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Mojave Desert biological soil crusts promote grass seed germination via surface structure

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ABSTRACT

Biological soil crusts (biocrusts) are common in arid landscapes, where they alter the surface structure and nutrient content of soils. Biocrusts can have both positive and negative effects on seed germination, but the mechanisms of these effects are less understood. In this study, we investigated whether biological soil crusts promote or inhibit grass seed germination in the eastern Mojave Desert. Additionally, we tested whether this effect is due to the surface structure or the chemical composition of the soil crust. We compared algal, moss, and lichen crust, and found that across all these biocrust types, surface structure is most beneficial to grass seed germination. Seeds preferentially germinated on intact pieces of soil crust rather than on crumbled crust. The different biocrust types did not differ in moisture retention. While moss crusts had lower pH and lower respiration rates than lichen crusts, these factors did not affect the rate of grass seed germination between the different types of crust.

Keywords: biological soil crust, biocrust, Mojave Desert, seed germination, soil water retention

INTRODUCTION

It is estimated that about 12% of Earth's terrestrial surface is covered by biological soil crust, and in arid and semiarid regions cover is even higher at 70% (Belnap et al. 2016, Rodriguez-Caballero et al. 2018). Biocrusts can be classified into different types based on the dominant species in the crust, including algal crusts, lichen crusts, and moss crusts. These types of biocrusts differ in their ecological functions (Pietrasiak 2014). In hot deserts, biocrusts can provide ecosystem services such as soil aggregation, carbon and nitrogen fixation, and water retention (Belnap et al. 2016, Chamizo et al. 2016). The extreme temperature changes and water scarcity of these ecosystems mean that biological soil crusts may be crucial in stabilizing soils and supporting vascular plants (Belnap 2003).

However, biological soil crusts do not always benefit plants. While some studies have found that biocrusts have positive effects on plant germination (Rivera-Aguilar et al. 2005, Godínez-Alvarez et al. 2011), others have found negative effects on germination through the prevention of root penetration or secretion of plant-inhibiting chemicals (Prasse and Bornkamm 2000, Deines et al. 2007, Escudero et al. 2007, Song et al. 2017). Different types of soil crust (Pietrasiak 2014) may also differ in their effects on plants. For instance, moss crust often facilitates and lichen crust often inhibits plant germination (Mendoza-Aguilar et al. 2014, Havrilla et al. 2019).

Nonetheless, it is unclear whether these effects of soil crust on plant germination are primarily due to the changes biocrusts make to surface structure or to soil chemistry. Soil crusts alter characteristics of the soil surface such as temperature and water retention. For example, moss and cyanobacterial soil crusts can decrease the albedo of the soil surface, raising its temperature (Couradeau et al. 2016, Xiao and Bowker 2020). Moss crusts and lichen crusts trap dust and fine particles more efficiently due to their complex morphology, resulting in a higher water-holding capacity and longer water retention (Pietrasiak 2014, Childs 1940, Hopmans 2011).

Biocrusts can also alter the chemistry of soils, which affects plant germination (Pietrasiak 2014, Escuerdo et al. 2007, Belnap et al. 2001). Measures of soil chemistry include electrical conductivity and pH, which can indicate soil quality and biological activity (Smith and Doran 1997). Soil pH determines the dominant plant species and microbially mediated processes, such as nitrogen and carbon cycling (Belnap et al. 2016, Chamizo et al. 2016). It also represents the buffering capacity of the biocrusts, which stabilizes the environment after disturbance. Mosses and lichens can produce weak acids that chemically weather rocks (Lian et al. 2008, Jackson 2015). Soil crusts have been found to increase pH of topsoil (García-Pichel and Belnap, 1996). Electrical conductivity is used as a proxy for the total cations or anions in the soil, which affects soil salinity and available nutrients. Soils in arid environments tend to be alkaline and have higher amounts of dissolved salts (Dregne 2011). Additionally, later successional stages of biocrusts can have higher rates of respiration (Zaady et al. 2000). However, it is less clear whether these differences in chemistry and biological activity between different types of biocrust affect seed germination.

