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Investigation of the importance of rock chemistry for saxicolous lichen communities of the New Idria serpentinite mass, San Benito County, California, USA

N Rajakaruna
San Jose State University, nrajakaruna@gmail.com

K Knudsen
University of California - Riverside

A Fryday
Michigan State University

R E. O'Del
United States Bureau of Land Management Hollister Field Office, 20 Hamilton Ct., Hollister, CA USA

N Pope
University of California - Davis

See next page for additional authors

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Authors

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Investigation of the importance of rock chemistry for saxicolous lichen communities of the New Idria serpentinite mass, San Benito County, California, USA

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Abstract: Although several lichen inventories exist for European ultramafic sites, only four surveys of serpentine lichens for North America have been published to date. Of those, only one has been conducted in California. We conducted a survey of saxicolous lichens from ultramafic rocks (including nephrite, partially serpentinized peridotite, and serpentinite) and non-ultramafic rocks (including silica-carbonate, shale, and sandstone) at the New Idria serpentinite mass, San Benito County, California. X-ray Fluorescence Analysis of the rocks from which the lichens were collected revealed significant elemental differences between the ultramafic and non-ultramafic rocks for 26 of the 32 major and trace elements analyzed. We identified a total of 119 species of lichenized and lichenicolous fungi; 60 species were restricted to ultramafic substrata, 19 to silica-carbonate, and 15 to shale and sandstone. Only 4 species were shared in common. A permutational multivariate analysis of variance (perMANOVA) test revealed significant differences in lichen assemblages between ultramafic and non-ultramafic rocks at the species level but not at the generic level, with species richness (alpha-diversity) significantly greater at the ultramafic sites. We suggest that, although differences in geochemistry clearly influence the lichen community composition, other factors, especially substratum age and the physical characteristics of the rock, are of equal, if not greater, importance. Of all the species collected, six, *Buellia aethalea*, *B. ocellata*, *Caloplaca oblongula*, *Rhizocarpon saurinum*, *Thelocarpon laureri*, and *Trapelia obtegens*, are reported new to California, along with an apparently previously undescribed *Solenopsora* sp. The rest of the species encountered are relatively frequent in the lichen flora of southern and central California, except *Aspicilia praecrenata*, a rare California endemic that we collected on both ultramafic and non-ultramafic rocks.

Key words: edaphic endemism, geobotany, serpentine, ultramafic

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Introduction

Lichens have an intimate and often inseparable relationship with their substratum, even leading to unique lichen-geoedaphic associations (Brodo 1973; Garty & Galun 1974; Wilson 1995). Although the geochemistry and mineralogy of rocks may play an important role in the occurrence of individual lichen species and assembly of lichen communities (Purvis & Halls 1996), the exact nature of such relationships or the mechanisms of such influences have not been thoroughly investigated.

Lichens are a dominant component of the biodiversity of many heavy metal-enriched sites, including mine tailings (Purvis & Halls 1996; Purvis & Pawlik-Skowrońska 2008; Rajakaruna *et al.* 2011) and ultramafic ('serpentine') substrata (Favero-Longo *et al.* 2004; Harris *et al.* 2007; Paukov 2009), at times displaying distinct species associations (Rajakaruna *et al.* 2011, and references therein). Despite extensive research on the effect of ultramafic substrata on vascular plants, little

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N. Rajakaruna and F. C. Olday: College of the Atlantic, 105 Eden Street, Bar Harbor, ME 04609, USA. Email: nrajakaruna@coa.edu
K. Knudsen: Department of Botany & Plant Sciences, 2117 Bachelor Hall, University of California, Riverside, CA 92521, USA.
A. M. Fryday: Herbarium, Department of Plant Biology, Michigan State University, East Lansing, MI 48824, USA.
R. E. O'Dell: United States Bureau of Land Management Hollister Field Office, 20 Hamilton Ct., Hollister, CA 95023, USA.
N. Pope: Department of Entomology, University of California Davis, One Shields Avenue, CA 95616, USA.
S. Woolhouse: Department of Biological Sciences, One Washington Square, San José State University, San José, CA 95192, USA.

research has been undertaken to describe lichen communities growing on ultramafic substrata (Favero-Longo *et al.* 2004; Rajakaruna *et al.* 2009). Ultramafic rock is primarily composed of ferromagnesian silicates [$<45\%$ silica (Si); $>18\%$ magnesium oxide (MgO); Brooks 1987; Coleman & Jove 1992]. Common ultramafic rock types include peridotites (dunite, wehrlite, harzburgite, lherzolite) and the secondary alteration products formed by their hydration within the Earth's crust, including serpentinite (Coleman & Jove 1992). Ultramafic rocks and soils derived from them are generally deficient in plant-essential nutrients such as nitrogen (N), phosphorus (P), potassium (K), sulphur (S); have a calcium (Ca) to magnesium (Mg) molar ratio (Ca:Mg) of less than 1; and have elevated levels of heavy metals such as nickel (Ni) and chromium (Cr) (O'Dell & Rajakaruna 2011, and references therein). Due to the intense selective pressure generated by such stressful edaphic conditions, ultramafic substrata promote speciation and the evolution of ultramafic endemism in phanerogams (Kruckeberg 1986; Rajakaruna 2004; Kay *et al.* 2011), contributing to unique floras with high rates of endemism and species with disjunct distributions (Harrison & Rajakaruna 2011). Interestingly, species-level ultramafic endemism is not a common phenomenon among cryptogams, including lichens (Alexander *et al.* 2007; Rajakaruna *et al.* 2009) where species- and community-level patterns appear to be more strongly influenced by macro- and micro-climate and the physical properties of the rock than by its mineral composition (Rajakaruna *et al.* 2009). In a comprehensive review of lichens found on ultramafic substrata worldwide, Favero-Longo *et al.* (2004) found co-occurrence of species characteristic of Ca-rich and Si-rich rocks and occurrence of species characterized by disjunct distribution patterns as common features of lichen communities in ultramafic environments. No consistent trends were detected in other features that are typical of phanerogams on ultramafics, such as paucity of species and occurrence of particular ecotypes. Several lichens collected from ultramafic substrata in Europe have been described as new to science, although it is unclear if these are truly ultramafic endemics, or species which are rare and were collected only from ultramafic substrata (Favero-Longo *et al.* 2004, with references therein). Moreover, most of the species first reported as restricted to ultramafic substrata are poorly differentiated from related species and have been collected from other substrata (Wirth 1972; Hafellner 1991). Whereas several recent lichen inventories exist for European ultramafic sites (Kossowska 2001; Favero-Longo *et al.* 2004, 2005; von Brackel 2007; Favero-Longo & Piervittori 2009), including the earliest known published study of the relationship between lichens and ultramafic substrata (Hegetschweiler & Stizenberger 1887), there are only a handful of published surveys to date of ultramafic lichens for North America (Ryan 1988; Sirois *et al.* 1988; Sigal 1989; Harris *et al.* 2007). Sirois *et al.* (1988) listed a total of 202 lichen taxa on Mt. Albert, Gaspésian Provincial Park, Québec, Canada, of which 157 were reported from partially serpentinized peridotite and 81 were restricted to this rock type. Of the taxa reported from ultramafic substrata, seven were new to North America, three were new to Canada, and 18 were new to Québec. They concluded that the ecological influences of ultramafic substrata on the lichens were similar to those observed on the region's vascular plants (Rune 1954), where many taxa are largely restricted to ultramafic substrata. A study of marine and maritime lichens collected from partially serpentinized peridotite rocks from Fidalgo Island, Skagit County, Washington, USA, found 61 species, including 15 species new to the state and one (*Verrucaria sandstedei* B. de Lesd.) new to North America (Ryan 1988). Only one study of lichens on ultramafic substrata is known to have been conducted in California (Sigal 1989), despite the strong focus there to elucidate the relationship between vascular plant species and ultramafic substrata (Alexander *et al.* 2007). Sigal (1989) reported 76 lichens from five ultramafic sites in central California. These included a collection of *Ramonia gylactiformis* (Zahlbr.) Vězda from peridotite and serpentinite at Complexion Springs in Lake

