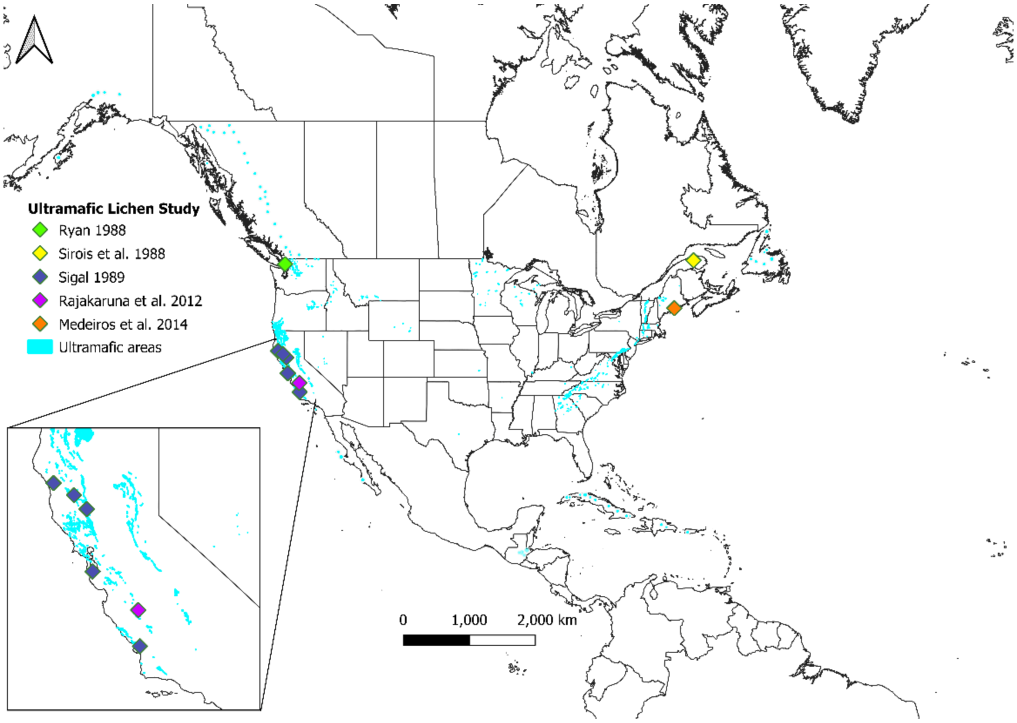

Figure 1. Sampling locations for five published studies focusing on ultramafic lichen communities in North America. Ultramafic areas within the lower 48 states of the USA are from Krevor et al. (2009). Ultramafic areas outside the lower 48 states are approximate locations of some of the major ultramafic formations in North America. Base layer sources are as follows: lower 48 states, U.S. Census Bureau (2018); Canada provincial/territorial boundaries, Statistics Canada (2019); all other country boundaries, Natural Earth (2021). Map is projected in WGS 84/Pseudo-Mercator (EPSG:3857).

Methods

Literature review and data compilation

We compiled information on every lichen taxon reported in each of six published studies that investigated lichen biotas of ultramafic substrates in North America (Figure 1 & Table 1; North America defined here to include Central America, Mexico, the Caribbean, the United States of America, Canada, Greenland, and Saint Pierre and Miquelon). The results of one of the studies, Harris et al. (2007), were included in a more recent study that added to the list of species for that location (Medeiros et al. 2014). Thus, for the purposes of this review, we only consider the ultramafic species list from the latter study. In addition, we conducted a literature search for published articles containing reports of lichens on ultramafic substrates. Taxonomic reports from 19 published articles and one lichen flora were added (see Table 2) resulting in an additional 105 taxa being included in the analyses. For this review, lichens considered to be growing on ultramafic substrates included taxa growing on other lichens (i.e., lichenicolous fungi, including lichenicolous lichens) and bryophytes (bryicolous lichens) that were themselves growing on ultramafic rocks or soils. Nomenclature mainly follows Esslinger (2019) with a small number of taxa following Index Fungorum (Index Fungorum Partnership 2021).

For all taxa identified in the literature review, we gathered available information on substrate affinity, habitat, and geographic range from selected herbarium records and online databases. These data were compiled into a single database that we used to investigate the characteristics of lichens occurring on ultramafic substrates in North America. It is important to note that a review of accessioned herbarium specimens reported from ultramafic substrates was beyond the scope of this review and was not conducted.

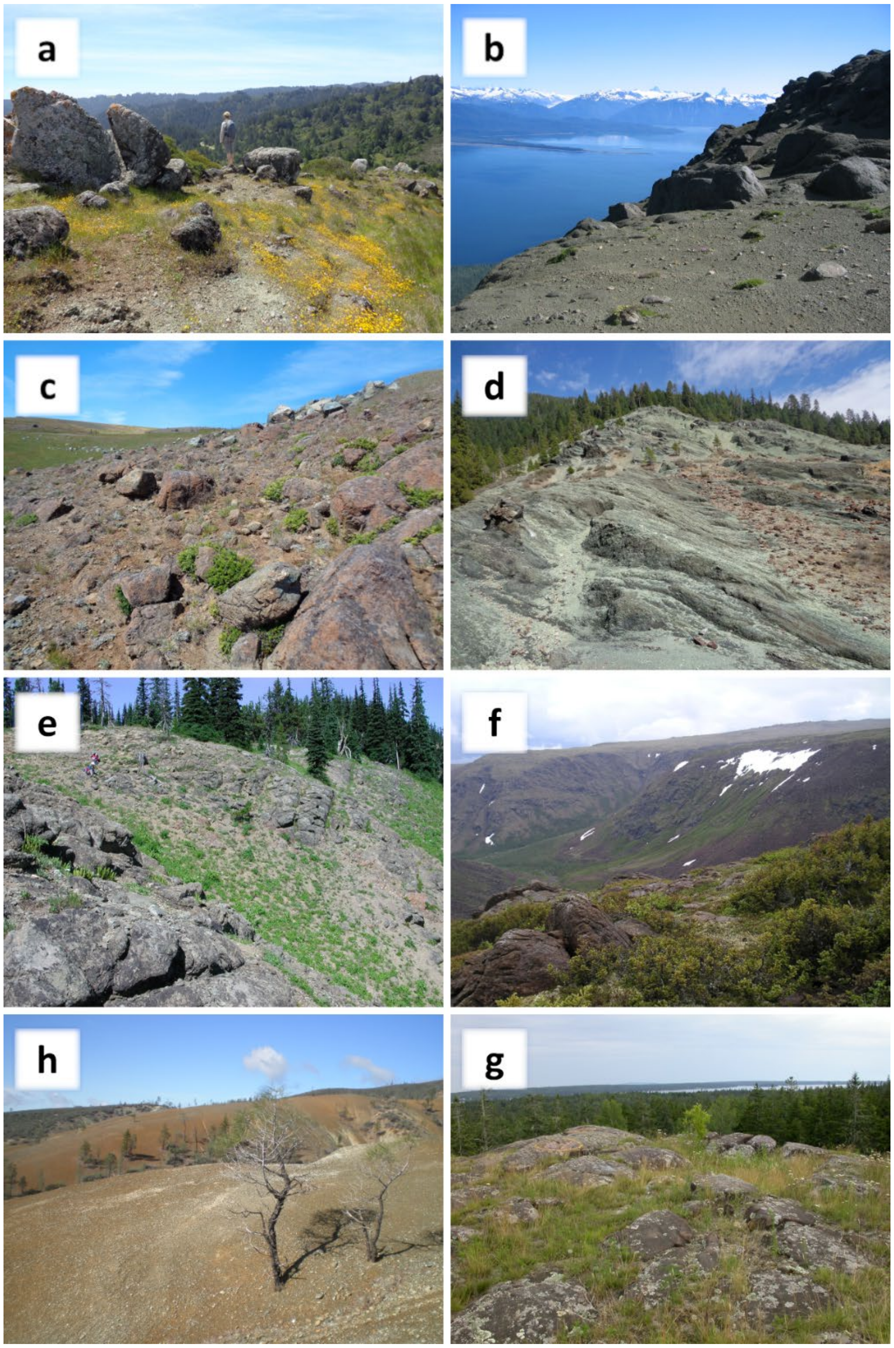

Figure 2. Examples of ultramafic rocks and soils in North America. (a) Ultramafic outcrop near Kneeland, Humboldt Co., CA, USA (Credit: Ryan O'Dell); (b) Kane Peak, AK, USA (Credit: US Forest Service by Karen Dillman); (c) Carson Ridge, Marin Co., CA, USA (Credit: Ryan O'Dell); (d) Ramshorn Creek, Sierra Co., CA, USA (Credit: Ryan O'Dell); (e) Olivine Mountain, BC, Canada (Credit: Gary Lewis); (f) Mont Albert, QC, Canada (Credit: Denise and Anthony Fernando); (g) Clear Creek, San Benito Co., CA, USA (Credit: Suzie Woolhouse); (h) Little Deer Isle, ME, USA (Credit: Nishanta Rajakaruna).

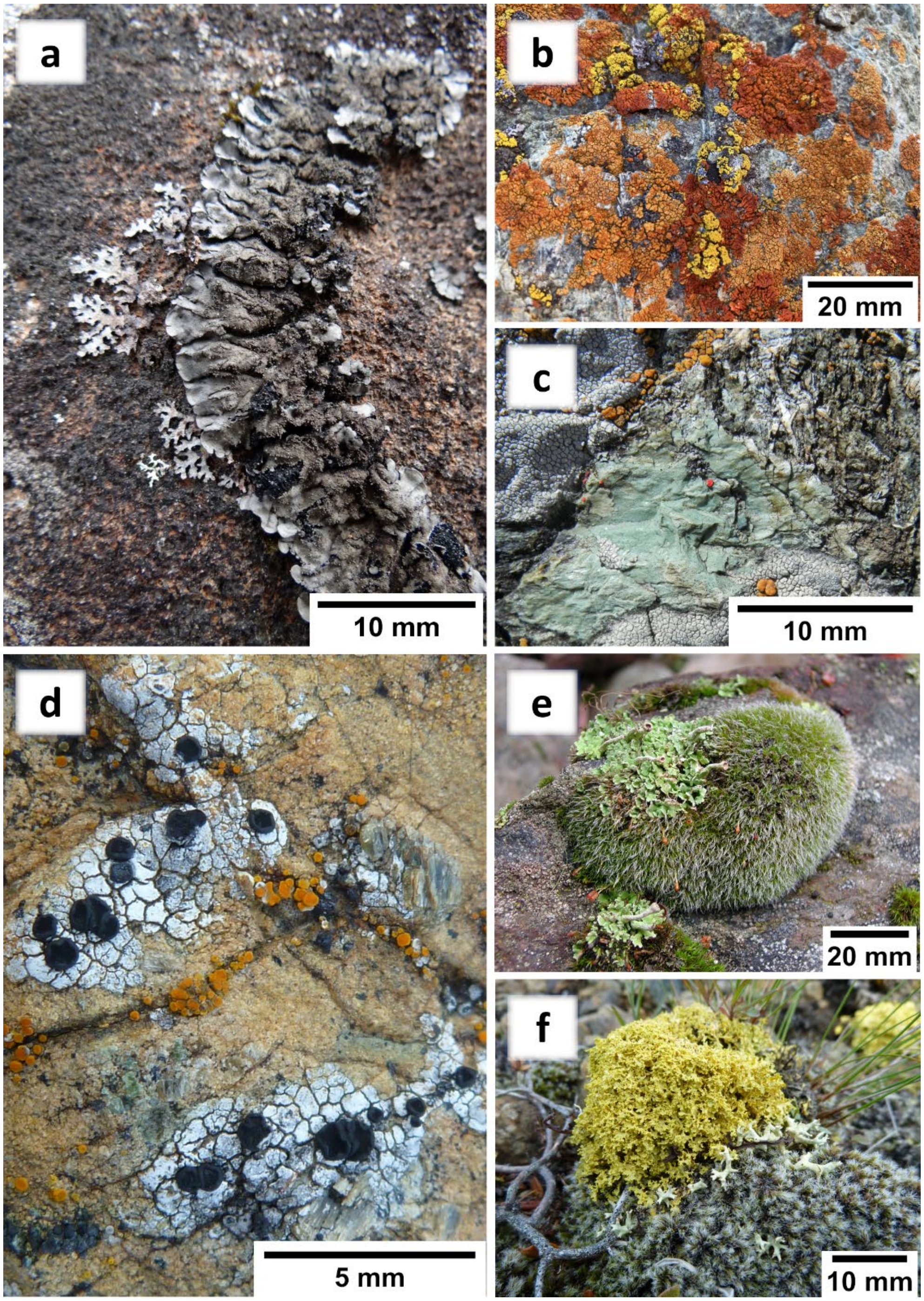

Figure 3. Lichens on ultramafic substrates in North America. (a) *Coccocarpia palmicola* at Little Deer Isle, ME, USA (Credit: Alan Fryday); (b) lichens on ultramafic outcrop in eastern San Luis Obispo Co., CA, USA (Credit: Michael Mulroy); (c) lichens on serpentinite, Irish Hills Nature Reserve, San Luis Obispo Co., CA, USA (Credit: Michael Mulroy); (d) saxicolous lichens including *Lecidea lapicida* (Ach.) Ach. in Mont Albert, QC, Canada (Credit: Jean Gagnon); (e) Cladonia sp. growing on moss, in BC, Canada (Credit: Gary Lewis); (f) *Vulpicida juniperina* (L.) J.-E. Mattson & M.J. Lai and other lichens growing among mosses in Mont Albert, QC, Canada (Credit: Jean Gagnon).

Table 1. Published studies of ultramafic lichen communities on the North American continent as of 2021.

Study	Locality	Latitude	Elevation range (m)	Average annual precipitation (cm)	Study type
Ryan (1988a)	Fidalgo Island, Skagit Co., Washington, USA	48.5	0-5	70.7*	Inventory of marine and maritime lichens of ultramafic rocks. Complemented by a quantitative ecological study of the same site (Ryan 1988b)
Sirois et al. (1988)	Mont Albert, Québec, Canada	48.9	900-1150	166	Compared lichen communities of serpentinized peridotite (ultramafic) and amphibolite (mafic) substrates using quantitative (relevé plot) sampling methods
Sigal (1989)	5 sites in northern and southern coast ranges, central California, USA	35.4-39.9	183-1,890	51-180	Compared ultramafic lichen communities along a latitudinal gradient in central California using inventory collecting methods
Rajakaruna et al. (2012)	New Idria, San Benito Co., CA, USA	36.3	841-1,422	50	Compared lichen communities of adjacent ultramafic and non-ultramafic substrates using inventory collecting methods
Medeiros et al. (2014)	Little Deer Isle, Hancock Co., Maine, USA	44.3	45	138	Compared lichens recorded from ultramafic substrates and non-ultramafic metal-enriched substrates using non-standardized inventory methods

*data acquired from outside source (Western Regional Climate Center 2021)

Table 2. Published floras and peer-reviewed articles including records of lichens on ultramafic substrates in North America.

Study	Locality	Details
Reed (1986)	Eastern North America (USA and Canada)	List of identified lichens and associated herbarium specimens collected from areas of serpentinite in eastern North America. Includes records of epiphytic lichen specimens in ultramafic habitats. Records included here are restricted to lichens confirmed from ultramafic rocks and soils.
Bratt and Wright (1995)	California, USA	An account of *Toninia* species known from California, including two taxa described as occurring on serpentine.
Doell and Wright (1996)	San Mateo County, California, USA	Inventory of macrolichens identified from Jasper Ridge Biological Preserve, San Mateo County, California. Includes records of three macrolichen species growing on serpentine.
Magney (1999)	California	Preliminary list of rare lichens known from California, including one taxon reported growing on serpentine.
Breuss and Bratt (2000)	California	Treatment of catapyrenioid lichens known from California. Provides species descriptions and distribution and ecology details for two taxa reported growing on serpentine.
Jørgensen (2000)	USA and Canada	Treatment of lichens in the family Pannariaceae in North America north of Mexico. Lists and provides descriptions of lichen taxa, including one taxon reported growing on serpentine.
Robertson and Robertson (2000)	California	Reports new and interesting lichen records from California, including records of four lichen taxa collected from serpentine.

Baltzo (2001)	San Mateo County, CA	Annotated list of lichens of the San Francisco watershed, including reports of six taxa occurring on serpentine.
Robertson and Robertson (2001)	California, USA	Reports of new and interesting lichen records from California, including two lichen taxa collected from serpentine.
Peterson (2003)	California, USA	Description of three *Umbilicaria* species new to California, including two species collected from an ultramafic rock outcrop in Del Norte County, California.
Lendemer (2004)	Maryland, USA	Descriptions of notable herbarium specimens from eastern North America. Includes one record of a newly described lichen, *Clavascidium lacinulatum* var. *atrans* (Breuss) M. Prieto from serpentine soil.
Lendemer (2008)	Eastern North America (USA)	Description of eastern disjunct populations of *Psora icterica* (Mont.) Müll. Arg. growing on serpentine barrens in Maryland and Pennsylvania.
Robertson and Robertson (2008)	Mt. Burdell Open Space, Marin Co., CA	List of lichens identified from a lichen foray, including 19 taxa growing on serpentine rocks and soils.
Doell et al. (2009)	Claremont Canyon, Alameda County, CA	List of lichens identified from various habitats within Claremont Canyon in Alameda County. Includes 14 taxa collected from serpentine.
Lendemer et al. (2009)	California	Summary of occurrences of the genus *Ramonia* in California. Describes a new species, *Ramonia extensa* Lendemer, K. Knudsen and Coppins, only known from its type locality on serpentine.
Benson et al. (2012)	San Francisco, Co., CA USA	Compilation of the results of lichen inventories carried out in the Presidio of San Francisco. Includes records of two species on serpentine.

Benson (2016)	Sedgwick Reserve, Santa Barbara Co., CA, USA	Reports lichens identified during forays at the 2016 California Lichen Society annual meeting in Southern California, including 18 records of lichens on serpentine from the Sedgwick Reserve.
McMullin et al. (2017)	Parc National de la Gaspésie, Québec, Canada	Reports 100 new records of lichens for Québec, Canada from Parc National de la Gaspésie. Includes one record of a lichen growing on serpentine rock.
Tucker (2017)	California, USA	Reports rare lichens collected in California by Judy and Ron Robertson. Includes one new record of a lichen growing on serpentine.

Table 3. Lichen species recorded from ultramafic substrates in North America in published literature. Alternative species names used in published studies and articles are given. Key to studies: a = Ryan 1988a; b = Sirois et al. 1988; c = Sigal 1989; d = Rajakaruna et al. 2012; e = Medeiros et al. 2014; Key to articles and floras: 1 = Reed 1986; 2 = Bratt and Wright 1995; 3 = Doell and Wright 1996; 4 = Magney 1999; 5 = Breuss and Bratt 2000; 6 = Jørgensen 2000; 7 = Robertson and Robertson 2000; 8 = Baltzo 2001; 9 = Robertson and Robertson 2001; 10 = Peterson 2003; 11 = Lendemer 2004; 12 = Lendemer 2008; 13 = Robertson and Robertson 2008; 14 = Doell et al. 2009; 15 = Lendemer et al. 2009; 16 = Benson et al. 2012; 17 = Benson 2016; 18 = McMullin et al. 2017; 19 = Tucker 2017. Substrate type for lichens is given for species considered to mostly occur on one or more of the following: bryophytes (bry - bryicolous), rocks (sax - saxicolous), soil (terr - terricolous) wood (lig - lignicolous), and bark (cort - corticolous). Substrate generalists known to occur on multiple substrates without clear specificity are denoted with "gen", and taxa considered lichenicolous (Lawrey and Diederich 2018) are denoted with "lich".

	Current Species Name	**Name used in study (if different)**	**Studies found**	**Substrate pH affinity**	**Substrate type**
1	*Acarospora americana* H. Magn.	—	d	—	—
2	*Acarospora fuscata* (Schrad.) Arnold	—	c, e, 1	acidic	sax
3	*Acarospora rosulata* (Th. Fr.) H. Magn.	—	d, 17	acidic	sax
4	*Acarospora schleicheri* (Ach.) A. Massal.	—	c, 1	neutral	terr
5	*Acarospora socialis* H. Magn.	—	d	—	sax
6	*Acarospora thamnina* (Tuck.) Herre	—	d	acidic	sax
7	*Alectoria ochroleuca* (Schrank) A. Massal.	—	b	acidic to neutral	terr
8	*Amandinea punctata* (Hoffm.) Coppins & Scheid.	*Buellia punctata* (Hoffm.) A. Massal.	c, e, 1	acidic to neutral	cort, lig
9	*Anaptychia palmulata* (Michx.) Vain.	—	e	—	—
10	*Arthonia glebosa* Tuck.	—	13	—	terr
11	*Arthonia phaeobaea* (Norman) Norman	—	a	acidic	sax
12	*Arthonia varians* (Davies) Nyl.	—	d	—	lich

13	*Arthonia* sp. 2	—	a	—	—
14	*Aspicilia cinerea* (L.) Körb.	—	c, 1	neutral	sax
15	*Aspicilia confusa* Owe-Larsson & A. Nordin	—	d	—	sax
16	*Aspicilia cuprea* Owe-Larsson & A. Nordin	—	d	—	sax
17	*Aspicilia pacifica* Owe-Larsson & A. Nordin	—	17	—	sax
18	*Aspicilia phaea* Owe-Larsson & A. Nordin	—	d	—	sax
19	*Aspicilia praecrenata* (Nyl. ex Hasse) Hue	—	d	—	sax, terr
20	*Aspicilia* cf. *caesiocinerea*	—	8	—	—
21	*Aspicilia* sp.	—	a	—	—
22	*Athallia holocarpa* (Hoffm.) Arup, Frödén & Søchting	*Caloplaca holocarpa* (Hoffm.) A.E. Wade	b, e	generalist	cort, lig
23	*Athallia scopularis* (Nyl.) Arup, Frödén & Søchting	*Caloplaca scopularis* (Nyl.) Lettau	e	acidic	sax
24	*Bacidia scopulicola* (Nyl.) A.L. Sm.	—	a	—	sax
25	*Bacidia* sp. 2	—	a	—	—
26	*Baeomyces rufus* (Hudson) Rebent.	—	b	neutral	sax, terr
27	*Bellemerea cinereorufescens* (Ach.) Clauzade & Cl. Roux	—	b	acidic	sax
28	*Biatora subduplex* (Nyl.) Printzen[1]	*Biatora vernalis* (L.) Fr.	b	generalist	gen
29	*Bibbya ruginosa* (Tuck.) Kistenich, Timdal, Bendiksby & S. Ekman subsp. *ruginosa*	*Toninia ruginosa* subsp. *ruginosa* (Tuck.) Herre	d, 2	—	sax, terr

30	*Bilimbia sabuletorum* (Schreb.) Arnold	*Mycobilimbia sabuletorum* (Schreb.) Hafellner	b	neutral	bry
31	*Blastenia ammiospila* (Wahlenb.) Arup, Søchting & Frödén	*Caloplaca cinnamomea* (Th. Fr.) H. Olivier	b	generalist	bry, terr
32	*Blennothallia fecunda* (Degel.) Otálora, P.M. Jørg. & Wedin	*Collema fecundum* Degel.	a	—	sax
33	*Bryobilimbia hypnorum* (Lib.) Fryday, Printzen & S. Ekman	*Lecidea hypnorum* Lib.	b	generalist	terr
34	*Bryocaulon divergens* (Ach.) Kärnefelt	*Coelocaulon divergens* (Ach.) R. Howe	b	—	terr
35	*Bryoplaca sinapisperma* (Lam. & DC.) Søchting, Frödén & Arup	*Caloplaca sinapisperma* (DC.) Maheu & A. Gillet	b	neutral to basic	bry, terr
36	*Bryoplaca tetraspora* (Nyl.) Søchting, Frödén & Arup	*Caloplaca tetraspora* (Nyl.) H. Olivier	b	neutral to basic	bry, terr
37	*Bryoria americana* Gyelnik	*Bryoria trichodes* (Ach.) Brodo & Hawksw.	1	—	cort
38	*Bryoria nitidula* (Th. Fr.) Brodo & D. Hawksw.	—	b	—	terr
39	*Buellia aethalea* (Ach.) Th. Fr.	—	d	acidic to neutral	sax
40	*Buellia badia* (Fr.) A. Massal.	—	c, d	acidic	lich
41	*Buellia dispersa* A. Massal.	*Buellia tergestina* J. Steiner & Zahlbr.	b, d	neutral	sax
42	*Buellia lepidastra* (Tuck.) Tuck.	—	e	—	—
43	*Buellia leptocline* (Flotow) A. Massal.	—	b	acidic	sax
44	*Buellia maculata* Bungartz	*Buellia stigmaea* Tuck.	1	—	sax
45	*Buellia nashii* Bungartz	—	d	—	sax
46	*Buellia ocellata* (Flotow) Körb.	—	d, e	acidic	sax

