National Park Service
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Natural Resource Stewardship and Science

Lichen Inventory and Visitor Use Study

Lava Beds National Monument

Natural Resource Report NPS/NRSS/IMD/NRR—2023/2547

ON THE COVER
A compilation of photos showing caves and lichen at Lava Beds National Monument
NPS

Lichen Inventory and Visitor Use Study

Lava Beds National Monument

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Abstract

Cave entrances in dry ecosystems provide important habitat for lichens because lichens are sensitive to environmental conditions at a fine scale and caves provide mesic, mild microclimates in otherwise harsh landscapes. The lichens associated with cave entrances at Lava Beds National Monument (LABE or the Monument) represent a unique floral component for the region and include many rare or little-known species. Despite the unique natural value of these communities, the impacts of visitor use on the lichens associated with the caves at the Monument are not fully known. The purpose of this study is to explore the effects of visitor use of caves and other ecological drivers on lichen communities at the Monument and provide managers with insight into this unique vegetation component.

Our goal was to sample lichen communities that are representative of the diversity of caves that occur at the Monument. We ultimately sampled 42 of the 80 selected caves, prioritizing sites that could be accessed relatively easily (e.g., within approximately two miles from roads) to ensure a large sample size. A total of 211 lichen taxa were observed in this study, 27 of which were new records for Lava Beds National Monument. Our observations, in combination with a recent checklist of lichen species from the Monument, bring the total number of lichen taxa known from the Monument to 288. The richness of lichen species in the 42 one-acre plots we sampled surrounding cave entrances ranged from 15 to 97 (mean 59 species).

Our study highlights that caves provide important habitat for lichens amid the semi-arid landscape of Lava Beds National Monument. Caves with deeper entrances and larger sink areas provide stronger microclimates, which in turn support more diverse lichen communities. Ice caves represent specialized habitats that host many rare or disjunct lichens. Larger and deeper caves may also provide better refugia from wildfire; almost all our study sites burned in the two years prior to sampling, but caves with deeper entrances and larger sink areas experienced a smaller amount of burned area in the immediate surroundings.

Although visitor use has the potential to disturb lichens and cause localized species extirpations, we found no differences in lichen richness at the plot scale among caves that experience high and low visitor use. These findings suggest that existing visitor infrastructure, such as railings and stairways, may be effectively mitigating visitor impacts, at least at the landscape scale.

Introduction

Cave entrances in dry ecosystems provide important habitat for lichens because lichens are sensitive to environmental conditions at a fine scale and caves provide mesic, mild microclimates in otherwise harsh landscapes. The lichens associated with cave entrances at Lava Beds National Monument (LABE or the Monument) represent a unique floral component for the region and include many rare or little-known species. Recent work within the Monument has resulted in the discovery of one macrolichen) and at least one microlichen that are new to science, highlighting the importance of the unique biodiversity of the area (McCune et al. 2014). Lichen species diversity in the Monument (Sheehy, 2017) is roughly equivalent to vascular plant species diversity (Smith, 2008) yet there is more to learn about the ecology of this important component of the Monument's vegetation.

Lichen communities associated with cave entrances in the Monument include disjunct species that are associated with the moderated microclimate provided by caves; many of these species do not occur in the surrounding landscape. Despite the unique natural value of these communities, the impacts of visitor use on the lichens associated with the caves at the Monument are not fully known. The purpose of this study is to explore the effects of visitor use of caves and other ecological drivers on lichen communities at the Monument and provide managers with insight into this unique vegetation component. The research was conducted under permit # Lava Beds National Monument - 2021 - SCI - 004.

Geologic history structures the rock substrates that provide much of the lichen habitat at the Monument. The Monument lies at 1,200–1,700 meters elevation at the juncture of the Great Basin section of the Basin and Range physiographic province to the east and the Cascade Mountains to the west. As such, it has been geologically influenced by both the Cascadia subduction zone and basin and range rifting, resulting in recent volcanic activity (KellerLynn, 2014).

The Monument is located on the north flank of the largest volcano by volume in the Cascade Range (600 km^3), the Medicine Lake shield volcano, which erupted most recently from several vents around 1,060 CE (KellerLynn, 2014). Most of the lava flows and lava tube caves in the Monument are basalt resulting from the eruption of Mammoth Crater and nearby vents that formed about 35,000 years ago. Lava tubes were formed as the free-flowing lava cooled on the outside and solidified into rock, allowing the hot lava inside the tubes to continue flowing northward until the Mammoth Crater eruption ceased (KellerLynn, 2014). Four other prominent lava flows spread projectile blobs of lava, uneven surface basaltic blocks, basaltic andesite, andesite, and pumice from 30,000 years ago to 1,100 years ago. These are represented in the Monument as the Schonchin flow from Schonchin Butte and Devils Homestead, the Ross flows from Fleener Chimneys and Black Crater, and the Callahan flow from Cinder Butte (Muffler et al., 2017).

Lava Beds National Monument supports important biodiversity of numerous taxonomic groups. It is home to a variety of wildlife including birds, coyotes, deer, elk, pronghorn antelope, porcupines, pika, woodrats, bats, as well as many invertebrate species. A 2005 biological assessment found substantial cavernicolous invertebrate diversity within the caves including flies, springtails, spiders, millipedes, mites, and diplurans. Additionally, many non-vascular plants not commonly observed in the area, such as mosses and ferns, occur in the Monument. The ability of such sensitive species to survive in the Monument is due to the climate-moderating effect of caves against harsh and arid outside conditions in the surrounding landscape (Taylor and Krejca, 2006).

Lichens are symbiotic associations of fungi, algae and bacteria that form stable thalli. Occurring in a wide variety of colors and on the physical scale of mosses and liverworts, lichens form a conspicuous component of the terrestrial vegetation in many environments, often completely covering their substrates, which typically include rocks and trees.

Humans have long been part of the ecological community in and around what is now the Monument. Although in recent times they are primarily Monument visitors, it is believed that humans have lived in the area for at least 11,000 years. Modoc people inhabited over 20 semi-permanent villages along the lakes and rivers in the vicinity of the monument prior to Euro-American colonization. Modoc people hunted deer, elk, waterfowl, and fish; gathered edible and medicinal plants; used tule reeds to make baskets, sleeping mats, and shoes; and carved and painted petroglyphs and pictographs on cave walls. As settlers invaded Modoc territory, tensions rose, eventually leading to the Modoc War of 1872–73, in which a small group of Modoc warriors held off hundreds of US Army soldiers using their intricate knowledge of the caves. The Modoc people were eventually overpowered, leading to their forced relocation to Oklahoma or to the Klamath Reservation where their descendants live to this day (Juillerat, 2015).

Though there is a long history of human use of caves in the Monument, little is known about the impacts today's visitors have on the caves and the organisms that inhabit them. Settlers used ice caves as a source of water for whiskey stills during prohibition. They ice skated on the frozen floors of ice caves, built a resort near Bearpaw Cave, and grazed sheep and cattle. The Forest Service initiated more intensive management in the 1920s, building roads, placing signs, and regulating grazing; the National Park Service assumed management when Lava Beds National Monument was established in 1925 (Brown, 2011). Among other projects, Civilian Conservation Corps crews built fences to preserve petroglyphs (Juillerat, 2015). Today, about 80,000 visitors enter the 22 developed caves annually (KellerLynn, 2014). Sensitive cave resources are protected in part by their remoteness and also by the Federal Cave Resources Protection Act of 1988 and associated regulations.

Methods

Cave Selection

Our goal was to sample lichen communities that are representative of the diversity of caves that occur at the Monument. We used a stratified random approach to select 80 caves across the full gradient of visitor use. We then modified the list by hand after field scouting to try to ensure an even range of cave sizes, since quantitative data on cave size was not available. Our goal was to sample the full spectrum of cave sizes in each visitor use class to the extent possible, so that cave size and visitor use would not be confounded. Some of these caves were later eliminated because of closure orders, accessibility issues, and time constraints. We ultimately sampled 42 of the 80 selected caves, prioritizing sites that could be accessed relatively easily (e.g., within approximately two miles from roads) so as to ensure a large sample size.

Sampling Approach

To capture the full diversity of lichens that is associated with each cave, we established a one-acre circular plot (31.8 m radius) centered at the entrance of each cave we studied. The plot consisted of all areas from the surrounding outer landscape surface through the sink and sheltered areas, into the twilight zone to the darkest area at the limit of the occurrence of photosynthetic organisms deep inside the cave.

Zones within each study plot were delineated as a way to represent the potential ecological niches occupied by the diversity of lichen species. Plots were divided into four ecological sampling zones: Rim, ink, sheltered and twilight. The zones are defined as follows:

- **Rim**: the at-grade area from the outer edge of the plot up to the rim of the sink.
- **Sink:** the area within the below-grade sink (including the underside of the overburden) but outside the aperture of the cave.
- **Sheltered:** from the edge of the aperture at drip line to four meters inside the cave.
- **Twilight:** from the inner edge of the sheltered zone to the deepest occurrence of a photosynthetic organism (lichen, moss or algae).

See Figures 1 and 2 for schematics of cave zones. These zones are inherently variable in size and some zones were absent at some caves (for example, the sink zone was sometimes absent at smaller caves).

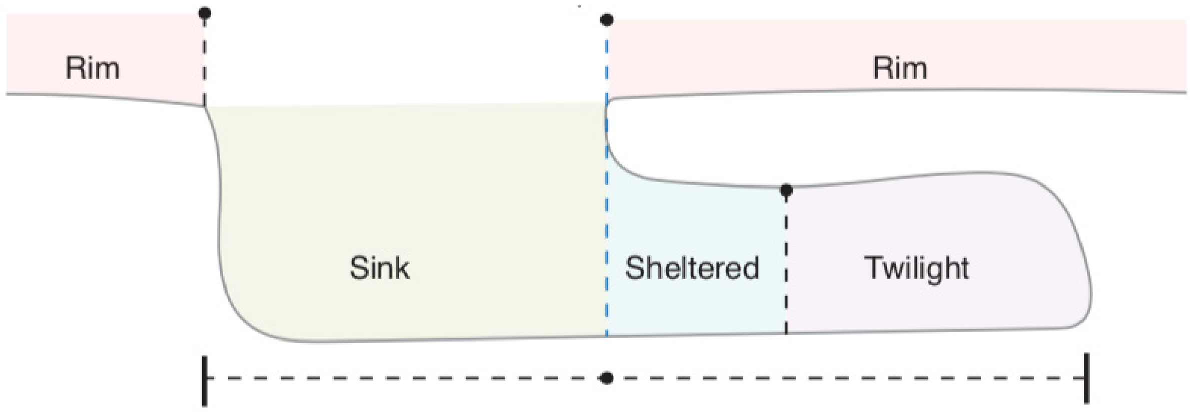

Figure 1. Schematic diagram of cave zones (original artwork by Callie Chappell).

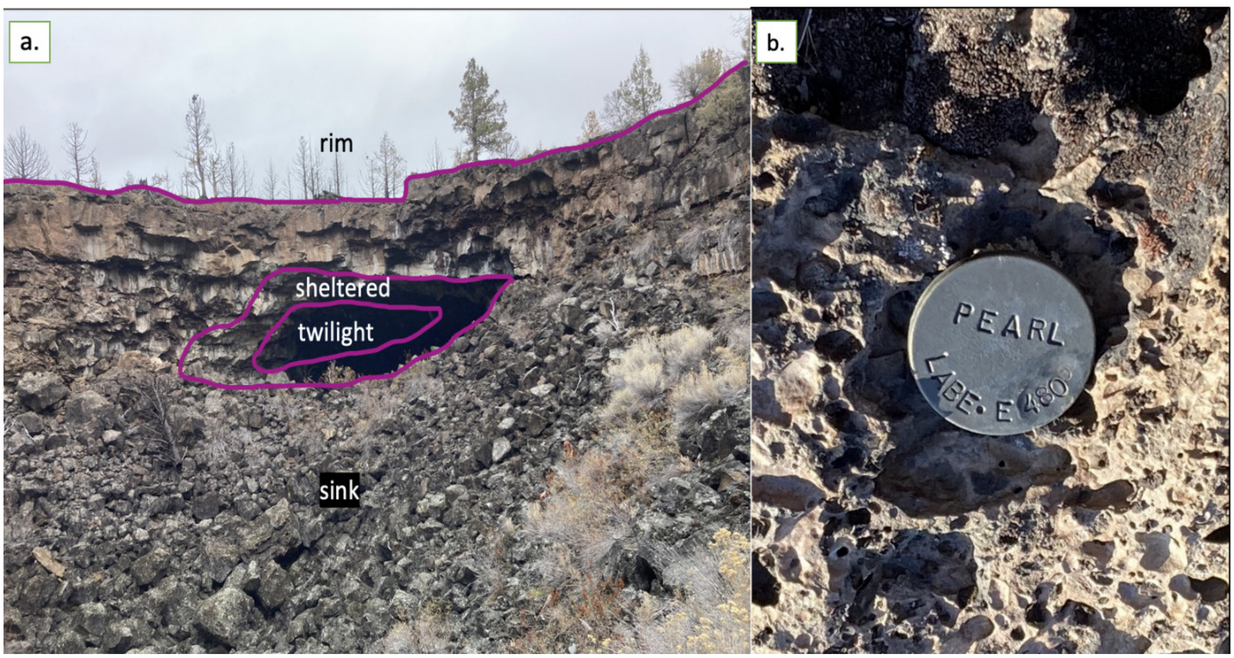

Figure 2. Photographic schematic of how the zones were divided for a typical cave (a). Permanent cave markers were used as plot centers of the circular 1-acre plots when available (b).

We searched each selected cave entrance and its surroundings for lichens, and we attempted to survey all aspects and microclimates in each plot to maximize lichen detection. For each of the four zones (Rim, Sink, Sheltered, Twilight) presence/absence data was collected for every lichen species encountered. Following a modified version of the Forest Inventory and Analysis program's lichen plot protocol (USDA Forest Service 2021), we searched each zone until no new lichen species were detected for ten minutes, and then moved on to the next zone.

All lichens that could not be positively identified to species in the field were identified to morphological group and photographed. We did not collect lichens. Species determinations from field observations and photographs were based on recent specimens collected by Steve Sheehy that are housed at the Monument (Sheehy, 2017) and collections made by Tonya M. Vanover that we received on loan from Eastern Washington University (Vanover, 2009).

Environmental data collected for each cave included the aspect of the cave entrance, the height of the upper edge of the cave entrance (meters above grade), the height of the lower edge of the cave entrance (meters above grade), the height of the center of the cave opening at the dripline, the width of the cave opening at the dripline, the thickness of the overburden, and the entrance type (vertical, horizontal, intermediate).

We measured four presence / absence visitor use variables (presence/absence of stairs or a ladder, a dirt trail, a paved trail, and trash / litter), which we then combined to form a visitor use impact index ranging from 0–4. We also assessed the degree of impact following the Lava Beds Cave Inventory Handbook (Sowers, 1992); since it appeared to be redundant with the visitor use impact index, we did not analyze it further.

For each zone, percent cover was visually estimated for each of the following botanical variables: native forbs, exotic forbs, native grass, exotic grass, moss, woody shrubs, and trees. Cover of each woody plant species was also recorded. We also recorded cover for several environmental variables: total burned area of each plot, bare soil, pumice/gravel, loose rock, and stable rock. The area of each zone was recorded as a percentage of the overall plot, which we then converted to square meters.

All lichen species or morphospecies (e.g., taxa that could only be identified to genus-level) were assigned a disturbance sensitivity rating based on gross morphology (e.g., functional groups). Species with the least potential for damage due to trampling were assigned low values (1) and species with the most potential for damage were assigned higher values (5–7).

The functional group disturbance sensitivity gradient was established as follows:

1. Species with little potential impact from trampling including low-profile crustose species and epiphytic species.
2. Species with moderately low potential for trampling impacts including squamulose and higher profile crustose species.
3. Species with a moderate potential for trampling impacts including foliose rock dwelling species.
4. Species with a moderately high potential for trampling impacts including umbilicate and fruticose rock dwelling species.
5. Species with a high potential for trampling impacts including species that inhabit soil (as opposed to rock).
6. Species with a very high potential for trampling impacts including vagrant lichens (coded as 7 in data analysis to weight the sensitivity of vagrant lichens higher).

Figure 3 shows examples of lichen species representative of the functional group disturbance sensitivity gradient.

