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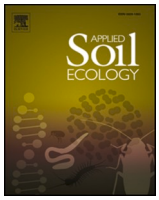

Simulated precipitation in a desert ecosystem reveals specific response of rhizosphere to water and a symbiont response in freshly emitted roots

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ABSTRACT

Soil microbiota plays a fundamental role in nutrient cycles and plant fitness. However, the response of bacterial and fungal communities interacting with plants to an increase in the water regime in natural ecosystems has yet to be extensively studied. To address this matter, we studied the response of rhizospheric and root endophytic microbial communities to simulated intense precipitation in a natural desert environment. We used amplicon sequencing to identify bacterial (16S) and fungal (ITS) communities of *Haloxylon salicornicum* (Moq) Bunge ex Boiss., a pivotal plant species in natural ecosystems with a high potential for land restauration. Bacterial community composition included mostly Actinobacteriota in roots and Chloroflexi in rhizospheres, whereas fungal communities were mostly represented by Ascomycota. The decomposition of beta diversity revealed a significant share of i) turnover for bacteria between compartments, ii) nestedness for fungi according to compartments, and iii) nestedness for bacteria in both rhizosphere and roots according to watering. Differential abundances analyses between watering conditions identified respectively i) 29 and 37 differentially abundant bacterial families, and ii) 7 and 6 differentially abundant fungal families for rhizosphere and roots. Watering induced a rapid response from little characterized microbiota potentially involved in nutrient recycling, such as rhizobia and dark septate endophytes. These results provided evidence of the fundamental role of rare and intense precipitation in modifying the microbial composition of roots and rhizosphere of one desert plant species. Moreover, little studied taxa potentially crucial to the plant health in desert environments such as dark septate endophytes and Planctomycetota were identified as pioneer taxa colonizing freshly emitted roots. Collectively, our results help to improve the understanding of desert taxa response to water availability, and may guide future research on natural ecosystems restauration.

1. Introduction

A third of terrestrial ecosystems are found in arid environments (Meigs, 1953) under high abiotic constraints, such as low nutrient and water availability. They may be described by the pulse-reserve paradigm (Noy-Meir, 1973), — a conceptual model — based on the assumption that episodic rainfall triggers biological activity and nutrient cycling. Plant growth is thus directly dependent on water availability. The role of microorganisms in nutrient cycling and plant establishment is even more critical in these ecosystems as plants are subjected to high abiotic stress (Soussi et al., 2016), which may be alleviated by microbes (Selosse et al., 2004). Both bacteria and fungi play key roles in nutrient cycling and ecosystem functioning (Delgado-Baquerizo et al., 2016). The pulse-reserve model was subsequently extended to account for microbial processes that shape the response of arid ecosystems to rainfall events (Collins et al., 2008). Overall, it suggests that pulse dynamics with respect to water availability are the driving factors of nutrient mineralization and biological activity in arid ecosystems.

There is current evidence that plant-microbiota interactions in arid ecosystems favor plant establishment (Molina-Montenegro et al., 2016)

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under the so-called 'fertility island' hypothesis (Schlesinger et al., 1995) *via* germination facilitation, increased water and nutrient acquisition (Toledo et al., 2022). It is crucial to determine how microbiota responds to periodic water input and the potential cascading consequences on ecosystems so as to be able to preserve them and understand the processes involved. It has been shown that soil microbial community composition can respond rapidly to water input and trigger CO_2 respiration, before returning to the initial drought conditions within a month (Armstrong et al., 2016). In the Chihuahua desert, microbial activity was significantly influenced by seasonal patterns of temperature and humidity, where carbon (C) and nitrogen (N) mineralization varied according to humidity pulses (Bell et al., 2008). The rapid response of bacteria has also been identified across diel-scale cycles in the Namib Desert, where changes in potentially active bacterial communities revealed by 454 pyrosequencing of 16S rRNA-derived cDNA, could occur within a single-day time frame (Gunnigle et al., 2017). Finally, in the Atacama Desert, where C availability is very low, rewetting was found to trigger soil microbial growth (Rosinger et al., 2023). Water also plays a key role in determining the microbial community composition by passive dispersal of the microorganisms through the aqueous phase of the soil habitat, as homogenization is essential for maintaining microbial diversity during drought (Šťovíček et al., 2017).

Moreover, arid ecosystems are highly vulnerable to global environmental changes such as increased temperature, precipitation temporality and intensity, and atmospheric carbon dioxide (Field and Barros, 2014). Climate change could teeter these fragile ecosystems towards mass biological extinction (Maestre et al., 2015), with associated ecosystem functionality loss (Philippot et al., 2013) and socioeconomic consequences (Field and Barros, 2014). Therefore, it is crucial to determine the responses of ecosystems to future climate change, which will affect the precipitation regimes (Field and Barros, 2014). Although some ecosystems may be subject to a decrease in mean annual precipitation in the future, others may receive more water under more extreme precipitation conditions (Zittis et al., 2022). In the Arabian Peninsula, Almazroui and Saeed (2020) used the RegCM4 model and showed that extreme precipitation could increase throughout Saudi Arabia, and participate to a greater extent in mean annual precipitation under Representative Concentration Pathway (RCP) 4.5 and 8.5 climatic scenarios. Moreover, the intensity of mesoscale convective systems, *i.e.*, a thunderstorm complex mainly responsible for triggering rainfall in arid regions often associated with heavy precipitation and flooding, has increased in the Arabian Peninsula (Nelli et al., 2021). Thus, microbial responses to current and future water inputs in natural ecosystems are essential for gaining deeper insight into the functioning of arid ecosystems.

