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PRACTICE AND TECHNICAL ARTICLE

Biological soil crusts are more prevalent in warmer and drier environments within the Great Basin ecoregion: implications for managing annual grass invasion

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Biological soil crusts (biocrusts) can thrive under environmental conditions that are stressful for vascular plants such as high temperatures and/or extremely low moisture availability. In these settings, and in the absence of disturbance, cover of biocrusts commonly exceeds cover of vascular plants. Arid landscapes are also typically slow to recover from disturbance and prone to altered vegetation and invasion by exotic species. In the sagebrush ecosystems, cover of annual, exotic, invasive grasses are lower where cover of biocrusts and vascular plants are greater, suggesting that biocrusts play a role in helping arid sites avoid conversion to dominance by invasive grasses. The conceptual framework for assessing ecological resistance and resilience (R&R) is used across the region to estimate the risk of invasion by annual grasses and the likelihood of recovery of native plants following disturbance. However, this framework does not currently account for biocrusts. We used data collected by the Bureau of Land Management Assessment, Inventory, and Monitoring program to relate biocrusts, specifically the presence of lichens and mosses, to the R&R framework. Lichens frequently occur on warm, dry sites, classified as lower R&R. Mosses frequently occur on sites classified as moderate or moderately low R&R. Without management practices that favor biocrusts in low-moderate R&R, these areas may be more vulnerable to transitioning from being dominated by shrubs to annual grasses. Under climate change scenarios, the area occupied by lower R&R sites is likely to increase, suggesting that the role of biocrusts in maintaining site resistance to invasion may also increase.

Key words: biocrusts, BLM AIM data, climate change, landscape monitoring framework, lichens, mosses, sagebrush ecosystems

Implications for Practice

- Overabundance of lichens and mosses in low and moderately low resistance and resilience (R&R) conditions, respectively, underscores that these generally hot and dry areas may have conservation value that is not fully represented by the vascular plant community.
- Because biocrusts, especially lichens, have been shown to suppress annual grass invasion, the abundance of lichens in lower R&R areas suggests that lichen protection in those areas may reduce invasion.
- Intact, low, or moderately low R&R sites could potentially be used as reference sites, increasing our understanding of the composition and ecology of plant communities, that include biocrusts, in the absence of anthropogenic disturbance.
- If climate change increases the distribution of lower R&R conditions, our results imply that the area favorable for biocrusts may increase.

Introduction

Biocrusts are organisms that live on the soil surface and include lichens, mosses, and algal crusts (including cyanobacteria). Biocrusts are increasingly recognized as "ecosystem engineers," given their ability to modify environmental conditions which influence vegetation. Biocrusts are associated with increased soil stability (Pérez 2021; Copeland et al. 2023), including areas that inherently have low stability such as sand dunes (Hagemann et al. 2017). Areas with high cover of biocrusts frequently have low cover of vascular plants, making the contributions of biocrusts to ecosystem functions notable in these systems (Belnap et al. 2003). The importance of this association can be envisioned

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when examining patches of bare soil and patches of vegetation. Innately bare soil often has an abundance of cyanobacteria which occupy the space that appears to be bare (sensu Condon & Pyke 2018*b*). Run-off from these "bare" areas leads to increased water availability for patches of vegetation in arid settings (Aquilar & Sala 1999), highlighting the critical importance of biocrusts as cover as well as their interactions with the plant community. Biocrusts are also associated with increased carbon fixation and reduced erosion and these associations are still present, although weaker, in the presence of disturbance (Rodríquez-Caballero et al. 2018).

In the sagebrush steppe, the frequency and extent of wildfire is increasing due to invasion by annual exotic grasses, such as cheatgrass (*Bromus tectorum* L.) (Balch et al. 2013). Threats of exotic annual grasses and subsequent changes to the wildfire regime, are placing iconic wildlife species such as the greater sage-grouse (*Centrocercus urophasianus*) at risk (Coates et al. 2016; O'Neil et al. 2020). Where wildfire is the sole disturbance, which is an extremely rare condition in the Great Basin, biocrusts, especially the lichen component, remain intact following fire (Condon et al. 2023). The persistence of biocrusts after wildfire is important to consider if maintaining low cover of cheatgrass is a management goal, because where cover of biocrusts is greater, cover of annual invasive grasses is lower (Daubenmire 1970; West 1990; Ponzetti et al. 2007; Condon & Pyke 2018*a*, 2018*b*).

