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Can biological soil crusts be prominent landscape components in rangelands? A case study from New Mexico, USA

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ABSTRACT

To sustainably manage rangelands, it is paramount that all agents of soil health are considered in conservation practices. Yet, our understanding of the extent and importance of biological soil crust (hereafter biocrust) as a component of rangeland health and quality is limited. The objective of this project was to quantify and characterize rangeland biocrusts within a region of New Mexico, USA, for which soil microbes have yet to be considered in rangeland health assessments: the Rio Puerco Watershed. Moreover, we examined the influence of biocrust on soil aggregate stability as key ecosystem service in a landscape prone to erosion. We further assessed the relationships between biocrust abundance and community composition with soil properties. We found that biocrusts covered an average of 41% of plant interspaces throughout all sampling locations (n = 20), with the most abundant types being incipient and light cyanobacterial crusts, which tend to be more cryptic in appearance. Soil surface stability was greater than subsurface stability and biocrust cover was positively related to soil surface stability. Light cyanobacterial and cyanolichen crusts were the primary biocrust types related to soil surface stability, especially on sites with unconsolidated subsurfaces. Physical soil crusts were also a major landscape component covering an average of 21% of the soil and were important for subsurface stability. These findings reflect the importance of biological and physical soil aggregating processes in dryland systems. Several environmental variables were related to biocrust community composition and aggregate stability, with surface soil texture, salt contents, pH, and soil nitrogen ions having the strongest relationships. This study expands the biocrust characterizations of drylands in a region that has received little attention. It further contributes new insights on how biocrust and soil microbial communities may play a role in influencing rangeland health, providing much needed data for a watershed characterized by its high susceptibility to soil loss.

1. Introduction

Drylands are characterized by limited primary productivity, low and unpredictable rainfall, and high potential evapotranspiration. They cover over 40% of earth's land surface (MEA, 2005; Reynolds et al., 2007; Hoover et al., 2019) and are home to 38% of the world's human population (MEA, 2005; Reynolds et al., 2007; Huang et al., 2015). These areas face increasing resource demands from the rapidly growing human population, which highlights the importance of understanding dryland ecosystems, their health, and their functions (MEA, 2005; Herrick et al., 2013).

A long history of dryland research exists on how abiotic factors, such as soil attributes, climate, and anthropogenic disturbance regimes, as well as ecosystem processes such as nutrient cycling, interact with aboveground macroscopic ecosystem components. For example, changes in temperature (Walker, 1992) and disturbance levels (Eldridge et al., 2013) have significantly influenced the structure of plant communities in drylands and caused major community shifts, as described in

Abbreviations: RPW, Rio Puerco Watershed; IC, incipient crust; LCC, light cyanobacterial crust; DCC, dark cyanobacterial crust, CLC, cyanolichen crust, GLC, green algal lichen crust, RMC, rough moss crust, and SMC, smooth moss crust; PC, physical soil crust; PC-CC, physical soil crusts that are covered with a thin cyanobacterial biofilm; nMDS, non-metric multidimensional scaling; RI, relative importance; EC, electrical conductivity; SAR, sodium absorption ratio; K, potassium; Mg, magnesium; Na, sodium; NO_3^-, nitrate; NH_4^+, ammonium; P, phosphorus.

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dryland state and transition models (Ritten et al., 2017). Although shifts in soil microbial communities may occur as well, information regarding their influence on site resilience is often missing from these state and transition models, despite the critical ecological roles soil microbes play in soil aggregation, biotic interactions, biogeochemical and hydrological cycling (Makhalanyane et al., 2015; Lee et al., 2016; Eldridge et al. 2020). In low resilience drylands, neglecting essential ecosystem components such as soil microbial communities limits our fundamental understanding of the structure and function of these systems. Therefore, it is important to improve our knowledge of how macroscopic and microscopic communities interact, which environmental pressures influence them, and how their community changes influence site properties like resilience and stability.

Examples of important soil microbial communities common to drylands are those forming biocrusts (Eldridge and Greene, 1994). Biocrust can be found within the first few centimeters of the soil surface in seemingly unpopulated plant interspaces. Microbes in biocrust assemble in complex communities of cyanobacteria, other bacteria, eukaryotic algae, fungi, lichen, and bryophytes (Belnap et al., 2016). These communities can be differentiated into biocrust types based on their dominant photoautotrophs: 1) incipient crusts are weakly consolidated, composed of primarily filamentous cyanobacteria and fungi, 2) light cyanobacterial crusts are largely formed by filamentous cyanobacteria, eukaryotic algae, and fungi, 3) dark cyanobacterial crusts are dominated by cyanobacteria producing dark sunscreen pigments which allow them to live on the soil surface, 4) lichen crusts are the result of symbiosis of fungi and either green algal (in green algal lichens, as known as chlorolichens) or cyanobacterial photobionts (in cyanolichens), and 5) bryophyte crusts are dominated by liverworts or mosses of different growth forms (millimeter small moss plants without hair-like extensions versus centimeter tall moss plants with or without hair-like extensions) (Pietrasiak et al., 2013). Bryophyte crusts can also be symbiotically associated with cyanobacterial species such as *Nostoc* spp. (Zhao et al., 2010; Pietrasiak et al., 2013; Arróniz-Crespo et al., 2014).

These biocrust types contribute differently to ecosystem functions (Evans and Johansen, 1999; Belnap, 2003; Bowker et al., 2013; Pietrasiak et al., 2013). For example, after a disturbance event, incipient crusts can aid in initial soil surface stabilization and aggregation (Pietrasiak et al., 2013). As the establishment of biocrust organisms progresses, light cyanobacterial crusts begin to form and provide increased soil stability. Many filamentous cyanobacteria produce sheaths or mucilage made up of various sticky polysaccharides, which cause soil particles to aggregate (Chock et al., 2019). Other exopolysaccharides are released into the soil solution and behave as chelating agents, improving nutrient availability (De Philippis and Vincenzini, 1998; Pereira et al., 2009; De Philippis et al., 2011; Kidron et al., 2012; Mota et al., 2016). These earlier successional types are important for the establishment of later successional crust types like dark cyanobacterial, lichen, and moss crusts, which have greater microbial biomass and exopolysaccharide production, increased abundance of nitrogen fixing taxa, and a development of root-like structures in lichens and mosses. These biocrusts influence soil hydrological processes more strongly, increase nutrient fixation, stabilize soil more effectively, and perform an overall wider range of ecosystem functions (Evans and Johansen, 1999; Maestre and Cortina, 2002; Eldridge et al., 2010; Kidron et al., 2012; Pietrasiak et al., 2013; Belnap et al., 2016; Faist et al., 2017). However, in actively managed rangelands an extensive coverage of late-successional biocrust types is less likely to occur due to frequent disturbance impacts (Garcia et al. 2015). Therefore, ecosystem service contributions by biocrusts in these rangelands may be restricted to the presence of early successional biocrust types.

As biocrust communities can impact the structure, biogeochemistry, and fertility of dryland topsoil, inherent physical and chemical soil properties reciprocally shape biocrust community composition and distribution. Soil texture, pH and electrical conductivity are well known drivers of variability in biocrust abundance and composition at local to ecoregional scales (Johansen et al, 2001; Bowker et al. 2016). In general, fine-textured soils with neutral to slightly alkaline pH and elevated electrical conductivity seem to foster biocrust development (Anderson et al., 1982; Johansen et al, 2001; Thompson et al., 2006). In contrast, relationships with specific elements such as nitrogen, phosphorus, potassium, and micronutrients are more complex and often site specific (Bowker et al. 2016). Further, unique feedbacks or unexpected complexities have been revealed at the local to regional scales, based upon parent material and geomorphology influences (Pietrasiak et al. 2011a, 2014). For example, fine texture, pH, and electrical conductivity did not necessarily impact biocrust development, but granitic gravel cover positively influenced biocrust establishment and functioning in the Mojave and Colorado Deserts (Pietrasiak et al. 2011a, 2014; Herrick et al., 2010). In another study, complex feedbacks between grazing, geomorphology, and soil texture were revealed in rangelands in the Monte Desert, Argentina (Garcia et al. 2015). With these known complexities across locations, understanding site specific relationships can help further guide our understanding of biocrust dynamics.

