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RESEARCH ARTICLE

Strategies for restoring the structure and function of lichen-moss biocrust communities

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Biological soil crusts (biocrusts) are crucial components of dryland ecosystems, but they are slow to recover following disturbance. Herein, we evaluated several methods for restoring lichen-moss biocrusts that included factorial applications of moss fragments in a water-slurry (1) with and without lichen fragments (to restore biocrust taxonomic structure), (2) with and without clay (to facilitate establishment), and (3) with and without jute ground cloth (to facilitate establishment). Three and four years after inoculation, moss and lichen cover was up to five and eight times higher on jute ground cloth than on bare ground, respectively. Lichen cover was six times higher in plots where lichen fragments were added. Clay amendments did not increase moss or lichen establishment. To understand the effects of biocrust recovery on soil properties, we measured soil inorganic nitrogen, microbial biomass carbon, and soil water availability in restoration and control plots. Restored biocrusts decreased inorganic NH_4-N availability by 67% when compared to controls 3 years after inoculation, but did not influence the availability of inorganic NO_3-N, soil water, or microbial biomass carbon. Our results demonstrate that adding a biocrust inoculant to jute ground cloth can expedite recovery of lichen-moss biocrust and reestablish its influence on soil properties within a few years.

Key words: biological soil crusts, ecosystem function, inorganic N, jute ground cloth, lichen, microbial biomass, moss, restoration

Implications for Practice

- Biocrusts provide important ecological services in drylands but are easily disturbed and slow to recover.
- In situ lichen-moss biocrust reestablishment can be accelerated by adding an inoculant with both lichen and moss to jute ground cloth.
- Reestablishing biocrusts begin regaining ecosystem function within a few years through their influence on soil inorganic nitrogen availability.
- Biocrust restoration expedites the recovery of biocrust structure and function, and should be considered individually and in combination with other restoration methods for its effectiveness at promoting community-level recovery from disturbance.

Introduction

Biological soil crusts (biocrusts hereafter) are complex communities of moss, lichen, and cyanobacteria that inhabit the soil surface in dryland ecosystems. Biocrusts are critical components of dryland systems that stabilize soil (Belnap & Gardner 1993; Zaady et al. 2014; Seitz et al. 2017), regulate water and nutrient cycling (Harper & Pendleton 1993; Pendleton et al. 2003; Chamizo et al. 2012, 2013; Weber et al. 2015), buffer soil temperatures (Gornall et al. 2009), and influence the establishment of vascular plants (e.g. Zaady et al. 1997; Briggs & Morgan 2011; Zhang et al. 2016; Slate et al. 2019*a*). Biocrusts are particularly sensitive to disturbance, and once disturbed are slow to reestablish (Belnap & Warren 2002; Weber et al. 2016) leaving disturbed soils prone to erosion (Rodríguez-Caballero et al. 2013; Chamizo et al. 2017), loss of soil nutrients (Barger et al. 2006; Chamizo et al. 2017), and plant invasions (Zhang et al. 2016; Slate et al. 2019*a*). Hence, the negative effects of biocrust disturbance on ecosystem function can be long-lasting without active restoration.

Recognition of the ecological importance of biocrusts has increased interest in developing strategies that expedite their recovery (reviewed in Bowker 2007), but available techniques remain limited. One of the more promising biocrust restoration techniques is also straightforward. Since biocrust organisms are able to regenerate vegetatively, biocrusts can be salvaged prior to disturbance or harvested from sites where biocrust cover is high and used as an inoculant to restore disturbed sites (Chiquoine et al. 2016; Condon & Pyke 2016; Antoninka et al. 2018; Chandler et al. 2018). However, the act of harvesting intact biocrusts generates disturbance itself (Antoninka

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et al. 2018), so techniques are needed that minimize the amount of biocrust inoculant needed. An additional challenge is that lightweight biocrust fragments can easily be washed or blown away (Kidron et al. 2012; Bu et al. 2016), rendering biocrust inoculations ineffective. Jute ground cloth has been successfully used as a substrate for the inoculation of moss biocrusts, where it is thought to increase the surface microtopography of soils and reduce the loss of biocrust fragments during wind and precipitation events (Condon & Pyke 2016). It is unknown, however, if jute ground cloth can also facilitate the establishment of other biocrust taxa like lichen. Additionally, coating biocrust fragments with clay could weigh the biocrust particles down and mitigate the loss of biocrust inoculants to erosion from wind and precipitation events. Clay coatings have been used to increase the mass/volume of very small seeds for incorporation in restoration seeding (Madsen et al. 2012), but this approach has not been applied to biocrust fragments.