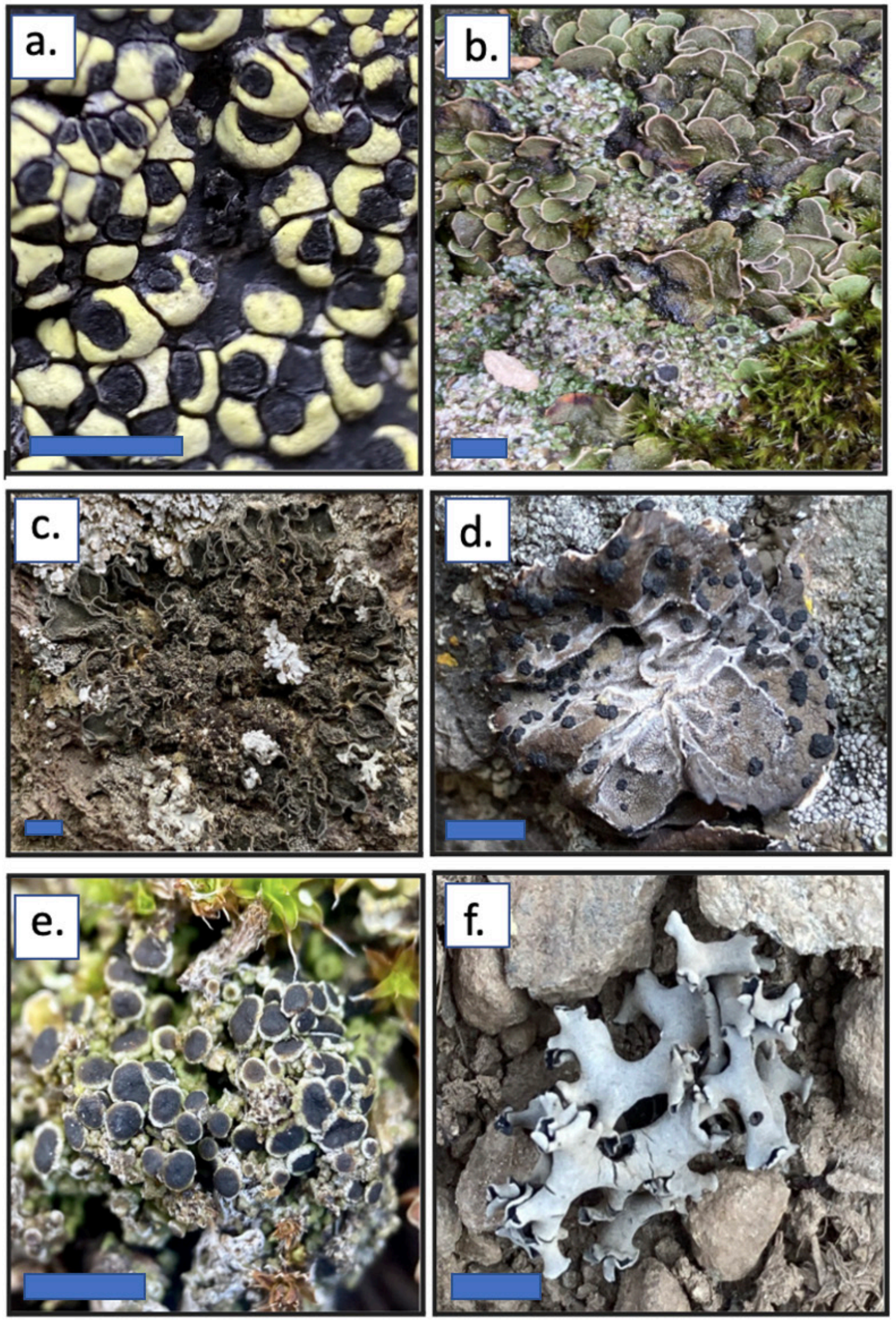

Figure 3. Examples of species representative of the functional group disturbance sensitivity gradient including: a. low profile crustose (*Rhizocarpon lecanorinum*), b. squamulose (*Psora nipponica*), c. foliose rock species (*Leptochidium albociliatum*), d. umbilicate (*Umbilicaria polaris*), e. soil dwelling crustose (*Rinodina olivaceobrunnea*) and f. vagrant species (*Dermatocarpon bachmannii*). Scale bars are 1 centimeter.

Data Analysis

Multiple regression was used to analyze how visitor impact, cave structure, and fire history influence total lichen richness and the and site-level mean trampling index (which was calculated based on the expected sensitivity of different lichen functional groups to trampling). For total lichen richness, we explored several candidate variables and selected variables with the strongest explanatory power to retain in the final model. We also kept the visitor use index in the final model since it was an original focus of this study. To better facilitate a comparison of our findings with previous research in the Monument, we ran another version of the lichen richness model with lichens occurring inside the cave only as the response variable.

An indicator species analysis was performed to determine whether individual species have affinities for specific zones (rim, sink, sheltered and twilight).

We used nonmetric multidimensional scaling ordinations with the Bray-Curtis dissimilarity metric to visualize lichen species composition across zones and across sites. To analyze and visualize “joint plots” as recommended by McCune and Grace (2002), we used the “envfit” function in the vegan package to identify environmental variables (including the visitor use impact index) and lichen functional groups that were significantly associated with lichen community composition. We determined that two-dimensional solutions were adequate if the stress was under 0.2.

We used exploratory data visualization to assess the abundance of different lichen functional groups across zones.

All analyses and data visualizations were performed in the R statistical programming language (R Core Team. 2019). We square-root-transformed sink area prior to analyses to improve its distributional properties and better meet model assumptions.

Results

A total of 211 lichen taxa were observed in this study (including taxa at the generic or family level that could not be identified to species, all referred to hereafter as “species” in some instances for simplicity). 27 of these species were new records for Lava Beds National Monument. See Appendix A for selected environmental variables from the caves we visited and Appendix B for lichen species we encountered. Our observations, in combination with a recent checklist of lichen species from the Monument (Sheehy, 2017), bring the total number of lichen taxa known from the Monument to 288 (Appendix C). The richness of lichen species in the 42 one-acre plots we sampled surrounding cave entrances ranged from 15 to 97 (mean 59 species).

Lichen species richness in the vicinity of caves was shaped by cave structure and fire history but was not measurably affected by visitor use (Figure 4, Appendix D). Plot-level lichen richness was negatively correlated with area burned ($P=0.052$). Lichen richness increased as the depth of cave entrances below the surrounding landscape increased ($P=0.015$), and in plots with larger sink areas ($P < 0.001$), presumably because deeper and larger caves and sinks produce more stable microclimates with cooler, more mesic conditions. The presence of permanent ice within caves was also associated with greater species richness (Figure 5). The richness of lichens inside the caves only also did not have a significant relationship with visitor use ($P=0.604$).

Lichen community composition and richness varied strongly among the four zones we examined at each study site (Figures 5 & 6). Each zone contained distinctive species that typically occurred in the same zone at many caves (although the twilight zone shared both of its indicator species with the sheltered zone; Table 1). The sink zone contained particularly high lichen diversity. Although the sink zone made up only 23% of the average plot’s area, a mean of 69% of all lichen species in each plot occurred in the sink zone. Plot-level lichen richness increased with increasing sink area when the sink made up less than ~30% of the plot (Figure 4).

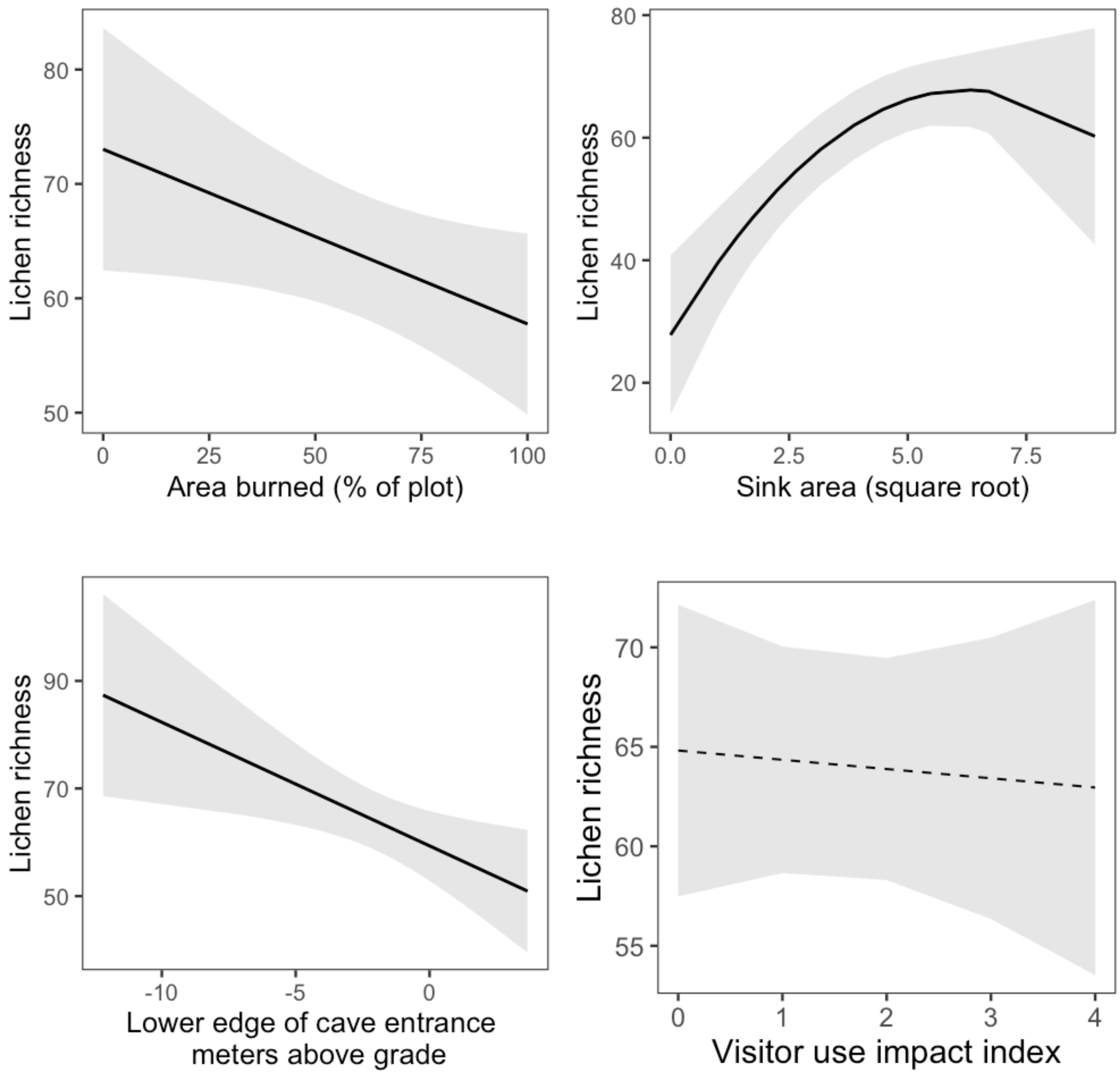

Figure 4. Drivers of site-level species richness across the 42 caves we sampled.

Table 1. Indicator species for specific cave zones. All species that are significant or marginally significant indicators (i.e., P-values < 0.1) are included. Species are ordered by overall indicator value for each zone.

Cave Zone	**Species**	**P-value**
Sink zone indicators	*Umbilicaria polyphylla*	0.01
	Xanthoparmelia coloradoensis	0.01
	Psora nipponica	0.01
	Parmelia saxatilis	0.01
	Cladonia fimbriata	0.01
	Phaeophyscia decolor	0.01

Table 1 (continued). Indicator species for specific cave zones. All species that are significant or marginally significant indicators (i.e., P-values < 0.1) are included. Species are ordered by overall indicator value for each zone.

Cave Zone	Species	P-value
Sink zone indicators (continued)	*Dimelaena thysanota*	0.01
	Xanthoparmelia plittii	0.01
	Peltigera rufescens	0.01
	Protoparmelia badia	0.01
	Rhizocarpon macrosporum	0.01
	Toninia ruginosa	0.01
	Physconia perisidiosa	0.01
	Leptochidium albociliatum	0.01
	Peltigera canina	0.01
	Bryoria fremontii	0.01
	Lepraria jackii	0.01
	Umbilicaria americana	0.01
	Cetraria chlorophylla	0.02
	Physcia tenella	0.02
	Acarospora socialis	0.01
	Psora himalayana	0.05
	Cladonia coniocraea	0.03
	Cladonia squamosa	0.03
	Cladonia pyxidata	0.04
	Parmelia sulcate	0.01
	Platismatia glauca	0.03
	Peltigera ponojensis	0.03
	Dermatocarpon miniatum	0.07
	Umbilicaria virginis	0.06
Sheltered and twilight zone indicators	*Flavoplaca citrina*	0.01
	Diplotomma alboatrum	0.01
Rim zone indicators	*Melanohalea multispora*	0.01
	Arthonia glebosa	0.01
	Lecanora albellula	0.01

Table 1 (continued). Indicator species for specific cave zones. All species that are significant or marginally significant indicators (i.e., P-values < 0.1) are included. Species are ordered by overall indicator value for each zone.

Cave Zone	Species	P-value
Rim zone indicators (continued)	*Letharia columbiana*	0.01
	Placynthiella oligotropha	0.01
	Acarospora schleicheri	0.09
	Hypogymnia imshaugii	0.05

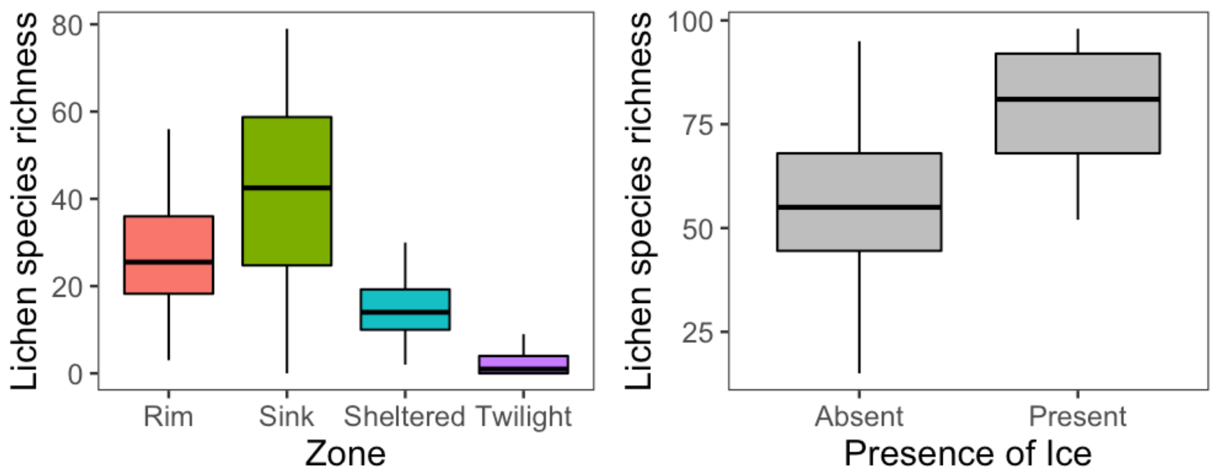

Figure 5. Lichen species richness. a. by zone, ranging from the landscape surrounding the cave topography (rim zone) to the deep interior of the caves (twilight zone). b. Comparison of total lichen species richness across all zones in ice caves (present) and caves without ice (absent).

Figure 6 shows that each of the four zones (rim, sink, sheltered, and twilight) tend to contain compositionally similar lichen communities across the caves we studied, and that there is some compositional overlap between adjacent zones. Each point represents one zone at one study site, and points that are closer together represent communities that contain similar species.

The site-level ordination suggested that lichen species composition at the landscape scale corresponds to a major gradient in correlated environmental variables, but not to visitor use. Caves with deeper entrances, larger sink areas, and more stable rock were more likely to contain ice; these caves were also less affected by fire (Figure 7). Few of the vegetation-related variables we measured had significant relationships with lichen communities, though mountain big sagebrush (*Artemisia tridentada* var. *vaseyana*) abundance had a significant relationship with lichen composition, and there was a trend towards more gelatinous cyanolichens in sites with more junipers (*Juniperus occidentalis*) cover and more moss cover.

Each point in Figure 7 represents one study site, and points that are closer together represent communities that contain similar species. Blue points represent ice caves, while black points represent caves without ice. The upper figure shows the ordination with vectors representing environmental variables, while the lower figure shows the ordination with the vectors representing functional groups (see pages 15–16 for functional group definitions).