47	*Buellia sequax* (Nyl.) Zahlbr.	*Buellia abstracta* (Nyl.) H. Olivier	d	neutral	sax
48	*Buellia spuria* (Schaer.) Anzi	—	c, 1	acidic to neutral	sax
49	*Buellia stellulata* (Taylor) Mudd	—	c, 8	neutral	sax
50	*Buellia vilis* Th. Fr.	—	c	acidic	sax
51	*Calogaya biatorina* (A. Massal.) Arup, Frödén & Søchting	*Caloplaca biatorina* (Trevis.) J. Steiner	d	basic	sax
52	*Calogaya lobulata* (Flörke) Arup, Frödén & Søchting	*Caloplaca lobulata* (Flörke) Hellb.	1	acidic to neutral	cort
53	*Caloplaca albovariegata* (B. de Lesd.) Wetmore	—	d	generalist	sax
54	*Caloplaca cerina* (Ehrh. ex Hedwig) Th. Fr.	*Caloplaca gilva* A. Zahlbr.	1	neutral to basic	cort
55	*Caloplaca cinnabarina* (Th. Fr.) Zahlbr.	—	1	—	sax
56	*Caloplaca demissa* (Körb.) Arup & Grube	—	d, 7	neutral	sax
57	*Caloplaca epithallina* Lynge	—	d	neutral	lich
58	*Caloplaca lithophila* H. Magn.	—	e	basic	sax
59	*Caloplaca* cf. *squamosa*	—	8	—	—
60	*Caloplaca* sp. 3	—	a	—	—
61	*Caloplaca* sp. 4	—	a	—	—
62	*Caloplaca* sp. 5	—	a	—	—
63	*Caloplaca* sp. 6	—	a	—	—
64	*Caloplaca* sp., Unknown #1	—	c	—	—
65	*Caloplaca* sp., Unknown #2	—	c	—	—
66	*Calvitimela aglaea* (Sommerf.) Hafellner	—	19	acidic	sax
67	*Candelaria concolor* (Dickson) Stein	—	c, d, 1	neutral to basic	gen

68	*Candelaria pacifica* M. Westb. & Arup	—	17	neutral to basic	cort, lig
69	*Candelariella aurella* (Hoffm.) Zahlbr.	—	a, d, e	basic	sax
70	*Candelariella citrina* B. de Lesd.	—	d	—	sax
71	*Candelariella efflorescens* Harris & Buck	—	1	neutral to basic	cort
72	*Candelariella rosulans* (Müll. Arg.) Zahlbr.	—	d, 17	generalist	sax
73	*Candelariella vitellina* (Hoffm.) Müll. Arg.	—	b, c, d, e, 1	acidic to neutral	sax
74	*Canoparmelia caroliniana* (Nyl.) Elix & Hale	*Pseudoparmelia caroliniana* (Nyl.) Hale	1	—	cort
75	*Catapyrenium cinereum* (Pers.) Körb.	—	c	neutral to basic	terr
76	*Catillaria chalybeia* (Borrer) A. Massal.	—	a	generalist	sax
77	*Catillaria lenticularis* (Ach.) Th. Fr.	—	c, e	neutral to basic	sax
78	*Catillaria* sp. 2	—	a	—	—
79	*Catolechia wahlenbergii* (Ach.) Körb.	—	b	acidic to neutral	sax
80	*Cetraria aculeata* (Schreb.) Fr.	*Coelocaulon aculeatum* (Schreb.) Link	b	acidic to neutral	terr
81	*Cetraria ericetorum* Opiz subsp. *ericetorum*	—	b	acidic to neutral	terr
82	*Cetraria islandica* subsp. *crispiformis* (Räsänen) Kärnefelt	—	b	acidic to neutral	terr
83	*Cetraria islandica* (L.) Ach. subsp. *islandica*	—	b	generalist	terr
84	*Cetraria laevigata* Rass.	—	b	—	terr
85	*Cetrariella delisei* (Schaer.) Kärnefelt & A. Thell	*Cetraria delisei* (Boy ex Schaer.) Nyl.	b	—	terr
86	*Chrysothrix candelaris* (L.) J.R. Laundon	—	a	acidic	gen

87	*Circinaria caesiocinerea* (Nyl. ex Malbr.) A. Nordin, Savić & Tibell	*Aspicilia caesiocinerea* (Nyl. ex Malbr.) Arnold	c	generalist	sax
88	*Cladonia acuminata* (Ach.) Norrlin	—	b, e, 1	neutral to basic	terr
89	*Cladonia amaurocraea* (Flörke) Schaer.	—	b	acidic	gen
90	*Cladonia apodocarpa* Robbins	—	1	—	terr
91	*Cladonia arbuscula* (Wallr.) Flotow	*Cladina arbuscula* (Wallr.) Hale & W. Culb.	1	acidic to neutral	bry, terr
92	*Cladonia atlantica* Evans	—	1	—	—
93	*Cladonia boryi* Tuck.	—	e, 1	—	—
94	*Cladonia cariosa* (Ach.) Sprengel	—	e, 1	acidic to neutral	terr
95	*Cladonia carneola* (Fr.) Fr.	—	b	acidic	lig, terr
96	*Cladonia cenotea* (Ach.) Schaer.	—	b	acidic	lig
97	*Cladonia chlorophaea* (Flörke ex Sommerf.) Sprengel	—	b, e, 1	acidic to neutral	gen
98	*Cladonia coccifera* (L.) Willd.	—	b, 1	acidic	terr
99	*Cladonia coniocraea* (Flörke) Sprengel	—	b, c, 1	acidic to neutral	lig
100	*Cladonia crispata* (Ach.) Flotow	—	b, 1	acidic	bry, terr
101	*Cladonia cristatella* Tuck.	—	e, 1	—	—
102	*Cladonia cryptochlorophaea* Asahina	—	e, 1	—	—
103	*Cladonia cyanipes* (Sommerf.) Nyl.	—	b	acidic	lig, terr
104	*Cladonia cylindrica* (Evans) Evans	—	1	—	—
105	*Cladonia decorticata* (Flörke) Sprengel	—	b	acidic	terr
106	*Cladonia deformis* (L.) Hoffm.	—	b	acidic	lig, terr
107	*Cladonia digitata* (L.) Hoffm.	—	b	acidic	lig, terr
108	*Cladonia dimorphoclada* Robbins	—	e, 1	—	—
109	*Cladonia farinacea* (Vain.) Evans	—	1	—	terr

110	*Cladonia furcata* (Hudson) Schrad.	—	b, 1	generalist	terr
111	*Cladonia glauca* Flörke	—	b	acidic	—
112	*Cladonia gracilis* subsp. *gracilis* (L.) Willd.	—	b, 1	acidic	lig, terr
113	*Cladonia grayi* G. Merr. ex Sandst.	—	e, 1	acidic	—
114	*Cladonia macilenta* Hoffm.	—	e	acidic	lig, terr
115	*Cladonia macilenta* var. *bacillaris* (Ach.) Schaer.	*Cladonia bacillaris* Nyl.	b, 1	—	lig, terr
116	*Cladonia macrophylla* (Schaer.) Stenh.	—	b	acidic	terr
117	*Cladonia mateocyatha* Robbins	—	1	—	terr
118	*Cladonia maxima* (Asahina) Ahti	—	b	—	bry, terr
119	*Cladonia mitis* Sandst.	*Cladina mitis* (Sandst.) Hustich	b, e, 1	acidic to neutral	terr
120	*Cladonia multiformis* G. Merr.	—	1	—	lig, terr
121	*Cladonia ochrochlora*	—	14	—	—
122	*Cladonia petrophila* R.C. Harris	—	1	acidic to neutral	sax
123	*Cladonia peziziformis* (With.) J. R. Laundon	*Cladonia capitata* (Michx.) Sprengel	1	acidic	terr
124	*Cladonia phyllophora* Hoffm.	—	b	acidic	terr
125	*Cladonia piedmontensis* G. Merr.	—	1	—	—
126	*Cladonia pleurota* (Flörke) Schaer.	—	b, e, 1	acidic	lig, terr
127	*Cladonia pseudorangiformis* Asahina	—	b	—	terr
128	*Cladonia pyxidata* (L.) Hoffm.	—	b, c, e, 1	acidic to neutral	terr
129	*Cladonia ramulosa* (With.) J. R. Laundon	*Cladonia pityrea* (Florke) Fr.	1	acidic	lig, terr
130	*Cladonia rangiferina* (L.) F.H. Wigg.	*Cladina rangiferina* (L.) Nyl.	b, 1	acidic to neutral	terr
131	*Cladonia rei* Schaer.	—	e, 1	acidic to neutral	terr
132	*Cladonia robbinsii* Evans	—	1	—	—

133	*Cladonia scabriuscula* (Delise) Nyl.	—	b	neutral	terr
134	*Cladonia squamosa* (Scop.) Hoffm.	—	b, e, 1	acidic	—
135	*Cladonia stellaris* (Opiz) Pouzar & Vězda	*Cladina stellaris* (Opiz) Brodo	b	acidic	terr
136	*Cladonia strepsilis* (Ach.) Grognot	—	1	acidic	bry, terr
137	*Cladonia subcariosa* Nyl.	*Cladonia clavulifera* Vain., *Cladonia polycarpoides* Nyl.	e, 1	neutral to basic	terr
138	*Cladonia subtenuis* (Abbayes) Mattick	*Cladina subtenuis* (des. Abb.)	1	—	—
139	*Cladonia subulata* (L.) F.H. Wigg.	—	b	neutral	terr
140	*Cladonia sulphurina* (Michx.) Fr.	—	b	acidic	lig, terr
141	*Cladonia symphycarpa* (Ach.) Fr.	—	e	basic	terr
142	*Cladonia turgida* Ehrh. ex Hoffm.	—	b, e, 1	acidic	terr
143	*Cladonia uliginosa* Ahti (Ahti)	*Cladonia stricta* var. *uliginosa* Ahti	b	—	terr
144	*Cladonia uncialis* (L.) F.H. Wigg.	—	b, e, 1	acidic to neutral	terr
145	*Clavascidium lacinulatum* (Ach.) M. Prieto	*Placidium lacinulatum* (Ach.) Breuss	13	basic	terr
146	*Clavascidium lacinulatum* var. *atrans* (Breuss) M. Prieto	*Placidium lacinulatum* var. *atrans* (Ach.) Breuss	11	—	terr
147	*Coccocarpia palmicola* (Sprengel) Arv. & D.J. Galloway	*Coccocarpia cronia* (Tuck.) Vain.	e, 1	neutral to basic	sax, terr
148	*Collema furfuraceum* (Arnold) Du Rietz	—	d	neutral	gen
149	*Collema subflaccidum* Degel.	—	e	neutral	gen
150	*Collemopsidium halodytes* (Nyl.) Grube & B.D. Ryan	*Pyrenocollema halodytes* (Nyl.) R. Harris	a	basic	sax
151	*Collemopsidium* sp. 2	*Pyrenocollema* sp. 2	a	—	—
152	*Collemopsidium* sp. 3	*Pyrenocollema* sp. 3	a	—	—
153	*Dactylospora urceolata* (Th. Fr.) Arnold	—	b	—	lich

154	*Dermatocarpon americanum* Vain.	—	13	—	sax
155	*Dermatocarpon leptophyllodes* (Nyl.) Vain. ex Hav.	—	d, e	—	sax
156	*Dermatocarpon luridum* (With.) J.R. Laundon	*Dermatocarpon weberi* (Ach.) Mann	b, 1	neutral	sax
157	*Dermatocarpon miniatum* (L.) W. Mann	—	c, e, 1, 8	neutral to basic	sax
158	*Dermatocarpon rivulorum* (Arnold) Dalla Torre & Sarnth.	—	b	acidic to neutral	sax
159	*Dibaeis baeomyces* (L.f.) Rambold & Hertel	—	e	acidic	terr
160	*Dimelaena oreina* (Ach.) Norman	—	d, 17	acidic to neutral	sax
161	*Dimelaena radiata* (Tuck.) Müll. Arg.	—	c	acidic to neutral	sax
162	*Dimelaena thysanota* (Tuck.) Hale & W.L. Culb.	—	d, 17	acidic	sax
163	*Diploschistes actinostoma* (Ach.) Zahlbr.	—	14	neutral to basic	sax
164	*Diploschistes muscorum* (Scop.) R. Sant.	—	14	neutral to basic	bry, terr
165	*Diploschistes scruposus* (Schreb.) Norman	—	c, 1, 14	neutral	sax
166	*Diplotomma alboatrum* (Hoffm.) Flotow	—	c	neutral to basic	gen
167	*Enchylium tenax* (Sw.) Gray	*Collema tenax* (Sw.)	1, 13, 14	neutral to basic	bry, terr
168	*Endocarpon* sp.	—	13	—	—
169	*Endococcus propinquus* (Körb.) D. Hawksw.	—	b	—	lich
170	*Ephebe lanata* (L.) Vain.	—	b, 1	acidic to neutral	sax
171	*Euopsis pulvinata* (Schaer.) Nyl.	—	c	acidic	sax
172	*Flavocetraria cucullata* (Bellardi) Kärnefelt & A. Thell	*Cetraria cucullata* (Bellardi) Ach.	b	neutral	terr

173	*Flavocetraria nivalis* (L.) Kärnefelt & A. Thell	*Cetraria nivalis* (L.) Ach.	b	neutral	terr
174	*Flavoparmelia baltimorensis* (Gyelnik & Fóriss) Hale	*Pseudoparmelia baltimorensis* (Gyelnik & Fóriss) Hale	1	—	sax
175	*Flavoparmelia caperata* (L.) Hale	*Pseudoparmelia caperata* (L.) Hale	e, 1	neutral	cort, lig
176	*Flavoplaca citrina* (Hoffm.) Arup, Frödén & Søchting	*Caloplaca citrina* (Hoffm.) Th. Fr.	a, 1	neutral to basic	sax
177	*Flavoplaca microthallina* (Wedd.) Arup, Frödén & Søchting	*Caloplaca microthallina* Wedd.	e	acidic to neutral	sax
178	*Flavopunctelia flaventior* (Stirton) Hale	—	c	acidic	gen
179	*Fuscopannaria cyanolepra* (Tuck.) P.M. Jørg.	*Parmeliella cyanolepra* (Tuck.) Herre	c	—	terr
180	*Fuscopannaria praetermissa* (Nyl.) P.M. Jørg.	*Pannaria praetermissa* Nyl.	b, e	neutral to basic	bry
181	*Fuscopannaria thiersii* P.M. Jørg.	—	6	—	—
182	*Gowardia nigricans* (Ach.) P. Halonen et al.	*Alectoria nigricans* (Ach.) Nyl.	b	acidic	terr
183	*Graphis scripta* (L.) Ach.	—	1	acidic to neutral	cort
184	*Gyalecta russula* (Körb. ex Nyl.) Baloch, Lumbsch & Wedin	*Belonia russula* Körb. ex Nyl.	b	neutral	sax
185	*Gyalolechia flavorubescens* (Hudson) Søchting, Frödén & Arup	*Caloplaca aurantiaca* (Lightf.) Th. Fr.	1	acidic to neutral	cort
186	*Heterodermia obscurata* (Nyl.) Trev.	—	1	acidic to neutral	bry, cort
187	*Heterodermia speciosa* (Wulf.) Trev.	—	1	acidic to neutral	gen
188	*Hydropunctaria maura* (Wahlenb.) C. Keller, Gueidan & Thüs	*Verrucaria maura* Wahlenb. ex Ach.	a	acidic	sax

189	*Hyperphyscia syncolla* (Tuck. ex Nyl.) Kalb	*Physciopsis syncolla* (Tuck.) Poelt.	1	—	—
190	*Hypogymnia physodes* (L.) Nyl.	—	b, 1	acidic to neutral	cort, lig
191	*Hypogymnia vittata* (Ach.) Parrique	—	b	acidic	cort
192	*Hypotrachyna horrescens* (Taylor) Krog & Swinscow	*Parmelina horrescens* (Taylor) Hale	1	acidic to neutral	cort
193	*Hypotrachyna livida* (Taylor) Hale	—	1	—	cort, sax
194	*Hypotrachyna minarum* (Vain.) Krog & Swinscow	*Parmelina dissecta* (Nyl.) Hale	1	acidic	cort
195	*Icmadophila ericetorum* (L.) Zahlbr.	—	b	acidic	lig, terr
196	*Ionaspis odora* (Ach.) Th. Fr.	—	b	acidic	sax
197	*Ionaspis* sp.	—	a	—	—
198	*Lecania pacifica* Zahlbr. ex B. D. Ryan & van den Boom	—	16	acidic to neutral	sax
199	*Lecania* sp. 1	—	a	—	—
200	*Lecania* sp. 2		a	—	—
201	*Lecanora albella* (Pers.) Ach.	*Lecanora pallida* (Schreb.) Rabenh.	1	acidic	cort
202	*Lecanora argentea* Oxner & Volkova	—	e	—	sax
203	*Lecanora argopholis* (Ach.) Ach.	—	c	neutral	sax
204	*Lecanora epibryon* (Ach.) Ach.	—	b	neutral to basic	bry, terr
205	*Lecanora gangaleoides* Nyl.	—	14	acidic to neutral	sax
206	*Lecanora hybocarpa* (Tuck.) Brodo	*Lecanora pseudochlarotera* Brodo ined.	1	acidic to neutral	cort
207	*Lecanora intricata* (Ach.) Ach.	—	d	neutral	sax
208	*Lecanora mellea* W.A. Weber	—	17	acidic to neutral	sax

209	*Lecanora placidensis* (H. Magn.) Knoph, Leuckert & Rambold	*Lecidea placidensis* H. Magn.	b	—	sax
210	*Lecanora polytropa* (Ehrh.) Rabenh.	—	b, c, e	acidic to neutral	sax
211	*Lecanora pseudistera* Nyl.	*Lecanora galactinula* Vain.	1	acidic to neutral	sax
212	*Lecanora pulicaris* (Pers.) Ach.	—	c	acidic	cort
213	*Lecanora rupicola* (L.) Zahlbr.	—	d	acidic to neutral	sax
214	*Lecanora sierrae* B.D. Ryan & T.H. Nash	—	d	acidic	sax
215	*Lecanora strobilina* (Sprengel) Kieff.	—	1	acidic	cort
216	*Lecanora xylophila* Hue	*Lecanora grantii* H. Magn.	a	—	cort
217	*Lecanora* cf. *dispersa*	—	a	—	—
218	*Lecanora* sp.	—	c	—	—
219	*Lecidea atrobrunnea* (Ramond ex Lam. & DC.) Schaer.	—	c, 14	acidic	sax
220	*Lecidea atrobrunnea* group	—	13	—	—
221	*Lecidea brunneofusca* H. Magn.	—	b	—	sax
222	*Lecidea cyrtidia* Tuck.	—	1	—	sax
223	*Lecidea fuscoatra* (L.) Ach.	—	c	acidic to neutral	sax
224	*Lecidea laboriosa* Müll. Arg.	—	d, 17	acidic	sax
225	*Lecidea tessellata* Flörke	—	b, c, d, 17	neutral	sax
226	*Lecidea umbonata* (Hepp) Mudd	—	b	neutral to basic	sax
227	*Lecidea* sp.	—	c	—	—
228	*Lecidea* sp. 1	—	a	—	—
229	*Lecidea* sp. 2	—	a	—	—
230	*Lecidella asema* (Nyl.) Knoph & Hertel	—	d	neutral	sax
231	*Lecidella carpathica* Körb.	—	b, c, d	generalist	sax

232	*Lecidella euphorea* (Flörke) Hertel	—	b	neutral	cort, lig
233	*Lecidella patavina* (A. Massal.) Knoph & Leuckert	—	e	basic	sax
234	*Lecidella scabra* (Taylor) Hertel & Leuckert	—	a	neutral	sax
235	*Lecidella stigmatea* (Ach.) Hertel & Leuckert	—	a, b, c, d, e	neutral	sax
236	*Lecidella wulfenii* (Hepp) Körb.	—	b	neutral	gen
237	*Lecidoma demissum* (Rutstr.) Gotth. Schneider & Hertel	—	b	acidic	terr
238	*Lepra amara* (Ach.) Hafellner	*Pertusaria amara* (Ach.) Nyl.	e	acidic to neutral	cort
239	*Lepra dactylina* (Ach.) Hafellner	*Pertusaria dactylina* (Ach.) Nyl.	b	—	bry, terr
240	*Lepra panyrga* (Ach.) Hafellner	*Pertusaria panyrga* (Ach.) A. Massal.	b	—	bry, terr
241	*Lepraria eburnea* J.R. Laundon	—	18	—	—
242	*Lepraria finkii* (B. de Lesd.) R.C. Harris	*Lepraria aeruginosa* (Wigg.) Sm.	e, 1	generalist	gen
243	*Lepraria neglecta* (Nyl.) Erichsen	*Lepraria caesioalba* (B. de Lesd.) J.R. Laundon, *Lepraria zonata* Brodo	e, 1	acidic to neutral	gen
244	*Lepraria normandinoides* Lendemer & R.C. Harris	—	e	—	gen
245	*Lepraria* sp.[2]	*Lepraria incana* (L.) Ach.	a, b	—	—
246	*Leprocaulon textum* (K. Knudsen, Elix & Lendemer) Lendemer & B.P. Hodk.	*Lepraria texta* K. Knudsen, Elix & Lendemer	d	—	sax
247	*Leptochidium albociliatum* (Desm.) M. Choisy	—	c, d, 3, 13	neutral	sax, terr

248	*Leptogium austroamericanum* (Malme) Dodge	—	1	—	cort
249	*Leptogium chloromelum* (Sw.) Nyl.	—	1	—	cort
250	*Leptogium cyanescens* (Rabenh.) Körb.	—	e	neutral	gen
251	*Leptogium* sp.	—	c	—	—
252	*Lichenomphalia hudsoniana* (H.S. Jenn.) Redhead et al.	*Botrydina viridis* (Ach.) Redhead & Kuyper	b	acidic	terr
253	*Lichenostigma elongatum* Nav.-Ros. & Hafellner	—	d	—	lich
254	*Lichenostigma subradians* Hafellner, Calatyud & Nav.-Ros.	—	d	—	lich
255	*Lichenothelia* spp.	—	17	—	—
256	*Lobaria pulmonaria* (L.) Hoffm.	—	e	neutral	cort
257	*Megaspora verrucosa* (Ach.) Arcadia & A. Nordin	*Pachyospora verrucosa* (Ach.) A. Massal.	b	neutral to basic	bry, terr
258	*Melanelixia glabroides* (Essl.) O. Blanco et al.	—	d	—	sax
259	*Melanelixia subaurifera* (Nyl.) O. Blanco et al.	*Melanelia subaurifera* (Nyl.) Essl.	a	neutral	cort, lig
260	*Melanohalea elegantula* (Zahlbr.) O. Blanco et al.	—	d	neutral	—
261	*Miriquidica plumbeoatra* (Vain.) A.J. Schwab & Rambold	*Lecidea plumbeoatra* Vain.	b	—	—
262	*Miriquidica pycnocarpa* (Körb.) Andreev	*Lecidea pycnocarpa* (Körb.) Ohlert	b	—	—
263	*Miriquidica scotopholis* (Tuck.) B.D. Ryan & Timdal	*Lecanora scotopholis* (Tuck.) Timdal	c, 17	—	sax