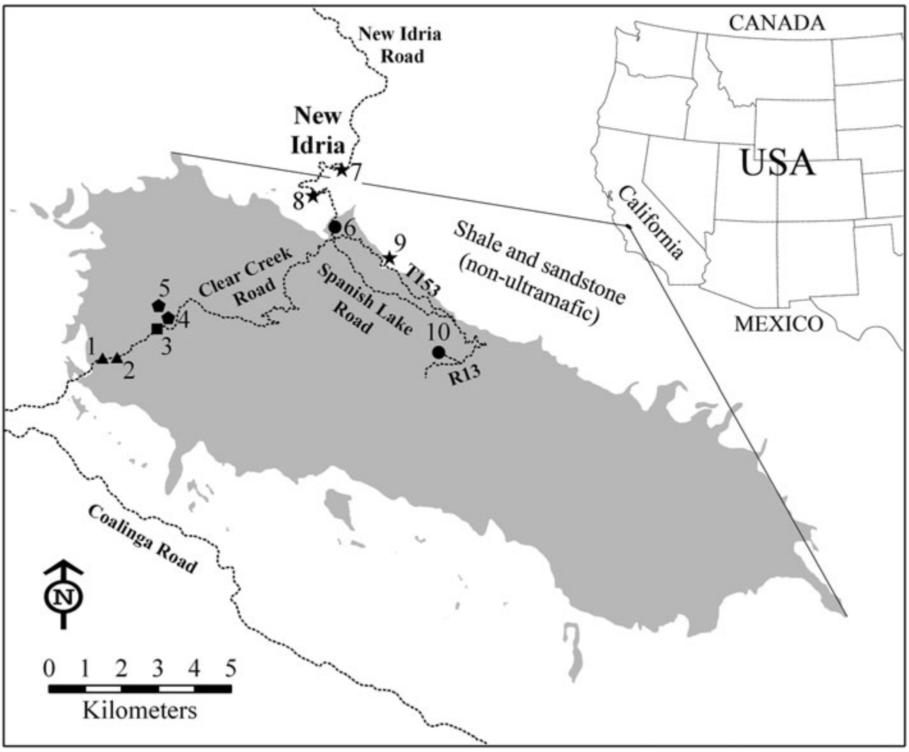

FIG. 1. Map of New Idria serpentinite mass showing sampling sites and their geological characteristics. Geology: ▨ =New Idria serpentinite (ultramafic), □ =Chert, shale, and sandstone (non-ultramafic). Collection locality geology: ▲ =Nephrite (ultramafic), ■ =Serpentinized peridotite (ultramafic), ⬟ =Silica-carbonate (non-ultramafic), ★ =Shale and sandstone (non-ultramafic), ● =Serpentinite (ultramafic). Numbers refer to collection sites given in Table 1. R13 & T153 are road numbers.

County that was recently recognized as a distinct species and described as new to science as *Ramonia extensa* Lendemer, K. Knudsen & Coppins (Lendemer *et al.* 2009). The taxon is still known only from the type collection on ultramafic rock and deserves further study to determine if it is a strict ultramafic endemic. A recent study by Harris *et al.* (2007) explored the lichen flora of a partially serpentinized peridotite outcrop on Little Deer Isle, Hancock County, Maine. Sixty-three species in 35 genera were found, with two species, *Buellia ocellata* (Flörke) Körb. and *Cladonia symphycarpia* (Flörke) Fr., being new reports for New England. The handful of available studies suggest that there may be an ultramafic substratum effect for lichens in North America, and that further study may reveal new species or interesting floristic associations.

Our study examines the saxicolous lichen flora of the New Idria serpentinite mass, San Benito County, California, USA (Fig. 1). Whereas previous studies have explored the geology (Van Baalen 1995), soils (Alexander *et al.* 2007), and their relationship to plant species (Lazarus *et al.* 2011) of this area, no studies to date have surveyed the cryptogamic biota of the area, including lichens. We present the lichen biota of nephrite (jade), partially serpentinized peridotite, serpentinite, silica-carbonate, shale, and sandstone rocks associated with, or adjacent to, the New Idria serpentinite mass, with relevant geochemical information for the rocks from which the species were collected.

Materials and Methods

Site description and field methods

The New Idria serpentinite mass, located in far southern San Benito and far western Fresno Counties, is one of the largest ultramafic masses in the South Coast Range of California, USA (36·3°N, 120·6°W; Figs 1, 2A). The lenticular mass of serpentinite is *c.* 22 km long, 8 km wide, and totals 13 000 ha. It forms the centre of an asymmetrical anticlinal dome that is flanked by Jurassic and Cretaceous-aged sedimentary rocks (shale and sandstone) of the Franciscan and Panoche formations (Van Baalen 1995). The serpentinite mass was derived from peridotite (harzburgite and dunite), which has been completely minerologically altered, sheared, and crushed to yield a nearly incoherent mass of pulverized serpentinite, (Fig. 2B; Van Baalen 1995), although some small, scattered hard outcrops of nephrite, serpentinite and partially serpentinized peridotite remain (Fig. 3). The serpentinite of the outcrops is typically hard, but can flake off into large flakes and plates, and the surface texture varies from lamellar to granular to vacuolar porous. The partially serpentinized peridotite of the outcrops is typically hard, but can be crumbly, and generally has a coarse granular surface texture. Boulders of nephrite (very hard; granular surface texture) are distributed throughout the serpentinite mass. The New Idria serpentinite mass also contains massive inclusions of silica-carbonate rocks, many of which contain cinnabar (mercury ore) deposits (Fig. 4A). Silica-carbonate rocks are typically hard with a vacuolar porous surface texture and have a dominant mineral composition of quartz, chalcedony, opal, ankerite, magnesite, and dolomite (Van Baalen 1995). Silica-carbonate forms from the precipitation of minerals from hydrothermal fluids of ultramafic origin within the serpentinite mass (Van Baalen 1995). The rocks contain $\gg$45% Si and $\ll$18% MgO and, therefore, although they are derived from hydrothermal fluids of ultramafic origin, silica-carbonate is classified as a non-ultramafic rock in this study. Cinnabar deposits also occur in Panoche shale and sandstone on the north-eastern edge of the New Idria serpentinite mass at New Idria (New Idria Mine Tailings; New Idria Camp Pit 2) and San Carlos Peak (San Carlos Peak Mine Pit; Fig. 5B). Cinnabar was mined at New Idria and San Carlos Peak from 1851 to 1972 (Gilbert 1984) and numerous large open mine pits and cinnabar-bearing tailing piles (tips) still remain.

The New Idria serpentinite mass is subject to a Mediterranean-type climate (cool wet winters and hot dry summers) with mean annual precipitation of 40–60 cm (Alexander *et al.* 2007) that primarily occurs between October and April. Snow is occasional during winter (December–February) and short-lived. Elevation range across the sampling localities varies from 841 m to 1422 m. Vegetative cover consists of chaparral at lower elevations and conifer forest at higher elevations. 'Moonscape' barrens, completely devoid of vegetation, are abundant and a prominent feature of the New Idria serpentinite mass (Figs 2, 3 & 5A).

On 22 February 2010 and 21–22 April 2011, we collected lichens from ultramafic rocks including nephrite ($n = 2$ sites), partially serpentinized peridotite ($n = 1$), and serpentinite ($n = 2$), and from non-ultramafic rocks including silica-carbonate ($n = 2$) and shale and sandstone ($n = 3$) adjacent to the New Idria serpentinite mass (Table 1; Fig. 1). For this study, sedimentary shale and sandstone are together considered a single rock type. All five non-ultramafic sites were extensively disturbed by mining as late as 1972, exposing fresh rock surfaces, in contrast to the little to no disturbance that has occurred at the ultramafic sites. As a result, the lichen community on the non-ultramafic sites represents a younger community than that on the ultramafic sites. Lichens were collected at each site until it was subjectively considered that the site had been well sampled. This varied from around 15 minutes (Sites 2, 3 and 8) to over an hour (Sites 1 and 10). It was considered that this was preferable to spending a fixed amount of time at each site, which would have resulted in disproportionate effort being expended on species-poor sites and would have resulted in these sites being over recorded. Representative rock samples, upon which the lichens were growing, were also collected. All lichen collections were identified by either the second or third authors, using standard reference works and comparison with named herbarium specimens or, for critical species, by experts in a particular group (see acknowledgments). All collections are permanently housed in the herbaria of either the College of the Atlantic (HCOA), University of California, Riverside (UCR), or Michigan State University (MSC). Nomenclature and naming authorities follow Index Fungorum Partnership (http://indexfungorum.org).

