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Review

Lichens of ultramafic substrates in North America: a review

Michael Mulroy[a], **Alan M. Fryday**[b], **Amanda Gersoff**[a], **Jason Dart**[c,d], **Rikke Reese Næsborg**[e], **and Nishanta Rajakaruna**[a,f]

[a]Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407, USA; [b]Herbarium, Department of Plant Biology, Michigan State University, East Lansing, MI 48824, USA; [c]Althouse and Meade, Inc., 1602 Spring Street, Paso Robles, CA 93446, USA; [d]Robert F. Hoover Herbarium, Biological Sciences Department, California Polytechnic University, San Luis Obispo, CA 93407, USA; [e]Santa Barbara Botanic Garden, Santa Barbara, CA 93105, USA; [f]Unit for Environmental Sciences and Management, North-West University, Potchefstroom 2520, South Africa

Corresponding author: **Michael Mulroy** (emails: mmulroy@calpoly.edu, mdmulroy21@gmail.com)

Abstract

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. This review examines geographic and ecological patterns of ultramafic lichen assemblages by synthesizing published reports of lichens of ultramafic substrates in North America, and by creating a database characterizing the ecology and habitat (substrate type, pH affinity, geographic distribution) for all taxa recorded in the literature. This effort yielded a total of 437 lichen species and infraspecific taxa reported from ultramafic substrates in the published literature. Lichen assemblages of ultramafic substrates vary in composition and are dominated by acidophytic taxa with a minor, but consistent, basiphytic 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.

Key words: lichen ecology, substrate properties, serpentine

Résumé

Les lichens sont parmi les formes de vie les plus importantes et les plus réussies des habitats riches en métaux, y compris les roches et les sols ultramafiques. La recherche sur les lichens des habitats ultramafiques est toutefois limitée, surtout sur le continent nord-américain. Cette revue examine les profils géographiques et écologiques des assemblages de lichens ultramafiques en synthétisant les rapports publiés sur les lichens des substrats ultramafiques en Amérique du Nord, et en créant une base de données caractérisant l'écologie et l'habitat (type de substrat, pH d'affinité, distribution géographique) pour tous les taxons enregistrés dans la littérature. Cela a permis d'obtenir un total de 437 espèces de lichens et de taxons infraspécifiques rapportés sur les substrats ultramafiques dans la littérature publiée. Les assemblages de lichens des substrats ultramafiques varient en composition et sont dominés par des taxons acidiphiles avec une composante basiphile mineure, mais constante. Les listes d'espèces des habitats ultramafiques de différentes régions géographiques variaient considérablement, ce qui suggère que des facteurs non liés au substrat, comme le climat, ont un effet important sur la composition des assemblages de lichens. Cependant, plusieurs études ont montré une différenciation claire entre la composition des lichens sur des habitats ultramafiques et non ultramafiques proches ou adjacents, ce qui suggère que les substrats ultramafiques abritent des assemblages de lichens uniques au niveau régional. [Traduit par la Rédaction]

Mots-clés : écologie des lichens, propriétés du substrat, serpentine

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 microorganisms that inhabit lichen thalli (Bates et al. 2012) has led some to argue that lichens are better thought of as microecosystems 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 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 our 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 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).