Important functions of biocrusts include their influence on soil water, carbon (C), and nitrogen (N) availability. Across biocrust types, biocrust communities dominated by moss tend to positively influence soil water infiltration and retention (Chamizo et al. 2017). In terms of biocrust restoration, the positive effects of reestablished biocrusts on soil water availability have been detected in as little as 2 years (Xiao et al. 2014). Soil water availability subsequently influences rates of soil C and N transformations, through its influence on soil microbial activity (e.g. Xiang et al. 2008). Over longer time spans, naturally reestablishing biocrusts are known to increase the availability of soil C and N (20+ years, Liu et al. 2014; 10+ years, Jia et al. 2017), but few studies have considered the effects of natural or assisted biocrust recovery on soil C and N in the short term or related these biogeochemical effects to soil water availability (Chiquoine et al. 2016; Williams et al. 2018). When natural biocrust reestablishment was evaluated 2 years after disturbance across four disparate European sites, total soil C and N was unchanged (Williams et al. 2018). In contrast, in the Mojave Desert, United States, assisted biocrust restoration increased soil inorganic N availability after only 18 months (Chiquoine et al. 2016). Neither of these studies measured soil water availability. Given that a central goal of most restoration projects is native vascular plant reestablishment, understanding how biocrust restoration influences soil moisture and fertility may help inform plant restoration strategies in dryland systems.

In this study, we initiated a field experiment to evaluate several methods (lichen addition, jute ground cloth, and clay addition) for restoring lichen-moss biocrusts while also examining how newly established biocrusts influenced soil nutrient and water availability. In all scenarios, we used small amounts (3 g per 0.25 m^2) of inoculant to evaluate the feasibility of restoring biocrusts with minimal impacts on biocrust source communities. We tested restoration methods for reducing the loss of biocrust fragments to wind and rain by adding biocrust fragments beneath, on top of, or without jute ground cloth and with or without a clay coating, hypothesizing that by combining jute ground cloth and clay we would increase biocrust establishment. Biocrusts in our study area included both moss and lichen, but mosses are generally more abundant than lichen in disturbed and recently tilled locations (Durham et al. 2018). Because of this, we inoculated restoration plots either with moss alone or moss and lichen, hypothesizing that though mosses should be first to establish, adding lichen fragments to our inoculant should expedite lichen establishment in our restored biocrusts. Finally, we evaluated how restored biocrust cover correlated with soil C, soil N, and soil water availability, hypothesizing that restored biocrusts would positively influence these soil properties during early establishment.

Methods

Site Description

Our study site was located in semiarid intermountain grasslands on MPG Ranch in western Montana. MPG Ranch is a 6,677 ha property located near Florence, Montana (46°40′48″N, 114°1′40″W; 1,024 m; www.mpgranch.com) that is managed with a focus on conservation and restoration. Mean annual precipitation is 325 mm (www.ncdc.noaa.gov) and occurs primarily in the winter and spring followed by hot, dry summers. Soils consist of gravelly loamy Mollisols (USDA Soil Taxonomy; www.websoilsurvey.sc.egov.usda.gov). Intact native grassland and shrubland communities are comprised of scattered perennial bunchgrasses, forbs, and shrubs with interspaces inhabited by biocrusts. Biocrust cover varies across the landscape from a mixture of bryophytes (mosses and liverworts) and lichens, to either mosses or lichens (Durham et al. 2018), with a physical microtopography characterized as rolling (Belnap 2001). The majority (63%) of the biocrust community on MPG Ranch is comprised of mosses from the genus *Syntrichia* and lichens from the genus *Cladonia*, but at least 94 other lichen and bryophyte species are also present with varying cover (Durham et al. 2018). The habitat is representative of biocrust communities over a large region of the intermountain west.

