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A spatiotemporal framework reveals contrasting factors shape biocrust microbial and microfaunal communities in the Chihuahuan Desert

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ABSTRACT

Biocrusts harbor soil-surface communities composed of autotrophic and heterotrophic microbiota that affect nutrient cycling, plant performance, soil hydrology and stability within drylands. Biocrust community composition is mostly thought to be driven by abiotic factors, but the structure of the bacteria, fungi, protist, and microfauna taxa are rarely documented simultaneously or over time. In this study, we examined the composition, abundance, and diversity of microbes (bacteria and fungi) and microfauna (protists and microscopic microfauna) in three types of biocrusts among two different vegetative habitats in the northern Chihuahuan Desert during three successive seasons. Microbial groups were identified by phospholipid fatty acid analyses (PLFA) and included actinobacteria, other gram-positive bacteria, other gram-negative bacteria, rhizobia arbuscular mycorrhizal fungi, and saprophytic fungi. Microfauna were enumerated via microscopy and included nematodes, tardigrades, rotifers, amoebae, ciliates, and flagellates. We found that microbial communities were most affected by biocrust type, whereas microfaunal communities were more influenced by sampling season. Season was also associated with different indicator taxa. Additionally, microbial communities were related to biocrust chemical properties—which changed with season and surrounding vegetation—while microfaunal communities were not. In cyanolichen-dominated crusts, but not others, the structure of microbial and microfaunal communities were strongly correlated. Our study highlights possible food web interactions and provides evidence that the co-occurring microbial and microfaunal taxa associated with biocrusts are temporally dynamic and structured by different drivers.

1. Introduction

Biological soil crusts (biocrusts) comprise diverse communities that live at and aggregate the soil surface of drylands globally (Ferrenberg et al., 2017). Biocrusts can contain cyanobacteria, bacteria, archaea, eukaryotic algae, fungi, lichens, bryophytes, and various protists and multicellular microfauna. In addition to housing substantial microscopic biodiversity, biocrusts can also affect dryland productivity by fixing nitrogen (N) and carbon (C) (Ferrenberg et al., 2017; Tucker et al., 2019), enhancing soil stability, influencing hydrology (Eldridge et al., 2020), and affecting plant recruitment and growth (Havrilla et al., 2019). Biodiversity within biocrusts and their associated ecosystem services are reported to vary with composition and type. For example, rates of N and C fixation (Barger et al., 2016; Guan et al., 2021; Tucker et al., 2019), surface energy balance (Rutherford et al., 2017), and effect on soil hydrology (Eldridge et al., 2020) depend on distinct biocrust types. Further study of the interactions among biotic groups within biocrusts of differing composition is needed for improving our knowledge of biodiversity and their influence on dryland ecosystems.

The dominant photoautotrophic members of a given biocrust—*i.e.*, cyanobacteria, eukaryotic algae, lichens, or bryophytes—are not only used to categorize biocrust type, but also often shape the larger microbial community with potential consequences for functionality (Pietrasiak et al., 2013, Moreira-Grez et al., 2019). For example, Maier et al. (2018) suggest that the photoautotrophic organisms used in classifying biocrusts strongly affect the surrounding soil environment by altering the physiological properties of the associated heterotrophic community; e.g. soil respiration and nitrification rates. Baran et al. (2015) demonstrated that metabolite exudates from *Microcoleus vaginatus*, a widespread and often dominant cyanobacterium of biocrusts, could enhance

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heterotrophic microbial diversity by providing an array of feeding niches. In addition, *M. vaginatus* associates with distinct groups of nitrogen fixing bacteria, increasing the nitrogen fixing potential of the biocrust up to 100-fold of the surrounding soil (Couradeau et al., 2019; Nelson et al., 2021).

Biocrusts also host metazoan microfauna and protists. Microfauna present in biocrusts typically range between 10 and 200 μm in diameter and include Nematoda, Rotifera, Tardigrada, Amoebozoa, Ciliophora, and Mastigophora. Of these groups, nematodes are often abundant and—as effective predators of bacteria and fungi—play an important role in regulating microbial communities and plant-available N near the soil surface (Gebremikael et al., 2016). Rotifers filter feed on bacteria and ingestible organic particles, while tardigrades consume a variety of live material—including lichens, algae, and other microfauna—with potential consequences on soil fertility and structure of microbial communities (Bonkowski, 2004). Biocrust communities also include many protists, which are often functionally and phylogenetically diverse due to their relatively fast growth and reproduction rates. Of the protists within biocrusts, amoebae, ciliates, and flagellates prey upon bacteria, algae, fungi, and other protists thereby shaping the dynamics of these groups (Darby and Neher, 2016). Collectively, given their impacts on soil food-webs and C and N dynamics, these microfauna can significantly alter the abundance, distribution, and dispersal rates of the microbiota (algae, bacteria, fungi) that form the core of biocrust communities, while also shaping soil nutrient cycles (Darby and Neher, 2016). Though microfauna are global modulators of decomposition rates and C and N cycling (De Graaff et al., 2015), they remain poorly studied in the context of dryland biocrusts. Furthermore, functional redundancy is often high within soil bacterial and fungal assemblages, thus buffering local ecosystem functions to a loss of biodiversity within these groups. Functional redundancy is not widely reported for soil microfauna, and a decrease in their diversity can negatively affect soil processes (De Graaff et al., 2015).

Our objective was to survey the bacteria and fungi—hereafter referred to as "microbes" or "microbial"—and microfauna (including protists) that co-occur in three biocrust types common to semi-arid drylands at our study site in the Chihuahuan Desert, New Mexico, USA. These types included light and dark cyanobacterial crusts (distinguished by the pigments they produce) and cyanolichen crusts. First, light cyanobacterial crusts (LCC)—among the most ubiquitous and inconspicuous biocrust types—are dominated by filamentous cyanobacteria (e.g., *Microcoleus* spp.) that stabilize soil by exuding exopolysaccharides (Weber et al., 2015) and eukaryotic algae (e.g., *Bracteacoccus, Chlorosarcinopsis,* and *Chlorella*; Pietrasiak et al., 2013). Second, dark cyanobacterial crusts (DCC) contain exopolysaccharide exuding taxa such as the heterocytous cyanobacteria (i.e., *Nostoc, Scytonema,* and *Hassallia*) that fix N and produce sunscreen-pigments that decrease albedo and increase soil temperature (Couradeau et al., 2016; Rutherford et al., 2017). Third, cyanolichen crusts (CLC) commonly consist of *Collema, Heppia,* and *Peltula* spp., which greatly enhance soil stability with their compact hyphae and rhizomorph networks (Pietrasiak et al., 2013) but vary in their ability to fix N (Torres-Cruz et al., 2018).

