Lichen diversity in serpentine habitats of the North Coast Range, California

Sarah Norvell Conway[1,3], Bruce McCune[2] and Terry W. Henkel[1]

[1] *Department of Biological Sciences, California State Polytechnic University, Humboldt, Arcata, CA 95521 U.S.A.;* [2] *Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331 U.S.A.*

Abstract. Macrolichen diversity and community composition were determined for an area of high botanical interest in the Coast Ranges of Northern California – the Horse Mountain Botanical Area (HMBA) in Six Rivers National Forest. The Coast Ranges have been suggested to have high lichen diversity, yet detailed site-specific macrolichen surveys are lacking for the area. The HMBA is characterized by the presence of ultramafic (serpentine) soils, contributing to its diverse assemblage of conifers. Here we present comprehensive data on macrolichens of the HMBA integrated with environmental variables at the landscape level. Twenty 0.4 ha sampling plots were positioned across the varying habitats of the HMBA and macrolichens were intensively sampled from all substrata. Out of 888 total collections, 119 macrolichen species in 52 genera were identified, 63 species were sequenced for the mycobiont internal transcribed spacer (ITS) region, and all species were vouchered. Microenvironmental influences on lichen community composition were ordinated with nonmetric multidimensional scaling (NMS). Within-plot measured environmental variables with strongest correlations to ordination Axis 1 were 1) total tree basal area, 2) proportion of conifer basal area relative to hardwoods, and 3) distance between plot center and nearest stream. Distinct macrolichen communities were found in plots containing primarily conifers versus mixed hardwood-conifer plots. All plots contained both nitrogen-fixing and pendulous forage macrolichens; in each of the three hardwood-dominated plots, nitrogen-fixing lichens composed nearly a third of the species total. When epiphytic macrolichen species richness and dominance within the HMBA were compared to data from other regional forests, the HMBA showed comparable community composition but averaged 39% higher species richness. Results from this study can help inform management of the HMBA as well as future taxonomic and ecological research on regional macrolichens.

Keywords. Cupressaceae, biodiversity, lichen biota, nonmetric multidimensional scaling, Pacific Northwest, Pinaceae, *Quercus*.

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In recent years, anthropogenic habitat destruction, resource exploitation and climate change have contributed to rapid loss of biodiversity at multiple scales (Ceballos et al. 2015; Pykälä 2019). Discovery of biodiversity, distribution and abundance of biotic taxa is essential to understanding ecosystem function and sustainability. Forest management practices depend upon the ability to distinguish species in well-functioning ecosystems compared to those in decline so that necessary interventions can be made. Moreover, a comprehensive understanding of species distributions and abundances can inform policies promoting sustainable resource use and mitigating climate change. Surveying and monitoring of ecosystems are critical for gaining such understanding and identifying areas with declining biodiversity (Lindenmayer et al. 2012).

Lichens are complex organisms composed of two or more trophic partners from different kingdoms that are mutualistically joined to form identifiable, self-replicating symbiotic species (Honegger 1993; Lücking et al. 2017). Lichen symbionts consist of a photosynthetic green alga and/or cyanobacterium (the "photobiont") partnered with a heterotrophic fungus (the "mycobiont"). Recent molecular studies

[3] Corresponding author's e-mail: humbotany@gmail.com
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have shown this symbiosis is more complex than previously understood, with additional fungi and microorganisms present in the lichen thallus along with the "core" symbionts (Spribille et al. 2022). Lichens can be attached to a wide range of biotic and abiotic substrata, and their community composition can vary greatly along gradients of elevation, moisture and substratum chemistry (Jovan & McCune 2004). Lichens provide habitat and sustenance to many different species across several trophic levels, including nesting materials and food for small vertebrates such as birds and flying squirrels (Graves & Dal Forno 2018; Maser et al. 1985), food for ungulates and terrestrial gastropods (Gerson & Seaward 1977; Holleman et al. 1979), and habitat for microinvertebrates such as oribatid mites, springtails and jumping spiders (Gerson 1973). Lichens influence terrestrial nutrient cycling through interception of throughfall mineral nutrients and fixation of atmospheric nitrogen by cyanolichens (Antoine 2004). Management practices impacting lichens will also affect these organisms and cycles.

Voucher specimens have long been crucial components of biodiversity research, as they provide references for species identification and historical records of their biogeography (Funk 2018; Rocha et al. 2014). With the advent of molecular techniques, GIS technology, and greater global communication, vouchers are now being digitally "extended" beyond the physical specimen to correspond to searchable online databases storing robust metadata including ecological, climatic, chemical, molecular and functional trait information (Webster 2017). With more data and accessibility, extended voucher specimens contribute to a digital information network facilitating a wide range of research (Lendemer et al. 2020).

Although lichen surveys have been conducted in North America for over a century, the understanding of lichens both locally and regionally has lagged that of well-studied Europe (Nash et al. 2002). Additionally, the number of trained lichen taxonomists capable of identifying specimens is steadily declining (Lücking 2020). In California, lichens are among the more poorly documented organismal groups, evidenced by the few published intra-state lichen inventories (Jovan & McCune 2004). Recent lichen studies from northern California, while limited to epiphytic lichens and lacking habitat details, suggested that the northern Coast Ranges of California may harbor the highest diversity of epiphytic macrolichens in the state (Carlberg 2013; Jovan 2002; Villella & Carlberg 2012; Williams & Sillett 2007).

The Horse Mountain Botanical Area (HMBA) is a protected area located in the Lower Trinity Ranger District of Six Rivers National Forest (SRNF) in Humboldt County, California (**Fig. 1**). The area overlaps the northern Coast Ranges and southern Klamath Mountains (Young 1978) and has complex ultramafic geology, serpentine soils, and a unique vascular flora with diverse conifers (Witte Scott 2010). The southern extent of the range of *Chamaecyparis lawsoniana* is located within the HMBA and a stand of serpentine-tolerant *Pinus jeffreyi* survives unusually close to the coast (Kauffmann 2013). The HMBA's diverse assemblage of conifers has suggested the presence of a potentially unique macrolichen community warranting further investigation (Király et al. 2013).