Elemental analysis

Elemental analysis (X-ray fluorescence) was conducted on pooled samples of 1–3 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 Thermo ARL Advant'XP+ wavelength dispersive sequential unit running at 60 keV and 60 mA with a rhodium target. Samples received as rock were prepared for analysis by chipping in a hardened steel jaw crusher then ground to a very fine powder in a tungsten carbide ring mill. The sample powder was weighed with di-lithium tetraborate flux at a 2:1 (low dilution) flux to rock ratio, mixed, then fused at 1000°C in a muffle oven for 45 min. Once cooled, the glass pellet was then re-ground, re-fused, and polished on diamond laps to provide a smooth flat surface for analysis. The concentration of elements was measured in *c.* 66 min under full vacuum with a 29 mm mask. The net intensities for all elements were corrected for line interferences and background slopes. Inter-element absorption and secondary enhancement effects were calculated using the fundamental

Fig. 2. A, general view of the New Idria serpentinite area, Site 5 (silica-carbonate rock) is just below horizon on the extreme right; B, close up of New Idria serpentinite mass near Site 5 (silica-carbonate rock) showing the generally fragmented nature of the substratum.

FIG. 3. Ultramafic outcrops. A, nephrite: large boulder at Staging Area (Site 1); B, serpentinite: over view of New Idria Reservoir (Site 6); C, serpentinite: close-up of a small part of San Benito Mountain Summit (Site 10).

FIG. 4. Non-ultramafic rock types studied. A, silica-carbonate: Clear Creek Mine just below horizon (Site 5); B, shale and sandstone: San Carlos Peak Mine (Site 9).

TABLE 1. *Locality and substratum information for Sites 1–10 from which lichens were collected*

Site	Locality	Coordinates	Elevation (m)	Substratum	Rock surface texture	Dominant slope aspect	Disturbance to rock surface	Sampling area (m^2)	Total area (m^2)
1	Staging Area 1	36°22′12.22″N 120°44′51.63″W	843	Nephrite	Fine granular to lamellar	South	None	59	59
2	Between Staging Area 1 and 2	36°22′12.08″N 120°44′42.16″W	835	Nephrite	Fine granular to lamellar	North-west	None	34	34
3	Clear Creek Road below Lower Silica-Carbonate Outcrop	36°22′31.60″N 120°43′54.50″W	914	Partially serpentinized peridotite	Coarse granular	South	None	9	9
4	Lower Silica-Carbonate Outcrop	36°22′41.79″N 120°43′40.06″W	955	Silica-Carbonate	Vacuolar porous	South-west	Mining (ceased ~1950?)	360	19 456
5	Upper Silica-Carbonate Outcrop	36°22′48.07″N 120°43′39.90″W	1014	Silica-Carbonate	Vacuolar porous	South-west	Mining (ceased ~1950?)	403	19 456
6	New Idria Reservoir	36°24′5.65″N 120°40′30.82″W	1164	Serpentinite	Lamellar	West	None	89	303
7	New Idria Mine Tailings	36°24′55.47″N 120°40′21.81″W	812	Shale and Sandstone (furnace tailings)	Clastic; medium to coarse grained	North-east	Mining (ceased ~1972)	1 833	156 191
8	New Idria Camp 2 Pit	36°24′33.42″N 120°40′52.60″W	1087	Shale and Sandstone	Clastic; medium to coarse grained	North	Mining (ceased ~1972)	555	154 072
9	San Carlos Peak Mine Pit	36°23′34.14″N 120°39′31.17″W	1426	Shale and Sandstone	Clastic; medium to coarse grained	South	Mining (ceased ~1972)	6 694	66 264
10	San Benito Mountain Summit	36°22′10.49″N 120°38′40.82″W	1602	Serpentinite	Vacuolar porous	South	None	42	433

parameters method. Approximately 105 diverse certified reference materials were employed for instrument calibration, and two internal standards were run on a regular basis to provide a continuous check on instrument performance.

Statistical analysis

Multiple permutational one-way ANOVAs with 999 permutations (Legendre 2007) and post-hoc comparisons implemented by package coin (Hothorn *et al.* 2008) were used to test the hypothesis that measured elemental concentrations differed across rocks collected from nephrite + partially serpentinized peridotite + serpentinite (collectively 'ultramafic'), silica-carbonate, and shale and sandstone sites (collectively 'non-ultramafic'). A Benjamini-Hotchberg correction for multiple comparisons was applied to the *P*-values from these 32 variables to control for false discovery rates (FDR), which is suitable for situations where explanatory variables are correlated between multiple tests (García 2003). A *t*-test was used to compare log-transformed species richness per 10 m × 10 m sampling area between ultramafic and non-ultramafic sites. A permutational multivariate analysis of variance (perMANOVA) with 999 permutations, function adonis of package vegan (Oksanen *et al.* 2011) was used to compare the assemblage of lichens among ultramafic vs. non-ultramafic sites. This comparison was chosen based upon the substantial differences in elemental composition between the two rock types. The sizes of the matrices included in the perMANOVA were 10 sites by 112 species and 44 genera. Lichenicolous fungi were excluded from the analysis because they are mostly species-specific and including them in the analysis would be equivalent to including their host species twice. Function adonis uses a dissimilarity matrix to statistically compare the squared deviations of multivariate group centroids, and is well suited to the analysis of biotic community assemblage where the presence or absence of many taxa must be compared across few regions (Anderson 2001; McArdle & Anderson 2001). Equal dispersion of group scores (analogous to a test for multivariate homogeneity of variances) was assessed using function betadisper in package vegan (Oksanen *et al.* 2011). Kulczynski distance (Faith *et al.* 1987) was chosen as an appropriate index of dissimilarity as it is robust to 'richness dependency', where site pairs with similar composition but differing richness receive high dissimilarity values (Hausdorf & Hennig 2005). To check for correlation between patterns of community assemblage and substratum elemental composition, a Mantel test (with 999 permutations; function mantel in package vegan) was employed using a Kulczynski distance matrix of beta diversity and a matrix of variance-scaled, mean-centred Euclidean distances for the correlated elemental variables. All statistical analyses were performed using R version 2.13.2 (R Development Core Team 2011).

Results

Rock chemistry

The composition of measured ultramafic, silica-carbonate, and shale and sandstone rocks differed significantly for 26 of 32 elements (Table 2; permutational one-way ANOVA; Benjamini-Hotchberg corrected $P < 0{\cdot}05$). Notable distinctions include significantly lower Ca:Mg ratios for ultramafic rocks and higher concentrations of heavy metals such as Ni and Cr. Additionally, non-ultramafic rocks were significantly higher compared to ultramafic rocks in rare earth elements such as Ba, Rb, Sr, V, Y, and Zr.

Floristics

We identified a total of 119 species of lichenized and lichenicolous fungi (Table 3), of which four, *Buellia ocellata*, *Caloplaca oblongula*, *Rhizocarpon saurinum*, and *Thelocarpon laureri*, are reported for the first time from California, and two, *Buellia aethalea* and *Trapelia obtegens*, are represented from California only by unpublished collections in the Consortium of North American Lichen Herbaria database (http://symbiota.org/nalichens). *Buellia aethalea* was collected from ultramafic rocks, *B. ocellata* from ultramafic and non-ultramafic rocks, and the other four species from non-ultramafic rocks. Additionally, a collection of a *Solenopsora* sp. from silica-carbonate rock does not correspond to any of the species of this genus currently listed as occurring in North America (Esslinger 2011), and is under further investigation by molecular methods to confirm its taxonomic status.

