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Interactions of Microhabitat and Time Control Grassland Bacterial and Fungal Composition

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Dryland grasslands are vast and globally important and, as in all terrestrial ecosystems, soil microbial communities play fundamental roles in regulating dryland ecosystem function. A typical characteristic of drylands is the spatial mosaic of vascular plant cover surrounded by interspace soils, where biological soil crusts (biocrusts)—a complex community of organisms including bacteria, fungi, algae, mosses, and lichens—are common. The implications of this heterogeneity, where plants and biocrust cover co-occur, are often explored in the context of soil fertility and hydrology, but rarely has the impact of these multiple microhabitat types been simultaneously explored to determine the influence on bacterial and fungal communities, key biological players in these ecosystems. Further, our understanding of the temporal dynamics of bacterial and fungal communities in grasslands, and of how these dynamics depend on the microhabitat within the ecosystem, is notably poor. Here we used a temporally and spatially explicit approach to assess bacterial and fungal communities in a grassland on the Colorado Plateau, and to link variation in these communities to edaphic characteristics. We found that microhabitat (e.g., vascular plant rhizosphere, biocrust, and below biocrust) was the strongest driver of differences in bacterial and fungal community richness, diversity, and composition. Microhabitat type also significantly mediated the impact of temporal change in shaping community composition. Taken together, 29% of the variation in bacterial community composition could be explained by microhabitat, date, and microhabitat-by-date interactions, while only 11% of the variation in fungal community composition could be explained by the same factors, suggesting important differences in community assembly processes. Soil microbial communities dictate myriad critical ecosystem functions, thus understanding the factors that control their compostition is crucial to considering and forecasting how terrestrial ecosystems work. Overall, this case study provides insights for future studies on the spatial and temporal dynamics of bacterial and fungal communities in dryland grasslands.

Keywords: biological soil crusts, diversity, temporal dynamics, fungi, bacteria

INTRODUCTION

Semiarid, arid, and hyperarid (hereafter, dryland) ecosystems cover over 40% of the terrestrial surface across the globe (Safriel et al., 2005) and ∼35% of the western US (Pointing and Belnap, 2012). Dryland grasslands play particularly important roles in drylands: grasslands are home to many endemic plants and animals, are critical for livestock and wildlife grazing, are hotspots of recreation, and are at risk under global change (Maestre et al., 2016). In dryland ecosystems in general, and in the high deserts of the southwestern US in particular, high climate variability is the norm, with temperature and precipitation fluctuating on timescales ranging from hours to seasons to centuries (Sheppard et al., 2002). The high variability in precipitation and temperature makes it a challenging environment for species survival; despite this, a diversity of plants and microorganisms have adapted to these conditions and these organisms have helped shape the unique landscape. This landscape is heterogenous, typically comprised of sparsely distributed plants and numerous types of biological soil crusts (biocrusts) covering the interspace soils among plants (Weber et al., 2016). Biocrusts are diverse and can be formed by cyanobacteria, algae, fungi, lichens, and/or mosses (Weber et al., 2016). The heterogeneity in dryland biota (e.g., vascular plants surrounded by interspace soils; **Figure S1**) creates a variety of diverse microhabitats, each with distinct soil bacterial and fungal communities (Grondin and Johansen, 1993; Wheeler et al., 1993; Bates et al., 2010, 2012; Steven et al., 2012, 2013, 2014; Yeager et al., 2012; Patzelt et al., 2014; Mueller et al., 2015; McHugh et al., 2017). These bacterial and fungal communities are key players in determining ecosystem functioning by contributing to soil stabilization, hydrology, and nutrient cycling (Belnap, 2006; Maestre et al., 2011, 2016; Bowker et al., 2013).

Our understanding of how microhabitats structure bacterial and fungal communities in drylands is far from complete. However, compared to our knowledge of microhabitat variation, even less is known about temporal variation in bacterial and fungal composition in arid grassland ecosystems. Early studies on seasonal changes in biocrusts used microscopy to look at changes in communities in response to climatic factors (Johansen, 1984; Johansen and Rushforth, 1985). A few more recent studies have tracked temporal variation in bacterial and fungal biomass and composition in drylands using chemical techniques (Bowker et al., 2002; Bell et al., 2009); for example, seasonal differences were observed in the community composition of desert cyanobacterial soil crusts (Bowker et al., 2002; Yeager et al., 2012). However, systematic assessments of dryland grassland bacterial and fungal communities through time are exceedingly rare. Nevertheless, studies from other ecosystems, including agricultural, mesic grasslands, alpine, arctic tundra, and rainforest systems, have shown the potential for dramatic temporal changes in bacterial and/or fungal community composition (Smit et al., 2001; Lipson et al., 2002; Griffiths et al., 2003; Wallenstein et al., 2007; Bjork et al., 2008; Matulich et al., 2015; Smith et al., 2015; Kivlin and Hawkes, 2016). Studies from other ecosystems have also examined the relative impacts of microhabitat variation (most often due to differences in plant composition) compared to the effects of season on bacterial and/or fungal composition (i.e., these studies have simultaneously assessed the control of spatial and temporal variation), with varied results. In both an alpine tundra (Bjork et al., 2008) and a rainforest (Kivlin and Hawkes, 2016), soil microbial community changes over time were of greater magnitude than differences attributed to association with a specific plant community. In contrast, plant composition (tussock or shrub) was a stronger regulator of microbial communities than season in Arctic tundra soils (Wallenstein et al., 2007). The variability in the magnitude of temporal versus microhabitat effects across ecosystems is perhaps not unexpected, as temporal changes at a location may be affected by numerous environmental (e.g., temperature, soil moisture) and ecological (e.g., dispersal) factors, and these factors may be highly variable and location dependent. Nevertheless, tracking seasonal dynamics concurrently with microhabitat controls has the potential to broaden our understanding of controls over the diversity of bacteria and fungi, especially those living in extreme environments (Schadt et al., 2003).