Because different biocrust communities provide various ecosystem functions and can be influenced by unique combinations of abiotic and biotic factors, the use of biocrust types can be an important management tool (Bowker et al., 2014). This may be particularly useful when biologically characterizing areas of interest, evaluating an area for expected and/or desired ecosystem services, and assessing an area's resistance and resilience to disturbance (Walker, 1992; Chilton et al., 2017). Yet, for many North American rangelands baseline data on biocrust abundance and composition are sparse, as they are often inconspicuous and not routinely considered as indicators for rangeland health and quality. Our objectives for this study were to 1) quantify the extent and characterize the diversity of biocrusts in managed drylands of the Rio Puerco Watershed; 2) contribute new insights on how biocrust soil microbial communities may influence rangeland health, contributing to soil stability in a managed landscape facing a high erosion potential; 3) investigate the edaphic factors that influence biocrust community abundance and composition within a rangeland setting. In conclusion, we offer management implications guided by the findings of our study, towards sustainable rangeland use in drylands.

2. Materials and methods

2.1. Study area

Approximately 50% of New Mexico, USA, is classified as rangeland. A large proportion of these lands face conditions typical of drylands, having a long history of land use including livestock grazing, and high susceptibility to soil loss. As a result, many areas in New Mexico face soil degradation and entrenchment such as found in the Rio Puerco Watershed (RPW). For example, in a sub-watershed of the Rio Puerco, Gellis et al. (2004) found sedimentation rates for alluvial valley floors to average 2.76 kg m^{-2} y^{-1}.

The Rio Puerco Watershed encompasses about 1.58 million ha and is located in west-central New Mexico representing the southernmost extent of the Colorado Plateau ecoregion, a cold desert with arid grasslands and shrublands at lower elevations transitioning into woodlands as elevation increases (Bailey, 1980). Precipitation occurs in the form of winter snowfall and monsoon rains, with the latter occurring mainly as intense convection storms from July through September. The mean annual precipitation ranges from 203 to 406 mm depending on location within the basin, with high inter-annual variability (Vincent, 1992; Scurlock, 1998; Greene et al., 1999). Dominant vascular plants include shrubs and subshrubs such as Wyoming big sagebrush (*Artemisia tridentata*), rubber rabbitbrush (*Ericameria nauseosa*), and broom snakeweed (*Gutierrezia sarothrae*). Warm season perennial grasses include blue grama (*Bouteloua gracilis*), sand dropseed (*Sporobolus cryptandrus*), and alkali sacaton (*Sporobolus airoides*) in lowland areas with finer soil texture. Cool season grasses are underrepresented but include western wheatgrass (*Pascopyrum smithii*) and Indian ricegrass (*Acnantherum hymenoides*) (Vincent, 1992).

Geologically the Rio Puerco Watershed is characterized by underlying Cretaceous and Tertiary marine shales and sandstones that have been sculpted into mesas and badlands. We focused our study on an area southwest of Cuba, New Mexico, in the Major Land Resource Area 36 (Southwestern Plateaus, Mesas, and Foothills, Fig. 1). The two dominant Ecological Sites within this region are the Sandy Savannah Ecological site and the Loamy Ecological Site. Salty Bottomland, Loamy Upland, and Limy Ecological Sites are also scattered throughout the region. Dominant soil classes within the area are Typic Torripsamments, Typic Torriorthents, and Ustic Haplargids (Soil Survey Staff, 2018). Within these Ecological Sites, soil texture is highly variable ranging from coarse-textured, deep soils, such as sandy loams, to finer-textured, poorly drained soils found mainly in lowlands (Gellis et al., 2004).

The Rio Puerco Watershed has a long history of human influence. Prior to European settlement the Rio Puerco Watershed was used for small areas of irrigated agriculture and populated by both Navajo and Pueblo people. During Spanish settlement unsustainable grazing practices were introduced (Scurlock, 1998; Aby et al., 2016). Since then, the watershed has experienced extensive soil degradation, driving a plant community shift from grasslands dominated by cool season species to a dense shrubland dominated by Wyoming big sagebrush (Greene et al., 1999; Coleman et al., 2001; Phippen and Wohl, 2003). Water quality and soil loss have been concerns in the Rio Puerco Watershed for decades (Gellis et al., 2004). Therefore, it has been the focus of management practices such as grazing through seasonal stocking and brush management in the form of herbicide application and mechanical treatments, with the goal of decreasing shrub cover while increasing herbaceous plant cover (BLM, 2012).

We performed our study in the northern portion of the Rio Puerco Watershed (Fig. 1) along the northern edges of the Rio Puerco River and the northeastern edges of the Arroyo Chico, a tributary of the Rio Puerco River (Fig. 1). Study sites were randomly established as part of a long-term monitoring project observing the effects of herbicide treatments on vegetation and soil biological community dynamics (Schallner, 2019). Our study was conducted before any herbicide treatments were applied. Sites were examined for biocrust abundance, composition, soil aggregate stability, and a suite of soil chemical and physical properties, with site being our experimental unit (n = 20, Fig. 1).

2.2. Biocrust quantification – cover and community composition

Soil cover, including biocrust, was estimated using the quadrat point intercept method with a 0.5 m^2 frame containing 25 intersections. Quadrat placement was performed using a 50 m "main" transect set up at each of the 20 sites (Fig. 2). Along this main transect there were a total of five perpendicular 15 m transects every 10 m (Fig. 2). For each 15-meter transect, two to three 0.5 m^2 quadrats were read between one and nine meters away from the perpendicular transects yielding a total of 13 quadrats scored per site (Fig. 2). Quadrats were placed in shrub interspaces, as that is where biocrusts are typically found to have the strongest impact on soil stability (Eldridge and Leys, 2003; Housman et al., 2007). In rare cases (<2%) where initial placement of quadrats would have included a shrub base, quadrats were moved to the nearest shrub interspace. This design yielded 325 soil cover points for each site (i.e., 13 quadrat locations × 25 intersections).

Soil cover was assessed following the methodology outlined in Belnap et al. (2001) and Herrick et al. (2017, Fig. 1D). Biocrust types were recorded as functional groups and were identified using morphological characteristics according to Pietrasiak et al. (2013) and Pietrasiak (2014). Groups distinguished included incipient crust (IC), light cyanobacterial crust (LCC), dark cyanobacterial crust (DCC), green algal lichen crust (GLC), cyanolichen crust (CLC), smooth moss crust (SMC) and rough moss crust (RMC) (Table 1). Presence of any physical or chemical crusting (PC), or physical crusting with presence of biological filaments attached as a thin biofilm to the physical crust surface (PC-CC), was also recorded but was not considered part of biocrust in a strict sense (Table 1). Evidence of physical crusting included vesicular pores, platy structure, and/or surface cracking; these occurred with finely textured soils. Soil with no aggregation was classified as soil cover category: "bare soil", which represented loose soil particles lacking any detectable aggregation and often associated with sandy textured soils in our study area (see Herrick et al., 2017). Presence of vascular plants was also recorded, including annual grasses, annual forbs, perennial grasses, and perennial forbs. We scored organic surface debris as woody litter, herbaceous litter, or animal dung.

2.3. Soil aggregate stability

At each site we collected a total of 18 surface samples (0–1 cm soil depth) and 18 subsurface samples (1–3 cm soil depth) following the soil depth recommendation by Herrick et al. (2001). In Herrick et al. (2001) a depth of 2–3 cm was associated with the soil layer most likely to be exposed if soil cover components such as vascular plants, biocrusts, or physical soil crusts would be removed by disturbance. Samples used for soil stability metrics were collected along the main transect tape at every 5, 15, 25, 35, and 45-meter mark as well as one meter from the top left side of each soil cover quadrat locations along the perpendicular 15 m transects (Fig. 2). We then performed the Field Soil Aggregate Stability Test according to Herrick et al., (2001, 2017). Briefly, this kit represents a tool to evaluate soil aggregate stability to slaking in water. It can be performed in the field without risking soil structure damage from transportation to a lab. Using visual observations and mechanical dipping in water, soil samples are rated using a scale of 0 for the lowest aggregate stability to 6 representing the highest stability.