By far the largest number of taxa (83) was collected from ultramafic rocks, with the two other rock types sampled, silica-carbonate (37) and shale and sandstone (28) (non-ultramafic rocks), being far less species-rich. A similar pattern is apparent for taxa collected from only one rock type, with ultramafic rocks (60) having far more taxa restricted to that substratum than the two non-ultramafic rock types: silica-carbonate (19), shale and

TABLE 2. *Elemental chemistry of ultramafic and non-ultramafic rocks from which lichens were collected. Major (Al-Ti) elements are reported as % weight, whereas the minor (As-Zr) elements are reported as ppm. Elemental analysis determined via X-ray Fluorescence (XRF) analysis. Original* P *values and Benjamini-Hotchberg q values (corrected p values) are from a permutational one-way ANOVA for each element across ultramafic (*n = 5*), silica-carbonate (*n = 2*), and shale and sandstone (*n = 3*) substrata. Significant values ($\leq 0{\cdot}05$) are in bold. Comparisons between substrata are denoted with superscripted letters adjacent to their respective means ± standard errors; different letters indicate a significant difference*

	Ultramafic rock					Non-ultramafic rock					Ultramafic	Non-ultramafic		
	Nephrite		Serpentinized peridotite	Serpentinite		Silica-carbonate		Shale and sandstone						
Site# →←	1	2	3	6	10	4	5	7	8	9	Nephrite; Serpentinized peridotite; Serpentinite (Mean ± SE)	Silica-Carbonate (Mean ± SE)	Shale and Sandstone (Mean ± SE)	*P*/q Value
Major Elements (%)														
Al_2O_3	0·26	0·28	4·48	1·47	0·22	15·04	15·44	12·46	13·64	15·48	1·28 ± 0·82^{A}	15·24 ± 0·2^{B}	13·86 ± 0·88^{B}	**0·005/ 0·011**
CaO	0·53	0	0·04	0·85	0·02	0·13	0·11	0·18	0·12	0·26	0·28 ± 0·17	0·12 ± 0·01	0·19 ± 0·04	0·855/0·883
FeO	4·95	5·38	8·21	6·1	8·64	0·2	7·6	4·27	5·9	3·69	6·66 ± 0·75	3·9 ± 3·7	4·62 ± 0·66	0·330/0·364
K_2O	0·03	0·01	0·01	0	0·01	2·41	2·69	6·99	1·67	3·33	0·01 ± 0·004^{A}	2·55 ± 0·14^{B}	4·00 ± 1·57^{B}	**0·011/0·017**
MgO	35·2	38·79	34·92	37·25	31·46	0·28	0·29	0·25	0·23	0·41	35·52 ± 1·24^{A}	0·29 ± 0·005^{B}	0·30 ± 0·06^{B}	**0·012/0·017**
CaO:MgO	0·015	0	0·001	0·023	0·001	0·461	0·377	0·734	0·52	0·629	0·008 ± 0·005^{A}	0·419 ± 0·042^{B}	0·628 ± 0·062^{B}	**<0·001/0·005**
MnO	0·108	0·098	0·167	0·111	0·098	0·002	0	0·082	0·02	0·016	0·116 ± 0·013^{A}	0·001 ± 0·001^{B}	0·039 ± 0·021^{B}	**<0·001/0·005**
Na_2O	0·04	0·01	0	0	0·01	4·61	6·03	1·1	6·17	5·23	0·01 ± 0·007^{A}	5·32 ± 0·71^{B}	4·17 ± 1·56^{B}	**0·008/0·015**
P_2O_5	0·017	0·007	0·007	0·005	0·01	0·041	0·1	0·141	0·09	0·118	0·009 ± 0·002^{A}	0·071 ± 0·03^{B}	0·116 ± 0·015^{B}	**<0·001/0·005**
SiO_2	16·63	43·01	39·88	41·62	48·08	72·13	61·25	70·54	64·52	66·99	37·84 ± 5·48^{A}	66·69 ± 5·44^{B}	67·35 ± 1·75^{B}	**0·007/0·014**
SO_3	0·02	0	0	0	0	0	0·31	0	1·42	0	0·004 ± 0·004	0·155 ± 0·155	0·473 ± 0·473	0·353/0·377
TiO_2	0·017	0·002	0·016	0·008	0·003	0·702	0·71	0·604	0·65	0·673	0·009 ± 0·003^{A}	0·706 ± 0·04^{B}	0·642 ± 0·02^{B}	**0·002/ 0·007**
Trace Elements (ppm)														
As	0	3	0	0	0	0	30	15	5	9	0 ± 0^{A}	15 ± 15^{A,B}	9·7 ± 2·9^{B}	0·072/ 0·085
Ba	36	7	28	16	7	501	608	831	414	850	18·8 ± 5·8^{A}	554·5 ± 53·5^{B}	698·3 ± 142·3^{B}	**<0·001/0·005**
Ce	3	0	0	3	0	42	34	21	28	45	1·2 ± 0·7^{A}	38 ± 4^{B}	31·3 ± 7·1^{B}	**0·002/0·007**
Cr	2766	2381	935	1971	999	104	115	112	111	103	1810 ± 367^{A}	110 ± 6^{B}	109 ± 3^{B}	**0·028/0·036**
Cu	7	3	3	8	3	8	54	112	62	52	4·8 ± 1·1^{A}	31 ± 23^{A,B}	75·3 ± 18·6^{B}	**0·012/0·017**
Ga	1	1	4	2	1	15	19	15	14	18	1·8 ± 0·6^{A}	17 ± 2^{B}	15·7 ± 1·2^{B}	**0·004/0·010**
La	2	4	0	1	1	21	21	12	12	24	1·6 ± 0·7^{A}	21 ± 0^{B}	16 ± 4^{B}	**<0·001/0·005**
Nb	0·4	0·7	0·7	0·6	0·3	9·4	9·5	5·9	9	8·4	0·54 ± 0·08^{A}	9·45 ± 0·05^{B}	7·77 ± 0·95^{B}	**<0·001/0·005**
Nd	2	1	1	3	1	17	13	14	11	20	1·6 ± 0·4^{A}	15 ± 2^{B}	15 ± 2·6^{B}	**0·009/0·015**
Ni	1839	1912	2074	1933	2662	22	17	105	22	115	2084 ± 149^{A}	20 ± 3^{B}	81 ± 29^{B}	**0·010/0·016**
Pb	1	3	42	1	3	12	8	10	10	17	10 ± 8	10 ± 2	12 ± 2	0·988/0·988
Rb	1	0	1	0	0	63	85	172	53	94	0·4 ± 0·2^{A}	74 ± 11^{B}	106·3 ± 34·9^{B}	**0·002/0·007**
Sc	6	5	13	8	5	9	10	22	15	17	7 ± 1·5^{A}	9·5 ± 0·5^{A,B}	18 ± 2^{B}	**0·009/0·015**
Sr	40	1	4	74	1	77	74	62	125	86	24 ± 14·5^{A}	75·5 ± 1·5^{A,B}	91 ± 18·4^{B}	**0·041/0·050**
Th	0	0	0	0	0	5	8	4	4	8	0 ± 0^{A}	6·5 ± 1·5^{B}	5·3 ± 1·3^{B}	**0·004/0·010**
U	0	0	1	0	0	1	4	2	2	2	0·2 ± 0·2^{A}	2·5 ± 1·5^{A,B}	2 ± 0^{B}	**0·017/0·023**
V	22	25	62	38	10	128	133	142	126	137	31·4 ± 8·9^{A}	130·5 ± 2·5^{B}	135 ± 4·7^{B}	**0·004/0·010**
Y	2	2	2	2	1	22	19	22	13	21	1·8 ± 0·2^{A}	20·5 ± 1·5^{B}	18·7 ± 2·8^{B}	**0·005/0·011**
Zn	38	40	51	41	31	4	25	113	17	82	40·2 ± 3·2	14·5 ± 10·5	70·7 ± 28·3	0·103/ 0·118
Zr	5	0	4	0	1	138	160	105	144	135	2 ± 1·1^{A}	149 ± 11^{B}	128 ± 11·8^{B}	**0·004/0·010**

TABLE 3. *112 lichen taxa and 7 lichenicolous fungi collected from 10 sites at the New Idria serpentinite mass. The six taxa in bold font are new reports or newly published records for California. Names marked with a * were reported from more than one ultramafic site by* Favero-Longo *et al. (2004), and those with a † by Sigal (1989). Nomenclature and naming authorities follow Index Fungorum Partnership* (http://indexfungorum.org)