Our study measured aspects of soil crust structure and chemistry in order to determine whether the primary influence of biological soil crusts on seed germination in the eastern Mojave Desert is physical or chemical. Structural variables included water retention and surface temperature, and chemical variables included pH, electroconductivity, and cellular respiration. We hypothesized that structure is the most important determinant of seed germination success in the eastern Mojave Desert due to water being the most limited resource (Pavlik 2008). Furthermore, we expect lichen and moss crusts to have higher surface temperatures due to their darker color, and higher water retention due to their more complex structure and morphology. We also expect moss and lichen crusts to have higher electrical conductivity and respiration rates due to more microbial activity. The soil pH should be lower for moss and lichen crusts due to their ability to chemically weather rocks. However, we predict that despite chemical differences, biocrust structure will be the most important determinant of seed germination due to its influence on moisture.

METHODS

2.1 Study Site

This study was conducted at the Sweeney Granite Desert Research Center, a 3,601-hectare reserve located within the Granite Mountains of the East Mojave Desert in San Bernardino County, California (34° 48’ 20” N, 115° 39’ 50” W). The research center is located between 1128 and 2071 meters in elevation with an annual average precipitation of 23 cm. This study took place over five days from May 3–8, 2022. The eastern Mojave Desert has a warm-temperate climate and is characterized by low rainfall and low humidity, except during monsoon season in the summer. This reserve consists of pinyon-juniper woodlands, creosote bush scrub, and wash scrub. Common plant species at the study site were yucca (*Yucca baccata*), creosote (*Larrea tridentata*), cholla (*Cylindropuntia* spp.), and juniper (*Juniperus osteosperma).* Our study focused on the biological soil crust located throughout the reserve.

2.2 Sampling Methods

Our sample area was within two habitat types; the creosote bush scrub and wash scrub located along the Al A. Allenson Trail, a trailhead near the Norris Camp facilities on the reserve. We sampled three general types of biological soil crust: algal crust, lichen crust, and moss crust. Using a spatula, we collected approximately 200 g of intact soil crust samples, which were placed on paper plates and transferred on a baking tray. In total, 45 samples were collected, (11 lichen crust samples, 11 moss crust samples, and 23 algal crust samples) and sample of varying thicknesses.

2.3 Bioassay

To study whether structure or nutrients in soil crust were contributing to plant success, a 5-day bioassay was conducted using Scotts® Turf Builder® Grass Seed Sun & Shade Mix® 2-0-0, which is made of 48% grass seeds and 50% Water Smart® Plus Fertilizer Coating. Seeds were thoroughly washed before using to remove fertilizer. Three types of soil crust were used: algal crust, moss crust, and lichen crust. To study the importance of structure; five (ten for algal crust) crumbled and five (ten for algal crust) intact replicates were used for all three types of soil crust, totaling to 40 soil crust bioassays. Our intact variants used soil crust samples that were cohesive and still held their shape, and crumbled variants were ground until fully disintegrated. Bioassays were conducted in plastic bowls using 30 g of soil and 10 seeds placed on top, and a wet paper towel as a liner. Samples were kept damp throughout the 5 days to ensure seed germination and placed next to an east facing window to ensure consistent temperature and lighting. On the final day bioassays were inspected by hand to record how many seeds had germinated. Germination was defined as any seed that had a root or shoot emerging.

2.4 Structural variables

To measure surface temperature, U.S. quarter-sized pieces of soil crust were placed on paper plates and left to sit in the sun. After one hour, a thermometer gun (CandyCare Infrared Thermometer Model No. OTB00016) was used to take three surface temperature measurements, which were averaged.

Soil water retention was obtained from the mass of water lost from each sample over the course of three hours. 5 mL of water was added to each sample and its initial mass was recorded. Samples were placed inside, avoiding any effects of direct sunshine or wind. Three hours later, the mass of each sample was measured again. Water loss was calculated as the difference between the two measurements. This water loss was divided by the initial mass of the sample to obtain percentage of water lost, an indication of the water retention capacity of each sample.

2.5 Chemical variables

To measure the chemical properties of different types of soil crust, 5 g of intact crust from each sample was weighed and dissolved in 20 mL tap water. This suspension was allowed to rest for 5 hours so that chemicals could dissolve into solution. The pH was determined by a calibrated HI98127 pH tester (HANNA Instruments), and electrical conductivity was measured by a COM-80S hydrotester (HM Digital, Inc.) in µS.

