COVER AND COMPOSITION OF BIOLOGICAL SOIL CRUST VARY AS A FUNCTION OF DISTURBANCE DUE TO LIVESTOCK IN A SONORAN DESERT GRASSLAND

By

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Abstract

Cryptic organisms are increasingly recognized for their influence on ecosystem function and services. Biological soil crusts are communities of aggregated soil particles, bryophytes, lichens, cyanobacteria, and other microbes that influence arid ecosystem function by provisioning soil nutrients, increasing soil water capacity, and reducing soil erosion. Biocrusts are broadly sensitive to mechanical disturbance, but knowledge gaps persist in our understanding of disturbance impacts to cover and composition of biocrusts. Because of their sensitivity to disturbance and importance in arid ecosystem function, biocrusts may provide important insight into ecological theory of disturbance in arid ecosystems. I assessed cover and composition of biocrusts across a gradient of disturbance by livestock in a Sonoran Desert grassland in southern Arizona. I found reductions in biocrust cover and shifts in biocrust communities under greater use by livestock. I argue that biocrust communities are negatively impacted by livestock use, but that some biocrust morphotypes may be more resilient to, or benefit from, some level of disturbance. This work provides new data about the composition and distribution of biocrusts in southern Arizona and contributes new insights about the potential impacts of livestock on these important elements of dryland ecosystems.

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Introduction

An emerging theme in ecology is that cryptic organisms influence ecosystem function and services in wild and human-altered lands[1]. In arid and semiarid environments, cryptic biological soil crusts (biocrusts) have important ecological roles. Biocrusts are made up of aggregated soil particles and communities of green algae, cyanobacteria, lichen, bryophytes, and free-living microfungi (Fig.1)[1, 2]. In regions with limited or strongly seasonal precipitation, biocrusts are often the primary contributor of soil nitrogen and frequently provide other nutrients key to vascular plant growth[3-5]. Biocrusts further influence ecosystem function by improving water holding capacity of soils otherwise poor in organic matter, and by reducing soil erosion due to wind and runoff[4-7]. In many cases biocrusts are important primary producers, particularly in landscapes that have been altered by disturbance[8,9]. As such, biocrusts are often considered important in early succession after major disturbance events[9,10].

Despite an increased recognition of the roles biocrusts play in arid ecosystem function, knowledge gaps persist regarding the factors that shape two fundamental characteristics of biocrust biology: cover (the amount of soil surface covered by biocrusts) and composition (the makeup of those biocrust communities)[11]. In the Sonoran Desert bioregion, biocrust cover and composition vary spatially and in terms of composition at landscape scales[2]. With increasing population pressure, greater outdoors activity for recreation, changes in grazing regimes, and a shifting climate, the Sonoran Desert region represents a compelling environment for understanding the responses of biocrusts to disturbance.

Ongoing investigations into the effects of disturbance have broadly clarified biocrust sensitivity to mechanical disturbances like trampling. However, questions remain about the factors that mediate this response[12-14]. Some studies have noted that different morphotypes of crusts (i.e., the unique combination of constituents present in a given biocrust) respond differently to disturbance, suggesting that some biocrust communities are more resistant to or may benefit from some degree of disturbance[12-14].

Current literature on biocrust disturbance has yet to fully capture shifts at the community level due to disturbances by cattle use, although some have presented evidence for these effects in sheep livestock systems[14]. Few studies exist which characterize disturbance impacts to biocrusts in the semi-arid grasslands of the Sonoran Desert bioregion, and none investigate potential for shifts in community composition resulting from cattle use.

Therefore, this study seeks to answer the following questions: Q1: What biocrust components are common in a representative grassland of the Sonoran Desert bioregion? Q2: Are biological soil crusts reduced along a gradient of disturbance by cattle?; Q2: Are some biocrust morphotypes favored under greater intensities of disturbance?