264	*Muellerella lichenicola* (Sommerf. ex Fr.) D. Hawksw.	—	b	—	lich
265	*Mycobilimbia berengeriana* (A. Massal.) Hafellner & V. Wirth	*Lecidea berengeriana* (Massal.) Th. Fr.	b	basic	bry, terr
266	*Mycoblastus sanguinarius* (L.) Norman	—	b	acidic	—
267	*Myelochroa aurulenta* (Tuck.) Elix & Hale	*Parmelina aurulenta* (Tuck.) Hale	1	—	cort, sax
268	*Myelochroa galbina* (Ach.) Elix & Hale	*Parmelina galbina* (Ach.) Hale	1	—	cort
269	*Myelochroa obsessa* (Ach.) Elix & Hale	*Parmelina obsessa* (Ach.) Hale	1	acidic to neutral	sax
270	*Myriospora scabrida* (Hedl. ex Magn.) K. Knudsen & Arcadia	—	d	acidic	sax
271	*Nephroma arcticum* (L.) Torss.	—	b	—	gen
272	*Nephroma bellum* (Sprengel) Tuck.	—	1	acidic to neutral	gen
273	*Nephroma parile* (Ach.) Ach.	—	e	acidic to neutral	sax
274	*Ochrolechia androgyna* (Hoffm.) Amold	—	b	acidic	gen
275	*Ochrolechia frigida* (Sw.) Lynge	*Ochrolechia lapuensis* (Vain.) Räsänen	b	acidic	bry
276	*Ochrolechia gyalectina* (Nyl.) Zahlbr.	—	b	—	gen
277	*Ochrolechia inaequatula* (Nyl.) Zahlbr.	—	b	acidic	—
278	*Ochrolechia upsaliensis* (L.) A. Massal.	—	b	basic	bry, terr
279	*Opegrapha rupestris* Pers.	*Opegrapha saxicola* Ach.	a	generalist	lich
280	*Pannaria rubiginosa* (Thunb.) Delise	—	e	neutral	cort
281	*Parmelia saxatilis* (L.) Ach.	—	a, b, e, 1	acidic	sax
282	*Parmelia sulcata* Taylor	—	b, e, 1	acidic to neutral	cort
283	*Parmeliopsis hyperopta* (Ach.) Arnold	—	b	acidic	cort
284	*Parmotrema crinitum* (Ach.) M. Choisy	—	e	acidic	cort

285	*Parmotrema hypoleucinum* (B. Stein) Hale	—	1	acidic to neutral	cort
286	*Parmotrema hypotropum* (Nyl.) Hale	—	1	acidic to neutral	cort
287	*Parmotrema perforatum* (Jacq.) A. Massal.	—	1	—	cort
288	*Parmotrema reticulatum* (Taylor) Choisy	—	1	acidic to neutral	cort
289	*Parmotrema subisidiosum* (Mull. Arg.) Hale	—	1	—	cort
290	*Peltigera aphthosa* group[3]	*Peltigera aphthosa* (L.) Willd.	b, 1	—	—
291	*Peltigera canina* group[3]	*Peltigera canina* (L.) Willd.	b, 1	—	—
292	*Peltigera didactyla* (With.) J.R. Laundon	—	e	neutral	terr
293	*Peltigera evansiana* Gyelnik	—	1	—	bry, terr
294	*Peltigera polydactylon* (Necker) Hoffm.	*Peltigera polydactyla* (Necker) Hoffm.	b, 1	—	terr
295	*Peltigera rufescens* (Weiss) Humb.	—	e, 1	neutral to basic	terr
296	*Peltigera scabrosa* Th. Fr.	—	b	acidic	gen
297	*Peltula bolanderi* (Tuck.) Wetmore	—	c, d, 13, 17	generalist	sax
298	*Peltula euploca* (Ach.) Poelt ex Ozenda & Clauzade	—	d, 13, 17	neutral	sax
299	*Peltula omphaliza* (Nyl.) Wetmore	—	c	neutral	sax
300	*Peltula zahlbruckneri* (Hasse) Wetmore	—	7	acidic to neutral	—
301	*Pertusaria octomela* (Norman) Erichsen	—	b	—	bry, terr
302	*Phaeophyscia adiastola* (Essl.) Essl.	—	e, 1	—	gen
303	*Phaeophyscia ciliata* (Hoffm.) Moberg	—	1	acidic to neutral	cort
304	*Phaeophyscia endococcina* (Körb.) Moberg	—	b	neutral	—

305	*Phaeophyscia orbicularis* (Necker) Moberg	—	a	generalist	cort
306	*Phaeophyscia pusilloides* (Zahlbr.) Essl.	—	1	acidic to neutral	cort
307	*Phaeophyscia rubropulchra* (Degel.) Essl.	—	e	neutral	—
308	*Phaeophyscia sciastra* (Ach.) Moberg	—	a, e	neutral to basic	sax
309	*Phylliscum demangeonii* (Moug. & Mont.) Nyl.	—	7	acidic to neutral	sax
310	*Physcia adscendens* (Fr.) H. Olivier	—	a, c	generalist	gen
311	*Physcia americana* G. Merr.	—	1	—	cort, sax
312	*Physcia biziana* (A. Massal.) Zahlbr.	—	d	neutral	gen
313	*Physcia caesia* (Hoffm.) Hampe ex Fürnr.	—	a, b, e, 1	neutral to basic	sax
314	*Physcia dimidiata* (Arnold) Nyl.	—	d	neutral	sax
315	*Physcia dubia* (Hoffm.) Lettau	—	b, 13	generalist	sax
316	*Physcia millegrana* Degel.	—	1	—	cort
317	*Physcia phaea* (Tuck.) J.W. Thomson	—	13	neutral	sax
318	*Physcia stellaris* (L.) Nyl.	—	c, 1	neutral	cort
319	*Physcia tenella* (Scop.) DC.	—	a, e	generalist	gen
320	*Physcia tribacia* (Ach.) Nyl.	—	8, 13, 14	neutral	sax
321	*Physconia americana* Essl.	—	d	—	gen
322	*Physconia californica* Essl.	—	d	—	cort
323	*Physconia enteroxantha* (Nyl.) Poelt	—	d	neutral	gen
324	*Physconia isidiigera* (Zahlbr.) Essl.	*Physconia grisea* (Lam.) Poelt f. *isidiigera* (Zahlbr.) Thomson comb. nov.	c, 13	neutral	—
325	*Physconia muscigena* (Ach.) Poelt	—	b, d	neutral to basic	bry, terr

326	*Physconia* sp.[4]	*Physconia distorta* (With.) J.R. Laundon	c	neutral	cort
327	*Placidium arboreum* (Schwein. ex E. Michener) Lendemer	*Dermatocarpon tuckermanii* (Rav.) Zahlbr.	1	—	cort
328	*Placidium lachneum* (Ach.) B. de Lesd.	*Catapyrenium lachneum* (Ach.) R. Sant.	c, 1, 3	neutral to basic	bry, terr
329	*Placidium pilosellum* (Breuss) Breuss	—	5	neutral to basic	bry, terr
330	*Placidium squamulosum* (Ach.) Breuss	—	e, 5	basic	bry, terr
331	*Placopyrenium stanfordii* (Herre) K. Knudsen	—	d	generalist	sax
332	*Placynthiella icmalea* (Ach.) Coppins & P. James	—	e	acidic	terr
333	*Placynthiella uliginosa* (Schrad.) Coppins & P. James	—	e	acidic	terr
334	*Placynthium nigrum* (Hudson) Gray	—	b, c	neutral to basic	sax
335	*Placynthium* sp.	—	a	—	—
336	*Platismatia glauca* (L.) W.L. Culb. & C.F. Culb.	—	b, 1	—	gen
337	*Polyblastia cupularis* A. Massal.	—	b	neutral to basic	sax
338	*Polyblastia hyperborea* Th. Fr.	—	b	—	sax
339	*Polyblastia* sp.	—	a	—	—
340	*Polycauliona bolacina* (Tuck.) Arup, Frödén & Søchting	*Caloplaca bolacina* (Tuck.) Herre	13, 17	acidic to neutral	sax
341	*Polycauliona candelaria* (L.) Frödén, Arup, & Søchting	*Xanthoria candelaria* (L.) Th. Fr.	a	generalist	cort, sax
342	*Polycauliona ignea* (Arup) Arup, Frödén & Søchting	*Caloplaca ignea* Arup.	d, 17	—	sax

343	*Polycauliona impolita* (Arup) Arup, Frödén & Søchting	*Caloplaca impolita* Arup.	d	—	sax
344	*Polycauliona luteominia* var. *bolanderi* (Tuck.) Arup, Frödén & Søchting	*Caloplaca bolanderi* (Tuck.) H. Magn.	c, 17	generalist	sax
345	*Polycauliona luteominia* (Tuck.) Arup, Frödén & Søchting var. *luteominia*	*Caloplaca laeta* H. Magn.	c	generalist	sax
346	*Polycauliona verruculifera* (Vain.) Arup, Frödén & Søchting	*Caloplaca verruculifera* (Vain.) Zahlbr.	a	generalist	gen
347	*Polyozosia albescens* (Hoffm.) S.Y. Kondr., Lőkös & Farkas	*Lecanora albescens* (Hoffm.) Flörke	a	neutral to basic	sax
348	*Polyozosia dispersa* (Pers.) S.Y. Kondr., Lőkös & Farkas	*Lecanora dispersa* (Pers.) Röhl.	e, 16	generalist	gen
349	*Polyozosia hagenii* (Ach.) S.Y. Kondr., Lőkös & Farkas	*Lecanora hagenii* (Ach.) Ach.	b	neutral to basic	gen
350	*Porocyphus coccodes* (Flotow) Körb.	—	e	neutral	sax
351	*Porpidia albocaerulescens* (Wulfen) Hertel & Knoph	*Huilia albocoerulescens* (Wulf.) Hertel	1	acidic	sax
352	*Porpidia cinereoatra* (Ach.) Hertel & Knoph	—	b	neutral	sax
353	*Porpidia crustulata* (Ach.) Hertel & Knoph	*Huilia crustulata* (Ach.) Hertel.	b, 1	acidic	sax
354	*Porpidia macrocarpa* (DC.) Hertel & A.J. Schwab	—	b	acidic	sax
355	*Porpidia subsimplex* (H. Magn.) Fryday	—	e	acidic	sax
356	*Porpidia tuberculosa* (Sm.) Hertel & Knoph	—	b	acidic to neutral	gen
357	*Protopannaria pezizoides* (Weber) P. M Jørg. & S. Ekman	*Pannaria pezizoides* (Weber) Trevis.	b	neutral	bry, terr
358	*Protoparmelia badia* (Hoffm.) Hafellner	—	9	acidic to neutral	sax

359	*Protoparmeliopsis garovaglii* (Körb.) Arup, Zhao Xin & Lumbsch	*Lecanora garovaglii* (Körb.) Zahlbr.	d	neutral	sax
360	*Protoparmeliopsis muralis* (Schreb.) M. Choisy	*Lecanora muralis* (Schreb.) Rabenh.	d, 1, 13,17	generalist	sax
361	*Protoparmeliopsis pinguis* (Tuck.) S. Y. Kondr.	*Lecanora pinguis* Tuck.	8	—	sax
362	*Psora globifera* (Ach.) A. Massal.	—	c	neutral	terr
363	*Psora icterica* (Mont.) Müll. Arg.	—	1, 12	—	terr
364	*Psora pacifica* Timdal	—	7, 13	—	terr
365	*Psoroma hypnorum* (Vahl) Gray	—	b	acidic	bry, terr
366	*Psorula rufonigra* (Tuck.) Gotth. Schneider	—	c, e, 1	neutral	lich
367	*Punctelia rudecta* (Ach.) Krog	*Parmelia rudecta* Ach.	1	—	—
368	*Punctelia stictica* (Delise ex Duby) Krog	—	14	acidic to neutral	sax
369	*Pycnothelia papillaria* (Ehrh.) Duf.	—	1	acidic	bry, terr
370	*Pyrenocarpon thelostomum* (Ach. ex J. Harriman) Coppins & Aptroot	—	e	—	—
371	*Pyrenopsis phaeococca* Tuck.	—	c	—	sax
372	*Ramalina farinacea* (L.) Ach.	—	a	neutral	cort
373	*Ramonia extensa* Lendemer, K. Knudsen & Coppins[5]	*Ramonia gyalectiformis* (Zahlbr.) Vězda	c, 15	—	sax
374	*Rhizocarpon bolanderi* (Tuck.) Herre	—	c, d	—	sax
375	*Rhizocarpon cinereovirens* (Müll. Arg.) Vain.	—	b	acidic	sax
376	*Rhizocarpon disporum* (Nägeli ex Hepp) Müll. Arg.	—	a, e	neutral	sax
377	*Rhizocarpon geminatum* Körb.	—	e	neutral	sax

378	*Rhizocarpon geographicum* (L.) DC.	—	b, c	acidic to neutral	sax
379	*Rhizocarpon grande* (Flörke ex Flotow) Arnold	—	c	acidic	sax
380	*Rhizocarpon hochstetteri* (Körb.) Vain.	—	b	acidic to neutral	sax
381	*Rhizocarpon reductum* Th. Fr.	—	e	acidic to neutral	sax
382	*Rhizocarpon superficiale* (Schaer.) Vain.	—	d	acidic	sax
383	*Rhizocarpon viridiatrum* (Wulfen) Körb.	—	c, d	neutral	sax
384	*Rhizoplaca chrysoleuca* (Sm.) Zopf	—	c	neutral	sax
385	*Rhizoplaca glaucophana* (Nyl. ex Hasse) W.A. Weber	—	d	—	sax
386	*Rhizoplaca melanophthalma* (DC.) Leuckert & Poelt	—	c, d	neutral	sax
387	*Rinodina confragosa* (Ach.) Körb.	—	d	acidic to neutral	sax
388	*Rinodina conradii* Körb.	—	b	neutral	gen
389	*Rinodina gennarii* Bagl.	—	a	neutral	sax
390	*Rinodina milvina* (Wahlenb.) Th. Fr.	—	d	neutral	sax
391	*Rinodina mniaroea* (Ach.) Körb.	—	b	—	bry, terr
392	*Rinodina mniaroeiza* (Nyl.) Arnold	—	b	—	—
393	*Rinodina rinodinoides* (Anzi) H. Mayerh. & Scheid.	—	17	acidic to neutral	sax
394	*Rinodina straussii* J. Steiner	—	d	basic	sax
395	*Rinodina tephraspis* (Tuck.) Herre	—	c	acidic	sax
396	*Rufoplaca oxfordensis* (Fink) Arup, Søchting & Frödén	*Caloplaca oxfordensis* Fink in Hedr.	1	—	sax
397	*Rusavskia elegans* (Link) S.Y. Kondr. & Kärnefelt	*Xanthoria elegans* (Link) Th. Fr.	b, e	basic	sax

398	*Rusavskia sorediata* (Vain.) S.Y. Kondr. & Kärnefelt	*Xanthoria sorediata* (Vain.) Poelt	b	neutral to basic	sax
399	*Scoliciosporum umbrinum* (Ach.) Arnold	—	b, e, 1	acidic to neutral	sax
400	*Scytinium californicum* (Tuck.) Otálora, P.M. Jørg. & Wedin	*Leptogium californicum* Tuck.	c, d	generalist	sax
401	*Scytinium lichenoides* (L.) Otálora, P.M. Jørg. & Wedin	*Leptogium lichenoides* (L.) Zahlbr.	d	neutral to basic	gen
402	*Scytinium palmatum* (Hudson) Gray	*Leptogium corniculatum* (Hoffm.) Minks [=*Leptogium palmatum* (Huds.) Mont.]	a, c	neutral	sax, terr
403	*Scytinium plicatile* (Ach.) Otálora, P.M. Jørg. & Wedin	*Leptogium plicatile* (Ach.) Leight.	a	neutral to basic	sax
404	*Scytinium rivale* (Tuck.) Otálora, P.M. Jørg. & Wedin	*Leptogium rivale* Tuck.	a	—	sax
405	*Scytinium subtile* (Schrad.) Otálora, P.M. Jørg. & Wedin	*Leptogium minutissimum* (Flörke) Th. Fr.	a	—	terr
406	*Scytinium tenuissimum* (Dickson) Otálora, P.M. Jørg. & Wedin	*Leptogium tenuissimum* (Dickson) Th. Fr.	a, d	neutral	cort, terr
407	*Solenopsora crenata* (Herre) Zahlbr.	—	9	—	sax, terr
408	*Sphaerophorus globosus* (Hudson) Vain.	—	b	acidic	bry, terr
409	*Spilonema revertens* Nyl.	—	a, e	—	sax
410	*Squamulea squamosa* (B. de Lesd.) Arup, Søchting & Frödén	*Caloplaca squamosa* (B. de Lesd.) Zahlbr.	c	generalist	sax
411	*Squamulea subsoluta* (Nyl.) Arup, Søchting & Frödén	*Caloplaca subsoluta* (Nyl.) Zahlbr.	d	generalist	sax
412	*Staurothele areolata* (Ach.) Lettau	—	d	neutral to basic	sax
413	*Staurothele elenkinii* Oxner	—	d	—	sax
414	*Staurothele rufa* (A. Massal.) Zschacke	—	a	neutral to basic	sax

415	*Stereocaulon alpinum* Laurer ex Funck	—	b	acidic	terr
416	*Stereocaulon glareosum* (Savicz) H. Magn.	—	b	acidic	terr
417	*Stereocaulon glaucescens* Tuck.	—	b, e	—	terr
418	*Stereocaulon incrustatum* Flörke	—	b	acidic	terr
419	*Stereocaulon paschale* (L.) Hoffm.	—	b	—	terr
420	*Stereocaulon saxatile* H. Magn.	—	1	—	sax
421	*Stereocaulon subcoralloides* (Nyl.) Nyl.	—	b	—	sax
422	*Stereocaulon tomentosum* Fr.	—	b, 1	acidic	sax
423	*Stigmidium marinum* (Deakin) Swinscow	—	a	—	lich
424	*Stigmidium squamariae* (B. de Lesd.) Cl. Roux & Triebel	—	d	—	lich
425	*Tephromela atra* (Hudson) Hafellner	—	b, c	neutral	sax
426	*Tetramelas papillatus* (Sommerf.) Kalb	*Buellia papillata* (Sommerf.) Tuck.	b	neutral to basic	bry, terr
427	*Thalloidima ioen* (Herre) S. Ekman & Timdal	*Toninia submexicana* de Lesdain	2, 4	—	sax, terr
428	*Thamnolia subuliformis* (Ehrh.) W.L. Culb.	—	b	—	terr
429	*Thelidium* sp.	—	c	—	sax
430	*Thelomma mammosum* (Hepp.) A. Massal.	—	13, 14	—	sax
431	*Tingiopsidium sonomense* (Tuck.) Hafellner & T. Sprib.	*Koerberia sonomensis* (Tuck.) Henssen	d	neutral	sax
432	*Toninia squalida* (Ach.) A. Massal.		c	neutral	sax, terr
433	*Toniniopsis aromatica* (Sm.) Kistenich et al.	*Toninia aromatica* (Turner) A. Massal.	c	—	sax, terr

434	*Trapelia involuta* (Taylor) Hert.	—	1	acidic to neutral	sax
435	*Trapelia* sp.	—	1	—	—
436	*Trapeliopsis granulosa* (Hoffm.) Lumbsch	—	b, e	acidic	gen
437	*Tremolecia atrata* (Ach.) Hertel	—	b	acidic	sax
438	*Tuckermannopsis ciliaris* (Ach.) Gyelnik	*Cetraria ciliaris* Ach.	1	—	gen
439	*Umbilicaria lambii* Imshaug	—	10	—	sax
440	*Umbilicaria phaea* Tuck.	—	c, d, 14	acidic to neutral	sax
441	*Umbilicaria polaris* (Schol.) Zahlbr.	*Umbilicaria krascheninnikovii* (Savicz) Zahlbr.	c	acidic to neutral	sax
442	*Umbilicaria rigida* (Hoffm.)	—	10	acidic	sax
443	*Usnea flavocardia* Räsänen	*Usnea wirthii* P. Clerc	14	acidic	cort, sax
444	*Vahliella leucophaea* (Vahl) P.M. Jørg.	*Pannaria leucophaea* (Vahl.) P. M. Jørg.	b, c	neutral	sax
445	*Verrucaria aethiobola* Wahlenb.	—	c	generalist	sax
446	*Verrucaria ceuthocarpa* Wahlenb.	—	a	acidic	sax
447	*Verrucaria degelii* R. Sant.	—	a	—	sax
448	*Verrucaria erichsenii* Zschacke	—	a	acidic	sax
449	*Verrucaria halizoa* Leighton	—	a	—	sax
450	*Verrucaria margacea* (Wahlenb.) Wahlenb.	—	c	neutral	sax
451	*Verrucaria muralis* Ach.	—	c	basic	sax
452	*Verrucaria nigrescens* Pers.	—	c, 1	neutral to basic	sax
453	*Verrucaria sandstedei* B. de Lesd.	—	a	—	—
454	*Verrucaria sphaerospora* Anzi	—	d	neutral to basic	sax
455	*Verrucaria viridula* (Schrad.) Ach.	—	c, 1	neutral to basic	sax

456	*Verrucaria* sp. 9	—	a	—	—
457	*Verrucaria* sp. 10	—	a	—	—
458	*Vulpicida juniperina* (L.) J.-E. Mattsson & M.J. Lai	*Cetraria tilesii* Ach.	b	basic	bry, terr
459	*Wahlenbergiella mucosa* (Wahlenb.) Gueidan & Thüs	*Verrucaria mucosa* Wahlenb.	a	—	sax
460	*Wahlenbergiella striatula* (Wahlenb.) Gueidan & Thüs	*Verrucaria striatula* Wahlenb. *ex* Ach.	a	—	sax
461	*Xanthocarpia crenulatella* (Nyl.) Frödén, Arup & Søchting	*Caloplaca crenulatella* (Nyl.) H. Olivier	d	basic	sax
462	*Xanthomendoza fallax* (Hepp ex Arnold) Søchting, Kärnefelt & S.Y. Kondr.	—	d	neutral	cort
463	*Xanthoparmelia conspersa* (Ach.) Hale	—	1	acidic to neutral	sax
464	*Xanthoparmelia cumberlandia* (Gyelnik) Hale	—	c, e, 1	acidic to neutral	sax, terr
465	*Xanthoparmelia hypomelaena* (Hale) Hale	—	1	acidic to neutral	sax
466	*Xanthoparmelia loxodes* (Nyl.) O. Blanco et al.	—	d	generalist	sax
467	*Xanthoparmelia mexicana* (Gyelnik) Hale	—	d, 14	acidic to neutral	sax, terr
468	*Xanthoparmelia plittii* (Gyelnik) Hale	—	e, 1	acidic to neutral	sax
469	*Xanthoparmelia schmidtii* Hale	—	3	—	sax
470	*Xanthoparmelia verruculifera* (Nyl.) O. Blanco et al.	*Neofuscelia verruculifera* (Nyl.) Essl.	d, 14	generalist	sax
471	*Xanthoparmelia viriduloumbrina* (Gyelnik) Lendemer	—	e	—	—
472	*Xanthoparmelia* sp.	—	13	—	—

473	*Xanthoparmelia* sp. 1	*Xanthoparmelia taractica* (Kremplh.) Hale[6]	1	—	sax, terr
474	*Xanthoparmelia* sp. 2	*Xanthoparmelia tasmanica* (Hook. F. & Taylor) Hale[7]	1	—	—
475	*Xanthoria parietina* (L.) Th. Fr.	—	e	generalist	gen
476	*Xanthoria* sp.	—	c	—	—

[1] Sirois et al. (1988) report *Biatora vernalis* but this is more likely *Biatora subduplex*, a species that was typically lumped with *B. vernalis* at the time of publication of the study - see Printzen and Tønsberg (1999).