Within the three biocrust types examined, we completed a simultaneous assessment of the microbial and microfaunal communities, across three seasons and in two habitats characterized by different vegetation communities: a black grama (*Bouteloua eriopoda* Torr.) dominated grassland and a tarbush (*Flourensia cernua* DC.) dominated shrubland. With an exploratory approach, we focused on these biocrusts and vegetation community states to better represent the potential influences of biocrust variability, while also aiming to improve our understanding of the temporal dynamics of microbial and microfaunal compositions within different biocrust types embedded in divergent vegetation communities. We characterized the microbes using phospholipid fatty acid analyses (PLFA) and characterized the microfauna using a modified tray extraction method and microscopic identification. We also analyzed the physical and biochemical properties of the biocrusts, and quantitatively determined whether the structure of microbial and microfaunal communities vary as a function of biocrust type, surrounding vegetation, or season. Finally, we quantified the relationship between the microbial and microfaunal groups to better understand the processes shaping the assembly of these communities and outline food-web interactions within biocrusts.

2. Methods

2.1. Study site and sampling method

This study was conducted between July 2017 and December 2018 at the Jornada Basin LTER within the Chihuahuan Desert of southern New Mexico (Fig. 1). We selected two vegetation community types common in the Jornada Basin, deciduous shrub-dominated, *Flourensia cernua* ("T", tarbush) and the perennial grass-dominated, *Bouteloua eriopoda* ("G", black grama). Four of the sites undergo continual cattle grazing (T_West. T_East, T_Taylor, G_Beetle) and two sites (G_IBPE and G_Ranch) have cattle excluded. The six sites (three grass and three tarbush) were characterized by line-point intercept, gap intercept, and canopy intercept in December 2018 to better understand vegetation and biocrust distribution. One grass site (G_IBPE) did not have cyanolichen crusts (CLC) present (Fig. 1), and all sites were abundant with light cyanobacterial crusts (LCC). Overall, grass sites had nearly five times more bare soil cover (16.1 %)—where plants and biocrusts were absent—compared to shrub sites (3.3 %). Cover of dark-cyanobacterial crusts (DCC) and CLC types were lower in the grass than shrub sites (4.1 % vs. 36.0 %, respectively).

During the 3 seasons—summer (26 June 2017), fall (13 October 2017), and spring (18 March 2018)—the six sites (Fig. 1) were sampled for each of the three biocrust types—LCC, DCC, and CLC (*Heppia/Peltula* spp.)—based on the biocrust classification scheme described by Pietrasiak (2014). This approach resulted in a total of 51 samples. Each sample consisted of a 300 g composite of one biocrust type collected within a 20 m^2 radius with each subsample collected a minimum of 20 m away from access roads and at least 20 cm away from plant bases. Only surface biocrusts were include in the samples, with depths ranging from 3 to 6 mm, as each crust type varied in thickness. Finger force was used to gently break the aggregates inside the composite sampling bag, which was stored at 4 °C for a maximum of two weeks before processing. Cumulative precipitation for the two weeks prior to sampling was greater in the fall than in the spring or summer (15.4, 2.8, and 3.0 mm, respectively).

2.2. Biocrust abiotic properties

To assess the variation in the soil environment of our sampling sites, we quantified a suite of biogeochemical properties from each biocrust sample. Soil chemical analyses were performed at Ward Laboratories, Inc (Kearney, NE, USA), and included: pH (Woodruff method), soluble salts (0.1 M $CaCl_2$), organic matter (OM, measured as LOI-%), cation exchange capacity (CEC meq/100 g soil, measured as sum of cations from NH_4 acetate extraction), and a suite of elements all measured in ppm including: nitrogen (N), sodium (Na, NH_4 acetate extraction), calcium (Ca, NH_4 acetate extraction), sulfur (S, Mehlich 3 ICAP), phosphorous (P, Olsen method), potassium (K, digestion method), magnesium (Mg, NH_4 acetate extraction), manganese (Mn, DTPA extraction), copper (Cu, DTPA extraction), zinc (Zn, DTPA extraction), iron (Fe, DTPA extraction). Soil moisture was measured using a gravimetric dry down of 10 g of homogenized biocrust at 105 °C for 24 h. A grain-size analysis was performed on fall samples only, as this was not considered to be a highly dynamic measure. Five g of homogenized biocrust sample were deflocculated using 10 mL of a dispersing agent (sodium hexametaphosphate; 50 g l^{-1}) and agitated for 24 h and a Malvern 2000 G Hydro particle-size analyzer (Malvern, United

