Ecological Research

NOTES AND INSIGHTS

Ultramafic Ecology 2025: Proceedings of the 11th International Conference on Serpentine Ecology

Slow Succession: A Comparison of the Saxicolous Lichens of a 50-Year-Old Abandoned Chromite Mine and a Nearby Undisturbed Ultramafic Outcrop

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Received: 16 January 2026 | **Revised:** 5 April 2026 | **Accepted:** 23 April 2026

Keywords: community ecology | cryptogams | dispersal | geoecology | ultramafic

ABSTRACT

Pioneering and succession are well-studied phenomena in the field of ecology but are poorly understood for lithic habitats dominated by cryptogams. Yet pioneering and establishment of epilithic communities constitutes a fundamental ecological process that provides a precursor to the formation of soil terrestrial communities. Abandoned mines offer an exciting opportunity to explore pioneering and succession of lithic habitats. In our study, we quantitatively compared the lichen communities of an approximately 50-year-old abandoned chromite mine to a nearby, undisturbed rock outcrop of similar ultramafic parent material. Our results reveal several differences between these two communities. The early successional community of the mined site had significantly lower lichen cover and species richness, as well as a species composition distinct from the late successional community of the undisturbed rock outcrop. The early successional community was characterized by relatively high cover and frequency of endolithic lichen taxa, which were mostly absent from the late successional community. Our results highlight the slow progress of pioneering and succession in newly exposed areas of rock and emphasize the importance of preserving undisturbed, late successional lithic habitats.

1 | Introduction

Rock outcrops and other lithic habitats support highly diverse communities of lichens, bryophytes, and vascular plants, including many habitat-restricted species. Rock-dwelling (saxicolous) lichens are frequently dominant in these habitats, often covering most of the available rock surfaces and forming diverse species assemblages. Although lithic habitats may be perceived as resilient compared to other cryptogam-dominated communities, they remain vulnerable to anthropogenic disturbances such as infrastructure development, quarrying, air pollution, recreational rock climbing, and fire (Cámara et al. 2011; Hauck 2010; Rydgren et al. 2011; Reding et al. 2022; Zabala et al. 2023). Post-disturbance recovery of saxicolous cryptogam communities is of interest for a variety of reasons, including, but not limited to, bioremediation of mined areas (Favero-Longo et al. 2006; Liulevičius et al. 2026) and habitat restoration for rare vascular plants (Riefner et al. 2003).

Lichens are among the first macroscopically visible pioneers of bare rock surfaces, although they are often preceded by endolithic and epilithic microbes growing within and on top of the rock surface, respectively. These include non-lichenized fungi, cyanobacteria, and green algae (Temina 1992; Cámara et al. 2011; Favero-Longo et al. 2015). Establishment rates of lichens are typically very slow, with visible epilithic lichens sometimes only appearing after several decades (Cámara et al. 2011). One reason for this is the slow growth rate of lichens, particularly of crustose lichens, which for many species has been measured at less than 1 mm per year (Armstrong and Bradwell 2010). Another likely reason is dispersal limitation in lichens, which at a minimum include a primary fungal (mycobiont) and photosynthetic (photobiont) component, and may also contain additional obligate members, at least in some taxa (Spribille et al. 2016). Therefore, dispersal in lichens requires dispersal of at least the primary mycobiont and photobiont, either together within an asexual propagule or independently. Finally, freshly exposed rock surfaces may have properties that inhibit establishment of lichens. New, unweathered rock surfaces may differ from older, weathered surfaces of undisturbed outcrops in many respects, including surface pH, elemental composition and availability, surface microtopography, and the epilithic and endolithic microbial community (Favero-Longo et al. 2015).