[2] This includes report of *Lepraria incana* from Sirois et al. (1988). *L. incana* was previously used for several species now recognized as distinct taxa.

[3] *Peltigera aphthosa* and *P. canina* were names previously used for several species that are now recognized as distinct taxa.

[4] *Physconia distorta* is now known not to occur in North America.

[5] The two study citations (Lendemer et al. 2009; Sigal 1989) are likely based on the same specimen and represent a single taxon.

The collection of *Ramonia gyalectiformis* from Complexion Springs mentioned in Sigal (1989) is presumed to be the same as the type specimen for the later described *R. extensa.*

[6] Specimens identified as *Xanthoparmelia taractica* from eastern North America are considered likely to be misidentifications of *X. viriduloumbrina* (Esslinger 2019).

[7] Records of *X. tasmanica* in North America are likely *X. hypofusca* (Esslinger 2019).

Substrate affinity

Of the 437 taxa identified to species recorded on ultramafic substrates in North America, 126 (29%) were not assigned a pH affinity category due to insufficient information in the literature. Roughly half (224; 51%) were designated a pH affinity category of Acidic, Acidic to neutral, or Neutral, and the remaining taxa (87; 20%) had a pH affinity of Generalist, Basic, or Neutral to basic (Table 4).

The largest proportion of lichen taxa recorded are saxicolous (186; 43%), with terricolous taxa (61; 14%) next most frequent, and only three bryicolous taxa (<1%). Forty-one lichens were classified as either saxicolous and terricolous (13; 3%) or terricolous and bryicolous (28; 6%). Forty-six (11%) predominantly epiphytic (i.e., corticolous and/or lignicolous [growing on exposed wood]) taxa were identified, as well as twelve (3%) lichenicolous taxa and 36 (8%) substrate generalists. Thirty-one taxa were not assigned a substrate type.

Table 4. North American ultramafic lichens categorized by substrate pH affinity. Thirty-nine taxa not identified to the species level are not included.

pH affinity category	Number of taxa	Percentage of total
Acidic	85	19.5%
Acidic to Neutral	70	16%
Neutral	69	16%
Neutral to Basic	40	9%
Basic	15	3.5%
Generalist	32	7%
N/A (unknown)	126	29%
Total:	**437**	**100%**

Species distributions

Of the 437 taxa identified to species, 52 are apparently restricted to North America (Table 5), with the remaining taxa more widely distributed. The nine species recorded in three or more of the five published studies focusing on lichens of ultramafic substrates are globally widespread, with most being cosmopolitan or nearly so (Table 6).

Table 5. **Lichen taxa apparently restricted to North America from lichens recorded on ultramafic substrates in North America in the published literature.** For key to studies, see Table 3.

Species Name	Studies found	Distribution within North America
Aspicilia confusa	d	Primarily southern and central parts of California
Aspicilia cuprea	d	Primarily southern and central parts of California
Aspicilia phaea	d	Southwestern United States, most records from southern and central California and the Great Basin (Nevada, Utah)
Aspicilia praecrenata	d	Primarily central and southern California: Los Angeles, San Luis Obispo, and San Benito counties, and the Channel Islands
Blennothallia fecunda	a	Coastlines of northwest Washington, British Columbia, and Alaska
Buellia lepidastra	e	Across United States
Buellia nashii	d	Primarily southwestern United States, Baja California, and mainland Mexico
Caloplaca albovariegata	d	Primarily western North America
Candelariella citrina	d	Western North America, northern Canada, Alaska, and Greenland
Cladonia apodocarpa[1]	1	Eastern North America
Cladonia atlantica	1	Eastern North America
Cladonia cristatella	e, 1	North America (primarily Eastern)
Cladonia cylindrica	1	North America (primarily Eastern)
Cladonia dimorphoclada	e, 1	Eastern North America
Cladonia mateocyatha	1	North America (primarily Eastern)
Cladonia petrophila	1	Eastern United States and Canada
Clavascidium lacinulatum var. *atrans*	11	Western and central North America, with disjunct eastern populations.

Dermatocarpon americanum	13	North America from Canada to Mexico, most records from southwestern United States and northern Mexico
Dimelaena thysanota	d, 17	Western North America from southern Canada to northern Mexico
Lecanora mellea	17	Western North America, primarily Canada
Lecanora placidensis	b	Northeastern United States
Lecanora sierrae	d	Western United States (mainly in the Sierra Nevada) and Baja California
Lecidea brunneofusca	b	Northeastern United States and southeastern Canada
Lecidea cyrtidia	1	North America (primarily Eastern)
Lepraria normandinoides	e	North America (primarily Eastern)
Leprocaulon textum	d	Central and southern California
Melanelixia glabroides	d	Western United States and Baja California, Mexico
Miriquidica scotopholis	c, 17	Western North America, primarily California and Baja California
Myelochroa obsessa	1	North America (primarily eastern)
Physcia americana[2]	1	Mainly eastern United States
Physcia millegrana	1	North America (primarily Eastern)
Physconia californica	d	Western North America, southern Oregon to Baja California
Placidium arboreum	1	United States (primarily eastern)
Polycauliona bolacina	13, 17	North America (primarily eastern)
Polycauliona ignea	d, 17	Northern California to southern Baja California
Polycauliona impolita	d	California, Baja California, and mainland Mexico (Sinaloa, Sonora, and Chihuahua provinces)
Polycauliona luteominia var. *bolanderi*	c, 17	Coastal, western North America south to northern Baja California
Polycauliona luteominia var. *luteominia*	c	Western North America (mainly coastal) and Caribbean islands
Porpidia subsimplex	e	Eastern North America
Protoparmeliopsis pinguis	8	Western North America from southern Canada to northern Mexico, primarily coastal
Psora pacifica	7, 13	Northern California to central Baja California, primarily coastal
Pyrenopsis phaeococca	c	North America, primarily northeastern United States and Great Lakes region

Ramonia extensa	c, 15	Known only from type locality: Complexion Springs, California on serpentine rock
Rhizoplaca glaucophana	d	California and Baja California
Rinodina straussii	d	Western North America, mainly western United States, but also Canada
Scytinium californicum	c, d	Mainly western North America from Alaska to Mexico
Scytinium rivale	a	Mainly western North America
Solenopsora crenata	9	Central and Southern California, coastal
Staurothele elenkinii	d	Mainly western North America
Stereocaulon glaucescens	b, e	Eastern North America
Umbilicaria lambii	10	Western North America, from Canada to California
Xanthoparmelia schmidtii	3	Southwestern United States

[1] *C. apodocarpa* has unverified records from Colombia.

[2] *P. americana* is included here although it has two records from the Hawaiian Islands, which are normally considered part of Oceania.

Table 6. Lichens recorded in 3+ studies of ultramafic lichens in North America. Key to studies: a = Ryan 1988a; b = Sirois et al. 1988; c = Sigal 1989; d = Rajakaruna et al. 2012; e = Medeiros et al. 2014

Species	**Studies found**	**pH affinity**	**Global distribution**
Candelariella aurella	a, d, e	Basic	Cosmopolitan
Candelariella vitellina	b, c, d, e	Acidic to neutral	Cosmopolitan
Cladonia pyxidata	b, c, e	Acidic to neutral	Cosmopolitan
Lecanora polytropa	b, c, e	Acidic to neutral	Cosmopolitan
Lecidea tessellata	b, c, d	Neutral	North America and Europe
Lecidella carpathica	b, c, d	Generalist	Widespread, mainly temperate
Lecidella stigmatea	a, b, c, d, e	Neutral	Widespread, mainly temperate
Parmelia saxatilis	a, b, e	Acidic	Widespread, mainly temperate and southern boreal regions
Physcia caesia	a, b, e	Neutral to basic	Widely distributed; arctic, boreal, and temperate zones

Discussion

Substrate affinities of ultramafic lichens of North America

This review of the literature on lichens of ultramafic substrates shows a high proportion of highly to somewhat acidophytic taxa, with a much smaller proportion of basiphytic taxa (Table 4). Taxa with a neutral pH affinity, as well as generalists tolerant of a wide range of pH levels, were also well-represented. This is somewhat consistent with the mix of acidophytic and basiphytic taxa that have often been observed on ultramafic substrates worldwide (Favero-Longo et al. 2004). It is important to note that basiphytic and acidophytic taxa co-occurred within the same sites for each of the five ultramafic lichen studies reviewed. In other words, the occurrence of a small number of weakly to strongly basiphytic taxa was a consistent feature of the sites surveyed in the reviewed studies, and not a result of a small number of sites with a highly basiphytic component. The pattern of consistent co-occurrence is better explained by the observation that basiphytic species are often found on the undersides of overhanging rock surfaces of ultramafic outcrops, rather than exposed surfaces where acidophytic species tend to predominate. This observed pattern could possibly be a result of accumulated nutrients, including bases, as well as higher calcium concentrations, in these sheltered microhabitats (Miller et al. 2005).

Species richness and diversity in ultramafic lichen assemblages

Measurements of species richness and diversity on ultramafic substrates in North America do not reveal any clear pattern of high or low diversity relative to non-ultramafic substrates. In the three studies comparing ultramafic and non-ultramafic lichen assemblages, two (Sirois et al. 1988; Rajakaruna et al. 2012) found a higher number of taxa on ultramafic substrates. However, in both studies, the authors noted potential confounding factors. In one study, much of the area of the non-ultramafic sites had been disturbed within the last 62 years, and thus harbored relatively young lichen communities compared to the undisturbed ultramafic sites (Rajakaruna et al. 2012). In the second study, the higher total number of taxa found on serpentinized peridotite - 157 taxa compared to 121 on mafic amphibolite - could be partly a result of the fact that among the 145 study plots, only 15 sampled amphibolite (Sirois et al. 1988). The third comparative study reported similar numbers of taxa between Pine Hill, Little Deer Isle, Maine, an ultramafic serpentinized peridotite site (82 taxa), and the nearby volcanic-origin, metal enriched rocks of Callahan Mine (84 taxa; Medeiros et al. 2014). However, comparison of species richness and diversity between sites was not an express objective of this study; the sampling area and survey effort were different between sites, and surveys were carried out by different workers (Harris et al. 2007; Medeiros et al. 2014), making comparisons of species richness between ultramafic and non-ultramafic substrates uninformative.

Globally, published accounts of lichens of ultramafic substrates have come to different conclusions regarding species diversity of ultramafic substrates in comparison to other rock types. In their review of lichens of metal-enriched environments, Purvis and Halls (1996) state that ultramafic substrates tend to have relatively low lichen species richness compared to other rock types. However, other studies present evidence of ultramafic substrates having comparable, or even higher species richness than adjacent rock types (Favero-Longo and Piervittori 2009; Paukov 2009). Thus, there does not appear to be broad agreement on the species diversity of ultramafic substrates compared to non-ultramafic substrates, which is also noted by Favero-Longo et al. (2004, 2018).

Composition of ultramafic lichen assemblages

Comparisons of lichen assemblages from the five studies reviewed here show a remarkably low overlap in species composition among ultramafic study areas (Table 3). This is at least partly attributable to the large differences in abiotic conditions present at the different geographic regions covered by the studies (Table 1; Figure 1). As one example, the New Idria serpentinite mass (California) sampled by Rajakaruna et al. (2012) and Little Deer Isle (Maine; Harris et al. 2007) differ in many respects, including mean annual temperature, elevation, precipitation, coastal proximity, and latitude. Thus, it is unsurprising that the two surveys found only five lichen species common to both study areas, which is 3% of the total number of taxa (165) inventoried from ultramafic substrates across both studies. Perhaps more interestingly, comparisons of lichen species inventories on ultramafic substrates within similar regions also reveal large differences in lichen species assemblages at regional and local scales. Rajakaruna et al. (2012) found substantial heterogeneity in lichen species composition (recorded as presence-only data) between five ultramafic sites in the New Idria serpentinite mass in San Benito County, CA. Fifty-four of the 79 species (68%) found on ultramafic substrates were recorded at only one of the five sampled sites, which all occur within a 5 km radius. In a study of the serpentine lichen biota of the northern and central California coast ranges, Sigal (1989) conducted inventories of five ultramafic outcrops distributed along a latitudinal gradient (Figure 1). The study recorded 76 species across the five sites but only two, *Candelariella vitellina* (Hoffm.) Müll. Arg. and *Circinaria caesiocinerea* (Nyl. ex Malbr.) A. Nordin et al., were found at every site. Three additional species were found at four of the five sites - *Acarospora fuscata* (Schrad.) Arnold, *Lecanora polytropa* (Ehrh.)

Rabenh., and *Leptochidium albociliatum* (Desm.) M. Choisy - and ten species were found at three of five sites: *Buellia badia* (Fr.) A. Massal., *Candelaria concolor* (Dickson) Stein, *Catillaria lenticularis* (Ach.) Th. Fr., *Cladonia coniocraea* (Flörke) Sprengel, *Dermatocarpon miniatum* (L.) W. Mann, *Lecidella carpathica* Körb., *Leptogium cyanescens* (Rabenh.) Körb., *Psorula rufonigra* (Tuck.) Gotth. Schneider,[1] *Vahliella leucophaea* (Vahl) P.M. Jørg., and *Xanthoparmelia cumberlandia* (Gyelnik) Hale. These species are mostly widespread, all occurring on multiple continents (CNALH 2022), and they vary in their pH affinity from acidophytic to basiphytic, with one species, *Lecidella carpathica*, a substrate pH generalist. Thirty-nine of the 76 species (51%) were observed at only one locality, and the remaining 22 were found at two localities (29%).

The observed pattern of high species turnover at varying spatial scales in ultramafic lichen communities in North America agrees with findings of low compositional similarity at the global scale (Favero-Longo et al. 2004). An azonal distribution of lichen species, where ultramafic lichen assemblage composition is similar across latitudinal, climatic, and other abiotic gradients, would suggest a strong, overriding effect of substrate on lichen assemblage composition, and this is not demonstrated in studies of ultramafic lichen assemblages in North America or elsewhere.

The patterns of species composition observed in ultramafic lichen assemblages appear, at first, relatively unremarkable, especially in comparison to ultramafic vascular plant assemblages (Kruckeberg 2002; Galey et al. 2017). However, it is important to note that, to date, large-scale, lithology-specific reviews of lichen biotas have only been

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[1] *Psorula rufonigra* is an obligate parasite on the lichen *Spilonema revertens* Nyl. We suspect that *S. revertens* was present in the study sites but was overlooked due to its small stature and similar appearance to free living cyanobacteria species.

conducted for lichens of ultramafic substrates (Favero-Longo et al. 2004; Favero-Longo et al. 2018), with no analogous studies of other rock types. This makes it difficult to put reviews of ultramafic lichen biotas into a broader context (Favero-Longo et al. 2018). Furthermore, comparative lichen floristic surveys of ultramafic and non-ultramafic at regional and local scales are uncommon (e.g., Favero-Longo and Piervittori 2009; Paukov and Trapeznikova 2005), and typically utilize species inventory methods as opposed to quantitative sampling methods, making identification of characteristic or dominant species difficult. However, the comparative studies that have been conducted, including three North American studies reviewed here (Sirois et al. 1988; Rajakaruna et al. 2012; Medeiros et al. 2014), reveal substantial differentiation between ultramafic and nearby non-ultramafic lichen biotas. Sirois et al. (1988) reported markedly different lichen assemblages on amphibolite, a mafic rock, and ultramafic partially serpentinized peridotite, which occur adjacent to each other on Mt. Albert, Québec. Rajakaruna et al. (2012) found statistically significant differences in lichen assemblages of ultramafic, silica-carbonate, and sedimentary shale and sandstone. Medeiros et al. (2014) also reported differences between inventories from nearby ultramafic and non-ultramafic areas. The differentiation across studies between ultramafic and non-ultramafic substrates suggests a substrate effect, though more research is clearly needed.

Ultramafic affinity, distributions, and disjunct populations

There is some direct and indirect evidence that ultramafic rocks and soils are important habitats for certain lichen taxa. These include taxa that appear to have some level of affinity for ultramafic substrates, as well as taxa with disjunct populations found on ultramafic substrates. Due to their inhospitability to vascular plants, the microclimates and microhabitats on ultramafic rocks and soils are often dramatically different from nearby habitats of non-ultramafic substrates (Brady et al. 2005; Cacho and Strauss 2014). This may lead to regionally unique microhabitats that support rare or endemic taxa, and/or disjunct populations restricted to these microhabitats. Lendemer (2008) describes eastern disjunct populations of *Psora icterica* (Mont.) Müll. Arg. in serpentine barrens in Maryland and Pennsylvania. *Psora icterica* was subsequently found in similarly open granite flat rock microhabitats in the Piedmont Plateau in Alabama (Hansen and Goertzen 2012). The authors suggested that the relatively open, arid microhabitats offered by serpentine barrens and granite flat rock environments shape the disjunct distribution of *P. icterica*, which was previously considered restricted to arid regions of western and central North America. *Clavascidium lacinulatum* var. *atrans* (Breuss) M. Prieto has a similar disjunct distribution to *P. icterica* and has been recorded co-occuring with the species on serpentine barrens in Maryland (Lendemer 2004). In the western United States, *Solenopsora crenata* (Herre) Zahlbr., a somewhat rare lichen apparently endemic to coastal California, has been characterized as fairly common on shaded serpentine in the northern San Francisco Bay Area (Robertson and Robertson 2001). *Solenopsora crenata* is described as occurring in coastal, open habitats in central and southern California and the Channel Islands (Ryan and Timdal 2002). As open coastal habitats become less common along the increasingly mesic central and northern coast of California, it seems plausible that ultramafic outcrops provide pockets of habitat for this species where it would otherwise not occur. These examples suggest that ultramafic habitats, which are often relatively open and arid due to a paucity of vascular plant cover, may serve as important refugia for various lichen taxa that would otherwise be locally or regionally absent. Other lichen species may have an affinity for the properties of ultramafic substrates themselves. One such species is *Fuscopannaria thiersii* P.M. Jørg., which is described as occurring on moist rock surfaces that are often iron-rich and is considered possibly a specialist of heavy metal-rich or ultrabasic (i.e., serpentinite) rocks (Jørgensen 2000). Lastly, *Ramonia extensa* Lendemer, K. Knudsen & Coppins may be a specialist on ultramafic substrates, though classifying it as such at this time is untenable since currently it is only known from its type locality in Lake County, California (Lendemer et al. 2009). We suggest that there are likely numerous examples of lichen taxa with significant degrees of affinity for ultramafic substrates in North America. Furthermore, although there is scant evidence of ultramafic endemism for lichens in North America or elsewhere, endemism of infraspecific taxa and distinct genotypes, as well as ultramafic habitats shaping regional and local species distributions, are possibilities that remain largely unexplored.

Future Research Directions

This review highlights the meaningful work done characterizing taxonomic diversity of lichens of ultramafic rocks and soils in North America, providing further evidence for trends identified by earlier global accounts (Favero-Longo et al. 2004, 2018), while adding an increased focus on the North American continent. However, this review also reveals gaps in the knowledge of lichens on ultramafic substrates in North America, including gaps in survey coverage. Lichen biotas of large areas of ultramafic rocks and soils remain relatively unknown with no published data. These areas include orogenic ultramafics in boreal parts of Alaska and Newfoundland, as well as British Columbia, Washington, Oregon, and Baja California. Additionally, more localized areas of intracratonic (i.e., within the stable interior portion of the continent) ultramafic rocks occur in the central United States, and accounts of the lichen biotas of these are absent from the published literature. These include ultramafics of the Stillwater Complex in Montana, as well as other intracratonic complexes in Wyoming and Minnesota (Figure 1; Krevor et al. 2009). While published data for these areas appear to be scant to nonexistent, it is important to note that much untapped data is available from herbarium collections. Review of herbarium records was beyond the scope of this review but would provide a valuable avenue of research for future studies of lichens of ultramafic substrates.

In addition to filling geographical gaps in ultramafic lichen community data, there is a lack of quantitative data for lichens of ultramafic substrates, which significantly limits the ability to 1) accurately characterize ultramafic lichen communities; 2) explore similarities and differences between ultramafic lichen communities and 3) understand the effects of biotic and abiotic variation on these communities. The use of taxonomic inventory methods is informative and has the advantages of being more straightforward and less time consuming. However, inventories have significant limitations in the types of statistical analyses that can be used to make confident conclusions about taxonomic composition and relationships between composition and environmental factors. Sirois et al. (1988) recorded lichen species in relevé plots using Braun-Blanquet cover classes. This quantitative approach allowed them to draw conclusions about differences in taxonomic diversity (measured via the Shannon Index) and make robust conclusions about the dominant species present on ultramafic and amphibolite substrates. Ryan (1988*b*) recorded percent cover of each lichen species in quadrats placed along elevational transects on a rocky seashore. This approach allowed the author to demonstrate changes in percent cover and frequency in different intertidal zones and show how the dominant lichen species change along the elevational gradient in response to factors such as salt spray and manuring. Another important approach to characterizing diversity is the use of genetic studies, which may have the potential to uncover distinct genotypes of mycobionts and photobionts (Nadyeina et al. 2014; Jüriado et al. 2019; Ruprecht et al. 2020) occurring on ultramafic substrates.

Future studies would benefit from collection of substrate data, particularly elemental composition, but also mineralogy, hardness, and surface texture. Ultramafic rocks may vary significantly in concentrations of several elements (Coleman and Jove 1992), which are likely of significance for lichens (e.g., calcium). However, the only North American study that has collected elemental composition data is Rajakaruna et al. (2012). They reported differences in the elemental composition of rocks at different ultramafic and non-ultramafic lichen sampling sites and related this to the lichen inventories recorded from each site. Their study found a significant effect of rock elemental makeup on lichen assemblage composition and identified lichen species that were useful in distinguishing ultramafic from non-ultramafic rocks. However, the specific interactions between elemental composition and lichen composition were not explored, and the effects of particular elemental concentrations, bioavailability, pH, or other abiotic factors related to elemental composition remain unclear.

Conclusions

- Lichen assemblages of ultramafic rocks and soils in North America vary widely in composition but are generally characterized by acidophytic taxa and/or taxa with wide pH tolerance, with the consistent co-occurrence of a small number of basiphytic taxa. Ultramafic lichen assemblages show high species turnover at varying local, regional, and continental scales, suggesting that factors unrelated to the distinctive substrate properties of ultramafic rocks, and/or variation in the substrate properties of ultramafic rocks and soils, have larger effects on lichen assembly.

- Ultramafic substrates may harbor unique lichen biotas at regional scales within the North American continent. However, a lack of focused study on biotas of adjacent non-ultramafic lithologies limits the ability to compare lichen biotas between substrates and identify substrates and/or areas worthy of consideration for conservation.
- The microhabitat characteristics of ultramafic rocks and soils are likely an important factor for lichens of these substrates. The relative openness and aridity of such areas likely results in the disjunct populations of lichens found in eastern North America and elsewhere.
- Although lichens of ultramafic rocks and soils have received more study in North America than other lithologies, many aspects of ultramafic lichen biotas remain unexplored, and the lichen diversity of large regions of ultramafic rocks and soils remain poorly known. The state of knowledge of lichens of ultramafic habitats would benefit from future focused study of under-sampled areas as well as an increased focus on quantitative studies relating lichen community data to substrate, microhabitat, and climatic variation.