2.4. Soil physical and chemical characterization

To characterize soil physical and chemical properties associated with the topsoil and biocrusts we collected 18 soil cores at systematic places along the transects of each site (Fig. 2). We used a 6-cm diameter soil core to a 1-cm depth and composited the 18 soil core samples for subsequent laboratory analysis (Fig. 2). Samples were collected in dry conditions. We sieved composite soil samples through 2 mm mesh and analyzed texture, nutrient contents, pH, electrical conductivity (EC), and sodium absorption ratio (SAR) following standard protocols (U.S. Salinity Laboratory Staff, 1954; Gee and Or, 2002). Percent sand, silt, and clay were determined by a combined Bouyoucos hydrometer and wet sieving method (Gee and Or, 2002). Fine earth fraction was pretreated with 50 ml of 10% sodium hexametaphosphate, then shaken for 24 hr before determining percent clay with the hydrometer. The sample was separated next using a 0.053 mm mesh sieve and dried at 105 °C for 48 h. Recovered sand samples were processed by Brigham Young University's Environmental Analytical Laboratory (Provo, UT) to determine percent of very coarse sand, coarse sand, medium sand, fine sand, and very fine sand fractions.

Soil chemical properties were analyzed using saturated paste extracts by mixing 200 g of soil with deionized water until the soil reached saturation with a 4 hr incubation time (U.S. Salinity Laboratory Staff, 1954). The pH measurements were taken from pastes and analyzed using an Oakton pH 150 m. Each soil solution was then vacuum extracted for all other analyses. Extracts were assessed for electrical conductivity via Fisher Scientific Accumet pH meter, while calcium, magnesium, potassium, sodium, and sodium absorption ratio/sodicity was analyzed by inductively coupled plasma optical emission spectroscopy with an Optima 4300 DV ICP-OES from PerkinElmer Instruments. Ammonium and nitrate were analyzed with a Technicon auto-analyzer by Technicon Industrial Systems. Phosphorus was analyzed with Olsen-P method on a Spec-20 spectrophotometer from Thermo Spectronic.

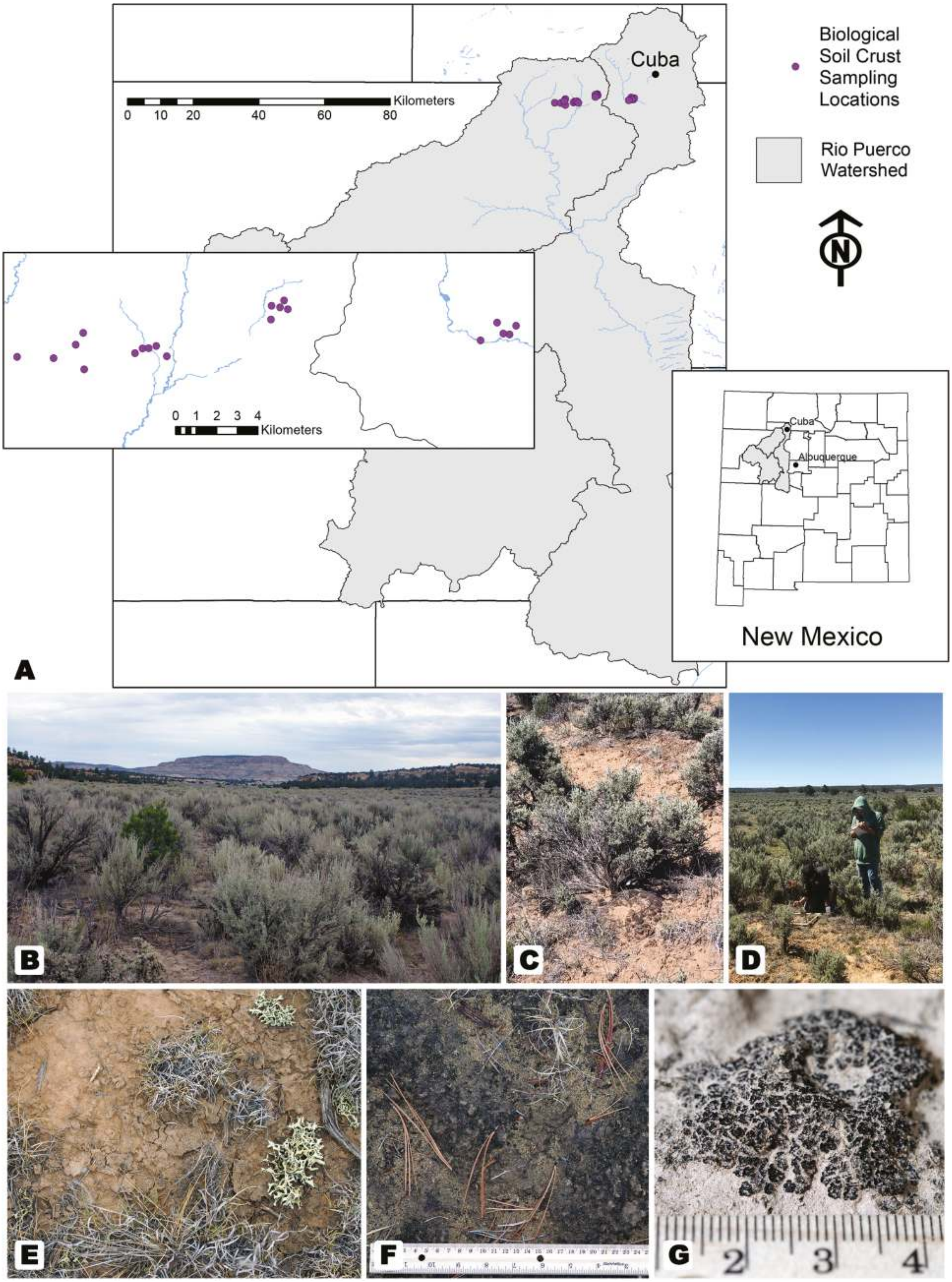

Fig. 1. Map and representative photographs of the study sites within the Rio Puerco Watershed (RPW), New Mexico. A) Map showing the location of the twenty study sites within the watershed; B) Landscape view of the sagebrush communities; C) Late successional biocrusts growing in association of sagebrush; D) Cover measurements using the quadrat point intercept method; E) Typical biocrust communities in RPW rangelands during dry season; F) Typical biocrust communities in RPW rangelands during wet season; G) Close up of cyanolichen *Collema* sp.

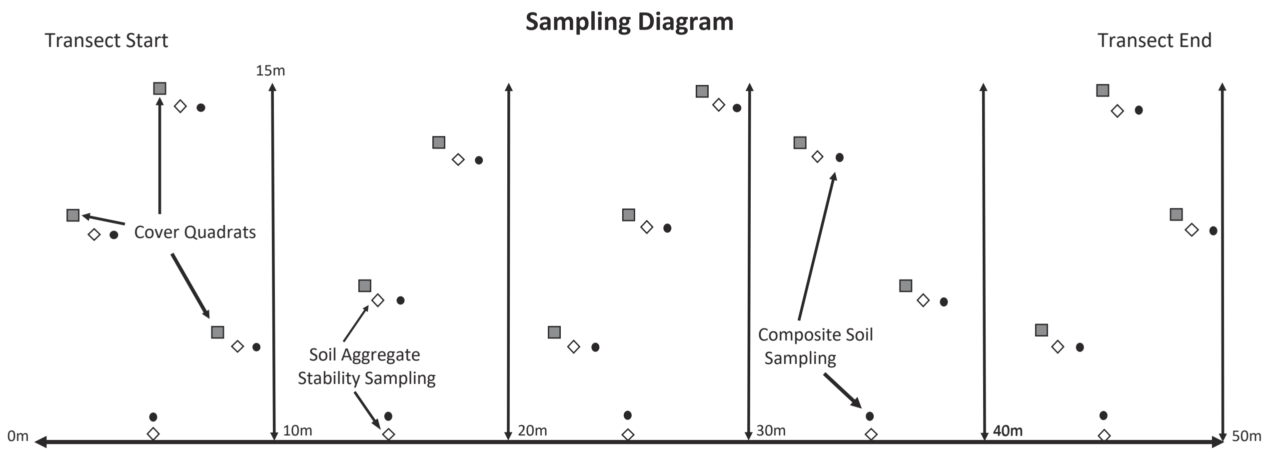

Fig. 2. Sampling schematic showing transect, quadrat, soil aggregate, and composite soil sampling placement.

Table 1
Breakdown of the various functional groups of physical and biological soil crust types used for cover characterization and observed throughout the region of the Rio Puerco Watershed studied.