Through a field study coupled with characterization of biocrust components via microscopy, I evaluated the following predictions:

$P1_0$: *Biocrusts containing cyanobacteria, lichen, and mosses are present in Sonoran Desert grasslands*

$P2_0$: *Biocrust cover does not vary with intensity of use by livestock*
$P2_a$: *Biocrust cover is reduced with increasing use by livestock*

$P3_0$: *Biocrust composition is similar across intensity of use by livestock*
$P3_a$: *Biocrust composition shifts with increasing intensity of use by livestock to favor more resilient biocrust constituents*

Methods

The Santa Rita Experimental Range (SRER) is an approximately 21,000-hectare research range that lies at the base of the Santa Rita Mountains in southeastern Arizona. The landscape of the region is characterized by alluvial fans with a shallow slope at the elevations where this study was conducted. Vegetation communities at the SRER have shifted in recent history, including expansion of velvet mesquite (native; *Prosopis velutina*) and Lehmann's lovegrass (introduced; *Eragrostis lehmanniana)* across most of the range[15]. Common understory vegetation additionally includes *Opuntia* spp. and other cactaceae, perennial grasses, and annual forbs.

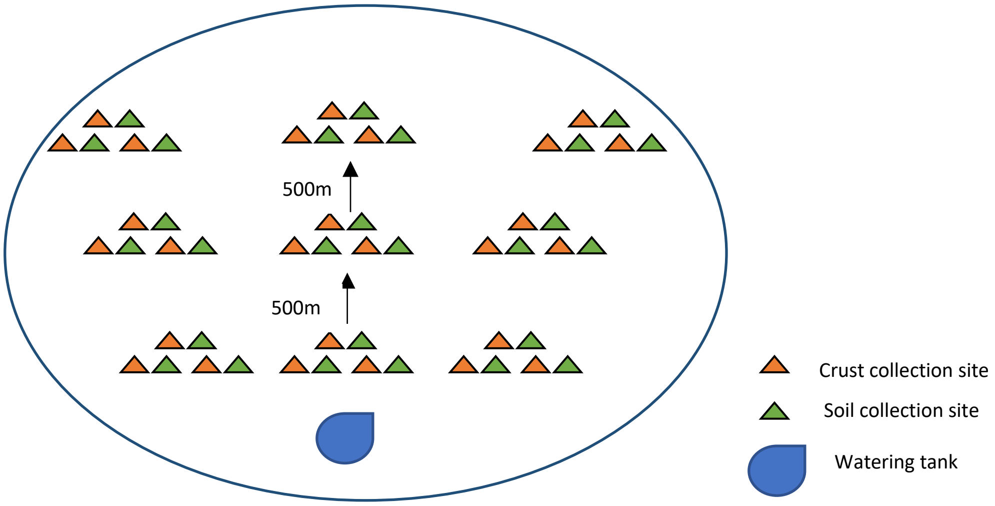

***Fig. 1**. Study design at one of three plots considered at Santa Rita Experimental Range. For each plot, nine collection 'sites' with 6 samples at each (3 biocrust and 3 bare soil) were considered.*

Experimental design

I established one plot on each of three pastures at SRER. Each plot contained a cattle watering tank. The distance between watering tanks was 3.2 km, corresponding to distances between plots.

The three pastures considered in this study are geographically adjacent and are similar in terms of soil, precipitation, and vegetation characteristics (Table 2). Historical use by cattle is similar between the SR and 5S pastures, and roughly two times more on the W plot across its recorded history (Table 1).