Chapter 2: The role of rock: a quantitative comparison of lichen communities of ultramafic versus sandstone outcrops across a coastal-to-inland gradient

Introduction

Saxicolous (i.e., rock-dwelling) lichen assemblages are understudied, yet are important contributors to biodiversity and ecosystem functioning at scales ranging from local to global. As a group, lichens growing on rocks often form highly diverse communities. Substrate-specific studies report very high taxonomic richness over small areas (e.g., John 1989, quartzite sandstone), regions (Rutherford and Rebertus 2022, granite), as well as on continental and global scales (Favero-Longo et al. 2018; Mulroy et al. 2022). Although we are not aware of a published global estimate of the number of saxicolous lichen taxa, the number is certainly several thousands of taxa. Uncertainty about the number of saxicolous lichens is likely due to the challenge of collecting crustose lichens, which are generally the dominant saxicolous growth form, from rocks. In addition to their contribution to biodiversity, saxicolous lichens contribute to soil formation and nutrient cycling through their interactions with rock substrates (Brodo 1973). They are among the first colonizers of newly exposed rock surfaces and may play important roles in primary succession (Garibotti et al. 2011), in part through the ability of photobionts to fix carbon, and, in the case of lichens containing cyanobacteria, nitrogen. Though saxicolous lichens are less well-known for their interactions with other organisms than terricolous (i.e., soil-dwelling) and epiphytic lichens, they do have documented relationships with higher plants, (e.g., coastal *Dudleya* species and *Niebla* lichens [Riefner et al. 2003], and maritime Antarctic plant communities and *Usnea antarctica* [Bokhorst et al. 2016]). Despite their ecological relevance, relatively little is known about the biotic and abiotic factors that determine lichen community assembly on rocks, especially compared with more well-studied epiphytic and terricolous lichen communities.

It is common knowledge among lichenologists that different types of rocks host distinctive assemblages of lichens. The most noticeable differences are between 1) high-calcium rocks, such as limestone, which support distinctive assemblages of so-called calcicolous (or calciphilous) lichens, and 2) siliceous rocks, such as granite, which support very different assemblages of silicicolous lichen taxa (Brodo 1973). Other distinctive lichen communities appear on nutrient-enriched areas of rock, such as below bird perches and areas with high atmospheric nitrogen pollution (Brodo 1973), or rocks with high heavy metal content (Purvis and Halls 1996). The effects of specific rock properties on lichen assemblages have also received attention. Rock elemental composition (Purvis and Halls 1996; Rajakaruna et al. 2012) and water retention capacity (Garty and Galun 1974) have both been shown to influence lichen assemblage composition. Rock surface texture is also thought to play an important role (Brodo 1973) but is difficult to quantify. Rock elemental composition plays a fundamental role in determining the rock surface pH environment, and pH is thought to play a paramount role in determining lichen community assembly (Gilbert and James 1987). Some lichens have been associated with specific elements, including metals such as iron (Purvis and Halls 1996; Lendemer and Tripp 2015). The degree of rock weathering also appears to be important to lichens, and has been experimentally shown to affect a variety of rock properties important to lichens. Marques et al. (2015) demonstrated significant differences in weathered vs. unweathered schist for porosity, pH, and elemental composition, and showed that weathered schist is more bioreceptive (i.e., susceptible to colonization) by free-living cyanobacteria. Woolhouse et al. (1985) observed community differences on a gneiss rock face with surfaces of different ages, and they described a pattern of succession to account for these differences.

A handful of studies have been undertaken to quantify or describe differences in lichen communities between different rock substrates (Pentecost 1980; Sirois et al. 1988; Favero-Longo and Piervittori 2009; Paukov 2009; Rajakaruna et al. 2012; Aho et al. 2014). Although methodologies were highly variable, these studies all reported distinct lichen communities occurring on different rock types. Ultramafic lichen communities have received more attention than lichen communities on other substrates, but studies of ultramafic lichens are nonetheless uncommon and typically utilize inventory methods (e.g., Rajakaruna et al. 2012; Sigal 1988). Reviews on lichens of ultramafic substrates suggest that ultramafic lichen biotas are relatively unremarkable (Favero-Longo et al. 2004, 2018; Mulroy et al. 2022), especially when compared with the specialized vascular plants of ultramafics. Some notable characteristics of ultramafic communities include the consistent mix of co-occurring acidophytic (low pH preferring) and basiphytic (high pH preferring) taxa, and the occurrence of disjunct populations of taxa known from more arid environments. In studies of lichen communities of ultramafic and other rock types, it often remains unclear which substrate properties are most responsible for the observed community differences because rock substrates can vary in many ways that may be of significance to lichens. Most ecological studies of saxicolous lichens measure only a few environmental variables, and recording the elemental composition of rock substrates is rare (but see Rajakaruna et al. 2012).

The effects of environmental gradients on saxicolous lichen communities have received more attention than substrate effects. Studies have found changes in species composition along altitudinal gradients (e.g., Pintado et al. 2001; Favero-Longo and Piervittori 2009), including changes in lichen photobionts (Medeiros et al. 2021). Changes in functional diversity and species richness of saxicolous and terricolous macrolichens have been noted across a subarctic to arctic latitudinal gradient (Chagnon et al. 2021). Water availability also has large effects on saxicolous lichen communities. Giordani et al. (2013) showed that different functional guilds of saxicolous lichens respond in different ways to water runoff potential, and Aho et al. (2014) found changes in cliff face lichen composition along a localized aridity gradient. The effects of microhabitat characteristics, such as rock slope and aspect (John and Dale 1990; Paz-Bermudez et al. 2021) and solar irradiation (Bjelland 2003) have also been demonstrated to affect species composition. Individual species often respond to changes in microtopography such as rock convexity or concavity (Rutherford and Rebertus 2022). Changes in species composition and diversity across temporal gradients, where communities were compared on rock surfaces of different ages, have also been demonstrated for saxicolous lichens (Woolhouse et al. 1985; Pastore et al. 2014). As many of these studies note, environmental gradients, microhabitat, and mesohabitat variables that are measured are often highly interrelated, making it difficult to determine the precise mechanisms of lichen community assembly.

Maritime influence, a collective suite of conditions encompassing temperature regimes, precipitation, aerial salt deposition, among other abiotic factors, is associated with specialized lichen biotas that include saxicolous communities along the immediate shoreline and the intertidal zone (Fletcher 1973a,b), and lichens associated with coastal fog belts (Rundel 1978; Schieferstein and Loris 1992). Maritime influence gradient effects on saxicolous lichen communities have been shown to impact lichen communities at small scales along the immediate shoreline (Fletcher 1973b; Ryan 1988; Bjelland 2003). Quantitative studies of community changes across larger, regional-scale maritime gradients have been done for epiphytic lichen communities (e.g., Root et al. 2014) but are absent from the literature for saxicolous lichens. Notably, however, Rutherford and Rebertus (2022) found significant community differentiation between lakeshore and interior sites along Lake Superior, which is associated with environmental gradients similar to those associated with maritime influence.

The numerous environmental factors that can influence lichen communities often interact with one another in significant ways. One type of interaction that can occur is a dampening, or moderating, effect of one factor on another. This type of effect has been noted to occur in saxicolous lichens. In one study of saxicolous communities of north and south aspects of peaks in the Argentinian Andes, the effect of aspect on saxicolous lichen composition was found to be reduced at higher altitudes (Costas et al. 2021). Analogously, Aho et al. (2014) found that nearby limestone and andesite cliff communities were more differentiated in arid parts of cliffs, and became more compositionally homogenous with increasing water availability.

In this study, we compared regional lichen assemblages of two rock types, ultramafic and sandstone, along a maritime influence gradient. The primary goal of this study was to understand the effects of substrate properties, climate (temperature, precipitation, cloud cover, fog), microhabitat characteristics (rock slope and aspect, distance to the ground surface, rock microtopography), and mesohabitat characteristics (elevation, topography) on saxicolous lichen community composition. This study tested three hypotheses. (1) Differences in substrate properties between ultramafic and sandstone outcrops lead to distinct lichen communities on these substrates (*Substrate Hypothesis*) resulting in significantly different taxonomic compositions on ultramafic and sandstone outcrops. (2) Lichen communities would vary spatially across the regional maritime gradient where we sampled (*Maritime Gradient Hypothesis*), and lichen taxonomic composition would therefore be significantly different between coastal and inland sites. (3) Maritime influence factors would moderate the effects of substrate differences on lichen assemblage composition (*Maritime Moderation Hypothesis*) causing more composistional similarity between ultramafic and sandstone lichen assemblages near the coast than assemblages further from the coast.

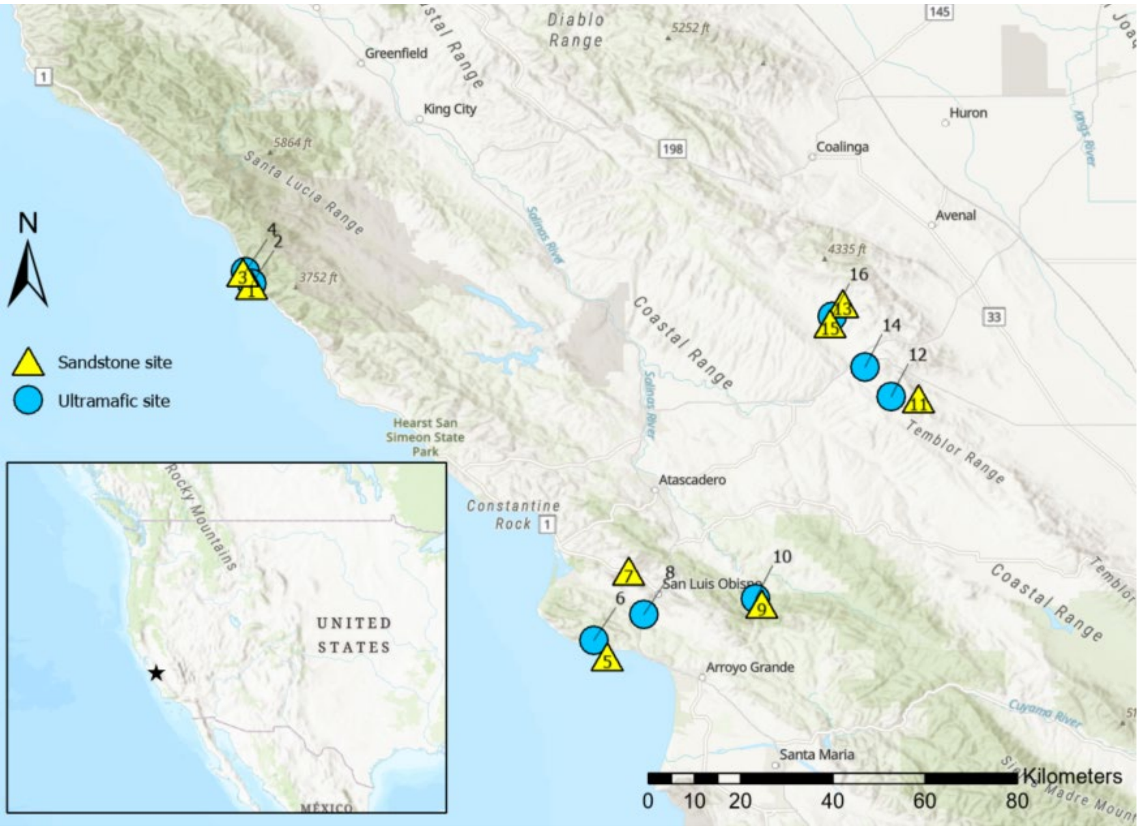

Figure 4. Map of lichen sampling sites. Numbers correspond to the following sites: 1: Willow Creek; 2: Willow Creek; 3: Jade Cove; 4: Jade Cove; 5: San Luis Hill; 6: Pecho Creek; 7: El Chorro; 8: Irish Hills; 9: Hi Mountain Road; 10: Rinconada; 11: James Parcel; 12: Still Parcel; 13: Serpent’s Back; 14: Parcel D; 15: Parcel B; 16: Parcel B

Table 7. Ultramafic and sandstone outcrop sampling sites.

	Study Site	Substrate	Distance to coast (km)	Elevation (m)	Location description and ownership/permitting authority	Vegetation	Study Site Coordinates	
1	Willow Creek	Sandstone	0.7	185	Outcrop along Los Burros Road, Los Padres National Forest, Monterey Ranger District.	Coastal scrub/chaparral.	35.890922, -121.454288	COASTAL
2	Willow Creek	Ultramafic	0.7	180	Outcrop along Los Burros Road, Los Padres National Forest, Monterey Ranger District.	Coastal scrub/serpentine grassland.	35.890896, -121.453720	
3	Jade Cove	Sandstone	0.1	40	Outcrops along coastal terrace near Jade Cove, Los Padres National Forest, Monterey Ranger District.	Coastal scrub/coastal prairie.	35.915923, -121.471301	
4	Jade Cove	Ultramafic	0.4	150	Outcrop along Plaskett Ridge Road, Los Padres National Forest, Monterey Ranger District.	Coastal scrub/chaparral and serpentine grassland.	35.913794, -121.466101	
5	San Luis Hill	Sandstone	0.5	195	Outcrops on San Luis Hill, Diablo Canyon Lands PG&E property.	Coastal scrub/grassland.	35.168239, -120.762267	
6	Pecho Creek	Ultramafic	1.8	150	Pecho Creek Canyon, Diablo Canyon Lands PG&E property.	Coastal scrub/chaparral.	35.196346, -120.787974	
7	El Chorro	Sandstone	13.7	232	Eagle Rock Trail, El Chorro Regional Park (San Luis Obispo County Parks).	Coastal scrub/grassland.	35.334910, -120.720379	INTERMEDIATE
8	Irish Hills	Ultramafic	8.2	101	Outcrop in Irish Hills Natural Reserve near Phyllis' Lookout, City of San Luis Obispo.	Coastal scrub/serpentine grassland.	35.246793, -120.690765	
9	Hi Mountain Road	Sandstone	22.1	782	Outcrop along Hi Mountain Road, Los Padres National Forest, Santa Lucia Ranger District.	Chaparral.	35.270776, -120.461254	
10	Rinconada	Ultramafic	21.7	735	Outcrop along Rinconada Trail, Los Padres National Forest, Santa Lucia Ranger District.	Chaparral.	35.277641, -120.473505	
11	James Parcel	Sandstone	71.2	494	Annette Road, Palo Prieto Conservation Bank, Kern Co.	Semi-arid annual grassland.	35.670399, -120.156352	IN

12	Still Parcel	Ultramafic	66.3	661	Annette Road, Palo Prieto Conservation Bank, San Luis Obispo Co.	Semi-arid annual grassland.	35.670775, -120.209593	
13	Serpent’s Back	Sandstone	70.6	497	Cholame Hills, California Flats Solar Project, Monterey Co. Semi-arid grassland.	Semi-arid annual grassland.	35.855402, -120.303888	
14	Parcel D	Ultramafic	65.5	420	Cholame Valley, Davis Road, Jack Ranch, San Luis Obispo County	Semi-arid annual grassland.	35.728148, -120.260432	
15	Parcel B	Sandstone	66.1	408	Cholame Hills, along Cottonwood Creek, Jack Ranch, Monterey Co.	Semi-arid annual grassland.	35.816563, -120.328580	
16	Parcel B	Ultramafic	67.3	414	Cholame Hills, along Cottonwood Creek, Jack Ranch, Monterey Co.	Semi-arid annual grassland.	35.826973, -120.324048	

Methods

Study Region

This study was conducted in western North America along the central coast of California, in the Central California Foothills and Coastal Mountains ecoregion (Griffith et al. 2016). The climate is Mediterranean, with cool, wet winters and warm, dry summers. Along the coast, summer fog is frequent and often extends into coastal valleys overnight (Western Regional Climate Center 2022). Common vegetation types include chaparral, coastal scrub, annual grassland, and oak woodland.

Sampling Locations

We sampled 16 rock outcrops across an approximately 70 km. coast-inland gradient of decreasing maritime influence in San Luis Obispo, Monterey, and Kern Counties (Figure 4; Table 7). Sites were selected as paired ultramafic and sandstone sites, with paired sites located as close together as possible. Distance between paired sites ranged from 0.05 km to 14.7 km. Six coastal sites – 3 ultramafic, 3 sandstone – were located between 0.1 and 1.8 km of the ocean. Four “intermediate” sites (2 ultramafic, 2 sandstone) were located between 8.1 and 22.1 km from the coast, with one site pair closer to the coast and lower elevation (Sites 7 and 8), and the other further inland and higher elevation (Sites 9 and 10). Six inland sites (3 ultramafic, 3 sandstone) were located between 65.5 and 71.2 km from the coast.

Site selection criteria

All sample sites were in areas where we could receive explicit permission to sample and collect lichen voucher specimens (Table 7). Within these areas, we chose rock outcrops with multiple aspects. To the extent possible, sites were centered around hilltops or ridgelines with moderate to high topographic exposure. All sites selected were under 1,000 m in elevation, were assessed to be relatively undisturbed by landslides, fires, or other recent disturbances, and had minimal canopy shading from trees or shrubs. For sandstone sites, we selected outcrops consisting of non-calcareous sandstone (i.e., sandstone with a non-calcareous cement). The presence of abundant calcium carbonate was assessed by testing samples of sandstone with dilute hydrochloric acid and checking for bubbling. Coastal sandstone sites targeted 10's of m-scale, lithic-rich sandstone blocks within Franciscan Complex mélange at Willow Creek and Jade Cove (Dibblee and Minch 2007), and a km-scale arkosic sandstone body at San Luis Hill that is also within the Franciscan Complex and mapped as the Point San Luis slab (Chapman et al. 2016). Intermediate distance sandstone sites targeted a km-scale, lithic-rich sandstone within the Franciscan Complex at El Chorro (Wiegers 2010) and outcrops of arkosic sandstone mapped as part of the Atascadero Formation (Dibblee and Minch 2004) at Hi Mountain Road. The inland sites targeted sandstone of the Temblor Formation at James Parcel (Dibblee and Minch 2005a), an unmapped sandstone layer within the Monterey Formation at Serpents Back (Dibblee and Minch 2005b), and an unnamed arkosic sandstone at Parcel B (Dibblee and Minch 2005b). All ultramafic sites across the study area targeted outcrops of partially serpentinized harzburgite consisting of relict olivine and orthopyroxene that 1) displayed similar degrees of weathering and serpentinization and 2) did not have abundant outcrop-scale smooth fault surfaces.

Sampling

At each sample site we randomly selected selected eight quadrat sampling locations. We used ArcGIS to create a set of numbered random points within the site boundaries. From each random point, we located the closest suitable rock face, alternating between north and south aspects of rocks, such that for each sampling site we had 4 north aspect quadrats and 4 south aspect quadrats. Criteria for a suitable rock for quadrat placement consisted of: 1) average rock slope between 30 and 90 degrees; 2) aspect for north-facing quadrats 0 ± 45 degrees, (between 315 and 45 degrees), and for south-facing quadrats 180 ± 45 degrees (between 135 and 225 degrees); 3) rock face sufficiently coherent to allow the quadrat to be placed on the rock so that an outline of the quadrat and quadrant lines could be drawn onto the rock face using chalk. For some sampled rock faces, there were multiple suitable sites for quadrat placement. In these cases, each suitable site was given a number and a random number generator was used to select the quadrat location.

At each quadrat, we first estimated the percent of bare rock, percent lichen cover, and percent non-lichen cover (bryophytes, vascular plants). Then a list of lichen morphospecies occurring within the quadrat was generated by close examination of the rock surface with 10x, 14x, and 20x loupes. Percent cover was estimated for each morphospecies using a modified version of Domin scale cover classes (10=91–100% cover; 9=76–90% cover; 8=51–75% cover; 7=34–50% cover; 6=26–33% cover; 5=11–25%; 4=4–10% cover; 3=<4% cover, many individuals; 2=<4% cover, several individuals; 1=<4% cover, few individuals; +=<4% cover, single individual.). For multivariate community composition analyses, lichen cover data was transformed by converting the "+" category to 1, 1 to 2, etc. so that the 11 cover classes ranged from 1 to 11. For all other analyses, cover classes were converted into percent cover midpoints.

Elemental composition of rock samples

Elemental analysis (X-ray fluorescence) was conducted on pooled samples of 1–2 rock fragments from 1–2 different rock samples from each site where lichens were collected. Pooling of fragments and samples was necessary because of the high cost of the procedure. Elemental concentrations for each sample pooled were determined for major (Al-Ti) and trace (As-Zr) elements. The analyses were carried out by the GeoAnalytical Laboratory, Washington State University, WA, USA, using an automated ThermoARL Advant'XP+ sequential X-ray fluorescence spectrometer. Rock samples were prepared for analysis by chipping, grinding to a very fine powder, weighing with di-lithium tetraborate flux (2:1 flux:rock), fusing at 1000 °C in a muffle oven, and cooling; the bead is then reground, refused and polished on diamond laps to provide a smooth flat analysis surface. The concentrations of 30 elements in the unknown samples were measured by comparing the X-ray intensity for each element with the intensity measured from standard samples, and two beads of pure vein quartz used as blanks for all elements except Si. Elemental concentrations for samples from each study site were obtained for 11 major elements and 19 trace elements. For one site, Jade Cove SS, we obtained XRF data for three different samples because there were observable differences in the sandstone substrate at different parts of the site. This site consists of scattered sandstone outcrops occurring on a coastal terrace within a <0.05 km^2 area.

Abiotic variable measurements

At each quadrat, we measured the average slope of the rock using a Suunto PM-5 handheld clinometer, and we measured the aspect using a Brunton Nexus 7DNL handheld compass. We assessed the microtopography of quadrat locations using the following variables: 1) microtopography of the rock surface (0=smooth, 1 = some cracks and ledges present, 2 = many cracks and ledges present); 2) undulation of the rock surface (i.e., heterogeneity of slopes and aspects of the rock surface at the quadrat location; 0=flat, 1 = moderate undulation, 2 = high undulation); 3) occurrences of overhanging rock surfaces within the quadrat area (recorded as either present or absent, overhang defined as any rock surface >90 slope and >1cm^2 surface area); and 4) distance of the quadrat location from the ground surface (<0.3 meters, 0.3-0.9 meters, >0.9 meters).

Voucher specimen identification

Lichen voucher specimens were collected for morphospecies at all sampling sites. Voucher specimens were collected outside of quadrats to preserve the sample units for future follow-up examinations. In some cases, representative morphospecies were unavailable due to their rarity and/or difficulty of collection. Identifications were conducted in the laboratory using light microscopy and the following chemical spot tests: 10% potassium hydroxide (K), sodium hypochlorite (bleach; C), and paraphenylenediamine (PD). Lugol's solution (IKI) was used for tissue staining. Collections were mostly identified using the keys provided in Lichens of the Sonoran Desert Region Volumes 1-3 (Nash et al. 2002, 2004, and 2007). However, a variety of other resources were utilized, including McCune & Geiser (2009), Brodo (2016), and McCune (2017).

Taxonomic Diversity

We measured taxonomic richness at the level of individual quadrats as well as at the site level. For quadrat-level richness – hereafter referred to as microhabitat richness – the total number of morphospecies identified during sampling was used. In a few cases, two morphospecies were later found to be the same taxon (e.g., fertile and sterile forms of *Peltula euploca* that were separated as distinct morphospecies in the field), and these were combined into a single species for microhabitat richness calculations. Estimating richness at the site level – hereafter mesohabitat richness – was more challenging and prone to potential error. We estimated mesohabitat richness by adding up the number of distinct morphospecies, including unidentified morphospecies, and then subtracted the number of unidentified *Aspicilia* morphospecies. In my experience of identifying and sampling lichens, *Aspicilia* species 1) frequently looked macroscopically different on different rock aspects; 2) often had fungal parasites that altered the appearance of the thallus; and 3) occasionally had thalli with few or no reproductive structures, making morphospecies assignment in the field particularly difficult for many individual thalli of *Aspicilia* taxa. For many of the sample sites, this led to the separation of numerous *Aspicilia* taxa where it appears likely that significantly fewer were truly present. For this reason, we felt that removing unidentified *Aspicilia* morphospecies would improve the accuracy of site richness estimates in most cases.

