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A watering manipulation in a semiarid grassland induced changes in fungal but not bacterial community composition

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ABSTRACT

Monsoon precipitation in the arid southwestern United States is an important driver of ecosystem productivity, delivering up to 50% of annual precipitation during the summer months. These sporadic rainfall events typify drying-rewetting cycles and impose a physiological stress on the soil microbial communities responsible for carbon and nutrient cycling. As one aspect of climate change is an intensification of the hydrologic cycle, understanding how soil microbial communities and the processes they mediate are impacted by moisture fluctuations is increasingly important. We performed a month-long watering manipulation in the field and characterized bacterial and fungal communities across five time points using high-throughput sequencing. Watering treatment had a significant impact on fungal community composition, and there was a trend toward decreased fungal diversity and OTU richness in watered plots. In contrast, no significant differences were observed in bacterial communities between watered and control plots nor among sampling times. These findings suggest that fungi are more sensitive than bacteria to changes in soil moisture.

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1. Introduction

Sporadic precipitation with varied temporal distribution dictates productivity in arid regions (Noy-Meir, 1973). For the southwestern United States, a shift from dry westerly winds to wet southeasterly winds results in a transition from an extremely dry spring to a wet summer. This wind shift, known as the North American monsoon, transports pulses of moisture from the tropical eastern Pacific Ocean, Gulf of California, and Gulf of Mexico (Hales, 1972; Brenner, 1974). Arizona and New Mexico receive up to half of their annual precipitation during the summer monsoon season (Climate Assessment for the Southwest, 2012), making this rain event crucial for ecosystem productivity and dynamics. As alterations in precipitation patterns are predicted due to climate change, it is critical to uncover how resilient ecosystem processes are to fluctuations in precipitation. Microbial processes, including organic matter decomposition and nitrogen cycling, are important contributors to ecosystem productivity, and yet the mechanisms behind microbial population dynamics in response to major changes in precipitation levels remain poorly understood.

In a descriptive study of soil microbial population dynamics in a semiarid grassland during the monsoon period in northern Arizona, select bacterial populations, including Actinobacteria and Firmicutes, responded immediately to an increase in soil moisture. However, overall bacterial community composition did not change significantly in response to increased soil moisture (McHugh et al., 2014). In contrast, fungal community composition shifted late in the season after the rains ceased, possibly in response to plant growth. These compositional shifts were driven primarily by increased abundances of Glomeromycota and Zygomycota. In general, the relative abundances of fungal phyla were more variable through time and with soil moisture fluctuations than those of bacterial phyla, suggesting the fungal community was more dynamic during the rainy period (McHugh et al., 2014). Many environmental parameters, including temperature, soil moisture, relative humidity, and photoperiod change during the monsoon season. In order to understand the mechanism behind microbial population dynamics, it is imperative to conduct manipulation experiments in which the impacts of altered environmental parameters on microbial community composition are investigated.

In a field manipulation with decreased precipitation and/or removal of the plant community, we measured the direct and

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interactive effects of these changes on bacterial and fungal communities at five time points during a summer season in a semiarid grassland site (McHugh and Schwartz, 2014). We found that soil microbial communities were sensitive to alterations in precipitation and plant assemblages, though the observed changes in community composition were not pronounced. These findings are significant in light of the growing recognition that the composition of microbial communities influences important ecosystem processes across a variety of spatial and temporal scales (Strickland et al., 2009; Allison et al., 2013).

In the present study, we report the results of a watering experiment in a semiarid grassland where we altered both the timing and frequency of precipitation by applying an entire monsoon period's moisture to soil during the dry season, prior to the advent of the summer rains. Using high-throughput sequencing, we describe the responses of bacterial and fungal communities to extreme moisture fluctuations. We hypothesized that abundant bacterial populations, including Actinobacteria and Firmicutes, would be immediately impacted by increased soil moisture, while the composite fungal community would change slowly in response to the watering manipulation.