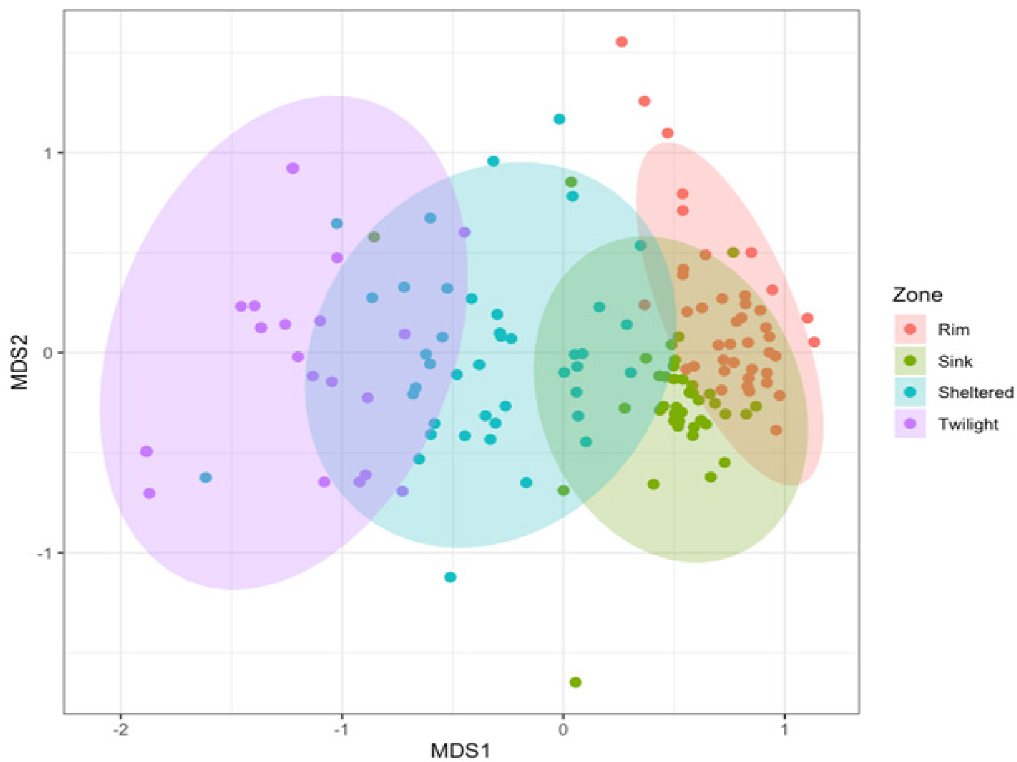

Figure 6. A nonmetric multidimensional scaling (NMDS) ordination of lichen community composition by zone.

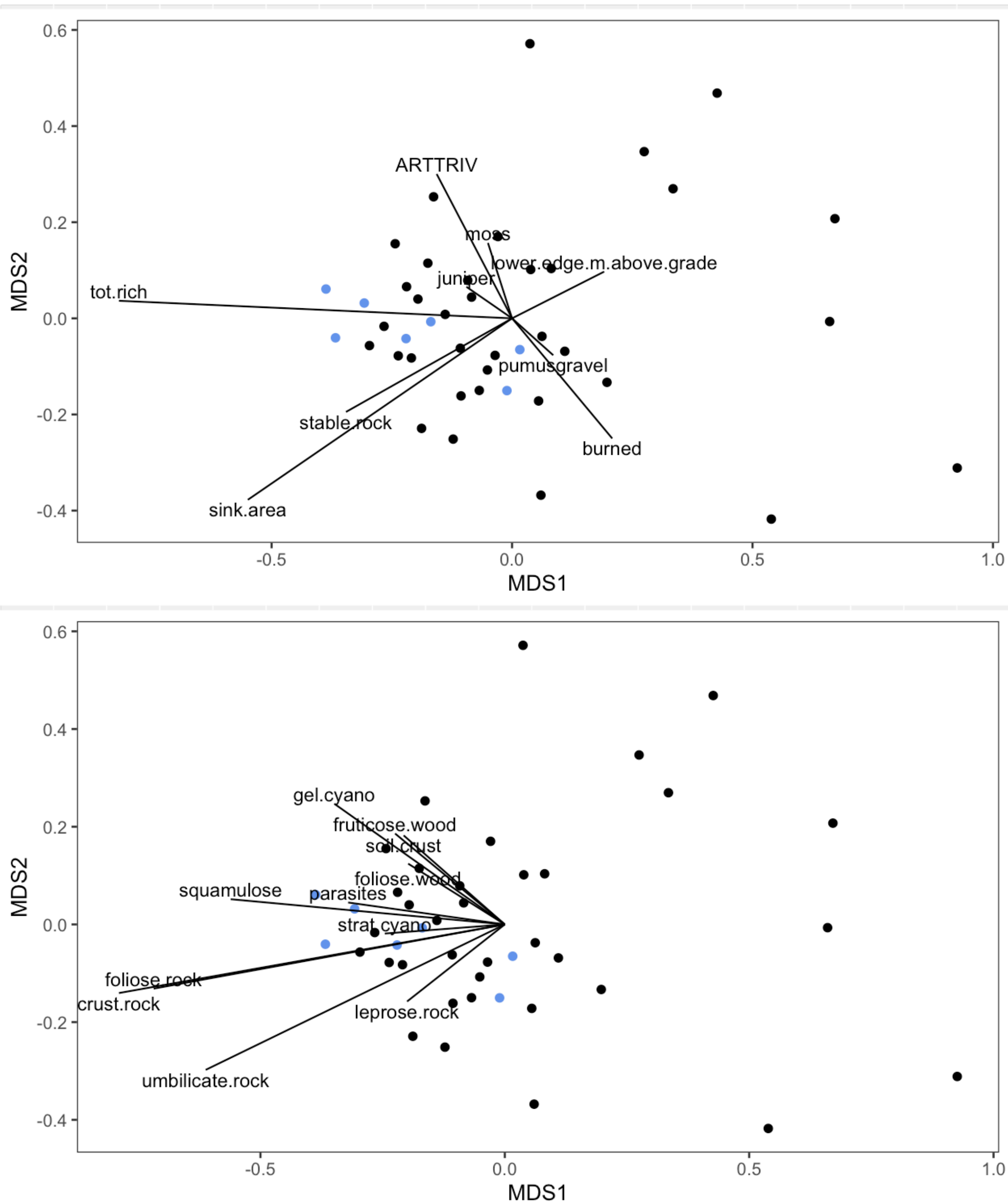

Figure 7. A Nonmetric multidimensional scaling ordination of lichen community composition by site showing a. environmental variables as vectors and b. functional groups as vectors.

Visitor use was not significantly related to the mean site trampling index (Figure 8), which represents the expected sensitivity of lichens to visitor use. This suggests that existing visitor use impact mitigation measures, such as paved trails, railings, and stairways, may be successfully preventing visitors from damaging the lichen flora, at least at a landscape scale. However, because we sampled lichen species at a relatively broad scale, our approach may not have detected fine-scale visitor impacts such as trampling in areas that are used as paths, since such effects are typically localized.

Overall, rock crusts were the most abundant lichen functional group, followed by rock-dwelling foliose lichens (Figure 9). Wood-dwelling lichens were somewhat less common, probably because rock was a more abundant substrate than wood at all caves. Cyanolichens were relatively rare and occurred most frequently in sink zones. Lichenicolous fungi (parasitic species), pin lichens and vagrant lichens were the rarest functional groups and occurred at few study sites.

Figure 9 shows how many species in each functional group occur in each zone associated with cave entrances on average. Summed average richness for all zones may be greater than total species richness for a study plot since the same species may occur in multiple zones. Full names for the functional groups are (from left to right): Crustose rock lichens (crust.rock), foliose rock lichens (foliose.rock), umbilicate rock chlorolichens (umbilicate.rock), squamulose chlorolichens (squamulose), leprose rock chlorolichens (leprose.rock), foliose wood chlorolichens (foliose.wood), crustose wood chlorolichens (curst.wood), soil crusts (green algal; soil.crust), fruticose wood chlorolichens (fruticose.wood), gelatinous cyanolichens (gel.cyano), stratified cyanolichens (strat.cyano), lichenicolous fungi (parasites), rock-dwelling pin lichens (rock.pins), and vagrant lichens (vagrant).

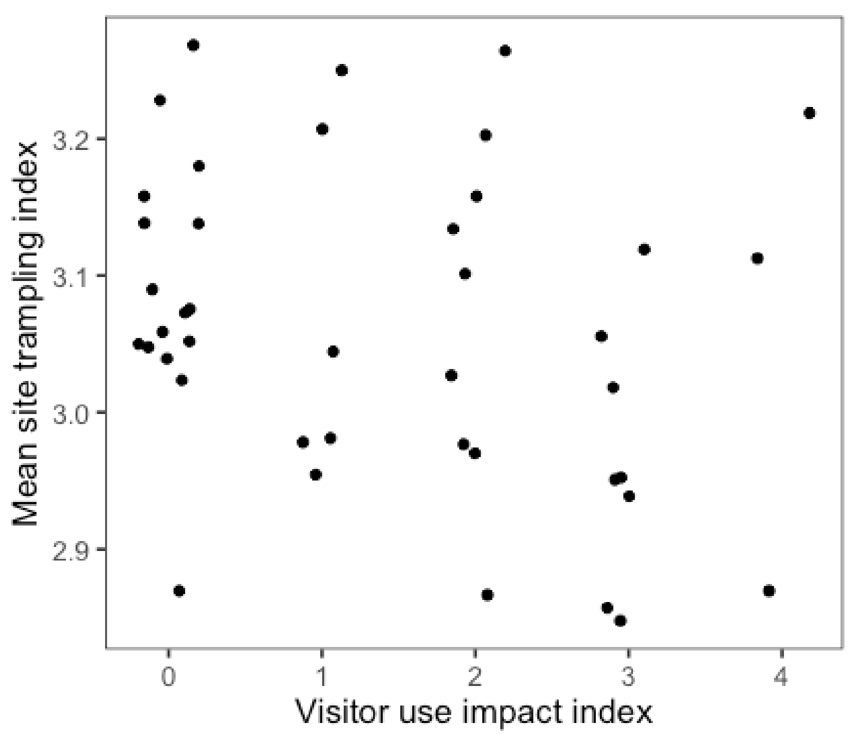

Figure 8. Relationship between the visitor use impact and the trampling index.

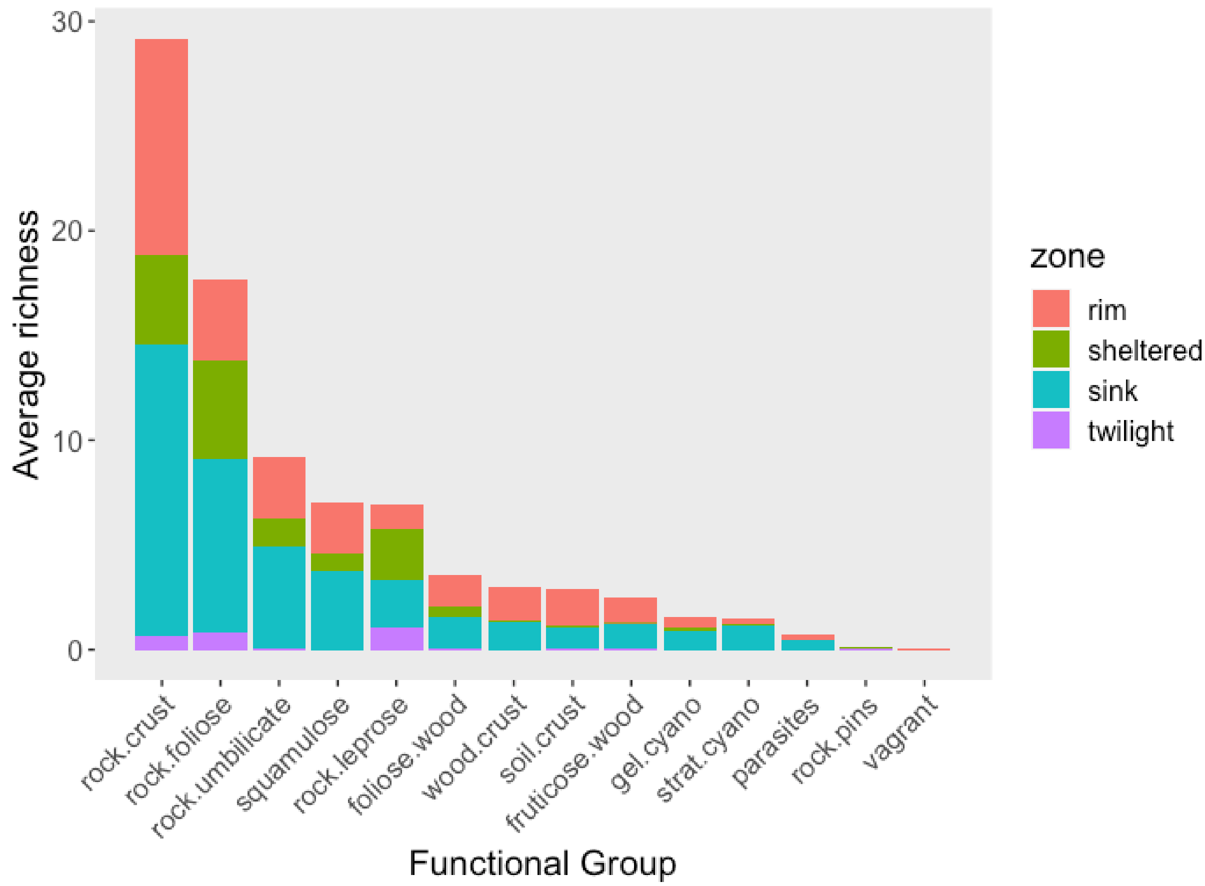

Figure 9. Lichen functional group richness by zone.

Indicator species

Indicator species analysis identified a number of species that are indicators of the different cave zones we sampled. Species can be indicators for either a single zone or multiple zones in combination. There were only two species that were indicators for the twilight and sheltered zones, and these two species were indicators for both zones in combination (Table 1; Figure 10). There were numerous indicator species for both the rim and sink zones (Figures 11 and 12). In addition to the results of our multivariate indicator species analysis based on zone, lichenicolous fungi appeared to be indicators of caves with deeper entrances and larger sink zones (Figure 13).

Flavoplaca citrina and *Diplotomma alboatrum* are the only two species that are indicator species for the sheltered and twilight zones (Figure 10). *D. alboatrum* is a parasite on *Flavoplaca* species, possibly helping it to occupy low light environments.

Figure 10. *Flavoplaca citrina* and *Diplotomma alboatrum* growing side by side in the twilight zone.

Many of the sink zone indicator species are strict rock dwellers (Figure 11).

Rim zone indicators include species that are obligate soil dwellers and epiphytic species (Figure 12). Soil and trees tended to occur in greater abundance on the rim as opposed to the sink, where stable rock made up the most abundant substrate.

Our results show that parasitic lichens typically occurred in caves with larger sinks and deeper entrances relative to the surrounding landscape (Figure 13).

Figure 11. *Dimelaena thysanota* and *Parmelia saxitilis* are two examples of sink zone indicator species.

Figure 12. *Acarospora schleicheri* and *Hypogymnia imshaugii* are two examples of rim zone indicator species.

Figure 13. Parasitic lichens (also known as lichenicolous lichens) are considered representatives of well-developed lichen communities.

Noteworthy Species

We found several notable species that represent disjunct populations, range extensions, or other unusual occurrences, including a number of species that typically inhabit wetter ecosystems west of the Cascades and Sierra Nevada. The occurrence of disjunct populations demonstrates the value of Lava Beds National Monument as a lichen refugium within the Modoc Plateau and the Pacific Slope more broadly. The occurrence records that are mapped below for each of these species are based on occurrence records in the Consortium of North American Lichen Herbaria (CNALH, 2022), an online database that aggregates herbarium specimen records from all major lichen herbaria in North America, South America, Europe and Asia that house significant collections of North American material. Brief descriptions of the identifying features and known range details for each species are presented below.

Agonimia tristicula (Figure 14a) is a rare peritheciate soil dwelling species, with uniquely shaped large spores. There is only one previously recorded collection from California and it is not recorded from Oregon. This species has been more commonly collected in British Columbia. This is a new record for Lava Beds National Monument (Figure 14b).