In order to estimate the cumulative number of species on sandstone and ultramafic rock outcrops across all sites, we extrapolated richness using the specpool function in the Vegan package using the Chao richness estimator (Oksanen et al. 2022). It is worth noting that since sampling only covered a subset of the rock microhabitats present, site-level and extrapolated richness estimates are likely to underrepresent the taxonomic richness of saxicolous lichens within and across sites. In addition to richness, microhabitat and mesohabitat diversity were calculated using the Shannon-Wiener diversity index.

Climate parameter measurements

For each site, climate data were obtained from several sources. We included mean annual precipitation, incidence of fog and low cloud cover, mean daily maximum temperature in July, and mean daily minimum temperature in January (Appendix I). Temperature and precipitation data were obtained from the PRISM 30-year normals from 1991-2020 (PRISM 2021). Incidence of fog and low cloud cover (FLCC) during summer months was obtained from Geostationary Operational Environmental Satellite (GOES) imagery data (Torregrosa et al. 2016). In addition to these variables, we initially hoped to develop an index of aerial salt deposition for individual sites. Later, we concluded that modelling salt deposition was not feasible at sufficiently fine scales to reliably characterize differences between sites, and so this was not done.

Data Analysis

Statistical analyses of community data were conducted in the program R (R Core Team 2021). Multivariate analyses used a Bray-Curtis distance matrix. We used non-metric multidimensional scaling (NMDS) to visually explore variation among communities, and permutational multivariate analysis of variance (perMANOVA) to test for the effect of environmental variables on community composition. NMDS was conducted using the metaMDS function in the Vegan package in R (Oksanen et al. 2022). perMANOVA was conducted using the adonis2 function in Vegan. perMANOVA analyses included blocking factors, and the blocking factor used depended on the nature of the variable. Blocking factors included rock type, paired site, and sample site. Permutations were assigned using the how function of the permute package (Simpson 2019), and blocks were assigned based on the type of group. We tested for differences in multivariate dispersion using the betadisper function in Vegan. Prior to analyzing community data, we removed taxa occurring in 2 or fewer quadrats (i.e., rare species), and we excluded quadrats where 30% or more of the total lichen cover was unidentified. Additionally, we used a Mantel test to look at correlation between community and elemental composition, and a partial Mantel test to account for spatial autocorrelation among sites. To do this we used the mantel and partial.mantel functions from the Vegan package, using 999 permutations and selecting the Pearson's correlation coefficient output. The community distance matrix for the Mantel test was the same as that used for NMDS and perMANOVA. The elemental composition matrix data is shown in Appendix II.

Taxonomic richness was analyzed at microhabitat (quadrat) and mesohabitat (site) scales. Differences in richness were examined in R using analysis of variance (aov function) and Welch paired samples t-tests (for mesohabitat) and two-sample t-tests (microhabitat) using the t.test function (R Core Team 2021). We calculated diversity using the Shannon-Wiener index, which was applied to the full site by species matrix of 134 taxa. Microhabitat and mesohabitat diversity indices were calculated using the diversity function in the Vegan package (Oksanen et al. 2022). For both community composition and diversity analysis, we looked at differences between rock types within the three coastal distance groups, such that we were comparing six groups: coastal sandstone, coastal ultramafic, intermediate sandstone, intermediate ultramafic, inland sandstone, and inland ultramafic.

Indicator Species Analysis

We used Indicator Species Analysis (ISA) to investigate whether there were differences in specific lichen taxa associated with different rock types, coastal distances, and other groups of samples (e.g., ultramafic-associated lichens, inland samples). ISA was performed using the multipatt function of the Indicspecies package (De Caceres and Legendre 2009). The same assigned blocks that were used for perMANOVAs were also used in ISA.

Results

Across all 16 sample sites (128 quadrat sample units), we identified 134 unique lichen taxa. Twenty of these are considered macrolichens (McCune and Geiser 2009) including 15 foliose taxa, three fruticose taxa, and two umbilicate taxa, with the remaining 114 taxa classified as microlichens including crustose, squamulose, endolithic, and minutely fruticose growth forms (Appendix III). Ten of the 134 taxa contain cyanobacteria as their primary photobiont (i.e. cyanolichens), with the remaining taxa containing green algae (chlorolichens). Eighty taxa were recorded on ultramafic rocks and 100 were recorded from sandstone, with 46 taxa recorded from both substrates. Chao-estimated richness for ultramafic was 101.7±12.6 (estimate±standard error), 141.3±17.9 for sandstone, and 168.7±15.3 across all sites (Table 8).

Of the 134 lichens identified, 62 (46%) were only recorded from a single site, with an additional 26 taxa (19%) recorded from only two sites. We recorded 22 taxa that have not been previously recorded on ultramafic rocks in the published literature from North America (Mulroy et al. 2022). The taxa present in the most quadrats (128 total) were *Polycauliona bolacina* (Tuck.) Arup, Fröden & Søchting (46), *Dimelaena radiata*

(Tuck.) Mull. Arg. (45), *Peltula bolanderi* (Tuck.) Wetmore (39), *Lecidella asema-carpathica* group[2] (35), *Peltula euploca* (Ach.) Poelt ex Ozenda & Clauzade (31), *Polycauliona ignea* (Arup) Arup, Fröden & Søchting (29), *Miriquidica scotopholis* (Tuck.) B.D. Ryan & Timdal (27), *Acarospora socialis* H. Magn. (24), *Protoparmeliopsis muralis* (Schreb.) M. Choisy (24), *Lichinella stipatula* Nyl. (22), *Candelariella vitellina* (Hoffm.) Mull. Arg. (20), and *Thelomma mammosum* (Hepp.) A. Massal. (20). The strongest indicator species for sample groups analyzed are included in Table 9.

The three most frequently occurring ultramafic taxa were *Peltula euploca, Peltula bolanderi*, and *Polycauliona bolacina*, which were found in all three coastal distance groups (coastal, intermediate, and inland). *Diplotomma alboatrum* (Hoffm.) Flotow and *Squamulea subsoluta* (Nyl.) Arup, Søchting & Fröden were also observed in at least one site within all coastal distance groups. *Lichinella stipatula*, *Thalloidima ioen* (Herre) S. Ekman & Timdal, *Lecidella asema-carpathica* group, *Acarospora socialis*, and *Candelariella citrina* B. de Lesd. were present at all inland ultramafic sites, and *Dimelaena radiata* occurred at all coastal ultramafic sites. On sandstone, *Acarospora socialis*, *Dimelaena radiata*, *Miriquidica scotopholis*, *Lecidella asema-carpathica* group, *Lecidea laboriosa* group, *Protoparmeliopsis muralis*, and *Thelomma mammosum* each occurred in at least four sites. *Dimelaena radiata* and *Thelomma mammosum* occurred within all coastal sandstone sites.

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[2] *Lecidella asema* and *L. carpathica* are readily distinguished in the laboratory using chemical spot tests. However, we found that separating these in the field was problematic since specimens of each taxon varied in color and often had scant thallus material, so we chose to combine them for the purposes of community analyses.

Substrate effects

Sandstone and ultramafic lichen assemblages showed large differences in elemental composition, and these differences were associated with differences in lichen community composition. The most notable differences in major element concentrations between ultramafic and sandstone elemental composition included higher silicon, aluminum, calcium, and potassium concentrations in the sandstones, and higher magnesium and iron concentrations in the ultramafics. For trace elements, ultramafics had higher nickel and chromium than sandstones, but lower barium, rubidium, strontium, zircon, niobium, and gallium concentrations (see Appendix II for rock elemental composition of individual sites).

We found significant differences between sandstone and ultramafic lichen taxonomic composition. A perMANOVA analysis comparing sandstone and ultramafic samples showed significant differences ($F = 9.83$, df = 1, 109, $R^2 = 0.082$, $p<0.001$) in composition between the two rock types, and this is visually represented in Figure 5. Multivariate dispersion, measured as average distance to the group median, was significantly higher in sandstone (0.64) than ultramafic (0.58; $F = 24.21$, df=1,109, $p<0.001$). Of the 100 taxa recorded from sandstone, 53 were only found on sandstone, and of the 81 taxa found on ultramafic rocks, 34 taxa were only found on ultramafic. Forty-seven taxa were found on both substrates. Lichen assemblage composition and rock elemental composition were significantly correlated (Mantel test; $r = 0.25$, $p<0.001$). A partial Mantel test accounting for spatial autocorrelation of samples also showed significant correlation ($r = 0.33$, $p<0.001$).

ISA identified seven taxa that were strongly associated with ultramafic rocks, and five that were associated with sandstone (Table 9). Lichen percent cover was higher in sandstone sites (70.3 ± 3.53%, mean and standard error) than in ultramafic sites (44.56±4.34%). Sandstone and ultramafic rocks overall did not have significant differences in richness or Shannon-Wiener diversity at either microhabitat or mesohabitat scales. (Table 8; Figures 6 and 7). Within coastal distance groups, coastal sandstone had higher microhabitat richness (10.79) than coastal ultramafic (7.21; Tukey HSD, p=0.01; Table 8). Differences between substrates in intermediate and inland samples were not statistically significant.

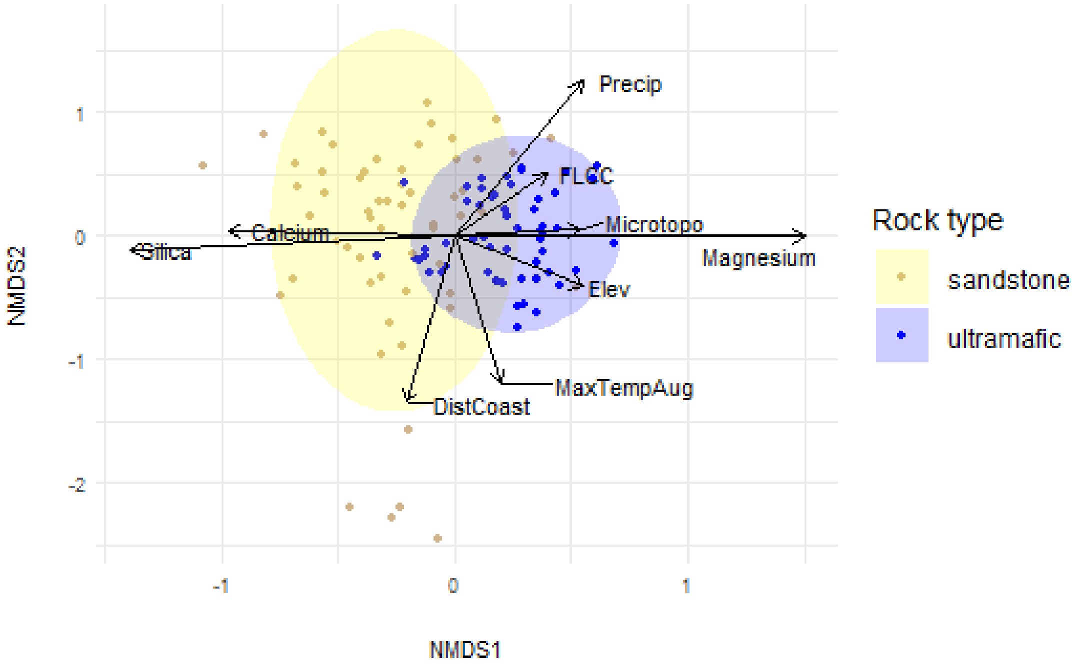

Figure 5. NMDS ordination of samples with overlaid vectors for selected environmental variables and ellipses representing 95% confidence intervals of the centroids for both ultramafic and sandstone quadrats. Key to vectors: Precip = precipitation; FLCC = fog and low cloud cover; Elev = elevation; DistCoast=Distance to coast (km); MaxTempAug = average maximum daily temperature in August; Magnesium = % Magnesium content (MgO) in rock samples; Silica = % Silica dioxide content (SiO_2); Microtopo = index of the prevalence of cracks and ledges in quadrats.

Table 8. Richness and Shannon-Wiener diversity measurements for individual sites. For microhabitat richness, extrapolated richness, diversity, and group averages, standard error is provided. The notation “UM” is used for ultramafic, and “SS” is used for sandstone.

Study Site Name	Microhabitat richness	Mesohabitat richness	Chao richness estimate	Microhabitat diversity	Mesohabitat diversity
Willow Creek SS	8.1±0.7	18	17.0±1.6	1.49 ± 0.06	2.11
Willow Creek UM	6.0 ± 0.6	23	27.7±11.6	1.11 ± 0.16	2.28
Jade Cove SS	8.8 ± 0.9	28	22.6±2.0	1.08 ± 0.20	2.37
Jade Cove UM	5.4 ± 0.4	19	29.0±14.5	0.99 ± 0.06	2.00
San Luis Hill SS	15.5 ± 1.3	47	37.8±11.0	1.64 ± 0.04	2.43
Pecho Creek UM	10.3 ± 1.2	33	35.9±9.4	1.54 ± 0.14	2.53
Coastal	**9.0±0.6**	**28±4.4**	**83.6±11.0**	**1.31±0.06**	**2.29±0.082**
Coastal SS	**10.8±0.9**	**31±8.5**	**54.7±5.8**	**1.40 ± 0.08**	**2.30±0.010**
Coastal UM	**7.21±0.6**	**25±4.2**	**63.1±15.4**	**1.21 ± 0.09**	**2.27±0.153**
El Chorro Regional Park SS	14.4 ± 0.7	42	46.8±11.2	1.70 ± 0.08	2.68
Irish Hills UM	8.8 ± 1.0	25	22.6±2.9	1.28 ± 0.15	2.26
Hi Mountain Road SS	9.1 ± 1.0	31	29.8±7.4	1.14 ± 0.19	2.46
Rinconada UM	9.3 ± 1.6	28	30.9±8.0	1.27 ± 0.18	2.52
Intermediate	**10.4±0.7**	**31.5±3.7**	**74.2±6.9**	**1.35±0.08**	**2.48±0.086**
Intermediate SS	**11.8±0.9**	**36.5±5.5**	**63.4±12.7**	**1.42±0.12**	**2.57±0.111**
Intermediate UM	**9.0±0.9**	**26.5±1.5**	**42.8±5.1**	**1.27±0.11**	**2.39±0.126**
James Parcel SS	7.1 ± 0.9	29	33.5±8.1	1.13 ± 0.14	2.27
Still Parcel UM	8.6 ± 1.3	24	36.4±15.2	1.34 ± 0.12	2.15
Serpent’s Back SS	9.0 ± 0.7	25	25.7±3.3	1.45 ± 0.12	2.24

Study Site Name	Microhabitat richness	Mesohabitat richness	Chao richness estimate	Microhabitat diversity	Mesohabitat diversity
Parcel D UM	12.3 ± 1.4	22	24.0±3.0	1.75 ± 0.07	2.65
Parcel B SS	5.1 ± 0.6	22	23.0±3.8	1.07 ± 0.09	2.33
Parcel B UM	8.0 ± 1.1	22	25.3±4.3	1.52 ± 0.22	2.07
Inland mean	**8.4±0.5**	**24±1.13**	**83.7±10.4**	**1.38±0.06**	**2.29±0.082**
Inland SS	**7.08±0.5**	**25.3±2.03**	**70.6±13.4**	**1.22±0.07**	**2.28±0.028**
Inland UM	**9.6 ± 0.8**	**22.7±0.667**	**46.6±9.8**	**1.54±0.09**	**2.29±0.182**
Sandstone	**9.6±0.5**	**30.2±3.46**	**141.3±17.9**	**1.34±0.05**	**2.36±0.060**
Ultramafic	**8.6±0.5**	**24.5±1.52**	**101.7±12.6**	**1.35±0.06**	**2.31±0.084**
All sites	**9.1±0.3**	**27.4±2.0**	**168.7±15.3**	**1.33±0.04**	**2.34±0.051**

Table 9. Strongest indicator species (index value >0.4) for sample unit groups. Groups include rock types (ultramafic and sandstone), rock aspects (north- and south-facing), and coastal distance groups (coastal, inland, and coastal plus intermediate). Statistic A is the sample estimate of the positive predictive value that a sample unit (quadrat) belongs to a given group given the presence of that species. Statistic B represents the sample estimate of the probability of finding the species in a quadrat within a group.

Species	A	B	Index value	p
Ultramafic				
Polycauliona bolacina	0.932	0.6317	0.75	<0.001
Peltula bolanderi	0.88836	0.52381	0.682	<0.001
Lichinella stipatula	1	0.34921	0.591	<0.001
Peltula euploca	0.81427	0.4127	0.58	<0.001
Polycauliona ígnea	0.79131	0.34921	0.526	<0.001
Thalloidima ioen	1	0.26984	0.519	<0.001
Polycauliona luteominia var. *bolanderi*	1	0.22222	0.471	<0.001
Sandstone				
Thelomma mammosum	0.99077	0.29688	0.542	<0.001
Acarospora socialis	0.81341	0.26562	0.465	0.017
Buellia tesserata	1	0.20312	0.451	<0.001
Xanthoparmelia mexicana	0.98506	0.17188	0.411	<0.001
Xanthoparmelia plittii	0.93002	0.17188	0.4	0.002
North-facing rock aspects				
Lecidella asema – L. carpathica group	0.95787	0.44615	0.654	<0.001
Physcia tribacia	0.95172	0.18462	0.419	0.003
South-facing rock aspects				
Dimelaena radiata	0.84113	0.40323	0.582	0.004
Peltula euploca	0.79012	0.37097	0.541	<0.001
Umbilicaria phaea	0.92492	0.17742	0.405	0.008
Coastal Sites				
Buellia tesserata	1	0.27083	0.52	<0.001
Pertusaria islandica	1	0.22917	0.479	<0.001
Tephromela atra	1	0.20833	0.456	<0.001
Aspicilia pacifica	0.98343	0.1875	0.429	<0.001
Coastal and Intermediate Sites				

Dimelaena radiata	1	0.5125	0.716	<0.001
Polycauliona bolacina	0.9449	0.4875	0.679	<0.001
Lecidella asema – L. carpathica group	1	0.4375	0.661	<0.001
Thelomma mammosum	1	0.25	0.5	0.002
Squamulea subsoluta	1	0.2125	0.461	0.002
Physcia tribacia	1	0.1875	0.433	0.009
Polycauliona luteominia var. *bolanderi*	1	0.175	0.418	0.024
Lecanora gangaleoides	1	0.1625	0.403	0.009
Inland Sites				
Polycauliona ignea	0.91585	0.55319	0.712	<0.001
Candelariella citrina	1	0.34043	0.583	<0.001
Umbilicaria phaea	0.94344	0.2766	0.511	<0.001
Caloplaca "tangerina"	1	0.23404	0.484	<0.001
Physconia enteroxantha	1	0.21277	0.461	<0.001
Aspicilia cf. *americana*	1	0.19149	0.438	<0.001
Lecania hassei	1	0.17021	0.413	0.002
High microtopography				
Peltula euploca	0.8234	0.4118	0.582	0.014
Moderate-high microtopography				
Peltula bolanderi	0.9130	0.4267	0.624	0.01
Low microtopography				
"Caloplaca marina"	1	0.3333	0.577	<0.001
Lecania hassei	0.8363	0.3333	0.528	<0.001
Physconia enteroxantha	0.7746	0.3333	0.508	0.008
Overhangs present				
Peltula euploca	0.8762	0.2917	0.506	0.023
Thalloidima ioen	0.9245	0.1806	0.4009	0.027
Overhangs absent				
Thelomma mammosum	0.94980	0.23214	0.470	0.005

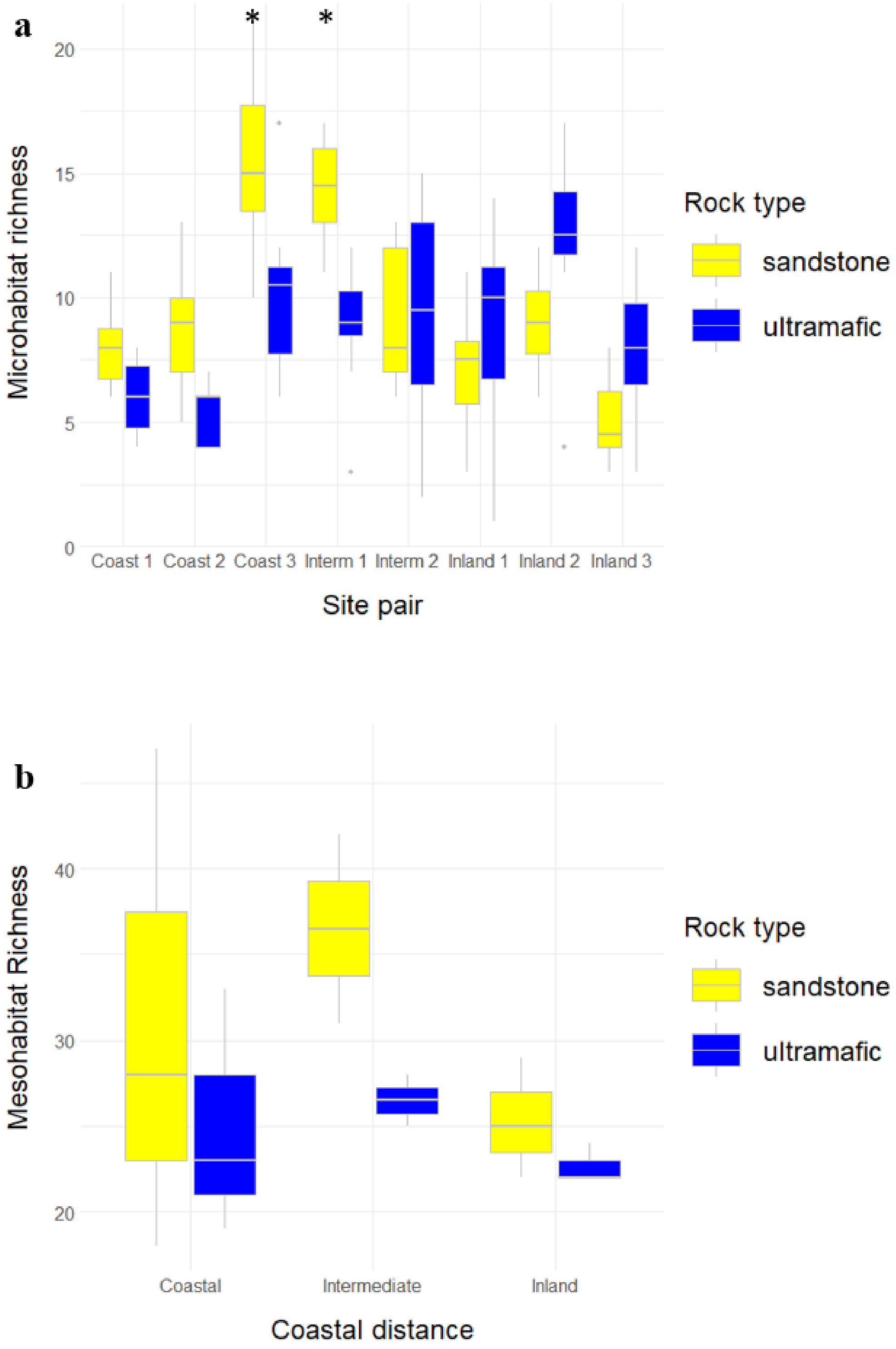

Figure 6. Microhabitat and mesohabitat differences in richness. a: microhabitat (quadrat-level) richness for paired sample sites (see Fig. 2 key to pairs). **b:** mesohabitat (site-level) differences for coastal distance groups. Asterisks (*) indicate statistically significant differences in richness between ultramafic and sandstone within a group.