Respiration was measured by the change in oxygen when hydrated soil crust was placed in dark, sealed jars. The remaining oxygen in the vial after three days, unused by the biocrust sample, was measured. Unused oxygen was measured by the volume of air consumed in rusting a piece of steel wool. First, 3 g of hydrated soil crust and 0.2 g of extra fine steel wool were placed in a 20 mL glass scintillation vial and inverted in a water bath inside a 4 oz. plastic specimen cup (Fig. 1). The initial water level inside the glass vial was marked, and samples were placed inside a cardboard box to prevent photosynthesis from occurring. After three days, the water level inside the small glass vial was marked again. The change in air volume was calculated as the volume of a cylinder ($V = \pi r^2 l$), with *r* as the radius of the glass vial and *l* as the change in water level in the small vial. The temperature of the water bath was also recorded, so that the volume of oxygen could be converted to moles of O_2 using the formula n = pVRT, where *n* is the number of moles of O_2, *p* is the air pressure (1 atm), *V* is the volume of oxygen consumed by rust, and *T* is the temperature.

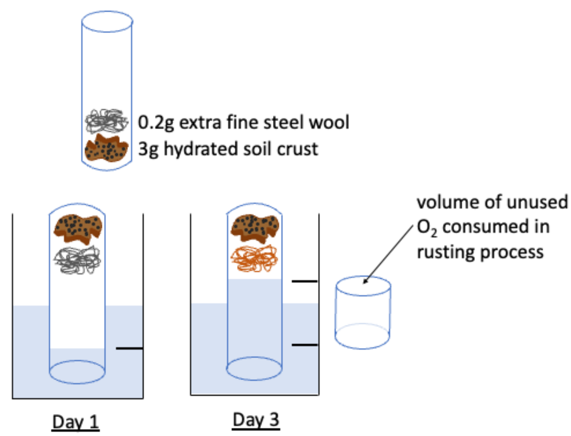

Figure 1. Procedure for measuring respiration of soil crust samples. Three grams of hydrated soil crust and 0.2g of extra fine steel wool were placed in a 20mL glass scintillation vial. This was inverted in a water bath inside a 4 oz plastic specimen cup, and initial water level in the scintillation vial was marked. Samples were placed in a dark box for three days, then the final water level in the scintillation vial was marked. The decrease in air volume was converted to moles of oxygen consumed in the process of rusting the steel wool using the formula n = pVRT. This amount of oxygen was considered unused by the soil crust sample, and therefore available for the rusting reaction. A higher amount of unused oxygen would mean lower respiration rates.

2.5 Statistical analyses

All statistical analyses were completed by JMP statistical software (v. 16) (SAS institute Inc.). A two-way ANOVA was conducted to investigate the effect of soil crust types (moss, lichen, thin algal, and thick algal), structure (intact or crumbled), and their interaction on seed germination. We also ran five separate ANOVAs to analyze the differences in surface temperature, water retention, pH, electrical conductivity, and respiration rate among the three types of soil crust (moss, lichen, and algal).

RESULTS

3.1 Seed germination

Intact soil crusts had higher seed germination rates than crumbled crusts ($N = 20$, $F = 7.42$, $p = 0.01$; Fig. 2), whereas germination did not differ across soil crust types ($N_{Algal} = 20$, N_{Lichen}, $N_{Moss} = 10$, $F = 1.60$, $P = 0.22$; Fig. 2). The interaction between soil crust types and intact or crumbled structure also had no effect on germination ($N_{Algal} = 10$, N_{Lichen}, $N_{Moss} = 5$, $F = 0.11$, $p = 0.91$; Fig. 2).

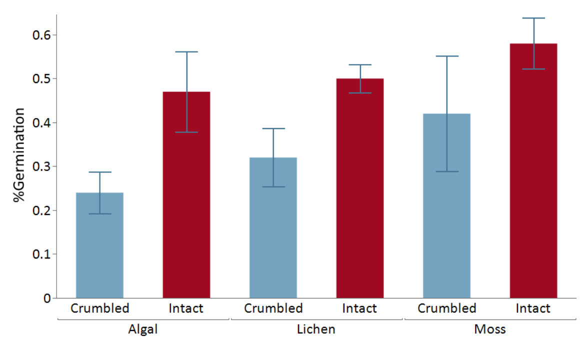

Figure 2. Effect of types and structure of biocrust on seed germination percentage. Three types of biocrust samples (algal, lichen, and moss crusts) were collected from the eastern Mojave Desert. Each type has five replicates of intact crust (ten for algal crusts) and five replicates of crumbled crust (ten for algal crusts), for a total of 40 samples. Intact soil crusts had higher seed germination rates than crumbled crusts ($N = 20$, $F = 7.42$, $p = 0.01$), whereas germination did not differ across soil crust types ($N_{Algal} = 20$, N_{Lichen}, $N_{Moss} = 10$, $F = 1.60$, $P = 0.22$). The interaction between soil crust types and structure also had no effect on germination ($N_{Algal} = 10$, N_{Lichen}, $N_{Moss} = 5$, $F = 0.11$, $p = 0.91$). The error bar represents +/- one standard error.

