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RESEARCH ARTICLE

A Comparative Study of Lichen and Bryophyte Communities on Sandstone and Ultramafic Bedrocks Along a Maritime Gradient in Central California

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ABSTRACT

Aims: Lichens and bryophytes are an often overlooked, yet dominant biotic component of rock outcrops and other lithic habitats. Saxicolous lichen and bryophyte communities are frequently species-rich and play important ecological roles, including rock weathering, soil formation, and vascular plant recruitment. In this study, we test whether saxicolous communities differ between two substrate types along a coastal to inland spatial gradient.

Location: Ultramafic and sandstone rock outcrops in central California in San Luis Obispo, Monterey, and Kern counties.

Methods: We sampled saxicolous communities of eight ultramafic and eight sandstone outcrop sites along a 70 km maritime influence gradient using 20 × 20 cm quadrats stratified between north- and south-facing rock aspects. For each quadrat, species composition, distance above the ground, and rock microtopography characteristics were recorded. For each site, rock elemental composition and climate parameters including rainfall, temperature, and fog were documented.

Results: We recorded 132 lichen and seven bryophyte taxa across 128 quadrats. Saxicolous communities were significantly different between ultramafic rock and sandstone, as well as between coastal, intermediate, and inland sites. Ultramafic rocks hosted fewer species overall but had a higher abundance and diversity of cyanolichens. The effect of rock type on species composition was mediated by maritime influence, with coastal samples showing greater cross-substrate differentiation than intermediate and inland samples.

Conclusions: Our results demonstrate the interactive roles of substrate, climate, and microtopography in shaping saxicolous communities. The role of substrate in structuring saxicolous communities is mediated by climate and accentuated by the different microtopography profiles of the ultramafic and sandstone rocks. Improving our understanding of how saxicolous communities vary across the landscape is an important step in identifying conservation priorities for these highly diverse and ecologically significant communities.

1 | Introduction

Rock outcrops are ecologically important habitats harboring distinctive plant, animal, and fungal communities, and they play important roles in maintaining landscape-level diversity (Chozas et al. 2022). Although often overlooked, assemblages of lichens and bryophytes that occupy rock outcrops, hereafter referred to as "saxicolous communities," frequently cover the majority of available rock surfaces with a high diversity of species. Species-rich communities of saxicolous bryophytes and lichens have been reported from various rock types across varying spatial scales (Foote 1966; Bates 1975; John 1989; Caners 2011; Favero-Longo et al. 2018; Mulroy et al. 2022; Rutherford and Rebertus 2022; Aragón et al. 2025). Saxicoles contribute to fundamental ecosystem processes, including soil formation, rock weathering, and nutrient cycling (Brodo 1973; Garibotti et al. 2011), pioneer new rock substrates and facilitate vascular plant recruitment (Riefner et al. 2003; Bokhorst et al. 2016), and serve as microhabitats for diverse invertebrate communities (Materna 2000). Despite their important ecological functions in lithic habitats, relatively little is known about the biotic and abiotic factors that shape saxicolous communities.

Rock type often explains variation in saxicolous community composition, in that distinct communities occur on different substrates (Pentecost 1980; Sirois et al. 1988; Paukov and Trapeznikova 2005; Briscoe et al. 2009; Favero-Longo and Piervittori 2009; Rajakaruna et al. 2012; Aho et al. 2014; Medeiros et al. 2014; Aragón et al. 2025). Moreover, some species are restricted to specific rock types (Brodo 1973; Gilbert 1996, 2000). The underlying drivers of this variation in community structure among different lithologies are not well-understood, but rock properties including elemental composition (Purvis and Halls 1996; Rajakaruna et al. 2012), water retention capacity (Garty and Galun 1974), surface pH (Gilbert and James 1987; Hauck et al. 2011), and rock surface texture (Brodo 1973) represent promising areas for further research.

The effects of climate and microhabitat gradients on saxicolous communities have received more attention than substrate effects. For example, saxicolous lichen communities have been found to vary with altitude (Pintado et al. 2001; Favero-Longo and Piervittori 2009), and the algal partner in the lichen symbiosis shifts across altitudinal gradients within the same lichen fungal taxon (Medeiros et al. 2021). Functional trait diversity and species richness of rock- and soil-dwelling lichens were found to change across a latitudinal gradient from the subarctic to the arctic (Chagnon et al. 2021). Water availability (Giordani et al. 2013; Aho et al. 2014), rock orientation (Alpert 1986; John and Dale 1990; Paz-Bermúdez et al. 2021), and solar irradiation (Bjelland 2003) all appear to influence saxicolous community composition. These and other gradients across which saxicolous community composition is quantified are often interrelated (i.e., multicollinear), which makes it difficult to determine the precise mechanisms of community assembly (Alın 2010).

Maritime conditions, which offer a unique regime of temperature, precipitation, aerial salt deposition, and other abiotic factors, are associated with specialized saxicolous communities dominated by lichens (Fletcher 1973a, 1973b; Rundel 1978; Schieferstein and Loris 1992). Variation in maritime influence affects saxicolous community composition across fine spatial scales along the immediate shoreline (Fletcher 1973b; Ryan 1988; Bjelland 2003). While coastal saxicolous communities change across broader scales of several kilometers (Bates 1975), an eventual change across a full maritime gradient from the thermally stable, damp coast to the thermally variable, arid interior has not been documented in the published literature. The nearest approximations come from studies of epiphytic lichens along a coast-to-inland gradient in Alaska (Root et al. 2014) and saxicolous lichens along a lake-effect gradient in Michigan (Rutherford and Rebertus 2022), both of which found changes in community composition.

In this study, we compare saxicolous communities between two distinct rock types, ultramafic rock and sandstone, along a regional-scale maritime influence gradient in central California. Our primary goal is to understand the roles of substrate (rock type, elemental composition, and microtopography characteristics) and climate (temperature, precipitation, cloud cover, and fog) on the species composition of saxicolous communities. The null hypothesis, that saxicolous community composition is not affected by variation in substrate or climate, was tested against three alternative hypotheses: (1) *Substrate Hypothesis*: Differences in substrate properties between ultramafic rocks and sandstone lead to distinct saxicolous communities on these substrates. (2) *Maritime Influence Hypothesis*: Differences in climatic conditions across the regional maritime gradient cause species composition to differ between coastal and inland sites. (3) *Maritime Moderation Hypothesis*: The milder climate brought about by maritime influence moderates the effects of substrate differences on species composition, leading to greater compositional similarity between ultramafic and sandstone substrates near the coast and increasing dissimilarity further inland.

2 | Materials and Methods

2.1 | Study Region

This study was conducted along the central coast of California, in the Central California Foothills and Coastal Mountains ecoregion (Griffith et al. 2016; Figure 1). The climate is Mediterranean-like, with cool, wet winters and warm, dry summers. Summer fog is frequent and often extends into coastal valleys overnight (Western Regional Climate Center 2022). Vegetation types include chaparral, coastal scrub, annual grassland, and oak woodland (Appendix S1). Compared to inland sites, coastal sites in this study have higher average annual precipitation (590 vs. 340 mm) and lower annual temperature fluctuation (13.7°C vs. 34.6°C; PRISM 2021; Appendix S2).