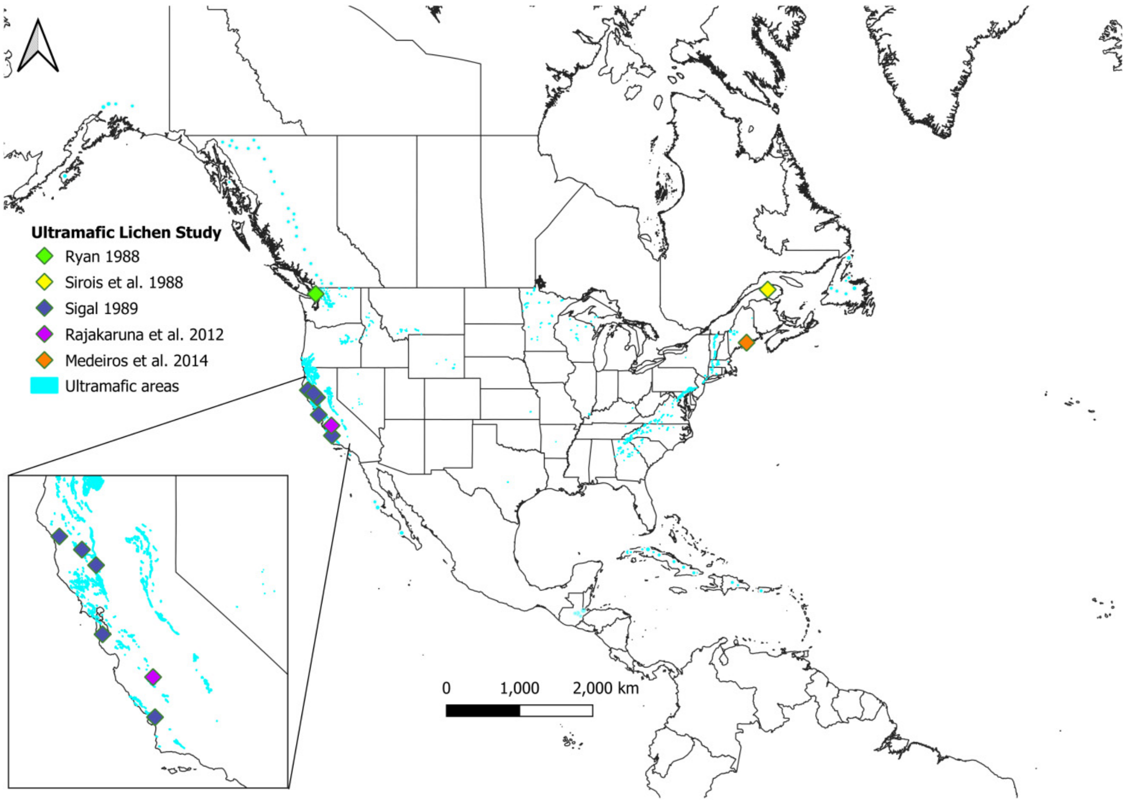
In addition to iron and magnesium, ultramafic rocks and soils are characteristically high in metals such as nickel, chromium, and cobalt. They are also typically low in nutrients essential to plants and other life forms, including nitrogen, phosphorus, potassium, and calcium (Kruckeberg 1992; Rajakaruna 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). While 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 2013*a*, 2013*b*; 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 2013*b*). 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 nonultramafic substrates often show marked differences in lichen species composition (e.g., Sirois et al. 1988; Favero-Longo and Piervittori 2009; Paukov 2009), 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;

Fig. 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).