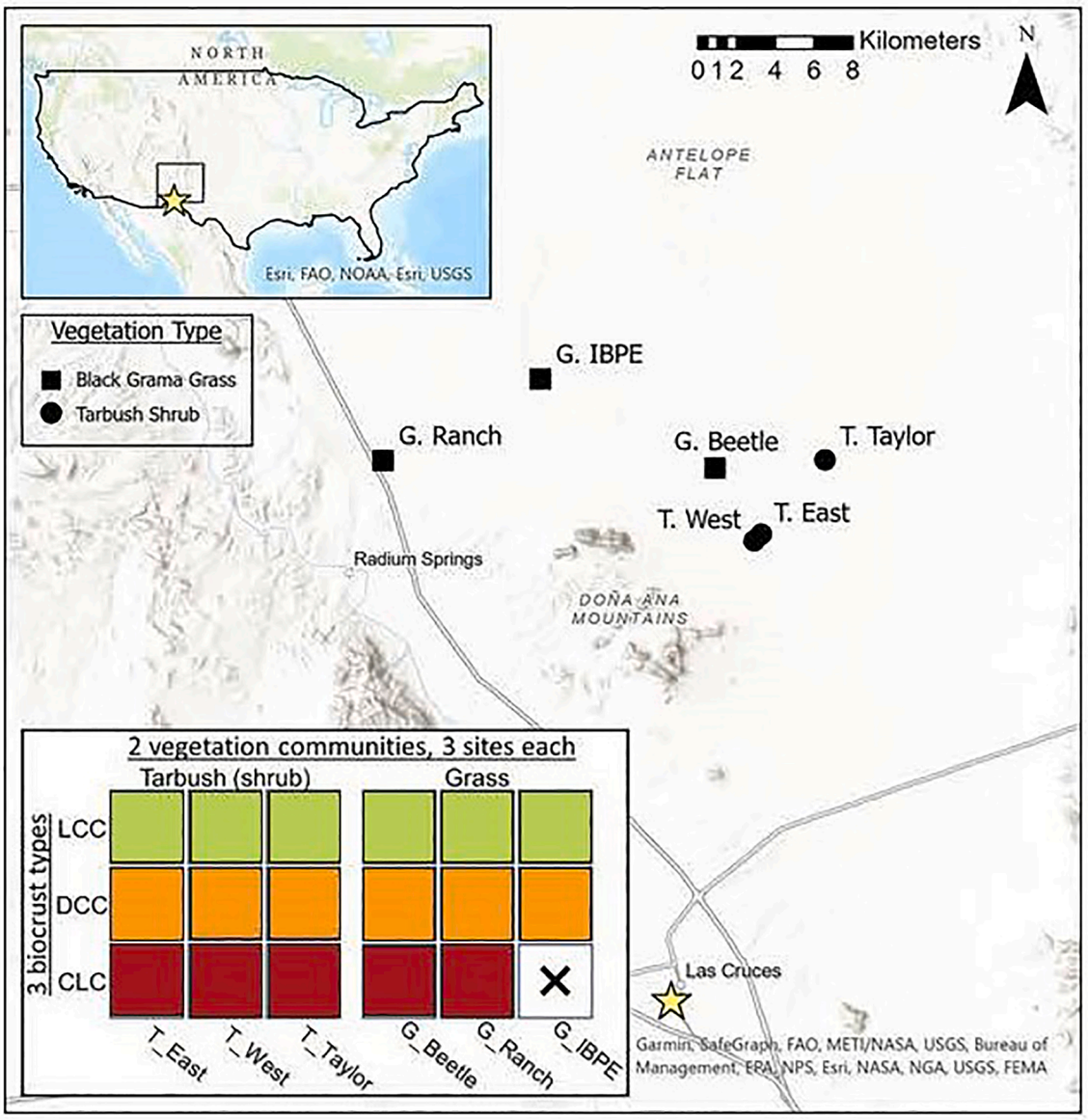

Fig. 1. Map of study site and conceptual diagram of the experimental design. Squares indicate sites with grass communities and circles indicate sites with shrub communities. At each site, composite samples of light cyanobacterial crusts (LCC), dark cyanobacterial crusts (DCC), and cyanolichen crusts (CLC) were collected, except for G_IBPE which did not have CLCs. Each site was sampled during the summer, fall and spring.

Kingdom). The Mastersizer software package version 5.6 was utilized to obtain the geometric standard deviation of each subsample by laser diffraction (Collins et al., 2017). The machine optical properties were set to a particle refractive index of 1.544 (silica) with absorption at 1. The pump and stirrer speeds were set to 2000 and 800 rpms, respectively. Three measurements of Powder Technology Inc. ISO 12103-1, A4 Coarse Test Dust were used to monitor machine precision and accuracy. Sample obscurations fell within an acceptable range (17% and 31%; Malvern Instruments Ltd 1999). For complete machine protocols, see Sperazza et al. (2004). Each sample was measured three times and reported as the mean.

2.3. Microbial and microfaunal identification

To characterize the bacteria and fungi (microbiota) at the time of sampling, phospholipid fatty acid analysis (PLFA) was used to quantify the biomass (ng/g) of arbuscular mycorrhizal fungi, saprophytic fungi, gram-positive bacteria, gram-negative bacteria, rhizobia, and actinobacteria for each biocrust composite during each season. The analyses were conducted at Ward Laboratories, Inc (Kearney, NE, USA) following Quideau et al., 2016 protocols.

To extract soil microfauna and protists, 85 g of homogenized biocrust was placed on top of two layers of large Kimwipes© in the strainer compartment of an extraction tray measuring 30 × 22 cm (modified after Whitehead and Hemming, 1965). The bottom compartment contained enough sterile deionized (DI) water to saturate and soak the biocrust sample for 16 h, after which all liquid was collected from the bottom of the tray. The tray was rinsed with DI water, and this liquid was also collected for examination. All liquid was strained through a 10-μm mesh sieve to isolate microfauna larger than 10 μm. The mesh was then flushed, producing approximately 50 mL of filtrate that was collected in a sterile beaker and mixed by pouring it back and forth four times into a separate sterile beaker. A 20 mL subsample was poured into a watch glass and microfauna were counted by tally marking each observation through a Zeiss AxioVert 100 inverted microscope. Based on previous studies (Bamforth, 2004, 2008; Darby et al., 2006), microfauna and protists were grouped into phyla or, if possible, into class which included: Nematoda, Tardigrada, Rotifera, Amoebozoa, Ciliophora

(Colpodea, Heterotchrichea, and Oligohymenophora) and Mastigophora (zooflagellates). Counts of microfauna for each sample were completed within a couple hours of sieving to preempt changes due to reproduction or mortality.

2.4. Statistical analysis

All analyses were performed in the R statistical environment (R Core Team, 2019). Analysis of univariate measure—i.e., Shannon diversity (H'), total biomass, and concentrations of soil biogeochemical variable—as a function of the fixed-effects of sampling season, vegetation community type, and biocrust community type were completed as permutational linear models using the package "lmPerm" (Wheeler et al., 2016); this approach allows for variance partitioning using sums of squares while eliminating the need for data to meet the assumption of a normal distribution. Multivariate analysis of microbial and microfaunal communities' responses to the same fixed factors were completed with PERMANOVAs, while tests for correlations of each community to the soil environment were measured with Mantel tests. Soil environmental properties were considered in a multivariate framework for comparison among sites and seasons using Principal Component Analysis (PCA). All of the aforementioned multivariate techniques—i.e., PERMANOVA, PCA, and Mantel tests—were completed with the package "vegan" (Oksanen et al., 2015). PERMANOVAs focused on microbial and microfaunal communities using Bray-Curtis distance matrixes while all analyses of soil properties utilized a Euclidean distance matrix. Multivariate plots were produced with the package "ggfortify" (Tang et al., 2016), and univariate plotting was performed in "ggplot2" (Wickham et al., 2016). To test the hypothesized relationship among microfauna and microbial taxa, while controlling for common issues with the mean–variance relationship in multivariate data sets, we used a multivariate generalized linear modeling approach (that controls for a mean–variance relationship) for community data in the package "mvabund" (Wang et al., 2012). We also used Indicator Species Analyses, performed using the package "indicspecies" (De Caceres et al., 2016) with the function "multipatt" and the corrected correlation function "r.g" and 9999 permutations, to find taxa that were significantly correlated with each sampling season, vegetation community type, and biocrust type.

3. Results

3.1. Biocrust environmental properties

To assess the variation in the soil environment of our sampling sites, we quantified a suite of biogeochemical properties from each biocrust sample. Regardless of vegetation type or biocrust state, many individual soil chemical properties were significantly correlated—a common pattern within soil biogeochemical pools (Fig. S1). The tarbush-dominated sites were higher in pH, OM, CEC, P, Ca, K, Zn, Fe, Cu, and soil moisture than black grama grass-dominated sites ($P < 0.05$ for all, Fig. 2, Fig. S2). The grass-dominated sites had larger soil particle size (mean surface area) relative to the tarbush-dominated sites. Using a PERMANOVA, we found that multivariate environmental properties considered in our study were most impacted by sample season ($R^2 = 0.33$, $P < 0.001$) followed by dominant vegetation type ($R^2 = 0.14$, $P < 0.001$) and biocrust community state ($R^2 = 0.10$, $P < 0.001$) (Table 1). Season also influenced several of the individual biogeochemical