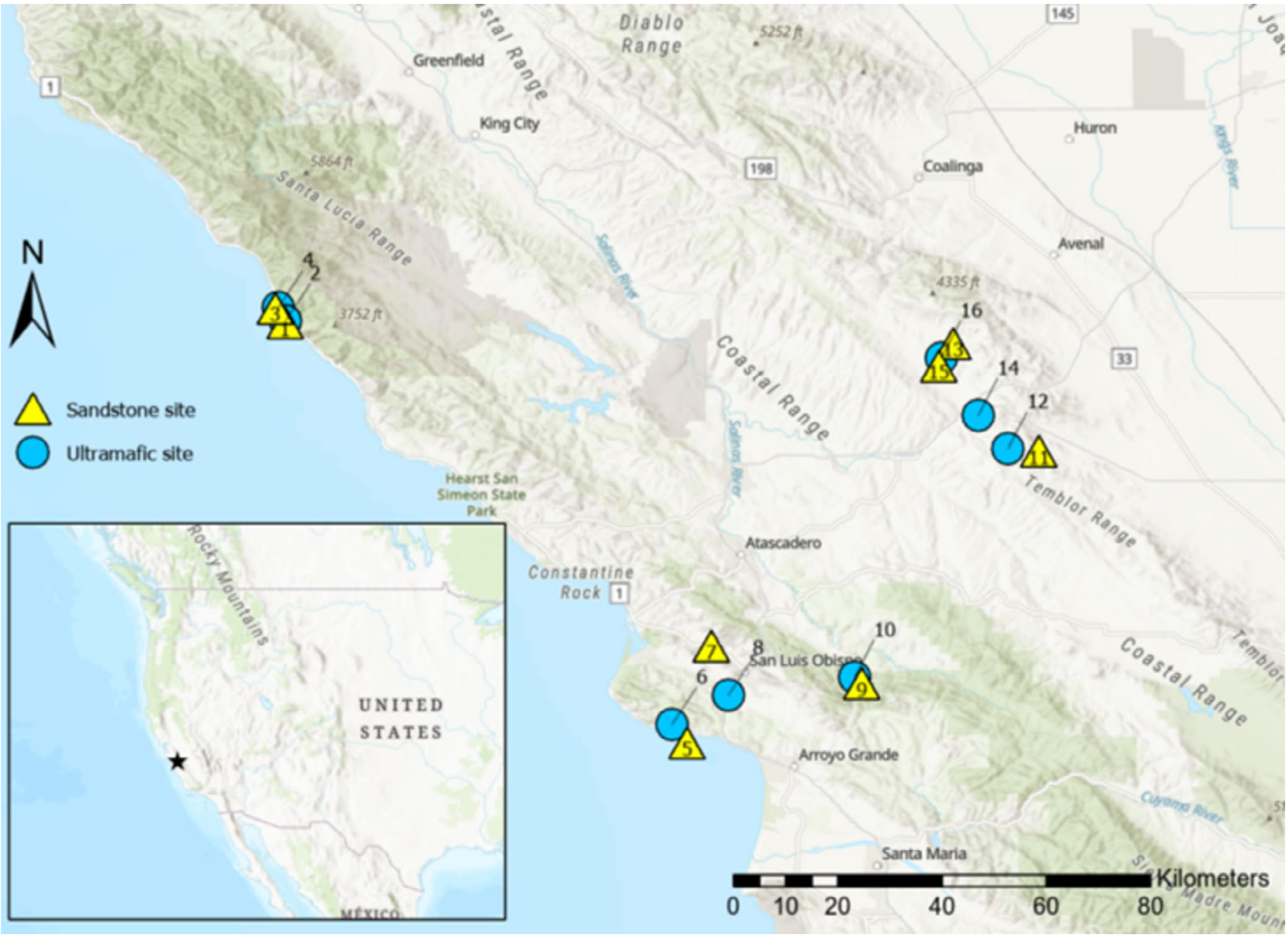

FIGURE 1 | Map of sampling sites. Sequential numbers (e.g., 1, 2; 3, 4) are paired sandstone and ultramafic sites. See Appendix S1 for site descriptions. Numbers correspond to the following sites: 1: Willow Creek; 2: Willow Creek; 3: Jade Cove; 4: Jade Cove; 5: San Luis Hill; 6: Pecho Creek; 7: El Chorro; 8: Irish Hills; 9: Hi Mountain Road; 10: Rinconada; 11: James Parcel; 12: Still Parcel; 13: Serpent's Back; 14: Parcel D; 15: Parcel B; 16: Parcel B.

We sampled 16 rock outcrop sites across a ca. 70-km coast–inland gradient of decreasing maritime influence in San Luis Obispo, Monterey, and Kern counties (Figures 1 and 2; Appendix S1). Sites were selected as paired ultramafic rock and sandstone sites. Paired sites were selected to be as close together as possible and varied from 0.05 to 14.7 km apart. Six sites were between 0.1 and 1.8 km of the nearest coastline (coastal sites), four sites were 8.1–22.1 km from the coast (intermediate sites), and six were 65.5–71.2 km from the coast (inland sites). Sites were located on hilltops or along ridgelines with moderate-to-high topographic exposure and met the following criteria: (1) <1000 m elevation; (2) unimpacted by recent disturbances (e.g., landslides, fires); (3) minimal shading from trees or shrubs; and (4) visually homogeneous rocks. The ultramafic rock sites were outcrops of partially serpentinized harzburgite consisting of relict olivine and orthopyroxene that displayed similar degrees of weathering and serpentinization and lacked abundant outcrop-scale smooth fault surfaces (i.e., slickensides). The sandstone sites varied subtly from lithic-rich arenite to arkosic arenite but displayed similar whole-rock geochemistry (Appendix S3) and were characterized by non-calcareous cements, which were assessed by applying dilute hydrochloric acid to unweathered rock surfaces.

2.2 | Sampling

We sampled each of 16 rock outcrop sites using eight randomly located 20×20 cm quadrats stratified between north- and south-facing rock aspects (Figure 2). Each quadrat was placed on a different individual rock within the site. Quadrat locations were generated by creating a set of random points for each site using ArcGIS software. From each point, we navigated to the nearest suitable quadrat location, alternating between north- and south-oriented rock faces. Suitable quadrat locations met the following criteria: (1) average slope between 30° and 90°; (2) aspect for north-facing quadrats $0° \pm 45°$, and for south-facing quadrats $180° \pm 45°$; (3) rock face large enough and with a sufficiently uniform slope and aspect to accommodate a quadrat. When a large rock face offered multiple quadrat placement options, the placement was selected at random.

Within each quadrat, we estimated percent cover of bare rock, lichens, bryophytes, and vascular plants. A list of taxa occurring within the quadrat was generated by close examination of the rock surface with 10×, 14×, and 20× loupes. Provisional names were given to each observed taxon, and percent cover was estimated for each taxon using Domin scale cover classes (Domin 1928).