Patchy landscapes with distinct microhabitats caused by the presence or absence of vascular plants or different soil surface covers (**Figure S1**) are ideal for examining temporal changes in dissimilar environments while keeping other factors, such as climate and land use history, constant. However, to our knowledge no study has simultaneously evaluated how dryland grassland bacterial and fungal communities vary by microhabitat type and through time, leaving interactions between these likely controls unexplored. Here, we assessed how microhabitats and time separately and together impact bacterial and fungal community composition in a semiarid grassland ecosystem. Specifically, we asked: (1) How do changes in community composition across microhabitats compare to changes across season? and (2) Do the temporal community dynamics differ with microhabitat type? We hypothesized that microhabitats would exert greater control over bacterial and fungal community composition than temporal variation. Microhabitats generally vary in pH, soil texture, sunlight/UV exposure, temperature, and other environmental factors that control the composition of the microflora (Steven et al., 2013). Furthermore, we hypothesized that within the interspace microhabitats, the below-biocrust communities would change less than the biocrust communities. This is because surface communities are likely subject both to more extreme climatic changes (e.g., Tucker et al., 2017) and higher rates of microorganism dispersal, which are buffered in subsurface soils. Understanding the relative roles of spatial and temporal variation can provide insights into the drivers of community assembly in extreme environments, and provide a baseline from which to understand the effects of anthropogenic changes on grassland bacterial and fungal communities.

MATERIALS AND METHODS

Study Site and Soil Sampling

This study was conducted in a semiarid grassland located near Castle Valley, Utah, USA and close to a long-term climate manipulation experiment on the Colroado Plateau (38°40′26.52″

N, 109°24′59.27″ W; Wertin et al., 2015). The site has a history of limited- to no direct anthropogenic impacts prior to establishment of the study and the soils are classified as sandy loam, calcareous, Rizno series (Grand County Soil Survey; Winkler et al., 2019). Air temperature and precipitation values were collected from a weather station located ∼200 m from the collection site (**Figure S1**). The average annual precipitation was 257 mm and the mean annual temperature 14.0°C during our study period (2013–2014). This was similar to longer-term averages (2006–2018) collected at the same weather station, where average annual precipitation was 236 mm and average annual temperature 14.3°C. Soil temperature was not measured at sampling locations, but in drylands, soil, and air temperatures are often highly correlated (Bell et al., 2008).

The site's vegetation was dominated by the native perennial grasses *Pleuraphis jamesii* (syn. *Hilaria jamesii;* James' galleta) and *Achnatherum hymenoides* (syns. *Stipa hymenoides* and *Oryzopsis hymenoides*; Indian ricegrass) and the exotic invasive grass *Bromus tectorum* (cheatgrass). Biocrust communities were dominated by the cyanobacterium *Microcoleus vaginatus*, the cyanolichens *Collema tenax* and *C. coccophorum*, and the moss *Syntrichia caninervis.* Soils were collected from three soil locations representing distinct general microhabitats: (1) rhizosphere samples were taken from beneath the base of the native perennial grass *P. jamesii* and the exotic invasive annual grass *B. tectorum*; (2) biocrust samples were collected from plant interspaces and included three types of biocrusts as characterized by the dominant organisms (lichen, moss, and cyanobacteria); and (3) soils underlying lichen-dominated and cyanobacteria-dominated biocrusts. At each sampling point, four replicates per microhabitat were collected. Microhabitat sampling locations within the site were randomly selected at each time point. Soil samples were taken monthly from April 2013 to April 2014, but due to extreme snow conditions, the study sites were not accessible from December 2013 to February 2014, resulting in a total of 10 sampling timepoints over the 13-month period. In addition to collecting soils for microbial community assessments, samples were concurrently collected from each microhabitat type for soil chemistry. Biocrust samples were collected at 0–0.5 cm, while rhizosphere and below-surface soil samples were collected from 0.5 to 5 cm.

To assess whether dust blowing in the area contained significant amounts of bacteria and fungi that might contribute to soil populations, we also analyzed samples collected from two nearby sites. Sample were collected using "Big Springs Number Eight" (BSNE; Fryrear, 1986) sediment collectors placed 15, 50, and 100 cm above the soil surface (Flagg et al., 2014). Samples from the three heights were pooled for microbial DNA extractions. Dust samples were collected at four timepoints during 2012 (March, July, September) and 2013 (February).