2. Material and methods

2.1. Site description and experimental design

This study was conducted in a semiarid, high-desert grassland north of Flagstaff, Arizona (35°34′20′N, 111°34′4′W, 1760 m above sea level, 230 mm of rain annually). Vegetation at the site consists mainly of perennial grasses (*Bouteloua eriopoda*,*Bouteloua gracilis*, *Sporobulus cryptandrus*, and *Pleuraphis jamesii*) with few shrubs (*Ericameria nauseousa*, *Gutierrezia sarothrae*). Soils are cindery and are classified in the U.S. Department of Agriculture Soil Taxonomic Subgroup of Typic Haplustolls. A Campbell Scientific (Logan, UT) weather station continuously collects precipitation and temperature data, along with other environmental parameters.

We performed a month-long watering experiment during June 2012, prior to the natural monsoon rains, when temperatures were elevated (daily mean 25.6 °C) and soil moisture content was extremely low (1.94% on average). Plants were physiologically dormant at this time and vegetation cover was patchy. No natural precipitation occurred during the experimental period, which extended from 1 to 30 June. A random block design was employed, with four blocks as replicates and 1.0 m spaces between blocks. Each block contained two 1.0 m x 1.0 m plots randomly designated as treatment plots or controls, and spaces of 1.0 m were left between plots in each block. Long-term monsoon precipitation averages for this grassland were used to design the watering regime (Fig. 1). A total of 78 mm of water was delivered to each treatment plot over a 28-day period. The approach mimicked the natural dry-wet cycles typical of monsoon precipitation (McHugh et al., 2014), with the greatest amount of moisture being delivered in the middle of the experiment.

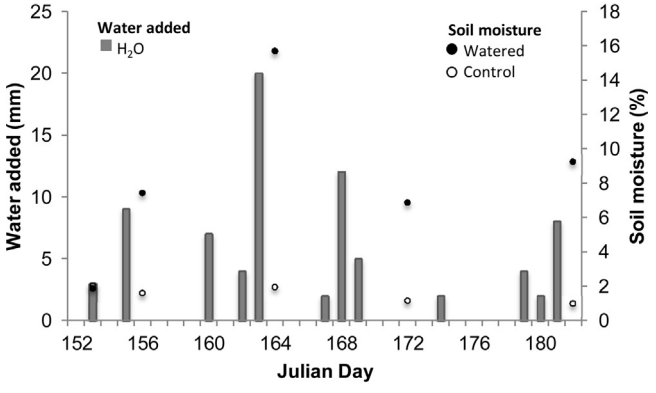

Fig. 1. Watering scheme and soil moisture content during the watering experiment. Error bars are standard error for means (n = 4).

2.2. Soil collection and moisture measurements

A Hydrosense II soil-water sensor with 12 cm rods (Campbell Scientific, Logan, UT, USA) was used to measure volumetric water content on each watering day, prior to irrigation. At five time points (experimental days 1, 4, 12, 20, and 30), one 5 cm (depth and diameter) soil core was collected from bare soil between plant patches within each plot, for a total of 40 cores. Soil cores were sieved (<2 mm), homogenized, and subsampled to determine gravimetric water content.

2.3. NO_3^- and NH_4^+

Soil NO_3^- and NH_4^+ were extracted from 10 g soil samples in 40 mL 2 M KCl solution in the field. Samples were transported back to the laboratory, shaken for 1 h, filtered through Whatman No. 1 filter paper and stored at −20 °C until further processing. Ammonium and NO_3^- extracts were analyzed colorimetrically with a Lachat analyzer.

2.4. Soil respiration

On the five soil collection days, a 40 g subsample of fresh soil from each core was weighed into a specimen cup, placed in a 1 L Mason jar, and sealed with a lid containing a rubber septum. CO_2 concentrations were measured for each sample with a LI-COR 6262. CO_2/H_2O gas analyzer (LI-COR Biosciences Inc., Lincoln, NE, USA). Gas samples were taken shortly after field collection and two days following collection to obtain a rate of CO_2 production. All jars were incubated in the dark at 23 °C. Remaining soil was stored at −40 °C until further processing.