3.2 Structural variables

Lichen crusts had higher surface temperatures than algal crusts ($N_{Algal} = 21$, $N_{Lichen} = 10$, $N_{Moss} = 11$, $F = 5.42$, $p = 0.008$; Fig. 3), but moss crusts did not significantly differ in temperature from the other types. In addition, there was no difference in water retention across the three types of biocrusts ($N_{Algal} = 23$, N_{Lichen}, $N_{Moss} = 11$, $F = 0.54$, $p = 0.58$; Fig. 4).

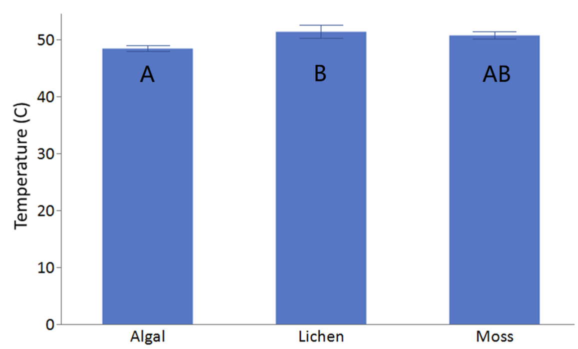

Figure 3. Effect of types of biocrust on surface temperature in degrees Celsius. ($N_{Algal} = 23$, N_{Lichen}, $N_{Moss} = 11$, $F = 5.4190$, $p = 0.0083$) Three types of biocrust samples (algal, lichen, and moss crusts) were collected from the eastern Mojave Desert. Their surface temperatures were measured after one hour under sunshine. Lichen crusts had a higher surface temperature than algal crusts. The error bar represents +/- one standard error.

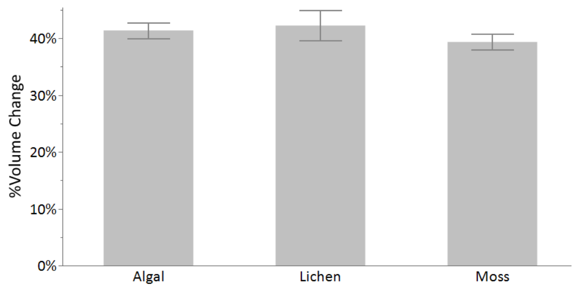

Figure 4. Effect of types of biocrust on water retention. (N_{Algal} = 23, N_{Lichen}, N_{Moss} = 11, F = 0.54, p = 0.58) Three types of biocrust samples (algal, lichen, and moss crusts) were collected from the eastern Mojave Desert. The water retention was measured as percent volume change (y-axis) three hours after adding 5 mL of water into the sample. No difference was founded in water retention across three types of biocrusts. The error bar represents +/- one standard error.

3.3 Chemical variables

Soil crusts containing moss were more acidic than the other two types, and the pH of algal and lichen crusts were not significantly different (N_{Algal} = 23, N_{Lichen}, N_{Moss} = 11, F = 8.08, p = 0.001; Fig. 5). While algal crusts had the lowest electrical conductivity, there was no difference between lichen and moss crusts (N_{Algal} = 23, N_{Lichen}, N_{Moss} = 11, F = 9.09, p = 0.0005; Fig. 6). Furthermore, measurements of O_2 consumption revealed that lichen crusts had higher respiration rates than moss crusts, but that neither differed from algal crusts (N_{Algal} = 9, N_{Lichen}, N_{Moss} = 6, F = 4.37, p = 0.03; Fig. 7).

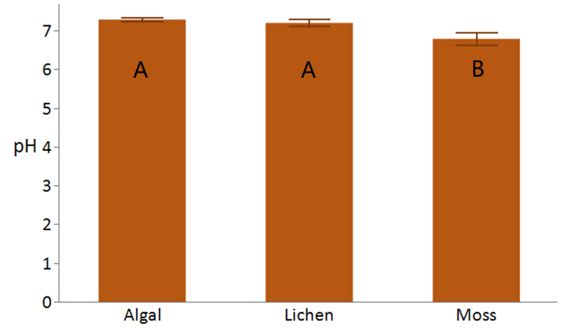

Figure 5. Effect of types of biocrust on soil pH. (N_{Algal} = 23, N_{Lichen}, N_{Moss} = 11, F = 8.08, p = 0.001) Three types of biocrust samples (algal, lichen, and moss crusts) were collected from the eastern Mojave Desert. Five grams of each sample was dissolved in 20 mL of water. Soil pH was measured five hours later using pH probe. Moss crusts were found to be more acidic than algal and lichen crusts. The error bar represents +/- one standard error.