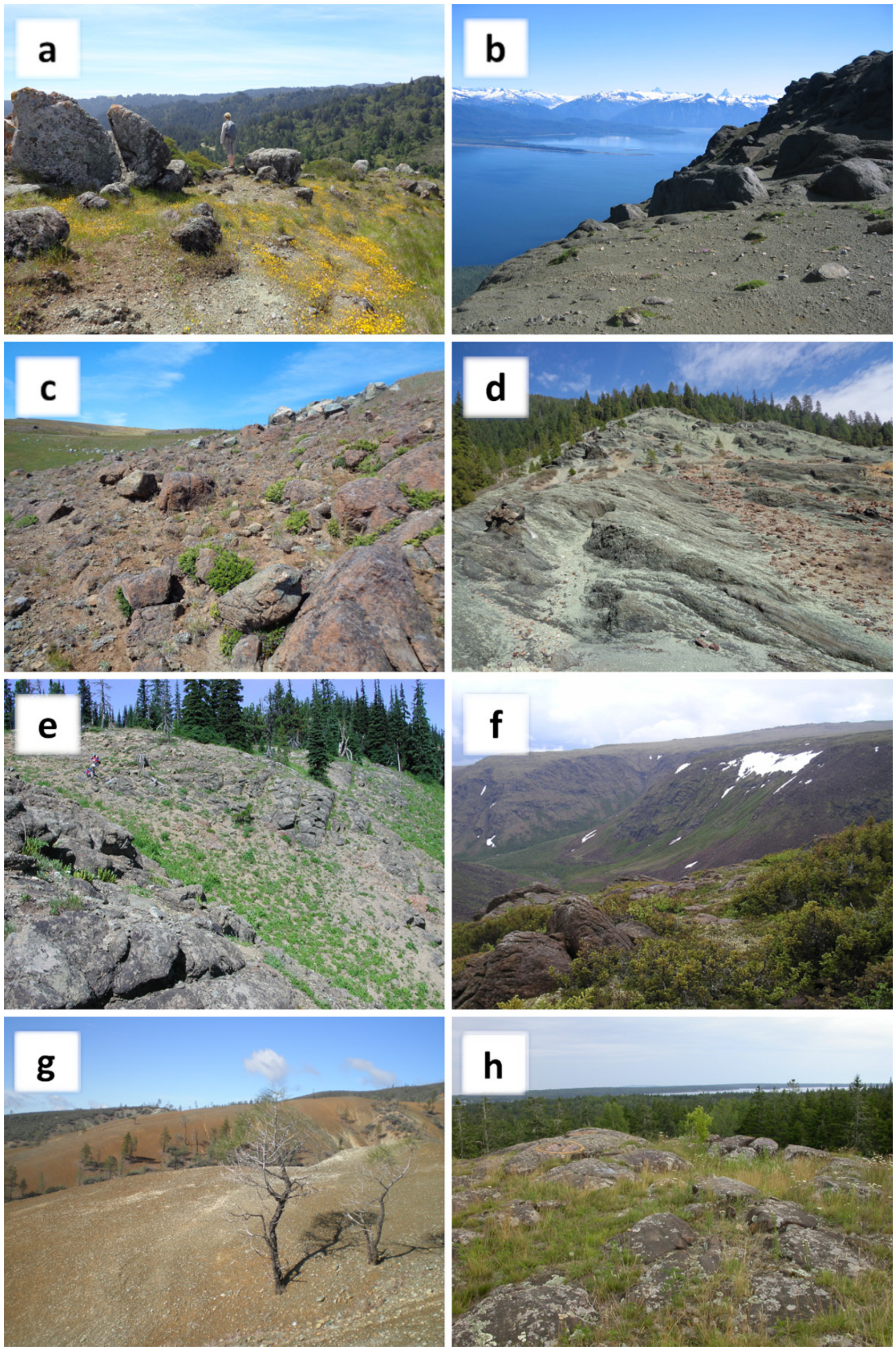


Favero-Longo and Piervittori 2009; Favero-Longo et al. 2018). In a worldwide review of studies investigating lichens of ultramafic substrates, Favero-Longo et al. (2004) found evidence for several ecological trends in ultramafic lichen communities. Perhaps most interestingly, their review indicated that 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 percentage 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), providing 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, to better understand patterns of lichen assemblages of ultramafic rocks and soils on the North American continent (see Figs. 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 America from the published literature. To the extent possible, we then compared the attributes of ultramafic lichen assemblages with those of nonultramafic substrates. We were interested in exploring (1) attributes of lichen taxa on ultramafic substrates; (2) similarities and differences of ultramafic and nonultramafic 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 nonultramafic habitats; (4) geographic distributions of lichens of ultramafic substrates (i.e., prevalence of widespread/cosmopolitan taxa versus taxa with restricted ranges); and (5) spatial variation in ultramafic lichen

Fig. 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).