2.5. Nucleic acid extraction and sequencing

Total genomic DNA was extracted from 0.5 g of soil in each sample using PowerLyzer PowerSoil DNA Isolation Kit according to the manufacturer's instructions, with an initial 10-min incubation at 70 °C followed by bead beating for 90 s (MO BIO Laboratories, Inc., Carlsbad, CA). High-throughput short amplicon sequencing on an Illumina MiSeq platform was performed at Northern Arizona University's Environmental Genetics and Genomics Laboratory. The 16S rRNA gene was amplified using primers 515f and 806r, which target the hypervariable V4 region (Caporaso et al., 2012). The fungal ITS region was amplified using primers ITS4_Fun and 5.8S_Fun, which target ITS2 (Taylor, 2014).

Bacterial and fungal samples were prepared for sequencing using an approach described previously (McHugh and Schwartz, 2014). All samples were quantified by PicoGreen (Molecular Probes, Eugene, OR) fluorescence and normalized to 1 ng/μL before amplification. Samples were processed in two barcoded primer PCR steps (Berry et al., 2011). First, each sample was amplified in triplicate, 8 μL-PCRs containing 1 mM of each primer, 0.01U/μL Phusion HotStart II Polymerase (Thermo Fisher Scientific, Waltham, MA), 1X Phusion HF buffer (Thermo Fisher Scientific), 3.0 mM $MgCl_2$, 6% glycerol, and 200 μM dNTPs. PCR conditions were as follows: 95 °C for 2 min, 15 cycles of 30 s at 95 °C (25 cycles for ITS), 30 s at 55 °C, and 4 min at 60 °C. Initial PCR products were pooled, diluted 10-fold, and used as template in the subsequent tailing reactions with region-specific primers. These reactions were identical to initial PCR reagent concentrations and cycling

conditions, except that amplification was carried out for 20 cycles rather than 15. Tailing products were quantified by PicoGreen fluorescence, and the normalized amounts were combined into a final sequencing pool. A bead cleanup procedure was used to remove unincorporated primers according to the protocol described in Rohland and Reich (2012). The purified pool was quantified by PicoGreen fluorescence, denatured, and loaded at 8 pM onto an Illumina MiSeq for a 2 × 150 paired-end run.

2.6. Data analysis

Overlapping paired-end reads were merged with Ea-utils at a 5% maximum mismatch and a 30 bp minimum overlap (Aronesty, 2011). QIIME 1.7.0 was used to demultiplex, quality filter, and analyze joined fastq files (Caporaso et al., 2010b). Default parameters were used to eliminate low-quality reads, with the exception of the Q-score threshold, which was set at 30.

The 16S rRNA sequences were clustered into operational taxonomic units (OTUs) by 97% sequence identity using UCLUST and the Greengenes database version 13_5 (Edgar, 2010; McDonald et al., 2012). The most abundant sequence for each OTU was aligned with the PyNAST algorithm (Caporaso et al., 2010a) and then used to generate taxonomic assignments with the RDP classifier (Wang et al., 2007). Sequences classified as archaea were removed from the OTU table to limit downstream analyses to the domain bacteria. Additional quality filtering was applied, discarding any OTUs with a number of sequences that accounted for less than 0.005% of the total number of sequences (Bokulich et al., 2013). After bacterial libraries were rarefied so that sequencing efforts did not affect diversity comparisons, alpha diversity was computed using observed species, Chao1, and phylogenetic diversity (Faith and Baker, 2007) metrics. Bacterial community composition was assessed with UniFrac pairwise distance between samples (Lozupone and Knight, 2005).

Fungal sequences were clustered into OTUs with USEARCH61 (Edgar, 2010) using a 94% sequence similarity (Hoffman and Arnold, 2010; McHugh and Schwartz, 2014). Taxonomy was assigned to ITS reads with BLAST using the UNITE 12_11 reference database (Koljalg et al., 2013). The minimum total observation count for fungal OTUs was set at 0.005% (Bokulich et al., 2013). Fungal libraries were rarefied, and alpha diversity was computed using observed species and Chao1 metrics. Bray-Curtis dissimilarities were used to assess fungal community composition.