Arid sites experience fewer years with favorable conditions for recovery following a disturbance, resulting in a slower rate of recovery compared with more productive sites (Bainbridge 2007). Within the Great Basin, U.S.A., this dynamic is captured by the conceptual framework for assessing geographic patterns in ecological resilience to disturbance (recovery potential) and resistance to invasive annual grasses (R&R), which is commonly used to guide land management actions (Chambers et al. 2014, 2023). The R&R framework originally used soil temperature and moisture regimes to evaluate R&R combined across the region. Sites with lower R&R are more prone to invasion by exotic annual grasses and are slower to recover from disturbance as opposed to sites with higher R&R (Table 1; Chambers et al. 2014). The R&R framework has recently been refined, with a new product that uses predictive soil water availability and climatic variables derived largely from ecohydrological models as predictive variables and categorizes resilience and resistance separately (Chambers et al. 2023). These two R&R categories were best predicted by combinations of mean temperature, coldest month temperature, climatic water deficit, and summer and driest month precipitation. Although biocrusts abundance is known to be higher in arid sites and sites with higher temperatures (Garcia-Pichel et al. 2013; Ding & Eldridge 2020) including across the western United States (Condon & Pyke 2020), the relationship of biocrusts to estimated R&R categories remains unclear. For instance, in Australia, the response of biocrusts to disturbances can interact with soil type (Vega-Cofre et al. 2023). Characterizing the relationship between biocrusts and R&R can help inform management priorities and strategies. If biocrusts are more common on low R&R sites, managing for biocrusts in these areas is particularly important to minimize annual grass invasion and to maintain ecosystem functions such as hydrologic cycling, nutrient cycling, and the prevention of soil erosion. Here, we used the extensive monitoring dataset maintained by the Bureau of Land Management (BLM) to assess biocrust abundance (presence/absence) across categories of both R&R products. We hypothesized that lichen and moss would occur more frequently on warmer, drier sites categorized as having lower R&R, compared with more productive sites. We also had a unique opportunity to see if similar patterns in the presence of lichen and moss were detected with the first R&R product based on soil temperature and moisture regimes in comparison with the second R&R products that utilized models of soil water availability and climate.

Table 1. Resistance and resilience categories by soil temperature and moisture (Chambers et al. 2014).

R&R Class	*Soil Temperature*	*Soil Moisture*	*Combination*
Low	Mesic	Aridic	Mesic-aridic
Moderate	Mesic	Aridic	Mesic-xeric
	Frigid	Xeric	Frigid-aridic
	Cryic		Frigid-xeric
			Cryic-xeric
High	Frigid	Xeric	Frigid-xeric
	Cryic		Cryic-xeric

Methods

We assessed the presence and absence of lichens and mosses by R&R categories from both the 2014 (Chambers et al. 2014) and 2023 products (Chambers et al. 2023) by intersecting R&R maps with data from the Landscape Monitoring Framework of the Assessment, Inventory, and Monitoring (LMF-AIM; https://www.blm.gov/aim) Program of the BLM (Fig. 1). LMF-AIM is the program created by the BLM to provide monitoring of resource conditions to support management decisions (Toevs et al. 2011). The R&R 2014 product defines three categories with resistance and resilience (R&R) combined (low, moderate, and high), based on soil moisture and temperature regimes or more explicitly the number of days per year that the soil is dry or moist and above a given temperature. The R&R 2023 product defines resistance and resilience separately and categorizes both resistance and resilience into four categories (low, moderately low, moderate, and moderately high), based on long-term climate norms (1980–2019). The 2014 product does not test separate seasons, but the 2023 product does. We used locations where LMF-AIM data had been collected within the extent of the Great Basin region as defined by EPA Level 3 Ecoregions, specifically the Northern Basin and Range, the Central Basin and Range, and the Snake River Plain. We used data collected between 2011 and 2021, reflecting all available data at the time of our analysis. We only used locations that were classified in both the 2014 and 2023 products. Observed occurrences were compared with what would be expected by chance in a contingency table. A chi-square goodness of fit test was used to determine if the differences between observed occurrences by category were statistically significant (Ramsey & Schafer 2002).