The primary goal of this study was to improve our understanding of succession following disturbance in a saxicolous lichen community. To accomplish this, we compared the lichen communities of two neighboring ultramafic rock sites: (1) the early successional lichen community of a chromite mine area that had been abandoned for approximately 50 years; and (2) a late successional lichen community of an undisturbed rock outcrop site ca. 1.3 km away. We hypothesized that compared to the late successional community, the early successional community would have (1) a different lichen species composition; (2) lower lichen cover; and (3) lower lichen species richness. We also hypothesized that the early-successional community would have a higher prevalence of asexually reproducing species due to their ability to disperse both the photobiont and mycobiont simultaneously. Lastly, we hypothesized that spore size could play a role in a lichen's ability to disperse to new areas. Therefore, we predicted that sexually reproducing species at the early successional community would have smaller spores than sexually reproducing species at the undisturbed site.

2 | Methods

2.1 | Study Areas

The mined and undisturbed sites are both located on ultramafic rock within Irish Hills Natural Reserve in San Luis Obispo County, California, USA (Figure 1). The mined site, hereafter referred to as the early successional community, is located at 35.243892°, −120.704430°, at an elevation of 280 m within chaparral habitat classified as the leather oak chaparral alliance (CNPS 2025). The mined site was estimated to have been abandoned in the 1970s, such that the lichen community there is approximately 50 years old. This was estimated by comparing historical aerial imagery between 1956 and 1994. New ground disturbance was visible in 1969 aerial imagery, but by 1994, most of the mine footprint had reestablished chaparral growth. Although much of the mined area has since been recolonized by native chaparral vegetation, the portion of the mine sampled for this study consisted of mostly bare, exposed upland habitat on a predominantly north-facing slope (Figures 1 and 2), characterized by large rocks, bare mineral soil, and scattered shrubs. The undisturbed site, hereafter referred to as the late successional community, lies approximately 1.3 km east-northeast of the early successional community (35.246803°, −120.690513°; 100 m elevation) and is situated within an open grassland classified as the needle grass grassland alliance (CNPS 2025). The site is centered on a hilltop and includes multiple slope aspects.

2.2 | Lichen Community Sampling

We sampled the saxicolous lichen community at both sites using 20 × 20 cm sample plots stratified between north-facing and south-facing rock aspects. Plots were established using a 20 × 20 cm quadrat. Eight sample plots were taken at each site for a total of 16 samples study-wide. The undisturbed rock

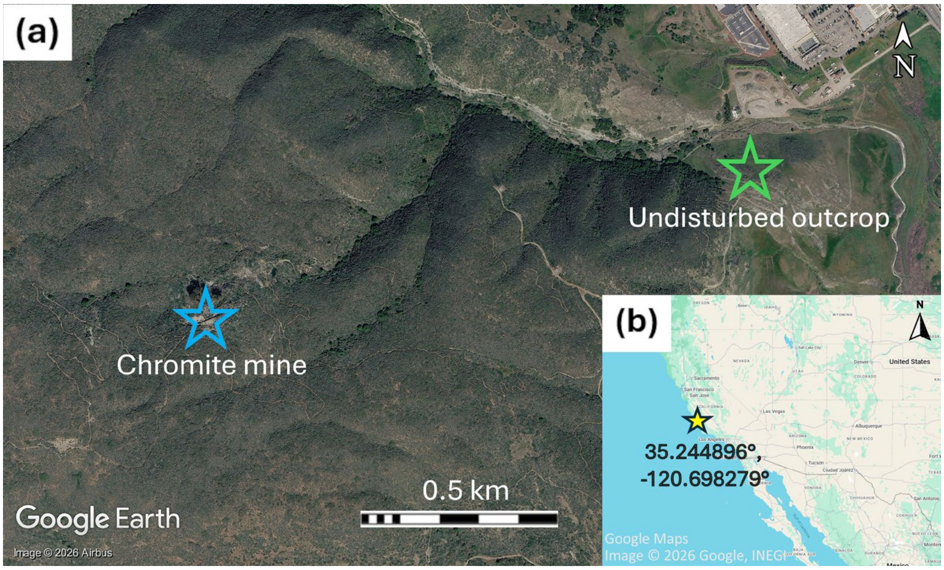

FIGURE 1 | (a) Map of the relative locations of the undisturbed ultramafic rock outcrop site (late successional community) and the disturbed chromite mine site (early successional). (b) Location of study area in North America. Imagery sources: (a) Google Earth imagery 03/2024, Airbus (b) Google Maps 2026, Google, National Institute of Statistics and Geography (INEGI).