		Ultramafic rock				Non-ultramafic rock					Number of Sites		
		Nephrite	Serpentinized peridotite		Serpentinite		Silica-Carbonate			Shale and Sandstone	Ultramafic rock	Non-ultramafic rock	Total
	Taxon	Site 1	Site 2	Site 3	Site 6	Site 10	Site 4	Site 5	Site 7	Site 8	Site 9			
	Acarospora americana H. Magn.	x	.	.	.	x	.	x	x	x	x	2	4	6
	A. oligospora (Nyl.) Arnold	.	.	.	.	.	.	x	.	.	.	.	1	1
	A. rosulata (Th. Fr.) H. Magn.	x	.	.	.	.	.	.	.	.	.	1	.	1
	A. socialis H. Magn.	x	.	.	.	.	.	x	.	.	x	1	2	3
	A. thamnina (Tuck.) Herre	.	.	.	.	x	.	.	.	.	.	1	.	1
	Aspicilia confusa Owe-Larss. & A. Nordin	x	.	.	.	x	.	.	.	.	.	2	.	2
	A. cuprea Owe-Larss. & A. Nordin	.	.	.	.	x	.	.	.	.		1	.	1
	A. phaea Owe-Larss. & A. Nordin	x	.	.	x	x	.	x	.	.	.	3	1	4
	A. praecrenata (Nyl.) Hue	x	x	.	.	x	x	x	.	.	.	3	2	5
	Buellia abstracta (Nyl.) H. Olivier	x	.	.	.	.	.	.	.	.	.	1	.	1
*	***B. aethalea* (Ach.) Th. Fr.**	.	.	.	.	x	.	.	.	.	.	1	.	1
†	*B. badia* (Fr.) A. Massal.	x	.	.	x	.	.	.	.	.	.	2	.	2
	B. dispersa A. Massal.	x	x	.	.	.	.	.	.	.	.	2	.	2
	B. nashii Bungartz	x	.	.	.	.	.	.	.	.	.	1	.	1
*	***B. ocellata* (Flörke) Körb.**	.	.	.	.	x	.	.	.	.	x	1	1	2
	Caloplaca albovariegata (B. de Lesd.) Wetmore	.	x	.	.	.	.	.	.	.	.	1	.	1
	C. arenaria (Pers.) Müll. Arg.	.	.	.	.	.	.	.	.	.	x	.	1	1
	C. biatorina (Trevis.) J. Steiner	x	.	.	x	.	.	x	.	.	x	2	2	4
	C. crenulatella (Nyl.) H. Olivier	x	.	.	.	.	.	.	.	.	.	1	.	1
	C. demissa (Körb.) Arup & Grube	x	.	.	.	.	.	.	.	.	.	1	.	1
	C. epithallina Lynge	.	.	.	.	x	.	.	.	.	.	1	.	1
	C. ignea Arup	x	.	x	.	.	.	.	.	.	.	2	.	2
	C. impolita Arup	.	.	x	.	x	.	.	.	.	.	2	.	2
	C. ludificans Arup	.	.	.	.	.	x	.	.	.	.	.	1	1
	C. luteominia (Tuck.) Zahlbr.	.	.	.	.	.	x	.	.	.	.	.	1	1
	***C. oblongula* (H. Magn.) Wetmore**	.	.	.	.	.	.	x	.	.	.	.	1	1
	C. subsoluta (Nyl.) Zahlbr.	.	.	.	.	x	.	.	.	.	.	1	.	1
†	*Candelaria concolor* (Dicks.) Jatta	.	.	.	x		.	.	.	.	.	1	.	1
*	*Candelariella aurella* (Hoffm.) Zahlbr.	.	.	.	.	x	x	.	.	.	.	1	1	1
	C. citrina B. de Lesd.	.	.	.	.	.	.	x	.	.	.	.	1	1
	C. rosulans (Müll. Arg.) Zahlbr.	x	.	.	x	x	.	x	.	.	.	3	1	4
* †	*C. vitellina* (Hoffm.) Müll. Arg.	x	.	.	.	x	.	.	.	.	x	2	1	3
	Collema coccophorum Tuck.	.	.	.	.	.	.	x	.	.	.	.	1	1
*	*C. furfuraceum* Du Rietz	x	.	.	.	.	.	.	.	.	.	1	.	1
	Dermatocarpon leptophylloides (Nyl.) Zahlbr.	x	.	.	.	.	.	.	.	.	.	1	.	1
	D. reticulatum H. Magn.	.	.	.	.		.	x	.	.	.	.	1	1
	Dimelaena oreina (Ach.) Norman	x	.	.	.	.	.	.	.	.	.	1	.	1
	D. thysanota (Tuck.) Hale & W.L. Culb.	x	.	.	.	x	.	.	.	.	.	2	.	2
	Koerberia sonomensis (Tuck.) Henssen	x	.	.	.	.	.	.	.	.	.	1	.	1
*	*Lecanora intricata* (Ach.) Ach.	.	.	.	.	x	.	.	.	.	.	1	.	1
	L. garovaglii (Körb.) Zahlbr.	x	.	.	x	.	.	.	.	.	x	2	1	3
*	*L. muralis* Rabenh.	x	.	.	x	.	.	.	.	.	x	2	1	3
* †	*L. rupicola* (L.) Zahlbr.	.	.	.	.	x	.	.	.	.	.	1	.	1
	L. sierrae B.D. Ryan & T.H. Nash	x	.	.	.	.	.	.	.	.	x	1	1	2
	Lecidea laboriosa Müll. Arg.	.	.	.	x	.	.	.	.	.	x	1	1	2
* †	*L. tessellata* Flörke	x	.	.	x	x	.	.	.	.	.	3	.	3
	Lecidella asema (Nyl.) Knoph & Hertel	.	.	.	x	.	.	.	.	.	.	1	.	1