Field Experiment

We established a field experiment to evaluate several methods for restoring lichen-moss biocrusts: (1) lichen addition, (2) jute ground cloth, and (3) clay addition. Though our study site was flat, biocrust fragments are very lightweight and can be dispersed by light winds and rains (Kidron et al. 2012; Bu et al. 2016), even on sites with no slope. To minimize the loss of biocrust fragments from wind and rain, we incorporated jute ground cloth into the study to increase soil surface microtopography and varied whether biocrust fragments were added beneath or on top of jute ground cloth. We also coated biocrust fragments with clay to weigh them down and further reduce losses during wind and precipitation events. Restoration plots were inoculated with moss or moss and lichen fragments to evaluate how inoculating restoration plots with one or both of our dominant biocrust taxa influenced the cover, by dominant taxa, of the restored biocrusts. We also investigated the influence of restored biocrusts on soil properties.

Our field experiment was located inside a large fenced common garden that had been tilled and lined with ground cloth

5 months prior to the experiment. We cut away the ground cloth and established two-hundred and sixty 0.25 m^2 restoration plots marked by wooden stakes (Fig. 1). Moss biocrust recovery appears to be greatest when biocrust fragments are added in fall (Condon & Pyke 2016; Bu et al. 2018) so we established our plots in October of 2013. In June 2013, we collected, dried, and ground moss biocrusts (with no visible lichen present) from MPG property into small fragments (<0.5 cm) with a coffee grinder. In specimen cups, we added 3 g of dried moss fragments to 50 mL water (Scarlett 1994) to create a slurry and generate an application rate of 12 g moss per m^2. Half of the moss-water slurries were amended with 3 g of kaolin clay (±clay; EPK Clay, Edgar Minerals, Edgar, FL, U.S.A.). Lichen biocrusts were collected from MPG property in June 2013, dried, and ground. Half of the moss-water slurries (±clay) received 3 g of lichen inoculant while the other half did not (±lichen). We used landscape staples to attach jute ground cloth to the ground and applied each of the various slurries on top of jute, beneath jute, or onto bare soil (Forestry Suppliers Inc., Jackson, MS, U.S.A.). Each treatment combination was replicated 20 times. Twenty additional plots were installed as experimental controls and treated with 50 mL of water but no moss, lichen, or clay was added. Plots were randomly assigned as treatment or control within our experimental garden area. Thus, we created a fractional factorial design and included 260 plots with 20 fully randomized replicates of moss addition (+moss only) * ground cloth (no jute, on top of jute, beneath jute) * clay addition (±clay) * lichen addition (±lichen) combinations with 20 control plots having no moss, no ground cloth, no clay, and no lichen (Table S1). We focused this design on moss addition (i.e. we did not replicate all combinations of no moss addition) in order to emphasize treatments likely to promote biocrust restoration success, because the full factorial design would have nearly doubled the number of plots, with most no-moss addition control treatments likely resulting in little biocrust establishment. None of our experimental plots received additional water, but weeds were removed by hand to minimize the disturbance of developing biocrusts.

Measurements

To measure changes in cover, we photographed each plot by attaching a camera to a tripod mounted 47 cm over each 0.25 m^2 quadrat. All plots were photographed on a single day immediately following a rain event in early May of 2016 and 2017 while biocrusts were fully hydrated. Percent cover of moss (2016) and lichen (2018) was determined from these photos using ImageJ (Schneider et al. 2012).

Analyses of our 2016 measures of moss percent cover (methods described below) revealed that jute ground cloth positively influenced moss reestablishment and demonstrated that no other