For both bacterial and fungal datasets, the QIIME-generated distance matrices were imported into Primer 6 (Primer-E; Lutton, Ivy Bridge, United Kingdom) and visualized using nonmetric multidimensional scaling (NMS). We determined the effects of experimental treatment and time on the structure of bacterial and fungal communities with permutational multivariate analysis of variance (PerMANOVA) in Primer. Analysis of variance was used to assess the impact of time and watering treatment on soil moisture content, inorganic N concentrations, soil respiration rates, and alpha diversity (SAS Institute Inc., Cary, NC, USA). For bacterial and fungal communities, organisms representative of watering treatment and control groups were identified by performing indicator species analysis in the R statistical platform (R Core Team, 2012) using the labdsv package.

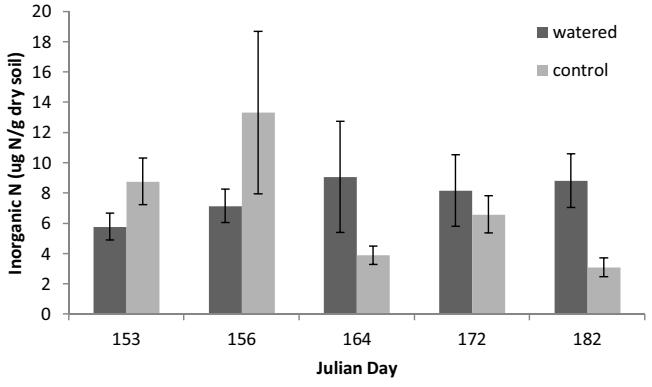

Fig. 2. Inorganic N concentrations in watered and control plots. Error bars are standard error for means (n = 4).

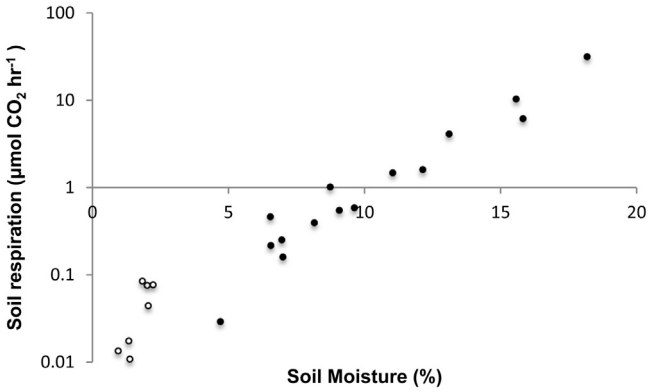

Fig. 3. Soil respiration in watered (closed circle) and control (open circle) plots at different moisture contents over the course of the experiment. Respiration measurements are $\log_{10}$, and negative values are not shown.

3. Results

With the exception of the first soil collection, which occurred prior to watering, soil moisture content throughout the experiment was significantly higher in watered plots than in untreated control plots ($p < 0.001$, Fig. 1). Inorganic N concentrations in control plots were initially higher than those in watered plots, however this pattern shifted by the middle of the experiment (Fig. 2). When N pool data from the first two collection dates were excluded to account for natural variation among experimental plots prior to the start of the study, there was a significant effect of watering on inorganic N concentrations ($p = 0.022$). Increased water availability resulted in significantly greater soil respiration rates in watered plots, and the relationship between soil CO_2 efflux and soil moisture content was exponential ($p < 0.001$, Fig. 3).

High-throughput sequencing produced 1,979,015 bacterial sequences and 2174 OTUs. Sequences per sample ranged from 27,490 to 59,973, with an average of 43,897. Rarefaction curves reached an asymptote, indicating the sampling effort was sufficient to capture the diversity within our soils. Bacterial communities were dominated by the phyla Actinobacteria, Proteobacteria, and Acidobacteria, with few differences observed between control and watered plots (Fig. 4a). On average, Actinobacteria showed no response to water addition, while members of the Firmicutes phylum increased in abundance by experimental day 4 (Julian Day 156) in response to small moisture pulses. Indicator species analysis revealed that Acidimicrobiales AKIW874, Acidobacteria, and Verrucomicrobia were indicators of the watering treatment, while Staphylococcus, Acetobacteraceae, and Betaproteobacteria MND1 were indicators of the control (Table 1). NMS ordination showed that bacterial communities in watered plots were indistinguishable from those in control plots, and this lack of differentiation was supported by PerMANOVA ($p = 0.332$, $F = 1.12$; Fig. 5a). Alpha diversity was similarly unaffected by watering.