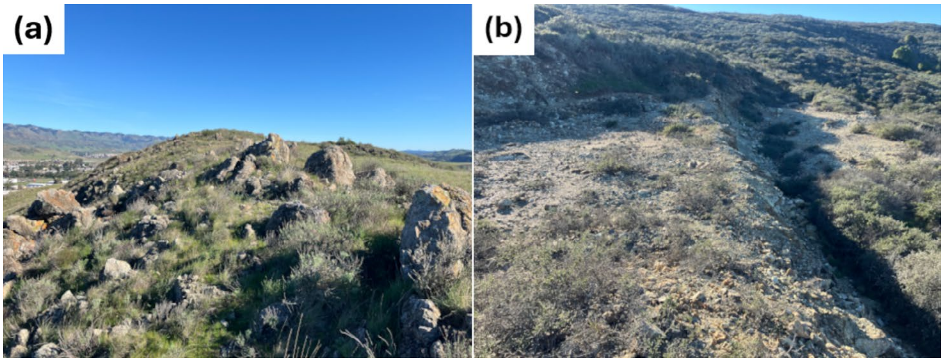

FIGURE 2 | (a) Late successional community. (b) Early successional community.

outcrop was sampled in 2021 as part of a separate study of ultramafic and sandstone cryptogam communities (Mulroy et al. 2025), and the same sampling approach was subsequently used for the earlysuccessional community in 2024. Each sample plot was taken from a different individual rock. Sample plot locations were generated by creating a set of eight random points for each site using ArcGIS software. From each point, we navigated to the nearest suitable sample plot location, alternating between north- and south-oriented rock faces. Suitable sample plot locations met the following criteria: (1) average slope between 30° and 90°; (2) aspect for north-facing sample plots 0° ± 45°, and for south-facing sample plots 180° ± 45°; (3) rock face large enough and with a sufficiently uniform slope and aspect to accommodate a 20 × 20 cm quadrat. When a large rock face offered multiple sample plot placement options, the placement was selected at random by giving a number to each potential location on the rock, and then using a random number generator to provide a number until it matched one of the numbered plot locations. The quadrat was then placed on the rock with the observer looking away from the rock to prevent bias in the placement location.

For each sample plot, we estimated percent cover of bare rock, lichens, bryophytes, and vascular plants. A list of taxa occurring within the sample plot 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). Lichen voucher specimens were collected for each field-identified taxon from each site. Voucher specimens were identified in the laboratory using standard lichen microscopy and chemical spot test techniques and regional lichen keys (Nash et al. 2002, 2004, 2007). Lichen nomenclature follows North American Lichen Checklist (Esslinger 2021). We also assessed four microhabitat variables for each sample plot: (1) fine-scale microtopography ($0 =$ smooth, $2 =$ some cracks and ledges $\gtrsim 1$ mm, $4 =$ many cracks and ledges $\gtrsim 1$ mm); (2) broad-scale microtopography ($0 =$ flat, $2 =$ moderate undulation, $4 =$ high undulation); (3) overhangs (present or absent, defined as any rock surface $> 90°$ slope and > 1 cm^2 surface area); and (4) distance from ground ($1 \leq 0.3$ m, $2 = 0.3$–0.9 m, $3 \geq 0.9$ m). For spore measurements, we used spore length as a proxy for spore size, and used the spore size data provided in species descriptions in Nash et al. (2002, 2004, 2007). Only taxa that reproduce primarily sexually and that were positively identified to the species level were included in spore size analyses.

2.3 | Statistical Analysis

Community analyses were conducted in R (R Core Team 2021), using the package vegan (Oksanen 2025) and using a proportional dissimilarity matrix for multivariate procedures. To visualize community variation between the two sites, we performed nonmetric 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. The final stress of the NMDS solution was 0.103 and was repeated 17 times; 183 runs using randomized data yielded higher values. To test for differences in species composition between sites, we used permutational multivariate analysis of variance (PERMANOVA) using adonis2 with the default options. We tested for group differences in species richness, lichen cover, and spore size, using Wilcoxon tests via the wilcox_test function of the coin package (Hothorn et al. 2006). To examine the relationship between sample plot distance from the ground and other variables, we used Kruskal–Wallis tests via the kruskal.test function (R Core Team 2021). For all tests, statistical significance was assessed at $\alpha \leq 0.05$.