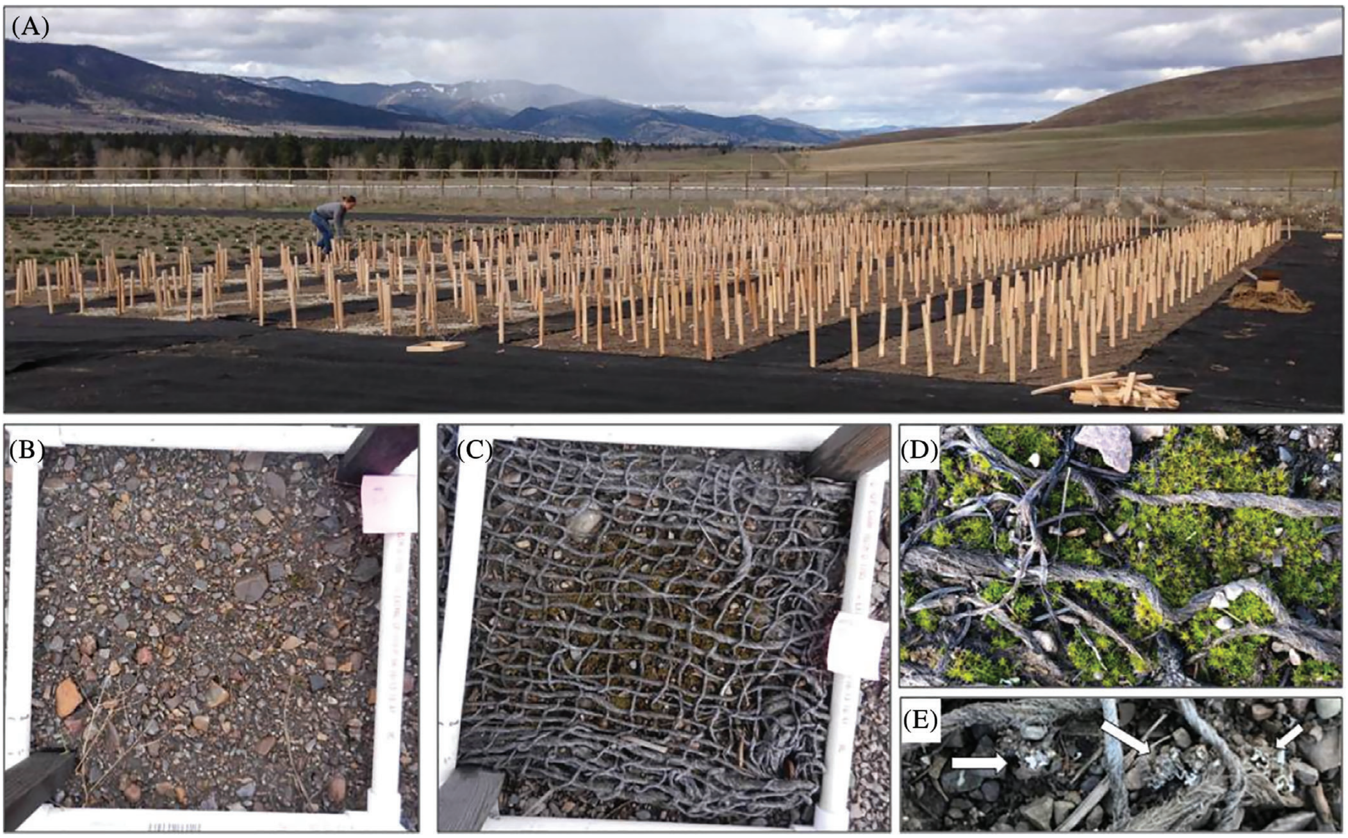

Figure 1. Field-based biocrust restoration experiment. Two hundred sixty plots were installed in October 2013 (A). By June 2016, little to no biocrusts had established in plots without jute ground cloth (B). However, the presence of jute ground cloth facilitated moss (C, D) and lichen (E) biocrust establishment.

treatment or treatment combination influenced moss reestablishment. Therefore, for our soil analyses we sampled soils only from jute ground cloth plots and control plots as specified below.

In order to understand how differences in moss cover (lichen were not present at this time) influenced soil inorganic N availability and soil water availability, we randomly selected 10 restoration plots with jute ground cloth and 5 control plots during the morning on 12 July, 2016. We extracted and combined three 2-cm deep soil samples (approximately 35 g) from each plot within a 1-hour period of time. Soils were subsequently sieved and gravimetric water content (GWC) was determined by mass for all soil samples within 48 hours. To extract inorganic soil N, comprised of ammonium (NH_4^+) and nitrate (NO_3^-), we added about 15 mL of soil to 50 mL of 2 M KCl. The mixture was placed on a lab shaker for 1 hour, allowed to settle overnight at 4°C, filtered and sent to Ward Laboratories (www.wardlab.com) for colorimetric determination of NH_4-N and NO_3-N (Solórzano 1969; Doane & Horwath 2003). Soil N data were corrected for soil moisture content.