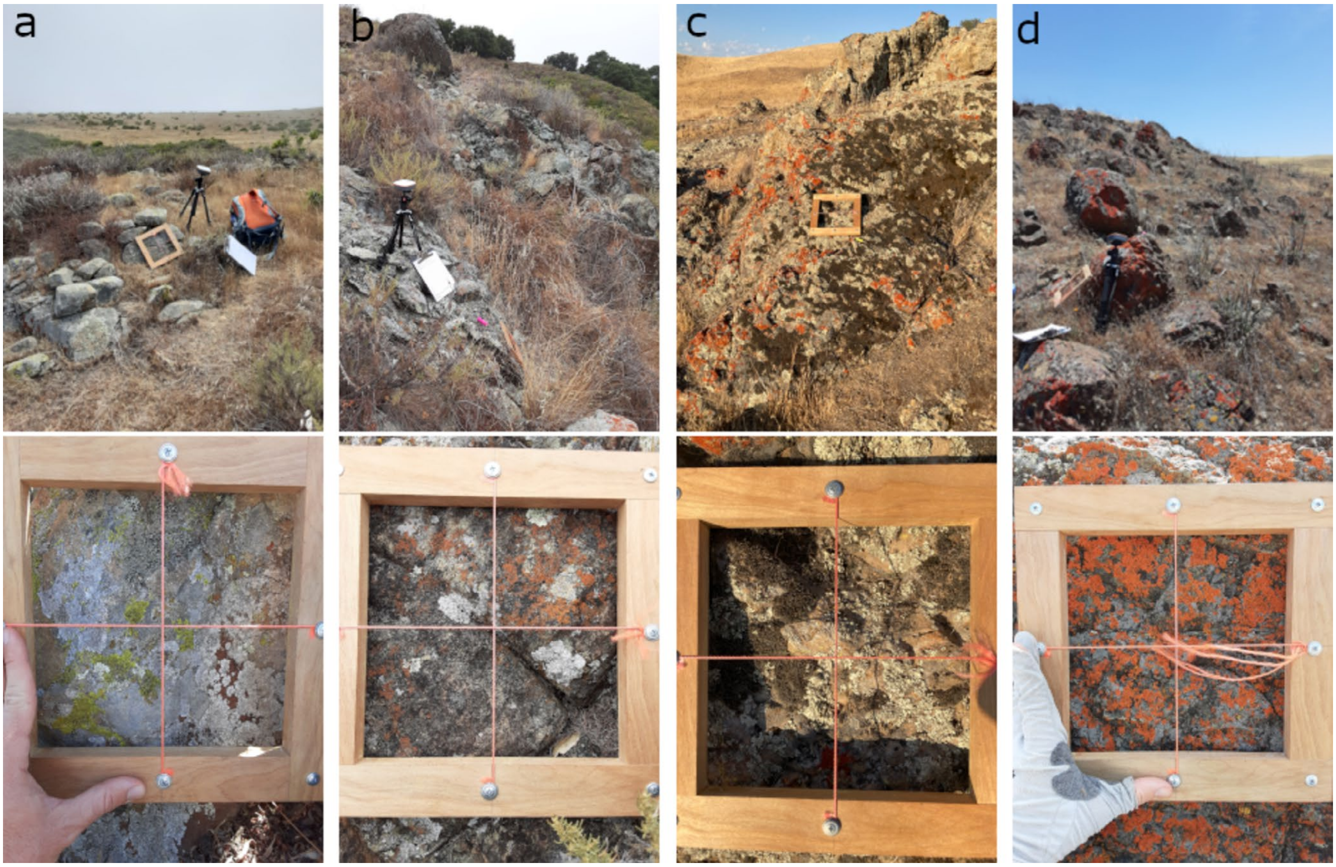

FIGURE 2 | Photographs of representative sampling sites and north-facing quadrat samples. (a) San Luis Hill coastal sandstone site and quadrat. (b) Pecho Creek coastal ultramafic rock site and quadrat. (c) Serpent's back inland sandstone site and quadrat. (d) Parcel D inland ultramafic rock site and quadrat.

Lichen and bryophyte voucher specimens were collected for each field-identified taxon from each site, although in some cases representative lichen specimens were unavailable due to rarity and/or difficulty of collection. Although collection of identifiable voucher specimens was not always possible, we attempted to identify as many of the observed taxa as possible, and we revisited sites to resolve uncertainties in the community dataset.

2.3 | Specimen Identification

Lichens and bryophytes were identified in the laboratory using light microscopy and, for lichens, standard chemical spot tests, with the aid of dichotomous keys (Nash et al. 2002, 2004, 2007; Flora of North America Editorial Committee 2007, 2014; McCune and Geiser 2009; Brodo 2016; McCune 2017a, 2017b; Knudsen et al. 2023). Lichen nomenclature mainly follows Esslinger (2021) with a small number of taxa following Index Fungorum (Index Fungorum Partnership 2021). Bryophyte nomenclature follows the Bryophyte Nomenclator (Brinda and Atwood 2025). Voucher specimens are housed at the Robert F. Hoover Herbarium (OBI).

2.4 | Elemental Composition of Rock Samples

Whole-rock elemental analysis was conducted on fragments from 1 to 2 representative samples of unweathered bedrock from each site. Elemental concentrations were determined for major and trace elements (Appendix S3). Samples were analyzed by the GeoAnalytical Laboratory, Washington State University, WA, USA, using an automated ThermoARL Advant'XP+ sequential X-ray fluorescence (XRF) spectrometer (for elemental composition data and XRF methodology, see Appendix S3). At the Jade Cove sandstone site, which consisted of closely scattered outcrops occurring on a coastal terrace, we obtained XRF data at four different sub-sites due to observable differences in the rocks.

2.5 | Microhabitat and Climate Variables

We collected data on abiotic characteristics at both site and quadrat scales (Table 1). At the quadrat level, we measured slope and aspect using a clinometer and compass. We assessed five quadrat-scale microhabitat variables: (1) Rock aspect (north- or south-facing); (2) fine-scale microtopography (0 = smooth, 2 = some cracks and ledges $\gtrsim 1$ mm, 4 = many cracks and ledges $\gtrsim 1$ mm); (3) broad-scale microtopography (0 = flat, 2 = moderate undulation, 4 = high undulation); (4) overhangs (present or absent, defined as any rock surface $> 90°$ slope and $> 1\,cm^2$ surface area); and (5) distance from ground ($1 \leq 0.3$ m, $2 = 0.3$–0.9 m, $3 \geq 0.9$ m). At the site level, apart from rock type and distance from the coast, we obtained data for five climate variables: average daily maximum and minimum temperature of the warmest month (August) and coldest month (January), respectively, annual precipitation, incidence of summer fog and low cloud

TABLE 1 | Explanatory variables used in this study.