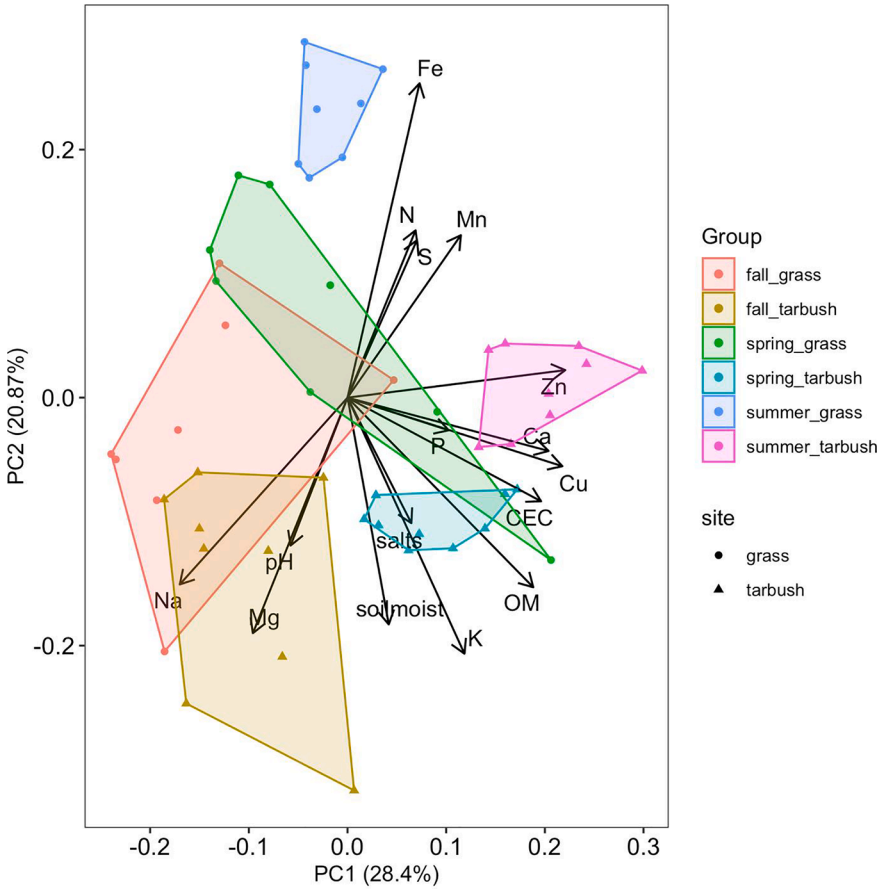

Fig. 2. Principal component plot of multivariate soil properties across three sampling seasons (i.e., fall, spring, or summer) in shrub vs. grass communities. The hulls represent the spread of the multivariate soil properties associated with season and site, and the arrows indicate eigenvector of the PCA. The arrow's direction indicates increasing values and lengths for the loading score– e.g., fall tarbush samples are characterized by greater values of Mg and pH.

Table 1
Results of PERMANOVA testing for effects of season, vegetation, and biocrust type on microbial and microfaunal communities, and soil properties.

	Microbiota			Microfauna			Soil Properties		
Fixed effects	*F-statistic*	R^2	*P*	*F-statistic*	R^2	*P*	*F-statistic*	R^2	*P*
Season	15.197	0.19	0.001	11.677	0.28	0.001	17.404	0.33	0.001
Vegetation	14.107	0.09	0.001	1.738	0.02	0.141	14.926	0.14	0.001
Biocrust	22.881	0.30	0.001	5.108	0.12	0.003	5.197	0.10	0.001
Season: Vegetation	3.899	0.05	0.013	0.602	0.01	0.786	2.566	0.05	0.006
Season: Biocrust	4.433	0.11	0.001	1.393	0.07	0.151	0.575	0.02	0.961
Vegetation: Biocrust	2.635	0.03	0.060	2.589	0.06	0.009	0.634	0.01	0.839
Season: Vegetation: Biocrust	2.197	0.05	0.056	1.189	0.39	0.256	0.766	0.03	0.783

Biotic responses were transformed to Bray-Curtis distance matrices and soil properties to a Euclidean distance matrix for PERMANOVA.

properties (Fig. S2), with pH, salts, N, P, S, Mg, Mn, Fe, Cu, Ca, CEC, Na, and soil moisture all differing significantly among seasons ($P < 0.05$ for all, Fig. 2, Fig. S2).

3.2. Biocrust microbial composition

When considering the measures of biomass and diversity of the bacterial and fungal community (hereafter referred to as "microbial" for simplicity), we found gram-negative bacteria followed by saprotrophic fungi as the most abundant microbial groups (Fig. 3A, Fig. 4C). Overall microbial biomass was significantly impacted by season, vegetation, and biocrust type (Fig. 4C, Table S1), while microbial diversity was only influenced by vegetation (Fig. S3, Table S2). Microbial biomass was greatest in the spring relative to the fall and summer ($F_{(2,48)} = 7.646$, $P < 0.005$), and overall the lowest in light-cyanobacterial biocrust (LCC) type compared to cyanolichen (CLC) and dark-cyanobacterial (DCC) biocrusts ($F_{(2,48)} = 13.51$, $P < 0.0001$, Fig. 3A, Fig. 4C). Both biomass and diversity of the microbiota was greater at the tarbush-dominated than at the black grama grass-dominated sites (hereafter referred to as "shrub" and "grass" sites, respectively, for convenience) ($F_{(1,49)} = 4.722$, $P < 0.05$, $F_{(1,49)} = 5.815$, $P < 0.05$, respectively, Fig. S3).

A PERMANOVA analysis of multivariate composition across seasons and among vegetation and biocrust community states indicated that microbial composition was most impacted by biocrust community state ($R^2 = 0.28$, $P < 0.001$) followed by sampling season ($R^2 = 0.19$, $P < 0.001$) and vegetation site type ($R^2 = 0.09$, $P < 0.001$, Table 1). Mantel