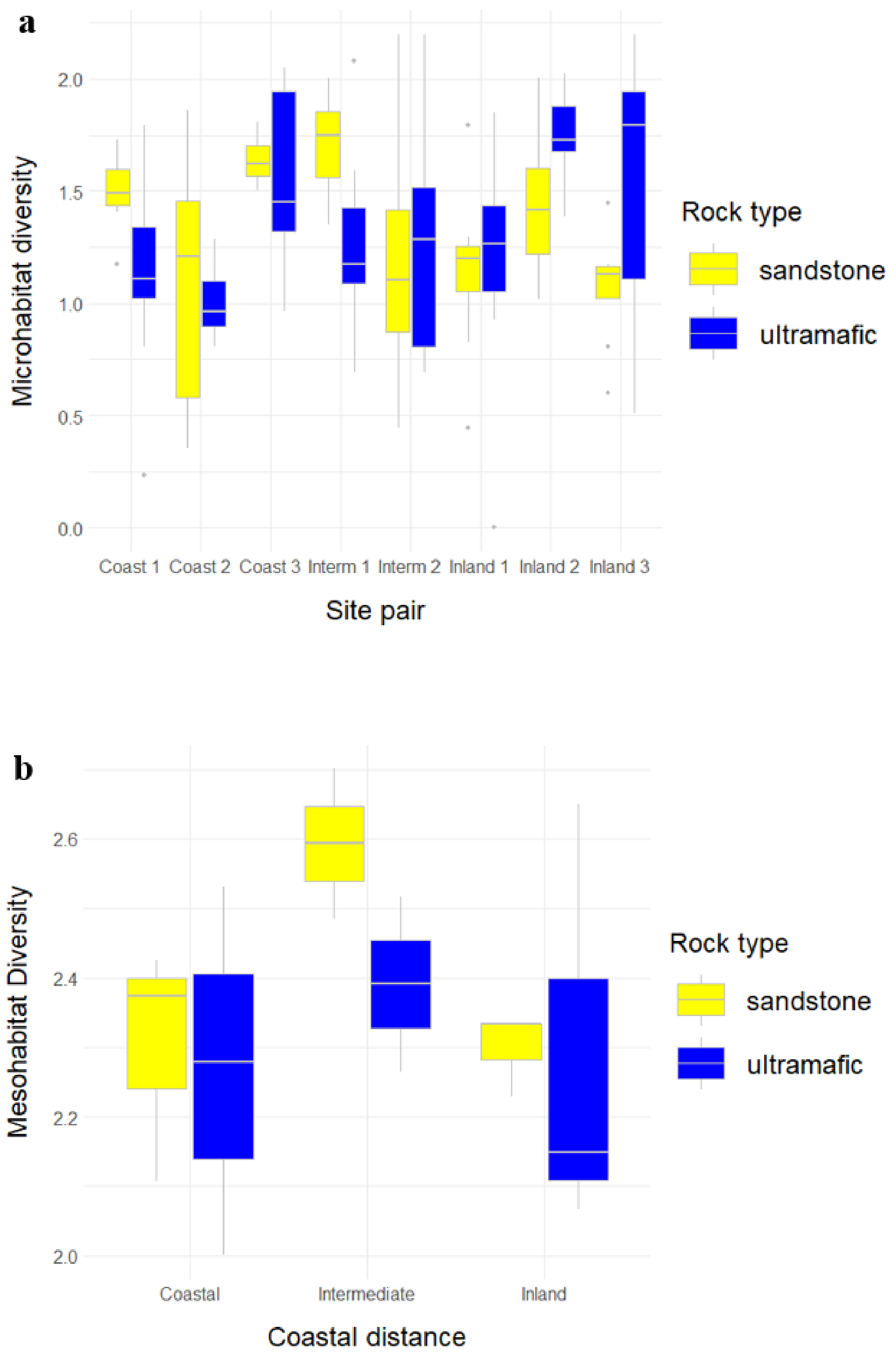

Figure 7. Shannon-Wiener diversity for microhabitat and mesohabitat. a: microhabitat (quadrat-level) diversity for paired sample sites (see Fig. 2 key to pairs). **b:** mesohabitat (site-level) differences for coastal distance groups.

Table 10. Results of perMANOVA for tested categorical and continuous variables. Variables in bold are statistically significant at the $\alpha = 0.05$ level.

Categorical variables	F	DF	R^2 value	p-value	Blocking factor
Site	**7.2485**	**15**	**0.53369**	**<0.001**	**None**
Rock type	**9.8312**	**1**	**0.08273**	**<0.001**	**Paired site**
Coastal distance	**8.5365**	**2**	**0.13650**	**<0.001**	**Rock type**
Rock type/coastal distance interaction	**3.6735**	**2**	**0.05108**	**<0.001**	**None**
Aspect (North or South)	**4.0584**	**1**	**0.03308**	**<0.001**	**Sample site**
Microtopography	**3.8361**	**1**	**0.03421**	**0.013**	**Sample site**
Undulation	0.9305	1	0.00830	0.299	Sample site
Overhangs	1.2902	1	0.01151	0.298	Sample site
Continuous variables					
Calcium (% CaO)	**6.9287**	**1**	**0.05977**	**<0.001**	**Paired site**
Magnesium (%MgO)	**9.6819**	**1**	**0.08158**	**<0.001**	**Paired site**
Silicon (%SiO_2)	**8.4808**	**1**	**0.07219**	**<0.001**	**Paired site**
Coastal distance (km)	**12.537**	**1**	**0.10316**	**<0.001**	**Rock type**
Elevation (m)	**8.2527**	**1**	**0.07038**	**<0.001**	**Rock type**
Maximum temperature in August	**12.006**	**1**	**0.09922**	**<0.001**	**Rock type**
Minimum temperature in January	**12.538**	**1**	**0.10316**	**<0.001**	**Rock type**
Precipitation	**9.7598**	**1**	**0.08218**	**<0.001**	**Rock type**
Fog and low cloud cover (FLCC)	**7.1605**	**1**	**0.06164**	**<0.001**	**Rock type**

Maritime gradient effects

Coastal, intermediate, and inland samples were significantly different from each other, and this is visualized in Figure 8. Inland samples were compositionally different from coastal samples (F = 10.89, df=1,82, R^2 = 0.117, p<0.001) and intermediate samples (F = 8.45, R^2 = 0.109, df = 1,69, p<0.001). Coastal and intermediate samples were also compositionally different, though the size of the difference was smaller (F = 4.46, R^2 = 0.067, df = 1,65, p<0.001). There were no significant differences in multivariate dispersion between coastal distance groups (F = 0.94, df = 2,108, p = 0.395). ISA identified a number of taxa associated with coastal, coastal-plus-intermediate, and inland samples, but none for intermediate or intermediate-plus-inland sample groups (Table 9). There were no significant differences in microhabitat or mesohabitat richness or Shannon-Wiener diversity across coastal distance groups (Table 8). Within individual rock types, there were significant differences in microhabitat richness between coastal distance groups (ANOVA: df=5, F= 5.69, p<0.001) for sandstone, but not for ultramafic. Inland sandstone samples had lower richness (7.8) than both coastal sandstone (10.8, TukeyHSD p=0.005) and intermediate sandstone (11.8; TukeyHSD p=0.001).

Sandstone and ultramafic communities had significant differentiation in each coastal distance group. Pairwise comparisons of taxonomic composition between ultramafic and sandstone rocks show that sandstone and ultramafic were significantly different within each coastal distance group (coast: F=8.34, df=1,38, R^2=0.18, p<0.001; intermediate: F=4.76, df=1,25, R^2=0.16, p<0.001; inland: F=6.42, df=1,42, R^2 = 0.13, p<0.001). The magnitude of the difference (i.e., the R^2 value) was highest for the coastal group and lowest for the inland group.

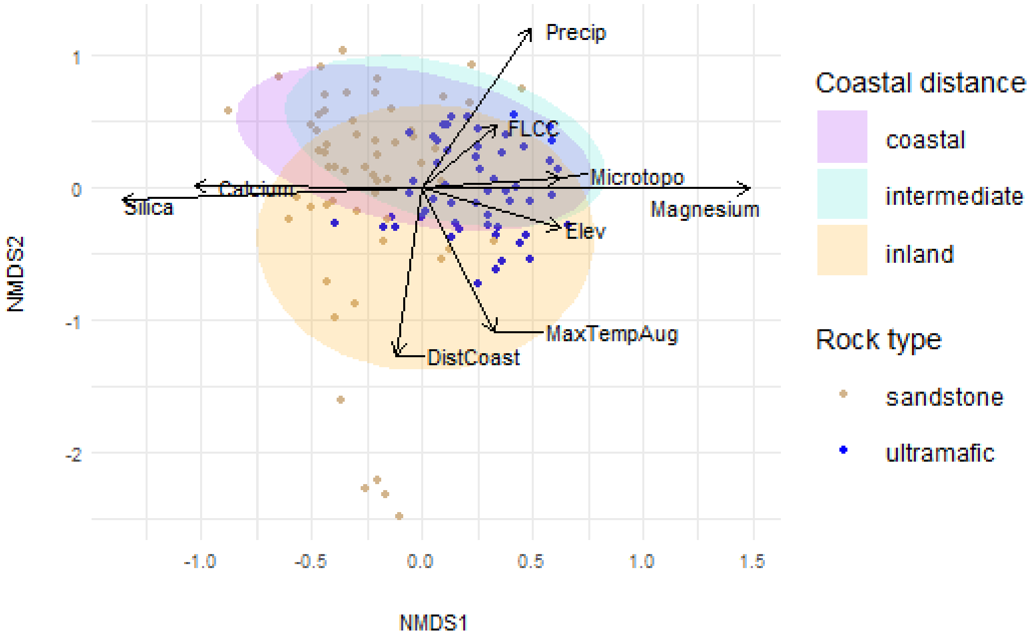

Figure 8. NMDS ordination of samples with overlaid vectors for selected environmental variables and ellipses represent 95% confidence intervals of the centroids for coastal, intermediate, and inland samples. See Figure 5 key to vectors.

Microhabitat, Microtopography, and Climate

We analyzed the effects of 17 categorical and continuous variables thought to have potential significance to lichens (Table 10). Most variables were associated with differences in lichen communities, though many were highly correlated with one another. Coastal distance was negatively correlated with precipitation, fog and low cloud cover, and minimum temperature in January, and positively correlated with maximum daily temperature in August and elevation. Ultramafic quadrat samples had a higher average microtopography index (1.20) than sandstone (0.68), as well as slightly higher mean undulation index (0.93 versus 0.83), and a higher prevalence of overhangs (71% of quadrats versus 40% for sandstone).

Since sampling was stratified across north and south rock aspects, we were able to examine the effects of this variable in greater depth. There were significant compositional differences between north and south aspects for both sandstone (F=2.40, R^2 = 0.04, df=1, 55, p=0.004) and ultramafic (F=3.27, R^2 = 0.06, df=1, 52, p=0.002). Microhabitat richness was significantly higher on north-facing rock aspects (10.12) than south-facing aspects (8.05; Welch 2-sample t-test, t = 3.08, df = 125.2, p = 0.003), and this was true for both sandstone (North mean = 10.45; South mean = 8.77) and ultramafic (North mean = 9.78; South mean = 7.55; Figure 9). Lichen percent cover showed a similar pattern to richness, with northern aspects having higher cover (68.7%) than southern aspects (45.8%; Figure 9). There were larger percent cover differences between aspects on ultramafic (north mean: 61.5%, south mean: 27.1%) than on sandstone (north mean: 75.7%, south mean: 64.5%). For both ultramafic and sandstone, coastal quadrats had lower differences in percent cover between aspects than inland quadrats (Figure 9). Both north and south aspects had strongly associated indicator taxa that were identified by ISA (Table 9).

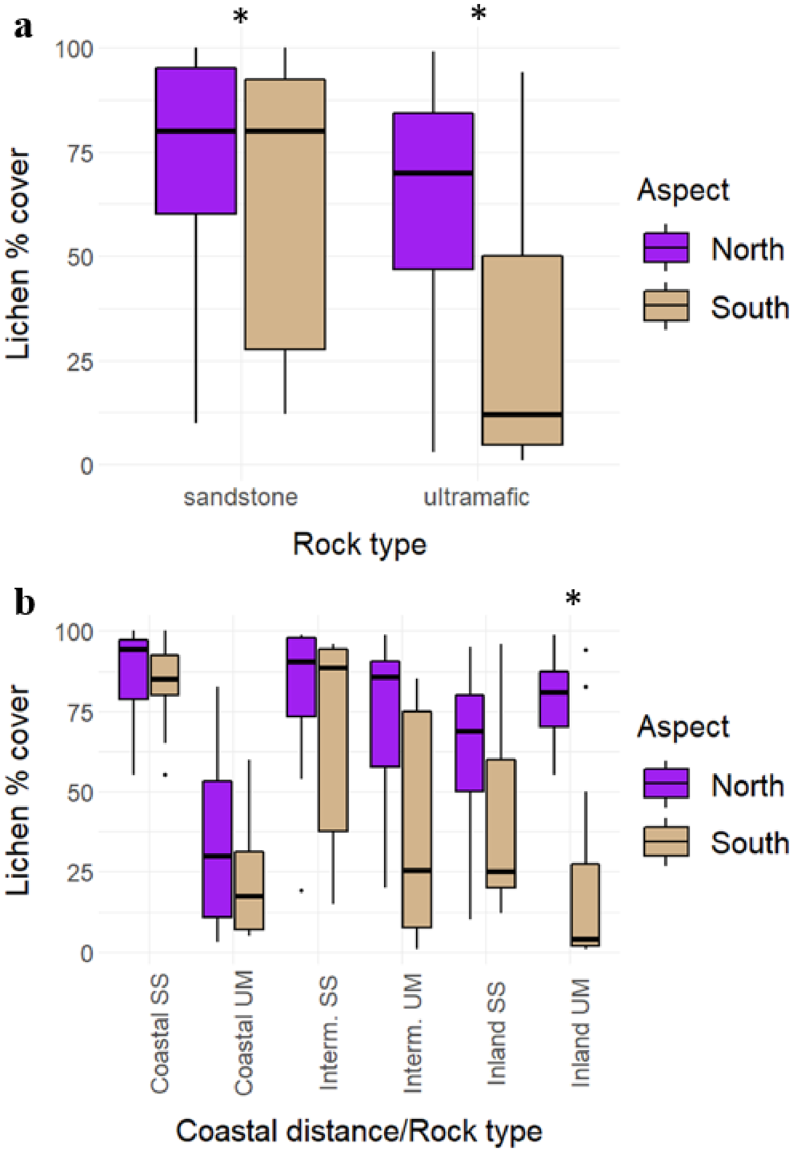

Figure 9. Lichen cover relationships with aspect. a: differences in lichen cover between north and south aspects between aggregated sandstone and ultramafic samples. **b:** differences in cover for each coastal distance plus rock type category. "UM" and "SS" denote ultramafic and sandstone, respectively. Asterisks (*) indicate statistically significant differences in cover between north and south aspects within a group.

Discussion

Substrate effects

The results of this study provide strong support for the *Substrate Hypothesis*. Lichen communities on sandstone and ultramafic are significantly different from one another both compositionally and in several other respects. Sandstone and ultramafic rocks each had distinctive suites of strongly associated lichen taxa. Compared to ultramafic lichen communities, sandstone communities were characterized by higher lichen percent cover and smaller differences in lichen percent cover between north and south aspects. Sandstone on average had higher mesohabitat richness and diversity, and a larger number of taxa were found on sandstone (100) than ultramafic rocks (81). Interestingly, the sites with the highest and lowest mesohabitat richness were both coastal sandstone sites. The low mesohabitat richness sandstones at Willow Creek and Jade Cove were qualitatively different than other sandstones sampled. Two attributes of the sandstones at these sites were particularly apparent. For one, both sites had higher rock hardness than the other sampled sandstone sites, and no observed exfoliation of outer layers of sandstone, which was often observed at other sandstone sites. Exfoliation has been proposed as an important factor in structuring both plant and lichen communities of cliff faces (Aho and Weaver 2006; Larson and Kelly 1991). It seems possible that modest rates of exfoliation prevent the formation of a climax community of a small number of species, and that newly exposed areas of rock provide room for less competitive species to persist at a given site. Differences in lichen communities between substrate surfaces of different ages have been documented in the literature. Pastore et al. (2014) found the lichen diversity was positively associated with intermediate time since disturbance as lichens slowly recolonized newly exposed rock surfaces. Woolhouse et al. (1985) proposed a pattern of succession to account for observed community compositional differences between gneiss rock faces of different ages. Differences in communities of hard-weathering and soft-weathering rocks have also been quantified (Favero-Longo and Piervittori 2009). A second notable difference in the sandstones of Jade Cove and Willow Creek was the higher smoothness of the rock surfaces, which contrasts with the rough surface texture of most other sandstone sites. A second hypothesis is that smoother rock surfaces are more difficult for lichens to colonize, leading to lower species richness. Surface texture is thought to be an important factor in structuring lichen communities (Brodo 1973), and smooth rock surface slopes may lack microsites for spores and asexual propagules to settle. Further investigation would be necessary to test either hypothesis, and was beyond the scope of the current study.

At the microhabitat scale, it is noteworthy that coastal site pairs, as well as the more coastal of the two intermediate site pairs (i.e., Interm 1 in Figures 6 and 7), each had higher richness and diversity on sandstone than ultramafic rock. For the remaining four more inland site pairs, ultramafic richness and diversity were higher in each case. Although there is not a clear explanation for this, we suggest that the greater microtopography of ultramafic rocks creates a higher diversity of microhabitats for lichens, including cracks and overhangs associated with higher moisture availability. Moisture is likely less of a limiting factor in lower-elevation coastal areas with more moderate temperatures, higher precipitation, and more summertime fog, and more important in arid interior, higher-elevation sites that receive less summertime fog.

Interestingly, cyanolichens comprised a larger proportion of the ultramafic lichen biota than the sandstone biota. Of the ten cyanolichen taxa recorded in this study, six were found only on ultramafic outcrops. Two others, *Peltula bolanderi* and *Peltula euploca*, were indicators of ultramafic rocks (Table 9) but were also found on sandstone. *Leptochidium albociliatum* was found on two ultramafic sites and one sandstone site, and one taxon, *Pyrenopsis* sp. (Nyl.) Nyl., was recorded only in a single sandstone quadrat. The ultramafic affinity of the two most frequently recorded cyanolichens observed in this study, *Peltula bolanderi* and *Peltula euploca*, may be explained by their strong affinity toward quadrats with high microtopography (Table 9). *Lichinella stipatula*, another ultramafic indicator species in this study, often occurs along rock cracks and seepage tracks in the Sonoran Desert region (Nash et al. 2007). Ultramafic rocks had a higher average microtopography and prevalence of overhangs than sandstone. Thus, it may be that cyanolichen occurrence on ultramafic rocks is associated with the high microtopography characteristic of the ultramafic rocks in this study. The association of cyanolichens with ultramafics in this study may explain the restriction of *Thalloidima ioen* to ultramafic substrates. *Thalloidima ioen*, similar to other taxa in the *Toninia* group (sensu Timdal 1991), is closely associated with cyanolichens and may be a facultative or obligate cyanolichen parasite when young, and in agreement with this study, most collections of this species are from mafic (basalt) and ultramafic (serpentine) substrates (Timdal 1991).

Another interesting pattern we noted was the occurrence of lichen taxa typical of calcareous, high-pH rocks on both ultramafic and sandstone outcrops. Although the rock surface pH was not measured in this study, the elemental composition was measured.

Between-site differences in geochemistry were higher for sandstone than for ultramafic, and sandstones sampled came from a range of geologic formations. In contrast, ultramafic outcrops were rather uniform in terms of geochemistry and geologic origin. This may in part account for the higher number of species found on sandstone in this study, as well as the greater apparent dispersion in sandstone composition shown in Figures 5 and 6.

The percent calcium of ultramafic outcrops samples was consistently low across ultramafic sites (mean±s.e.: 0.42±0.21, range: 0.04% to 1.75%). Calcium content of sandstone samples was slightly higher and varied more between sites (2.56 ±0.69, 0.09% to 6.52%; Appendix II). Two inland sandstone outcrops, Parcel B and James Parcel, contained species that are generally considered calciphiles and/or high-pH preferring, including *Candelariella aurella* (Hoffm.) Zahlbr., *Diplotomma venustum* (Körb.) Körb., *Lecania hassei* (Zahlbr.) W.J. Noble, and *Verrucaria furfuracea* (B. de Lesd.) Breuss, among others. However, the occurrence of calcicolous taxa was intermittent within sites, suggesting that rock calcium concentrations may vary significantly within these sites. Alternatively, the occurrence of calcicolous taxa could be explained by some other substrate variable that raised the pH at the rock surface in these areas. It is generally unclear whether differences in lichen communities result mainly from differences in elemental concentrations, or positively correlated substrate properties such as the pH of the rock surface environment. Some recent resources group lichens according to pH tolerance rather than affinity to specific elements (e.g., basiphytic and acidophytic lichens; Nimis 2022). Variation in the degree of rock weathering may also explain the patchy distribution of basiphytic taxa. Weathering processes can alter the rock surface environment substantially, leading to differences in lichen communities on rocks with different patterns and degrees of weathering (Woolhouse et al. 1985; Favero-Longo and Piervittori 2009).

The co-occurrence of acidophytic and basiphytic lichens on ultramafics is a well-documented phenomenon (Favero-Longo 2004; Mulroy et al. 2022), and we did observe basiphytic and neutrophilic (neutral pH preferring) lichens among a prevalent component of acidophytic taxa. Highly to somewhat basiphytic taxa found on ultramafic sites included *Diplotomma alboatrum* (Hoffm.) Flotow, *Physcia caesia* (Hoffm.) Hampe ex Fürnr, *Rusavskia elegans* (Link) S.Y. Kondr. & Kärnefelt, *Xanthocarpia crenulatella* (Nyl.) Frödén, Arup & Søchting, (Mulroy et al. 2022), and *Lichinella nigritella* (Lettau) P. P. Moreno & Egea (Nimis 2022), among others. Several of the cyanolichens recorded on ultramafic rocks are considered neutrophilic, including *Peltula euploca*, *Leptochidium albociliatum*, and *Collema furfuraceum* (Arnold) Du Rietz (Mulroy et al. 2022). The majority of taxa and lichen cover of ultramafic samples consisted of acidophytic species.

Maritime influence effects

The *Maritime Gradient Hypothesis* was well supported by the results of this study. Each coastal distance group was compositionally distinct. The inland lichen community group was the most strongly differentiated; intermediate and coastal groups were more compositionally similar. The collective climate factors related to maritime influence appeared to have a strong effect on composition similar in magnitude to the effect of rock type. Coastal and intermediate sites were characterized by small differences in lichen percent cover between north and south rock aspects, and there was a suite of taxa identified by ISA that were strongly associated with coastal plus intermediate sites. A smaller number of taxa were associated with only coastal sites (Table 9). Inland sites showed large differences in percent cover between north and south rock aspects, particularly on ultramafic rocks, and included strongly inland-associated lichen taxa (Table 9). Taxonomic richness and diversity at both mesohabitat and microhabitat scales were rather variable across the maritime gradient; substrate and microhabitat factors appear to be more important in explaining richness and diversity than maritime influence.

Since maritime influence is a collective set of environmental factors, it is challenging to identify the specific factors that are most important for lichen community assembly. In coastal vascular plant communities in the region of this study, intermittent aerial salt deposition appears to suppress dominant plant species, allowing a greater diversity of vascular vegetation to persist in coastal shrub communities when compared to more inland shrub communities (Baxter and Parker 1999; Wrubel and Parker 2018). This provides support for an intermediate disturbance hypothesis, which posits that a level of disturbance plays a role in promoting taxonomic diversity in vascular plant assemblages. The influence of aerial salt deposition on lichen communities in this study remains an open question, since this was not measured nor estimated. We believe the influence of salt deposition merits further investigation.