Variable	Abbreviated name	Variable type and units	Scale
Explanatory variables			
Rock type	Rock type	Nominal—ultramafic rock vs. sandstone	Site
Distance from the coast	Dist coast	Ordinal—coastal, intermediate, inland	Site
Annual precipitation	Precip	Numeric—mm	Site
Mean maximum daily temperature in August	Min temp	Numeric—°C	Site
Mean minimum daily temperature in January	Max temp	Numeric—°C	Site
Fog and low cloud cover	FLCC	Numeric—# of hours with FLCC in summer months	Site
Elevation	Elevation	Numeric—m	Site
Aspect	Aspect	Nominal—north vs. south	Quadrat
Overhangs	Overhangs	Nominal—present or absent	Quadrat
Fine-scale microtopography	Microtopo1	Ordinal with five levels	Quadrat
Broad-scale microtopography	Microtopo2	Ordinal with five levels	Quadrat
Height from ground surface	Height	Ordinal with three levels	Quadrat

cover (FLCC), and elevation. Temperature and precipitation data were obtained from the PRISM 30-year 1991–2020 normals modeled at 800 m resolution (Daly et al. 2008; PRISM 2021). The mean number of hours with FLCC during summer months (June–September, 1999–2009) was obtained from Geostationary Operational Environmental Satellite (GOES) imagery data (Torregrosa et al. 2016).

2.6 | Data Analysis

All analyses were conducted in R (R Core Team 2021), with the aid of the package vegan (Oksanen 2025) and using a proportional dissimilarity matrix for multivariate procedures. One quadrat sample was excluded from analyses due to a lack of positively identified taxa, yielding a community matrix of 127 quadrat samples. To visually explore variation among communities, we performed non-metric multidimensional scaling (NMDS) on the community matrix using the *metaMDS* function, specifying a "bray" distance matrix, 200 minimum and 999 maximum random starting configurations, 999 maximum iterations, and a convergence tolerance of 1×10^{-7}. We selected a two-dimensional solution after computing stresses using *dimcheckMDS* (goeveg package, Goral and Schellenberg 2021). The final stress of the NMDS solution was 0.154 and was repeated once; 225 runs using randomized data yielded higher values. To aid interpretation, we rotated the solution using the *varimax* function of the stats package (R Core Team 2021) and then rescaled to half-change units using *postMDS*. We then overlaid vectors for environmental variables using *envfit*. The NMDS solution was substantiated by comparing it to a detrended correspondence analysis (DCA) ordination run in parallel (see Appendix S4).

To test for group differences in species composition, we applied permutational multivariate analysis of variance (PERMANOVA) using *adonis2* with the default options. The PERMANOVA model included rock type, distance from the coast, and rock type * distance from the coast as an interaction term. We used pairwise a posteriori tests to compare (1) coastal, intermediate, and inland samples, and (2) ultramafic rock and sandstone samples within each of these groups. We tested for differences in rock surface characteristics between groups using Wilcoxon tests via the *wilcox.test* function (R Core Team 2021). For all tests, statistical significance was assessed at $\alpha \leq 0.05$.

To better understand how variation was partitioned among different spatial scales, we conducted a split-plot generalized linear model (GLM) using the two NMDS axis quadrat scores as response variables (cf. Auestad et al. 2008). We partitioned the variation explained at three hierarchical levels: groups of quadrat samples with the same rock type and coastal distance categories (e.g., coastal sandstone and inland ultramafic), sites, and quadrats. NMDS axis scores were tested against 23 explanatory variables at each level. Explanatory variables tested included those in Table 1 minus distance from the coast, plus the concentrations of the 10 major elements and two trace elements, chromium and nickel, from rock samples (Table 2). For the Jade Cove sandstone site, the elemental composition was averaged across the four sub-sites. All variables except for categorical variables—rock type, aspect, and overhangs—were zero-skewness transformed prior to split-plot GLM analysis (Økland et al. 2001). For each NMDS axis, we calculated the fraction of total variation explained (FVE) at each spatial scale by dividing its sum of squares (SS) by the total SS for the NMDS axis. For each explanatory variable at each level, the variable SS was divided by the level SS to yield the proportion of level variation explained by the variable. *p* values were generated for each test but do not represent a formal test of significance due to the high levels of correlation between explanatory variables. Split-plot GLM analyses using the identity link function and a

TABLE 2 | Elemental concentrations of ultramafic rock and sandstone for selected major and trace elements.

	Major elements (% weight)										Trace elements (ppm)	
	SiO_2	TiO_2	Al_2O_3	FeO	MnO	MgO	CaO	Na_2O	K_2O	P_2O_5	Ni	Cr
Ultramafic rock	39.63 ± 0.32	0.04 ± 0.01	13.59 ± 1.13	8.21 ± 0.20	0.13 ± 0.01	35.24 ± 0.52	0.42 ± 0.21	0.01 ± 0.00	0.01 ± 0.00	0.03 ± 0.02	2516 ± 151	3003 ± 209
Sandstone	67.85 ± 2.72	0.55 ± 0.09	1.57 ± 0.29	4.03 ± 0.72	0.06 ± 0.01	2.02 ± 0.41	2.56 ± 0.69	3.73 ± 0.58	2.10 ± 0.37	0.17 ± 0.04	32 ± 7	91 ± 15

Note: Concentrations are mean ± standard error.

normal error distribution were conducted using the *aov* function in R. Pearson's correlation coefficients for each explanatory variable—NMDS axis relationship were calculated using the *cor.test* function (R Core Team 2021). Correlations between abiotic variables and between elemental concentrations are shown in Appendices S5 and S6, respectively.

3 | Results

We identified 132 lichen and seven bryophyte taxa in the 128 sampled quadrats. Lichens occurred in all quadrats, whereas bryophytes, which were all mosses, occurred in 27 quadrats—14 ultramafic and 13 on sandstone. Two quadrats contained vascular plants—annual graminoids—which were not included in the community matrix. Lichens consisted of 21 macrolichens and 111 microlichens (Appendix S7). Ten lichen taxa contained a cyanobacterium as their primary photobiont (i.e., cyanolichens), while the remaining taxa contained a green alga (chlorolichens). Forty-nine lichens occurred on both ultramafic rock and sandstone, 30 were restricted to ultramafic rock, and 53 were only observed on sandstone. Of the seven bryophytes, one was restricted to ultramafic rock and four were found only on sandstone (Appendix S7).

Sandstone and ultramafic rocks had distinct rock elemental compositions. On average, compared to ultramafic rock, sandstone had higher concentrations of silicon, aluminum, calcium, and potassium, whereas ultramafic rocks contained more magnesium, iron, nickel, and chromium (Table 2; Appendix S3). Most elemental concentrations were strongly correlated with one another (Appendix S6). The two rock types also differed in their average microtopography. Ultramafic rocks had a rougher fine-scale microtopography index (1.20) than sandstone (0.68; Wilcoxon test: $W = 3158.5$, $p < 0.001$) and a higher frequency of overhangs present (72% of quadrats) than sandstone (41%; Wilcoxon test: $W = 2688.0$, $p < 0.001$). Broad-scale microtopography was also higher on average in ultramafic rocks (0.92 vs. 0.82 in sandstone), but the difference was not significant (Wilcoxon test: $W = 2284.0$, $p = 0.24$).

The two-dimensional NMDS ordination of the community matrix shows partial separation of the inland community group from the coastal and intermediate groups along NMDS 1, as well as greater compositional variation within the inland group (Figure 3a). Figure 3b shows partial separation between the ultramafic and sandstone groups along NMDS 2, with greater variation within the sandstone group.