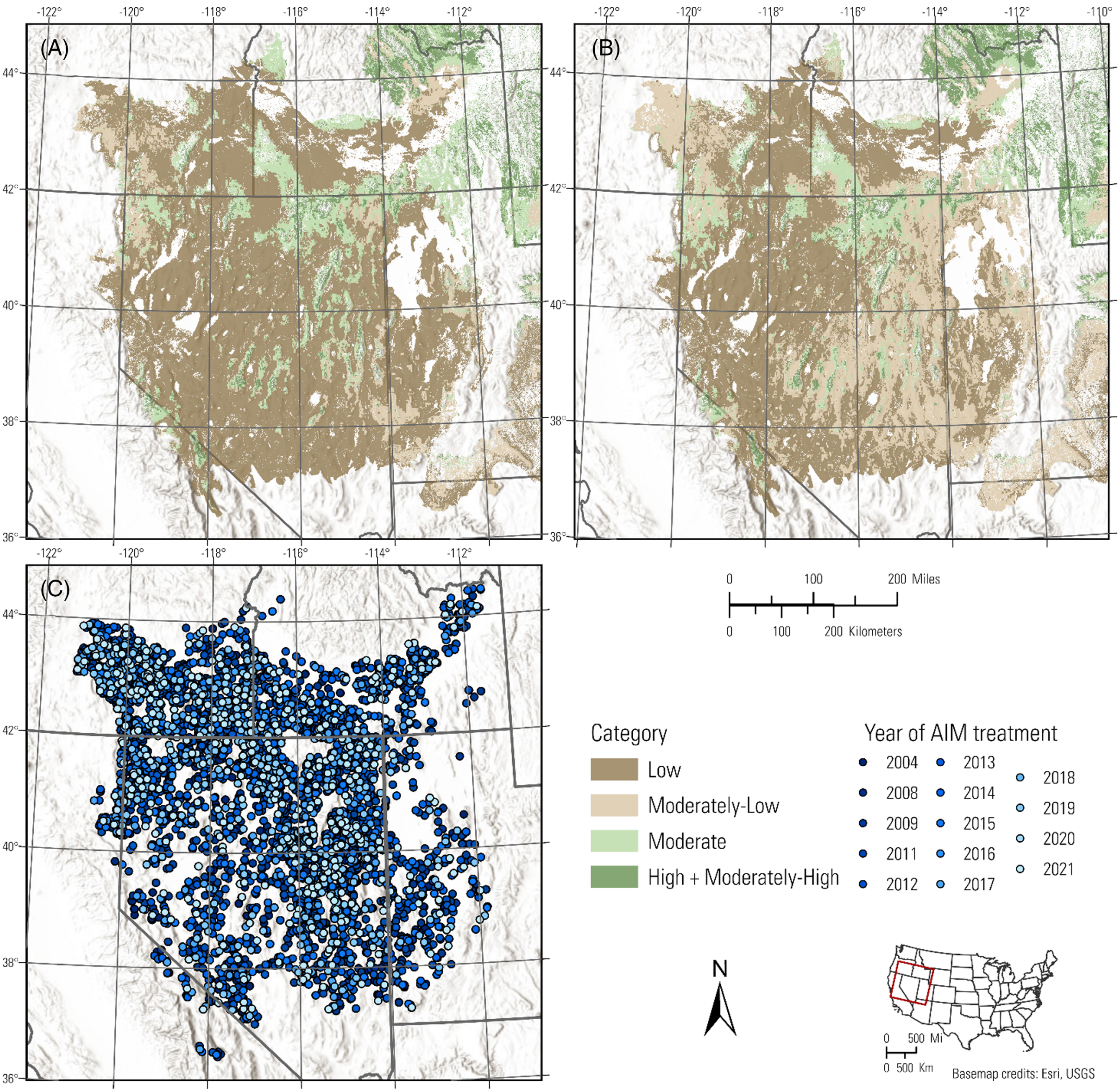

Figure 1. Map showing the distribution of the (A) Resistance 2023 layer, (B) Resilience 2023 layer, and (C) AIM (Assessment, Inventory and Monitoring Program of the Bureau of Land Management) plots across the Great Basin and used in our analysis. Plots are color coded by the year of survey. Resistance and Resilience (2023) categories were produced by Chambers et al. (2023).

Tukey comparisons were used to identify differences in the means of lichen and moss presence by R&R 2014, Resilience 2023, and Resistance 2023 categories (Tukey 1991).

Results

Across the Great Basin, the presence of lichens differed by R&R 2014 and both Resistance 2023 and Resilience 2023 products by category (R&R 2014 $\chi^2_{2,7753} = 174.18$, $p = <0.001$; Resistance 2023 $\chi^2_{3,7752} = 126.92$, $p = <0.001$; Resilience 2023 $\chi^2_{3,7752} = 130.71, p = <0.001$) (Table S1; Fig. 2). Lichens more frequently occurred in the low R&R 2014 