3 | Results

3.1 | Lichen Community Composition

Across both study sites, 28 lichen taxa were observed: 15 in the early successional community and 20 in the late successional community (Table 1). Eight lichen species were found only at the early successional community, and 13 were unique to the late successional community. Seven lichen species were found at both sites. With the exceptions of the foliose *Peltula bolanderi* (Tuck.) Wetmore, *P. euploca* (Ach.) Poelt ex Ozenda and Clauzade, *Physcia tribacia* (Ach.) Nyl., and *Xanthoparmelia plittii* (Gyelnik) Hale, all lichens were crustose (including squamulose, endolithic, and microfruticose growth forms). These same four foliose lichens were also the only taxa recorded that reproduce primarily asexually. *Xanthoparmelia plittii* produces asexual propagules with a defined cortex called isidia, whereas the other three produce small, grain-like, ecorticate asexual propagules called soredia. The difference in average spore lengths for the primarily sexually reproducing lichen species found at the early successional (11

TABLE 1 | Number of sample plot occurrences at early successional and late successional communities for each lichen taxon recorded.

Species	Early successional	Late successional
Acarospora americana H. Magn.	2	—
Aspicilia sp.	1	1
Athallia cf. *holocarpa*	4	—
Bibbya ruginosa (Tuck.) Kistenich et al.	—	3
Buellia cf. *sequax*	2	—
Buellia dispersa (A. Massal.) A. Massal.	—	1
Buellia halonia (Ach.) Tuck.	—	1
Candelariella vitellina (Hoffm.) Müll. Arg.	3	4
Dimelaena radiata (Tuck.) Müll. Arg.	3	7
Diplotomma alboatrum (Hoffm.) Flotow	1	—
Lecidea sp.	2	—
Lecidella asema (Nyl.) Knoph and Hertel	2	5
Lichinella stipatula Nyl.	1	4
Miriquidica scotopholis (Tuck.) B.D. Ryan and Timdal	—	2
Monerolechia badia (Fr.) Kalb	—	2
Monerolechia californica (H. Magn.) Elix	—	2
Peltula bolanderi (Tuck.) Wetmore	—	1
Peltula euploca (Ach.) Poelt ex Ozenda and Clauzade	—	4
Physcia tribacia (Ach.) Nyl.	—	2
Placopyrenium stanfordii (Herre) K. Knudsen	—	2
Polycauliona bolacina (Tuck.) Arup, Frödén, and Søchting	3	7
Polycauliona ignea (Arup) Arup, Frödén, and Søchting	—	1
Polycauliona luteominia var. *bolanderi* (Tuck.) Arup, Frödén, and Søchting	8	1
Squamulea subsoluta (Nyl.) Arup, Søchting, and Frödén	—	4
Verrucaria muralis Ach.	1	—
Verrucaria sp.	3	—
Xanthocarpia crenulatella (Nyl.) Frödén, Arup, and Søchting	2	—
Xanthoparmelia plittii (Gyelnik) Hale	—	2

species; 12.54 μm) and late successional (16 species; 12.94 μm) communities was not significantly different (Wilcoxon test: $Z = 0.3961$, $p = 0.692$).