Here we studied the response of *Haloxylon salicornicum* (Moq.) Bunge ex Boiss microbiota, an Amaranthaceae species highly tolerant to environmental stresses and of interest for arid land restoration (Rathore et al., 2015; Singh et al., 2015), to simulated heavy rainfall. Implantation of this species in desert regions improves and stabilizes the soil nutrient parameters in the vicinity of the plants (Rathore et al., 2015). Through the 'fertility island' effect, *H. salicornicum* also enables other plants to become established, it is thus a key species for restoring arid lands and curbing desertification (Rathore et al., 2015; Singh et al., 2015). Microorganisms can rapidly adapt to changing abiotic conditions, have a short life cycle, and perform key functions in ecosystems (Delgado-Baquerizo et al., 2016; Elena and Lenski, 2003). However, the response in their diversity and composition after *in situ* precipitation, and the identity of pioneer taxa that colonize freshly emitted roots is still poorly understood in desert ecosystems. This is particularly true in this remote region of Saudi Arabia, where there is a significant lack of studies on soil and plant microbial diversity, hindering our understanding of these fragile ecosystems. In this study, we aimed at identifying community composition changes in both the root and rhizosphere of *H. salicornicum* following an experimentally induced precipitation *in situ*. We also aimed at identifying the differentially abundant taxa in freshly emitted roots, to gain insights into pioneer taxa colonizing roots. Additional functional inferences were also investigated to identify the genomic potential changes occurring after rainfall. We hypothesized that (i) community scale metrics such as alpha and beta microbial diversity would not be affected by the watering treatment, while (ii) taxa specific to the drought condition would inform us about the microbial composition capable of withstanding severe desert constraints, and (iii) differentially abundant taxa known to be linked to plant development and nutrient acquisition would be present in freshly emitted roots.

2. Material and methods

2.1. Field site

The field study took place *in situ* in March 2022, in a natural hyper-arid desert ecosystem located in the Sharaan natural reserve in AlUla region (Medina Province, Saudi Arabia; 26° 53′ 24.51″ N, 38° 14′ 1.20″ E). The mean annual precipitation in the region is approximately 40 mm. No significant precipitation was recorded during the previous rainy season from October 2020 to May 2021, and this was confirmed by the fact that no ephemeral vegetation was able to develop (Supplemental information; Fig. S1). This was an optimal setting for testing the effect of prolonged drought on microbial communities and the differential effect of simulated precipitation on microbiota abundance.

2.2. Sampling design

A total of 16 stress-tolerant *H. salicornicum* (Amaranthaceae) individual plants were chosen in a natural environment site. Eight of them served as a drought control (no addition of water), while the other eight plants were watered twice every 7 days (equivalent to 40 mm of precipitation each time), with water extracted from a fossil water table at 140 m depth. These two weekly water treatments, *i.e.*, equivalent to 80 mm of precipitation, simulated the heavy precipitation conditions that likely will regularly occur in the region according to the climate change previsions. The rhizospheric soil and roots of each watered ($n = 8$ for roots and $n = 8$ for rhizosphere) and control plants ($n = 8$ for roots and $n = 8$ for rhizosphere) were sampled 11 days after the first watering treatment, for a total of 32 samples, using sterile equipment and stored at 4 °C until laboratory analysis. This delay allowed watered plants to respond to changes in water availability and produce new roots. Thus, freshly emitted roots were sampled from each watered individual plant, while persistent roots were sampled for the controls. Each root was traced to the trunk to ensure it belonged to each *H. salicornicum* individual and were preserved in a 2 % cetrimonium bromide solution. The rhizospheric soil was collected *in situ* as the soil attached to the roots, and sieved to 2 mm. At the sampling site, five soil samples (hereafter called 'bulk soil') were also collected at least 2 m away from any plants.

2.3. Soil parameters

To characterize soil composition of the bulk and rhizosphere soils, we measured the relative abundance of soil chemical elements (from magnesium to uranium) using X-ray fluorescence (XRF). Soils in this region are very sandy and low in nutrients (*e.g.*, nitrogen) and organic matter content. This method, which enables fine analysis of atomic compositions, is the most suitable for this ecosystem. Triplicate soil samples were pressed at 20 t for 2 min with 1:3 v:v of SpectroBlend® (SCP Science). Each pellet was then analyzed in triplicate with an XRF S1 Titan analyzer (Bruker) using the 'geoexploration' parameter with a total exposure time of 105 s. The nine measurements were then calibrated according to the limit of optical detection (LOD) of each analyzed element (provided by Bruker). A pH meter (pH Meter Knick 766, Knick international) was used to assess pH in a 1:5v:v of H2O.