Maritime gradient effects on community differentiation across substrates

Sandstone and ultramafic communities remained significantly differentiated within coastal, intermediate, and inland sample groups. The *Maritime Moderation Hypothesis*, which predicted greater community compositional similarity between ultramafic and sandstone sites in coastal areas and greater differentiation in inland areas, is not supported. In fact, the magnitude of the difference between substrates slightly decreased with further distance from the coast, though the observed trend was weak. One possible explanation for this result is that aridity, or some other factor related to coastal distance, tends to override substrate differences in inland areas, and homogenization is occurring in the opposite direction along the gradient. Another possibility is that the higher humidity in coastal areas alters the chemical environment (i.e., elemental availability, pH) of the rock surface in such a way that differences in the microenvironment are accentuated in coastal areas. It is also possible that future studies carried out at different scales would demonstrate moderating effects related to coastal distance. In their study comparing communities of limestone and andesite cliffs along an aridity gradient, Aho et al. (2014) observed a dampening effect across a very small area. A comparative study of ultramafic and sandstone lichens in intertidal to supralittoral areas along the coast, or a study taking place across a larger coast-inland transect, might have yielded different results.

Microhabitat and Microtopography

Although effects of rock aspect on lichen taxonomic composition were minor relative to climate factors and substrate type, northern rock aspects had substantially higher microhabitat richness and lichen percent cover. This pattern is in contrast to the pattern observed by Paz-Bermudez et al. (2021) in their study comparing lichen communities on north and south aspects of church walls in Spain, where they estimated consistently higher richness on southern aspects than northern aspects. Multiple studies have found larger thalli (Armstrong 2002) and/or higher lichen growth rates (Haworth et al. 1986) on southern aspects in high-latitude areas of the Northern Hemisphere. Armstrong (1975) suggested that differential growth rates between different rock aspects at different times of year were a result of the interaction between thallus moisture content, temperature, and light availability. The results of this study suggest that the microclimate of north facing aspects is more amenable to most lichens in the study region, leading to higher richness and lichen cover. This is also suggested by the higher number of indicator taxa for northern rock aspects (11) than for southern aspects (4; Table 9). We suggest that the higher richness and lichen cover on northern aspects demonstrates that moisture availability is more limiting to lichen growth than light availability for most taxa in the region.

Limitations

This study had several caveats that constrain the conclusions that can be confidently made from this study's results. First, this study did not account for possible differences in substrate within sites, since only 1-2 samples were collected at each site (the single exception is the Jade Cove sandstone site, where we collected four samples due to qualitative substrate differences that we observed in the field). Second, we did not account for several variables that we believe may have been of significance for lichens. Several unmeasured substrate properties may be of particular importance: rock hardness, rock mineralogy, and the pH of the surface environment. Rock hardness, which relates to the weathering rate of the substrate, has clear effects on lichen communities (Woolhouse et al. 1985; Favero-Longo and Piervittori 2009). A rock's mineral composition, which is distinct from elemental composition, can affect rock bioavailability of elements, which results from differences in the chemical structures of minerals (Purvis and Halls 1996). Mineralogy can interact with pH to control element bioavailability (e.g., Liu et al. 2022). Rock surface pH has also been shown to affect the ability of lichen secondary metabolites to bind metals, and this has been correlated to lichens' substrate pH affinities (Hauck et al. 2009). The landform aspect of sample units (i.e., their position on the larger rock outcrop) was not recorded and may significantly contribute to the rock surface microclimate. Finally, we did not incorporate eastness, westness, and rock slope angle into analyses, and these would presumably have some effect on microclimate conditions.

Another limitation to this study was the inherent challenge of lichen identification both in the field when distinguishing morphospecies, as well as in the laboratory. Some taxa showed substantial phenotypic plasticity, and we commonly observed what appeared to be single lichen individuals varying in their appearance in different parts of a thallus. Some lichen taxonomic groups are highly cryptic. In general, the sampling approach was to be aggressive in separating taxa into multiple morphospecies, and later lump conspecific morphospecies after lab identification. A related challenge was collecting voucher specimens with enough material for identification. In some cases, morphospecies identified in quadrats could not be found outside of quadrats (or individuals that were found could not be collected from their locations on rock surfaces). In other cases, voucher specimens collected could not be confidently identified. There were several reasons for this, including lack of expertise in certain groups, an inability to find measurable spores, a lack of reproductive structures in the voucher collection, parasites that altered the appearance of the thallus, and insufficient material. Collectively, these challenges influenced the accuracy of quadrat cover data, and it is certain that some lichen taxa that occurred in quadrats were overlooked. However, we believe that the majority of lichen taxa, and particularly taxa that occurred in multiple sample units, were accurately recorded. We are also confident that the collected data are adequate to draw conclusions about compositional similarities among most sample units. As stated in the

Methods section, samples with a large proportion of unidentified lichen cover were excluded from the community analyses.

Future Research Directions

Future studies of saxicolous communities would benefit from increased attention on seldom-measured, yet likely important factors such as substrate-water relations and the rock surface pH environment, which have traditionally not been measured rigorously in lichenological studies, including ours [see Aho and Weaver (2006) for rigorous methods to measure pH and substrate water relations]. Studies that include careful measurements of these factors in addition to elemental concentrations of calcium and other elements at rock surfaces could help clarify the relative importance of these factors, which are often highly correlated, in structuring saxicolous lichen communities.

We also advocate for more studies that compare paired ultramafic and non-ultramafic lichen biotas. In the study region, sandstone outcrops are the most commonly available rock type near ultramafic outcrops. However, these substrates are very different not only in their elemental composition, but also in their structure and associated properties. In order to gain a better understanding of the effects of geochemistry on lichens, it would be valuable to conduct studies comparing ultramafic lichen biotas to more similar volcanic-origin substrates such as basalt, granite, and others. Additionally, studies comparing the genetics and physiology of taxa occurring on different rock types could elucidate cryptic diversity and mechanisms of adaptation to specific substrates.

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Appendix I. Site-level abiotic measurements.

	Study Site	**Distance to coast (km)**	**Precip (mm)**	**Max temp Aug (°C)**	**Min temp Jan (°C)**	**FLCC**
1	Willow Creek SS	0.67	648.158	8.58	21.7	5.09
2	Willow Creek UM	0.71	741.914	8.25	21.8	5.09
3	Jade Cove SS	0.1	566.906	9.41	17.99	3.18
4	Jade Cove UM	0.37	698.678	8.56	21.67	6.86
5	San Luis Hill SS	0.47	408.792	7.45	21.48	6.69
6	Pecho Creek UM	1.8	491.753	6.57	20.33	9.51
7	El Chorro SS	13.7	514.224	5.06	25.02	4.62
8	Irish Hills UM	8.17	461.492	6.18	24.19	6.79
9	Hi Mountain Road SS	22.1	651.686	5.74	31.45	2.4
10	Rinconada UM	21.7	640.818	4.69	31.84	2.4
11	James Parcel SS	71.2	322.529	1.75	34.96	2.97
12	Still Parcel UM	66.3	351.625	2.08	34.82	2.97
13	Serpent's Back SS	70.6	340.365	0.46	35.97	2.46
14	Parcel D UM	65.5	349.988	0.55	35.99	2.9
15	Parcel B SS	66.1	324.319	0.84	36.09	2.37
16	Parcel B UM	67.3	324.607	0.92	36.11	2.37

Appendix II. Elemental composition of rock samples taken from each lichen sample site. Major elements are reported as percent weight, and trace elements are reported in parts per million (ppm). Means of elemental concentrations are provided along with the standard error for both ultramafic and sandstone sites. *For the Jade Cove sandstone site, we collected four different rock samples due to observable differences in the rocks within sampled areas. Site abbreviations are as follows: Jade = Jade Cove, Will = Willow Creek, Pech = Pecho Creek, Iris = Irish Hills, Rinc = Rinconada, ParD = Parcel D, Stil = Still Parcel, ParB = Parcel B, SLHi = San Luis Hill, Chor = El Chorro Regional Park, HiMt = Hi Mountain Road, Jpar = James Parcel, SerB = Serpent's Back.

Ultramafic:	**Jade**	**Will**	**Pech**	**Iris**	**Rinc**	**Stil**	**ParD**	**ParB**	**mean ± s.e.**
Major elements (%)									
SiO2	40.71	38.02	40.85	39.48	39.1	40.07	39.49	39.34	39.63 ± 0.32
TiO2	0.06	0.052	0.01	0.075	0.04	0.019	0.03	0.007	0.04±0.01
Al2O3	2.19	1.97	0.15	2.25	2	1.33	2.15	0.51	1.57±0.29
FeO*	8.94	8.62	8.31	8.84	7.85	7.67	8.12	7.32	8.21±0.20
MnO	0.129	0.158	0.061	0.107	0.146	0.138	0.161	0.118	0.13±0.01
MgO	34.2	36.95	35.8	32.56	35.88	36.07	34.1	36.31	35.24±0.52
CaO	1.75	0.72	0.11	0.06	0.04	0.5	0.1	0.1	0.42±0.21
Na2O	0.02	0	0.02	0.01	0.01	0	0	0.01	0.01±0.00
K2O	0.01	0	0.01	0.01	0.01	0.01	0.02	0.01	0.01±0.00
P2O5	0.01	0.014	0.012	0.013	0.011	0.02	0.024	0.152	0.03±0.02
SO3 ≥	0.08	0.09	0.09	0.08	0.09	0.11	0.09	0.11	0.09±0.00
Sum	88.03	86.52	85.33	83.41	85.09	85.83	84.2	83.88	85.29±0.54
LOI %	11.48	12.65	13.82	15.51	14.01	13.4	15.11	15.32	13.91±0.50
Trace elements (ppm)									
Ni	2268	2428	3386	2926	2502	2238	2174	2210	2516.50±151.36
Cr	2240	2931	3444	4046	3154	2606	3202	2406	3003.45±209.00
Sc	11	12	2	15	12	9	13	6	9.75±1.47
V	59	64	18	88	69	55	74	33	57.52±7.99
Ba	16	7	3	8	16	15	39	10	14.00±3.96
Rb	0	0	0	0	0	0	0	0	0.04 ±0.03
Sr	7	1	2	2	3	5	5	3	3.31±0.63
Zr	2	1	1	2	1	3	1	1	1.56 ±0.29
Y	3	2	1	2	0	1	2	0	1.26 ±0.35
Nb	0	0	0	0	0	0.1	0	0	0.01±0.01
Ga	1	3	1	2	0	1	1	0	1.14 ±0.32
Cu	23	38	3	32	58	14	34	4	25.65 ±6.63
Zn	50	68	68	72	56	55	59	43	58.88±3.52
Pb	0	0	0	1	0	0	0	0	0.21 ±0.16
La	2	2	0	1	1	0	0	1	0.89 ±0.27
Ce	0	0	0	0	0	7	0	0	0.87 ±0.83

Th	0	1	0	0	0	1	0	1	0.42 ±0.15
Nd	1	1	1	5	3	2	1	0	1.87 ±0.51
U	0	0	0	0	1	0	0	0	0.13±0.09

Sandstone:	**Jade1**	**Jade2***	**Jade3***	**Jade4***	**Will**	**SLHi**	**Chor**	**HiMt**	**Jpar**	**SerB**	**ParB**	**mean ± s.e.**
Major elements (%)												
SiO2	58.6	54.07	53.08	71.47	64.46	71.34	69.92	75.36	72	77.72	78.35	67.85 ±2.72
TiO2	0.726	0.944	1.036	0.42	0.914	0.435	0.54	0.453	0.121	0.224	0.285	0.55 ±0.09
Al2O3	18.25	18.49	18.82	13.56	14.63	13.9	10.36	12.72	7.33	10.3	11.1	13.59 ±1.13
FeO*	5	7.6	7.36	3.56	5.88	3.1	5.29	2.66	0.54	1.91	1.41	4.03 ±0.72
MnO	0.064	0.115	0.128	0.063	0.085	0.055	0.139	0.016	0.017	0.01	0.005	0.06 ±0.01
MgO	2.85	3.24	4.12	1.7	3.01	1.31	1.9	0.22	3.15	0.34	0.35	2.02 ±0.41
CaO	3.19	6.52	5.25	0.63	2.41	0.55	4.19	0.09	4.47	0.56	0.29	2.56 ±0.69
Na2O	6.69	5.63	6.02	5.14	3.95	3.77	2.48	2.61	0.8	1.49	2.5	3.73 ±0.58
K2O	2.1	0.87	0.38	1.65	1.28	2.63	0.6	3.13	4	3.22	3.26	2.10 ±0.37
P2O5	0.246	0.207	0.24	0.088	0.126	0.148	0.079	0.07	0.461	0.143	0.025	0.17 ±0.04
SO3 ≥	0.06	0.06	0.06	0.09	0.06	0.07	0.09	0.05	0.07	0.25	0.09	0.09 ±0.02
Sum	97.72	97.69	96.44	98.29	96.76	97.23	95.49	97.34	92.89	95.92	97.58	96.67 ±0.45
LOI %	1.7	2.08	3.31	1.47	2.83	2.54	4.32	2.65	6.86	3.88	2.09	3.07 ±0.46
Trace elements (ppm)												
Ni	53	61	61	38	61	26	32	8	9	9	1	32.55 ±7.15
Cr	115	137	145	59	158	62	138	26	43	92	23	90.70±15.23
Sc	18	26	29	8	19	7	19	5	3	3	3	12.55 ±2.95
V	120	204	172	65	141	68	142	68	17	46	34	98.07 ±18.42
Ba	2520	978	271	239	422	882	922	596	761	777	934	845.58 ±185.54
Rb	45	22	12	49	43	84	16	109	73	85	86	56.73 ±9.87
Sr	281	788	566	228	140	289	184	192	109	183	143	282.07 ±63.02
Zr	179	179	185	129	173	150	63	175	59	147	141	143.67 ±13.46
Y	24	32	31	22	24	11	16	14	9	7	5	17.70 ±2.88
Nb	9.4	8.6	8.8	10.1	6.9	8.4	0.8	9.9	1.1	4	5.2	6.65 ±1.02
Ga	15	29	19	15	17	15	9	14	6	10	10	14.54 ±1.79
Cu	31	81	17	26	22	11	22	11	2	10	2	21.26 ±6.61
Zn	57	75	91	74	87	53	55	41	8	26	16	52.91 ±8.43
Pb	3	5	3	14	7	10	4	14	8	7	12	8.03 ±1.21
La	24	18	17	23	18	15	5	24	9	12	14	16.49 ±1.83
Ce	48	45	39	48	32	42	10	45	10	23	24	33.44 ±4.35
Th	9	7	7	10	7	7	1	11	3	4	5	6.34 ±0.93
Nd	22	22	20	22	18	11	7	18	6	10	10	15.17 ±1.90
U	2	2	2	4	2	2	0	4	1	4	1	2.15 ±0.40

Appendix III. List of lichen species recorded in quadrats. Blue site titles are ultramafic sites and tan site titles are sandstone sites. Presence at a site is indicated by an `x`. A species' status as an indicator for a sample unit group is provided using the following group codes: UM = ultramafic, SS = sandstone, C = coastal sites, I = inland sites, C-Int = coastal plus intermediate, N = north-facing rock quadrats, S = south-facing rock quadrats. Lichen type designations include: Mic = microlichen, Mac = macrolichen, Fol = foliose, Fru = fruticose, Umb = umbilicate, and Cy = cyanolichen. An asterisk after the name indicates a taxon that to my knowledge has not been previously reported on ultramafic rock in North America (Mulroy et al. 2022). Sites are denoted by numbers: 1 = Jade Cove UM; 2 = Willow Creek UM; 3=Pecho Creek UM; 4=Irish Hills UM; 5=Rinconada UM; 6=Still Parcel UM; 7=Parcel D UM; 8=Parcel B UM; 9=Jade Cove SS; 10=Willow Creek SS; 11=San Luis Hill SS; 12=El Chorro SS; 13=Hi Mountain Road SS; 14=James Parcel SS; 15=Serpent's Back SS; 16=Parcel B SS.

Taxon	**Type**	**Indicator group(s)**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Acarospora americana	Mic							x			x		x					
*Acarospora elevata**	Mic	UM, I							x									
*Acarospora obnubila**	Mic													X		x		
*Acarospora obpallens**	Mic													X	x			
Acarospora robiniae	Mic											x		X				
Acarospora rosulata	Mic	I															x	x
Acarospora socialis	Mic	SS						x	x	x	x		x	X		x	x	
Acarospora sp. 2	Mic										x		x					
Aspicilia cf. *americana*	Mic	I															x	x
Aspicilia brucei	Mic														x			
Aspicilia cf. *caesiocinerea*	Mic																x	
*Aspicilia cyanescens**	Mic	UM, I							x									

Taxon	**Type**	**Indicator group(s)**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
*Aspicilia fumosa**	Mic						x							X				
Aspicilia “gray squam”	Mic	UM					x											
Aspicilia phaea	Mic				x		x		x			x			X	x		
Aspicilia pacifica	Mic	SS, C				x						x	x					
Bibbya ruginosa	Mic					x												
*Buellia abstracta**	Mic	C		x									x					
Buellia badia	Mic			x		x							x	X	x			
Buellia dispersa	Mic				x	x							x	X				
*Buellia halonia**	Mic	SS				x					x		x	X				
*Buellia maritima**	Mic					x					x							
Buellia sequax	Mic	SS, C										x		X				
Buellia stellulata	Mic													X				
Buellia tesserata	Mic	SS, C									x	x						
Caloplaca cf. *atroflava* (short isthmus)	Mic			x	x										x			
Caloplaca cf. *epithallina*	Mic															x		
Caloplaca dark undescribed	Mic	UM						x										
"Caloplaca marina"	Mic							x		x						x		
Caloplaca marina ssp. *americana*	Mic										x							

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*Caloplaca peliophylla**	Mic	C			x					x			x					
Caloplaca saxicola	Mic													X		x		
Caloplaca “tangerina”	Mic	SS, I								x						x		x
Caloplaca teicholyta	Mic															x		
Candelaria pacifica	Mic	N						x	x				x		x			
Candelariella aurella	Mic																	x
Candelariella citrina	Mic	UM, N, I						x	x	x						x		
"Candelariella orange"	Mic															x		
Candelariella rosulans	Mic	SS											x			x		
Candelariella vitellina	Mic				x	x	x							X	x			
Catillaria chalybeia	Mic		x															
Chrysothrix sp.	Mic										x							
*Circinaria arida**	Mic	UM, I								x								
Cladonia spp.	Mac													X	x			
Collema furfuraceum	Mic, Cy		x															
*Dimelaena californica**	Mic	S		x		x					x			X			x	
Dimelaena oreina	Mic																x	

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Dimelaena radiata	Mic	S, C-Int	x	x	x	x					x	x	x	X			x	
Diploschistes actinostomus	Mic													X	x			
Diploschistes muscorum	Mic	N												X				
Diplotomma alboatrum	Mic			x			x	x		x								
Diplotomma venustum	Mic																	x
Dirina catalinarae f. sorediata	Mic										x							
Flavopunctelia flaventior	Mac, Fol													X				
Fuscopannaria sp.	Mic, Cy						x											
Lecania brunonis	Mic													X				
Lecania hassei	Mic	SS, I														x		x
Lecanographa hypothallina	Mic										x							
Lecanora gangaleoides	Mic	SS, N, C-Int	x	x							x		x	X				
Lecanora cf. *mellea*	Mic																x	
Lecanora bicincta	Mic													X				
Lecanora subcarnea	Mic											x						
Lecidea laboriosa group	Mic	SS			x								x	X	x	x	x	

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Lecidea mannii	Mic														x			
Lecidea tessellata	Mic						x											
Lecidella asema/carpathica	Mic	N, C-Int	x	x	x	x					x	x	x	x	x			
Lecidella patavina-stigmatea group[16]	Mic														x	x		
*Lepraria “*gray-green”	Mic	N			x		x								x		x	
Lepraria “white”	Mic														x			
Leptochidium albociliatum	Mic, Cy						x		x							x		
*Lichinella nigritella**	Mic, Cy									x								
*Lichinella stipatula**	Mic, Cy	UM			x	x	x			x								
Melanohalea elegantula	Mic											x		x				
Miriquidica scotopholis	Mic				x	x		x			x	x		x			x	
Myriolecis flowersiana	Mic															x		x
*Myriolecis semipallida**	Mic									x							x	
Myriospora scabrida	Mic	UM								x								
Niebla homalea	Mac, Fru											x						

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Niebla laevigata	Mac, Fru										x							
Niebla combeioides	Mac, Fru										x							
Peltula bolanderi	Mic, Cy	UM	x	x	x	x	x	x	x	x			x				x	x
Peltula euploca	Mac, Umb, Cy	UM, S	x	x	x	x	x		x	x			x				x	x
Peltula obscurans var. *deserticola**	Mic, Cy		x															
*Pertusaria islandica**	Mic	UM, C	x	x														
*Phaeophyscia hirsuta**	Mac, Fol				x								x					
Physcia adscendens	Mac, Fol												x					
Physcia phaea	Mac, Fol				x													
Physcia tribacia	Mac, Fol	SS, N, C-Int	x		x	x					x		x	x				
*Physcia tenellula**	Mac, Fol						x											
Physconia enteroxantha	Mac, Fol	N, I					x	x	x							x		x
Physconia isidiigera	Mac, Fol												x					
*Placidium acarosporoides**	Mic							x		x						x		
Placidium squamulosum	Mic			x														

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Placopyrenium stanfordii	Mic	UM				x			x	x								
Polycauliona bolacina	Mic	UM, C-Int	x	x	x	x	x	x	x				x				x	
Polycauliona ignea	Mic	UM, I	x		x	x		x	x	x							x	x
Polycauliona impolita	Mic	N						x					x	x				x
Polycauliona luteominia var. *bolanderi*	Mic	UM, C-Int		x	x	x	x											
Polycauliona luteominia var. *luteominia*	Mic		x	x														x
Polycauliona nashii	Mic															x		
Polycauliona stellata	Mic														x			
Polysporina simplex	Mic																x	
Protoparmeliopsis muralis	Mic							x	x	x			x	x			x	x
Protoparmeliopsis muralis var. *brunneola**	Mic								x									
Psora pacifica	Mic				x													
Psora sp. 2	Mic				x													
Pyrenopsis sp.	Mic, Cy																	x
Rhizocarpon bolanderi	Mic						x											

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Rhizocarpon distinctum	Mic											x						
Rhizocarpon viridiatrum	Mic						x											
Rhizoplaca glaucophana	Mac	UM							x									
Rinodina sp.	Mic																	x
*Rinodina pacifica**	Mic						x											
Rusavskia elegans	Mic	UM, I							x	x								
Sarcogyne hypophaea	Mic															x		
Sarcogyne similis	Mic																	x
Scytinium sp.	Mic, Cy						x											
Squamulea squamosa	Mic	UM, I	x						x	x							x	
Squamulea subsoluta	Mic	UM, C-Int		x	x	x				x			x	x				
Solenopsora cf. *crenata*	Mic		x				x											
*Staurothele drummondii**	Mic	UM, I						x		x								
Tephromela atra	Mic	SS, C									x	x						
Thalloidima ioen	Mic	UM			x		x		x	x								
Thelomma mammosum	Mic	SS, C-Int			x						x	x	x	x				
Umbilicaria phaea	Mac, Umb	S, I						x	x						x		x	x

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Verrucaria furfuracea	Mic	SS, I														x		x
*Verrucaria subdivisa**	Mic	N, C	x								x	x						
Xanthocarpia crenulatella	Mic			x											x		x	
*Xanthomendoza fulva**	Mac, Fol								x									
Xanthoparmelia cumberlandia	Mac, Fol													x				
*Xanthoparmelia lineola**	Mac, Fol	SS, N															x	
Xanthoparmelia mexicana	Mac, Fol	SS			x								x				x	
*Xanthoparmelia neoconspersa**	Mac, Fol	SS, C										x						
Xanthoparmelia plittii	Mac, Fol	SS				x								x	x	x		