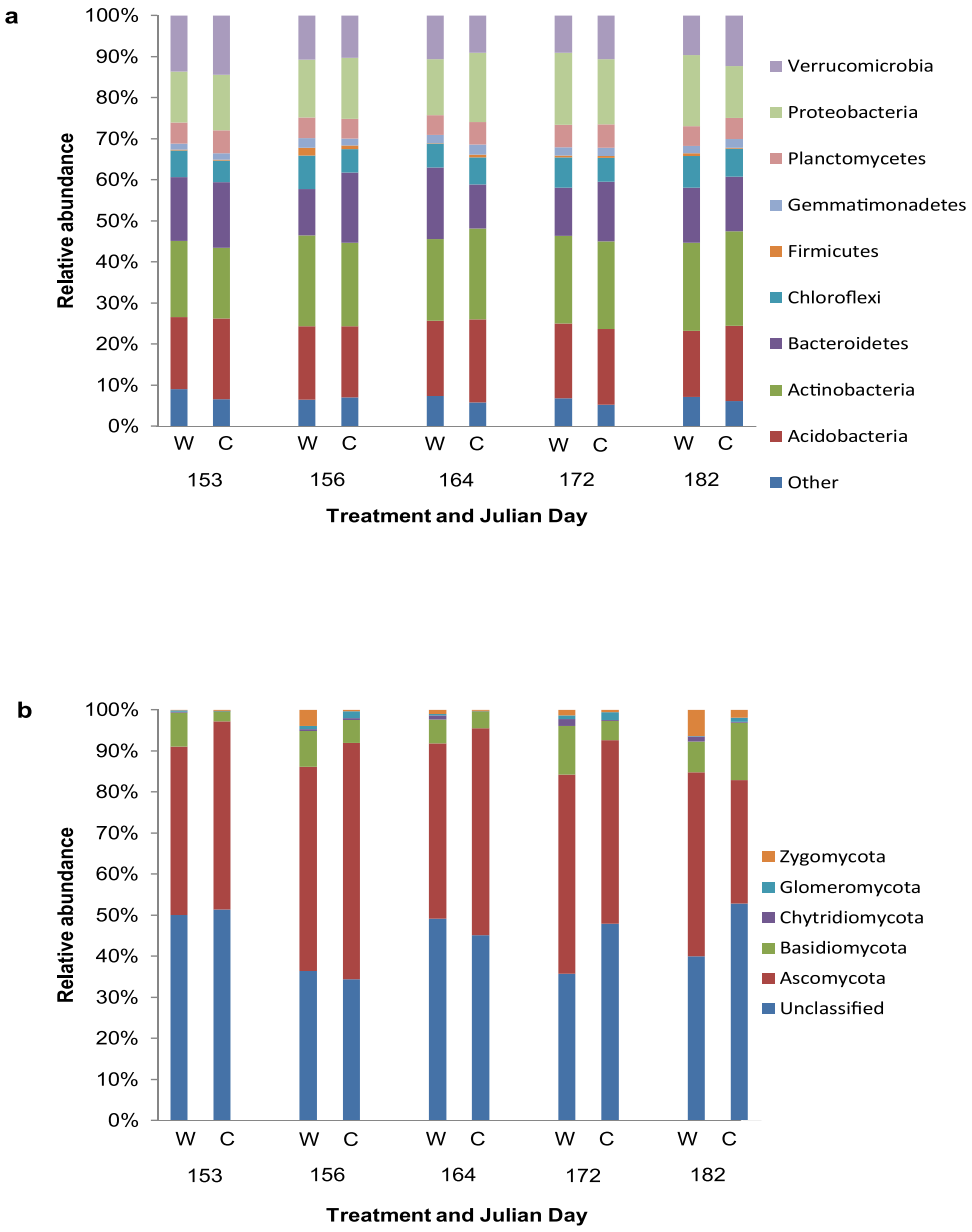

Fig. 4. Relative abundances of dominant bacterial (a) and fungal (b) phyla in watered (W) and control (C) plots as determined by high-throughput sequencing of the 16S rRNA gene and ITS region, respectively.