Soil Chemistry

In order to characterize soil chemical differences among microsites, bulk soil chemistry measurements were obtained for composite samples from fall (October and November 2013) and spring (April and May 2014) (e.g., organic matter, total carbon, and nitrogen; **Table S1**) as soil chemical sampling at all timepoints was beyond the capacity of the project. Spring and late summer/fall are times of year when vascular plants are most active in this region (Wertin et al., 2015), thus April–May and October–November samplings were selected in order to best elucidate differences between plant-associated vs. interspace soil characteristics. Soil chemical analyses were performed by the Colorado State University Soil, Water, and Plant Testing Laboratory (Fort Collins, CO; www.soiltestinglab.colostate.edu) using their standard "routine soil and overburden" approach. Additionally, pH was measured for all individual samples at each timepoint. This was done by suspending 1 g of sample in 10 ml of distilled water. Samples were homogenized using a vortexter, allowed to settle for ∼5 min, and pH was measured using a Mettler Toledo pH meter (Mettler-Toledo, LLC, Ohio, USA).

Molecular Methods

Total nucleic acids were extracted from 0.5 g of soil using the Fast DNA for Soil kit (MP Biomedical) according to the manufacturer's instructions (http://www.mgp.cz/files/kity/FastDNASPINkit.PDF). To quantify changes in soil microbial communities over time and across microhabitats, we examined bacterial and archaeal (hereafter referred to as bacterial) and fungal communities using Illumina high throughput sequencing. Samples were prepared for sequencing on the Illumina MiSeq platform using a two-stage protocol described previously (Mueller et al., 2015). To target the bacterial community, we amplified the V3–V4 region of the 16S ribosomal RNA gene using the F515-R806 primer pair and for the fungal communities, we amplified the LSU D2 hypervariable region using the LR22R-LR3 primer pair (Mueller et al., 2015). Paired-end 250 bp sequences were generated using the Illumina MiSeq platform. A single 12 bp barcode was generated from the combinatorial barcodes and overlapping reads were joined into a single sequence using PEAR (Zhang et al., 2014) with a minimum overlap of 20 bp. Samples were de-multiplexed using QIIME (Caporaso et al., 2010) and any sequence with a mismatch to the barcode or forward primer was removed. Additional quality filtering and OTU clustering was conducted using UPARSE (Edgar, 2013) to remove any sequence with an expected error rate >0.5 and singleton sequence putative chimeras were identified against all *de novo* sequences and eliminated using UCHIME. OTUs were delineated at 97% sequence similarity for both 16S and LSU sequences. Representative sequences for each OTU bin were classified using the Ribosomal Database Project (RDP) online classifier tool (http://rdp.cme.msu.edu/) against the RDP LSU database and the 16S rRNA gene databases (Wang et al., 2007). Sequences classified to Phylum or Domain with a bootstrap <80% were removed from downstream analysis. OTU tables with taxonomic classifications are provided for fungi and bacteria (**Tables S2, S3**). Cyanobacteria are included in bacterial OTU analysis in RDP, however, additional classification for Cyanobacteria sequences were also performed using DECIPHER (Murali et al., 2018) with the Genome Taxonomy Database (Parks et al., 2018) (**Table S4**). Bacterial and Fungal OTU tables were exported for analysis in R (www.R-project.org). Using the OTU tables, we generated a rarefied composition table, randomly drawing the lowest common number of

sequences (n = 1,023, fungi and n = 1,663, bacteria). We then calculated a Bray-Curtis distance matrix that was used in the remaining analyses (Oksanen et al., 2018). Richness and shannon diversity of rarified OTU matrix libraries was also calculated in R. Fastq files used in this analysis were deposited to the MG-RAST database (mgp87567, https://www.mg-rast.org/linkin.cgi?project=mgp87567). Data can be downloaded from MG-RAST ID links for bacteria (mgm4824928.3) and fungi (mgm4824929.3). Additionally, we have added a supplemental metadata file for deposited sequence data (**Table S5**).

Statistical Analyses

To test for differences in bacterial and fungal richness and diversity across microhabitat and sampling date and to estimate the variance explained by each factor, we used a two-way ANOVA design with microhabitat and date as main fixed factors, and a microhabitat-by-date interaction. Differences in pH across microhabitat and date were also assessed using a two-way ANOVA. For significant factors, Tukey's HSD *post-hoc* tests were used to identify which groups within these factors were significantly different from each other. Using the same factors of microhabitat, date, and microhabitat-by-date, for the multivariate metric of community composition we performed a permutational multivariate analysis of variance (PERMANOVA), using type III partial sums of squares under a reduced model with 999 permutations. We estimated the percent of variation that could be attributed to each significant term for both the ANOVA and PERMANOVA analyses (Quinn and Keough, 2002). Analyses were run separately for bacteria and fungi.

We assessed correlations between environmental parameters, including air temperature, precipitation, and pH, and community metrics (richness, diversity, and composition). For precipitation, we used the cumulative precipitation over the 2 weeks prior to the sampling date (**Figure S2**). Pearson's correlations were used for univariate community metrics (richness, diversity), while Mantel tests were used for multivariate community metrics. For Mantel tests, each environmental parameter (pH, precipitation, air temperature) was used to generate a Euclidean distance matrix, while Bray-curtis distance matrices were used for bacterial and fungal community composition.