Anaptychia elbursiana (Figure 15a) is a calciphile found more commonly in the Great Basin and other arid areas to the east. Material from Lava Beds National Monument is not well developed but conforms morphologically to the species. This is an example in the data set of a species on the western fringe of its range in the Lava Beds National Monument. There are only a few collections from Southern California while most are from Nevada (Figure 15b).

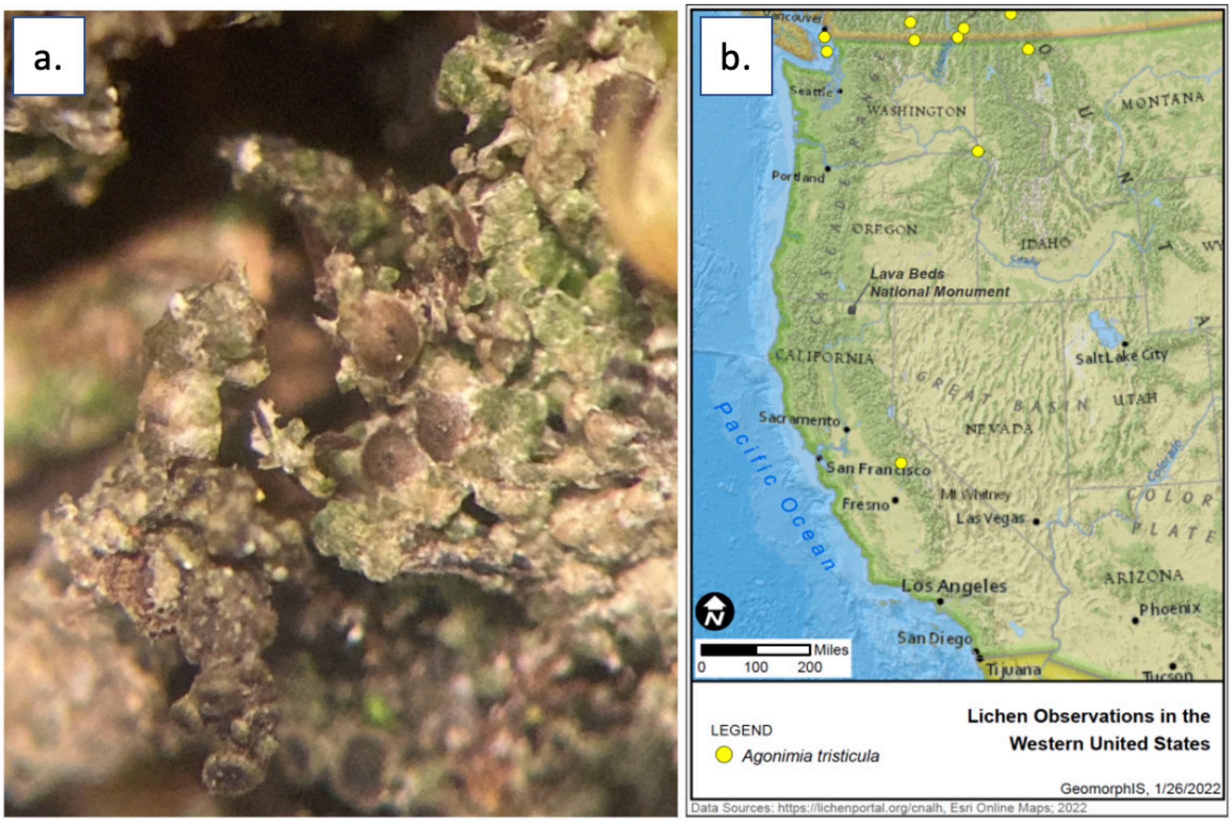

Figure 14. *Agonimia tristicula* (a) close-up and (b) range.

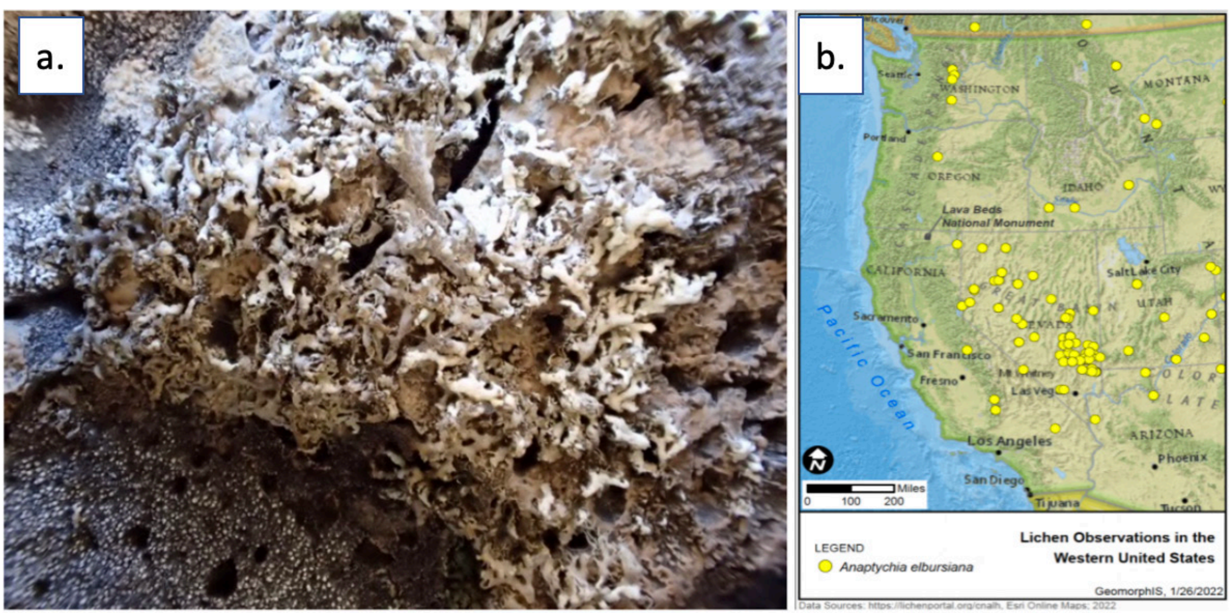

Figure 15. *Anaptychia elbursiana* (a) close-up and (b) range.

Aspicilia reptans (Figure 16a) is a vagrant species mostly found in the intermountain west that has not been previously recorded in California. It is most common in Eastern Oregon. This is an example of a species on the western edge of its range in Lava Beds National Monument (Figure 16b). Difficult to spot, this species is highly susceptible to trampling due to its delicate structure. It was only found in the rim zone in one location where it is susceptible to the impacts of recent fires. This location was an unburned patch within the fire perimeter; the population may have been more extensive in the area before the recent fire.

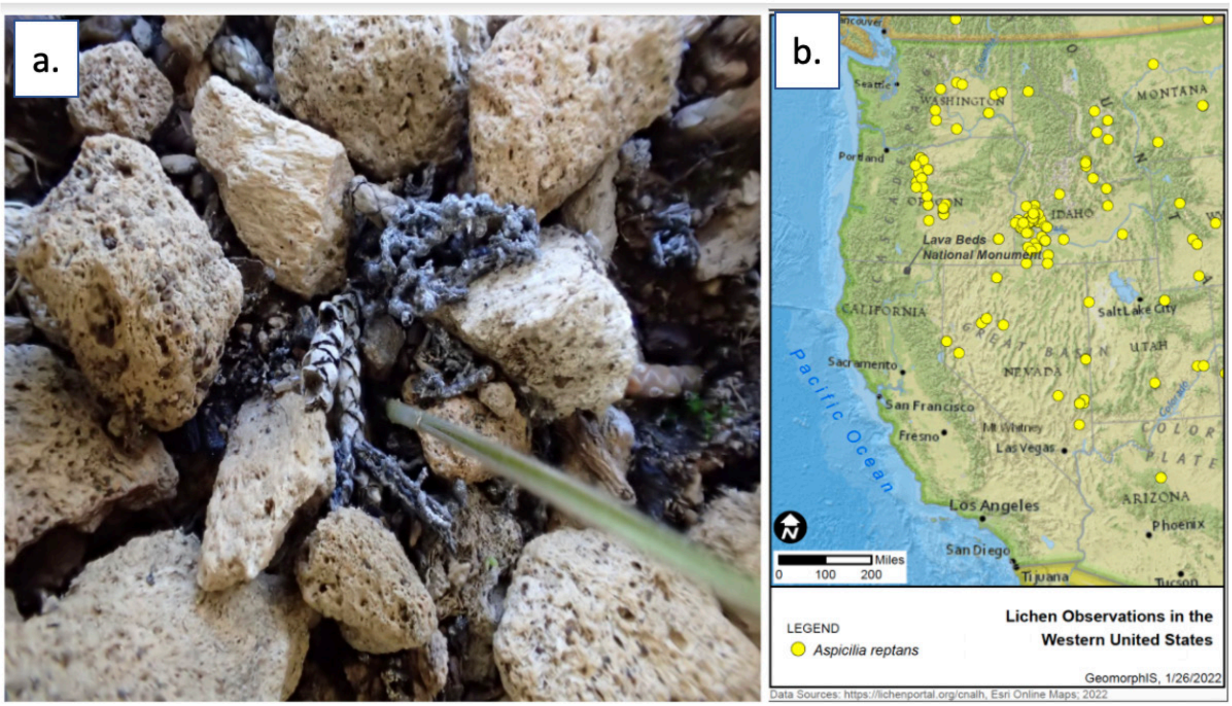

Figure 16. *Aspicila reptans* close-up photo (a) and (b) range.

Chaenotheca cinerea (Figure 17a) is a rare pin lichen with a typically superficial white to grayish-white thallus and pins with a whitish pruina in the upper half of the pin and a brown spore mass. There are a few records in the Pacific Northwest with the nearest recorded occurrence in the central Cascades of Washington State (figure 17b). This species is highly susceptible to trampling, and was found on wood and rock in two ice caves. The identification of this species is tentative and needs further investigation to confirm.

Chaenotheca furfuracea (Figure 18a) is a pin lichen with greenish stalks and a greenish exciple that nearly match the color of the powdery thallus. This species is somewhat common on the westside of the Cascade Range but is disjunct in Lava Beds National Monument and not otherwise known from the Modoc Plateau (Figure 18b). This species was found on the rock walls in the sink of an ice cave, which is an uncommon substrate for the species as it is typically found on soil, exposed rootlets, bark, or wood. Interestingly this species has been recorded in a disjunct population in an ice cave in Pennsylvania (Lendemer et al. 2009).

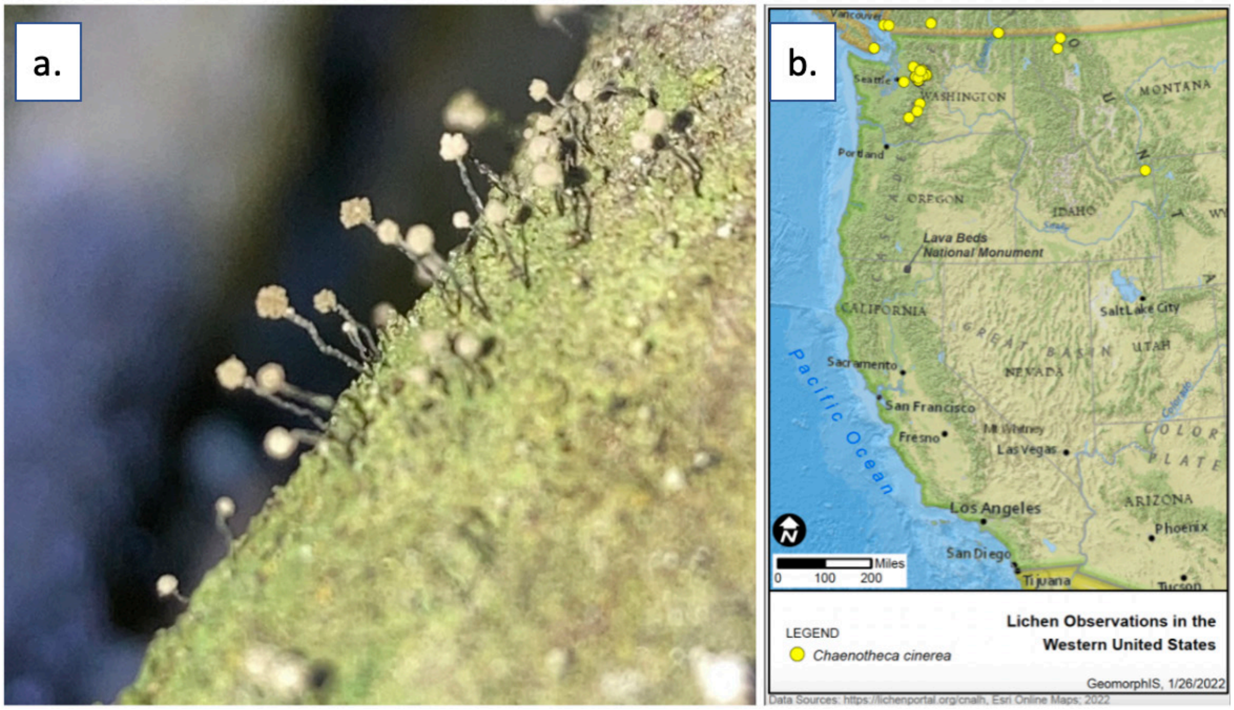

Figure 17. *Chaenotheca cinerea* (a) close-up and (b) range.

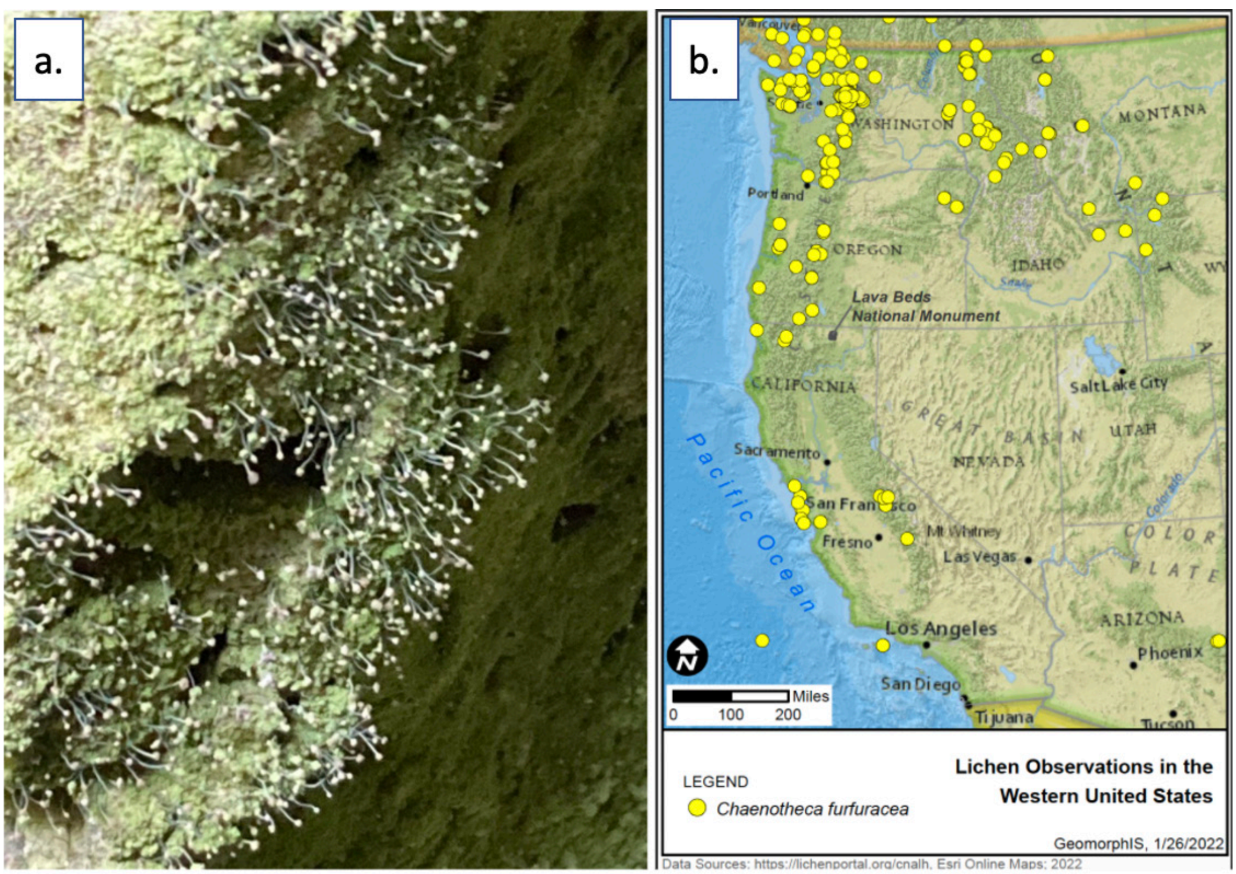

Figure 18. *Chaenotheca furfuracea* (a) close-up and (b) range.