To determine how moss cover influenced soil C, we measured soil microbial biomass C which responds more quickly to changes in soil quality than soil organic carbon (Smith & Paul 1990). We sampled approximately 30 g soil from 15 randomly selected experimental restoration plots with jute ground cloth and 5 control plots on 23 July, 2017 in the same manner as described above. As before, GWC was determined by mass on soil subsamples from each plot. Soil microbial biomass C was measured on fresh soil as chloroform labile C (Vance et al. 1987). Briefly, soil subsamples (approximately 10 g per plot) were extracted in 35 mL of 0.5 M K_2SO_4, placed on a lab shaker for 1 hour, allowed to settle overnight, filtered, and frozen until analyzed. A second soil subsample from each plot was fumigated with ethanol-free chloroform for 7 days and then extracted as described above and frozen. Filtered samples were sent to Ward Laboratories for determination of total organic C with a combustion analyzer. The difference in organic C between unfumigated and fumigated samples is proportional to microbial biomass C. Microbial biomass C data were corrected for soil water content.

Statistical Analyses

All analyses were conducted in R version 3.5.1 (R Core Team 2018). Prior to analyses and for each response variable (moss or lichen cover), we made a histogram of the residuals to check the assumption of normality and created a scatter plot of the residuals and estimated fitted values to check the assumption of homoscedasticity. To account for the skewness of the data, we used a generalized linear model (GLM) to understand which treatment (jute ground cover, clay addition, or lichen addition) and treatment combinations generated the most moss cover (lichen were not visible prior to fall 2017). Moss percent cover (2016) was treated as the response variable and the ground cover (no jute, on jute, beneath jute), clay addition (±clay), lichen addition (±lichen) treatments and their interactions were treated as fixed factors. Lichen cover was first censused in 2018. We used a GLM to understand how lichen percent cover (response variable) was influenced by the jute ground cloth, clay addition, and lichen addition treatments and their interactions (fixed factors). For both GLMs, we accounted for overdispersion by applying the gamma family and log-link function. X^2 and p values were estimated using the Anova function in the car package (Fox & Weisberg 2011) and post-hoc contrasts were conducted with the emmeans package when appropriate (Lenth 2018).

In order to understand how biocrust reestablishment influenced soil properties, we compared the levels of soil inorganic N (NH_4-N or NO_3-N), moisture (GWC), and microbial biomass C in biocrust restoration plots where biocrusts established (plots with jute ground cloth that were inoculated with mosses) with those of control plots (no moss inoculation) with Welch's t tests to account for heteroscedasticity. When soil properties varied between biocrust restoration plots and control plots ($p < 0.10$), we investigated the relationship between moss cover and the soil property with weighted regression analysis using the R package MASS (Venables & Ripley 2002).

Results

In 2016, mosses covered 1.5% of our control plots where no moss or lichen fragments were added as compared to an average cover of 17 or 3.5% in experimental plots treated with moss fragments and with or without jute ground cloth, respectively (jute addition treatments combined). Across all experimental restoration plots, moss cover (primarily *Syntrichia ruralis*; Fig. 1D) was higher when jute ground cloth was present (jute addition treatments combined; Tables S2, S3; Fig. 2A). However, there was no difference in moss cover among experimental treatments where moss fragments were added on top of or beneath jute ground cloth (Table S3). Moss cover in restoration plots with jute ground cloth (jute addition treatments combined) was 4.8 times greater than moss cover in plots with no jute ground cloth. Lichen and clay addition treatments and their interactions had no effect on moss cover (Table S2).

Lichen cover was 0.1% in control plots where no moss or lichen was added but ranged from 0 to 8% cover in experimental plots that were initiated with a moss or moss and lichen inoculant. Like moss cover, lichen cover (primarily species of *Cladonia*; Fig. 1E) was higher in restoration plots with jute than without jute ground cloth (jute addition treatments combined; Tables S2, S3; Fig. 2B). However, lichen cover did not vary among all experimental plots where lichen was added beneath rather than on top of jute ground cloth (Table S3). When combined, restoration plots inoculated with lichen had 127% greater lichen cover than restoration plots that were not inoculated with lichen (Table S2). A significant interaction between ground cover treatment and lichen inoculation indicated that the influence of ground cover treatment and lichen inoculation varied depending on the other factor. Thus, this interaction resulted in much lower lichen cover when no lichen fragments were added to experimental plots with and without jute ground cloth as compared to the same ground cover treatments with lichen inoculation (Fig. 2B).