The fungal sequencing effort generated 1,205,219 sequences and 259 OTUs. Sequences per sample ranged from 14,277 to 49,764. Fungal phyla were dominated by Ascomycota and Basidiomycota, and as much as 50% of the community was taxonomically unclassified (Fig. 4b). Indicator species analysis showed that Herpotrichia, Glomeromycota, Poculum, and Ampelomyces were indicators of the watering treatment, while Spizellomyces, Taifanglania, Aspergillus, and Saccharomyces were indicators of the control (Table 2). NMS ordination showed separation of fungal communities across the five time points, with communities from experimental days 20 and 30 (Julian Days 172 and 182) being most distinct (Fig. 5b). PerMANOVA revealed that watering treatment ($p = 0.003$, $F = 2.19$) and time ($p = 0.024$, $F = 1.34$) had a significant impact on fungal community composition. A trend toward decreased diversity in watered plots at the end of the experiment was observed (Julian Days 172 and 182, Chao1 $p = 0.070$, observed species $p = 0.100$).

4. Discussion

Soil water content influences microorganisms directly and indirectly through changes in oxygen concentrations and nutrient

Table 1
Representative bacterial taxa in watered and control plots, as determined by indicator species analysis.

Treatment	Taxon	Indicator Value	Probability
Watered	Acidimicrobiales, AKIW874	0.9179	0.02850
Watered	Acidobacteria, other	0.8630	0.02670
Watered	Verrucomicrobia, other	0.8470	0.02660
Watered	Chlorobi	0.8064	0.02860
Watered	Chloroflexi, P2-11E	0.7213	0.02990
Control	Staphylococcus	0.9976	0.02870
Control	Acetobacteraceae, other	0.6636	0.02860
Control	Betaproteobacteria, MND1	0.5940	0.02720
Control	Beijerinckiaceae	0.5751	0.02730

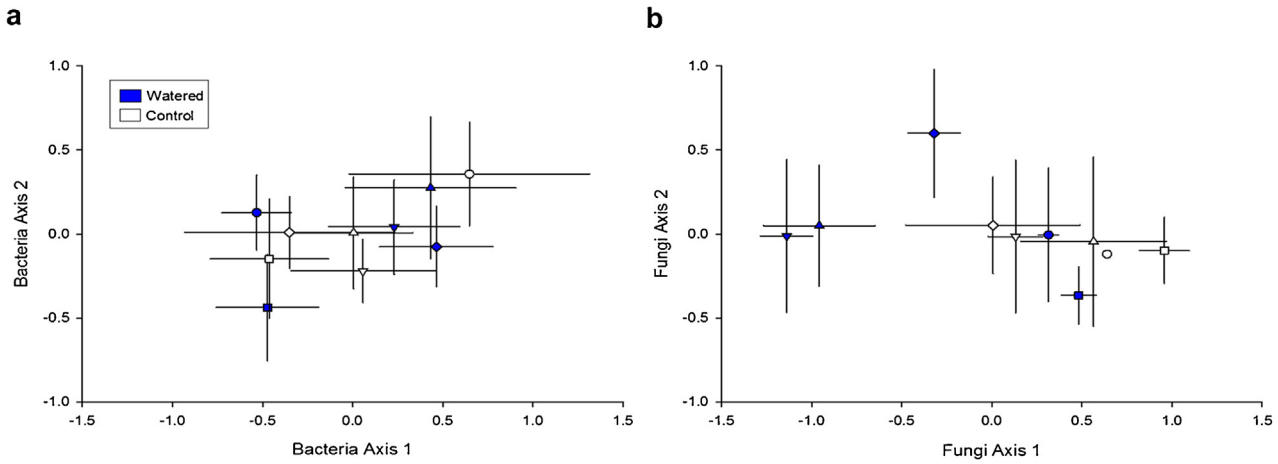

Fig. 5. Nonmetric multidimensional scaling ordinations of bacterial (a) and fungal (b) community composition through time calculated from weighted UniFrac distances and Bray-Curtis dissimilarities, respectively. Shapes represent sampling dates according to the following convention: square, Julian Day 153; diamond, Julian Day 156; circle, Julian Day 164; triangle, Julian Day 172; upside-down triangle, Julian Day 182.