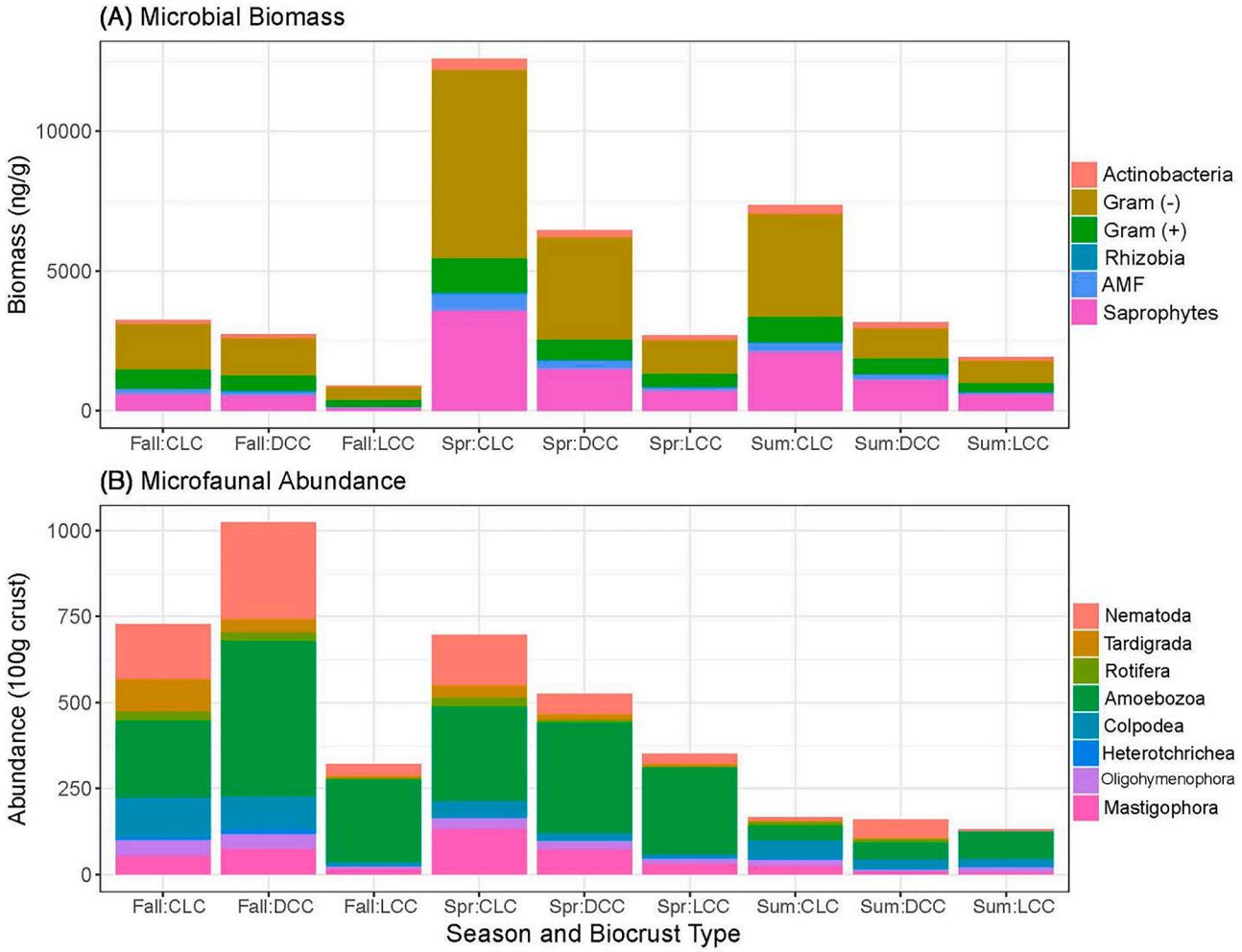

Fig. 3. (A) Microbial biomass (ng/g) of biocrusts and (B) microfaunal abundance within a 100 g biocrust sample from the fall (Fall), spring (Spr), and summer (Sum) seasons within cyanolichen crust (CLC), dark cyanobacterial crusts (DCC), and light cyanobacterial crusts (LCC) types.

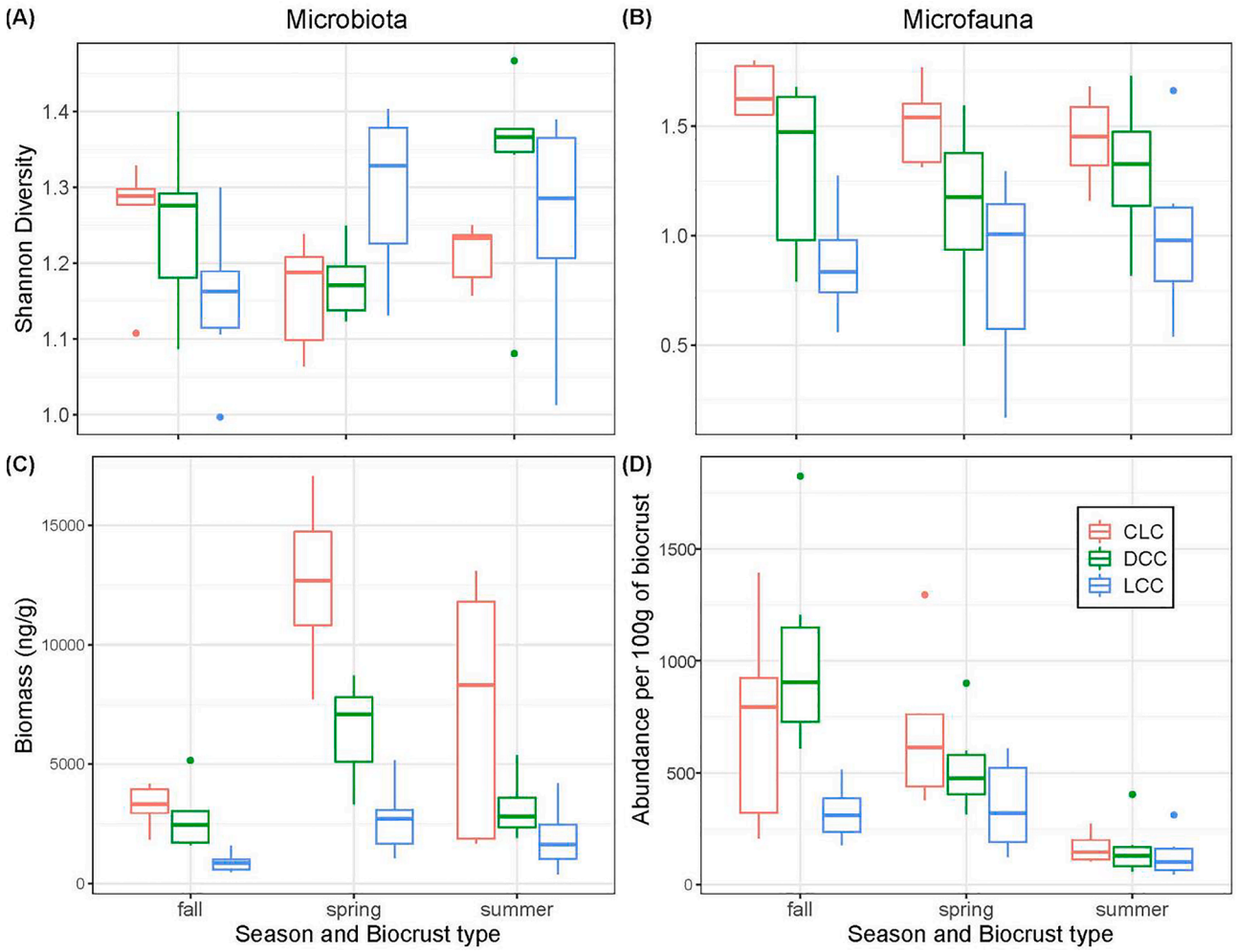

Fig. 4. Biomass, abundance, and diversity of microbiota (bacteria and fungi) and microfauna within each biocrust type (CLC cyanolichen crust, DCC dark cyanobacterial crust, LCC light cyanobacterial crust) and season. (A) Shannon diversity of microbiota, (B) Shannon diversity of microfauna, (C) biomass of microbiota, and (D) abundance of microfauna.

tests, used to assess the correlation between the microbial composition and soil physiochemical properties, indicated that microbes significantly correlated with the soil environment in only the spring season ($r = 0.35$, $P < 0.01$, Table 2). Microbial composition had significant, but relatively weak relationships to the soil properties in both vegetation community types ($r = 0.33$ and 0.23 in shrub and grass, respectively; $P < 0.05$ for both, Table 2). Comparing among crust types, disregarding season and vegetation, the strongest associations between microbial and soil properties were found in CLC ($r = 0.57$, $P < 0.01$, Table 2) versus DCC and LCC types ($r = 0.19$ and 0.19, respectively, $P < 0.05$ for both, Table 2). Collectively, these results provide additional support for significant influences of season, biocrust type, and vegetation community types on the biocrust microbial community assembly.