Code	Functional Group ID	Field Characterization
PC	Physical crust	Soil surface crusting with no signs of algal filaments or other evidence of biological soil crusting. Presence of vesicular pores, platy structure, and/or soil surface cracking.
PC-CC	Physical crust with cyanobacterial biofilm	Evidence of both physical crusting and presence of biological filaments (e.g., cyanobacterial, algal, or fungal filaments) forming a thin layer atop of physical soil crust
IC	Incipient crust	Weakly aggregated and very cryptic biological soil crust. Less developed in comparison to other later successional biological soil crust types. Often populated by filamentous cyanobacteria and fungi.
LCC	Light cyanobacterial crust	More developed, yet still cryptic, biological soil crust that is typically dominated by filamentous cyanobacteria and eukaryotic green algae.
DCC	Dark cyanobacterial crust	Biological soil crust presented by darkening of the soil surface. Often dominated by heterocytous (nitrogen-fixing) cyanobacteria that produce sunscreen pigments.
CLC	Cyanolichen crust	Soil lichens with a cyanobacterial photobiont. Common cyanolichens observed in the region of the Rio Puerco Watershed include: *Collema* spp. and *Peltula* spp.
GLC	Green algal lichen crust	Soil lichens with a green algal photobiont. Common green algal lichens observed in the region of the Rio Puerco Watershed include: *Clavascidium lacinulatum* and *Aspicilia* spp.
SMC	Smooth moss crust	Moss crust in the form of a smooth carpet on the soil surface. Most commonly observed in the region of the Rio Puerco Watershed include: *Bryum* spp.
RMC	Rough moss crust	Moss crust with more pronounced morphological features (e.g., awns or extended midribs) and typically found to be larger. Most commonly observed in the region of the Rio Puerco Watershed include: *Syntrichia* spp.

2.5. Statistical analyses

All statistical analyses were completed with R Version 3.4.3 (R Core Team, 2017). We used descriptive statistics to characterize biocrust abundances (cover) and their variability. A paired *t*-test was used to compare the soil surface and subsurface aggregate stability scores. Normality of soil cover was tested using the Shapiro-Wilk test with the *shapiro.test* function. Due to lack of normality in many variables, subsequent correlation analyses were performed using the Spearman's rank correlation, a non-parametric alternative that returns the ranked correlation coefficient, rho (Spearman, 1904). We first correlated surface and subsurface aggregate stability indices to abundance of physical and biological soil crusts. To assess the relationships between biocrust functional group abundance, biocrust community composition, and soil variables, we then used Spearman correlation analysis, multiple linear regression analysis, and non-metric multidimensional scaling (nMDS). Significance of relationships was tested against a threshold of 0.05. Correlograms were used to visualize the strength of linear correlations between bare soil, physical crusts, and biocrust functional groups with soil chemical and physical variables. We conducted multiple linear regression models with soil chemical characteristics only, soil physical characteristics only, and the combination of physical and chemical characteristics, to investigate which of these affect different biocrust types the most. We also estimated the relative importance (RI) value of each soil property from linear regression models, quantifying the contributions of individual variables to the R^2 of the linear regression models (Grömping 2006, 2007). Further, we used nMDS to investigate the similarities/dissimilarities of biocrust types in ordination space calculated with Bray Curtis dissimilarities within the *vegan* package (Oksanen et al., 2018). We then used the *envfit* function to relate and visualize the effects of soil environmental variables on biocrust community composition. Soil variables included: % clay content, % very fine, medium, and very coarse sand, available water content, surface aggregate stability index, subsurface aggregate stability index, pH, EC, SAR, NO_3^-, P, K, NH_4^+, Ca, Mg, and Na contents, A Mantel test was employed to relate environmental variables to biocrust composition by correlating our BSC compositional matrix with the environmental data matrix (Oksanen et al., 2018). Data and R code are available at GitHub under the following link: https://github.com/npietras/Stovall_et_al_RangelandBiocrust.

3. Results

3.1. Extent and composition of biocrust in rangelands of the northern Rio Puerco Watershed

Biocrust, regardless of successional type, covered an average of 41.15 ± 5.95% (mean ± SE) of the shrub interspace soil surface throughout the study areas, with total cover ranging from 0% to 79.1% across sites (Fig. 3A, Table 2). Cyanobacterial crusts were the dominant crust type and alone covered up to 78.8% of shrub interspaces. Within cyanobacterial crusts functional groups such as incipient (19.60 ± 3.90%) and light cyanobacterial crust types (19.17 ± 4.32%) were the most abundant (Table 2; Fig. 3B). Cover percentages of dark cyanobacterial, lichen, and moss biocrusts were very low for all study areas (Fig. 3B). Lichen crusts reached a maximum of 5.8% and moss crusts covered a maximum of 4.6%. The most common lichens observed throughout the sites included the cyanolichen *Collema* spp. and the green algal lichen *Clavascidium lacinulatum*. Common moss crusts