availability. We successfully manipulated soil moisture content in our experiment, increasing soil moisture up to 10-fold in the irrigated plots. The approach involved gradually delivering an entire monsoon season's worth of water over a month-long period. While others have simulated yearly rainfall by applying all the water at the beginning of the study period (e.g., Liu et al., 2002), we felt that incremental application more realistically simulated monsoon precipitation. By adding water on several occasions during the experiment, we established wetting and drying cycles that may be important in structuring soil microbial communities. The wet-dry cycles associated with monsoon season impose a physiological stress that can affect both the community composition and metabolism of soil microorganisms (Schimel et al., 2007). We documented soil moisture contents above field capacity (21.5%) in our monsoon observational study (McHugh et al., 2014), and similar moisture levels were achieved in this experimental manipulation.

A significant increase in microbial activity was observed in response to watering. Soil respiration is typically low in dry soils and shows an instantaneous increase after rains (Holt et al., 1990; Grahammer et al., 1991). Soil moisture affects soil respiration directly through its influence on root and microbial activities, and indirectly through physical and chemical changes (Schimel and Clein, 1991; Raich and Schlesinger, 1992). Other research has shown that soil drying reduces solute diffusion and limits the supply of substrates to microorganisms (Griffin, 1981). As soil water potential decreases, so does the activity of microorganisms (Griffin, 1981; Harris, 1981). Reduced demand results in the accumulation of mineral and organic substrates during dry times, and this leads to a cascade of events following rewetting. Carbon previously bound in soil aggregates becomes mobilized, intracellular osmolytes are released, and metabolic and enzymatic activities increase, subsequently promoting respiration and nutrient mineralization (Fierer and Schimel, 2003; Schimel et al., 2007; Xiang et al., 2008; Borken and Matzner, 2009). Our results are consistent with these observations. CO_2 efflux rose immediately with the first watering event and reached a peak on experimental day 12 (Julian Day 164). Evidence of microbial activity was also provided by our nutrient data, which showed increased N mineralization at later stages in the watered plots compared to controls. Respiration in watered plots declined in the second half of the experiment, even though soil moisture remained elevated on subsequent days. Others have shown that microbial respiration in response to dry-wet pulses is lessened with successive events as microorganisms become acclimated to these episodes (Fierer and Schimel, 2003). Microbial respiration rates in control plots remained near zero for the duration of the study, possibly due to substrate limitation that occurs when hydrological connectivity is lost (Manzoni and Katul, 2014). The strong exponential relationship we observed between microbial respiration rates and soil moisture content indicates that, even in the driest of times, some microorganisms survive and are able to quickly respond to a beneficial change in their environment. As CO_2 flux data from several precipitation manipulation studies show signs of temperature sensitivity in wetted treatments (e.g., Liu et al., 2008; Zhang et al., 2010; Thomas et al., 2011), studies of this nature should take care to monitor soil temperature, as it may determine the size of the respiration response to wetting (Chatterjee and Jenerette, 2011).

Table 2
Representative fungal taxa in watered and control plots, as determined by indicator species analysis.

Treatment	Taxon	Indicator Value	Probability
Watered	Herpotrichia	0.9462	0.0046
Watered	Glomeromycota	0.9164	0.0131
Watered	Poculum	0.8567	0.0122
Watered	Ampelomyces	0.6851	0.0438
Control	Spizellomyces	0.9093	0.0074
Control	Taifanglania	0.8835	0.0276
Control	Chatomium	0.8811	0.0207
Control	Aspergillus	0.7746	0.0135
Control	Saccharomyces	0.7586	0.0173

Water addition resulted in a significant change in fungal community composition, possibly by expanding the habitat available for fungal growth. Microhabitat differentiation on soil aggregates has been documented (Hattori, 1988; Chenu et al., 2001), and it has been postulated that partitioning of bacteria and fungi into inner and outer portions of soil aggregates can result in fungi being more sensitive to drying-rewetting stress (Hattori, 1988). Furthermore, a recent microcosm experiment supports the idea that fungal communities are more sensitive than bacterial communities to non-extreme changes in moisture, and as moisture conditions fluctuate, certain fungal populations can become more dominant (Kaisermann et al., 2015). Our results did not support the hypothesis that fungi, by virtue of their filamentous structure, are better adapted than bacteria to soil drying (Wilson and Griffin, 1975; Gordon et al., 2008). Signs of water limitation in soil fungi from dry sites have also been noted in other aridland soils