Table 2
Results of Mantel tests, using Spearman correlations to relate microbial community composition to soil properties among seasons, vegetation, and biocrust types.

Fixed Effects	Microbiota-Soil properties		Microfauna-Soil properties		Microbiota-Microfauna	
	r	P-value	*r*	P-value	*r*	P-value
All	0.23	<0.01	0.06	0.11	−0.06	0.91
Fall	0.01	0.44	−0.22	0.94	0.09	0.22
Spring	0.35	0.01	0.04	0.33	0.05	0.30
Summer	−0.10	0.74	0.23	0.02	−0.09	0.79
Tarbush	0.33	<0.01	0.08	0.18	−0.01	0.91
Grass	0.23	0.03	−0.04	0.68	0.09	0.13
CLC	0.57	<0.01	0.24	0.03	0.30	0.01
DCC	0.19	0.02	0.24	0.01	0.11	0.13
LCC	0.19	0.04	0.01	0.45	−0.03	0.57

The microbial community data was transformed to a Bray-Curtis distance matrix and the soil properties were transformed to a Euclidean distance matrix prior to Mantel tests.

Using indicator species analyses, we found that gram-negative and -positive bacteria, and arbuscular mycorrhizal fungi (AMF) had strong association to the spring season, while actinobacteria and saprophytes were associated with summer and spring (Table 3). Three of 6 microbial groups had significant indicator values for shrub-dominated sites, while grass sites had no indicator taxa (Table 3). Considering biocrust types, gram-positive and -negative bacteria, arbuscular mycorrhizal fungi (AMF), saprophytes, and actinobacteria were significantly associated with CLC, while the DCC and LCC biocrusts had no indicator microbial groups (Table 3).

3.3. Biocrust microfaunal composition

Considering abundance and diversity patterns, Amoebozoa was the most abundant microfaunal group across all biocrust types (Fig. 3B). In addition, microfaunal abundance was impacted most by season and biocrust type (Fig. 4B, Table S3). We observed the lowest abundance in the summer relative to spring and fall seasons (Fig. 3B, Fig. 4D, $F_{(2,48)} =$

Table 3
Indicator Species Analysis* showing microbial and microfaunal taxa that were significantly (P < 0.05) correlated (r) with different seasonal, vegetation, and biocrust groupings.

Group†	Indicator taxa*	r	p-value
Fall	Colpodea	0.394	0.011
	Heterotrichea	0.365	0.019
	Nematoda	0.361	0.012
	Tardigrada	0.316	0.041
Fall + Spring	Amoebozoa	0.602	<0.001
	Mastigophora	0.463	0.002
Spring	Gram-neg	0.505	0.007
	AMF	0.416	0.006
	Gram-pos	0.327	0.048
Spring + Summer	Actinobacteria	0.435	0.004
	Saprophytes	0.428	0.004
Tarbush	Actinobacteria	0.453	0.001
	Saprophytes	0.375	0.005
	AMF	0.320	0.019
	Rotifera	0.281	0.037
CLC	Gram-pos	0.583	<0.001
	Gram-neg	0.558	<0.001
	AMF	0.508	<0.001
	Saprophytes	0.491	0.001
	Actinobacteria	0.397	0.010
CLC + DCC	Colpodea	0.435	0.004
	Mastigophora	0.397	0.011
	Rotifera	0.348	0.029
	Nematoda	0.319	0.042

*All biota were characterized above the species level resulting in "indicator taxa" instead of species as implied by the analysis name; AMF = arbuscular mycorrhizal fungi, Gram-neg = gram-negative bacteria, Gram-pos = gram-positive bacteria. †The analysis was performed on groups that included sampling seasons (spring, summer, and fall), dominant-vegetation type (shrub vs. grass), and biocrust type (LCC, DCC, and CLC); only significant results are shown.

12.38, P < 0.0001), with no difference between vegetation sites ($F_{(1,49)}$ = 0.085, P > 0.5). Among the biocrust types, DCC had the greatest mean abundance of microfauna ($F_{(2,48)}$ = 3.5, P < 0.05, Fig. 3B, Fig. 4D). Microfaunal diversity was only impacted by biocrust type (Table S4), where CLC was the most diverse and LCC was the least ($F_{(2,48)}$ = 15.98, P < 0.0001, Fig. 3B, Fig. 4D).

A PERMANOVA revealed that season explained roughly twice as much variation in the microfaunal community assembly (R^2 = 0.28, P < 0.001) than the combined influences of biocrust (R^2 = 0.12, P < 0.01) and vegetation site types (R^2 = 0.02, P > 0.05) (Table 1). This indicated that observed differences in microfaunal composition resulted primarily from significant influences of sampling season, followed by biocrust type, then vegetation site type. A Mantel test found no significant correlation among the microfaunal community and soil properties, (R^2 = 0.004, P > 0.1; Table 2). However, when considered within seasons and biocrust types, there was a relationship among the microfauna and soil properties in the summer (r = 0.23, P < 0.05) and in CLC and DCC community states of biocrusts, but not in any other seasons or in the LCCs (Table 2).

Indicator species analysis found that 4 of the 5 microfaunal taxa had significant associations to the fall and 2 taxa to the spring and fall (Table 3). On the site level, shrub sites were associated with Rotifera, while the biocrusts types CLC and DCC were associated with Colpodea, Mastigophora, Rotifera, and Nematoda. The LCC biocrust type had no indicator microfaunal taxa.

3.4. Interactions between biocrust microbial and microfaunal communities

Despite potential interactions among the microbiota and microfauna, a Mantel test did not reveal a correlation among these groups at large. When considering the biocrust types individually, there was a significant relationship among microbial and microfauna communities in the CLC biocrust type (R^2 = 0.09, P < 0.05, Table 2). Multivariate approaches typically suffer from a positive mean–variance relationship that introduces bias into their calculation (Warton and Hui, 2017). Thus, we followed the Mantel test with a multivariate GLM approach that controls for this issue (Wang et al., 2012). In this GLM, we considered the multivariate microfaunal abundance as a response to microbial biomass. This framing places microbes into the predictor role and microfauna the response role, thereby hypothesizing a "bottom-up" influence of microbes on microfauna, many of which feed upon bacteria and fungi. This view was based on a presumption of more rapid turnover times for bacteria and fungi and the greater dispersal potential of microfauna allowing them to track dynamics of their prey. The GLM indicated that microfaunal community significantly related to the biomass of gram-positive (P = 0.002, deviance reduction = 43.01) and gram-negative bacteria (P = 0.01, deviance reduction = 27.86), which positively impacted the overall microfaunal abundance (Fig. S6). Considering specific microfaunal responses, we found that gram-positive bacteria had a significant positive effect on Nematoda (P = 0.006, deviance reduction = 11.03) and Colpodea abundance (P = 0.002, deviance reduction = 13.51), while gram-negative bacteria had a significant positive effect on the abundance of Mastigophora (P = 0.012, deviance reduction = 9.98).