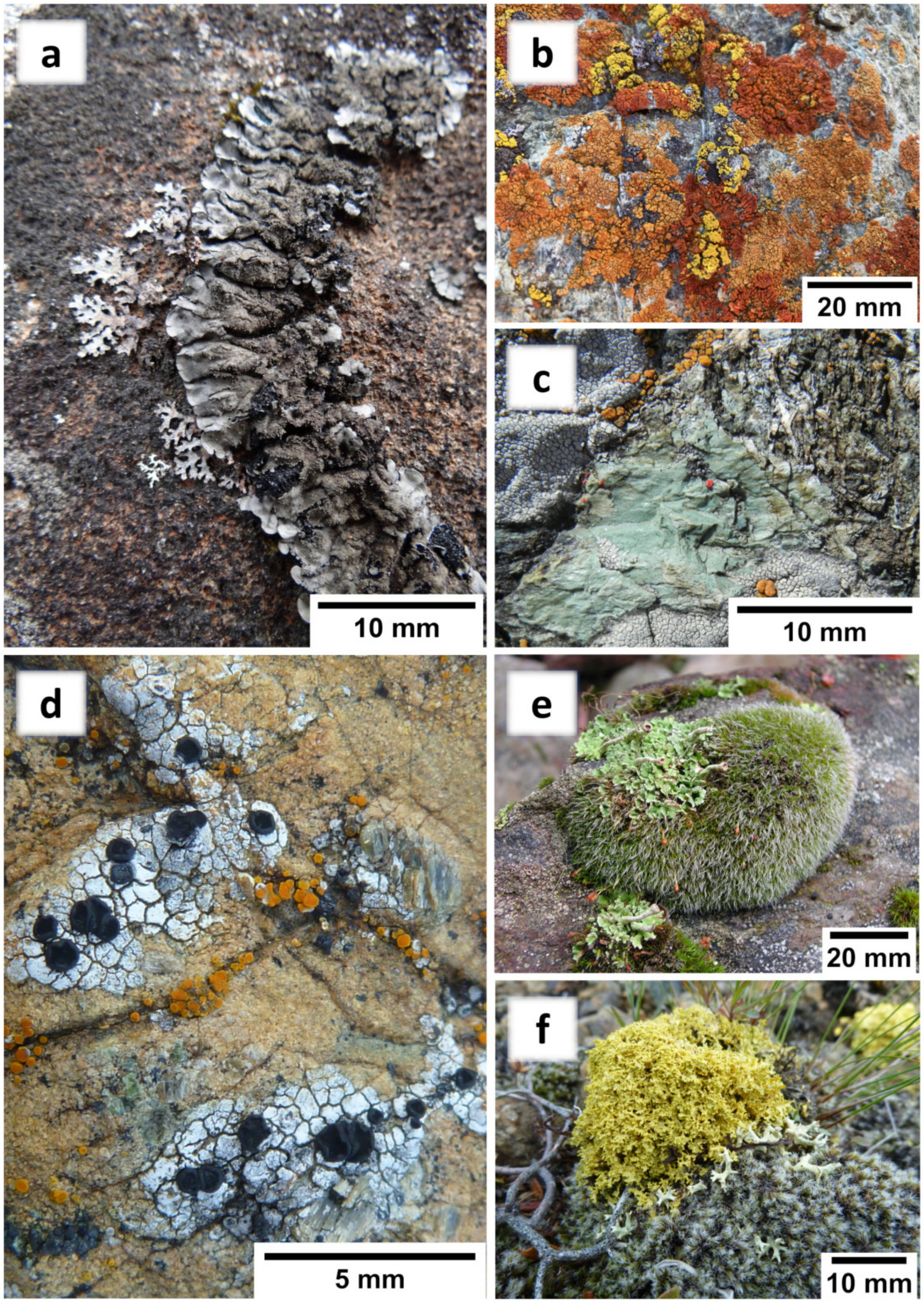
assemblages, including an assessment of the relative importance of abiotic factors on assemblage composition. Lastly, we sought to identify gaps in our knowledge of ultramafic lichens in North America to help focus future research and surveys.