Correlations between temporal distance and community similarity for each individual microhabitat were calculated using Mantel tests. Pairwise temporal distances were measured based on the number of days that separated each sampling time point. All statistical analyses were conducted using the statistical platform R with the packages vegan, phyloseq (McMurdie and Holmes, 2013), picante (Kembel et al., 2010), and ecodist (Goslee and Urban, 2007). $P \leq 0.05$ were defined as significant.

RESULTS AND DISCUSSION

Soil Chemistry Across Microhabitats and Time

Soil chemistry measurements showed significant differences among habitat types (**Table S1**). Organic matter (OM) ranged from 1.5 to 6.1% and was highest in moss biocrust [5.0% (fall), 6.1% (spring)] and lowest in soils below lichen biocrusts [1.6% (fall), 1.5% (spring)] (**Table S1**). Total nitrogen (N) concentrations ranged from 0.03 to 0.17% and were higher in the lichen biocrust (0.08–0.17%) and moss biocrust (0.08–0.10%) compared to the other microhabitats. Carbon (C) concentrations were highest in the lichen biocrust [2.5% (fall), 3.5% (spring)]. C:N ratios varied across microhabitat type, with higher C:N ratios in the soil beneath cyanobacteria and lichen biocrusts, and lower C:N ratios in lichen, moss and cyanobacteria biocrusts (**Figure S3**). The pH was sampled more intensively with measurements taken from each microhabitat at each sampling date. The pH varied across both microhabitats and time, but there was no interaction [two-way ANOVA; microhabitat: $F_{(6,140)} = 86.5$, $p < 0.001$, date: $F_{(9,140)} = 6.7$, $p < 0.001$, microhabitat-by-date: $F_{(54,140)} = 1.3$, $p = 1.24$] (**Figures S4, S5**).

Microhabitats Are the Strongest Driver of Differences Across Microbial Community Richness Diversity and Composition

Bacterial richness differed across microhabitat type, while fungal richness did not [two-way ANOVA; microhabitat: $F_{(7,143)} = 95.1$, $P < 0.001$ (bacteria), $F_{(7,143)} = 1.87$, $P = 0.08$ (fungi), **Figures 1A,B**]. Bacterial richness was highest in the rhizosphere soils (*B. tectorum* and *P. jamesii*) and below lichen biocrusts (**Figures 1A,B**). Despite the lack of differences in richness for fungi, both bacterial and fungal diversity (Shannon index) differed across microhabitats [two-way ANOVA; microhabitat: $F_{(7,143)} = 46.3$, $P < 0.001$ (bacteria), $F_{(7,143)} = 4.0$, $P < 0.001$ (fungi)]. Bacterial diversity was also highest for the rhizosphere soils and below lichen and was lowest for cyanobacteria biocrust and dust samples (**Figure 1C**). Bacterial diversity has previously been found as lower in biocrusts compared to surrounding soil communities (Gundlapally and Garcia-Pichel, 2006). Furthermore, cyanobacteria-dominated biocrusts generally are early in the successional sequence of biocrust organisms for these ecosystems (Belnap, 2003) and thus bacterial communities may not be as developed as in other microhabitats. Fungal diversity was lowest in the lichen crust, but similar across all other habitats (**Figure 1D**).

Supporting our first hypothesis, microhabitat type was the strongest driver of differences in community composition for both bacteria and fungi [PERMANOVA; microhabitat: $F_{(7,143)} = 13.3$, $P = 0.001$ (bacteria), $F_{(7,143)} = 5.4$, $P = 0.001$ (fungi), **Figure 2**]. Overall, microhabitat explained an average 13.3% of estimated variation in bacterial community metrics, and 7.5% of estimated variation for fungal community metrics (**Figure 3**). Such differences in microbial communities in soils separated by only a few centimeters speaks to the role of microhabitat in structuring community patterns across a range of scales (Maier et al., 2018). Further, the microbial composition, and in particular the bacterial composition of soil associated with the invasive plant species *B. tectorum*, was distinct from composition associated with the native *P. jamesii*, as well as the biocrust communities (**Figure 1**, **Figures S5–S8**). Plant invasions, such as the spread of *B. tectorum*, an exotic annual grass that now dominates a large portion of the western US, are changing