In the present study, macrolichens were sampled from sites within the HMBA using standard inventory protocols. The work resulted in many collected lichen specimens with roughly one third curated as vouchers. Molecular data in the form of internal transcribed spacer (ITS) regions were obtained from the majority of taxa. Macrolichen community composition within the HMBA was evaluated using nonmetric multidimensional scaling (NMS), and functional trait values were quantified for all plots. This study provides a baseline assessment of the macrolichen diversity in the HMBA, which can be used to inform conservation strategies and aid in future taxonomic and molecular studies.

Materials and Methods

Study site. The HMBA is a 445 ha area located roughly 35 km from the Pacific Ocean with a central location of 40°52′27″N, 123°43′20″W, and with elevations ranging from ~1200–1500 m. The climate is typically Mediterranean with cool, wet winters and warm, dry summers with periodic maritime fogs. Snowfall occurs throughout winter, with snowpack persisting on north-facing slopes until early June (Witte Scott 2010). Thirty-year average monthly temperatures and precipitation were 3.5°C and 14.8 cm in January and 18.7°C and 0.9 cm in July, with an annual trend of increasing monthly temperatures and declining precipitation over the same time period (PRISM Climate Group 2023). Soils throughout the HMBA are derived from weathering of the underlying iron and magnesium-rich

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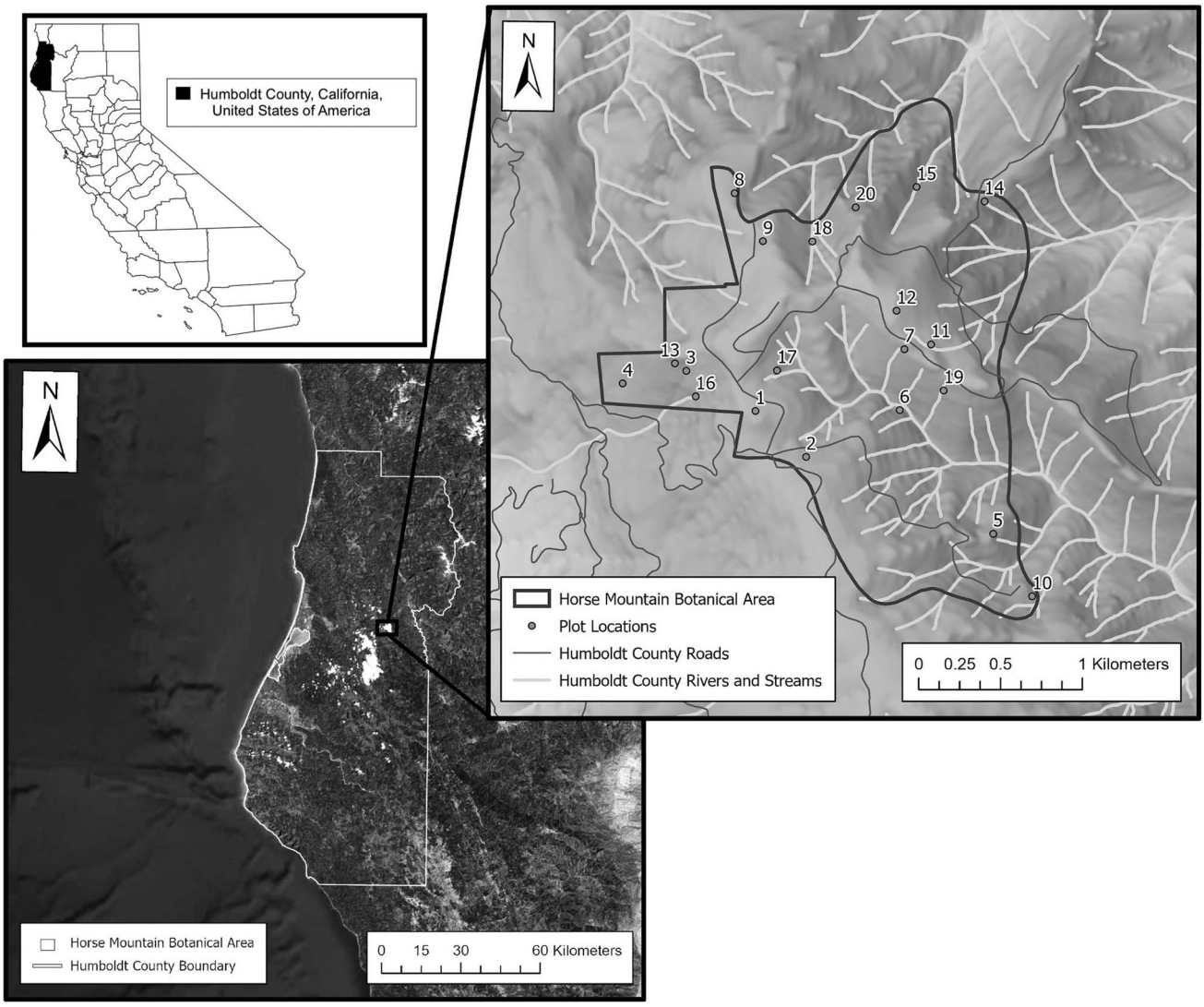

Figure 1. Location of Humboldt County within California (top left), location of the Horse Mountain Botanical Area in Humboldt County (bottom left) and expanded view of the Horse Mountain Botanical area showing study plot locations (right).

serpentinite and peridotite (Alexander 2011; Le Maitre et al. 2002).