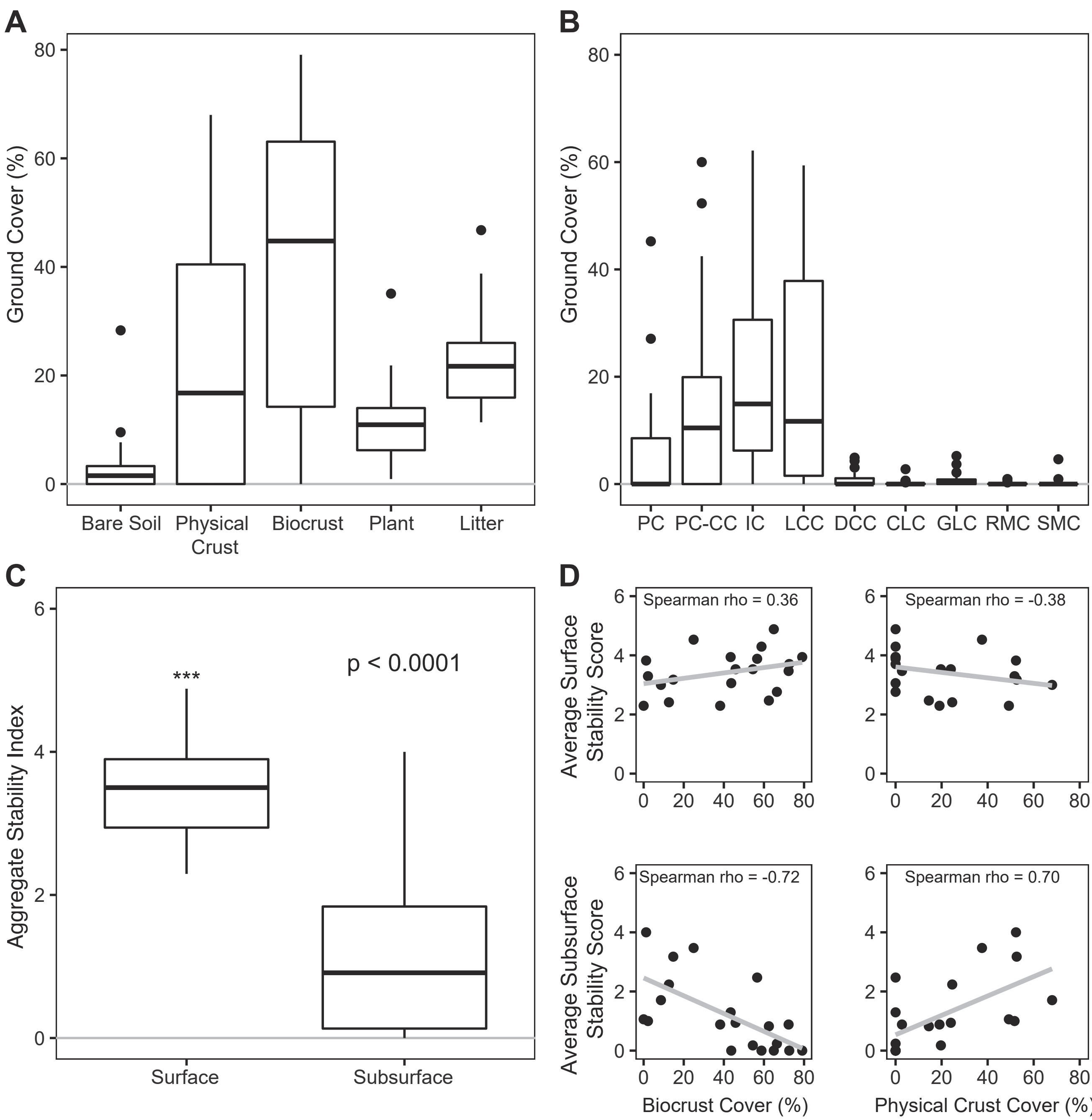

Fig. 3. A) Boxplot showing the percent ground cover for categories recorded plant interspaces in the Rio Puerco Watershed: BS = bare soil; PC = crust formed predominantly by physical processes which includes physical crusts and physical crusts with a thin cyanobacterial/algal biofilm layer atop; BSC = biocrusts including incipient, light cyanobacterial, dark cyanobacterial, cyanolichen, green algal lichen, rough moss, and smooth moss crusts; Grass = annual and perennial grasses; Forb = annual and perennial forbs; Litter = woody and herbaceous litter as well as animal dung; B) boxplot of biocrust cover broken down into crust community types. Biocrust types include: IC = incipient crust; LCC = light cyanobacterial crust; DCC = dark cyanobacterial crust, CLC = cyanolichen crust, GLC = green algal lichen crust, RMC = rough moss crust, and SMC = smooth moss crust. PC-CC is a physical soil crust covered with a cyanobacterial/algal biofilm. C) Boxplot demonstrating the difference in soil aggregate stability score between surface and subsurface aggregates for the rangelands studied in the RPW.

Table 2
Table with percent ground cover of uncrusted soil (BS), physical soil crusts (PC, PC-CC), and biocrust functional groups (all other) observed throughout the region of the Rio Puerco Watershed studied. BS = bare soil, PC = physical soil crust, PC-CC = physical crust with cyanobacterial/algal biofilm, LCC = light cyanobacterial crust, DCC = dark cyanobacterial crust, GLC = green algal lichen crust, CLC = cyanolichen crust, SMC = smooth moss crust, RMC = rough moss crust.

	Soil Crust Characteristics by Functional Groups (% Ground Cover)									
Site ID	BS	PC	PC-CC	IC	LCC	DCC	CLC	GLC	RMC	SMC
MPT2	0.0	16.9	20.6	3.7	11.7	4.9	2.8	1.9	0.0	0.0
MPT3	0.0	0.0	52.3	0.0	0.0	0.9	0.3	0.0	0.0	0.0
MPT6	0.6	0.0	0.0	30.2	36.3	4.3	0.6	0.3	0.9	0.0
MPT7	0.0	0.0	0.0	18.5	38.2	0.0	0.0	0.0	0.0	0.0
MPT8	28.3	0.0	0.0	32.0	11.7	0.0	0.0	0.0	0.0	0.0
VWT3	1.2	0.0	0.0	14.8	37.9	0.3	0.6	5.2	0.0	0.0
VWT5	2.8	0.0	0.0	32.6	10.5	0.0	0.0	0.3	0.0	0.0
VWT7	0.0	0.0	0.0	23.7	41.2	0.0	0.0	0.0	0.0	0.0
VWT8	0.3	0.0	0.0	40.9	37.9	0.0	0.0	0.0	0.3	0.0
VWT10	1.9	2.8	0.0	7.1	59.4	2.2	0.0	3.7	0.0	0.0
JPT1	0.9	1.5	17.5	15.1	19.1	3.1	0.0	0.0	0.9	0.0
JPT2	6.2	0.0	14.5	12.0	49.2	0.0	0.0	0.0	0.3	0.9
JPT3	0.0	10.2	42.5	11.7	0.6	0.3	0.0	2.2	0.0	0.0
JPT4	0.0	8.0	60.0	2.8	0.9	0.0	0.0	0.3	0.0	4.6
JPT5	7.7	7.1	16.9	23.4	19.4	1.5	0.3	0.6	0.6	0.0
SPT1	9.5	27.1	22.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SPT2	2.8	45.2	6.5	0.0	1.5	0.0	0.0	0.6	0.0	0.0
SPT3	4.0	10.2	14.5	11.1	1.5	0.0	0.0	0.0	0.0	0.0
SPT4	3.1	0.0	19.7	50.5	2.5	0.0	0.0	1.5	0.0	0.0
SPT5	2.8	0.0	0.0	62.2	4.0	0.0	0.0	0.3	0.0	0.0
Mean	**3.6**	**6.4**	**14.4**	**19.6**	**19.2**	**0.9**	**0.2**	**0.8**	**0.2**	**0.3**
Min	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Max	**28.3**	**45.2**	**60.0**	**62.2**	**59.4**	**4.9**	**2.8**	**5.2**	**0.9**	**4.6**

observed throughout the sites included smooth moss crusts with *Bryum* spp. and rough moss crusts with *Syntrichia* spp. With all functional groups combined, biocrust made up the dominant biological cover of the shrub interspaces throughout the study area (Fig. 3A) while only 11.78 ± 1.84% of the interspaces were covered by vascular plants including annual and perennial grasses and forbs. Litter covered 22.66 ± 2.12% of the interspace. Unconsolidated bare soils were rare at only 3.60 ± 1.44% ground cover, while physical crusts (including physical crust with an algal layer) covered an average of 20.80 ± 5.16% with a maximum of 68.00% in one site (Table 2, Fig. 3A).

3.2. *Soil aggregate stability and its relationships to biological and physical soil crusting*

Throughout the study area soil surface stability was greater than subsurface stability ($p < 0.001$, t-statistic = 6.87). The average soil surface stability score for all sites was 3.4. Corresponding average soil subsurface stability score was 1.33 (±0.30) (Table 2). Soil subsurface stability had higher variability across sites compared to soil surface stability (Fig. 3C). Spearman's rank correlation analysis revealed that total biocrust cover was significantly and positively correlated to soil surface stability (rho = 0.36) while cover of physical crust was significantly negatively correlated with surface stability (rho = -0.38, Fig. 3D). Subsurface aggregation showed the opposite trend where subsurface stability strongly decreased with increasing biocrust cover (rho = -0.72) but stability strongly increased with greater physical soil crust cover (rho = 0.69, Fig. 3D, Fig. 4A). Cover of light cyanobacterial and cyanolichen crusts were positively correlated with an increase in soil surface stability (rho = 0.38 and 0.49, respectively). Bare, i.e., unconsolidated, soil was negatively correlated with both surface and subsurface stability (rho = -0.51 and −0.31, respectively). Soil chemical and physical factors significantly relating to surface stability included the coarse sand fraction (rho = 0.55), potassium (rho = 0.67), and ammonium (rho = -0.54). Salt content and fine textures positively related to soil subsurface aggregate stability and included SAR (rho = 0.51), sodium (rho = 0.60), percent clay (rho = 0.68), and percent silt (rho = 0.85). Nitrate content (rho = -0.53) and percent sand (rho = -0.82) correlated negatively with subsurface stability.

3.3. *Relating physical and chemical soil properties to biocrust*

Sand was the most variable soil fraction across sites with a maximum of 85% and a minimum of about 7% sand content (58.02 ± 4.53, Table S1). Clay had the narrowest range with a max of about 45% and a min of 11% (19.37 ± 1.97, Table S1). With respect to soil surface chemical properties, most factors had a wide range of variability throughout the sites (Table S2). SAR levels ranged from 0.09 to 13.10, where very sodic soils start at about 13. The EC levels within the sites had a mean of 3.59 and ranged from 1.53 to over 8 dS/m, where values > 4 dS/m indicate saline conditions. The soil pH within the sites ranged from 4.5 to 7.32, with a mean of ca. 6.09 (±0.17). Soil salts such as Ca and Mg were not as variable in comparison to other chemical characteristics. Ca content ranged from 0.37 to 3.52 meq/L. Mg content ranged from 0.13 to 1.02 meq/L. K and NO_3^- were highly variable with K content ranging from 0.01 to 39.90 mg/L and NO_3^- content ranging from 0.09 to 29.50 mg/L. Other forms of soil nitrogen such as NH_4^+ ranged from 0.02 to 2.53 mg/L and were not nearly as variable. P content ranged between 0.01 and 16.30 mg/L (Table S2).