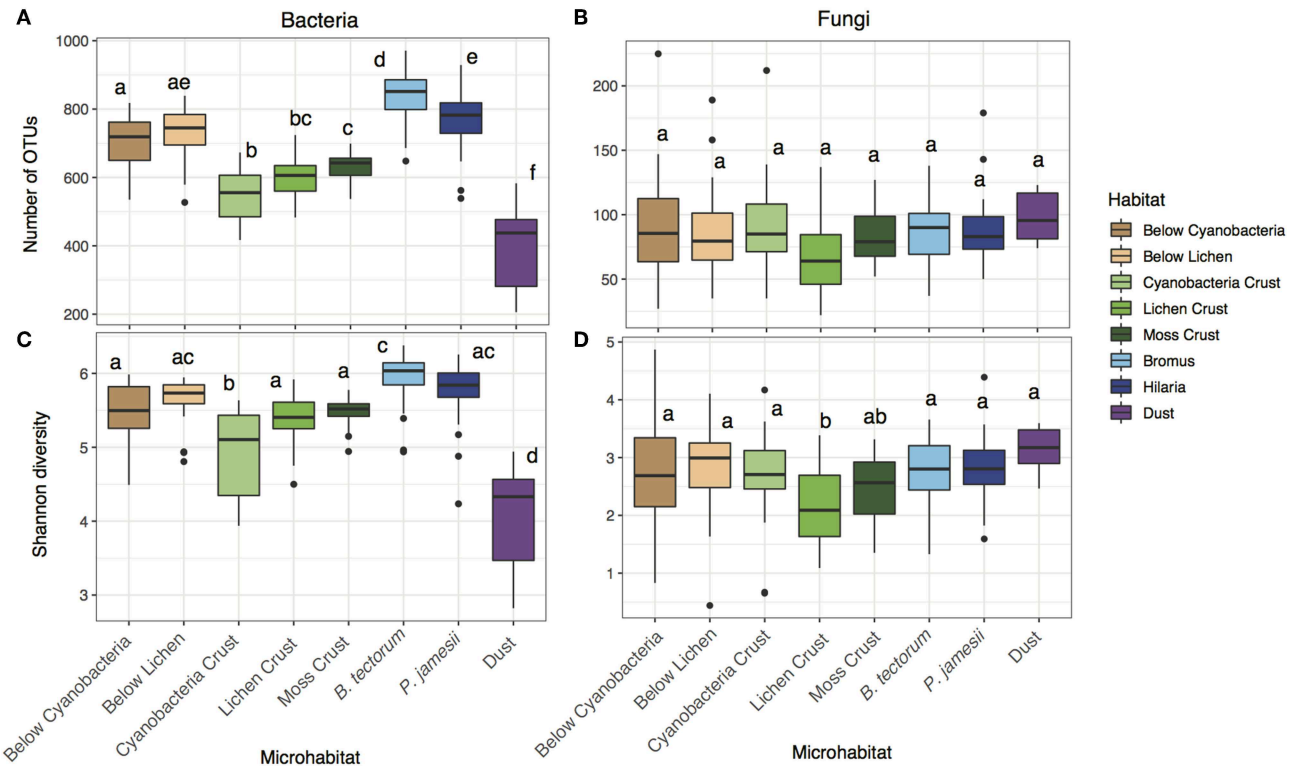

FIGURE 1 | Microhabitat variation in **(A)** bacterial richness, **(B)** fungal richness, **(C)** bacterial diversity, and **(D)** fungal diversity.

western U.S. drylands in many ways (Chapin et al., 2000; Belnap and Phillips, 2001; Compagnoni and Adler, 2014; Bradley et al., 2018). Among other influences, *B. tectorum* has altered plant biodiversity and nutrient cycling (Sperry et al., 2006; Norton et al., 2008), as well as microbial and microfaunal composition (Belnap and Phillips, 2001; Kuske et al., 2002; Belnap et al., 2005). For example, *B. tectorum* can reduce the ability of fungi to consume N (DeCrappeo et al., 2017). In addition, biocrusts have been shown to enhance *B. tectorum* growth likely through impacts on soil fertility (Ferrenberg et al., 2018). Our data support the conclusion that invasion by *B. tectorum* creates a new microhabitat type that helps dictate the extant soil microbial community.

Many fungal taxa were common across rhizosphere soils of *P. jamesii* and *B. tectorum* (**Figures S6, S8**, **Table S6**). In addition, a number of fungal genera were most highly associated with *B. tectorum,* including *Sclerotinia* (plant pathogenic fungi), *Saccobolus*, *Zygopleurage*, *Karstenula* (saprotroph), *Neofabraea* (plant pathogen/saprotroph), *Hydropisphaera*, and *Microsphaeropsis* (saprotroph) (**Figure S8**, **Table S6**), as well as the bacterial genus *Massilia*, a copiotrophic root colonizing bacteria (Ofek et al., 2012) (**Figure S9**, **Table S6**). In the biocrust communities, the fungal genus *Endocarpon* was characteristic of cyanobacteria and lichen bicrusts, but was found in much lower abundance in rhizosphere soil communities. Fungal genera *Psora, Hymenelia, and Aspicilia* were also abundant in lichen biocrusts, while *Basidiomycetes* were more common in cyanobacteria biocrusts. Moss biocrusts were characterized by *Iodophanus,* also found in the plant-associated soils, as well as *Lamprospora* and *Umbilicaria*. Generally, microbial communities in moss biocrusts were more similar to the rhizosphere soils, which is interesting given that mosses are plants and, like plant roots, have structures called rhizines embedded in the soil (Jones and Dolan, 2012). Mosses in this area fix more CO_2 compared with earlier-successional (e.g., cyanobacterial) biocrusts (Tucker et al., 2018), and thus carbon supply to the soil microbial community could be part of what supports a similar community between vascular plant roots and the soils beneath moss rhizines. Differences in the bacterial and fungal composition of biocrusts compared to non-biocrust samples may also be related to the soil depth. This study was limited to coarsely surveying complex communities through molecular techniques, future studies using additional techniques such as microscopy, culturing, and functional assays are needed to confirm the identity of and further characterize the microorganisms forming these complex communities.