Vegetation types within the HMBA include the *Quercus vacciniifolia* Shrubland Alliance, *Pinus jeffreyi* Forest and Woodland Alliance, *Pseudotsuga menziesii - Notholithocarpus densiflorus* Forest and Woodland Alliance, and *Abies concolor - P. menziesii* Forest and Woodland Alliance (Sawyer et al. 2009; Witte Scott 2010). Most of the HMBA is dominated by conifers, but it also contains outlying patches of hardwoods including *Acer macrophyllum, Quercus chrysolepis* and *Quercus garryana.*

Plot locations were selected by traversing the HMBA and making qualitative observations to identify sites with high lichen diversity and variation in substrata following an 'intuitive controlled survey' method (Whiteaker et al. 1998). Fully randomized surveys were not employed as they are insufficient at capturing maximum diversity in lichens over heterogeneous landscapes, as many lichen species have specific niches (Peterson & McCune 2003). Twenty circular 0.4 ha plots (**Fig. 1**) were set up with the goal of maximizing environmental variation captured within the study. Field work was conducted between May and October 2021.

Specimen collection. Plots were surveyed using the standard lichen field sampling protocol of the Forest Inventory and Analysis (FIA) Program of the USDA Forest Service (Will-Wolf 2010 2011). The goal was to

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Table 1. Forest Inventory and Analysis (FIA) relative abundance categories for lichen species.

Abundance Code	Description	Parameters
1	rare	1-3 individuals in lichen plot
2	uncommon	4-10 individuals in lichen plot
3	common	>10 individuals in lichen plot but less than half of the boles and branches have the subject species present
4	abundant	more than half of all FIA-designated substrates in lichen plot have the subject species present

determine for each plot the presence and abundance of all macrolichen taxa. Each plot survey was conducted within a two-hour search time and covered all woody substrata above a height of 0.5 m. Woody substratum taxa included *Abies concolor, Acer macrophyllum, Arctostaphylos* spp., *Calocedrus decurrens, Chamaecyparis lawsoniana, Pinus jeffreyi, Pinus lambertiana, Pinus monticola, Pseudotsuga menziesii, Quercus chrysolepis, Quercus garryana, Quercus vacciniifolia* and *Rhododendron occidentale*.

Since the permitting and training requirements for tree climbing are often prohibitive, it has been customary for macrolichen surveys to use litterfall to sample for canopy species (Miller et al. 2017; Will-Wolf et al. 2002). The Horse Mountain area features numerous tree root disease centers with abundant treefalls that allow ground sampling of canopy epiphytic lichens (Hawkins & Henkel 2011).

A supplementary survey was performed paralleling FIA protocols to assess previously unsurveyed natural substrata, including rocks, soil, bryophytes, downed woody debris, stumps and bases of standing trees below 0.5 m. Specimens collected during initial 'epiphyte' surveys and those collected during supplementary 'ground' surveys were separated for analysis purposes. Species known to have been collected during 'epiphyte' surveys were not recollected during 'ground' surveys for the same plot.

Macrolichen specimens were collected with attached substrata and labeled with plot number, collector, collection number, description or taxon sight identification, substratum, substratum taxon and relative abundance value. An abundance value of 1 (low) to 4 (high) was assigned to each specimen following FIA lichen survey protocols (McCune et al. 1997) (**Table 1**).

Plot data collection. Plot center coordinates were recorded with the iPhone 11 Avenza Maps application using the Military Grid Reference System (MGRS) standard (**Supplementary File S1**). These data were then imported into ArcGIS Pro Version 2.5 (Esri 2021) for further analysis. A Garmin GPSMAP 64st was used to verify the accuracy of coordinates obtained with Avenza Maps; location data were equivalent between both devices. A map of plot locations was generated in ArcGIS Pro using datasets obtained from the USDA Natural Resource Conservation Service Geospatial Data Gateway, the National Map, Humboldt County GIS, and the USDA Forest Service. Slope, aspect, and distance to the nearest stream were determined for each plot center using the Slope, Aspect, and Near spatial analysis tools in ArcGIS Pro. Elevation was calculated from the Digital Elevation Model (DEM). Tree basal area was estimated within each plot using a wedge prism (Jim-Gem® Square Cruising Prism) with a basal area factor (BAF) of 10 ft^2/acre. For each plot, five 360° sweeps were made with the wedge prism, one from plot center and one from each cardinal direction at the plot border. Trees included by the prism were counted and recorded as either hardwoods or conifers (Šálek & Zahradník 2008). Counts from the five sweeps were averaged for each plot and multiplied by the BAF to calculate total basal area. Plot metadata are given in **Supplementary File S2**.

Locations of the 20 FIA plots nearest to the HMBA (**Supplementary File S3**) were selected for macrolichen community comparison using ArcGIS Pro; plots within 15 km of the coast were excluded due to differences in macrolichen communities relative to inland plots. While no FIA plots were located within the boundaries of the HMBA, all selected FIA comparison plots were within ~ 75 km of the study site.

Specimen determinations. Lichen specimens were identified to species using macro- and micromorphology, ultraviolet light, lichen chemical spot-testing, and keys (Brodo 2016). Standard spot tests were performed using undiluted commercial bleach, an aqueous solution of 10% potassium hydroxide, and crystalline p-phenylenediamine dissolved in 95% ethanol (Lumbsch 2002; McCune & Geiser 2009). A subset of specimens in the genus *Usnea* were subjected to thin-layer chromatography (TLC) using solvents B′ and C following the standard methods and Rf tables of Culberson (1972; C. Culberson pers.

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comm.). Representative specimens were extracted for barcode sequences as described below.

Voucher specimens. Voucher specimens were curated for each inventoried species using the extended specimen concept (Lendemer et al. 2020). Three separate collections per species were curated where possible and deposited into the Cal Poly Humboldt Lichenarium (HSC), which serves as a voucher specimen repository for regional lichen studies. Vouchers and associated metadata were accessioned into the Consortium of Lichen Herbaria (CLH) via Symbiota software following the Darwin Core Standard (Gries et al. 2014).