category, the low Resilience 2023 category, and the low and moderately low Resistance 2023 categories (Fig. 2). The observed presence of lichen compared with what was expected by chance differed in the low category of the R&R 2014 product (Table S2), the low category of the Resistance 2023 product (Table S3), and the low and moderately low categories of the Resilience 2023 product (Table S4). The presence of mosses also differed by R&R 2014 and both Resistance 2023 and Resilience 2023 categories (R&R 2014 $\chi^2_{2,7753} = 99.32$, $p = <0.001$;

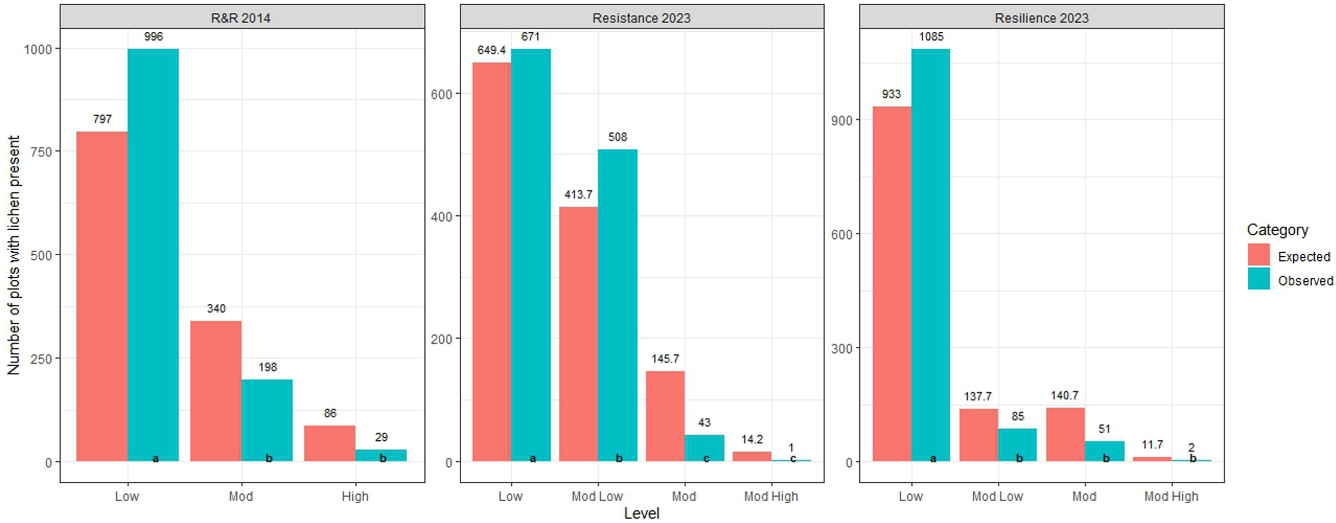

Figure 2. Number of plots with lichen observed as present versus number of plots with lichen expected to be present given chance by resistance and resilience categories defined by Chambers et al. 2014, 2023. "Mod" is an abbreviation for moderate. Letters hovering at the zero line are the results of Tukey comparisons among the means of observed presence by R&R category.