Biocrusts (cyanobacteria, lichen, and moss) were dominated by Cyanobacteria and Thaumarchaeota (*Nitrososphaera*). The most abundant Cyanobacteria was *Microcoleus* (*Phormidiaceae*) (**Table S4**), which has previously been described as the most dominant cyanobacteria in Colorado plateau biocrusts (Garcia-Pichel et al., 2001). Other abundant Cyanobacterial families included *Coleofasciculaceae* and *Nostocaceae* (**Table S4**). The highest relative abundances of Thaumarchaeota were found

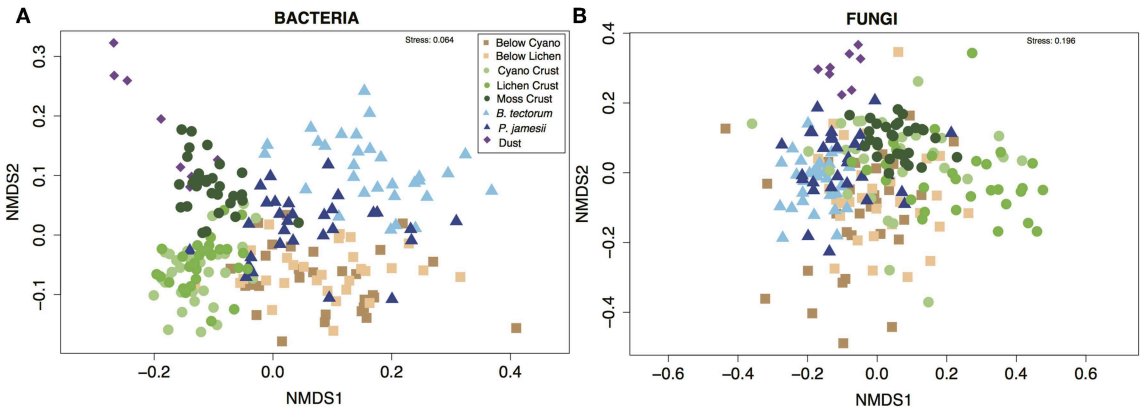

FIGURE 2 | Non-metric multidimensional scaling (NMDS) ordinations showing **(A)** bacterial and **(B)** fungal community composition across different microhabitat types.

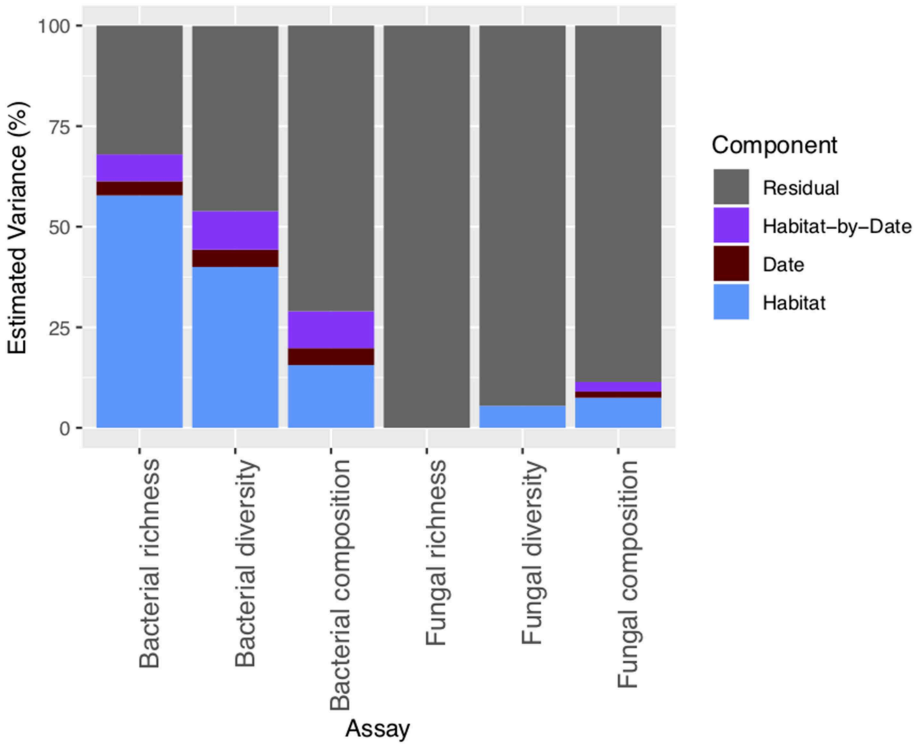

FIGURE 3 | Percentage of estimated variation across bacterial and fungal richness, diversity, and composition metrics explained by the microhabitat, date, and microhabitat-by-date.