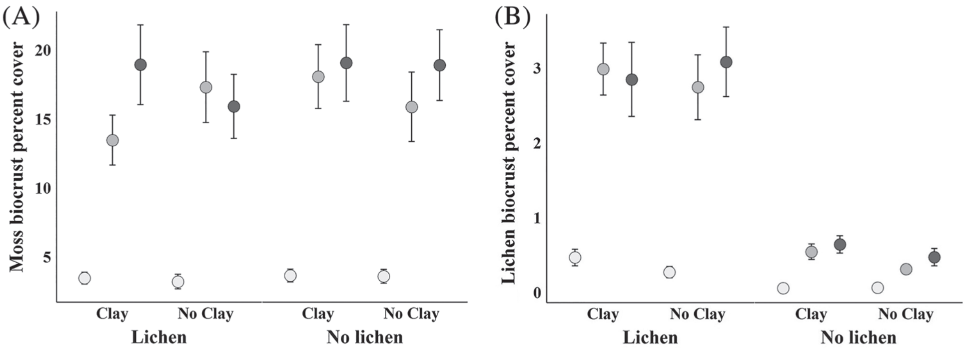

Figure 2. Biocrust reestablishment in restoration plots 3 (A) and 4 (B) years after experimental installation. Moss biocrust fragments were added to plots treated with different ground cover treatments (no jute = open, on jute = light gray, under jute = dark gray), lichen addition treatments (lichen or no lichen), and clay addition treatments (clay or no clay). Moss biocrust percent cover was measured most recently in 2016 (A). Lichen biocrust percent cover was quantified in 2018 (B); mean ± SE. Moss and lichen cover were highest when jute ground cloth was present and not influenced by the clay addition treatment. We found no differences in moss or lichen cover in plots where biocrust fragments were added on top of or beneath jute ground cloth.

Inorganic NH_4-N levels were lower in biocrust restoration plots than in control plots (Fig. 3A; Table S4) and negatively associated with moss cover ($r^2 = 0.213$, $p = 0.083$). However, there was no difference in soil inorganic NO_3-N, soil GWC, or soil microbial biomass C levels between control and biocrust restoration plots (Fig. 3B–D; Table S4).

Discussion

Biocrusts are integral components of dryland ecosystems that are sensitive to disturbance and slow to reestablish without assistance. We found that lichen-moss biocrust establishment can be enhanced over natural biocrust recovery by using relatively straightforward and logistically practical in situ approaches. Moss and lichen cover was up to 33 and 76 times higher in our restoration plots than in our control plots where no moss or lichen fragments were added 3 and 4 years after inoculation, respectively. While the absolute coverage of moss and lichen was still relatively low (highest average cover was 17% for moss and 3% for lichen), our results suggest that when compared with previous successful biocrust restoration studies (e.g. Condon & Pyke 2016), these restoration techniques can expedite recovery of the structure and function of lichen-moss biocrusts using lower-level inoculations that minimize impacts to donor communities.

Biocrust Reestablishment

Our finding that jute ground cloth increased moss establishment corroborates other recent studies (Condon & Pyke 2016). However, this study is the first to demonstrate that jute ground cloth can also increase lichen establishment. Jute ground cloth is thought to protect lightweight biocrust fragments from wind and water dispersal while also creating a higher moisture microclimate (Condon & Pyke 2016). For moss and lichen, opportunities for growth are limited to the brief periods of hydration that follow precipitation events (Belnap & Lange 2003). Hence, methods that create higher moisture microclimates (Condon & Pyke 2016) or prolong hydration with shade (Bu et al. 2018) tend to have a positive influence on biocrust growth. Jute ground cloth also enhances soil surface microtopography which can expand the surface boundary layer and slow drying. The fact that no differences were observed when adding biocrust fragments beneath or on top of jute ground cloth suggests there is some latitude in the manner in which this technique is deployed.