Methods

Literature review and data compilation

We compiled information on every lichen taxon reported in each of six published studies that investigated lichen

Fig. 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).



biotas of ultramafic substrates in North America (Fig. 1 and Table 1; North America is defined here to include Central America, Mexico, the Caribbean, the USA, 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 18 published articles and one lichen flora were added (see Table 2), resulting in an additional 105 taxa being included in analyses. Lichens considered to be growing on ultramafic

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

Study	Locality	Latitude	Elevation range (m)	Average mean precipitation (cm)	Study type
Ryan (1988*a*)	Fidalgo Island, Skagit Co., WA, USA	48.5	0–5	71*	Inventory of marine and maritime lichens of ultramafic rocks. Complemented by a quantitative ecological study of the same site (Ryan 1988*b*)
Sirois et al. (1988)	Mont Albert, QC, 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)	Five sites in Northern and Southern Coast Ranges, CA, USA	35.4–39.9	183–1890	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	841–1422	50	Compared lichen communities of adjacent ultramafic and nonultramafic substrates using inventory collecting methods
Medeiros et al. (2014)	Little Deer Isle, Hancock Co., ME, USA	44.3	45	138	Compared lichens recorded from ultramafic substrates and nonultramafic metal-enriched substrates using nonstandardized inventory methods

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

substrates included taxa growing on other lichens (i.e., lichenicolous lichens, including some nonlichenized fungi) 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 our 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.

Substrate affinity

We attempted to characterize the substrate pH affinity for each taxon identified. To do this, we compiled species substrate affinity information available from several sources: (1) where available, substrate pH affinity information was gathered from species descriptions in Lichens of the Greater Sonoran Desert Region (Nash et al. 2002, 2004, 2007); (2) for some taxa, substrate pH affinity information was obtained from LIAS.net (LIAS 2021); (3) for widely distributed species, pH affinity information from the Information System on Italian Lichens (ITALIC) database and the Nimis lichen herbarium database were also referenced (Nimis 2016, 2021). Based on an assessment of the totality of these sources, we assigned each lichen species to one of six substrate pH affinity categories: acidic, acidic to neutral, neutral, neutral to basic, basic, and generalist. For many species, there was insufficient information to make a confident pH affinity assignment, and in such cases affinity categories were not assigned. Despite our efforts to provide accurate substrate pH affinity information for as many taxa as possible, this categorization is likely prone to bias (e.g., from uneven distribution in substrate type for collections of a given taxon, as well as geographic bias in collections and observations). As a result, the substrate pH affinity categorizations provided here should be considered provisional and not necessarily fully reflective of a taxon's substrate pH affinity across its entire range.

In addition to pH affinity, we designated substrate types for each lichen taxon according to its degree of restriction to one or more substrates. Substrate-type designations were based on available information from the same sources referenced for substrate pH affinity designations. Substrate-type designations should also be considered provisional, as a full inventory of online herbarium records for each species was not undertaken. Similar to pH affinity, for some taxa information on substrate is scant and collections may be biased toward certain substrates or regions. In some cases, a lichen's substrate specificity was unclear due to insufficient information, and in these cases a provisional substrate type was not designated.

North American endemism

We created a list of taxa reported from ultramafic substrates that currently appear to be endemic to North America. The distributions of lichen species were obtained from the Global Biodiversity Information Facility (GBIF; GBIF Secretariat 2021) and the Consortium of North American Lichen