in the soils underlying the cyanobacteria and lichen crusts (**Figure S7**), which were the most alkaline microhabitats with the highest C:N ratio (**Figures S3, S4**). Thaumarchaeota are ammonia-oxidizing archaea, that have previously been reported as significant contributors to biocrusts that may be important in soil crust N cycling (Soule et al., 2009; Marunsenko et al., 2013; Maier et al., 2018). Furthermore, previous work has found that soils ammonia-oxidizing archaea abundances are generally higher in more alkaline and NH_4^+ limited soils (Gubry-Rangin et al., 2011). A number of other abundant bacteria genera in this study including *Streptomyces, Rubrobacter*, *Paracoccus*, *Massilia*, *Bacillus*, and *Spirosoma* have also been previously characterized in biocrusts from the Southwestern U.S. Colorado plateau region (Gundlapally and Garcia-Pichel, 2006) (**Figure S9**).

Mineral soil inputs of dust are most often discussed as nutrient inputs but less often considered as inputs of biological (microbial) material. Even so, an abundance of taxa known to play important roles in biocrusts have been documented

in indoor and outdoor airborne environments (Despres et al., 2012; Barberan et al., 2015; Warren et al., 2019). We found that both the bacterial and fungal composition of dust were distinct from the soil samples (**Figure 2**). Furthermore, bacterial richness and diversity were lower in dust samples, while fungal dust samples did not differ from soils (**Figure 1**). This may be because fungal spores are generally tougher and thus less likely than bacterial cells to be degraded during the time span and harsh conditions of air travel and deposition (Kuske, 2006). Common fungal genera found in dust samples in higher abundances than in the other microhabitats we sampled included *Ochrocaldosporium*, *Thelebolus*, *Chaetosphaeronema*, and *Camarosporium* (**Figure S8**, **Table S6**). *Thelebolus* is known for ability as a thermophile to survive in extreme temperature conditions (de Hoog et al., 2005), while *Camarosporium* is known as a fungal plant pathogen (Wanasinghe et al., 2017). Dust samples were dominated by the bacterial genera *Zhihengliuella, Oxalicibacterium,* and *Hymenobacter* (**Figure S9**, **Table S7**). *Hymenobacter* has been characterized as a common atmospheric bacterium (Yooseph et al., 2013; Barberan et al., 2015). The most abundant phyla in dust samples was Deinococcus-Thermus (**Figure S7**), recognized as the most extremophilic phylum of bacteria (Theodorakopoulos et al., 2013).

Correlations Between Microbial Diversity and Environmental Parameters

Precipitation and pH were the two environmental parameters that significantly correlated with changes in microbial diversity in the grassland microhabitats, although these relationships were relatively weak. Both bacterial and fungal richness and diversity were positively correlated with pH [$R^2 = 0.34, p < 0.001$ (bacteria richness) and $R^2 = 0.13$, $p = 0.05$ (bacteria diversity), $R^2 = 0.15$, $p = 0.03$ (fungal richness), and $R^2 = 0.21$, $p = 0.003$ (fungal diversity)]. pH ranged from 6.9 to 8.4 where more alkaline soils had greater richness and diversity (**Figure 1**, **Figure S4**). Bacterial and fungal composition were significantly correlated with pH (Mantel test; $R = 0.21$, $p = 0.001$ and $R = 0.06$, $p = 0.03$, respectively). Considering climate controls, bacterial diversity was positively correlated with precipitation ($R^2 = 0.14$, $p = 0.04$), while both fungal richness and diversity were negatively correlated with precipitation ($R^2 = -0.15$, $p = 0.04$ and $R^2 = -0.14$, $p = 0.05$, respectively). These results are consistent with previous studies showing that, across global soils, changes in pH are correlated with changes in bacterial community composition (Fierer and Jackson, 2006; Rousk et al., 2010), but manipulative studies would be needed to test for causation.

Temporal Changes in Microbial Community Richness Diversity and Composition

Bacterial richness and diversity [two-way ANOVA; date: $F_{(13,143)} = 4.5$, $P < 0.001$ (richness), $F_{(13,140)} = 4.0$, $P < 0.001$ (diversity)] showed significant temporal variability, as well as a significant microhabitat-by-date interaction [two-way ANOVA; microhabitat-by-date: $F_{(54,143)} = 1.8$, $P < 0.001$ (bacterial richness), $F_{(54,143)} = 1.8$, $P < 0.001$ (bacterial diversity)]. In contrast, fungal richness and diversity showed no significant temporal variability. Both bacterial and fungal composition changed significantly across the sampling dates [PERMANOVA; date: $F_{(13,143)} = 2.9$, $P < 0.001$ (bacteria), $F_{(13,143)} = 1.5$, $P = 0.001$ (fungi)] (**Figures S6B, S7B**); however overall sampling date explained much less of the variation in community composition than microhabitat (**Figure 3**). Some fungal communities may be more stable over time than bacteria because of their extensive hyphal structures that allow them to regulate moisture availability which can change rapidly over time in dryland ecosystems (Bapiri et al., 2010; Yuste et al., 2011; Barnard et al., 2013). However, some soil fungi have also been shown to be sensitive to moisture conditions (Meisner et al., 2018).