The species compositions of the early successional and late successional communities were distinct (PERMANOVA: $F = 8.47$, df = 1,14, $p < 0.001$; Figure 3). At the early successional community, the most frequently occurring lichen was *Polycauliona luteominia* var. *bolanderi* (Tuck.) Arup, Frödén, and Søchting, which occurred in all eight sample plots. The second-most frequent was *Athallia* cf. *holocarpa*, with four sample plot occurrences. All other lichen taxa at the early successional community were found in fewer than half of sample plots. At the late successional community, *Dimelaena radiata* (Tuck.) Müll. Arg. and *Polycauliona bolacina* (Tuck.) Arup, Frödén, and Søchting were most frequent, each occurring in seven sample plots. Almost all occurrences of endolithic lichens—*Athallia* cf. *holocarpa*, *Lecidea* sp., *Polycauliona luteominia* var. *bolanderi*, *Verrucaria* sp., and *Xanthocarpia crenulatella* (Nyl.) Frödén, Arup, and Søchting—were from the early successional community. All three facultative and obligate lichenicolous taxa—*Bibbya ruginosa* (Tuck.) Kistenich et al., *Monerolechia badia* (Fr.) Kalb., and *M. californica* (H. Magn.) Elix—were only found in the late successional community.

3.2 | Species Richness and Percent Cover

Mean sample plot species richness was higher in the late successional community (8.75 ± 0.98; mean ± standard error) than the early successional community (4.88 ± 1.01; Wilcoxon test: $Z = -2.44$, $p = 0.015$; Figure 4). Similarly, lichen percent cover was higher in the late successional community (73% ± 11%) than the early successional community (16% ± 5%; Wilcoxon test: $Z = -2.63$, $p = 0.009$; Figure 5). Differences in richness and cover between sites were not explained by microtopography, which did not differ significantly between sites for fine-scale (Wilcoxon test: $Z = 0.79$, $p = 0.43$) or coarse-scale ($Z = 0.28$, $p = 0.7816$) microtopography. Although sample plots at the late successional community were significantly higher from the ground surface than the early successional community on average (Kruskal–Wallis test: $\chi^2 = 4.3493$, df = 1, $p = 0.037$), we did not observe a significant effect of distance from the ground on either richness (Kruskal–Wallis test: $\chi^2 = 2.8947$, df = 2, $p = 0.235$) or lichen cover (Kruskal–Wallis test: $\chi^2 = 3.591$, df = 2, $p = 0.166$).

4 | Discussion

Our study indicates that after half a century, the early successional community is distinct from the undisturbed community

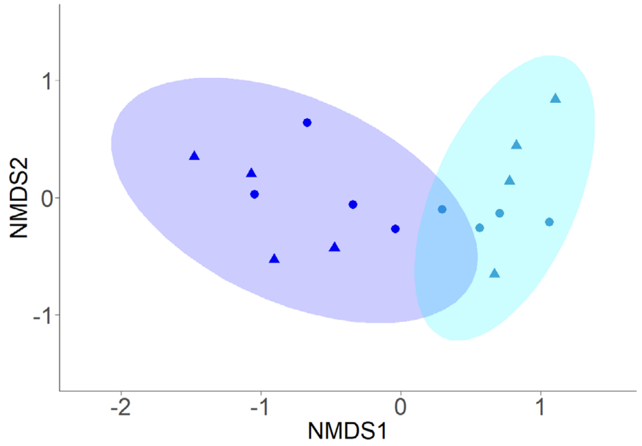

FIGURE 3 | Nonmetric multidimensional scaling (NMDS) ordination of community dataset samples ($n = 16$ sample plots). Ellipses are 95% confidence intervals of the centroids for the early successional (dark blue) and late successional (light blue) communities. Triangles represent samples taken from south-facing rock aspects, and circles are samples from north-facing aspects.

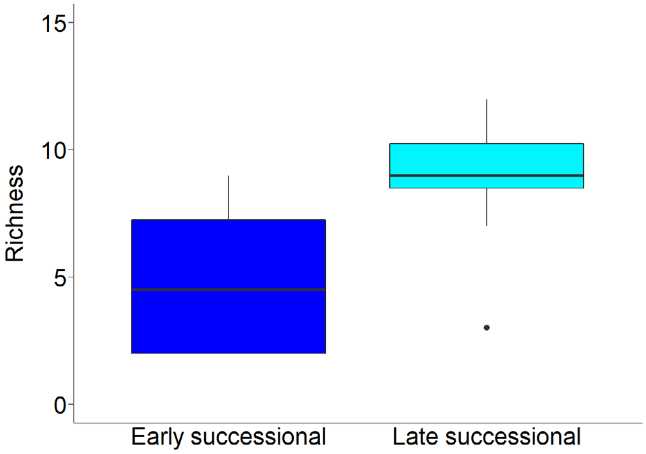

FIGURE 4 | Lichen species richness compared between early successional and late successional communities. Lichen species richness was significantly higher in the late successional community ($p = 0.015$).