Table 1. *Average grazing use intensity across 5, 10, and 30 years and number of biocrust communities sampled per pasture. AUY = Animal Units Per Year. All history includes all recorded grazing intensity history for the pasture until 2020 (one year prior to survey and collections). Data sets were provided by the Santa Rita Experimental Range Digital Database. Funding for the digitization of these data was provided by USDA Forest Service Rocky Mountain Research Station and the University of Arizona.*

Plot	Avg. AUY/ha all history	Avg. AUY/ha 1990-2020	Avg. AUY/ha 2010-2020	Avg. AUY/ha 2015-2020	Number of biocrusts collected
W	0.042	0.036	0.024	0.026	27
SR	0.021	0.016	0.018	0.018	24
5S	0.020	0.015	0.018	0.017	24

In each plot, a piosphere design was used to approximate disturbance intensities (Fig. 1)[16]. At each cattle tank, three 1000m transects were established. Along each transect, three sample points were defined: 50m, 500m, and 1000m from the cattle tank. Distance from watering tank was considered as a proxy for intensity of use by cattle, where increasing proximity to the tank was considered increasing use[16]. At each sample point along each transect, three biocrust samples and three bare soil samples were collected.

I collected biological soil crusts and soil samples at SRER in September 2021. I collected samples and metadata for 75 individual biocrust communities across three pastures at SRER (Table 1). At each sample point, a 1m^2 quadrat was placed around a representative biocrust. Within each quadrat I recorded metadata including biocrust cover and abundance, vegetation cover and abundance, and dominant biocrust morphotype.

Biocrust collections were dried in the lab to prevent mold growth. Field characterizations of morphotype were confirmed via dissecting microscope, and crusts containing lichens were identified to genus[17]. I confirmed lichen identities with descriptions from the Consortium of North American Lichen Herbaria lichen portal[18].

Table 2. *Soil type and description for study pastures at Santa Rita Experimental Range. Soil characteristics were similar across all pastures. Data sets were provided by the Santa Rita Experimental Range Digital Database. Funding for the digitization of these data was provided by USDA Forest Service Rocky Mountain Research Station and the University of Arizona.*

Plot	Soil Type	Soil Description
5S	Hayhook-Pajarito complex	2-15% gravel, loamy sand; mixed parent material; well drained; moderately rapid permeability; water capacity low to moderate; Slow runoff
	Agustin sandy loam	5-15% gravel, sandy loam; mixed parent material; well drained, moderately rapid permeability; low to moderate water capacity; slow runoff
SR	Hayhook-Pajarito complex	2-15% gravel, loamy sand; mixed parent material; well drained; moderately rapid permeability; water capacity low to moderate; Slow runoff
W	Combate-diaspar complex	5-20% gravel; loamy sand; mixed parent material; well drained; moderately rapid permeability; water capacity low; slow runoff
	Hayhook-Pajarito complex	2-15% gravel, loamy sand; mixed parent material; well drained; moderately rapid permeability; water capacity low to moderate; Slow runoff
	Sasabe-Baboquivari complex	0-10% gravel, sandy loam; mixed parent material; well drained, moderately slow permeability; water capacity high; slow to medium runoff

Results

Biocrusts were abundant in all three study plots at SRER. Biocrust composition included cyanobacteria, lichen, and moss (Fig. 2). Among 75 biocrust samples, I defined 24 unique biocrust morphotypes, which accounted for unique combinations of cyanobacterial type, lichen species, and presence/absence of moss (Table 3).

Black and green cyanobacteria were present in 89.4% (n = 66) of biocrusts. Mosses or other bryophytes were observed in 23.6% of crusts (n = 18). Lichens were present in 31.5% (n = 24) of crusts sampled, including *Endocarpon* spp., *Collema* spp., *Placidium* spp., *Peltula* spp., and two unidentified species. Moss species identifications are not reported as the features required for identification were not present at the time of collection.