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)	CA, USA	An account of *Toninia* species known from California, including two taxa described as occurring on serpentine
Doell and Wright (1996)	San Mateo Co., CA, 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)	CA, USA	Preliminary list of rare lichens known from California, including one taxon reported growing on serpentine
Breuss and Bratt (2000)	CA, USA	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)	CA, USA	Reports new and interesting lichen records from California, including records of four lichen taxa collected from serpentine
Baltzo (2001)	San Mateo Co., CA, USA	Annotated list of lichens of the San Francisco watershed, including reports of six taxa occurring on serpentine
Robertson and Robertson (2001)	CA, USA	Reports of new and interesting lichen records from California, including two lichen taxa collected from serpentine
Peterson (2003)	CA, 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)	MD, 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, USA	List of lichens identified from a lichen foray, including 19 taxa growing on serpentine rocks and soils
Doell et al. (2009)	Claremont Canyon, Alameda Co., CA, USA	List of lichens identified from various habitats within Claremont Canyon in Alameda County. Includes 14 taxa collected from serpentine
Lendemer et al. (2009)	CA, USA	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, QC, 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)	CA, USA	Reports rare lichens collected in California by Judy and Ron Robertson. Includes one new record of a lichen growing on serpentine

Herbaria (CNALH), which shows collection records for locations in North America and elsewhere (CNALH 2021). A taxon was considered potentially endemic to North America if there were no records outside of North America, or if scant records outside of North America appeared to be in error.

Results

After updating the nomenclature of all lichens reported from the published literature examined for this review, a total of 437 currently accepted lichen taxa (including lichenicolous fungi) identified to the species or infraspecies level were recorded (Table 3). In addition, Table 3 includes 33 taxa that were identified only to the genus level, three taxa belonging to a species complex and identified to the "group" level, and three taxa that were considered similar to known taxa but whose identities were not confirmed (denoted by "cf."). Of the taxa listed in Table 3, 371 were recorded in one or more of the five published studies that were the main focus of this review (Table 1). An additional 105 taxa were added from other published literature (Table 2).

Substrate affinity

Of the 437 taxa identified to species recorded on ultramafic substrates in North America, 126 (29%) were not assigned a

Table 3. Lichen species recorded from ultramafic substrates in North America in the published literature.

	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*	*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	—	—

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Table 3. Continued

	Current species name	Name used in study (if different)	Studies found	Substrate pH affinity	Substrate type
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

Table 3. Continued

	Current species name	Name used in study (if different)	Studies found	Substrate pH affinity	Substrate type
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

Table 3. Continued

	Current species name	Name used in study (if different)	Studies found	Substrate pH affinity	Substrate type
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

Table 3. Continued

	Current species name	Name used in study (if different)	Studies found	Substrate pH affinity	Substrate type
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

Table 3. Continued

	Current species name	Name used in study (if different)	Studies found	Substrate pH affinity	Substrate type
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.†	*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.) Arnold	—	b	acidic	gen

Table 3. Continued

	Current species name	Name used in study (if different)	Studies found	Substrate pH affinity	Substrate type
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‡	*Peltigera aphthosa* (L.) Willd.	b, 1	—	—
291	*Peltigera canina* group‡	*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

Table 3. Continued

	Current species name	Name used in study (if different)	Studies found	Substrate pH affinity	Substrate type
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.	*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

Table 3. Continued

	Current species name	Name used in study (if different)	Studies found	Substrate pH affinity	Substrate type
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[‖]	*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

Table 3. Continued

	Current species name	Name used in study (if different)	Studies found	Substrate pH affinity	Substrate type
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 vermicularis* (Sw.) Schaer.	*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

Table 3. Continued

	Current species name	Name used in study (if different)	Studies found	Substrate pH affinity	Substrate type
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¶	1	—	sax, terr
474	*Xanthoparmelia* sp. 2	*Xanthoparmelia tasmanica* (Hook. F. & Taylor) Hale**	1	—	—
475	*Xanthoria parietina* (L.) Th. Fr.	—	e	generalist	gen
476	*Xanthoria* sp.	—	c	—	—

Note: Alternative species names used in the published studies and articles are given. Key to studies: a, Ryan 1988*a*; 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; 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".

*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).

†This includes report of *Lepraria incana* from Sirois et al. (1988). *Lepraria incana* was the name previously used for several species now recognized as distinct taxa.