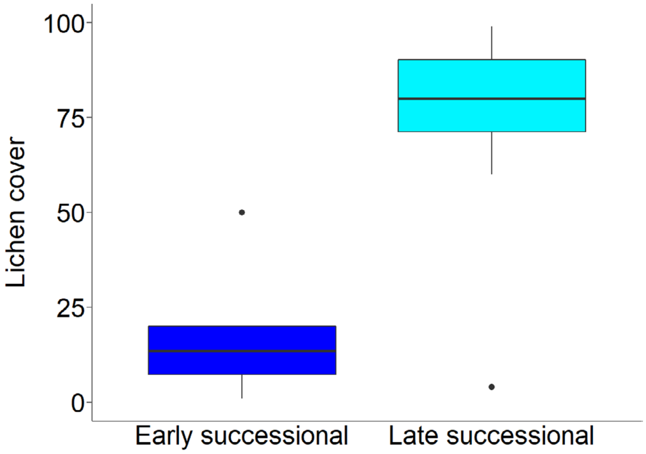

FIGURE 5 | Lichen percent cover compared between early successional and late successional communities. Lichen cover was significantly higher in the late successional community ($p = 0.009$).

in multiple ways, including community composition, percent cover of the rock surface, and species richness. This difference may be due in part to dispersal limitations within both the mycobiont and photobiont components of the lichens. The establishment of photobionts in newly formed or disturbed habitats may be a particularly important step in lichen community formation and ecological succession. Photobiont establishment might be expected to exert significant priority effects on lichen species composition; however, priority effects in lichen communities have been poorly studied. In a comparison of lichen establishment in limestone quarries over a 30-year time series, Temina (1992) found that different quarry communities displayed convergence in community composition over time, suggesting a limited role of priority effects on succession in that case. See also Root and Dodson (2016) for a discussion of priority effects in terricolous lichen communities. Some photobionts may be able to disperse and survive independently of the lichen symbiosis (Sanders 2005), while others may only be able to disperse via asexual symbiotic lichen propagules (Rikkinen et al. 2002; Peksa et al. 2022). Interestingly, all lichens observed in the early successional community lacked asexual symbiotic propagules. The four species that primarily reproduce asexually via soredia or isidia—*Peltula bolanderi, P. euploca, Physcia tribacia, and Xanthoparmelia plittii*—were found exclusively in the late successional community. These results do not support the hypothesis that asexual reproduction facilitates early successional establishment. Instead, the pattern suggests that photobionts likely colonized early successional habitats independently of mycobionts. Peksa et al. (2022) demonstrated that some photobionts are shared among terricolous, corticolous, and saxicolous lichen communities, which raises the possibility of photobiont acquisition from the chaparral corticolous or underlying terricolous communities that bound the mined area. For mycobionts, dispersal to disturbed sites may be limited by factors such as the number and size of meiospores produced (Morando et al. 2017). Our comparison of ascospore sizes between the species present at the early and late successional communities indicates that average spore sizes are approximately equivalent between the two. This suggests that spore size might not have been a limiting factor for mycobiont dispersal to the early successional community, at least within the range of spore sizes among the species observed.