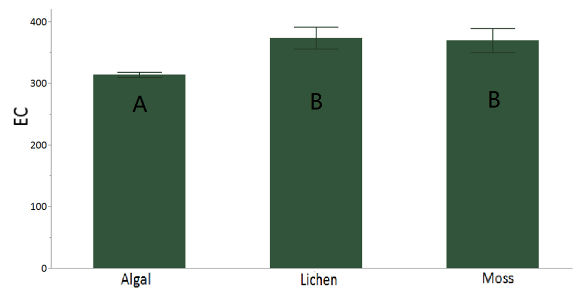

Figure 6. Effect of types of biocrust on electrical conductivity in µS. (N_{Algal} = 23, N_{Lichen}, N_{Moss} = 11, F = 9.09, p = 0.0005) Three types of biocrust samples (algal, lichen, and moss crusts) were collected from the eastern Mojave Desert. Five grams of each sample was dissolved in 20 mL of water. Electrical conductivity (EC) was measured five hours later using hydrotester. Algal crusts were found to have lower EC than moss and lichen crusts. The error bar represents +/- one standard error.

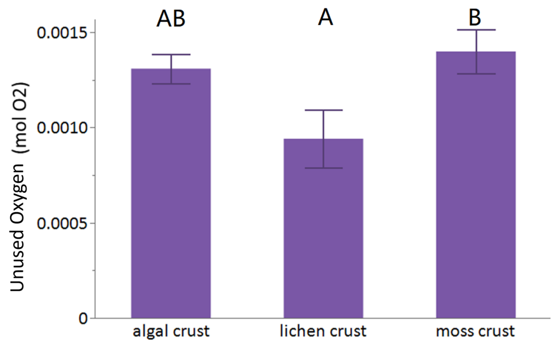

Figure 7. Respiration of difference types of biocrusts in mol of oxygen. (N_{Algal} = 9, N_{Lichen}, N_{Moss} = 6, F = 4.37, p = 0.03) Three types of biocrust samples (algal, lichen, and moss crusts) were collected from the eastern Mojave Desert. The amount of unused oxygen in the air was measured after different types of soil crusts were rehydrated and placed in a dark box for three days. Lichen crusts were found to have higher respiration levels than moss crusts, since they had less unused oxygen in the vial after three days, but neither differed from the algal crust. Standard error bars are pictured, and labels not containing the same letter are significantly different.

DISCUSSION

As we expected, our bioassay found that in the Mojave Desert, the structure of biological soil crust, rather than its chemical properties, is what facilitates seed germination. Despite differences in chemical properties between algal, lichen, and moss crusts, germinating seeds did not have a preference for biocrust type. Across all biocrust types, seeds preferred to germinate on intact pieces of biocrust rather than crumbled pieces. One possible explanation for the lack of crust type preference is that water is the most limiting factor for plant germination in deserts (Pavlik 2008), and all types of intact biocrust play an important role in retaining water in the local hydrologic cycle. Both external morphology and inner filaments of soil crust increase water absorptivity and retention and reduce soil porosity (Belnap 2006). These factors all increase available water, making soil crust structure the most important factor for facilitating plant germination.

Furthermore, we used grass seeds that are non-native to the Mojave Desert to test different types of soil crusts in this study. Even though grass seed germination could be treated as an indicator, native annual plants would be a better choice in the future study. Desert annual plants are adapted to extremely dry climates, making their seeds germinate only under certain conditions (Philippi 1993). This might cause them to have specific requirements on biocrusts that are different from those of grass seeds. Additionally, some studies have found that biocrust effects on plant germination are species-specific (Escudero et al. 2007, Godínez-Alvarez et al. 2011). Future studies could examine the effects of different biocrust types on various species of native Mojave Desert plants.