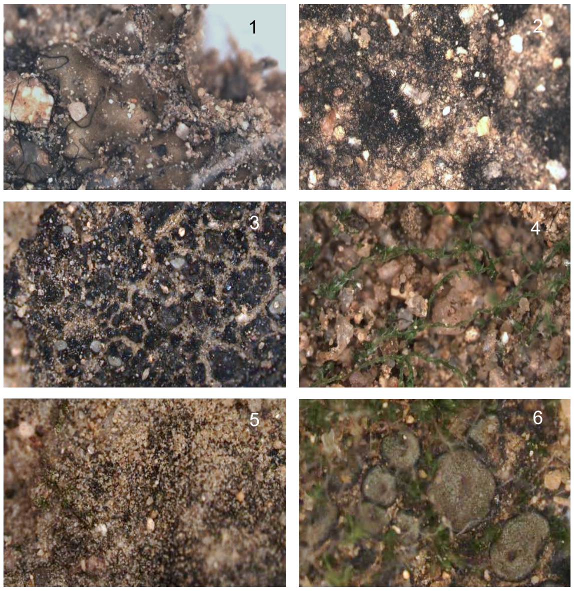

Fig. 2. Representative biocrusts from SRER, collected September 2021: 1, cyanobacteria and lichen; 2, cyanobacteria; 3, lichen; 4, moss; 5, cyanobacteria and moss; 6, moss and lichen.

Across all pastures, biocrust cover increased with distance from watering tank (logit-transformed biocrust cover, analyzed via linear regression with pasture as a random effect: $r^2 = 0.19$, $P =$ 0.0084, Fig. 3). Model exploration indicated that this relationship was not further explained by variation in vegetation cover (linear regression, $r^2 = 0.17$, $P = 0.0339$). Average biocrust cover across all pastures was 10% at 50m from the watering tank, 24% at 500m from the watering tank, and 21% at 1000m from the watering tank.

Biocrust cover differed between the points closest to water tanks (50m) and those 500m and 1000m away (post-hoc t-tests, respectively: 50m-500m, $P = 0.0028$; 50m-1000m, $P = 0.0093$). Cover was similar at 500m and 1000m ($P = 0.6509$).

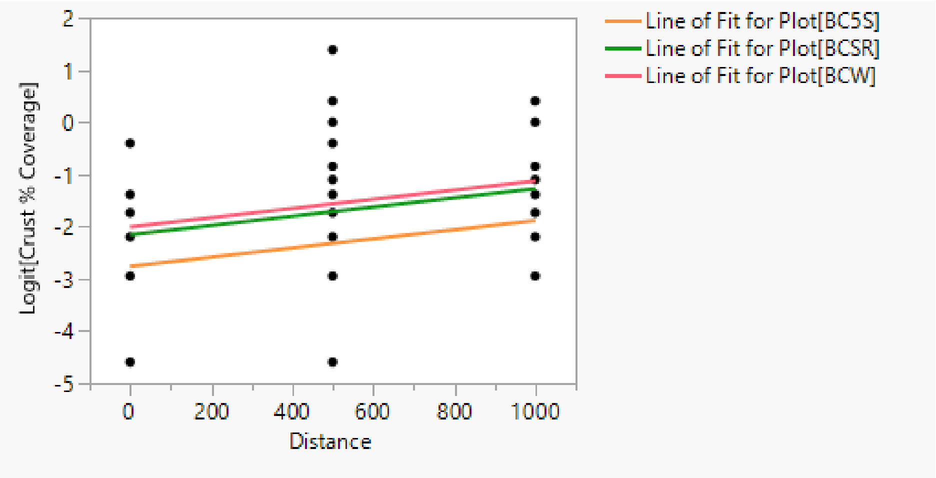

***Fig.3.** Logit-transformed percent cover of biocrusts increased with distance from water tanks linear regression with pasture as a random factor. Colors correspond to pastures: blue = 5S, red = SR, green = W. X-axis: distance from tank, in meters.*

Biocrusts that included lichens and/or mosses were more common on the W pasture than 5S or SR pastures (Table 1, chi-sq = 10.24, dF = 2, *P* = 0.0060). Mosses and lichens were present in 33.0% (n = 8) of crusts on the 5S plot, 20.8% of crusts on the SR plot (n = 5), and 63.0% (n = 17) of crusts sampled in the W pasture. Lichens and mosses were more common at greater distance from the watering tanks, whereas cyanobacteria were more common near the tanks (Fig. 4, chi-sq = 7.43, dF = 2, *P* = 0.0244).