4. Discussion

Overall, we found that biocrust soil chemical properties differed across sampling season, between surrounding vegetation, and among biocrust type. The composition and abundance of the microbial (bacteria and fungi) and microfaunal (protists and microfauna) components in biocrusts were also significantly influenced by season and biocrust type, while dominant vegetation type was far less influential in shaping these communities. In order of importance, microbial compositoin was shaped primarily by biocrust type then by season; this group was also more strongly correlated with soil properties than the microfauna, which were most responsive to season followed by biocrust type. We found a striking relationship between the microbial and microfaunal groups only in CLCs (cyanolichen crusts), and gram-negative and -positive bacteria had significant impacts on microfaunal taxa. Viewed collectively, results from our study revealed not only spatiotemporal variation in microbial and microfaunal communities associated with biocrusts of this system, but also differences in the rank order of the drivers influencing community assembly among these co-occurring groups.

4.1. Parsing the effects of vegetation and season on biocrust microbiota

Microbial biomass and diversity of biocrusts were greatest in shrub dominated communities (Fig. S4). Notably, soils at these sites had significantly smaller grain size particles and greater OM and CEC compared to grass sites (Fig. S2). Higher CEC reduces leaching of nutrients from soils, while OM can help retain nutrients and soil moisture, which may have facilitated greater microbial diversity. Moreover, we found that actinobacteria, saprophytic fungi, and AMF were indicator taxa of shrub site biocrusts (Table 3). Previous studies in the Tabernas Desert found Actinobacteria as abundant biocrust components, with up to 45 genera detected (Maier et al., 2014; Nagy et al., 2005). Furthermore, the presence of AMF could suggest plant–microbe interactions facilitated by the biocrust, though mechanisms of nutrient transfer remain unclear (Zhang et al., 2016a, Zhang et al., 2016b). Because edaphic factors are key determinants of biocrust type in drylands (Bowker et al., 2016), vegetation scale soil properties may generate microhabitats with distinct microbial communities (Eldridge et al., 2006).

Saprophytic fungi and gram-negative bacteria were the most abundant microbial groups throughout our study (Fig. 3A). Saprophytic fungi degrade the majority of lignin cellulose found in soils (De Boer et al.,

2005), whereas gram-negative bacteria target more easily decomposable plant-derived C for energy. The abundance of these two groups may indicate a response to varying concentrations and forms of organic inputs to the soil that are collectively shaped by climate, vegetation, biocrust composition, or edaphic properties.

Overall, sampling season was the second strongest factor in explaining variance in microbial composition in biocrusts (Table 1). With biomass as a rough proxy for activity, this finding agrees with prior reports of fungal activity being greater in spring than fall, where saprophytic fungi function remained relatively similar across years in a Chihuahuan Desert grassland (Bell et al., 2009). Furthermore, actinobacteria and saprophytic fungi were found to be indicator taxa for the summer biocrusts, which may suggest their ability to withstand lower soil moisture and drive nutrient cycles in the predominantly warm, dry summer when aboveground primary productivity typically slows or stalls. This relationship may be reflected in seasonal climate patterns and biocrust physical properties, which affects net degradation and mineralization rates of organic matter by saprophytes and actinobacteria. Additionally, actinobacteria in biocrusts were shown to dominate processes involved with ammonium uptake and P, K, and Fe solubilization (Miralles et al., 2021). Rates of photosynthesis in biocrusts of our same study system were greater in the spring and in lichen dominated biocrusts relative to other seasons and biocrusts, while nitrogenase activity was lowest in summer (Housman et al., 2006). Because biocrusts can a be a dominant source of nutrients and major carbon sink, it is important to understand when microbial activity occurs in typically nutrient limited drylands (Evans and Ehleringer, 1993; West, 1991).

4.2. Parsing the effects of vegetation and season on biocrust microfauna

In our study, Rotifera were a significant indicator taxon within shrub biocrusts, which may be a reflection on the sites' distinct microbial diversity, higher soil moisture, and smaller grain sized particles. As filter feeders, rotifers prey upon small cells (bacteria and unicellular algae), and, along with other microfauna, play an important role in regulating microbial communities, dispersing spores, and mobilizing nutrients (Darby and Neher, 2016). Rotifers can generally withstand extreme environmental conditions as they have been found to inhabit South African biocrusts, cool desert biocrusts, and Antarctic soils (Darby et al., 2010; Dumack et al., 2016; Velasco-Castrillón et al., 2014).

Amoebozoa were the most abundant microfaunal group, which has been observed before in drylands (Bamforth, 2008; Fiore-Donno et al., 2019). As the dominant protist, they have diverse feeding strategies and are capable of mineralizing N in both wet and dry conditions (Kuikman et al., 1989). They can undergo rapid population growth and can access bacterial biofilms and colonies in small pore spaces (Bonkowski, 2004). Furthermore, as indicator taxa in the fall and spring, amoeba and nematodes were the most abundant when microfaunal abundance was greatest. Nematodes are also important predators of bacteria, fungi, and cyanobacteria; thus, these groups may strongly alter microbial composition and nutrients found in biocrusts.

Sampling season was the strongest factor influencing microfaunal abundance and composition in biocrusts (Table 1, Table S3). Early summer in the Chihuahuan Desert is hot and dry, followed by a late-summer monsoon season when most annual precipitation occurs (Wainwright, 2006). This finding is consistent with reports from temperate grasslands where bacterivorous protist abundance peaked in spring and decreased in summer; in particular, Cercozoa (amoeboid) communities of this system changed significantly in relation to soil moisture and organic matter deposition (Fiore-Donno et al., 2019). Generally, patterns in microfaunal abundance have also been linked to soil texture in various biomes (Berg and Bengtsson, 2007; Simpson et al., 2012), indicative of "bottom-up" drivers whereby soil environments structure soil microfaunal communities (Berg, 2012).

Significant correlations between biocrust abiotic properties and associated microfauna were limited to the summer (Table 2), which suggests they have different sensitivities to climatic patterns than their co-occurring bacterial and fungal counterparts (Figs. 3, 4). A lack of significant correlations to the soil properties in some seasons could indicate that unmeasured abiotic factors shape these groups or that biotic filters (e.g., competition, facilitation, and/or predation) have great influence at various times of year on biocrust biota. Microfauna may also migrate below the biocrust or encyst in response to abiotic stresses. Stochastic processes—e.g., dispersal, demographic stochasticity, or chance access to a spatiotemporally dynamic pool of resources (i.e., the "lottery hypothesis," Sale, 1978)—could also shape the assembly of soil microbiota in dryland biocrusts as demonstrated in other semiarid systems (e.g., Ferrenberg et al., 2013; Ferrenberg et al., 2016).