In contrast to jute cloth, addition of clay to the inoculant did not affect moss or lichen reestablishment. It is possible that coating biocrust fragments in another substrate (e.g. gypsum or perhaps a water absorbent coating) could yield different results, but jute ground cloth may provide enough protection for biocrust fragments to alleviate losses to wind and precipitation.

There is a growing awareness that biocrust restoration strategies should rely less on established biocrusts as a source material for restoration (e.g. Antoninka et al. 2018), because harvesting intact biocrusts generates disturbance that is an undesirable side effect of restoration. For this reason, one of our goals was to evaluate the efficacy of reestablishing biocrusts using a relatively small amount of source inoculant. Our low-volume inoculation approach was not quite as effective as more intensive methods, but it did reestablish biocrusts. In our study, moss fragments were applied at an inoculation rate of 12 g moss per m^2 and covered 17% on average of plot surfaces containing jute ground cloth 2.5 years after inoculation. In another study, moss fragments applied at an inoculation rate of 43.5 g moss per m^2 covered 25% on average of plots containing jute ground cloth (for the same moss species) after 1.5 years of inoculation (Condon & Pyke 2016). When large amounts of salvaged biocrusts are available and the area needing restoration is small, biocrust communities may be quickly reestablished (18 months) even in dry locations such as the Mojave Desert by placing clumps of salvaged biocrusts onto bare ground (Chiquoine et al. 2016). Methods are being developed that will provide restoration practitioners with cultivated biocrust inoculant from greenhouses and growth chambers (reviewed in Antoninka et al. 2018). Such use of

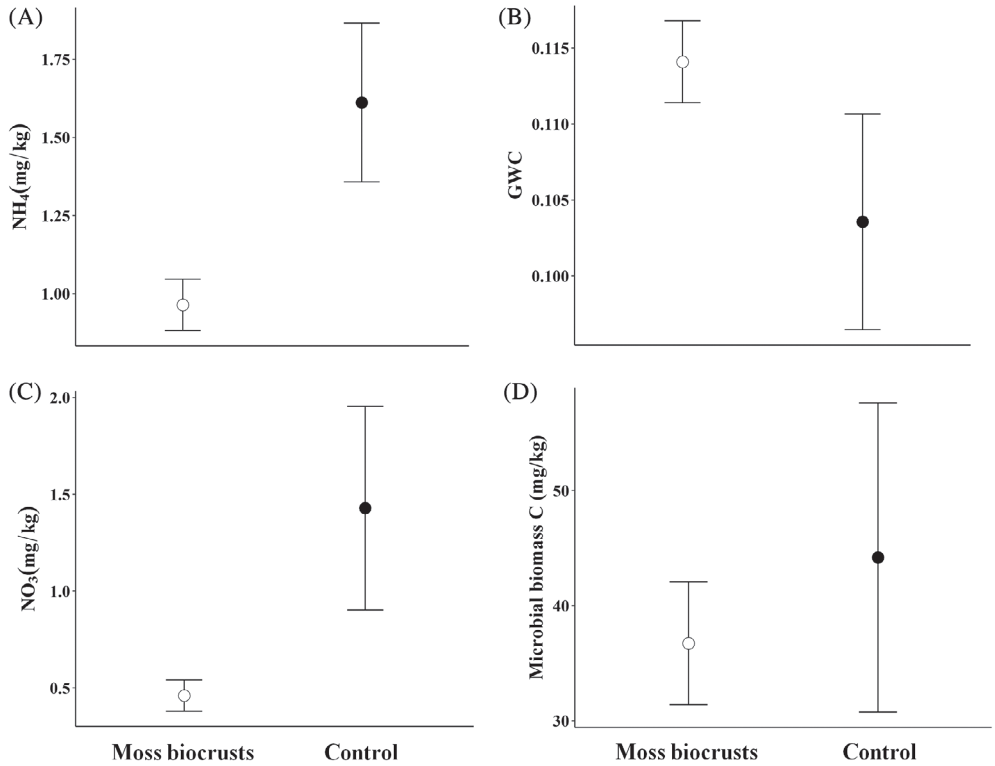

Figure 3. Relative abundance of soil inorganic NH_4-N (A), NO_3-N (B); mean ± SE.

cultivated biocrusts should alleviate the concern of creating a secondary disturbance, but until biocrust production capacity can meet the demands for restoration material there will be a need to maximize the efficiency of biocrust restoration using minimal source inoculum.