We first examined which soil variables related to the abundance (cover) of individual biocrust types. Spearman correlation analysis showed that the relationships between soil chemical properties and biocrust cover varied greatly across biocrust types (Fig. 4). The strongest relationships were found between covers of incipient, light cyanobacterial, and physical soil crusts with soil texture. Specifically, incipient and light cyanobacterial crusts strongly correlated with percent sand, particularly with percent medium sand, while negatively relating to finer particle sizes (Fig. 4). In contrast, physical crusts correlated strongly and positively with % clay, silt, and very fine sand while relating negatively to coarser particle sizes. Incipient and light cyanobacterial crusts also had negative correlations with sodium content and SAR. Cover of incipient crusts was also negatively correlated with pH while light cyanobacterial crusts related positively to nutrient contents including magnesium, calcium, and potassium (Fig. 4). Dark cyanobacterial, cyanolichen, and rough moss crust cover had stronger correlations with chemical properties than with physical properties. Respectively, dark cyanobacterial crusts correlated moderately to strongly with increasing pH and sodium content while rough moss crusts

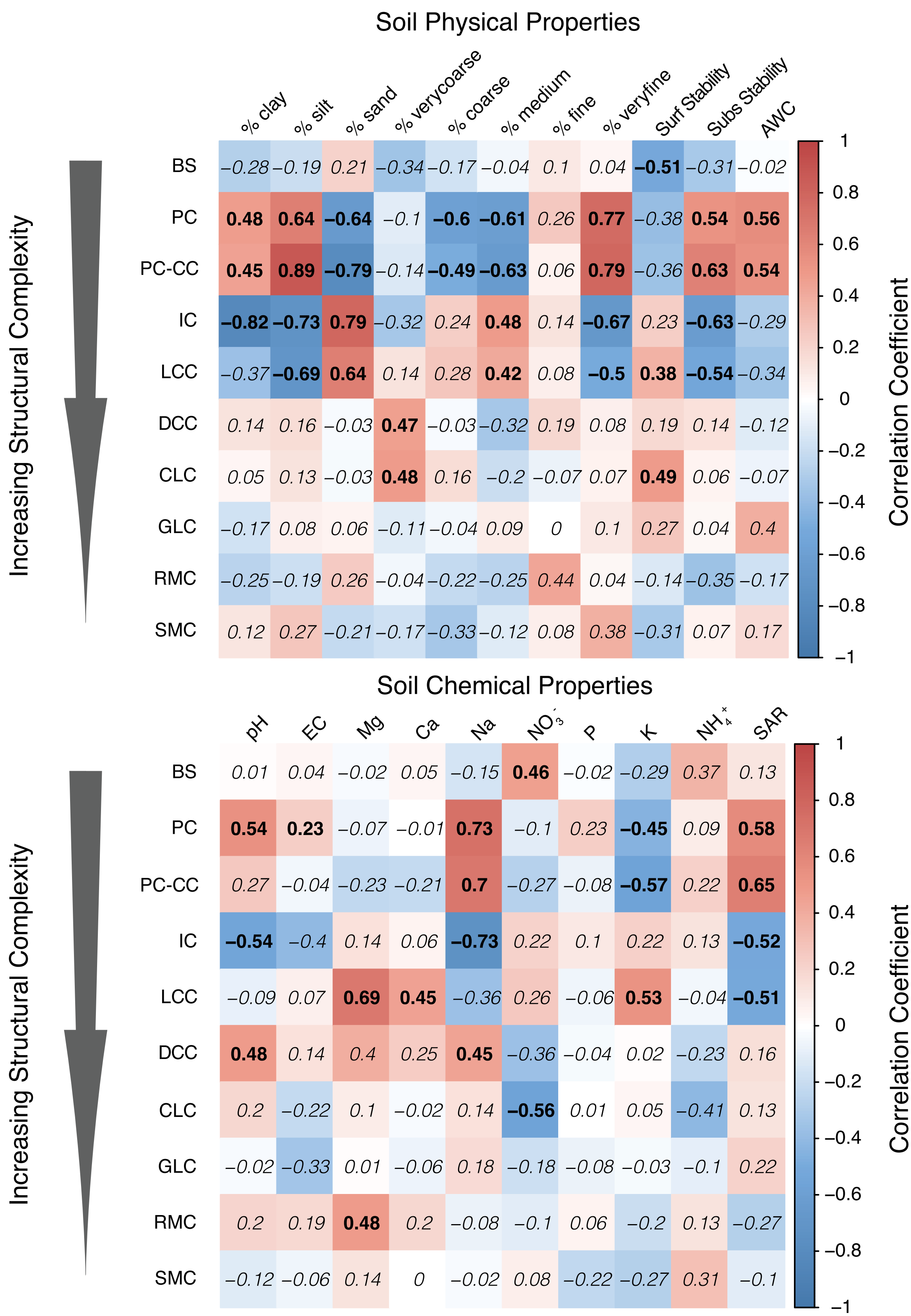

Fig. 4. Correlation heat map relating bare soil, physical crusts, and biocrust types to soil physical and chemical properties. Soil crust types are arranged according to structural complexity starting with the least structurally complex soil crust type to the most complex and include bare soil and physical crusts (PC and PC-CC) in the uppermost rows, followed by incipient biocrust (IC), light cyanobacterial crust (LCC), dark cyanobacterial crust (DCC), green algal lichen crust (GLC), cyanolichen crust (CLC) and moss crust types with rough and smooth moss crusts that have conspicuous structures below and above ground and are listed in the lowest rows.

correlated strongest with magnesium content (Fig. 4). Cyanolichen crusts cover had positive correlations with pH and sodium, but these relationships were not significant. Both dark cyanobacterial and cyanolichen crusts correlated negatively with increasing nitrate and ammonium contents. Smooth moss crust cover was mainly positively correlated with ammonium and very fine sand contents and negatively with % coarse sand. Green algal lichen crust cover had no significant correlation with any of the soil properties assessed.

We also explored the relationships between soil characteristics and the dissimilarities of biocrust functional groups across the sites (beta diversity of functional groups) through the use of nMDS ordination (stress = 0.138; Fig. 5). Sites that were located closer together (Fig. 1) were not spatially autocorrelated in biocrust composition, i.e., geographically closer sites did not plot together but rather were intermixed with more distant sites (Fig. 5). Soil surface characteristics that played a role in biocrust community assembly were those related to soil particle size and salt content like K, Mg, and Na as well as sodicity (SAR). The nMDS ordination also demonstrated that finer textured soils more closely associated with characteristics of physical crusting, such as SAR, salinity, and higher pH. Cyanobacteria crust types of more well-developed crusts like cyanolichens and dark cyanobacterial biocrusts associated with the environmental factors related to physical crusting and salinity. Incipient and light cyanobacterial crust types associated with coarse textured soils, lower salt content but higher potassium and magnesium content (Fig. 5). Mantel test results showed that texture, in particular percent sand content (r = 0.67) and the very fine sand fraction (r = 0.37) were the strongest associating factors for biocrust community structure. Mantel test results also showed that SAR explained a modest portion (r = 0.37) of the variation in biocrust distribution.

Results of multiple linear regression generally agreed with the results of our correlation and nMDS analyses. Overall, the comparison between linear regression models with the three data sets (physical properties, chemical properties, and the combination of chemical and physical characteristics) showed that the combination of physical and chemical properties explained a larger amount of the variability in the biocrust crust compositional data, but also that their particular effects varied for different biocrust types supporting the results of our correlation analysis (Fig. 4, S1-S3).

4. Discussion

4.1. Biocrusts as rangeland components

We found that biocrust is the dominant living ground cover within the shrub interspaces in comparison to herbaceous plant cover in Rio Puerco Watershed rangelands (Schallner, 2019). Incipient and light cyanobacterial crusts made up most of the ground cover in these managed drylands. Similar patterns have been observed for hot desert systems such as the Mojave Desert, where climate dictates the dominance of cyanobacterial crusts (Belnap et al., 2008; Pietrasiak et al., 2011a, 2011b, 2014a). In contrast, cool deserts such as the Colorado Plateau and the Great Basin typically contain a higher amount of lichen and moss crusts (Belnap, 2006; Deines et al., 2007). Our study area is located at the southernmost extent of the Colorado Plateau ecoregion.