Richness of lichen species was similar between plots SR and W, with four and five species represented at each respectively. In contrast, only two lichen species were represented at the 5S plot.

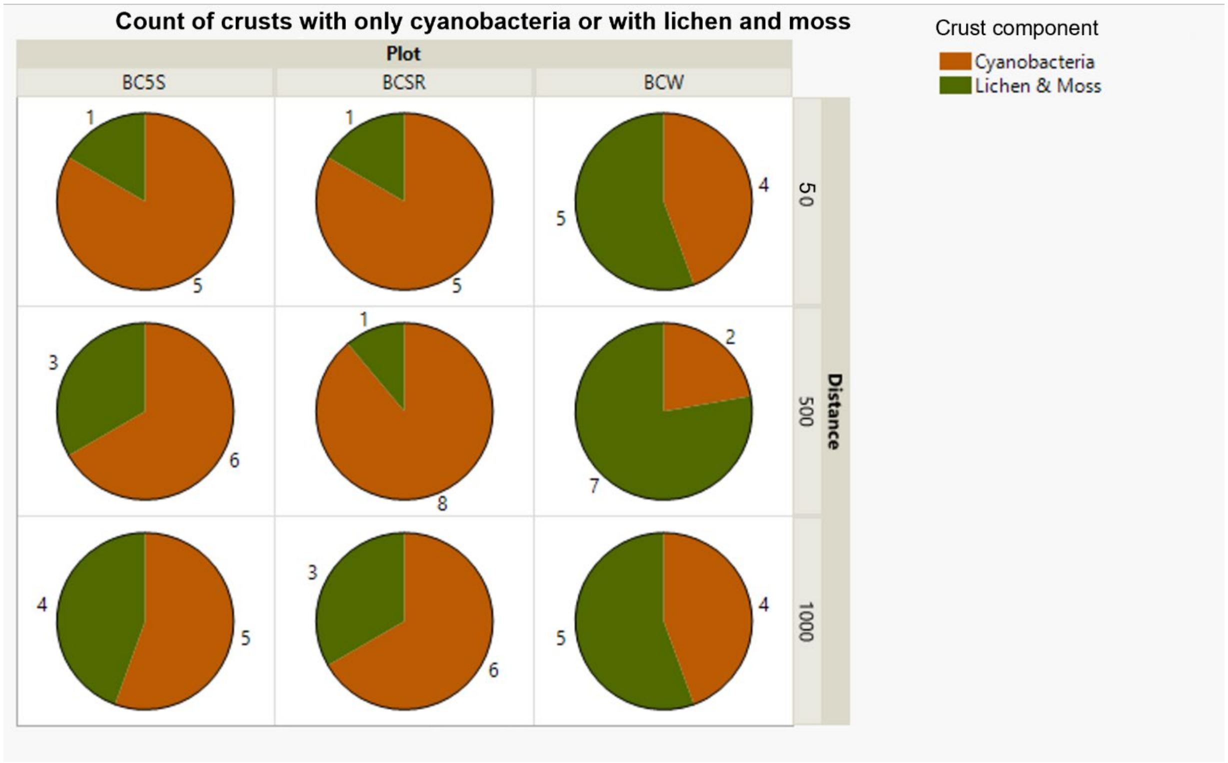

Fig.4. *Count of observed biocrusts with lichens or mosses present (green) vs. those that contain only cyanobacteria (orange) across three study pastures and three distances (m) from watering tank. Biocrusts containing lichens and mosses tended to be more common on plots with greater historical grazing use (BCW, see Table 1 for historical grazing intensity), and at greater distances from watering tank.*