Microhabitat Type Mediates the Impact of Temporal Change in Shaping Microbial Community Composition in a Semi-arid Grassland

For both bacteria and fungi, a significant microhabitat-by-date interaction was observed [PERMANOVA; microhabitat-by-date: $F_{(54,143)} = 1.5$, $P < 0.001$ (bacteria), $F_{(54,143)} = 1.1$, $P = 0.006$ (fungi)]. Bacterial and fungal composition were both significantly correlated with temporal distance (time between sampling points) for four out of the seven microhabitats, including cyanobacteria biocrust, below lichen, and plant-associated soil (*B. tectorum* and *P. jamesii*) (**Table 1**). In addition, bacterial composition was significantly correlated with temporal distance for the microhabitat moss biocrust (**Table 1**). These results partially support our second hypothesis that biocrust communities would change the most, and below-biocrust communities would change the least, over time. Surface soils typically experience greater climatic variability (Tucker et al., 2017), which may drive stronger temporal changes in the cyanobacteria biocrust communities. However, lichen and moss biocrust composition did not change significantly over time. This higher stability, despite the location on the surface may be because these biocrusts occur in later successional stages than cyanobacteria biocrusts (Belnap, 2003) and thus may be better established and more resistant to fluctuations in moisture and temperature. Other morphological characteristics of moss and

TABLE 1 | Correlations between community composition in each microhabitat and temporal distance (Mantel tests).

	Bacteria		Fungi	
Microhabitat	***R***	***p*-value**	***R***	***p*-value**
Cyano crust	**0.3179**	**0.001**	**0.1728**	**0.006**
Lichen crust	0.0237	0.333	−0.08984	0.943
Moss crust	**0.5311**	**0.001**	0.1083	0.069
Below cyano	0.05871	0.221	0.08592	0.128
Below lichen	**0.1789**	**0.008**	**0.1622**	**0.02**
P. jamesii	**0.2837**	**0.001**	**0.2106**	**0.006**
B. tectorum	**0.4218**	**0.001**	**0.1705**	**0.016**

Significant correlations ($p < 0.05$) are shown in bold.

lichen biocrusts may also increase resilience. The rhizosphere communities also showed a temporal correlation with bacterial community composition. The strongest correlation was with *B. tectorum*, which is an annual invasive C_3 grass that can germinate in September, expand roots over the winter, and then grow between March and April (Belnap and Phillips, 2001). The perennial C_4 grass *P. jamesii's* rhizophere microbial composition was also significantly correlated with time, but more weakly than *B. tectorum.* Temporal changes in these rhisozphere bacterial communities are likely associated with both plant life-cycles and development stage, which have been shown to influence rhizosphere communities (Houlden et al., 2008; Philippot et al., 2013; Li et al., 2014).

Differences in Semiarid Grassland Bacterial and Fungal Community Dynamics

Taken together, ∼29% of the variation in bacterial community composition could be explained by microhabitat, date, and microhabitat-by-date interaction, while only around 11% of variation in fungal community composition could be explained by the same factors (**Figure 3**). The low amount of variation explained by the environmental factors tested suggests that either fungal composition is driven by environmental factors not measured in the current study or that fungal assembly is more stochastic. Studies in other ecosystems have found that fungal communities exhibit highly stochastic assembly processes compared to bacteria, where environmental selection processes are the stronger drivers (Schmidt et al., 2014; Powell et al., 2015; Jiang et al., 2018). Our data suggest that these patterns may hold in dryland ecosystems as well.

The Future of Microbial Diversity in Semiarid Grasslands

Dryland grasslands are currently highly impacted by a variety of global changes, including altered precipitation, increased temperature and nutrient deposition, and physical disruption (Maestre et al., 2016; Plaza et al., 2018). Dryland grasslands are typically resource limited and can show low resistance and resilience to both abiotic and biotic perturbations (Barger et al., 2006; Belnap and Sherrod, 2009; Kuske et al., 2012; D'Odorico et al., 2013; Steven et al., 2018), thus the spatial heterogeneity in these landscapes is unlikely to remain static. The differences in composition across microhabitats in this study highlight the importance of spatial heterogeneity in shaping the overall diversity of microbial communities in grassland ecosystems. The microhabitats can be very close to one another, distanced by only a few centimeters or less, yet the communities observed here showed strong variation among locations and across time. While this study only examined microhabitats within a single grassland site for a single year, we expect that across larger spatial scales (multiple sites), we will see similar strong effects of microhabitat variation. The role of microhabitat heterogeneity and climatic variability in shaping diverse dryland landscapes remains an important question, and future studies that explore this variation and its consistency (or lack thereof) across multiple sites would be extremely valuable. This case study of the temporal and spatial structure of bacterial and fungal communities is one step to understanding the variability and assembly controls over microbial composition in drylands.

AUTHOR CONTRIBUTIONS

MA analyzed the data and wrote the first draft. RM analyzed the sequence data. LG-G conducted DNA extraction, PCR amplification, and prepared information for sequencing. JB, CK, and SR conceived the study and the monthly sampling.

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SUPPLEMENTARY MATERIAL

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