4.3. Biocrust community states impact soil microbiota and microfauna

We found that biocrust microbial composition and biomass were most influenced by biocrust type relative to other factors—leading to the supposition that the dominant photoautotrophic components of biocrusts regulate associated bacterial and fungal communities. Multiple studies on biocrust microbes support this, having revealed different bacterial communities among various biocrust community states (Chilton et al., 2018; Maier et al., 2018; Moreira-Grez et al., 2019; Pombubpa et al., 2020). Biocrust forming cyanobacteria exudates provide a diversity of feeding niches for soil bacteria, which in turn promotes the coexistence and diversity of bacterial taxa (Baran et al., 2015). In our study, microbial composition in DCC (dark cyanobacterial crusts) and CLC (cyanolichen crusts) had greater biomass and diversity than LCC (light cyanobacterial crusts; Fig. 4) and more microbial indicator taxa (Table 3). Prior work revealed that biocrusts characterized as DCC or CLC generally have greater microbial biomass and rates of C and N fixation than those classified as LCC (Housman et al., 2006). The genera *Scytonema* and *Nostoc*, not only produce sunscreens but can also develop heterocytes—specialized cells that fix atmospheric N_2, and these genera are more abundant in DCC and CLC than LCC crust types (Housman et al., 2006; Pietrasiak et al., 2013; Yeager et al., 2004). In addition to larger inputs of C and N, DCCs and CLCs could shape distinct microbial communities by producing sunscreens, which may serve as a photoprotectant for co-occurring microbial communities (Garcia-Pichel et al., 1992; Wada et al., 2013).

Among the biocrust types, bacteria and fungi found in LCC were the least related to soil chemical properties, possibly due to LCC's dynamic microbial composition and low overall biomass and diversity. Microbial composition within CLC, however, was strongly associated with soil chemical properties. Generally, pH is a strong mediator of bacterial diversity, while OM increases soil fertility, and CEC is a direct indicator of dissolved solids and a possible predictor of fungal community composition (Zhang et al., 2016a, Zhang et al., 2016b). Higher nutrient availability within CLC could be linked to the greater abundance of biomass-degrading microorganisms, specifically the gram-negative bacteria and saprophytic fungi (Fig. 2B). CLC and DCC are also characterized by rougher microtopography, which promotes the accumulation of dusts and small particles at the surface (Belnap et al., 2016)—a function that can promote fertility and capture dispersing microbes. Furthermore, lichens have greater enzymatic capabilities than algae and cyanobacteria occurring alone (McGuire et al., 2010), supporting greater food-web complexity and thereby promoting diversity in associated microorganismal communities (Wardle et al., 2004).

Following strong seasonal effects, microfaunal diversity and abundance were most influenced by biocrust type. Microfaunal diversity may also be linked to the dominant photoautotroph or associated microbial components of biocrusts through predation. Beyond direct feeding activity, microfauna may also benefit from sunscreen pigments produced by photoautotrophic components. Although we did not characterize microfauna based on buccal cavity, nematodes and tardigrades have been observed ingesting filamentous cyanobacteria (Darby and Neher,

2016). Additionally, biocrusts can promote the longevity of soil moisture after precipitation (George et al., 2003), which could create a "microrefugia" for protists and support greater microfaunal activity (Darby and Neher, 2016). Notably, we found almost all groups of microbes and microfauna to be associated in CLCs with strong correlations to soil chemical properties. Biocrusts classified as CLC generally have greater concentrations of OM and CEC, supporting more microbial and microfaunal biomass and generally more complex food-webs.

4.4. Links between microbial and microfaunal taxa in biocrusts

Despite possible interactions among the microbes and microfauna, a significant correlation of these communities from a Mantel test was limited to the CLC type. We used microbial biomass as a predictor of the microfaunal composition and of individual taxa in a multivariate GLM approach, hypothesizing a "bottom-up" influence of bacterial and fungal biomass on microfauna. In support of this hypothesis, we found gram-positive and -negative bacteria influenced the abundance of some microfauna. Specifically, gram-positive bacteria positively correlated with nematode abundance, as did gram-negative bacteria to flagellates. Because microfaunal grazing can impact bacterial diversity and abundance (Rønn et al., 2002) and has been shown to alter the composition of nitrifying and denitrifying bacteria (Mengel, 1996), feeding links among microfauna and microbiota may be more common in CLC than other biocrust types due to the higher inputs of N provided by the biocrust taxa. Links between these two groups could also be shaped by dispersal, mutualisms, and pathogenic relationships (Oliverio et al., 2020). Gram-negative bacteria have been shown to be a preferred food for some protists (Rønn et al., 2002), and may be linked to the high number of observed flagellate counts in the spring CLCs. However, a study of *C. elegans* revealed nematodes to be a potential dispersal vector of both gram-positive and -negative bacteria in soil (Anderson et al., 2003), highlighting a possible link among these groups that would create covariance and contradict a "bottom-up" view.

Furthermore, we observed fluctuating seasonal patterns of microbial and microfaunal abundance in biocrusts. The microfauna were most abundant in the fall when microbial biomass was low (Fig. 3). The fall also corresponded with many microfaunal indicator taxa and high levels of soil moisture. Because microfaunal grazing can alter microbial biomass and nutrient retention (Geisen et al., 2018), we hypothesize that the greater abundance of microfauna we observed in the fall could be a driver of low microbial biomass observed at the same time (Fig. 4). Similarly, in the spring and summer, microbial biomass was high and correlated strongly with soil chemical properties, while microfaunal abundance was low. These patterns may indicate a fluctuating dominance between microbial and microfaunal coupled processes that are dependent on seasonal dynamics. For example, studies have shown that sunlight (UV) exposure can stimulate microbial degradation of organic matter (Day et al., 2018; Lin et al., 2018), thus the spring and summer may select for microbes and associated microfauna suited to withstand UV and desiccation to decompose photodegraded C sources. Future studies, possibly using isotopic markers with greater species resolution, is needed to better disentangle food-web linkages among the bacteria, fungi, and microfauna of different biocrust types.

5. Conclusion

We examined the composition, abundance and diversity of microbiota and microfauna of different biocrusts, sampled across three seasons and between sites dominated by different vegetation in the Chihuahuan Desert. Large variation in soil chemical properties across seasons, vegetation types, and biocrust community states were noted. Additionally, microbial and microfaunal communities varied as a function of both season and biocrust community state—with differences in their order of importance for explaining variation within the two groups. Vegetation, characterized as shrub- or grass-dominated communities, had an influence on shaping the microbial composition and no significant influence on the microfaunal composition. A seasonally dynamic soil environment produced changes in the abundance of some microbial and microfaunal taxa. Nevertheless, correlations among the two groups and soil properties were modest to weak—a result that suggested either key influences of unmeasured abiotic factors in shaping these groups or of biotic filters (e.g., competition, facilitation, and/or predation) playing important roles for their community assembly. This latter possibility is supported in part, by a significant correlation of the abundance of microfauna to some bacterial and fungal taxa. While we completed analyses intended to uncover influences of deterministic processes on the community assembly of microbes and microfauna, simultaneous influences of stochastic processes are not only possible, but highly likely given their reported role in the assembly of soil communities (Nemergut et al., 2013; Ferrenberg et al., 2016). Considering these observations, further efforts to disentangle the processes shaping these diverse biotic communities hosted by biocrusts is warranted, particularly in light of global change pressures that are anticipated to increase inter-annual climate variability and disturbances that may de-couple nutrient cycles in dryland systems.

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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Data accessibility

The data that support the findings of this study are openly available through the Environmental Data Initiative (EDI) at https://doi.org/10.6073/pasta/f6d3e8aec341ad9a7558b59c0f357db4.

Ethical approval

The authors declare that this paper does not contain any study with human participants or animals.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2021.115409.

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