Ophioparma ventosa (Figure 19a) is a striking species with a white thallus and red apothecia, earning it the fitting common name “alpine bloodspot lichen.” With a UV+ white medulla and accessory stictic acid and thamnolic acid or atranorin, this species is distinctive. The nearest known recorded sites for this species are in Washington state, although it is also known from Oregon (McCune 2017). Formerly discovered by Steve Sheehy in Devil’s Homestead, locations within the Monument are the only currently known sites in California (Figure 19b).

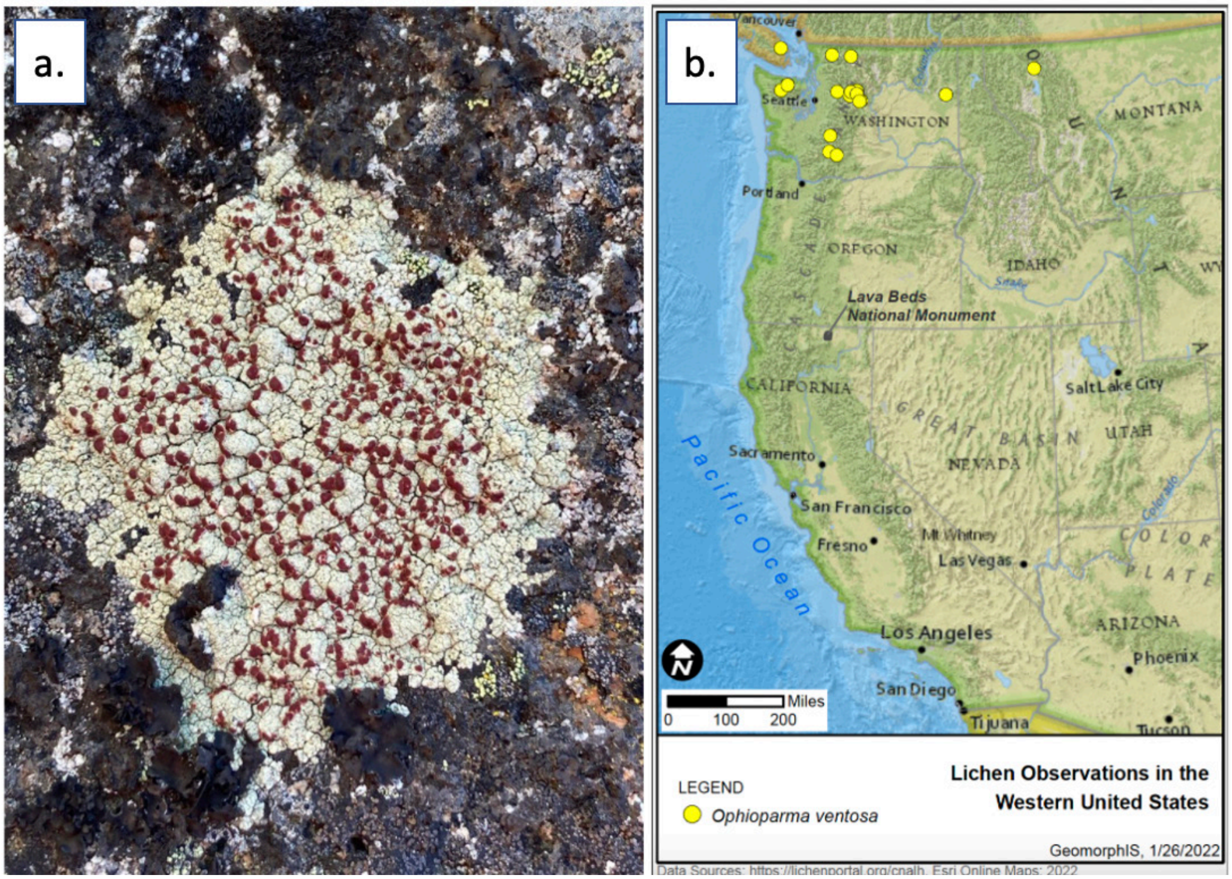

Figure 19. *Ophioparma ventosa* (a) close-up and photo and (b) range.

Easily distinguished by its marginal, linear soralia and thallus lacking tomentum, Peltigera collina (Figure 20a) is a relatively common foliose species on the westside of the Cascade Range. It is uncommon on the east side of the Cascades, with the nearest occurrences to the west and north (Figure 20b). This species was found high on a shaded wall ledge in the sink zone of an ice cave.

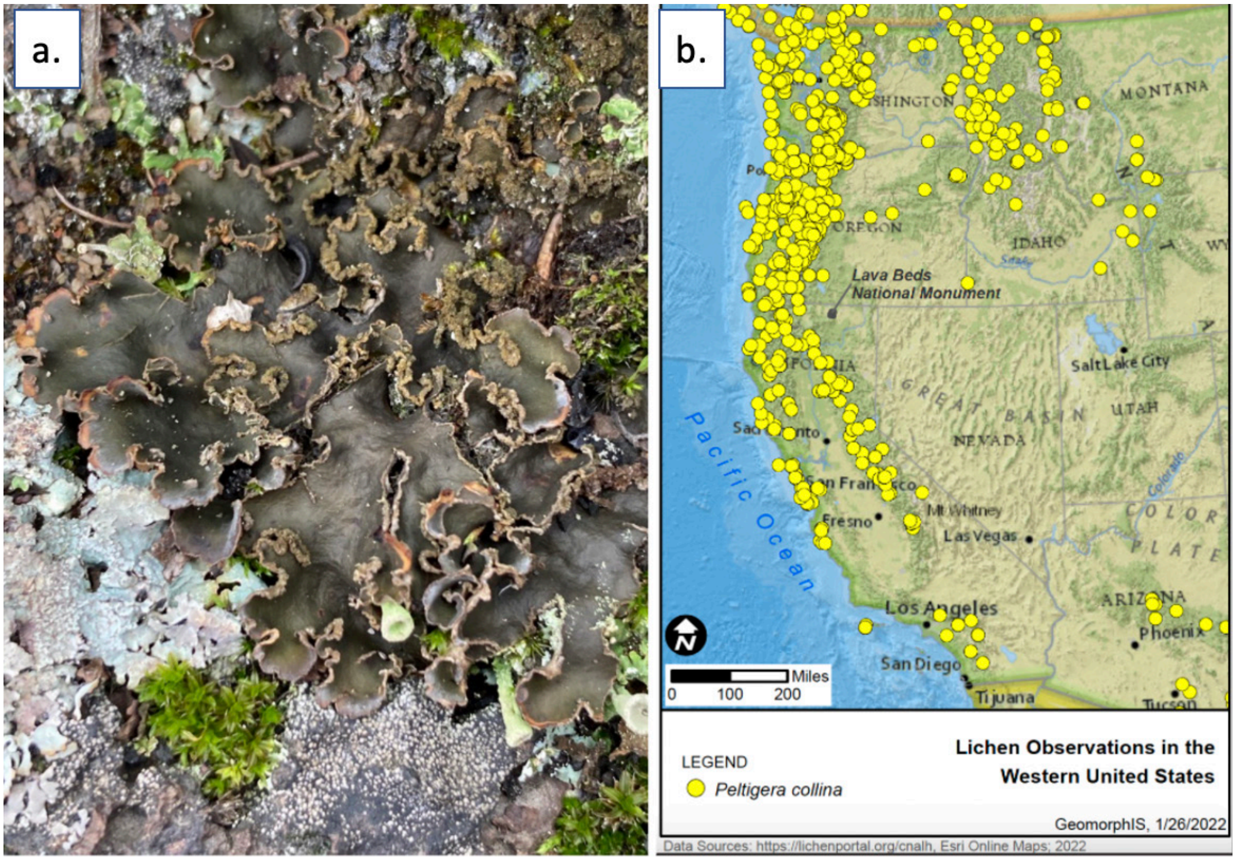

Figure 20. *Peltigera collina* (a) close-up photo and (b) range.

Psoroma hypnorum (Figure 21a) arises from small squamules, with a red-brown to dark brown disc up to 5 mm wide with a thalline margin. It is typically found in moist habitats, among bryophytes or on soil, mostly in montane regions, particularly in spruce-fir forests along the Cascade crest and west in the region, with few records in California (Fig 21b). This species was found in an ice cave.

The iron oxide in *Tremelecia atrata* (Figure 22a) gives it a red to rusty red surface. It is endemic to North America and is typically found on conifer wood or granites, schists or other acidic rocks in open humid habitats. There are three known sites in California (Figure 22b). Most records in the Pacific Northwest are to the north in Washington and Idaho.

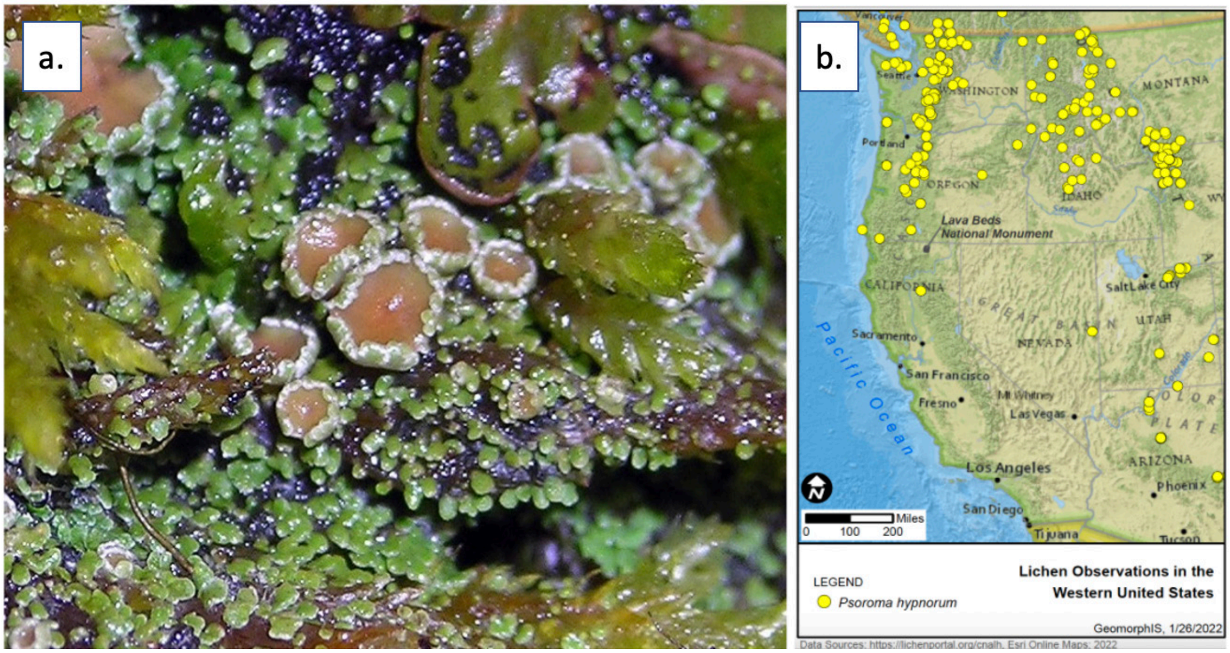

Figure 21. *Psoroma hypnorum* (a) close-up photo and (b) range.

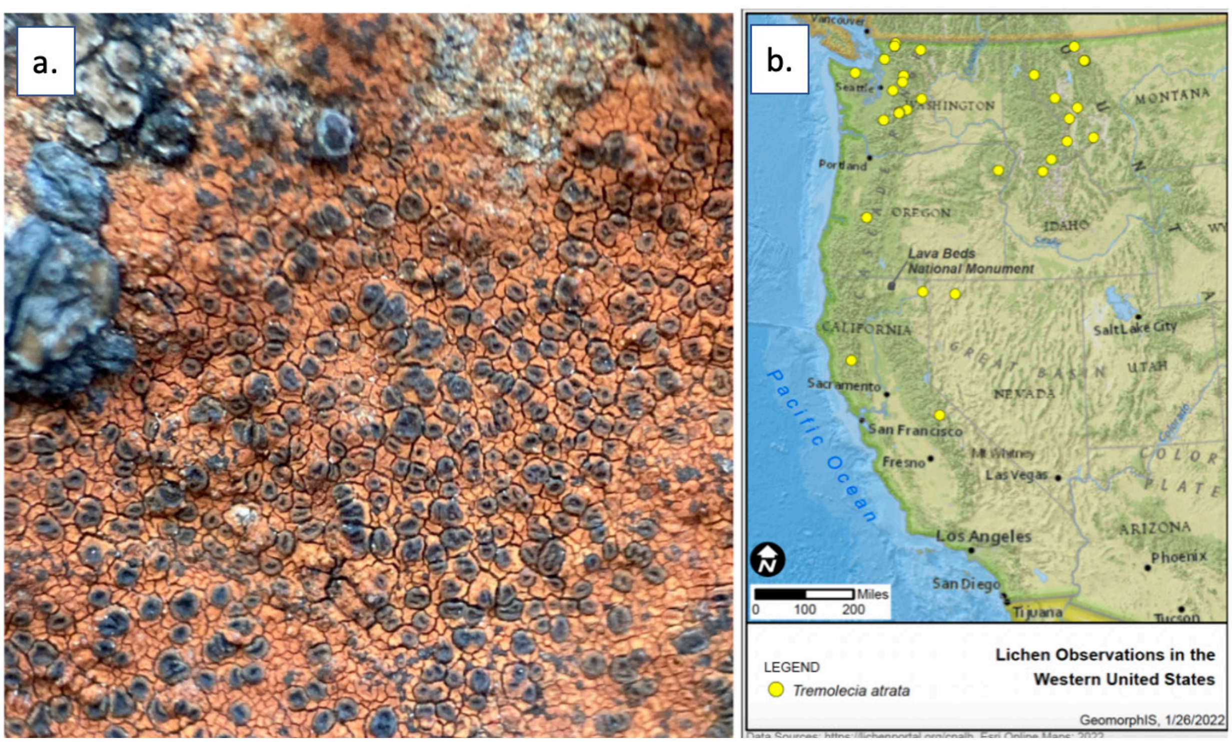

Figure 22. *Tremolecia atrata* (a) close-up and (b) range.

Discussion

Our study highlights that caves provide important habitat for lichens amid the semi-arid landscape of Lava Beds National Monument. Caves with deeper entrances and larger sink areas provide stronger microclimates, which in turn support more diverse lichen communities. Ice caves represent specialized habitats that host many rare or disjunct lichens. Larger and deeper caves may also provide better refugia from wildfire; almost all our study sites burned in the two years prior to sampling, but caves with deeper entrances and larger sink areas experienced a smaller amount of burned area in the immediate surroundings, probably because the large expanses of rock and pronounced topography create fire breaks and fire-sheltered areas.

Although visitor use has the potential to disturb lichens and cause localized species extirpations (Vanover, 2009), we found no differences in lichen richness at the plot scale among caves that experience high and low visitor use. These findings suggest that existing visitor infrastructure, such as railings and stairways, may be effectively mitigating visitor impacts, at least at the landscape scale. Visitors would be most likely to harm lichens by trampling them or scraping them off walls used as handholds, but even heavily used caves typically have large areas of lichen habitat that are inaccessible to direct contact from visitors. While visitor use may have localized impacts that our study did not detect, our findings highlight that visitor use does not appear to reduce lichen diversity at a landscape scale currently.

Our results contrast with a previous study of lichens in cave entrances at the Monument that found that visitor use reduces lichen cover, species richness and diversity on cave walls (Vanover, 2009). Vanover (2009) focused on areas that are analogous to the sheltered and twilight zones in our study and surveyed lichen community composition using small quadrats on cave walls. In contrast, our study examined lichen patterns at a broader spatial scale and concluded that at a landscape scale, there is not a significant impact of visitor use on lichen richness, on species that are likely to be sensitive to trampling specifically (e.g., vagrant lichens), or on species composition. Even when we analyzed only species recorded inside the cave interior, we did not find a significant effect of visitor use on lichen richness or the richness of sensitive species.