Resistance 2023 $\chi^2_{3,7752} = 68.789$, $p = <0.001$; Resilience 2023 $\chi^2_{3,7752} = 129.08$, $p = <0.001$) (Table S5; Fig. 2). Mosses more frequently occurred in the moderate R&R category in the R&R 2014 product and the moderately low Resistance 2023 and Resilience 2023 categories (Fig. 3). The observed presence of moss compared with what was expected by chance differed in the low and moderate categories of the R&R 2014 product (Table S2) and the low and moderately low categories of the Resilience 2023 product (Table S4). The observed presence of moss did not differ from what was expected by chance by category in the Resistance 2023 product (Table S3).

Discussion

Restoration of native plant communities is notoriously difficult in dryland ecosystems (Kildisheva et al. 2016), and those challenges contribute to the widespread degradation of drylands around the world (Reynolds et al. 2007). To our knowledge, our findings represent the first evidence of clear positive associations between biocrusts and the soil characteristics selected to predict plant recovery following disturbance in sagebrush ecosystems. Our findings also suggest that incorporating biotic components into a more holistic approach in land management is especially important in the Great Basin where restoration is challenging because of the prevalence of relatively warm and

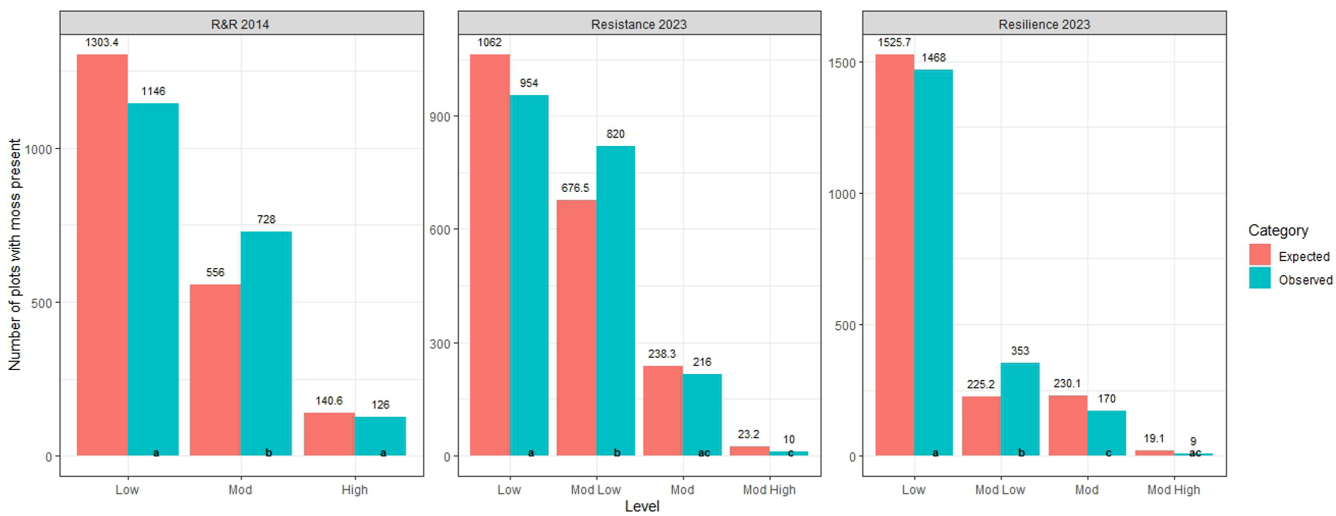

Figure 3. Number of plots with moss observed as present versus number of plots with moss expected to be present given chance by resistance and resilience categories defined by Chambers et al. 2014, 2023. "Mod" is an abbreviation for moderate. Letters hovering at the zero line are the results of Tukey comparisons among the means of observed presence by R&R category.

dry soils. Restoration practices that promote moss and lichen cover within low R&R areas (sites with relatively less soil moisture and higher temperatures) would likely support recovery of native vegetation because these areas generally exhibit slower recovery and greater chance of invasion by invasive grasses compared with higher R&R environments.