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

§*Physconia distorta* is now known not to occur in North America.

‖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*.

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

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

pH affinity category due to insufficient information in the literature. Approximately 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

Table 4. North American ultramafic lichens categorized by substrate pH affinity.

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%

Note: 39 taxa not identified to the species level are not included.

(11%) predominantly epiphytic (i.e., corticolous 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.

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).

Discussion

Substrate affinities of ultramafic lichens of North America

Our 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 nonultramafic substrates. In the three studies comparing ultramafic and nonultramafic 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 nonultramafic 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 nonultramafic substrates uninformative.

Globally, published accounts of lichens of ultramafic substrates have come to a range of 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. 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 nonultramafic 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 and Fig. 1). As one example, the New Idria serpentinite mass (CA, USA) sampled by Rajakaruna et al. (2012) and Little Deer Isle (ME, USA; 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

Table 5. Lichen taxa apparently restricted to North America from lichens recorded on ultramafic substrates in North America in the published literature.

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 USA, 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 USA
Buellia nashii	d	Primarily southwestern USA, 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	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 USA 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 USA 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 USA
Lecanora sierrae	d	Western USA (mainly in the Sierra Nevada) and Baja California
Lecidea brunneofusca	b	Northeastern USA 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 USA 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†	1	Mainly eastern USA
Physcia millegrana	1	North America (primarily eastern)
Physconia californica	d	Western North America, southern Oregon to Baja California
Placidium arboreum	1	USA (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 USA 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 USA, but also Canada

Table 5. Continued

Species name	Studies found	Distribution within North America
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 USA

Note: For key to studies, see Table 3.
C. apodocarpa has unverified records from Colombia.
†*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 more than three studies of ultramafic lichens in North America.

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

Note: Key to studies: a, Ryan 1988*a*; b, Sirois et al. 1988; c, Sigal 1989; d, Rajakaruna et al. 2012; e, Medeiros et al. 2014.

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, USA. 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 biotas of the Northern and Southern Coast Ranges in California, Sigal (1989) conducted inventories of five ultramafic outcrops distributed along a latitudinal gradient (Fig. 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 2021), 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 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 nonultramafic habitats at regional and local scales are uncommon (e.g., Favero-Longo and Piervittori 2009; Paukov and Trapeznikova 2005), and typically utilize species

[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.

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 nonultramafic 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 Mont Albert, QC, Canada. 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 nonultramafic areas. The differentiation across studies between ultramafic and nonultramafic 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 nonultramafic substrates (Brady et al. 2005; Cacho and Strauss 2014). This may lead to regionally unique microhabitats that support rare or endemic taxa, as well as 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-occurring with the species on serpentine barrens in Maryland (Lendemer 2004). In the western USA, *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 research topics that remain largely unexplored.

Future research directions

Our 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 state of 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 USA, 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 (Fig. 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 are 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 our 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 (1988b) recorded percentage cover of each lichen species in quadrats placed along elevational transects on a rocky seashore. This approach allowed the author to demonstrate changes in percentage 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 bird 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 by Rajakaruna et al. (2012). They reported differences in the elemental composition of rocks at different ultramafic and nonultramafic 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 nonultramafic 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 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 possibly 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 nonultramafic lithologies limits our ability to compare lichen biotas between substrates as well as identify substrates and areas worthy of consideration for lichen 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.
- While 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 undersampled areas as well as an increased focus on quantitative studies relating lichen community data to substrate, microhabitat, and climatic variation.

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Author information

Author ORCIDs

Michael Mulroy https://orcid.org/0000-0003-0796-7567
Alan M. Fryday https://orcid.org/0000-0002-5310-9232
Amanda Gersoff https://orcid.org/0000-0001-8197-5392
Jason Dart https://orcid.org/0000-0002-5656-066X
Rikke Reese Næsborg https://orcid.org/0000-0001-8187-1040
Nishanta Rajakaruna https://orcid.org/0000-0002-9021-6918

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