(Cregger et al., 2012). One noticeable response to increased soil moisture was in the phylum Zygomycota, where relative abundances were higher with increased soil moisture content. These organisms are known to form mutualistic symbiotic relationships with plants, and some are molds that are involved in the decomposition of plant material (Kendrick, 2000). Higher variability in fungal relative abundances with moisture fluctuations in the field setting (Zumsteg et al., 2013; McHugh et al., 2014) further supports the notion of increased fungal sensitivity to moisture. Additionally, we observed that fungal diversity and OTU richness were lower in watered plots at the conclusion of the experiment. This finding, in combination with large differences between fungal community composition of watered and control plots towards the end of the experiment (Julian Days 172 and 182), indicates that fungi in this grassland ecosystem gradually respond to drying-rewetting cycles. The delayed change in fungal community composition with simulated pulses of precipitation is consistent with what we observed previously in a descriptive study during the monsoon season at this field site (McHugh et al., 2014).

Our NMS ordination of bacterial communities from all plots and time points showed no significant changes in community composition with watering. While the indicator species analysis identified certain organisms as representative of the watering treatment, there were no obvious interpretations of the identity of these taxa. Researchers have previously postulated that moisture fluctuations, like those that occur during monsoon season, may modify the composition of soil microbial communities by selecting for taxa that can tolerate extreme changes in water potential (Harris, 1981; Atlas, 1984; Fierer et al., 2003). However, other studies conducted in the laboratory (Fierer et al., 2003; Griffiths et al., 2003) and the field (Landesman and Dighton, 2010) have documented bacterial resistance to water stress, possibly due to adaptations that allow these organisms to avoid desiccation and withstand moisture fluctuations. It was only when we compared bacterial communities from watered and control plots on individual sampling dates that we saw a significant community shift in the watered plots (Supplementary Fig. S1). This difference was observed on experimental day 12 (Julian Day 164), by which point we had applied 55% of monsoon precipitation. In a microcosm study with California agricultural soils, it was observed that microbial community composition changed very little at moisture contents less than or equal to field capacity, perhaps due to adaptation to low moisture conditions (Drenovsky et al., 2004). After experimental day 12 when more water was added to the treatment plots, we saw a decline in respiration rates, and bacterial communities in watered and control plots began to resemble each other once more. It is possible that labile C was exhausted by this point, as repeated dry-wet cycles can heighten C and N losses from soil (Schwinning et al., 2004). Plants likely play an important role in maintaining the availability of labile C in soil through, for instance, root exudation. In our experiment, plants did not grow vigorously, likely because elevated atmospheric temperatures and high rates of evaporation prevented moisture retention in soil. While there is merit in the experimental approach used in our study, it is important to acknowledge that precipitation manipulations do not exactly replicate the environmental conditions that occur with natural precipitation (Beier et al., 2012).

Because our study was conducted during the hottest and driest month in northern Arizona, the water addition occurred without a change in atmospheric relative humidity. During the study period, average relative humidity ranged from 8 to 14%, while it typically exceeds 50% during monsoon season. Though some degree of foliar greening occurred in the watered plots, we did not see a substantial response from grasses, which are the dominant vegetation type at the field site. Increased relative humidity and plant growth are changes that occur concurrently with monsoon precipitation. Since these two factors remained relatively constant during our experiment, we were able to isolate the influence of moisture fluctuations on soil microorganisms.

5. Conclusions

We found that fungal community composition changed gradually after irrigation of a semiarid grassland, while the bacterial community appeared highly resilient to changes in soil moisture. These results suggest that shifting precipitation patterns impact fungal communities in soil more strongly than bacteria, and that fungi may mediate climate-change associated alterations in ecosystem processes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pedobi.2016.04.003.

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