Surface temperature in the sun differed across algal, lichen, and moss crusts, but this did not influence germination rates in the experiment since seeds were kept inside. We predicted that darker lichen crusts would have a higher surface temperature than lighter-colored algal crusts and our findings confirmed this. However, moss crusts were not different in temperature from the other types of crusts, as was predicted. This result may be due to the green color of some mosses, which would not have lowered the albedo as much as the dark brown and black lichens. Additionally, the filamentous structure of moss crusts may help to disperse heat despite being darker in color (Xiao and Bowker 2020). Moss crusts can increase soil surface temperature when dry, but decrease soil surface temperature when wet (Xiao and Bowker 2020). Knowing this, it may be interesting to conduct a seed germination experiment outside in the sun, where differences in surface temperatures between the different types of crust could influence germination rates. Temperature of the soil crust surface is crucial, since seeds have an optimal temperature for germination (Roberts 1988), and for desert plants high heat can even speed up germination (Capon and Van Asdall 1967, Chawan 1971). These differences in surface temperature could affect the distribution of desert plants due to species-specific optimal germination temperatures.

This study did not find differences in water retention between the different types of crust. This did not agree with predictions, since we expected moss crusts to have a higher water retention based on previous findings (Pietrasiak 2014). As for cyanobacteria and gelatinous lichens, they have also been found to have high water retention, absorbing ten times their volume in water (Belnap and Eldridge 2003). In our study, lichens did not show greater water retention ability than the other types of biocrust, possibly due to experimental design. In situ, water loss is mostly driven by run-off and permeation into deep soil layers, but the main source of water loss in this experiment was evaporation. Even though lichen crusts have a strong ability to prevent water runoff, it is possible that water absorbed by the thallus has greater surface contact with surrounding dry air, causing a faster evaporation rate.

Chemical composition was found to be distinct across different types of soil crusts as well, but it resulted in no differences in plant germination. Moss crusts were more acidic than algal or lichen crusts. This might be caused by the weak acid produced by moss that speeds up chemical weathering of rock (Lian et al. 2008, Jackson 2015). However, some lichens produce weak acid (Lian et al. 2008, Jackson 2015). Further studies about individual lichen or moss species are needed to completely understand how they contribute to soil chemical properties. The pH value of algal and lichen soil crusts were overall basic, which agrees with previous studies (Belnap 2006). This also explained the existence of cyanobacteria in both lichens and biocrusts, since the optimal soil pH for them to grow, photosynthesize, and fix nitrogen is slightly alkaline (Smith and Doran 1997, Nayak 2007, Mangan et al. 2016). Furthermore, the fact that soil pH does not impact seed germination also agrees with previous findings. Studies on many plant species, including creosote (*Larrea tridentata)*, found that pH had no influence on seed germination, only on plant growth (Barbour 1968, Pérez-Fernández et al. 2006, Ma et al. 2015).

The low electrical conductivity for algal crusts indicated the least salt content and least soluble nutrients out of all of the crust types. This result was surprising since the cyanobacteria present in algal crust was thought to contribute more to nitrogen fixation in the Mojave Desert than lichen or moss crusts (Pietrasiak 2014). In this case, different levels of nitrogenous compounds should influence both germination rate and germination percentage. However, electrical conductivity measured not only the nitrogenous compounds but all cations and anions, including micronutrients. The higher dust-trapping ability of lichen and moss crusts (Pietrasiak 2014) would also contribute to a higher trapping of mineral and fine particles, leading to a high soil salinity.

This experiment showed that lichen crusts have a higher level of respiration than moss crusts during the three days after rehydration, since they had less unused oxygen in the vial after three days. This was not in agreement with predictions, since we predicted that mosses would have the highest respiration rate since they require more moisture (Pietrasiak 2014), and could therefore have higher rates of biological activity in general. However, it is possible that moss crusts simply have fewer heterotrophic taxa than lichen crusts, possibly due to the more complex morphology of the moss crowding out other taxa. Regardless, we found that the seeds did not respond to the differences in respiration between the different types of biological soil crusts, as their germination rates were higher on intact pieces of soil crust regardless of crust type.

These findings have important implications for conservation and environmental management. Both chemical and physical differentiations across types of biocrusts highlight the importance of conserving a variety of biocrust types, which create environmental variation that could improve local biodiversity. The importance of structure for plant germination across all types of biocrusts suggests that mechanical disturbance (such as trampling by humans and livestock) should be limited for all places with biological soil crusts. The mere presence of microorganisms in the soil is not sufficient to maintain ecosystem function - biocrusts must retain an undisturbed surface structure in order to promote plant germination.

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