Table 3. *Continued*

	Ultramafic rock					Non-ultramafic rock					Number of Sites		
	Nephrite	Serpentinized peridotite		Serpentinite		Silica-Carbonate			Shale and Sandstone		Ultramafic rock	Non-ultramafic rock	Total
Taxon	Site 1	Site 2	Site 3	Site 6	Site 10	Site 4	Site 5	Site 7	Site 8	Site 9			
* † *Lecidella carpathica* Körb.	x	.	.	x	x	.	x	.	.	.	3	1	4
* † *L. stigmatea* (Ach.) Hertel & Leuckert	x	.	.	.	.	.	x	.	.	.	1	1	2
Lepraria texta K. Knudsen *et al.*	x	.	.	.	.	.	.	.	.	.	1	.	1
† *Leptochidium albociliatum* (Desm.) M. Choisy	x	.	.	x	.	.	x	.	.	.	2	1	3
† *Leptogium californicum* Tuck.	x	.	.	.	.	.	.	.	.	.	1	.	1
L. lichenoides (L.) Zahlbr.	.	x	.	.	.	.	x	.	.	.	1	1	2
* *L. tenuissimum* (Hoffm.) Körb.	x	.	.	.	.	.	.	.	.	.	1	.	1
Lichenothelia tenuissima Henssen	.	.	.	.	.	.	x	.	.	.	.	1	1
Melanohalea elegantula (Zahlbr.) O. Blanco *et al.*	.	.	.	.	x	.	.	.	.	.	1	.	1
Melanelixia glabroides (Essl.) O. Blanco *et al.*	.	.	.	.	x	.	.	.	.	.	1	.	1
Myriospora scabrida (H. Magn.) K. Knudsen & L. Arcadia	.	.	.	x	.	.	x	.	.	.	1	1	1
† *Peltula bolanderi* (Tuck.) Wetmore	x	.	.	.	.	.	.	.	.	.	1	.	1
P. euploca (Ach.) Poelt ex Ozenda & Clauzade	x	.	.	.	.	.	.	.	.	.	1	.	1
Physcia biziana (A. Massal.) Zahlbr.	x	.	.	.	x	.	.	.	.	.	2	.	2
P. stellaris (L.) Nyl.	.	.	.	.	.	.	.	.	x	.	.	1	1
P. dimidiata (Arnold) Nyl.	.	.	.	x	.	.	.	.	.	.	1	.	1
Physconia americana Essl.	.	.	.	x	x	.	.	.	.	.	2	.	2
P. californica Essl.	.	.	.	x	x	.	.	.	.	.	2	.	2
P. enteroxantha (Nyl.) Poelt	x	.	.	x	.	.	.	.	.	.	2	.	2
P. isidiomuscigena Essl.	.	.	.	.	.	.	.	.	.	x	.	1	1
* *P. muscigena* (Ach.) Poelt	.	.	.	.	x	.	.	.	.	.	1	.	1
Placidium lacinulatum (Ach.) Breuss	.	.	.	.	.	.	x	.	.	.	.	1	1
P. squamulosum (Ach.) Breuss	.	.	.	.	.	.	x	.	.	.	.	1	1
Placopyrenium stanfordii (Herre) K. Knudsen	x	.	x	.	.	.	.	.	.	.	2	.	2
Placynthiella hyporhoda (Th. Fr.) Coppins & P. James	.	.	.	.	.	.	.	.	x	.	.	1	1
Polysporina simplex (Taylor) Jatta	.	.	.	.	.	.	.	x	.	.	.	1	1
Protoblastenia rupestris (Scop.) J. Steiner	.	.	.	.	.	.	.	.	.	x	.	1	1
Psora luridella (Tuck.) Fink	.	.	.	.	.	.	x	.	.	.	.	1	1
Psorotichia hassei Fink ex J. Hedrick	.	.	.	.	.	x	.	.	.	.	.	1	1
P. montinii (A. Massal.) Forssell	.	.	.	.	.	.	.	x	.	.	.	1	1
† *Rhizocarpon bolanderi* (Tuck.) Herre	x	x	.	.	x	.	.	.	.	.	3	.	3
R. disporum (Nägeli ex Hepp) Müll. Arg.	.	.	.	.	x	.	.	.	.	.	1	.	1
* † *R. geographicum* (L.) DC.	.	.	.	.	x	.	.	.	.	.	1	.	1
***R. saurinum* (W.A. Weber) Bungartz**	.	.	.	.	.	.	x	.	.	.	.	1	
R. superficiale (Schaer.) Malme	.	.	.	.	x	.	.	.	.	.	1	.	1
* † *R. viridiatrum* (Wulfen) Körb.	.	x	.	x	x	.	.	.	.	.	3	.	3
Rhizoplaca glaucophana (Hasse) W.A. Weber	x	.	.	.	.	.	.	.	.	.	1	.	1
† *R. melanophthalma* (DC.) Leuckert	.	.	.	.	x	.	.	.	.	.	1	.	1
Rinodina bischoffii (Hepp) A. Massal.	.	.	.	.	.	.	x	.	.	.	.	1	
* *R. confragosa* (Ach.) Körb.	.	.	.	.	x	.	.	.	.	.	1	.	1
* *R. gennarii* Bagl.	.	.	.	x	.	.	.	.	.	.	1	.	1
R. milvina (Wahlenb.) Th. Fr.	.	.	.	x	.	.	.	.	.	.	1	.	1
R. obnascens (Nyl.) H. Olivier	.	.	.	.	.	x	x	.	.	.	.	2	2
R. straussii J. Steiner	.	.	.	x	.	.	x	.	.	.	1	1	2
Sarcogyne arenosa (Herre) K. Knudsen & S.M. Standl.	.	.	.	.	.	.	x	x	.	.	.	2	2
***Solenopsora* sp.**	.	.	.	.	.	.	x	.	.	.	.	1	1
Staurothele areolata (Ach.) Lettau	.	.	.	.	x	.	.	.	.	.	1	.	1
S. elenkinii Oxner	.	.	.	.	.	x	.	.	.	.	.	1	1
***Thelocarpon laureri* (Flot.) Nyl.**	.	.	.	.	.	.	.	x	.	.	.	1	1

Table 3. *Continued*

	Ultramafic rock					Non-ultramafic rock					Number of Sites		
	Nephrite		Serpentinized peridotite	Serpentinite		Silica-Carbonate		Shale and Sandstone			Ultramafic rock	Non-ultramafic rock	Total
Taxon	Site 1	Site 2	Site 3	Site 6	Site 10	Site 4	Site 5	Site 7	Site 8	Site 9			
Toninia ruginosa ssp. *ruginosa* (Tuck.) Herre	x	.	.	.	.	.	x	.	.	.	1	1	2
Trapelia glebulosa (Sm.) J. R. Laundon	.	.	.	.	.	.	.	x	.	.	.	1	1
***T. obtegens* (Th. Fr.) Hertel**	.	.	.	.	.	.	.	x	x	.	.	2	2
† *Umbilicaria phaea* Tuck.	.	.	.	.	x	.	x	.	.	x	1	2	3
Verrucaria calkinsiana Servít	.	.	.	.	.	.	.	x	.	.	.	1	1
V. fuscoatroides Servít	.	.	.	.	.	.	x	.	.	x	.	2	2
V. nigrofusca Servít	.	.	.	.	.	.	.	.	.	x	.	1	1
V. sphaerospora Anzi	.	.	.	x	.	.	.	.	.	.	1	.	1
Xanthomendoza fallax (Arnold) Søchting *et al.*	x	.	.	.	.	.	.	.	.	.	1	.	1
Xanthoparmelia cumberlandia (Gyeln.) Hale	x	.	.	.	.	.	.	.	.	.	1	.	1
X. loxodes (Nyl.) O. Blanco *et al.*	.	.	.	.	x	.	.	.	.	.	1	.	1
X. mexicana (Gyeln.) Hale	.	.	.	x	.	.	.	.	.	.	1	.	1
X. subplitti Hale	.	.	.	.	.	.	.	.	.	x	.	1	1
X. verruculifera (Nyl.) O. Blanco *et al.*	.	.	.	x	x	.	.	.	.	.	2	.	2
* *Xanthoria elegans* (Link) Th. Fr.	.	.	.	.	x	.	.	.	.	.	1	.	1
X. fulva (Hoffm.) Poelt & Petut.	.	.	.	.	.	.	.	.	.	x	.	1	1
Total number of lichens reported from:													
Locality	**41**	**6**	**3**	**24**	**37**	**7**	**29**	**8**	**4**	**17**			
Rock type	**44**		**3**	**53**		**34**		**26**					
Rock category	**79**					**54**							
Total number of lichens restricted to:													
Locality	**18**	**1**	**0**	**7**	**17**	**3**	**12**	**5**	**2**	**6**			
Rock type	**20**		**0**	**27**		**16**		**14**					
Rock category	**58**					**33**							
Total number of lichens shared between (shaded):													
ultramafic/silica-carbonate	**11**												
ultramafic/shale and sandstone	**6**												
silica-carbonate/shale and sandstone						**2**							
ultramafic/silica-carbonate/shale and sandstone	**4**												
Lichenicolous Fungi													
Arthonia varians (Davies) Nyl. (on *Lecanora rupicola*)	.	.	.	.	x	.	.	.	.	.	x	.	.
Endococcus stigma (Körb.) Stizenb. (on *Acarospora socialis*)	.	.	.	.	.	.	x	.	.	.	.	x	.
Lichenostigma cosmopolites Hafellner & Calat. (on *Xanthoparmelia subplitti*)	.	.	.	.	.	.	.	.	.	x	.	.	x
L. elongatum Nav.-Ros. & Hafellner (on *Aspicilia* spp.)	x	.	.	.	.	.	.	.	.	x	x	.	x
L. subradians Hafellner *et al.* (on *Acarospora socialis*)	x	.	.	.	.	.	x	.	.	.	x	x	.
Stigmidium epistigmellum (Nyl. ex Vouaux) Kocourk. & K. Knudsen (on *Caloplaca ludificans*)	.	.	.	.	.	x	x	.	.	.	.	x	.
S. squamaria (B. de Lesd.) Cl. Roux & Triebel (on apothecia of *Lecanora muralis*)	.	.	.	x	.	.	.	.	.	.	x	.	.