The majority of observed community variation in this study was found within the broadest hierarchical level rock type * distance from the coast (Table 3). For NMDS 1, 48.0% of variation was explained at the hierarchical level rock type * distance from the coast, followed by quadrats (40.4%) and finally sites (11.6%; Table 3). At the rock type * distance from the coast level, climate variables including precipitation and temperature explained large amounts of variation (Table 3). At the sites level, fine- and broad-scale microtopography and overhangs explained the most variation, while at the quadrats level, none of the measured variables explained appreciable variation and only overhangs were significant (Table 3). NMDS 2 had a similar amount of variation explained by rock type * distance from

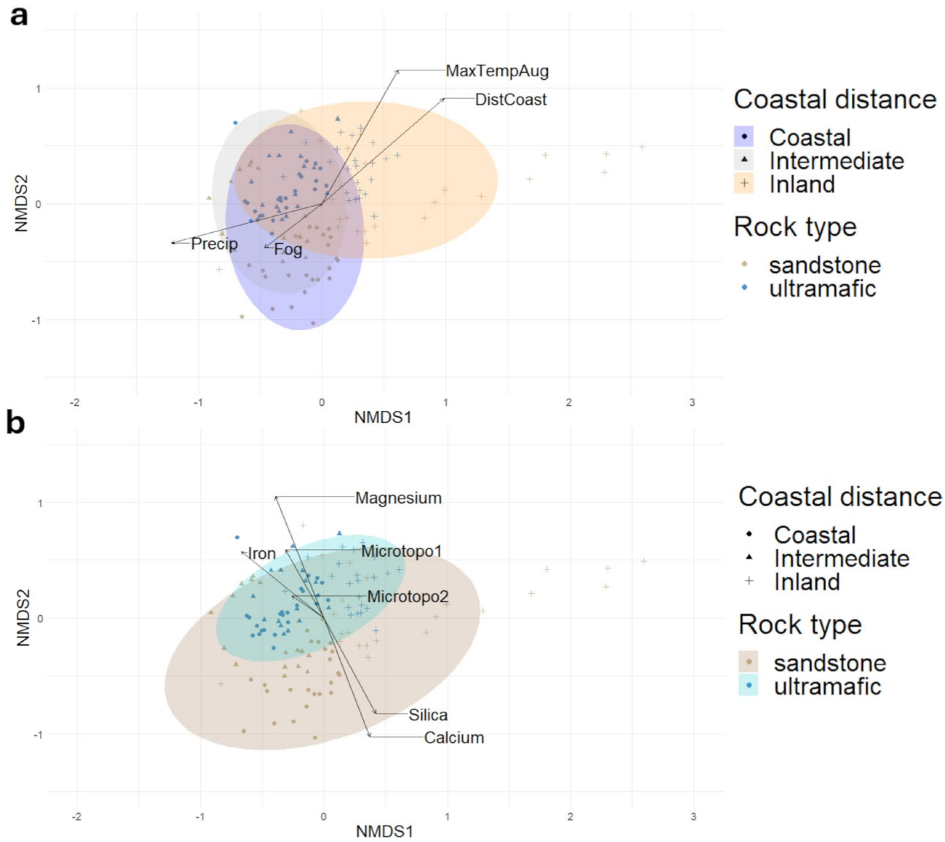

FIGURE 3 | NMDS ordination of community dataset samples ($n = 127$ quadrats). (a) Maritime influence and climate. Ellipses represent 95% confidence intervals of the centroids for coastal, intermediate, and inland samples. See Table 1 for the key to vectors. (b) Substrate. Ellipses represent 95% confidence intervals of the centroids for both ultramafic and sandstone quadrats. See Table 2 for the key to vectors.

the coast (52.3%), but the remaining explained variation was distributed more evenly between sites (27.4%) and quadrats (20.3%). At the rock type * distance from the coast level, broad-scale microtopography and several elemental concentrations, including titanium, aluminum, and sodium, explained the largest amounts of variation within that level. At the sites level, iron and chromium concentration explained the most variation, while at the quadrats level, none of the measured variables explained appreciable variation.

3.1 | Substrate Hypothesis

The species compositions of sandstone versus ultramafic rock quadrats were distinct (PERMANOVA: $F = 12.43$, df = 1, 121, $p < 0.001$; Table 4; Figure 3b). The two rock types were separated along NMDS 2, which was highly correlated with many elemental concentrations as well as fine-scale microtopography (Table 3; Figure 3b). Ultramafic rocks were characterized by high cover and abundance of several *Polycauliona* species, cyanolichens including *Peltula bolanderi*, *P. euploca*, and *Lichinella stipatula*, and *Thalloidima ioen*, among others. Characteristic sandstone taxa included *Acarospora socialis*, *Lecidea laboriosa* group, *Protoparmeliopsis muralis, Xanthoparmelia mexicana*, and *X. plittii* (Figure 4; Appendix S7). Cyanolichens comprised a larger part of the ultramafic rock biota than the sandstone biota. They occurred in 45 of 64 ultramafic rock quadrats, and averaged 6.1% cover, compared to 10 of 64 quadrats and 0.9% cover for sandstone. Six of the 10 cyanolichens recorded in this study only occurred on ultramafic rock, compared to 24 of 122 chlorolichens (Appendix S7).

3.2 | Maritime Influence Hypothesis

The species compositions of coastal, intermediate, and inland quadrat samples were significantly different from one another (PERMANOVA: $F = 10.14$, df = 2, 121, $p < 0.001$; Table 4; Figure 3b). The inland group was separated from the coastal and intermediate groups along NMDS 1, which was most strongly correlated with climate variables including precipitation and temperature. Coastal and inland composition were the most distinct, followed by inland and intermediate, and finally coastal and intermediate (Table 4; Figure 3b). Coastal quadrats were dominated by several species of lichens including *Dimelaena radiata, Lecanora gangaleoides, Lecidella asema*, and *Polycauliona bolacina*, while inland quadrats were characterized by the lichens *Candelariella citrina, Physconia enteroxantha, and Umbilicaria phaea*, as well as the moss *Grimmia laevigata* (Figure 4; Appendix S7).

3.3 | Maritime Influence—Substrate Interactions

Sandstone and ultramafic rock communities were significantly different across the maritime gradient, but the effect of substrate on species composition was dependent on distance from the coast (PERMANOVA: $F = 4.04$, df = 2, 121, $p < 0.001$; Table 4). Pairwise comparisons between ultramafic rock and sandstone within

TABLE 3 | Relationships between saxicolous community gradients (NMDS quadrat score response variable) and the different zero-skewness transformed explanatory variables ($n=127$ quadrats) evaluated at three levels—rock type * distance from the coast (e.g., coastal sandstone, inland ultramafic), sites, and quadrats—by split-plot GLM (identity link, normal errors).