Another important factor in lichen community formation and succession could be ecological interactions between species. For example, lichenicolous lichens are associated with their host lichens. For the lichenicolous species *Monerolechia californica* and *Bibbya ruginosa*, their respective host lichens—*Dimelaena radiata* and cyanolichens (i.e., lichens containing cyanobacteria as the primary photobiont)—were found at higher frequencies in the late successional community. The more generalist lichenicolous lichen *Monerolechia badia* also may have benefited from higher cover and diversity of multiple host species at the late successional community. Conversely, the presence of higher cover and species richness of lichens at the late successional community may have competitively excluded some of the eight species that were only found at the early successional community. One of the species found only at the early successional community, *Verrucaria muralis* Ach., has been described as a pioneer species (Nimis 2025), and was also reported from mined sites in Estonia and Maine (Temina 1992; Rajakaruna et al. 2011). There is also evidence that endolithic lichens, which were almost exclusively found at the chromite mine, are early successional species that become displaced by epiliths later in succession in other saxicolous habitats in temperate regions (Favero-Longo et al. 2006, 2015). For example, in a study of gneiss surfaces, Favero-Longo et al. (2015) found that endolithic lichens were prominent members of 25- and 75-year-old abandoned gneiss quarries, but were mostly absent from adjacent undisturbed gneiss outcrops with high epilithic lichen cover.

A variety of additional factors may have contributed to differences in the lichen communities of the early and late successional communities. Although we did not observe significant differences in the surface microtopography of the rocks at the two study sites, it is possible that there were unmeasured differences in rock surface characteristics that influenced the lichen community. For example, there may have been microscopic differences in rock microtopography caused by much higher weathering of rocks at the late successional community. Weathering might improve the potential for photobiont and mycobiont community acquisition by creating additional microsites for propagules to settle, and it may also create localized differences in porosity and moisture content (Moses et al. 2014) that could be beneficial to lichen symbiont establishment. Furthermore, although both sites are part of the same ultramafic bedrock area, there could be differences in rock elemental composition between the two sites, and any differences could have been further accentuated by rock weathering at the late successional community. There is a substantial body of literature focused on lichens of metal-rich substrates, including abandoned mines and ultramafic rocks, which indicates that metal-rich rocks may harbor distinctive lichen assemblages (Purvis and Halls 1996; Favero-Longo et al. 2004, 2018; Rajakaruna et al. 2011, 2012; Medeiros et al. 2014; Mulroy et al. 2022, 2025). Although the elemental composition of rock at the early successional community was not assessed, it is plausible that it differed from that of the undisturbed outcrop in elemental composition and heavy metal content (see Mulroy et al. 2025 for elemental composition of rock sample from the late successional community).

Finally, it is important to note that although there is very limited research on lichen succession in lithic habitats, there is a substantial body of research on the effects of forest management and stand age on epiphytic lichen communities. Epiphytic communities have a very slow rate of succession, with late successional communities continuing to accumulate biomass (McCune 1993) and increase in richness and diversity beyond 100 years (Moning and Müller 2009; Miller et al. 2021). Other studies demonstrate that conserved forest stands serve as important refugia for rare lichen species that are absent from managed stands (Ardelean et al. 2015; Frati and Brunialti 2023). A similar pattern may extend to late successional saxicolous and terricolous lichen communities, underscoring the need for further research on their successional dynamics.

5 | Conclusion

Our study provides further evidence that saxicolous lichen communities have a slow successional process that lasts multiple decades, and perhaps centuries, at least within the Mediterranean-like climates where the studies on saxicolous lichen succession have taken place to date. The slow rate of lichen reestablishment of cover and species richness is relevant for bioremediation and restoration of disturbed or newly created lithic habitats, which may benefit from higher lichen cover (Favero-Longo et al. 2006). The extended timeframes required for the restoration of saxicolous communities underscore the importance of conservation in protecting rare lichen assemblages, as meaningful recovery occurs only over multi-decadal periods.

Acknowledgments

The authors thank Bob Hill and the San Luis Obispo Office of Sustainability and Natural Resources for granting permission to sample lichens in Irish Hills Natural Reserve for this study. We also thank Carson Sanzone, Jack Poole, Jacob Mull, Lili Menkal, and Michael Gottlieb for their enthusiastic field support. We thank Alan Fryday and an anonymous reviewer for their insightful reviews of the manuscript. Finally, we acknowledge the Chumash and Salinan tribes, who have traditionally been stewards of the land where this study took place.

Conflicts of Interest

Nishanta Rajakaruna is an Associate Editor-in-Chief for the Special Issue on Serpentine Ecology and took no part in the peer review and decision-making processes for this paper.

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