Our findings highlight that management practices that reduce visitor impacts on lichen communities may be critical for maintaining landscape-scale lichen diversity at sites with high visitor use, since there is little doubt that visitor use has the potential to do great harm to lichen communities. The careful placement of railings, stairways, and other infrastructure at high-use caves channels visitor travel into defined corridors and limits potential visitor contact with natural surfaces. This likely explains why caves that experience frequent visitor traffic nonetheless frequently contain diverse, high-quality lichen communities. Continuing to mitigate visitor use impacts through such infrastructure is an important consideration for long-term management. Visitor impacts on lichens should be monitored regularly in the future, and should also be studied at finer scales using quadrats or other fine-scale sampling approaches.

Numerous regionally rare lichen species occurred in the mild environments associated with cave entrances. Several of these species typically occur in wetter habitats west of the Cascade and / or

Sierra Nevada ranges, although other species were found at the western edges of their Great-Basin-centric ranges. Mesic-adapted species that are apparently unable to otherwise survive in the semi-arid landscape of Lava Beds thrive in the benign environment of the cave entrances.

"Cold traps" associated with caves, and especially ice caves, have well-documented effects on vascular plant vegetation (Balch, 1900; Domínguez-Villar, 2013; Coles and Gilbertson, 1994). Though there have been few previous ecological studies of lichens associated with caves, numerous new lichen species have been described from caves (Etayo and Breuss, 1994; Etayo and Van Den Boom, 1995). Ice caves are known to be an especially important habitat for lichens and may contain relict lichen populations that have survived since the last glacial maxima in ice cave refugia (Lendemer et al., 2009; Dirig, 1994; Etayo, 1991). Similar to our findings here, disjunct species associated with cave microclimates have also been documented in Pennsylvania (Lendemer et al., 2009). Despite the differences in the lichen floras of Pennsylvania and Northern California, *Chaenotheca furfuracea* has been reported as a disjunct in Pennsylvania ice caves, as well as at two ice caves in the Monument that we sampled.

In an era of climate change, microclimates may be important as refugia for species that are sensitive to a changing climate. Our research highlights that cave entrances may be especially important for supporting species at the edges of their ranges of environmental tolerance in semi-arid ecosystems like those found at Lava Beds National Monument.

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Lisa Foster, Support biologist (SummitWest)

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Bruce F. Goff, Senior Reviewer/Editor (GeomorphIS)

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Appendix A. Selected environmental data across all study sites

Table 2. Selected environmental and lichen community data across study sites. Variables that are not included here can be found in the associated data file.

Cave code	Lower entrance meters above grade	Impact index	Presence of Ice	Total lichen richness	Percent burned	Average trampling index
B020	−2.4	0	Present	52	100	3.04
B180	−0.6	1	Absent	45	98.4	3.04
B200	−1.4	2	Absent	54	63	3.26
C510	−0.3	0	Absent	83	79	3.27
C580	−0.3	0	Absent	34	49.52	3.06
E260	3.7	0	Absent	55	66.5	3.07
E480	−0.9	0	Absent	40	94.5	3.05
E720	−2.1	2	Absent	79	69.2	3.20
L030	−7.0	4	Present	81	7.3	3.11
L040	−4.6	1	Present	93	52.3	2.98
L220	−6.4	0	Present	91	16	3.09
L255	0.6	3	Absent	55	83.5	3.06
L288	−0.3	0	Absent	38	29.4	3.16
L290	0.0	3	Absent	47	72	2.85
L295	−0.9	2	Absent	75	67.7	3.03
L340	−3.0	4	Absent	69	50	2.87
L350	−0.9	0	Absent	59	0	3.14
L383	−1.5	0	Absent	87	16.5	3.02
L400	−6.1	2	Present	98	12.4	3.13
L415	−1.8	0	Absent	64	69.3	3.05
L480	−2.4	3	Absent	85	0.6	3.12
L490	−1.2	3	Absent	21	98	2.86
L550	1.8	2	Absent	44	56	2.98
L610	−1.5	1	Absent	53	0	2.98
L630	−0.9	4	Absent	33	17	3.22

Table 2 (continued). Selected environmental and lichen community data across study sites. Variables that are not included here can be found in the associated data file.

Cave code	Lower entrance meters above grade	Impact index	Presence of Ice	Total lichen richness	Percent burned	Average trampling index
L780	−0.9	2	Absent	77	76.5	3.16
L790	−4.0	0	Absent	50	37.5	3.18
L800	−12.2	2	Present	80	73	3.10
L840	−0.9	0	Absent	23	99.5	2.87
L860	−0.3	2	Absent	15	97.52	2.87
M150	−1.8	2	Absent	67	82	2.97
M180	−1.5	3	Absent	49	89.3	2.94
M2000	−4.9	1	Absent	45	20	2.95
M235	0.0	1	Absent	24	97	3.25
M265	−6.1	0	Absent	95	49.2	3.14
M310	−3.0	3	Absent	63	57.4	2.95
M340	−6.1	0	Absent	78	60.8	3.05
M350	−0.9	3	Present	55	59.4	3.02
M390	−1.2	1	Absent	59	63	3.21
M400	−1.5	0	Absent	57	47.5	3.23
V715	−0.9	0	Absent	53	90.25	3.08
V780	−0.9	3	Absent	61	74	2.95

Appendix B. Lichen species encountered in the 42 study plots we sampled in the vicinity of caves

Table 3. List of lichen species encountered and their frequency by zones and trampling index values from Lava Beds National Monument. This list includes all taxa that were encountered during this study and includes trampling index scores and total frequency and frequency by zone. Trampling index scores were not assigned for lichenicolous fungi. The summed frequency for all zones may be greater than the total species frequency since the same taxa may occur in multiple zones at the same site; total frequency represents the total number sites where each taxon occurred. Trampling index values were not assigned for lichenicolous fungi.

Species	Trampling Index	Rim Zone Frequency	Sink Zone Frequency	Sheltered Zone Frequency	Twilight Zone Frequency	Total Species Frequency
Acarospora badiofusca	2	0	0	1	0	1
Acarospora bullata	2	16	10	5	0	24
Acarospora elevata	1	1	2	0	0	3
Acarospora fuscata	2	17	18	1	0	28
Acarospora schleicheri	5	3	0	0	0	3
Acarospora socialis	2	2	6	0	0	8
Acarospora species	2	1	0	0	1	2
Acarospora thamnina	4	21	21	1	0	27
Acarospora veronensis	2	8	5	0	0	11
Acolium inquinans	1	6	3	1	0	8
Agonimia tristicula	5	0	0	1	0	1
Alectoria imshaugii	4	1	1	0	0	1
Amandinea punctata	1	16	24	1	0	26
Anaptychia elbursiana	4	0	4	1	0	5
Arthonia glebosa	5	14	1	0	0	15
Aspicilia cinerea	2	4	2	0	0	5
Aspicilia filiformis	7	1	0	0	0	1
Aspicilia pacifica	2	7	4	2	0	13
Aspicilia reptans	5	0	1	0	0	1
Aspicilia species	2	15	18	9	0	28
Athallia holocarpa	1	0	0	0	1	1
Bellemerea sanguinea	2	0	1	0	0	1

Table 3 (continued). List of lichen species encountered and their frequency by zones and trampling index values from Lava Beds National Monument. This list includes all taxa that were encountered during this study and includes trampling index scores and total frequency and frequency by zone. Trampling index scores were not assigned for lichenicolous fungi. The summed frequency for all zones may be greater than the total species frequency since the same taxa may occur in multiple zones at the same site; total frequency represents the total number sites where each taxon occurred. Trampling index values were not assigned for lichenicolous fungi.

Species	Trampling Index	Rim Zone Frequency	Sink Zone Frequency	Sheltered Zone Frequency	Twilight Zone Frequency	Total Species Frequency
Bibbya ruginosa	2	3	12	0	0	14
Bryoplaca jungermanniae	5	7	7	0	0	12
Bryoria fremontii	4	0	9	0	0	9
Buellia badia	1	0	3	1	0	3
Buellia epigaea	5	0	1	0	0	1
Buellia species	2	0	1	0	0	1
Buellia species nova	2	1	3	1	0	5
Buellia terricola	5	0	1	0	0	1
Calicium tigillare	1	1	0	0	0	1
Calogaya saxicola	2	0	1	3	2	6
Caloplaca demissa	3	0	1	2	0	3
Caloplaca epithallina	–	9	17	0	0	21
Caloplaca species	2	1	1	1	1	4
Caloplaca subpyraceella	5	1	0	0	0	1
Candelaria pacifica	3	14	17	11	2	30
Candelariella efflorescens	1	1	2	0	0	3
Candelariella rosulans	2	33	26	7	0	37
Candelariella vitellina	2	28	27	13	0	36
Carbonea vitellinaria	–	1	0	0	0	1
Chaenotheca cf. *cinerea*	7	0	0	1	1	2
Chaenotheca furfuracea	7	0	0	1	1	2
Chaenotheca species	7	0	1	0	0	1
Chrysothrix chlorina	3	2	24	16	2	31
Circinaria caesiocinerea	2	20	10	13	1	30
Circinaria cf. *arida*	2	15	22	12	1	31

Table 3 (continued). List of lichen species encountered and their frequency by zones and trampling index values from Lava Beds National Monument. This list includes all taxa that were encountered during this study and includes trampling index scores and total frequency and frequency by zone. Trampling index scores were not assigned for lichenicolous fungi. The summed frequency for all zones may be greater than the total species frequency since the same taxa may occur in multiple zones at the same site; total frequency represents the total number sites where each taxon occurred. Trampling index values were not assigned for lichenicolous fungi.

Species	Trampling Index	Rim Zone Frequency	Sink Zone Frequency	Sheltered Zone Frequency	Twilight Zone Frequency	Total Species Frequency
Cladonia chlorophaea	4	22	28	14	0	39
Cladonia coniocraea	4	0	5	1	0	6
Cladonia fimbriata	4	6	20	3	0	22
Cladonia pocillum	4	0	1	0	0	1
Cladonia pyxidata	4	1	5	0	0	6
Cladonia species	4	28	24	12	0	39
Cladonia squamosa	4	1	5	0	0	6
Cladonia verruculosa	4	2	3	0	0	5
Dermatocarpon leptophyllodes	4	1	0	0	0	1
Dermatocarpon miniatum	4	0	5	2	0	7
Dermatocarpon reticulatum	4	3	21	18	1	26
Dimelaena thysanota	1	1	15	1	1	15
Diploschistes muscorum	5	17	8	0	0	22
Diploschistes scruposus	2	22	32	5	0	35
Diplotomma alboatrum	2	1	1	8	11	17
Enchylium tenax	4	6	4	1	0	9
Evernia prunastri	4	1	0	0	0	1
Flavoplaca citrina	3	2	4	27	21	33
Hypocenomyce scalaris	4	6	5	0	0	10
Hypogymnia imshaugii	4	3	0	0	0	3
Hypogymnia tubulosa	4	0	1	0	0	1
Lecanora albellula	1	17	6	0	0	20
Lecanora bicincta	2	8	5	1	0	11
Lecanora cenisia	2	2	4	2	0	7
Lecanora mellea	2	2	7	3	0	11

Table 3 (continued). List of lichen species encountered and their frequency by zones and trampling index values from Lava Beds National Monument. This list includes all taxa that were encountered during this study and includes trampling index scores and total frequency and frequency by zone. Trampling index scores were not assigned for lichenicolous fungi. The summed frequency for all zones may be greater than the total species frequency since the same taxa may occur in multiple zones at the same site; total frequency represents the total number sites where each taxon occurred. Trampling index values were not assigned for lichenicolous fungi.

Species	Trampling Index	Rim Zone Frequency	Sink Zone Frequency	Sheltered Zone Frequency	Twilight Zone Frequency	Total Species Frequency
Lecanora pseudomellea	2	5	9	0	0	13
Lecanora rupicola	2	31	31	9	1	40
Lecanora semitensis	2	0	2	0	0	2
Lecanora species	2	4	1	0	0	5
Lecanora swartzii	2	1	4	1	0	5
Lecidea atrobrunnea	2	33	32	7	1	39
Lecidea cascadensis	2	0	2	1	0	3
Lecidea fuscoatra	2	1	3	0	0	4
Lecidea laboriosa	1	1	0	0	0	1
Lecidea lactea	2	0	1	0	0	1
Lecidea lapicida	2	1	3	0	0	4
Lecidea protabacina	2	0	1	0	0	1
Lecidea tessellata	2	14	21	6	0	26
Lecidea turgidula	1	7	3	0	0	9
Lecidella carpathica	2	0	1	0	1	2
Lepraria eburnea	3	0	1	1	0	2
Lepraria jackii	3	0	6	0	0	6
Lepraria neglecta	3	39	36	23	2	42
Lepraria subalbicans	3	1	1	0	0	2
Leprocaulon adhaerens	3	0	2	3	0	4
Leprocaulon knudsenii	3	5	21	33	19	41
Leprocaulon species	3	0	1	0	0	1
Leptochidium albociliatum	5	1	11	1	0	11
Letharia columbiana	4	15	6	1	1	16
Letharia vulpina	4	27	22	1	0	35

Table 3 (continued). List of lichen species encountered and their frequency by zones and trampling index values from Lava Beds National Monument. This list includes all taxa that were encountered during this study and includes trampling index scores and total frequency and frequency by zone. Trampling index scores were not assigned for lichenicolous fungi. The summed frequency for all zones may be greater than the total species frequency since the same taxa may occur in multiple zones at the same site; total frequency represents the total number sites where each taxon occurred. Trampling index values were not assigned for lichenicolous fungi.

Species	Trampling Index	Rim Zone Frequency	Sink Zone Frequency	Sheltered Zone Frequency	Twilight Zone Frequency	Total Species Frequency
Lichinaceae species	4	0	1	0	0	1
Megaspora verrucosa	5	0	1	0	0	1
Melanelixia fuliginosa	3	0	0	1	0	1
Melanohalea elegantula	3	4	3	2	0	8
Melanohalea exasperatula	3	15	11	5	0	22
Melanohalea multispora	3	18	6	0	0	21
Miriquidica garovaglii	2	3	2	0	0	5
Miriquidica griseoatra	2	2	1	0	0	3
Montanelia panniformis	3	0	2	0	0	2
Montanelia tominii	3	0	1	0	0	1
Myriolecis dispersa	1	0	1	0	0	1
Myriolecis hagenii	2	0	1	0	0	1
Nodobryoria abbreviata	4	3	3	0	0	4
Nodobryoria oregana	4	2	2	0	0	4
Ochrolechia turneri	1	0	1	0	0	1
Ochrolechia upsaliensis	5	0	1	0	0	1
Ophioparma ventosa	2	0	1	0	0	1
Pachypeltis invadens	–	0	1	0	0	1
Parmelia barrenoae	3	8	6	0	0	13
Parmelia hygrophila	3	0	1	0	0	1
Parmelia saxatilis	4	1	20	4	0	21
Parmelia sulcata	3	0	5	1	0	6
Parmeliopsis ambigua	3	1	3	1	0	3
Parmeliopsis hyperopta	3	0	1	0	0	1
Parvoplaca tiroliensis	5	9	5	1	1	13

Table 3 (continued). List of lichen species encountered and their frequency by zones and trampling index values from Lava Beds National Monument. This list includes all taxa that were encountered during this study and includes trampling index scores and total frequency and frequency by zone. Trampling index scores were not assigned for lichenicolous fungi. The summed frequency for all zones may be greater than the total species frequency since the same taxa may occur in multiple zones at the same site; total frequency represents the total number sites where each taxon occurred. Trampling index values were not assigned for lichenicolous fungi.