DNA sequencing and analysis. Nuclear ITS regions of voucher specimens were obtained following the DNA extraction and PCR analysis protocols for lichens used by the McCune Lab in the Department of Botany and Plant Pathology at Oregon State University (unpublished), as summarized in **Supplementary File S4**. Products were sequenced with forward and reverse reads (Eurofins MWG Operon Inc., Kentucky, U.S.A.). A set of gelatinous lichen specimens was sent to Molecular Solutions LLC in Portland, Oregon for DNA amplification and sequencing. Sequence data analysis was performed using Geneious version 10.0.9 (Kearse et al. 2012). Raw sequence quality was assessed and two reads per sample were aligned using the *de novo* assembly tool. Consensus sequences were generated, trimmed, annotated, and deposited in the GenBank National Institutes of Health sequence database.

Data analysis. Data analyses were performed using multivariate analysis software PC-ORD Version 7 (McCune & Grace 2002; McCune & Mefford 2016). Matrices were generated for analysis in PC-ORD, including abundance matrices of all identified macrolichens from both 'epiphyte' and 'ground' surveys, a plot metadata matrix, a functional trait matrix, and abundance matrices of the 20 FIA plots nearest to the study site. Abundance values were combined for individual taxa collected during 'epiphyte' and 'ground' surveys within the same plot following FIA protocol (Will-Wolf & Neitlich 2010).

Gamma diversity was estimated with first and second-order jackknife and Chao2 estimators as part of the species-area function in PC-ORD. The species-area curve and confidence bands were generated by resampling the data with replacement.

An ordination was produced in PC-ORD using 'slow and thorough' NMS with the all-species abundance matrix, plot metadata matrix, and functional trait matrix. The Sørensen distance measure was employed with tie penalization, a maximum of six axes and 500 iterations, and a test of significance was based on 250 randomizations. After confirming the consistency of interpretation among multiple NMS solutions, we interpreted a two-dimensional NMS solution with a final stress of 15.7, and randomized test $p = 0.004$.

To compare our sample with nearby FIA plots, we used an indicator species analysis (ISA, Dufrêne & Legendre 1997) in PC-ORD using the 'epiphyte survey' species abundance matrix after appending the FIA plots. An explanatory matrix defined two groups (our study plots vs. FIA plots). Dominance curves were graphed in PC-ORD for subsets of data to illustrate the log(abundance) against rank abundance in each group. Boxplots of species richness comparing subsets were created in RStudio Version 2022.07.0 (RStudio 2020).

Abundance-weighted totals of functional trait values were generated by multiplying the all-species abundance matrix by the functional trait matrix using the 'Calculate SU × Traits Matrix' tool in PC-ORD. Most traits in the functional trait matrix were qualitative traits recorded as binary values. These traits include the ability to fix nitrogen (0=chlorolichen, 1=cyanolichen), obligation to rocky substrata (0=not obligated, 1=rock-obligated), and forage value for wildlife (0=thallus not pendulous, 1=thallus pendulous). Nitrophily scores were assigned using the 'Nitrogen Deposition at Peak Frequency' values listed in McCune & Geiser (2009), which occur on a scale from 0.8 to 8 kg N/ha/yr. For species with no calculated nitrophily value, scores were assigned based on similar species or given a neutral value if no similar species were listed. The nitrophily trait was subdivided into 'rock nitrophiles' and 'epiphytic nitrophiles' and assigned binary values (rock nitrophiles: 1=nitrophilic and rock-obligated; epiphytic nitrophiles: 1=nitrophilic and primarily epiphytic). In the resulting matrix, referred to as the sample unit (SU) × trait matrix, each element is the proportion of total abundance in a given plot with a particular trait (McCune 2015).

Results

A total of 888 lichen specimens were collected from the HMBA. Of these specimens, 865 macrolichens

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were identified to species, and these grouped into 119 species from 52 genera and 17 families (**Supplementary File S5**). Nine morphospecies could not be identified below the genus or family levels due to poor specimen condition or lack of propagules, and 14 microlichens were not identified. Lichens not identified to species were excluded from data analyses. Curated extended voucher specimens numbered 287. Thirty-four of the vouchered taxa appear to be the first documented records for Humboldt County in CLH. Among the identified species, 59% had foliose thalli, 23% were fruticose, and 18% were squamulose. Macrolichen species richness per plot ranged from 20 to 44 species and averaged 35 species. Thirty-five species occurred only once, and 21 species occurred only twice. Four species occurred in all 20 plots: *Cladonia transcendens, Hypogymnia imshaugii, Platismatia glauca* and *Platismatia stenophylla*. Gamma diversity was estimated with first and second-order jackknife estimators at 153 and 167 total species, respectively, had sampling been exhaustive in the area. The Chao2 estimate in the bias-corrected form was 146 total species. The species-area curve showed that most species were recovered by $\sim$ 10 plots with the curve gradually flattening between 10–20 plots. The all-species abundance matrix is provided in **Supplementary File S6**.

The ordination of the full set of plots with all macrolichen species (20 plots with 119 species) yielded a stable two-dimensional solution (final stress = 15.7; randomization test, $p = 0.004$) (**Fig. 2**). Roughly 80% of total variance in the dissimilarity matrix is represented by the first two axes (cumulative $r^2 = 0.798$). Pearson correlations with Axes 1 and 2 are displayed in **Table 2**. The conifer vector has the strongest correlation with Axis 1 ($r = –0.771$).

The SU $\times$ traits matrix (**Supplementary Files S7 & S8**) revealed that all plots contained macrolichens with cyanobacterial photobionts and forage value, 65% of plots contained rock-obligates, and 35% of plots contained nitrophilic macrolichens (mainly *Physcia* spp.). Three plots had 30% of species richness represented by cyanolichens. Half of all plots had 20% or more species richness represented by pendulous lichens with forage value (mainly *Alectoria*, *Bryoria* and *Usnea* spp.).

The inclusive alpha diversity of the 20 HMBA 'epiphyte' plots and the 20 nearest FIA plots was 106 species. Twenty-eight species occurring in the FIA plots were not found in the HMBA, and 19 HMBA species were not found in the FIA plots. Boxplots depicting species richness in the HMBA 'epiphyte' plots versus surrounding FIA plots are shown in **Fig. 3**. Results of dominance curves generated for HMBA 'epiphyte' plots and surrounding FIA plots are listed in **Table 3**.