TABLE 4. *Results from perMANOVA with 1000 permutations, showing differences in lichen community assembly between ultramafic and non-ultramafic (silica-carbonate and shale and sandstone) rocks at the species and generic level*

	df	*F*	R^2	*P* value
Species (112)				
Substratum	1	1·812	0·185	0·020
Residuals	8	.	0·815	.
Total	9	.	1	.
Genera (44)				
Substratum	1	1·651	0·171	0·164
Residuals	8	.	0·829	.
Total	9	.	1	.

sandstone (15). Data for taxa occurring on more than one substratum were ultramafic and silica-carbonate (11), ultramafic and shale and sandstone (6), silica-carbonate and shale and sandstone (2). Interestingly, only four species (*Acaropsora americana, A. socialis, Caloplaca biatorina*, and *Umbilicaria phaea*) occurred on all three rock types (Table 3).

Lichen-substratum relations

Species richness per 10 m × 10 m sampling area was significantly greater at the ultramafic sites (*t*-test; $t = 5{\cdot}51$, $P = 0{\cdot}002$; see Table 4), despite the wide range in species richness per site within each site group (Table 3), which was due, at least in part, to differences in the range of microhabitats present. Species richness standardized by area surveyed may not be an entirely accurate measure of alpha-diversity, as species-area curves are asymptotic. However, undisturbed ultramafic areas had a much greater species richness than disturbed non-ultramafic areas, despite the much smaller average size of the former (Table 1). The perMANOVA revealed significant differences in lichen assemblage between ultramafic and non-ultramafic sites at the species level ($P = 0{\cdot}020$, 112 variables) but not at the generic level ($P = 0{\cdot}164$, 44 variables; see Table 5). Dispersion of group scores was equal between ultramafic and non-ultramafic sites ($P = 0{\cdot}683$, $H_0 =$ no difference between groups). Species richness per 10 m × 10 m sampling area and site scores from the species-level perMANOVA indicate that silica-carbonate sites supported lichen communities intermediate between ultramafic and shale and sandstone (see Table 6). However, we did not include silica-carbonate as a separate factor in our analysis due to small sample size. The most useful taxa in distinguishing groups by the perMANOVA are summarized in Table 6. Lichen species assemblage and elemental composition among sites were weakly correlated (Mantel test; $r = 0{\cdot}273$, $P = 0{\cdot}02$).

Discussion

The importance of rock mineralogy, including elemental geochemistry, in determining the composition of saxicolous lichen communities has long been recognized (Purvis & Halls 1996). However, as pointed out by Brodo (1973), attempts to analyze the distribution of saxicolous lichens according to their lithochemistry are not very common (e.g. Werner 1956), and studies that directly associate quantitatively assessed mineralogy or elemental chemistry of host rocks to the presence of lichen species or the assemblage of lichen communities are rare (e.g. Boyle *et al.* 1987). The exact nature of this substratum-level influence on lichens (i.e. whether chemical and/or textural) also appears to be obscure, although complex interactions between lichens and rocks and lichens and elements are often cited (Richardson 1995; Wilson 1995; Purvis 1996; Shimizu 2004; Hauck *et al.* 2007). Purvis (1996) states that systematic description of lichen communities

TABLE 5. *Species and genera that contribute substantially (absolute scores above the 95th percentile) to distinguishing ultramafic and non-ultramafic lichen communities in the perMANOVA model. 'Score' is the relative weight given to the taxon by the analysis. 'Occurrence' lists the sites where a given taxon occurred, with cross-over between substrata in bold font and, for genera, number of subtaxa given in parentheses*

Taxon	Score	Occurrence
Ultramafic		
Genus		
Buellia	0·3	1(4), 2(1), **4**(1), **5**(2), 10(1)
Caloplaca	0·5	1(4), 2(1), 3(2), **4**(1), **5**(3), 6(2), 7(2), 10(2)
Lecanora	0·2	1(3), **4**(2), **5**(2), 10(3)
Leptogium	0·2	1(2), 2(1), **7**(1)
Peltula	0·2	1(2)
Placopyrenium	0·2	1(1), 3(1)
Species		
Aspicilia confusa	0·2	1, 10
A. phaea	0·2	1, **5**, 6, 10
Buellia badia	0·2	1, 6
B. dispersa	0·2	1, 2
Caloplaca ignea	0·2	1, 3
C. impolita	0·2	3, 10
Candelariella rosulans	0·2	1, **5**, 6, 10
Dimelaena thysanota	0·2	1, 10
Lecidea tessellata	0·3	1, 6, 10
Lecidella carpathica	0·2	1, **5**, 6, 10
Physconia americana	0·2	6, 10
P. californica	0·2	6, 10
P. enteroxantha	0·2	1, 6
Placopyrenium stanfordii	0·2	1, 3
Rhizocarpon viridiatrum	0·3	2, 6, 10
Xanthoparmelia verruculifera	0·2	6, 10
Non-ultramafic		
Genus		
Physconia	−0·4	**1**(1), 4(3), 5(3), **10**(1)
Rinodina	−0·6	4(3), 5(1), **6**(1), 7(3)
Species		
Acarospora americana	−0·2	**1**, 5, 7, 8, 9, **10**
Rinodina obnascens	−0·2	4, 5
Sarcogyne arenosa	−0·2	5, 7
Trapelia obtegens	−0·2	7, 8
Verrucaria fuscoatroides	−0·2	1, 9

in relation to rock mineralogy, elemental chemistry, and geochemical processes is critical to advance understudied areas of lichenology, particularly physiological ecology and evolution. Thus, despite the obvious relationship between substratum and lichens, there still remains a critical need for the systematic description and characterization of lichen communities in relation to specific lithologies and chemical environments.

Our study is one of only a few to relate lichen occurrence to geochemistry of individual rocks (Boyle *et al.* 1987) (Table 2). Only four species were shared in common between all three substrata, suggesting substantial differences in lichen community composition between ultramafic and non-ultramafic rocks at both the species and generic levels (Tables 5 & 6). Brodo (1973) lists texture, water relations, and chemistry as the main factors that determine the composition of a lichen biota of a substratum. However, determining whether the differences we observed in lichen assemblages

TABLE 6. *Species richness values for sites (see Table 3), and per square decametre (see Table 1) compared with total lichen samples collected. Site scores are from a perMANOVA model of lichen species assembly between ultramafic* (n = 5) *and non-ultramafic* (n = 5) *sites*

Site	Substratum class	Total number of samples collected	Species Richness/Site Area	Species Richness/10 m^2	Site Score (perMANOVA)
1	ultramafic	45	41	6·94	−0·137
2	ultramafic	4	6	1·76	−0·113
3	ultramafic	3	3	3·33	−0·154
4	non-ultramafic	7	7	0·19	0·077
5	non-ultramafic	37	29	0·72	0·080
6	ultramafic	28	24	2·70	−0·117
7	non-ultramafic	10	8	0·04	0·156
8	non-ultramafic	2	4	0·07	0·148
9	non-ultramafic	27	17	0·03	0·086
10	ultramafic	38	37	8·80	−0·115

were due to the elemental content of the rocks, their physical properties, or age of the exposed rock surfaces was beyond the scope of this study. Generally, ultramafic rock outcrops are thought to support lichen taxa characteristic of exposed, sunny areas, those that have wide ecological amplitude, or taxa that colonize stressful habitats with reduced competition (Purvis 1996; Favero-Longo *et al.* 2004; Harris *et al.* 2007). Additionally, the lichen biota of ultramafic substrata appears to consist of a mixture of species having a high affinity for Si-rich and Ca-rich rocks (Purvis 1996; Favero-Longo *et al.* 2004). The lichen biota of the New Idria serpentinite mass is generally consistent with these characteristics, and confirms the higher species diversity on ultramafic rocks than on other rock types already reported from other sites (Gilbert & James 1987; Sirois *et al.* 1988; Piervittori *et al.* 2004; Harris *et al.* 2007; Favero-Longo & Piervittori 2009), although this may be due to the physical properties of the rock and/or the history of disturbance (see below). Wirth (1972) characterizes the ultramafic lichen communities of Central Europe by the absence or scarcity of lichens typical of Si-rich rocks [e.g. *Rhizocarpon geographicum*, *Acarospora fuscata*, *Lasallia pustulata*, *Lecanora rupicola*, *Xanthoparmelia conspersa* (as *Parmelia conspersa*)], the absence of species typical of base-rich rocks, and the occurrence of species at the northernmost limit of their ranges. Interestingly, the only two species found during the present study that were reported as scarce on ultramafic rocks by Wirth (viz. *Rhizocarpon geographicum* and *Lecanora rupicola*) occurred only on ultramafic rocks, which supports the hypothesis that the physical properties of the rock may be more important in determining lichen assemblages than their mineralization.