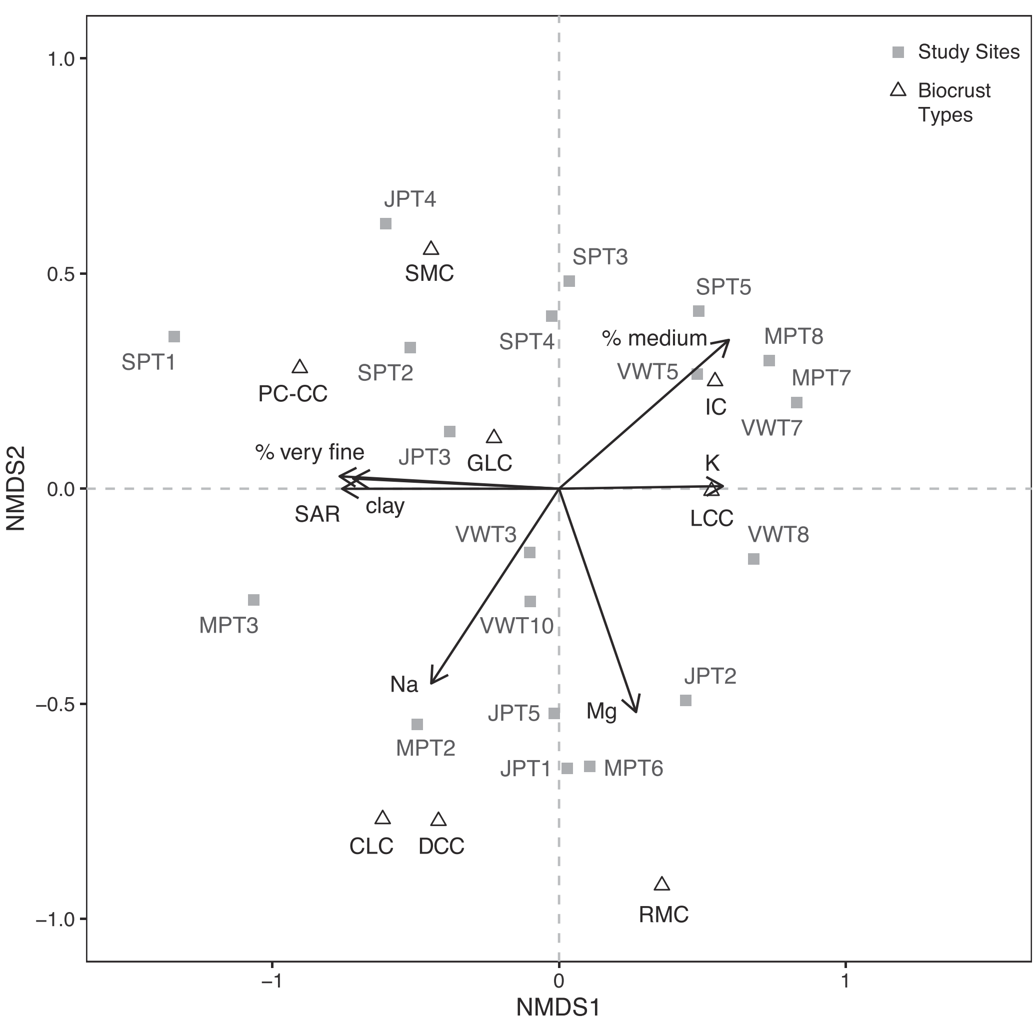

Fig. 5. NMDS ordination plot showing environmental variables that had significant correlations with the first two ordination axes and showed the strongest effects on soil crusts. Biocrust types include: IC = incipient crust; LCC = light cyanobacterial crust; DCC = dark cyanobacterial crust, CLC = cyanolichen crust, GLC = green algal lichen crust, RMC = rough moss crust, and SMC = smooth moss crust. PC-CC represents physical soil crusts that are covered with a thin cyanobacterial/algal biofilm.

Thus, climatically, this region has the potential to contain greater abundances of lichen and moss biocrusts. However, historical and contemporary land uses with associated physical disturbances may contribute to a reduction in lichen and moss crusts (Ferrenberg et al., 2015; Kuske et al., 2012). Thus, the fact that the Rio Puerco Watershed as a working landscape is periodically grazed could explain the dominance of early successional biocrust types such as incipient and light cyanobacterial crusts in the interspaces. Cyanobacteria dominating these crust types possess characteristics, such as high motility, faster growth, and colonization, that may allow for a higher resilience to periodic grazing.

As biocrusts recover from disturbance, early successional biocrust can act as precursor for later successional communities. Once later successional types have established, they often implement a wider range of ecological functions further enhancing soil stability (Pietrasiak et al., 2013; Faist et al., 2017). Portions of the Rio Puerco Watershed that are frequently grazed will likely not allow for full development of biocrust, as it has been shown that trampling effects are detrimental to late successional biocrust development (Ferrenberg et al., 2015; Garcia et al., 2015). Still, in the Rio Puerco Watershed rangelands surveyed, later successional biocrust types including moss and lichen crusts often were found tucked underneath sagebrush shrub canopies similar to Garcia et al., (2015, Fig. 1). The refugia provided by shrubs can thus allow for secondary succession to take part more quickly in recolonizing disturbed areas. Future monitoring studies could explore the biocrust recolonization potential from such shrub refugia.

4.2. Biocrusts and physical crusts contribute to soil aggregate stability

Within shrub interspaces, where cyanobacterial cover was common, surface soil aggregates were much stronger than subsurface aggregates. The stronger aggregation of the soil surface thus serves as a protective layer (Bowker et al., 2014; Bowker et al., 2018), keeping the underlying soil in place. This is of particular significance in areas with inherently high erosion potential like the Rio Puerco Watershed (Greene et al., 1999; Phippen and Wohl, 2003). Our findings agree with the literature that biocrust cover can enhance soil surface stability and potentially reduce erosion (Belnap and Büdel, 2016, Chamizo et al. 2017, Gao et al. 2017). In addition to soil surface stability aiding in reduced erosion potential, biocrust can influence soil surface roughness (Belnap 2006) which has also been demonstrated to reduce erosion (Faist et al. 2017).

The overall aggregate stability of the soil subsurface layer was much more variable than the surface layer. Interestingly, subsurface stability increased with increased presence of physical crusts. Physical crusts can be much thicker than biocrusts and accumulate via long term broad-scale additions of allochthonous material by wind or water deposition (Valentin and Bresson 1992). Nonetheless physical crusts often are much less stable than biocrust aggregates when subject to water inputs (Herrick et al. 2001, 2017). The subsurface aggregation alternatively may be much more heterogeneous due to variability of inherent soil properties such as soil texture, mineralogy, and chemistry (Herrick et al. 2001). The Rio Puerco Watershed is defined by its variable sedimentary parent materials scattered throughout the area, including sandstones and shales. Sandstones present largely in the form of outcrops and mesas, often associated with coarser textured, sandy loam soils whereas shales are often found in association with more lowland depositional areas and finer textured soils (Phippen and Wohl, 2003). The spatial variability in soil texture and mineralogy thus could help explain the spatial variability in subsurface soil aggregation.

4.3. Soil physical properties related to biocrust abundance and community composition

Soil surface texture, pH, and salt content were most influential in governing biocrust abundance and community composition in our study. Soil texture has been considered a common driver of biocrust composition and distribution at the regional scale (Pietrasiak et al., 2011a, 2011b, 2014a; Bowker et al., 2016, 2018; Faist et al., 2020). In general, fine textured soils are associated with higher lichen and moss crust cover due to higher inherent soil stability and generally more beneficial microhabitat conditions (Root and McCune, 2012; Belnap et al., 2016). In contrast, sandy textured soils often harbor poorly developed biocrusts, such as incipient crusts, or support biocrusts dominated by light cyanobacterial crusts (Pietrasiak et al., 2011b). Biocrusts have challenges establishing in coarse textured soils due to the lower water and nutrient holding capacities (Pietrasiak et al., 2011b), a much lower degree of chemical and physical surface interactions by the inorganic sand particles (Belnap and Gardner, 1993), and bigger particle and pore sizes that require a stronger "glue" to form stable biocrust aggregates (Belnap and Gardner, 1993; Rozenstein et al., 2014, Chock et al. 2019). Additionally, sandy soils in drylands often indicate geomorphic active environments, such as eolian or alluvial driven systems (Pietrasiak et al., 2011a, 2014a; Garcia et al., 2015). In our study, incipient and light cyanobacterial crusts were positively correlated with coarse textured soils. Although, based on our correlative results, we cannot imply causal relationships, potential mechanistic feedbacks should be investigated in future studies. For example, filamentous cyanobacteria species capable of producing copious amounts of sticky exopolysaccharides can be expected as early colonizers in incipient or as dominant community member in light cyanobacterial crusts (Campbell 1979; Garcia-Pichel and Pringault, 2001; Pietrasiak et al., 2014b; Mühlsteinová et al. 2014a, 2014b). These taxa also have an ability to move throughout the soil surface matrix in search of more favorable conditions, or weave their way back to the surface when they are buried by sediment moved by geomorphic forces (Garcia-Pichel and Pringault, 2001; Thomas and Dougill, 2007; Williams et al. 2012). Therefore, these groups may have a higher tolerance for loosely aggregated, sandier soils (Chock et al., 2019).