A total of 81 ITS rDNA sequences were generated through this study, representing 63 taxa (**Table 4**). All inventoried species underwent DNA extraction and PCR protocol, though many attempts were unsuccessful. Several good-quality ITS sequences did not closely match any sequences in GenBank and deserve more scrutiny, primarily from the genera *Alectoria*, *Letharia* and *Leprocaulon*. Three specimens from the HMBA and their sequences were used in the description of the new species *Hypogymnia tuckerae* (McCune & Conway 2022).

Discussion

Sampling and diversity. Species-area analysis of all inventoried plots suggested that the HMBA was effectively sampled to provide baseline data on the macrolichen diversity present. Further sampling efforts could, however, result in the recovery of additional macrolichen taxa. Epiphytic macrolichens appeared more diverse than in regional FIA plots, although it is difficult to compare the total number of taxa identified from within the HMBA to surrounding areas due to a lack of comparable published inventories. This difference may be due to environmental variation or sampling errors (McCune et al. 1997). Cryptic species are also difficult to recognize in the field (Lauriault & Wiersma 2019). Dominance analyses showing the ten most abundant species from study plots and regional FIA plots indicated four of the ten species were shared between the two groups, both listing *Hypogymnia imshaugii* as the most dominant. The FIA plots in the surrounding area had more dominance of mesic-associated species, such as *Alectoria sarmentosa*, *Bryoria pseudofuscescens*, and the cyanolichens *Lobaria pulmonaria* and *Lobaria anthraspis*. None of the top ten lichens at HMBA are considered serpentine specialists, although the abundance of *Alectoria lata* is unusual in the broader region and needs further study as to whether the local populations represent an environmental expression of *A. sarmentosa* or are genetically distinct.

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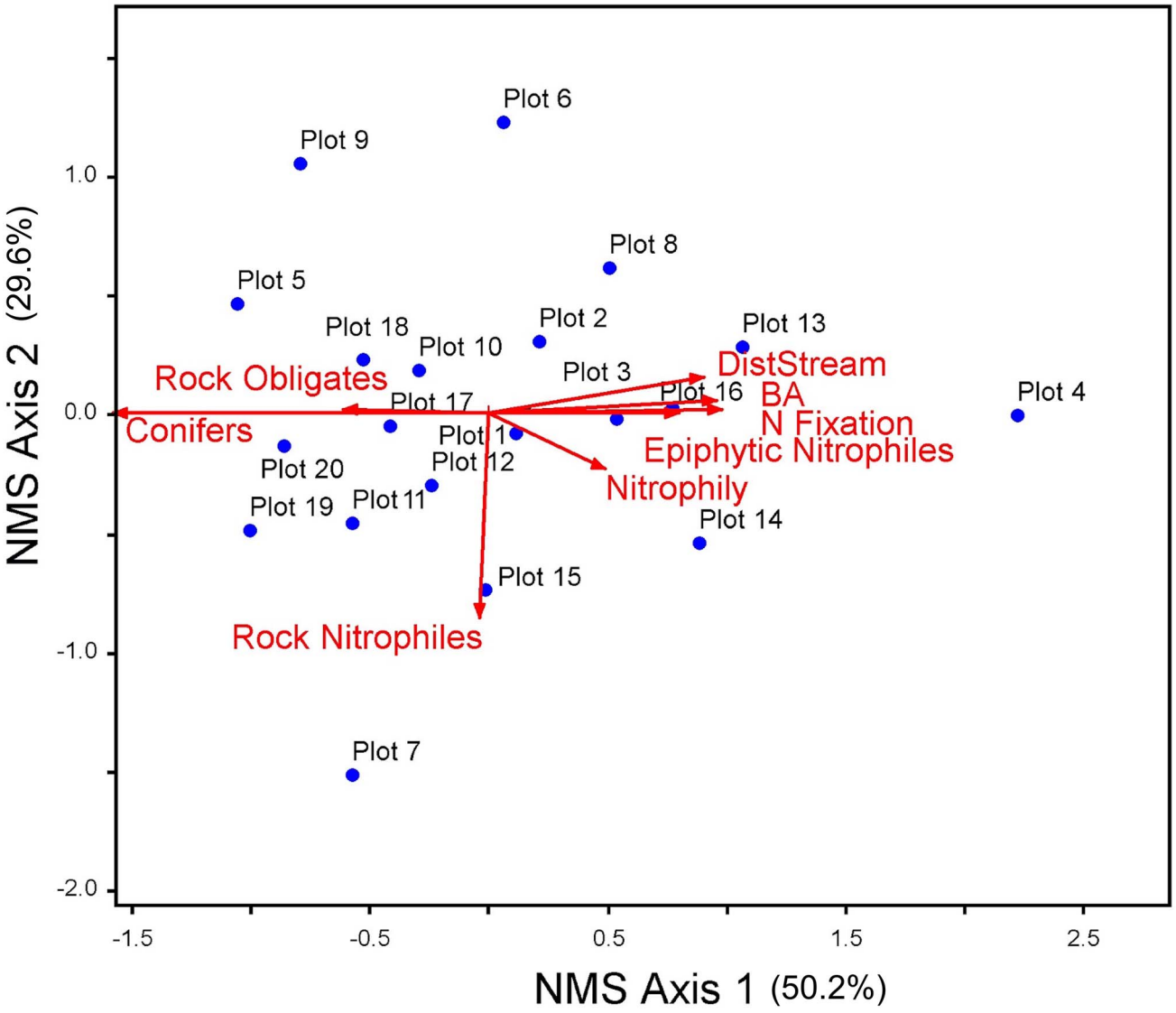

Figure 2. NMS ordination of all study plots (Plots 1–20) in species space based on 119 macrolichen species identified from the Horse Mountain Botanical Area. Roughly 80% of total variance is represented by Axis 1 (50.2%) and Axis 2 (29.6%), with cumulative $r^2 = 0.798$. Radiating lines represent the strength and direction of correlations with environmental variables and functional traits: BA = estimated plot basal area, Conifers = percentage of plot basal area contributed by conifers, DistStream = distance from nearest stream to plot center, Epiphytic Nitrophiles = presence of lichen species that are both nitrophilic and epiphytic, N Fixation = presence of cyanolichens, Nitrophily = presence of lichen species with an affinity for nitrogen-rich environments, Rock Nitrophiles = presence of lichen species that are both nitrophilic and obligated to rocky substrata, Rock Obligates = presence of lichen species obligated to rocky substrata. The conifer vector had the strongest correlation with Axis 1 ($r = -0.771$).