The R&R 2014 product has been commonly utilized as a tool for assessing potential recovery of native vegetation following disturbance, often with wildlife species in mind (Crist et al. 2019). Sites classified as having low R&R, especially in Wyoming big sagebrush dominated plant communities with depleted understories, have been predicted to transition to annual invasive grasses following fire (Miller et al. 2011; Coates et al. 2016; O'Neil et al. 2020). Ricca et al. (2018) employed this framework in the development of a conservation planning tool focused on the greater sage-grouse, where efforts to restore sagebrush were modeled as having lower success on low R&R sites and low R&R sites were predicted to be converted to annual invasive grasses following fire. Ricca et al. (2018) discuss the refinement of management options with finer scale (interpreted as being on the ground) knowledge of a site. Our results highlight the importance of this caveat. If biocrusts are present on a site prior to disturbance, the site is less likely to transition to high cover of annual grasses following disturbance (Condon & Pyke 2018a).

The R&R 2023 classifications are largely predicted by mean temperature, climatic water deficit, summer precipitation, and coldest month temperature (Chambers et al. 2023). Because we saw few differences in the trends related to the number of plots with lichen and moss present between the two versions of the framework, soil temperature and moisture regimes appear to do as good of a job as modeled climatic variables in predicting the presence of lichen and moss by R&R category with two exceptions. Lichens frequently occurred on low and moderately low category sites in the Resistance 2023, suggesting that both mean temperature and precipitation in July, August, and September are important for lichens as the moderately low category was defined by these factors (Chambers et al. 2023). Because mosses most frequently occurred on sites that were classified as having moderate R&R 2014 or moderately low R&R 2023, temperature may play a vital role in controlling the distribution of these organisms, as both Resistance 2023 and Resilience 2023 were largely predicted by mean temperature, but Resistance 2023 was also predicted by temperature in the coldest month. This corroborates work highlighting the importance of overwintering and minimum temperatures in winter months in predicting the distribution of mosses in the region (Condon & Pyke 2016, 2020). Although the two products appear similar when examining biocrusts categorized by lichen and moss, differences were more pronounced when comparing R&R categories that favor lichens (mostly lower R&R) as opposed to mosses (moderate or moderately low R&R).

The ecoregions that are classified as having the greatest proportion of total area of low R&R are northern and central basin and range, the core of the Great Basin region. Over the extent of sagebrush ecosystems and sage-grouse management units, which encompasses the boundary of the Great Basin, it is anticipated that cool season soil moisture will increase, as will temperatures (Bradford et al. 2020). As mesic and thermic soil temperature regimes expand, cryic and frigid conditions will contract (Bradford et al. 2019), and overall R&R may decrease (Chambers et al. 2023). Compared with other components of the plant community, big sagebrush (*Artemisia tridentata* subsp.) may be relatively resilient to these changes, especially if precipitation increases can partially counteract elevated atmospheric demand from warmer temperatures and/or if the size of precipitation events become larger, allowing for increases in water content in the subsurface root zone of shrub species (Holdrege et al. 2023). However, the frequency and extent of fire may still lead to reductions in the cover of big sagebrush (Balch et al. 2013). Interspaces between shrubs can be occupied with forbs, grasses and biocrusts. Since the last glacial period, forbs and perennial grasses have been shown to decline with increasing aridity (Anderson & Inouye 2001; Nowak et al. 2017), although recent work has shown a fair amount of variability in climate niches of specific annual and perennial forbs (Barga et al. 2018). The threat of fire highlights the need to maintain interspaces between plants and provides reasons to account for biocrusts with the R&R framework, as the lichen component of biocrusts has been shown to survive fire when fire is the only disturbance (Condon et al. 2023). The role of biocrusts in hindering invasion by annual grass may increase in importance with anticipated changes in climate. A recent study conducted by Root et al. (2023), found overall loses to biocrusts on paired sites with and without fire, although they were not able to account for compounding disturbances. We anticipate the response of biocrusts to fire found by Condon et al. (2023) will be corroborated by future studies, in other regions, when researchers can account for compounding disturbances.