Table 3. *Frequency of unique biocrust morphotype occurrence across each plot as a percent of total crusts sampled on that plot. Morphotypes were characterized via examination on a dissecting microscope, and all visible crust components were included. Morphotype characterizations are cyanobacterial type (black/green), lichen genus, and presence/absence of moss.*

Plot	black	green	black, green	black, moss	moss	black, green, moss	Endocarpon	Endocarpon, moss	black, Endocarpon, moss	black, green, Endocarpon, moss	Placidium	black, Placidium	black, green, Placidium	black, Placidium, moss	black, green, Placidium, moss	black, Peltula	Peltula moss	black, Peltula, moss	black, green, Peltula, moss	Collema	green, Collema	Collema, moss	Unknown lichen	black, Unknown lichen
W	0.1	0.03	0.40	0.03		0.03	0.07		0.03		0.03	0.03		0.03	0.07	0.03				0.03			0.07	
5S	0.88											0.08						0.04						
SR	0.04		0.23	0.08	0.04	0.04		0.04		0.04		0.15	0.04			0.04	0.04	0.04	0.04		0.04	0.08		0.04

Discussion

Biological soil crusts influence ecosystem function and services in arid ecosystems and may be impacted by land uses like livestock grazing. To gather insight on the influence of disturbance by cattle on biological soil crusts in the Sonoran Desert bioregion I evaluated the cover and composition of biological soil crusts across gradients of cattle use in a southern Arizona grassland.

I predicted that biocrust cover would be reduced and biocrust communities would shift under greater disturbance. I found that biocrust cover and community composition varied relative to the intensity of use by cattle across three pastures at SRER. Increasing cover by biocrusts with distance from watering tank is consistent with predicted negative effects of trampling by cattle, and the findings of previous studies[8,14,19]. Model exploration indicated that variation in vegetation cover did not improve model fit. Thus, edaphic and topographic factors that structure vegetation and biocrust distribution are likely not responsible for variation in biocrust cover.

Biocrust cover varied among pastures with a range of historical grazing use intensities (Table 1). Given that biocrust cover differed as a function of distance from tanks, acute disturbances may have a stronger influence on local biocrust cover than does chronic land use by cattle. In that scenario, expedient biocrust recolonization would be expected to foster short-term recovery. Alternatively, disturbance-related reductions in biocrust cover could be offset by other functions of cattle use such as nutrient deposition. Such inputs could lead to similar or increased biocrust cover in pastures with greater cattle use when compared to those with lesser use[14].

Dominant biocrust morphotypes varied as a function of distance from water tanks. Bryophytes and lichens may be more resilient to disturbance by cattle than cyanobacteria or may benefit from some moderate levels of disturbance. Crusts containing bryophytes and lichens may also benefit from nutrient-deposition by cattle[20].

Importantly, the study sites used in this work were not chosen randomly. Water tanks are not distributed randomly across the landscape, and their position may speak to topography or other factors that could influence our interpretation. Similarly, estimates of cover were made in a $1m^2$ area around a central biocrust, which were nonrandomly selected. Finally, more visible crusts – especially those that are larger or more developed, may have been selected, potentially leading to biases in our morphotype data or coverage estimates. To address these concerns, I made an effort to collect crusts across the range of development wherever possible. Collections occurred during the summer monsoon season in an especially wet year, which may have caused increased visibility of cryptic biocrusts[17].

In future steps, microfungal DNA extracted from collected biocrusts will be sequenced using the high-throughput Illumina MiSeq platform. Bioinformatic analysis of sequencing data will provide insight into microfungal community-level shifts across livestock use intensities. Additionally, bioinformatic data will contribute to the limited data available on common microfungal constituents among biocrust morphotypes in the Sonoran Desert bioregion. These data may inform our understanding of the unique mycological niches of biological soil crusts in Sonoran Desert grasslands. Furthermore, these data will enable contribution to the disturbance ecology literature, particularly as it relates to ongoing controversy in the acceptance of the intermediate disturbance hypothesis broadly, and in mycological applications[21].

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