Molecular data. Sequence data from the nuclear ITS region can be a useful adjunct for species delimitation in lichenized fungi (Kelly et al. 2011; Schoch et al. 2012). In this study, 81 ITS rDNA sequences were generated from 63 taxa, representing the majority of macrolichen taxa recovered from the HMBA. Initial BLAST results indicated that eight of our sequences were from species previously not deposited in GenBank, including *Collema nigrescens, Fuscopannaria thiersii, Leptochidium albociliatum, Lobaria hallii, Scytinium californicum, S. subaridum, S. tacomae*, and the recently described *Hypogymnia tuckerae*. Excepting *H. tuckerae*, most of these species are regionally common, highlighting the dearth of publicly available lichen sequence data (Lücking et al. 2014). Our GenBank records will allow retroactive re-identification of the species in this study as the taxonomy of lichens advances.

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Table 2. Pearson correlations with ordination axes, N = 22. Variables are plot elevation, plot slope, DistStream = distance from nearest stream to plot center, BA = estimated plot basal area, Conifers = percentage of plot basal area contributed by conifers, N Fixation= presence of cyanolichens, Rock Obligate = presence of lichen species obligated to rocky substrata, Forage = presence of pendulous lichen species with forage value for wildlife, Nitrophily = presence of lichen species with an affinity for nitrogen-rich environments, RockNitroph = presence of lichen species that are both nitrophilic and obligated to rocky substrata, and EpiNitroph = presence of lichen species that are both nitrophilic and epiphytic.

Variable	Axis 1	Axis 2
Elevation	−0.298	−0.062
Slope	−0.079	−0.196
DistStream	0.608	0.161
BA	0.616	0.069
Conifers	−0.771	0.148
N Fixation	0.617	−0.005
Rock Obligate	−0.477	0.160
Forage	−0.028	0.253
Nitrophily	0.406	−0.360
RockNitroph	−0.167	−0.558
EpiNitroph	0.552	−0.093

Some lichen species are morphologically indistinguishable and only reliably identified using molecular data (Altermann et al. 2016; Boluda et al. 2016). Several BLAST results from this study conflicted with previously determined species identifications. A specimen identified as *Alectoria lata*, a common species in the study with several regional records on CLH, matched GenBank vouchers of *A. imshaugii* and *A. sarmentosa* (both 99.8% pairwise identity) before matching with an *A. lata* voucher (97% pairwise identity). *Alectoria lata* was originally described from

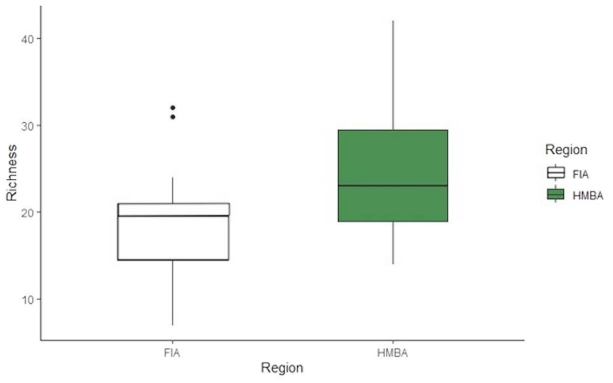

Figure 3. Median number of macrolichen species per plot from 20 Horse Mountain Botanical Area 'epiphyte' plots and that from 20 nearest Forest Inventory and Analysis plots. Boxes show median and the 1st and 3rd interquartile ranges. Whiskers extend to 1.5 × interquartile range. Dots are outliers.

Table 3. The ten most abundant species in all 20 Horse Mountain Botanical Area 'epiphyte' plots and nearest 20 FIA plots in descending order.

Rank	HMBA	FIA
1	*Hypogymnia imshaugii*	*Hypogymnia imshaugii*
2	*Platismatia glauca*	*Esslingeriana idahoensis*
3	*Letharia vulpina*	*Alectoria sarmentosa*
4	*Tuckermannopsis platyphylla*	*Letharia vulpina*
5	*Platismatia stenophylla*	*Tuckermannopsis platyphylla*
6	*Alectoria imshaugii*	*Tuckermannopsis orbata*
7	*Alectoria lata*	*Lobaria pulmonaria*
8	*Esslingeriana idahoensis*	*Parmelia sulcata*
9	*Parmeliopsis hyperopta*	*Lobaria anthraspis*
10	*Nodobryoria oregana*	*Bryoria pseudofuscescens*

Mexico (Brodo & Hawksworth 1977), and while specimens keying to *A. lata* on Horse Mountain appear morphologically distinct from *A. imshaugii* and *A. sarmentosa*, it is possible that *A. lata* belongs within *A. sarmentosa* (McMullin et al. 2016). Further taxonomic and molecular work is required.

Letharia specimens sequenced during this study were selected as archetypal examples of either *L. columbiana* or *L. vulpina*, two species that are morphologically distinct. Sequencing results indicated the presence of a third species, *L. lupina*, recently described in a study that attempted to disentangle the taxonomy of the genus in Western North America (Altermann et al. 2016). Of three *Letharia* sequences generated for this study, none had a match consensus on GenBank. As previous studies have suggested, sequencing more loci may be necessary for accurate species delineation in *Letharia* (Kroken & Taylor 2001).