Species	Trampling Index	Rim Zone Frequency	Sink Zone Frequency	Sheltered Zone Frequency	Twilight Zone Frequency	Total Species Frequency
Peltigera canina	5	3	12	1	0	13
Peltigera collina	5	0	1	0	0	1
Peltigera didactyla	5	3	3	0	0	6
Peltigera ponojensis	5	2	5	0	0	7
Peltigera rufescens	5	2	14	1	0	15
Pertusaria flavocunda	2	0	1	0	0	1
Phaeophyscia decolor	4	2	15	0	0	16
Phaeophyscia orbicularis	4	0	1	0	0	1
Phaeophyscia sciastra	4	0	1	0	0	1
Physcia adscendens	3	1	0	0	0	1
Physcia biziana	4	7	28	29	6	38
Physcia caesia	4	3	7	12	5	24
Physcia dimidiata	4	1	4	2	0	6
Physcia dubia	4	5	8	10	2	20
Physcia occidentalis	4	0	15	18	4	29
Physcia tenella	3	0	5	0	0	5
Physconia americana	4	0	1	1	0	2
Physconia enteroxantha	4	9	24	15	0	30
Physconia isidiigera	4	1	3	0	0	3
Physconia muscigena	4	1	2	3	0	5
Physconia perisidiosa	4	2	14	5	0	19
Placidium squamulosum	4	1	0	0	0	1
Placynthiella icmalea	1	1	0	0	0	1
Placynthiella oligotropha	5	8	2	0	0	10
Placynthiella uliginosa	5	2	0	0	0	2

Table 3 (continued). List of lichen species encountered and their frequency by zones and trampling index values from Lava Beds National Monument. This list includes all taxa that were encountered during this study and includes trampling index scores and total frequency and frequency by zone. Trampling index scores were not assigned for lichenicolous fungi. The summed frequency for all zones may be greater than the total species frequency since the same taxa may occur in multiple zones at the same site; total frequency represents the total number sites where each taxon occurred. Trampling index values were not assigned for lichenicolous fungi.

Species	Trampling Index	Rim Zone Frequency	Sink Zone Frequency	Sheltered Zone Frequency	Twilight Zone Frequency	Total Species Frequency
Platismatia glauca	3	0	4	0	0	4
Pleopsidium flavum	2	14	29	12	1	35
Polycauliona luteominia	1	0	2	0	0	2
Polychidium muscicola	5	0	2	0	0	2
Protoparmelia badia	2	0	12	1	0	12
Protoparmeliopsis garovaglii	3	2	3	2	0	7
Protoparmeliopsis muralis	3	31	29	20	1	42
Pseudephebe pubescens	3	10	19	0	0	23
Pseudothelomma occidentale	1	2	1	0	0	3
Pseudothelomma ocellatum	1	1	2	0	0	3
Psora cerebriformis	4	0	2	0	0	2
Psora globifera	4	3	5	0	0	6
Psora himalayana	4	2	6	0	0	8
Psora luridella	4	0	2	0	0	2
Psora nipponica	4	10	26	2	0	28
Psoroma hypnorum	5	0	1	0	0	1
Rhizocarpon disporum	2	14	22	2	0	26
Rhizocarpon dymalinae	–	0	1	0	0	1
Rhizocarpon eupetraeum	2	0	0	1	0	1
Rhizocarpon geographicum	2	39	34	7	1	42
Rhizocarpon grande	2	28	34	10	0	39
Rhizocarpon lecanorinum	2	17	27	1	0	29
Rhizocarpon macrosporum	2	4	15	4	0	19
Rhizoplaca chrysoleuca	4	17	20	1	0	28
Rhizoplaca melanophthalma	4	23	31	16	0	38

Table 3 (continued). List of lichen species encountered and their frequency by zones and trampling index values from Lava Beds National Monument. This list includes all taxa that were encountered during this study and includes trampling index scores and total frequency and frequency by zone. Trampling index scores were not assigned for lichenicolous fungi. The summed frequency for all zones may be greater than the total species frequency since the same taxa may occur in multiple zones at the same site; total frequency represents the total number sites where each taxon occurred. Trampling index values were not assigned for lichenicolous fungi.

Species	Trampling Index	Rim Zone Frequency	Sink Zone Frequency	Sheltered Zone Frequency	Twilight Zone Frequency	Total Species Frequency
Rhizoplaca phaedrophthalma	2	7	14	2	1	18
Rinodina bolanderi	5	0	1	0	0	1
Rinodina confragosa	2	3	15	14	0	20
Rinodina juniperina	1	3	1	0	0	4
Rinodina olivaceobrunnea	5	2	2	0	0	3
Rusavskia elegans	3	10	30	23	5	34
Rusavskia sorediata	3	0	3	0	1	4
Sagedia mastrucata	2	0	2	0	0	2
Scytinium intermedium	4	1	0	0	0	1
Scytinium lichenoides	4	15	32	6	0	34
Scytinium tenuissimum	4	1	0	0	0	1
Staurothele areolata	2	0	4	3	0	7
Staurothele drummondii	2	3	18	10	2	23
Stenocybe procrastinata	1	4	2	0	0	6
Tephromela atra	1	0	1	1	0	1
Tetramelas chloroleucus	1	0	1	0	0	1
Tetramelas papillatus	5	0	1	0	0	1
Thalloidima sedifolium	5	11	12	0	0	16
Trapeliopsis flexuosa	1	0	1	0	0	1
Trapeliopsis glaucopholis	2	1	1	0	0	1
Trapeliopsis granulosa	1	6	6	1	0	12
Tremolecia atrata	2	0	2	0	0	2
Tuckermanopsis chlorophylla	4	1	6	0	0	6
Umbilicaria americana	4	0	6	0	0	6
Umbilicaria hyperborea	4	33	31	8	0	40

Table 3 (continued). List of lichen species encountered and their frequency by zones and trampling index values from Lava Beds National Monument. This list includes all taxa that were encountered during this study and includes trampling index scores and total frequency and frequency by zone. Trampling index scores were not assigned for lichenicolous fungi. The summed frequency for all zones may be greater than the total species frequency since the same taxa may occur in multiple zones at the same site; total frequency represents the total number sites where each taxon occurred. Trampling index values were not assigned for lichenicolous fungi.

Species	Trampling Index	Rim Zone Frequency	Sink Zone Frequency	Sheltered Zone Frequency	Twilight Zone Frequency	Total Species Frequency
Umbilicaria nodulospora	4	13	27	0	0	32
Umbilicaria phaea	4	30	33	12	0	40
Umbilicaria polaris	4	2	4	0	0	5
Umbilicaria polyphylla	4	3	22	0	0	23
Umbilicaria torrefacta	4	0	1	0	0	1
Umbilicaria virginis	4	0	3	0	0	3
Xanthomendoza fulva	4	12	8	4	0	19
Xanthomendoza mendozae	4	0	14	31	9	35
Xanthomendoza montana	3	3	2	0	0	5
Xanthoparmelia coloradoensis	4	7	24	0	0	24
Xanthoparmelia cumberlandia	3	32	30	10	0	41
Xanthoparmelia loxodes	3	21	24	4	0	30
Xanthoparmelia plittii	3	6	16	0	0	18
Xylographa parallela	1	0	1	0	0	1

Appendix C. Updated checklist of all lichen species known from Lava Beds National Monument

Table 4. Updated checklist of all lichen species known from Lava Beds National Monument. This species list includes records from Sheehy (2017) and additional records provided by Tom Carlberg, Katherine Glew and Eric Peterson. Species recorded during this study are indicated in the right-hand column with an x. Species found in our study that occurred only in ice caves are in the middle column are indicated with an x. Taxa from our study that could not be identified to species level are not included here.

Lichen Species	Ice Cave Only	Recorded in this study
Acarospora badiofusca (Nyl.) Th. Fr.	–	X
Acarospora bullata Anzi	–	X
Acarospora elevata H. Magn.	–	X
Acarospora fuscata (Schrader) Arnold	–	X
Acarospora schleicheri (Ach.) A. Massal.	–	X
Acarospora socialis H. Magn.	–	X
Acarospora thamnina (Tuck.) Herre	–	X
Acarospora veronensis A. Massal.	–	X
Acolium inquinans (Sm.) A. Massal.	–	X
Agonimia tristicula (Nyl.) Zahlbr.	–	X
Ahtiana sphaerosporella (Müll.Arg.) Goward	–	–
Alectoria imshaugii Brodo & D. Hawksw.	–	X
Alectoria sarmentosa (Ach.) Ach.	–	–
Amandinea punctata (Hoffm.) Coppins & Scheid.	–	X
Anaptychia elbursiana (Szatala) Poelt	–	X
Arthonia glebosa Tuck.	–	X
Aspicilia cinerea (L.) Körb.	–	X
Aspicilia cyanescens Owe-Larss. & A. Nordin	–	–
Aspicilia filiformis Rosentreter	–	X
Aspicilia knudsenii Owe-Larss. & A. Nordin	–	–
Aspicilia mansourii Sohrabi	–	–
Aspicilia olivaceobrunnea Owe-Larss. & A. Nordin	–	–
Aspicilia pacifica Owe-Larss. & A. Nordin	–	X
Aspicilia reptans (Looman) Wetmore	–	X

Table 4 (continued). Updated checklist of all lichen species known from Lava Beds National Monument. This species list includes records from Sheehy (2017) and additional records provided by Tom Carlberg, Katherine Glew and Eric Peterson. Species recorded during this study are indicated in the right-hand column with an x. Species found in our study that occurred only in ice caves are in the middle column are indicated with an x. Taxa from our study that could not be identified to species level are not included here.

Lichen Species	Ice Cave Only	Recorded in this study
Aspicilia verrucigera Hue	–	–
Athallia cf. saxifragarum (Poelt) Arup, Frödén & Søchting	–	–
Athallia holocarpa (Hoffm.) Arup, Frödén & Søchting	–	X
Bellemerea alpina (Sommerf.) Clauzade & Cl. Roux	–	–
Bellemerea sanguinea (Krempelh.) Hafellner & Cl. Roux	–	X
Bibbya ruginosa (Tuck.) Kistenich, Timdal, Bendiksby & S. Ekman	–	X
Blastenia ferruginea (Huds.) A. Massal.	–	–
Bryobilimbia hypnorum (Lib.) Fryday, Printzen & S. Ekman	–	–
Bryoplaca jungermanniae (Vahl) Søchting, Frödén & Arup	–	X
Bryoria fremontii (Tuck.) Brodo & D. Hawksw.	–	X
Bryoria fuscescens (Gyelnik) Brodo & D. Hawksw.	–	–
Bryoria pseudofuscescens (Gyelnik) Brodo & D. Hawksw.	–	–
Bryoria tortuosa (G. Merr.) Brodo & D. Hawksw.	–	–
Buellia badia (Fr.) A. Massal.	–	X
Buellia epigaea (Pers.) Tuck.	X	X
Buellia terricola A. Nordin	–	–
Calicium tigillare (Ach.) Pers.	–	X
Calogaya saxicola (Hoffm.) Vondrák	–	X
Caloplaca aggregata Kantvilas & S.Y. Kondr.	–	–
Caloplaca demissa (Körb.) Arup & Grube	–	X
Caloplaca epithallina Lynge	–	X
Caloplaca stillicidiorum (Vahl) Lynge	–	–
Caloplaca subpyraceella (Nyl.) Zahlbr.	–	X
Candelaria concolor (Dickson) Stein	–	–
Candelariella efflorescens R.C. Harris & W. R. Buck	–	X
Candelariella rosulans (Müll.Arg.) Zahlbr.	–	X

Table 4 (continued). Updated checklist of all lichen species known from Lava Beds National Monument. This species list includes records from Sheehy (2017) and additional records provided by Tom Carlberg, Katherine Glew and Eric Peterson. Species recorded during this study are indicated in the right-hand column with an x. Species found in our study that occurred only in ice caves are in the middle column are indicated with an x. Taxa from our study that could not be identified to species level are not included here.

Lichen Species	Ice Cave Only	Recorded in this study
Candelariella vitellina (Hoffm.) Müll.Arg.	–	X
Carbonea vitellinaria (Nyl.) Hertel	–	X
Catapyrenium rufescens (Ach.) Breuss	–	–
Chaenotheca cinerea (Pers.) Tibell	X	X
Chaenotheca furfuracea (L.) Tibell	X	X
Chrysothrix chlorina (Ach.) J. R. Laundon	–	X
Circinaria cf. arida Owe-Larsson, A. Nordin & Tibell	–	X
Circinaria caesiocinerea (Nyl. ex Malbr.) A. Nordin, Savić & Tibell	–	X
Circinaria contorta (Hoffm.) A. Nordin, Savić & Tibell	–	–
Cladonia cariosa (Ach.) Sprengel	–	–
Cladonia chlorophaea (Flörke ex Sommerf.) Sprengel	–	X
Cladonia coniocraea (Flörke) Sprengel	–	X
Cladonia fimbriata (L.) Fr.	–	X
Cladonia pocillum (Ach.) O.J. Rich.	–	X
Cladonia pyxidata (L.) Hoffm.	–	X
Cladonia squamosa Hoffm.	–	X
Cladonia subulata (L.) Weber ex F. H. Wigg.	–	–
Cladonia verruculosa (Vain.) Ahti	–	X
Clavascidium lacinulatum (Ach.) M. Prieto	–	–
Dermatocarpon bachmannii Anders	–	–
Dermatocarpon leptophyllodes (Nyl.) Vainio ex Hav.	–	X
Dermatocarpon miniatum (L.) W. Mann	–	X
Dermatocarpon reticulatum H. Magn.	–	X
Dimelaena thysanota (Tuck.) Hale & Culb.	–	X
Diploschistes muscorum (Scop.) R. Sant.	–	X
Diploschistes scruposus (Schreber) Norman	–	X

Table 4 (continued). Updated checklist of all lichen species known from Lava Beds National Monument. This species list includes records from Sheehy (2017) and additional records provided by Tom Carlberg, Katherine Glew and Eric Peterson. Species recorded during this study are indicated in the right-hand column with an x. Species found in our study that occurred only in ice caves are in the middle column are indicated with an x. Taxa from our study that could not be identified to species level are not included here.

Lichen Species	Ice Cave Only	Recorded in this study
Diplotomma alboatrum (Hoffm.) Flotow	–	X
Enchylium tenax (Sw.) Gray	–	X
Endocarpon pulvinatum Th. Fr.	–	–
Evernia prunastri L. Ach.	–	X
Flavoplaca citrina (Hoffm.) Arup, Frödén & Søchting	–	X
Fuscidea recensa var. arcuatula (Arnold) Fryday	–	–
Hertelidea botryosa (Fr.) Kantvilas & Printzen	–	–
Heteroplacidium congestum (Breuss & McCune) Breuss	–	–
Hypocenomyce scalaris (Ach. ex Lilj.) M. Choisy	–	X
Hypogymnia apinnata Goward & McCune	–	–
Hypogymnia imshaugii Krog	X	X
Hypogymnia tubulosa (Schaer.) Hav.	X	X
Kaernefeltia merrillii (Du Rietz) Thell & Goward	–	–
Lecanora albellula Nyl.	–	X
Lecanora allophana f. sorediata Nyl.	–	–
Lecanora argopholis (Ach.) Ach.	–	–
Lecanora bicincta Ramond	–	X
Lecanora cenisia Ach.	–	X
Lecanora laxa (Śliva & Wetm.) Printzen	–	–
Lecanora mellea W.A. Weber	–	X
Lecanora mughicola Nyl.	–	–
Lecanora polytropa (Hoffm.) Rabenh.	–	–
Lecanora pseudomellea B.D. Ryan	–	X
Lecanora reagens Norman	–	–
Lecanora rupicola (L.) Zahlbr.	–	X
Lecanora semitensis Tuck.	–	X

Table 4 (continued). Updated checklist of all lichen species known from Lava Beds National Monument. This species list includes records from Sheehy (2017) and additional records provided by Tom Carlberg, Katherine Glew and Eric Peterson. Species recorded during this study are indicated in the right-hand column with an x. Species found in our study that occurred only in ice caves are in the middle column are indicated with an x. Taxa from our study that could not be identified to species level are not included here.