Bates (1978) suggested that lichen communities on ultramafic rocks were affected by the low availability of essential macronutrients such as N, P, K, S, and C, and/or high concentrations of Mg. Combined Ca deficiency and Mg toxicity results in the extreme adverse substratum condition of Ca:Mg molar ratio $\ll 1$ (Brooks 1987). Ca is a plant-essential macronutrient and required in much higher concentrations than Mg (Marschner 2002). The two cations compete with each other for uptake at the root, and vascular plants with Type I cell walls (dicotyledon and most monocotyledon plants) contain cell walls that are highly dependent upon Ca-bridged pectins to maintain cell wall integrity (Marschner 2002; O'Dell & Rajakaruna 2011). Unlike most vascular plants, the cell walls of fungi lack pectin (Kirk *et al.* 2011) and therefore fungi probably do not depend on an adequate supply of Ca to maintain cell wall integrity. It is thus unlikely that the chemistry of ultramafic substrata affects the fungal component of lichens in the same way that it affects vascular plants. It is possible, however, that the green algal (Chlorophyta; cell wall type similar to Type I) symbiont of lichens may be adversely affected by ultramafic substrata in the same manner as vascular plants since Ca-deficiency symptoms have been demonstrated for the non-lichenized, green algae *Scenedesmus intermedius* Chod. in a laboratory setting (Adam & Issa 2000).

Heavy metal toxicity is another possible influence of ultramafic substrata on lichen species diversity and cover. Ultramafic substrata contain elevated concentrations of Ni, Cr, and other heavy metals (Brooks 1987). Many lichen species secrete oxalic acid, which weathers ultramafic rock and dissolves metals bound in minerals, thus increasing their bioavailability (e.g. Wilson *et al.* 1981). It is possible that the heavy metals contained in ultramafic rocks could potentially be toxic to lichens. Likewise, lichens growing on ultramafic rocks may be physiologically adapted to tolerate high heavy metal concentrations, such as that demonstrated on Fe and Cu smelter slag (Lange & Ziegler 1963). Substitution of heavy metals by magnesium in one chemical compound in *Tephromela atra* (Huds.) Hafellner (as *Lecanora atra*) on serpentinites was reported by Wilson *et al.* (1981) as a possible method of avoiding the effects of toxic elements. More generally, it is evident that oxalates of a range of elements can form directly as a result of precipitation by reaction with oxalic acid during lichen growth (Purvis 1984). Ultramafic rocks (nephrite, partially serpentinized peridotite, serpentinite) analyzed from lichen collection sites of the New Idria serpentinite mass have 37 times as much Ni (2084 ppm vs. 109 ppm) and 16 times as much Cr (1810 ppm vs. 56 ppm) than the non-ultramafic rocks analyzed (silica-carbonate; shale and sandstone). Which element or combination of elements may be critical in limiting lichen colonization remains elusive without element- and species-specific studies exploring the tolerance of various lichens to the significant elemental differences we observed among the rocks studied (Table 2).

The fact that the patterns of diversity and cover of lichens on ultramafic as compared to non-ultramafic rocks can be widely variable (Favero-Longo *et al.* 2004, and references therein), suggests climate, elevation, history of land use, and other biotic and abiotic factors may complicate the substratum-level influence on lichens. The diverse lichen community we documented on ultramafic rocks of the New Idria serpentinite mass could be the result of the physical properties of the substratum (texture of the rocks) rather than due solely to their mineralogy. Ultramafic rocks of the sites from which we collected were typically hard with lamellar, granular, or vacuolar porous surface texture. In contrast, the non-ultramafic rocks were typically softer with vacuolar surface texture in the case of the silica-carbonate rock, and granular surface texture in the case of the shale and sandstone rock. Overall, the non-ultramafic rocks tended to have more friable surfaces that may be too unstable to permit the establishment of a diverse lichen biota. Similarly, hard-weathering serpentinites of alpine habitats were shown to host higher lichen diversity and cover than soft-weathering rocks such as calc-schists (Favero-Longo & Piervittori 2009).

An alternative explanation may be the difference in rock surface ages between the ultramafic and non-ultramafic sites. Most, or portions, of the non-ultramafic sites have been extensively disturbed by mining within the past 62 years, creating fresh rock surfaces, whereas virtually none of the ultramafic sites have been disturbed within the same time period (and probably for much longer).

Our study is the second account published to date of lichens collected from ultramafic rocks of the biodiverse California Floristic Province (Myers *et al.* 1999). Sigal (1989) provided the earlier account of ultramafic-associated lichens in central California, excluding the New Idria serpentinite mass, reporting 76 taxa from five sites. Although taxonomic concepts have changed since Sigal's study, and in some cases it is not possible to ascertain which species was actually recorded in her study, we report approximately the same number of species (83), only 15 of which were also reported in the earlier study (Table 3). The reasons for this are unclear, but possible factors are that Sigal also included species reported from soil, and that three out of the five study sites were significantly further north in the state than the New Idria serpentinite mass. To date, no endemic lichens have been reported from any of the ultramafic sites in California (or North America), although further taxonomic and phylogenetic studies may reveal distinct ecotypes or species. It is intriguing that despite the well-known phenomenon of ultramafic (or substratum-level) endemism in vascular plants (Anacker *et al.* 2011), species-level endemism is not a common phenomenon among cryptogams, including lichens (Sigal 1975) and bryophytes (Shaw *et al.* 1987; Lepp 2001; Briscoe *et al.* 2009). It is tempting to hypothesize that species- and community-level processes are more strongly influenced by other abiotic or biotic factors (e.g. microclimate, rock texture) than rock or soil mineralogy and, perhaps, the processes of speciation in cryptogams are less affected by isolation due to substratum chemistry (and other edaphic factors), known to be immensely important in generating diversity among vascular plants (Kruckeberg 1986; Rajakaruna 2004; Kay *et al.* 2011).

Of the 83 taxa (including four lichenicolous fungi) that we collected from ultramafic substrata, only 20 (Table 3) were included in the list of *c.* 250 lichen taxa reported by more than one ultramafic survey given by Favero-Longo *et al.* (2004). This is largely explained by the lack of studies devoted to lichens on ultramafic substrata in western North America. Interestingly, the two species from ultramafic substrata new to California were also two of those already reported from this substratum elsewhere by Favero-Longo *et al.* (2004): *Buellia aethalea* is a frequent species of hard, silica-rich rocks in Europe, and *B. ocellata* is a frequent species on ultramafic substrata (Favero-Longo *et al.* 2004) and was reported as new to New England from partially serpentinized peridotite by Harris *et al.* (2007). The two species reported from silica-carbonate are rare species, apparently restricted to calcareous sandstone in western USA, although *R. saurinum* has recently been reported from soft, aeolian sandstone in eastern Iran (Moniri *et al.* 2010). The two species reported from shale and sandstone are widespread but inconspicuous species that have probably been overlooked by previous workers.

Ultramafic substrata and other edaphically unusual habitats are undergoing drastic changes due to ever-expanding development, deforestation, mining, exotic species invasions, and atmospheric deposition of pollutants such as heavy metals or previously limiting nutrients such as nitrogen (Williamson & Balkwill 2006; Rajakaruna & Boyd 2008; Harrison & Rajakaruna 2011). Such changes can have a drastic impact on the biota of these unique habitats. Floristic surveys in support of conservation efforts should be encouraged to document the wealth of biological diversity being frequently lost from such sites worldwide. These sites, perhaps one of the last remaining under-studied frontiers of genetic diversity, should be better explored to generate data for effective conservation planning.

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