In our study, we found that adding lichen fragments to moss inoculants significantly increased lichen abundance in restored biocrusts. The fact that lichen did reestablish, albeit at a much lower rate, in plots that did not receive lichen fragments suggests that lichen propagules were either present in mosses but not obvious or that they accumulated in mosses naturally. Such passive inoculation could be beneficial from a restoration perspective when not all components of the biocrust community are amenable to cultivation. Nonetheless, lichen addition significantly increased lichen presence in the restored biocrusts. Without inoculation, lichens are rarely present until 10–20 years after a disturbance (Callison et al. 1985; Johansen 2001; Hilty et al. 2004) so adding lichen fragments to biocrust restoration inoculants may drastically increase the rate of lichen recovery because of the potential for vegetative growth. Mixed biocrust inoculants may also establish levels of diversity within the biocrust community more quickly and reestablish levels of ecosystem multifunctionality (Bowker et al. 2010; Bowker & Antoninka 2016). Though in the current study lichen was not present for long enough to test this hypothesis, we are continuing to monitor these plots to examine long-term effects of the treatments on ecosystem processes.

Effects of Restored Biocrusts on Soil Properties

Since mosses were present for longer and in greater abundance than lichen in our restoration plots, we focus on mosses in discussing biocrust restoration effects on ecosystem function. Moss cover did not appear to affect soil moisture or microbial biomass C, but this could be due to the timing of our sampling (mid-summer when soil water content was lowest), our method for measuring soil moisture (see Susha Lekshmi et al. 2014), and/or the duration of the study (Jia et al. 2017). We did find that restoration plots with mosses had lower inorganic NH_4-N than control plots within 3 years of establishment. In contrast, inorganic NO_3-N levels did not vary between restoration plots with mosses and control plots. Mosses lose C and N during cycles of desiccation and rehydration as a result of cellular damage: resources that can be carried away from rehydrating mosses in precipitation, transferred to soil, and accessed by soil microbes (Slate et al. 2019*b*). As mosses reestablished, rehydration-related pulses of C and N may have promoted soil N immobilization, accounting for lower NH_4-N levels measured in plots with moss versus no-moss control plots. Alternately, though mosses primarily rely on atmospheric N they can also assimilate soil N (Jauhiainen et al. 1998; Ayers et al. 2006) which could also explain our results, with neither hypothesis being mutually exclusive. Since biocrusts can influence native and exotic plant establishment (Hernandez & Sandquist 2011; Zhang et al. 2016; Condon & Pyke 2018; Slate et al. 2019*a*), this ability of biocrusts to reduce soil N could promote native over exotic plant establishment in systems like ours where disturbance increases soil N availability (Pearson et al. 2018).

Over time, the addition of organic matter from restored mosses should stimulate N mineralization and promote an overall increase, rather than decrease, in soil inorganic N availability (Sedia & Ehrenfeld 2005; Hu et al. 2014). Further, as lichen biocrusts increase in cover in our restoration plots, nitrification may be inhibited leading to a greater abundance of available N as NH_4-N or as dissolved organic N (Delgado-Baquerizo et al. 2010) and potentially promoting different forms and amounts of soil N than are predicted for soils beneath restored mosses. More work is needed to better understand these relationships between biocrust organisms and soil nutrient availability and whether the patterns found previously can be generalized to other systems. Importantly, this sort of fine-scale nutrient heterogeneity can influence plant community composition and productivity providing another example of how increasing diversity in biocrust inoculants could impact ecosystem function (Maestre et al. 2005; Wijesinghe et al. 2005; Maestre & Reynolds 2007). A next step would be investigating how these biocrust restoration techniques can be used in combination with native plant restoration strategies to expedite whole-community recovery in dryland systems.

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Supporting Information

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

Table S1: Table showing our experimental design.
Table S2: Results of analyses comparing biocrust cover by treatment.
Table S3: Results of pairwise comparisons of moss or lichen cover by ground cover treatment.
Table S4: Results of analyses comparing soil properties beneath restored biocrusts and control plots.

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