	NMDS1										
		Rock type * distance from the coast					**Sites**			**Quadrats**	
	SS	**20.448**					**4.958**			**17.199**	
	FVE	**0.480**					**0.116**			**0.404**	
	df	**5**					**10**			**111**	
	Explanatory variable	**SS_{expl}/ SS_{group}**	***p***	***c***	**SS_{expl}/SS_{site}**	***p***	***c***	**SS_{expl}/ SS_{quad}**	***p***	***c***	***r***
1	Rock type (sandstone)	0.041	0.653	−	na	na	na	na	na	na	na
2	Aspect (north)	0.067	0.621	−	0.028	0.622	+	0.006	0.414	+	na
3	Microtopo1	0.045	0.686	−	**0.450**	**0.024**	−	0.003	0.590	−	−0.171
4	Microtopo2	0.028	0.751	+	**0.432**	**0.028**	−	0.020	0.133	−	−0.125
5	Overhangs (absent)	0.108	0.526	−	**0.488**	**0.017**	−	**0.049**	**0.019**	−	na
6	Height	0.006	0.884	+	0.034	0.585	−	0.006	0.421	−	−0.047
7	Precip	**0.859**	**0.008**	−	0.292	0.086	−	na	na	na	−0.684
8	Min temp	**0.778**	**0.020**	−	0.020	0.681	+	na	na	na	−0.602
9	Max temp	0.584	0.077	+	0.077	0.409	−	na	na	na	0.511
10	FLCC	0.509	0.112	−	0.227	0.138	+	na	na	na	−0.297
11	Elevation	0.291	0.270	+	0.066	0.445	−	na	na	na	0.240
12	SiO_2	0.094	0.554	+	0.000	0.986	+	na	na	na	0.224
13	TiO_2	0.006	0.885	−	0.089	0.372	−	na	na	na	−0.080
14	Al_2O_3	0.012	0.834	+	0.260	0.109	−	na	na	na	0.047
15	FeO	0.244	0.320	−	0.000	0.962	+	na	na	na	−0.349
16	MnO	0.283	0.277	−	0.019	0.685	+	na	na	na	0.286
17	MgO	0.067	0.619	−	0.146	0.247	+	na	na	na	−0.180
18	CaO	0.020	0.788	+	0.019	0.689	+	na	na	na	0.104
19	Na_2O	0.015	0.819	+	0.000	0.951	+	na	na	na	0.089
20	K_2O	0.130	0.482	+	0.054	0.492	−	na	na	na	0.251
21	P_2O_5	0.195	0.381	+	0.000	0.960	−	na	na	na	0.277
22	Cr	0.059	0.650	−	0.049	0.954	+	na	na	na	−0.167
23	Ni	0.053	0.630	+	0.000	0.543	−	na	na	na	−0.174
	NMDS2										
		Rock type * distance from the coast					**Sites**			**Quadrats**	
	SS	**10.152**					**5.312**			**3.943**	
	FVE	**0.523**					**0.274**			**0.203**	
	df	**5**					**10**			**111**	
	Explanatory variable	**SS_{expl}/ SS_{group}**	***p***	***c***	**SS_{expl}/SS_{site}**	***p***	***c***	**SS_{expl}/SS_{quad}**	***p***	***c***	***r***
1	Rock type (sandstone)	0.513	0.109	+	na	na	na	na	na	na	na

(Continues)

TABLE 3 | (Continued)

	Explanatory variable	SS_{expl}/ SS_{group}	p	c	SS_{expl}/SS_{site}	p	c	SS_{expl}/SS_{quad}	p	c	r
2	Aspect (north)	0.293	0.267	–	0.042	0.545	–	0.013	0.226	+	na
3	Microtopo1	0.575	0.081	+	0.011	0.761	–	0.002	0.634	+	0.279
4	Microtopo2	**0.671**	**0.046**	+	0.029	0.617	–	0.000	0.920	+	0.079
5	Overhangs (absent)	0.331	0.233	na	0.162	0.220	na	0.002	0.649	na	na
6	Height	0.024	0.770	–	0.002	0.900	+	0.001	0.814	–	−0.034
7	Precip	0.202	0.371	–	0.023	0.660	–	na	na	na	−0.329
8	Min temp	0.379	0.193	–	0.007	0.810	+	na	na	na	−0.417
9	Max temp	0.428	0.159	+	0.294	0.085	+	na	na	na	0.537
10	FLCC	0.163	0.427	–	0.200	0.167	–	na	na	na	−0.369
11	Elevation	0.358	0.210	+	0.314	0.073	+	na	na	na	0.512
12	SiO_2	0.426	0.160	–	0.128	0.280	+	na	na	na	−0.455
13	TiO_2	**0.788**	**0.018**	–	0.145	0.248	–	na	na	na	−0.678
14	Al_2O_3	**0.685**	**0.042**	–	0.013	0.743	–	na	na	na	−0.605
15	FeO	0.252	0.311	+	**0.640**	**0.003**	–	na	na	na	0.259
16	MnO	0.205	0.368	+	0.127	0.281	–	na	na	na	0.159
17	MgO	0.483	0.125	+	0.058	0.477	–	na	na	na	0.499
18	CaO	0.527	0.102	–	0.277	0.096	–	na	na	na	−0.563
19	Na_2O	**0.661**	**0.049**	–	0.045	0.531	+	na	na	na	−0.577
20	K_2O	0.419	0.165	–	0.024	0.651	+	na	na	na	−0.458
21	P_2O_5	0.325	0.238	–	0.082	0.394	–	na	na	na	−0.433
22	Cr	0.436	0.129	+	**0.531**	**0.016**	–	na	na	na	0.447
23	Ni	0.244	0.148	+	0.782	0.107	–	na	na	na	0.461

Note: For each response variable, and at each level, the total SS (sum of squares) and FVE (fraction of total variation explained) are given. The variation explained (SS_{expl}/SS_{scale} level) by each explanatory variable is given for all three scales and two NMDS axes. Models with $p \leq 0.05$ are bolded. Model coefficients (c) show the sign of the relationship (+/−), and Pearson's correlation coefficient (r) is provided for each NMDS axis–explanatory variable relationship. For binary explanatory variables, the baseline value is given in parentheses.

coastal, intermediate, and inland quadrats showed that each group was significantly different from the others. The largest cross-substrate difference was found in coastal quadrats ($R^2=0.163$), followed by intermediate ($R^2=0.151$), and finally inland quadrats ($R^2=0.118$; Table 4). Many taxa showed affinities toward specific combinations of rock type and coastal distance. Examples include the moss *Vinealobryum nicholsonii* (Appendix S7) and the lichens *Pertusaria islandica* and *Polycauliona luteominia* var. *bolanderi* on coastal ultramafic rock, and the lichens *Buellia halonia, B. tesserata, Tephromela atra*, and *Thelomma mammosum* on coastal sandstone (Figure 4).

4 | Discussion

4.1 | Substrate Hypothesis

Our results demonstrate significant differentiation between sandstone and ultramafic rock communities (Figure 3b). Ultramafic substrates are well known as difficult substrates for vascular plants, thought to be a result of their high heavy metal content, low concentrations of essential nutrients, and low calcium:magnesium ratios (Rajakaruna and Boyd 2014). As a result, ultramafic soils often host unique vascular plant communities and have high rates of edaphic endemism (Garnica-Díaz et al. 2023). Although lichens and bryophytes appear to be less affected by the ultramafic environment, the limited number of comparative studies done has shown differentiation between ultramafic cryptogam communities and those of adjacent non-ultramafic rocks (Sirois et al. 1988; Briscoe et al. 2009; Mulroy et al. 2022). It may be that some of the factors that limit vascular plants on ultramafic substrates also work to filter out some lichens and bryophytes, which could partly explain the observed community differentiation, as well as lower total richness, on ultramafic rock compared to sandstone in our study.