Immediately to the southeast of the Great Basin, in the Colorado Plateau, warming and altered precipitation experiments have resulted in stressors to biocrusts (Ferrenberg et al. 2015). Predicted increases in soil temperatures are likely to lead to expansions of the low R&R category, in addition to pushing parts of the Great Basin outside of the current R&R framework (Bradford et al. 2019). Warming may not be lethal to some lichens if relative humidity is maintained or if photosynthesis occurs in the morning hours (Baldauf et al. 2020). We anticipate that because additional changes in the Great Basin include increases in cool season moisture (Bradford et al. 2020), these changes may translate into expansions of the moderate R&R 2014 category, which is also where we most frequently observed mosses. Increases in the abundance of mosses has been observed following warming in experimental settings (de Guevara et al. 2018).

One potential caveat of our work is that the technicians that collected data associated with the LMF-AIM framework, that we used in this analysis, may have had different amounts of experience in recognizing lichens and mosses. This is largely why we decided to analyze the data as presence/absence as opposed to using abundance values. Over the last few years, we have begun participating in the trainings that the field technicians attend prior to collecting this data. We anticipate that this technology transfer (Bozeman 2000), will allow us to answer additional questions related to the ecology and management of biocrusts in the future. We hope to expand future studies on the relationships between lichen and mosses and the R&R framework to greater portions of the western United States. This expansion would allow us to focus on greater amounts of area that are classified as belonging to the higher R&R categories and determine if the same relationships hold true.

We anticipate that considering the role of biocrusts in ecosystem services might assist land managers and scientists in confronting climate vulnerability as biocrusts, in general, positively affect water balance (Chamizo et al. 2016). The success of plant restoration efforts in arid environments often comes down to the availability of water (Bainbridge 2007). Biocrusts are associated with increased moisture storage (Eldridge et al. 2020). In west-central Argentina, on sites where most of the precipitation falls in the spring and summer, increased cover of both cyanobacteria and lichens demonstrates positive relationships with soil moisture (Garibotti et al. 2018). Transitions to warmer temperature regimes are expected to result in decreases in resilience to disturbance (Chambers et al. 2014), again, highlighting the potential role of biocrusts given their affinity for not just arid, but also sites with high temperatures (Condon & Pyke 2020), as well as the importance of biocrusts in maintaining soil moisture.

Land management treatments, with fire risk and climate change in mind, can be tailored to favor biocrusts. For example, biocrusts do not appear to be susceptible to many herbicides that are used to combat annual grasses and reduce shrub cover, both of which are the focus of fuel reduction treatments and efforts to protect rare plants (Condon & Gray 2020; Bishop et al. 2023; Slate et al. 2023). Our findings suggest the use of management options that would preserve these critical and often overlooked organisms in warm, dry settings could reduce the threat of invasion by annual grasses where it is high.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Number of plots with and without lichens by resistance and resilience categories defined by Chambers et al. 2014, 2023.

Table S2. Welch's *t* tests comparing the observed versus expected presence of lichen and moss by R&R 2014 categories defined by Chambers et al. 2014.

Table S3. Welch's *t* tests comparing the observed versus expected presence of lichen and moss by resistance 2023 categories defined by Chambers et al. 2023.

Table S4. Welch's *t* tests comparing the observed versus expected presence of lichen and moss by Resilience 2023 categories defined by Chambers et al. 2023.

Table S5. Number of plots with and without mosses by resistance and resilience categories defined by Chambers et al. 2023.

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