Lichen Species	Ice Cave Only	Recorded in this study
Lecanora swartzii (Ach.) Ach.	–	X
Lecidea atrobrunnea (Raymond ex Lam. & DC.) Schaer.	–	X
Lecidea brodoana Hertel & Leuckert	–	–
Lecidea cascadensis H. Magn.	–	X
Lecidea confluens (Weber) Ach.	–	–
Lecidea deplanaica (Hertel & Leuckert) McCune	–	–
Lecidea fuscoatra (L.) Ach.	–	X
Lecidea laboriosa Müll.Arg.	–	X
Lecidea lactea Flörke ex Schaer.	–	X
Lecidea lapicida (Ach.) Ach.	–	X
Lecidea mannii Tuck.	–	–
Lecidea protabacina Nyl.	–	X
Lecidea tessellata Flörke	–	X
Lecidea turgidula Fr.	–	X
Lecidella carpathica Körb.	–	X
Lecidoma demissum (Rustr.) Gotth. Schneider & Hertel	–	–
Lepra ophthalmiza (Nyl.) Hafellner	–	–
Lepraria diffusa (J.R. Laundon) Kukwa	–	–
Lepraria eburnea J. R. Laundon	–	X
Lepraria jackii Tønsberg	–	X
Lepraria neglecta (Nyl.) Erichsen	–	X
Lepraria subalbicans (I. M. Lamb) Lendemer & Hodk.	–	X
Lepraria vouauxii (Hue) R.C. Harris	–	–
Leprocaulon adhaerens (K. Knudsen, Elix & Lendemer) Lendemer & Hodk.	–	X
Leprocaulon knudsenii Lendemer & Hodk.	–	X
Leptochidium albociliatum (Desmaz.) Choisy	–	X

Table 4 (continued). Updated checklist of all lichen species known from Lava Beds National Monument. This species list includes records from Sheehy (2017) and additional records provided by Tom Carlberg, Katherine Glew and Eric Peterson. Species recorded during this study are indicated in the right-hand column with an x. Species found in our study that occurred only in ice caves are in the middle column are indicated with an x. Taxa from our study that could not be identified to species level are not included here.

Lichen Species	Ice Cave Only	Recorded in this study
Leptogium nanum Herre	–	–
Letharia columbiana (Nutt.) J.W. Thomson	–	X
Letharia vulpina (L.) Hue	–	X
Lobothallia alphoplaca (Wahlenb.) Hafellner	–	–
Massalongia carnosa (Dickson) Körb.	–	–
Megaspora verrucosa (Ach.) Hafellner & V. Wirth	–	X
Melanelixia fuliginosa (Fr. ex Duby) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	–	X
Melanelixia subaurifera (Nyl.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	–	–
Melanohalea elegantula (Zahlbr.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	–	X
Melanohalea exasperatula (De Not.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	–	X
Melanohalea multispora (A. Schneider) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	–	X
Melanohalea subolivacea (Nyl.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	–	–
Miriquidica garovaglii (Schaer.) Hertel & Rambold	–	X
Miriquidica griseoatra (Flotow) Hertel & Rambold	–	X
Montanelia disjuncta (Erichsen) Divakar, A. Crespo, Wedin & Essl.	–	–
Montanelia panniformis (Nyl.) Divakar, A. Crespo, Wedin & Essl.	–	X
Montanelia sorediata (Ach.) Divakar, A. Crespo, Wedin & Essl.	–	–
Montanelia tominii (Oxner) Divakar, A. Crespo, Wedin & Essl.	x	X
Myriolecis dispersa (Pers.) Śliva, Zhao Xin & Lumbsch	–	X
Myriolecis persimilis (Th. Fr.) Śliwa, Zhao Xin & Lumbsch	–	–
Nodobryoria abbreviata (Müll. Arg.) Common & Brodo	–	X
Nodobryoria oregana (Tuck.) Common & Brodo	–	–
Ochrolechia turneri (Sm.) Hasselrot	–	–

Table 4 (continued). Updated checklist of all lichen species known from Lava Beds National Monument. This species list includes records from Sheehy (2017) and additional records provided by Tom Carlberg, Katherine Glew and Eric Peterson. Species recorded during this study are indicated in the right-hand column with an x. Species found in our study that occurred only in ice caves are in the middle column are indicated with an x. Taxa from our study that could not be identified to species level are not included here.

Lichen Species	Ice Cave Only	Recorded in this study
Ochrolechia upsaliensis (L.) A. Massal.	X	X
Ophioparma rubricosa (Müll.Arg.) S. Ekma	–	–
Ophioparma ventosa (L.) Norman	X	X
Pachypeltis invadens (Lynge) Søchting, Frödén & Arup	X	X
Parmelia barrenoae Divakar, M. C. Molina & A. Crespo	–	X
Parmelia hygrophila Goward & Ahti	X	X
Parmelia saxatilis (L.) Ach.	–	X
Parmelia sulcata Taylor	–	X
Parmeliopsis ambigua (Hoffm.) Nyl.	–	X
Parmeliopsis hyperopta (Ach.) Arnold	X	X
Parvoplaca tiroliensis (Zahlbr.) Arup, Søchting & Frödén	–	X
Peltigera canina (L.) Willd.	–	X
Peltigera collina (Ach.) Schrader	X	X
Peltigera didactyla (With.) J. R. Laundon	–	X
Peltigera ponojensis Gyelnik	–	X
Peltigera rufescens (Weiss) Humb.	–	X
Peltula bolanderi (Tuck.) Wetmore	–	–
Pertusaria flavicunda Tuck.	–	X
Phaeophyscia adiastola (Essl.) Essl.	–	–
Phaeophyscia decolor (Kashiw.) Essl.	–	X
Phaeophyscia hirsuta (Mereschk.) Essl.	–	–
Phaeophyscia orbicularis (Necker) Moberg	X	X
Phaeophyscia sciastra (Ach.) Moberg	–	X
Physcia adscendens (Fr.) H. Olivier	–	X
Physcia biziana (A. Massal.) Zahlbr.	–	X
Physcia caesia (Hoffm.) Furnr.	–	X

Table 4 (continued). Updated checklist of all lichen species known from Lava Beds National Monument. This species list includes records from Sheehy (2017) and additional records provided by Tom Carlberg, Katherine Glew and Eric Peterson. Species recorded during this study are indicated in the right-hand column with an x. Species found in our study that occurred only in ice caves are in the middle column are indicated with an x. Taxa from our study that could not be identified to species level are not included here.

Lichen Species	Ice Cave Only	Recorded in this study
Physcia dimidiata (Arnold) Nyl.	–	X
Physcia dubia (Hoffm.) Lettau	–	X
Physcia occidentalis Essl. & McCune	–	X
Physcia subtilis Degel.	–	–
Physcia tenella (Scop.) DC.	–	X
Physcia tribacia (Ach.) Nyl.	–	–
Physconia americana Essl.	–	X
Physconia enteroxantha (Nyl.) Poelt	–	X
Physconia isidiigera (Zahlbr.) Essl.	–	X
Physconia muscigena (Ach.) Poelt	–	X
Physconia perisidiosa (Erichsen) Moberg	–	X
Pilophorus acicularis (Ach.) Th. Fr.	–	–
Placidium lachneum (Ach.) B. de Lesd.	–	–
Placidium squamulosum (Ach.) Breuss	–	X
Placynthiella icmalea (Ach.) Coppins & P. James	–	X
Placynthiella oligotropha (J. R. Laundon) Coppins & P. James	–	X
Placynthiella uliginosa (Schrader) Coppins & P. James	–	X
Platismatia glauca (L.) Culb. & C. Culb.	–	X
Pleopsidium flavum (Bellardi) Körb.	–	X
Polycauliona bolacina (Tuck.) Arup, Frödén & Søchting	–	–
Polycauliona luteominia (Tuck.) Arup, Frödén & Søchting	–	X
Polychidium muscicola (Sw.) Gray	–	X
Protoparmelia badia (Hoffm.) Hafellner	–	X
Protoparmelia ochrococca P.M. Jørg., Rambold & Hertel	–	–
Protoparmeliopsis garovaglii (Körb.) Arup, Zhao Xin & Lumbsch	–	X
Protoparmeliopsis muralis (Schreb.) M. Choisy	–	X

Table 4 (continued). Updated checklist of all lichen species known from Lava Beds National Monument. This species list includes records from Sheehy (2017) and additional records provided by Tom Carlberg, Katherine Glew and Eric Peterson. Species recorded during this study are indicated in the right-hand column with an x. Species found in our study that occurred only in ice caves are in the middle column are indicated with an x. Taxa from our study that could not be identified to species level are not included here.

Lichen Species	Ice Cave Only	Recorded in this study
Pseudephebe pubescens (L.) Choisy	–	X
Pseudothelomma occidentale (Herre) M. Prieto and Wedin	–	X
Pseudothelomma ocellatum (Körb.) M. Prieto and Wedin	–	X
Psora cerebriformis W.A. Weber	–	X
Psora decipiens (Hedwig) Hoffm.	–	–
Psora globifera (Ach.) A. Massal.	–	X
Psora himalayana (Church. Bab.) Timdal	–	X
Psora luridella (Tuck.) Fink	–	X
Psora montana Timdal	–	–
Psora nipponica (Zahlbr.) Gotth. Schneider	–	X
Psora tuckermanii R. Anderson ex Timdal	–	–
Psoroma hypnorum (Vahl) Gray	X	X
Pycnora praestabilis (Nyl.) Hafellner	–	–
Pyrenodesmia albovariegata B. de Lesd.	–	–
Rhizocarpon disporum (Naeg. ex Hepp) Müll.Arg.	–	X
Rhizocarpon dimelaneae Timdal	–	X
Rhizocarpon eupetraeum (Nyl.) Arnold	–	X
Rhizocarpon geographicum (L.) DC.	–	X
Rhizocarpon grande (Flörke ex Flotow) Arnold	–	X
Rhizocarpon lecanorinum Anders	–	X
Rhizocarpon macrosporum Räsänen	–	X
Rhizoplaca chrysoleuca (Sm.) Zopf	–	X
Rhizoplaca melanophthalma (DC.) Leuckert & Poelt	–	X
Rhizoplaca phaedrophthalma (Poelt) Leavitt, Zhao Xin & Lumbsch	–	X
Rinodina bolanderi H. Magn.	–	X
Rinodina confragosa (Ach.) Körb.	–	X

Table 4 (continued). Updated checklist of all lichen species known from Lava Beds National Monument. This species list includes records from Sheehy (2017) and additional records provided by Tom Carlberg, Katherine Glew and Eric Peterson. Species recorded during this study are indicated in the right-hand column with an x. Species found in our study that occurred only in ice caves are in the middle column are indicated with an x. Taxa from our study that could not be identified to species level are not included here.

Lichen Species	Ice Cave Only	Recorded in this study
Rinodina juniperina Sheard	–	X
Rinodina luridata (Körb.) H. Mayrh., Schneid. & Sheard	–	–
Rinodina olivaceobrunnea C.W. Dodge & Baker	–	X
Rinodina pyrina (Ach.) Arnol	–	–
Rinodina terrestris Tomin	–	–
Rinodina turfacea (Wahlenb.) Körb.	–	–
Rufoplaca arenaria (Pers.) Arup, Søchting & Frödén	–	–
Rusavskia elegans (Link) S.Y. Kondr. & Kärnefelt	–	X
Rusavskia sorediata (Vain.) S.Y. Kondr. & Kärnefelt	–	X
Sagedia mastrucata (Wahlenb.) A. Nordin, Savić & Tibell	–	X
Schaereria fuscocinerea (Nyl.) Clauzade & Cl. Roux	–	–
Scytinium intermedium (Arnold) Otálora, P.M. Jørg. & Wedin	–	X
Scytinium lichenoides (L.) Otálora, P.M. Jørg. & Wedin	–	X
Scytinium palmatum (Hudson) Gray	–	–
Scytinium subaridum (P.M. Jørg. & Goward) Otálora, P.M. Jørg. & Wedin	X	–
Staurothele areolata (Ach.) Lettau	–	X
Staurothele drummondii (Tuck.) Tuck.	–	X
Stenocybe procrastinata E. B. Peterson	–	X
Tephromela atra (Hudson) Hafellner	X	X
Tetramelas chloroleucus (Körb.) A. Nordin	X	X
Tetramelas papillatus (Sommerf.) Kalb	–	X
Teuvoa junipericola Sohrabi & S. Leavitt	–	–
Thalloidima sedifolium (Scop.) Kistenich, Timdal, Bendiksby & S. Ekman	–	X
Toninia squalida (Ach.) A. Massal.	–	–
Toninia tristis (Th. Fr.) Th. Fr.	–	–

Table 4 (continued). Updated checklist of all lichen species known from Lava Beds National Monument. This species list includes records from Sheehy (2017) and additional records provided by Tom Carlberg, Katherine Glew and Eric Peterson. Species recorded during this study are indicated in the right-hand column with an x. Species found in our study that occurred only in ice caves are in the middle column are indicated with an x. Taxa from our study that could not be identified to species level are not included here.

Lichen Species	Ice Cave Only	Recorded in this study
Trapeliopsis flexuosa (Fr.) Coppins & P. James	X	X
Trapeliopsis glaucopholis (Nyl. Ex Hasse) Printzen & McCune	–	X
Trapeliopsis granulosa (Hoffm.) Lumbsch	–	X
Trapeliopsis steppica McCune & Camacho	–	–
Tremolecia atrata (Ach.) Hertel	–	X
Tuckermanopsis chlorophylla (Willd.) Hale	–	X
Umbilicaria americana Poelt & T.H. Nash	–	X
Umbilicaria angulata Tuck.	–	–
Umbilicaria hyperborea (Ach.) Hoffm.	–	X
Umbilicaria nodulospora McCune, Di Meglio & M. J. Curtis	–	–
Umbilicaria phaea var. phaea Tuck.	–	X
Umbilicaria phaea var. coccinea Llano	–	X
Umbilicaria polaris (Schol.) Zahlbr.	–	X
Umbilicaria polyphylla (L.) Baumg.	–	X
Umbilicaria proboscidea (L.) Schrader	–	–
Umbilicaria torrefacta (Lightf.) Schrader	–	X
Umbilicaria vellea (L.) Ach.	–	–
Umbilicaria virginis Schaer.	X	X
Vahliella leucophaea (Vahl) P.M. Jørg.	–	–
Xanthocarpia erichansenii (S. Y. Kondr., A. Thell, Kärnefelt & Elix) Frödén, Arup & Søchting	–	–
Xanthocarpia tominii (Savicz) Frödén, Arup & Søchting	–	–
Xanthomendoza fulva (Hoffm.) Søchting, Kärnefelt & S.Y. Kondr.	–	X
Xanthomendoza mendozae (Räsänen) S.Y. Kondr. & Kärnefelt	–	X
Xanthomendoza montana (L. Lindblom) Søchting, Kärnefelt & S.Y. Kondr.	–	X
Xanthoparmelia angustiphylla (Gyelnik) Hale	–	–

Table 4 (continued). Updated checklist of all lichen species known from Lava Beds National Monument. This species list includes records from Sheehy (2017) and additional records provided by Tom Carlberg, Katherine Glew and Eric Peterson. Species recorded during this study are indicated in the right-hand column with an x. Species found in our study that occurred only in ice caves are in the middle column are indicated with an x. Taxa from our study that could not be identified to species level are not included here.

Lichen Species	Ice Cave Only	Recorded in this study
Xanthoparmelia coloradoensis (Gyelnik) Hale	–	X
Xanthoparmelia conspersa (Ehrh. ex Ach.) Hale	–	–
Xanthoparmelia cumberlandia (Gyelnik) Hale	–	X
Xanthoparmelia loxodes (Nyl.) O. Blanco, A. Crespo, Elix, D. Hawksw. & Lumbsch	–	X
Xanthoparmelia plittii (Gyelnik) Hale	–	X
Xanthoparmelia subhosseana (Essl.) O. Blanco, A. Crespo, Elix, D. Hawksw. & Lumbsch	–	–
Xanthoparmelia tasmanica (Hook. f. & Taylor) Hale	–	–
Xanthoparmelia verruculifera (Nyl.) O. Blanco, A. Crespo, Elix, D. Hawksw. & Lumbsch	–	–
Xylographa parallela (Ach.:Fr.) Fr.	X	X

Appendix D. Model results from a linear model for drivers of lichen species richness across the 42 study plots we sampled

Table 5. Model results from a linear model for drivers of lichen species richness across the 42 study plots sampled. Significant predictors are bolded and indicated by asterisk.

Term	Estimate	Standard error	P-value
(Intercept)	32.546	8.603	< 0.001
Burned area (% of plot) *	−0.153	0.076	0.052
Sink area (% of plot) *	12.822	3.096	< 0.001
Sink area^2 *	−1.028	0.362	0.007
Cave entrance m above grade *	−2.297	0.901	0.015
Visitor use impact index	−0.465	1.617	0.775

The Department of the Interior protects and manages the nation’s natural resources and cultural heritage; provides scientific and other information about those resources; and honors its special responsibilities to American Indians, Alaska Natives, and affiliated Island Communities.

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National Park Service
U.S. Department of the Interior

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