Interestingly, cyanolichens comprise a larger proportion of the ultramafic rock biota than the sandstone biota. We suspect that cyanolichens are associated with the rougher

TABLE 4 | Results of PERMANOVA testing the individual and interactive effects of abiotic variables on lichen and bryophyte species composition ($n = 127$ quadrats).

Source	df	Sum of squares	Mean squares	R^2	F	p
Rock type	1	4.059	4.059	0.077	12.43	< 0.001
Coastal distance (categorical)	2	6.623	3.312	0.125	10.14	< 0.001
Rock type * coastal distance	2	2.639	1.345	0.050	4.04	< 0.001
Residual	121	39.504	0.327	0.748		
Total	126	52.825				

Comparison[a]	df (parameter, residual)	Sum of squares	Mean squares	R^2	F	p
Coastal—intermediate	1, 78	1.660	1.660	0.054	4.47	< 0.001
Intermediate—inland	1, 77	3.293	3.293	0.101	8.63	< 0.001
Coastal—inland	1, 93	4.155	4.155	0.107	11.11	< 0.001
Coastal UM—coastal SS	1, 46	2.796	2.796	0.163	8.94	< 0.001
Intermediate UM—intermediate SS	1, 30	1.785	1.785	0.151	5.35	< 0.001
Inland UM—inland SS	1, 45	2.074	2.074	0.118	6.01	< 0.001

Note: "UM" and "SS" are abbreviations for ultramafic rock and sandstone.
[a]Pairwise a posteriori test among sample groups.

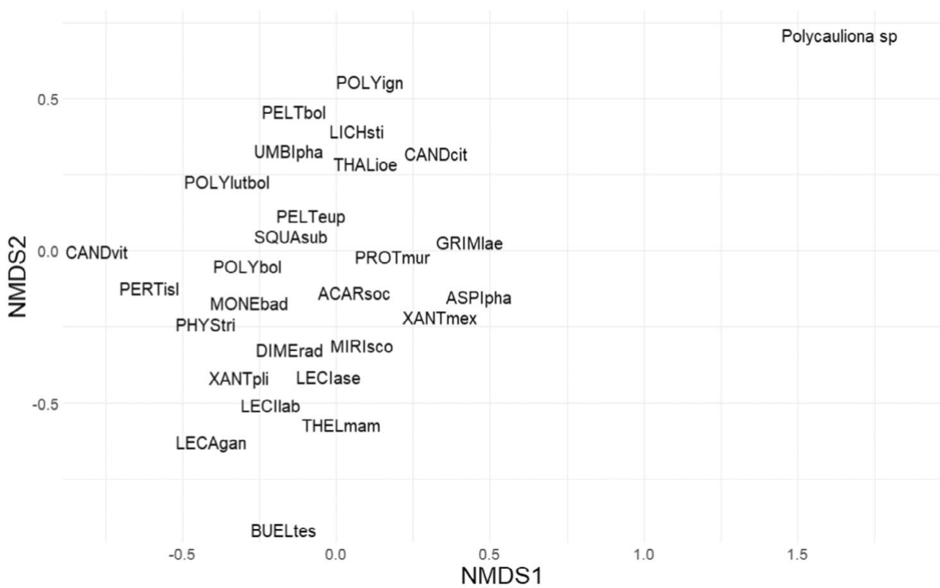

FIGURE 4 | NMDS species plot. The 28 species included occurred in 10 or more quadrats. Species abbreviations are the first four letters of the genus combined with the first three letters of the specific epithet, except for *Polycauliona* sp. See Appendix S7 for a complete list of taxa recorded.

microtopography of ultramafic rocks in comparison to sandstone in our study. Cyanolichens generally require hydration with liquid water to photosynthesize (Lange et al. 1986). Rock cracks may channel and retain water during condensation and precipitation, and moisture may persist beneath overhangs for longer periods. We therefore speculate that the relatively coarse microtopography of ultramafic rocks provides more opportunities for cyanolichen photosynthesis, resulting in their observed higher abundance and richness on ultramafic rocks compared to sandstone. In contrast, chlorolichens achieve high rates of photosynthesis under humid but not wet conditions (Lange et al. 1986), which could explain why there was not a similar association between chlorolichens and ultramafic rocks.

The effects of different rock surface properties on saxicolous communities are difficult to disentangle. For example, rock elemental composition affects surface pH, which in turn affects fundamental physiological processes such as the bioavailability of elements important to photosynthesis and metabolism. Rock surface pH and nutrient availability are highly relevant for saxicolous lichens and bryophytes. In some studies of cryptogam ecology, the importance of calcium and other elemental concentrations is emphasized, and species are described as calcicole and calcifuge (e.g., Palmer and Wilson 2021). Other studies emphasize pH tolerance and use the terms basiphytic (high-pH-associated) and acidophytic (low-pH-associated) to describe the pH associations of lichen species (e.g., Nimis 2024). Although we did not measure pH, calcium concentration was under 7% for all sites and was consistently lower in ultramafic rocks (mean ± standard error: 0.42% ± 0.21%) than sandstone (2.56 ± 0.69; Appendix S3). On sandstone, we recorded taxa typical of calcareous, high-pH rocks (Nimis 2024; Palmer and Wilson 2021). However, we also recorded some basiphytic/calcicolous taxa on ultramafic rocks. This apparent disconnect between measured calcium concentrations and the occurrence of calcicolous taxa can be reconciled when considering the variation within individual rock types. Heterogeneous distribution of calcium, along with variation in rock weathering, may lead to variation in the availability of calcium and other nutrients on different rock surfaces. Variation in rock weathering has observable effects on saxicolous communities (Woolhouse et al. 1985; Favero-Longo and Piervittori 2009). For ultramafic rock, the co-occurrence of basiphytic and acidophytic taxa is well documented (see Favero-Longo et al. 2004). One possible explanation for this co-occurrence is that highly textured rocks may facilitate the accumulation of cations along cracks and in underhangs via water flow, creating surfaces with localized higher pH. Basiphytic taxa encountered in this study include the lichens *Candelariella aurella*, *Diplotomma alboatrum*, *D. venustum*, *Lecania hassei*, *Lichinella nigritella*, *Physcia caesia*, *Rusavskia elegans*, *Verrucaria furfuracea*, and *Xanthocarpia crenulatella*, and the moss *Vinealobryum brachyphyllum*.

4.2 | Maritime Influence Hypothesis

Coastal, intermediate, and inland saxicolous communities were compositionally distinct, offering strong support for the *Maritime Influence Hypothesis*. The inland community group was the most compositionally distinct, whereas intermediate and coastal groups were more compositionally similar, likely as a result of those groups being spatially closer together (Figure 1; Appendix S1). The effect of maritime influence appears to have a slightly stronger effect than rock type in shaping the saxicolous communities in this study (Table 4).