A specimen identified as *Leprocaulon albicans* with apparent pseudopodetia was successfully sequenced, and BLAST results matched vouchers of *Lepraria neglecta* (between 97.8 and 98.2% pairwise identity). These results align with that of Lendemer & Hodkinson (2013), who found that all species of *Leprocaulon* likely belong in *Lepraria* s.str. and that they have evolved a fruticose growth form.

Environmental factors and macrolichen communities. The macrolichen community composition in the HMBA was closely linked to environmental factors. Ordination Axis 1 followed an environmental gradient from conifer-dominated, low basal area, stream-proximal plots to upland mixed hardwood-conifer plots with higher basal areas. Species primarily occurring in the hardwood-containing plots were

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Table 4. Taxa, voucher information, and GenBank accession numbers for macrolichens successfully sequenced in this study. A comprehensive species list is included in Supplementary File S5.

Taxon	Voucher	GenBank Accession No. (ITS)
Alectoria imshaugii	SNC52	OQ917170
Alectoria lata	SNC126	OQ917174
Alectoria sarmentosa	SNC127	OQ917175
Alectoria vancouverensis	SNC275	OQ917190
Bibbya ruginosa subsp. *ruginosa*	SNC827	OQ917241
Bryoria fremontii	SNC279	OQ917192
Bryoria fremontii	SNC744	OQ917234
Bryoria glabra	SNC278	OQ917191
Candelariella sp.	SNC736	OQ917231
Cetraria sphaerosporella	SNC615	OQ917224
Cladonia carneola	SNC832	OQ917242
Collema furfuraceum	SNC171	OQ917177
Collema nigrescens	SNC172	OQ917178
Esslingeriana idahoensis	SNC408	OQ917204
Evernia prunastri	SNC174	OQ917179
Fuscopannaria aurita	SNC738	OQ917232
Fuscopannaria pacifica	SNC613	OQ917222
Fuscopannaria pacifica	SNC614	OQ917223
Fuscopannaria thiersii	SNC653	OQ917229
Hypogymnia enteromorpha	SNC287	OQ913502
Hypogymnia imshaugii	SNC71	OQ917172
Hypogymnia tuckerae	SNC431	ON511157
Hypogymnia tuckerae	SNC442	ON511158
Hypogymnia tuckerae	SNC843	ON511159
Hypogymnia physodes	SNC15	OQ913503
Imshaugia aleurites	SNC67	OQ917171
Kaernefeltia merrillii	SNC406	OQ917203
Leprocaulon albicans	SNC245	OQ917184
Leptochidium albociliatum	SNC765	OQ917237
Letharia columbiana	SNC472	OQ917207
Letharia columbiana	SNC814	OQ917240
Letharia lupina	SNC413	OQ917205
Letharia lupina	SNC500	OQ917209
Letharia vulpina	SNC749	OQ917235
Lichenella stipatula	SNC260.1	OQ917187
Lobaria anthraspis	SNC570	OQ917213
Lobaria hallii	SNC184	OQ917180
Melanohalea multispora	SNC600	OQ917215
Montanelia panniformis	SNC220	OQ917182
Montanelia sorediata	SNC611	OQ917220
Nephroma helveticum	SNC639	OQ917227
Nephroma parile	SNC323	OQ917195
Nephroma resupinatum	SNC640	OQ917228
Nodobryoria oregana	SNC751	OQ917236
Normandina pulchella	SNC635	OQ917225
Parmeliopsis ambigua	SNC148	OQ917176
Peltigera collina	SNC638	OQ917226
Peltigera monticola	SNC863	OQ917243
Platismatia glauca	SNC389	OQ917199
Platismatia herrei	SNC390	OQ917200
Platismatia stenophylla	SNC584	OQ917214
Polychidium muscicola	SNC461	OQ917206
Polychidium muscicola	SNC612	OQ917221
Polychidium muscicola	SNC767	OQ917238
Psora nipponica	SNC251	OQ917185
Psoroma hypnorum	SNC328	OQ917196
Ramalina farinacea	SNC208	OQ917181
Scytinium californicum	SNC609	OQ917218
Scytinium californicum	SNC102	OQ917173
Scytinium californicum	SNC256	OQ917186
Scytinium californicum	SNC319	OQ917194
Scytinium californicum	SNC485	OQ917208
Scytinium californicum	SNC361	OQ917198
Scytinium polycarpum	SNC317	OQ917193
Scytinium pulvinatum	SNC739	OQ917233
Scytinium subaridum	SNC606	OQ917216
Scytinium tacomae	SNC47	OQ917169
Scytinium tacomae	SNC607	OQ917217
Scytinium tacomae	SNC610	OQ917219
Sphaerophorus tuckermanii	SNC329	OQ917197
Sphaerophorus venerabilis	SNC393	OQ917201
Toninia squalida	SNC796	OQ917239
Toninia squalida	SNC529	OQ917211
Tuckermannopsis chlorophylla	SNC718	OQ917230
Tuckermannopsis orbata	SNC7	OQ917168
Tuckermannopsis platyphylla	SNC228	OQ917183
Umbilicaria polyphylla	SNC271	OQ917189
Umbilicaria vellea	SNC269	OQ917188
Usnea barbata	SNC510	OQ917210
Usnea filipendula	SNC394	OQ917202
Waynea californica	SNC566	OQ917212

Collema furfuraceum, C. nigrescens, Lobaria hallii, L. scrobiculata, Physconia americana and *P. perisidiosa*. The few plots with significant proportions of hardwoods present occurred on hillsides and not in valleys near streams. Most HMBA streams are categorized as first-order streams, exhibiting either intermittent or ephemeral flow. Several plots in valley bottoms had moderate basal areas, high percentages of conifers, and were closer to streams than upland plots. Plots with the lowest basal area tended to be on exposed ridge tops with rocky outcrops and scattered, serpentine-stunted conifers. Species commonly occurring in these plots were *Cetraria sphaerosporella, Letharia columbiana, L. vulpina, Nodobryoria abbreviata* and *Vulpicida canadensis*. Plot elevation and slope had no demonstrable effect on macrolichen community composition in

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the HMBA. Within such a relatively small geographic area, it is not unusual for topographic factors to be insignificant (Jovan 2002; Jovan & McCune 2004).