Further, we found that cyanolichens and dark cyanobacterial crusts were associated with fine textured soils, although these relationships were less strong (Figs. 4 and 5). Within this study and others, it is challenging to know the directionality of this relationship. Fine textured soils can promote the development of lichen and cyanobacterial crusts (Belnap et al., 2001; Lalley et al. 2006) but there is also reason to consider the ability of biocrusts to trap dust increasing the number of fine particles in the surface soil over time (Danin and Ganor 1991; Gao et al. 2017). Yet, both crust types had overall low cover values in our study area. Their rare occurrence could mask stronger feedbacks with other soil characteristics or biological interactions, such as vascular plant establishment as influenced by soil properties.

Fine textured soils often co-occurred with a high level of physical crust cover, which points to potential formative processes for physical crust. For example, depositional physical crusts form when fine particles are transported to topographic low areas, where they settle out and accumulate over time to form a laminar crust (Valentin and Bresson 1992). Structural physical crust can form due to the rain splash effect in areas where surface soil is exposed, without living cover to disperse the impact of heavy raindrops hitting the ground. Dislodged particles fill in pore spaces at the soil surface and form a seal over time. Structural crusts are often an indication for poor soil health (Valentin and Bresson, 1992).

4.4. Soil chemical properties related to biocrust abundance and community composition

Additional noteworthy patterns in our study were apparent with selected soil chemical properties. At the local to ecoregional spatial scales, biocrust abundance and distribution is often related to chemical properties such as pH, SAR, EC, or nutrient content in ways that are often unique for individual sites (Ullmann and Büdel, 2003; Bowker et al., 2016). In our study we found strong relationships between pH (Fig. 4) and salt content (Figs. 4 and 5) with biocrust composition. Specifically, alkaline salty soils were associated with dark cyanobacterial and cyanolichen crusts, as supported by our results from the nMDS, Spearman correlations, and relative importance analyses (Figs. 4, 5, S1-3). Cyanobacteria are known to be salt and alkalinity tolerant and can sometimes be the only photoautotrophs present in salty alkaline surface soils (Singh, 1950; Danin and Barbour, 1982; Ullmann and Büdel, 2003; Sand-Jensen and Sand Jesperson, 2012). A follow up study could explore the salinity and alkalinity stress tolerances of Rio Puerco Watershed soil cyanobacteria. Such insights may provide valuable information for future restoration projects.

Rough moss crusts (*Syntrichia* dominated) at our study sites are positively correlated with magnesium and potassium content. Although we have a good understanding of ecophysiological responses to desiccation in *Syntrichia* and *Bryum* (see Tuba et al., 1996; Wu et al., 2012; Stark 2017; Greenwood et al., 2019) there is much opportunity for developing our understanding about nutrient requirements for metabolism and salt toxicity/tolerance in these mosses and in dryland mosses in general (Zhang et al., 2015; Wang et al., 2018). One study in Australia found a positive relationship of calcium (as calcium carbonate content) with several moss species within the genera *Desmatodon*, *Didymodon* and *Gigaspermum*, (Ullmann and Büdel, 2003) but our two genera (*Bryum, Syntrichia*) were not amongst the genera reported in the study. The biological impacts of biocrust communities on nutrient availability and mobilization are complex (Moreno-Jiménez et al. 2020). For example, Bowker et al. (2006) found positive associations of moss crusts with magnesium and potassium contents and the authors suggested that either the nutrient limitation hypothesis or biocrusts' ability to trap nutrient containing dust could explain the higher magnesium and potassium availabilities in moss crusts. Moreno-Jiménez et al. (2020) on the other hand explained a greater availability of nutrients in moss and lichen crusts as due to their impacts to hydrological cycling, which could in turn impact biogeochemical processes. These observations of biocrust being influenced by edaphic conditions could also be partly due to their interactions with vascular plants, whether facilitative or competitive (Havrilla et al. 2019). Future experimental studies are needed to investigate these intriguing associations and potential interactions across different biotic and abiotic characteristics.

4.5. Management implications

Our case study shows that biocrust can be a prominent component in a managed landscape. We also observed that biocrust occurrence linked positively with surface soil aggregate stability even though early successional biocrust types such as incipient and light cyanobacterial crusts dominated the shrub interspaces. Moreover, sparse patches of dark cyanobacterial crusts as well as several soil lichens and mosses could be found under or near shrubs (Fig. 1). Having a broad diversity of crust types at a site can be beneficial to ecosystem health due to a broader array of functions such as higher rates of carbon and nitrogen fixation and greater levels of soil stability. Despite biocrust's importance to dryland functioning and ecosystem health, rangeland management and conservation plans rarely incorporate biocrust in their management recommendations mostly due to a lack of awareness and their inherently cryptic appearance. Our findings raise many new questions such as 1) How can we best manage rangelands, increase rangeland health, and reduce soil loss by incorporating biocrusts in our management efforts?; 2) What degree of biocrust development is needed to obtain and maintain a healthy and sustainable rangeland soil?; and 3) What would be a desirable biocrust community composition and coverage needed to sustainably support land uses, while keeping soil loss to a minimum and acknowledging that biocrusts are vulnerable to disturbance.

With this in mind, a hypothesized management scenario at a specific rangeland site such as the Rio Puerco Watershed could be the following: If biocrusts are incorporated into management strategies perhaps a certain density of sagebrush should be maintained in these rangelands to provide biocrust refugia for highly functioning biocrust types including dark cyanobacterial, lichen, and moss crusts. Sagebrush refugia thus could function as a biocrust "seedbank" from which propagules can disperse to the plant interspaces to promote biocrust growth and (re-)establishment during the times when particular rangeland areas are excluded from grazing for forage recovery. While no extensive moss and lichen crust cover can be expected to establish in the shrub interspaces over a relative short recovery time (1–2 yrs) and due to the recurrence of trampling disturbance in a grazed landscape, our study suggests that early successional crust types could develop and still provide a considerable degree of soil stability to the system. However, if grazing frequency is too high, or duration is too long, soil stability and rangeland health would diminish. A long-term monitoring study could investigate whether such practice will yield the potential feedbacks hypothesized here.

5. Conclusions

For most managed drylands, little is known about the distribution and abundance of biocrusts in the landscape. Consideration of their impact to rangeland health is often missing in conservation planning, despite our growing understanding of their essential contributions to dryland ecosystem functioning. We found that biocrust contributed 41% of the ground cover in our case study, and most of the interspace cover was attributed to cryptic biocrust types such as incipient and light cyanobacterial biocrust types. Where biocrusts were present, soil aggregate stability was promoted emphasizing the role of biocrust in preventing soil erosion, an essential and desired ecosystem service in drylands. Different combinations of soil variables influenced biocrust abundance, diversity, and distribution. Biocrust types containing cyanobacteria, such as cyanolichens and dark cyanobacterial crusts, associated with the finer textures, high pH and salinity values; while early successional incipient and light cyanobacterial crusts associated with coarse textured soils with lower salt content.

The impact biocrusts may have on ecosystem services, such as soil erosion prevention in watersheds with high erosion potential like the Rio Puerco Watershed, carbon sequestration, nutrient cycling, and soil fertility can be valuable in dryland management. Yet, land managing tools such as state and transition models in ecological site descriptions rarely integrate biocrusts or soil microbial communities in their models and predictions. It is important that more becomes known about what types of biocrust and which coverage levels can be expected within a region of interest depending on management type and intensity applied. It is also practical to investigate what physical and chemical soil surface characteristics govern biocrust distribution. Such information will add valuable insights to our understanding of rangeland ecology, in addition to what we know about plant community dynamics with the ultimate goal of sustainably managing our rangelands as multilayered ecosystems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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