Since maritime influence represents a suite of environmental factors, it is challenging to identify the specific factors most important for saxicolous community assembly. Precipitation, temperature regime, fog and low cloud cover, and elevation were all highly correlated with one another and with distance from the coast (Appendix S2), but other factors related to maritime influence may also be important to saxicolous communities. In particular, the influence of aerial salt deposition, which we did not measure, merits future investigation, since it can vary substantially across short distances in coastal areas (Wrubel and Parker 2018; Haraguchi and Sakaki 2020). Certain species of maritime lichens and bryophytes have been shown to have varying sensitivities to salinity (Bates and Brown 1975; Nash and Lange 1988), which may in part explain the well-documented zonation of saxicolous communities along local-scale maritime gradients (Fletcher 1973b; Bates 1975; Ryan 1988; MacDonald et al. 2011).

4.3 | Maritime Moderation Hypothesis

The effect of rock type on saxicolous communities was highest in coastal sites, second highest in intermediate sites, and lowest in inland sites (Table 4). This negative interaction between distance from the coast and rock type was the opposite of our expectation from the *Maritime Moderation Hypothesis*. Our expectation was that a milder coast climate would allow lichens and bryophytes to tolerate a wider range of substrates. However, it may be that the higher humidity in coastal areas accentuates differences in the rock surface chemical environment (e.g., elemental availability, pH; Eppes et al. 2020). It is also possible that the interaction between maritime influence and substrate type is scale-dependent, such that studying longer coast–inland transects, or comparing ultramafic and sandstone communities in intertidal to supralittoral areas, might have yielded different results. For example, Aho et al. (2014) found a moderating effect of moisture across short (100-m) transects for cryptogamic communities of limestone and andesite cliffs.

4.4 | Scale-Dependence of Community Responses to Abiotic Variation

The large amount of variation explained within the highest hierarchical level, rock type * distance from the coast, supports the idea that substrate properties and coastal distance are two of the main drivers of community variation observed in this study. Since sites were selected to be as homogeneous as possible in terms of their elevation, topographic exposure, and vegetation structure, it is unsurprising that we observed a relatively small contribution from sites nested within rock type * distance from the coast. The higher contribution of sites to variation for NMDS 2 compared to NMDS 1 suggests that differences in rock properties within the ultramafic rock and sandstone may explain some variation within the sites level. The split-plot GLM results suggest that a possible source of variation is differences in elemental composition between sites. The lowest hierarchical level, quadrats, explains modest variation along both NMDS axes. Interestingly, none of the variables measured at the quadrat level appear to explain appreciable variation within this hierarchical level (Table 3). This is even more surprising when considering that quadrats were stratified between north and south aspects within each site. The apparent lack of contribution of aspect is particularly unexpected because of well-documented species-level affinities (Alpert 1986) and community differences (Paz-Bermúdez et al. 2021) on north and south aspects.

4.5 | Limitations

A central limitation of this study was the accurate characterization of substrate properties and local biotic variables that may be relevant to saxicolous community assembly. We did not measure rock surface pH or hardness, degree of weathering, or submillimeter microtopography. Nor did we account for within-site variation in substrate elemental composition among quadrats. We attempted to minimize these sources of variation by selecting sites with visually homogeneous rocks and taking representative rock samples. Additionally, the presence of nearby woody plants may affect rock surface microclimate through partial shading, and faunal manuring of rocks can affect the nutrient availability and pH of the rock surface (Langevin et al. 2024). We attempted to control for these biotic sources of variation by sampling open, unshaded rock outcrops and by sampling the sides of rocks rather than the upper surfaces where manuring effects are likely higher. Furthermore, although we selected paired ultramafic and sandstone sites to be as close together as possible, we were limited by the occurrence of suitable and accessible rock outcrop sites. Although we attempted to account for this by pairing sites with similar elevations and coastal distances, this introduced potential sources of biotic and abiotic variation that are related to distance.

5 | Conclusions and Directions for Future Research

This study improves our understanding of some of the drivers of saxicolous community variation at a regional scale, as well as how that variation is partitioned across spatial scales. Saxicolous communities are recognized as important nodes of biodiversity within larger landscapes that are increasingly exposed to anthropogenic threats (Fredericksen et al. 2003; Fitzsimons and Michael 2017; Azevedo et al. 2024). We believe that community studies are powerful tools for identifying priority habitats for conservation. These may include saxicolous communities that are regionally unique or distinctive, that host a high diversity of lichens and bryophytes, and that host locally, regionally, and/or globally rare lichen and bryophyte taxa.

Our results indicate that rock elemental composition is an important factor shaping saxicolous communities. Accordingly, we advocate its inclusion in future studies. Research on saxicolous communities would also benefit from incorporating seldom-measured, yet likely very important factors such as substrate water retention capacity, rock surface pH, and aerial salt deposition, none of which have been measured rigorously in saxicolous lichenological and bryological community studies, even though methods to measure these variables exist (Malloch 1972; Aho and Weaver 2006; Du and Hesp 2020). Rock surface pH affects the ability of lichen secondary metabolites to bind metals, which helps explain the substrate pH affinity differences among lichen taxa (Hauck et al. 2009). Rock hardness, which relates to the weathering rate of the substrate, has clear effects on lichen communities (Woolhouse et al. 1985; Favero-Longo and Piervittori 2009). Combining measurements of these factors with elemental concentrations at rock surfaces could help clarify the relative importance of these variables, which are often highly correlated, in structuring saxicolous communities.

To gain a better understanding of the effects of geochemistry on saxicolous communities, it would be valuable to compare lichen and bryophyte biotas of ultramafic rocks to more similar volcanic-origin rocks such as basalt and granite. In the study region, sandstone is the most common rock outcrop type near ultramafic outcrops. However, these substrates possess substantially different elemental compositions and structural properties. Finally, comparing the genetics and physiology of taxa occurring on different rock types could elucidate cryptic diversity and mechanisms of adaptation to specific substrates.

Author Contributions

M.M. and N.R. conceived of the study. M.M., J.D., N.R., R.R.N., and A.F. were responsible for the study design and methodology. M.M. and J.D. carried out the fieldwork. J.D., M.M., and A.F. carried out lichen identification, and K.K. identified the bryophytes. M.M., C.B.W., and R.R.N. carried out the ecological analyses. S.J. classified rock samples from study locations and interpreted geochemical data. M.M. wrote the manuscript, and all authors provided editorial input.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The datasets and code for analyses are available via the Open Science Framework (OSF) at https://doi.org/10.17605/OSF.IO/9GNRD (Mulroy 2025).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** jvs70072-sup-0001-AppendixS1.docx. **Appendix S2:** jvs70072-sup-0002-AppendixS2.docx. **Appendix S3:** jvs70072-sup-0003-AppendixS3.docx. **Appendix S4:** jvs70072-sup-0004-AppendixS4.docx. **Appendix S5:** jvs70072-sup-0005-AppendixS5.docx. **Appendix S6:** jvs70072-sup-0006-AppendixS6.docx. **Appendix S7:** jvs70072-sup-0007-AppendixS7.docx. **Appendix S8:** jvs70072-sup-0008-AppendixS8.docx.