Despite the relatively small size of the study area, overall spread of the plots in species space indicated that no two plots were exactly alike, demonstrating the variability of macrolichen species composition across this landscape. Further research in the area should measure additional environmental factors that more directly influence macrolichen community composition.

Macrolichen functional traits and community composition. Functional traits of lichen species can be utilized in combination with occurrence data to elucidate patterns of community composition along environmental gradients (Ellis et al. 2021; Nelson et al. 2015). Knowledge of these community patterns is useful to forest managers who must prioritize the health of particular taxa. The SU × trait matrix in this study showed that all plots contained both nitrogen-fixing and pendulous forage macrolichens. Such traits may play an important role in maintaining biodiversity in ecosystems (Rikkinen 2015). In each of the three hardwood-dominated plots (4, 13 & 14) nitrogen-fixing lichens composed nearly a third of the total species. The preference of certain nitrogen-fixing species for hardwood substrata is well known, and forest managers should take this into account when determining the conservation value of tree species (Cleavitt et al. 2009; Jovan & McCune 2004; Sillett & Goslin 1999). Specifically, hardwood and deciduous shrub retention in cutting units promotes biodiversity in many species groups, including birds, insects and lichens (Muir et al. 2002). Pendulous lichens provide essential nesting and foraging material for birds and mammals (Graves & Dal Forno 2018; Maser et al. 1985), which is important in areas like the HMBA with heavy winter snowpack. Some species of pendulous lichens are restricted to old-growth forests (Esseen et al. 1996; Lesica et al. 1991; Sillett et al. 2000), further emphasizing the need to conserve these stand types in the HMBA and elsewhere.

Exposed rocks occurred in all plots but not all plots contained rock-obligate macrolichens. Plots containing rock-obligates were primarily exposed conifer plots. Plot 5, with large boulders and outcrops, had the highest abundance of rock-obligate species. The rock-obligates vector has a different trajectory than the rock nitrophiles vector in the ordination, likely due to the influence of a single plot with a relatively high abundance of nitrophilic rock-obligates. Future research in the area should incorporate rock-type and soil analyses, with a focus on serpentine, to elucidate relationships between lichens and substratum chemistry (Sirois et al. 1988).

Less than half of the study plots contained nitrophilic macrolichens (Jovan & McCune 2005; McCune 2007), and where present, abundance values were generally low. The two plots with the highest nitrophile abundance (Plots 4 & 7) contained roughly 20% nitrophilic species, and several nitrophilic species collected were singletons in the study.

Our ordination showed similar axis correlations for nitrophily and nitrogen fixation, likely due to the known association of cyanolichens and select nitrophilic species with hardwoods. The nitrophily vector appears to be a compromise between rock nitrophiles and epiphytic nitrophiles.

Lichen Conservation Index. To further characterize the macrolichen community in the HMBA, lichen conservation index (LCI) values were assigned to HMBA species on a scale of 1 to 10. The scale corresponds to an estimate of the fidelity of a species to a forest stand of specific age, with 1 being the youngest stands and 10 being old-growth (Miller et al. 2020) (**Supplementary File S5**). Out of 79 taxa reported here, 24 ranked at 7 or higher, and only seven at 3 or below, suggesting that many species may be restricted to late-successional forests. Such findings reinforce the conservation value of older forests in the HMBA. The LCI, developed by Miller et al. 2020, combined experiential and empirical data to assign these values to regional epiphytic lichen species. Limitations to applying the LCI to this study include the regional focus of the index, which is primarily western Oregon and Washington. Additionally, the index does not include all epiphytic lichen species collected in this study.

Conclusions. This study represents the first exhaustive macrolichen community sampling and analysis for an area of high botanical interest in the Coast Ranges of northern California. As such, it provides insight into the diversity and distribution of macrolichens in the region. We found 119 macrolichen species identified from 888 collections, and the HMBA was shown to have high macrolichen diversity

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relative to a random sample of nearby forests in the FIA plot network. First taxa records for Humboldt County reiterated the need for more publicly available lichenarium records. Extended voucher specimens were curated to include molecular data to aid in the identification of cryptic lichen biodiversity within the study area and in future taxonomic research. Morphological and molecular analyses revealed the presence of a previously undescribed macrolichen species, *Hypogymnia tuckerae* (McCune & Conway 2022), as well as several cryptic species complexes, underscoring the importance of surveys and taxonomic research in the area.

Ordination results implicated several interacting environmental factors that may influence macrolichen community composition in the study area; the strongest gradient was from conifer-dominated, low basal area, stream-proximal plots to upland mixed hardwood-conifer plots with higher basal areas. Functional trait and dominance analyses further characterized macrolichen communities of the HMBA and could inform future monitoring efforts. Our study enhances understanding of complex lichen communities and reinforces the need for preserving this often-overlooked element of biodiversity.

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Supplementary documents online:

Supplementary File S1. Plot centroid spatial coordinates referenced to the WGS84 datum.

Supplementary File S2. Plot slope, aspect, elevation, distance to nearest stream, estimated total basal area, and proportion of basal area composed of conifers.

Supplementary File S3. Location coordinates of Forest Inventory and Analysis comparison plots.

Supplementary File S4. DNA Extraction and PCR protocols.

Supplementary File S5. Annotated species list of the HMBA.

Supplementary File S6. All-species abundance matrix for Horse Mountain Botanical Area.

Supplementary File S7. Functional trait matrix listing trait values for all study species.

Supplementary File S8. Abundance-weighted totals of species with particular functional traits.

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