2.4. Molecular analyses

Before DNA extraction, roots were washed with sterile water, flash frozen with liquid nitrogen and ground with a ceramic ball for 3 cycles of 30 s at 5.0 speed in a FastPrep-24™ 5G instrument from MP Biomedicals™ (Irvine, California, USA). DNA was extracted using the FastDNA Spin Kit for Soil (MP Biomedicals™), and the concentration was normalized to 0.3 ng.μL^{-1} before PCR amplification using with the Quant-i™ PicoGreen™ dsDNA Assay Kit (ThermoFisher Scientific). Bacteria were identified by amplification of the hypervariable region V3-V4 of the 16S rRNA gene using F479 (5′ CAGCMGCYGCNGTAANAC 3′) and R888 (5′ CCGYCAATTCMTTTRAGT 3′) primers (Terrat et al., 2015). Fungi were identified by amplification of the ITS2 region using ITS86F (5′ GTGAATCATCGAATCTTTGAA 3′) and ITS4 (5′ TCCTCCGCTTATTGATATGC 3′) primers (Op De Beeck et al., 2014).

All reactions were performed with Phusion™ High-Fidelity DNA Taq Polymerase (ThermoFisher Scientific) in triplicate with a technical negative control under the following conditions: initial 10 min denaturation; 35 denaturation cycles at 94 °C for 10 s, 20 s annealing at 55 °C, and 20 s extension at 72 °C, with a final 7 min extension at 72 °C. All reactions were then purified using Agencourt AMPure XP beads (Beckman Coulter Inc., Fullerton, California, USA). For 16S purification, an additional step for migration of the PCR products on 2 % agarose gel (80 V, 90 min) was performed to separate and recover the band specific to bacterial 16S (lower band, around 400 bp) and eliminate plant chloroplastic 16S DNA (higher band, < 600 bp, co-amplified during PCR). The recovered bands were purified using a QIAquick Gel Purification Kit (Qiagen, Hilden, Germany). MetaFast library preparation and amplicon sequencing were performed using Illumina Novaseq 6000 SP sequencer (Fasteris SA, Switzerland). Raw reads were processed with a pipeline using VSEARCH (Rognes et al., 2016) from Perez-Lamarque et al. (2022), and assigned to amplicon sequence variant (ASV) with 'usearch_global' options. The SILVA 138.1 and UNITE (v8.0) databases for bacteria and fungi, respectively, were used for taxonomic assignment (Kõljalg et al., 2020; Quast et al., 2012). Decontam was used to remove potential contaminant reads from the negative control amplifications based on the prevalence method (Davis et al., 2018).

2.5. Statistical analyses

All statistical analyses were performed using R software version 4.3.1 (R Core Team, 2022). To visualize the differences in soil parameters between rhizosphere and bulk soil, a PCA was performed on the centered log-ratio transformation on the atomic composition data of the elements.

For molecular data, only ASVs with a total abundance >100 reads in the dataset were retained for downstream analyses. In total, 15,682 ASVs were retained for 16S rRNA, distributed across 35 samples and 3,842,652 reads. For ITS, 751 ASVs distributed across 30 samples and 3,614,809 reads were retained. Detailed information about the analyses is available in the Supplemental information, Fig. S2.

We assessed changes in diversity under watered and not watered conditions for both the rhizosphere and roots using Hill numbers 0, 1, and 2 (diversity order q = 0 for the species richness; q = 1 for the exponential of Shannon diversity index; q = 2 for the inverse of Simpson diversity index) for both fungi and bacteria using the hilldiv package (Alberdi and Gilbert, 2019). Hill numbers allow sensitivity modulation towards abundant and rare ASVs, where the larger the q value, the less weight is given to rare ASVs. To further assess how the sequencing depth impacted the diversity measure, we also tested the coverage of each sample, which determine whether the sampling depth is sufficient to recover the diversity. We also tested the changes of species richness and evenness, defined as the effective number of ASVs, for different diversity orders within each sample (from q = 0 to q = 5) (Supplemental information, Fig. S3).

Beta diversity was visualized using non-metric multidimensional scaling (NMDS) with Bray-Curtis distances of Hellinger-transformed ASVs count tables. To assess microbial community compositional changes between conditions and compartments, permutational multivariate analysis of variance using distance matrices was performed for each amplicon using the adonis2 function of the vegan package (Oksanen et al., 2007). Conditions and compartments were used as independent variables for variation partitioning as well as their interaction.

To further investigate how the microbial community composition was affected by watering, we partitioned beta diversity into species spatial turnover and nestedness, which are the two antithetic processes that drive differences in beta diversity. Turnover, or species replacement, refers to the substitution of a species by a different one in another site. Nestedness is the gain or loss of a species in only one site, thus, an assemblage with lower diversity is a strict subset of an assemblage with higher diversity (Baselga, 2010). We used the betapart.pair.abund function in betapart to calculate the two abundance-based dissimilarity matrices using the Bray-Curtis distances (Baselga and Orme, 2012). The multiple response permutation procedure was then used to assess variations in species turnover and nestedness across the bulk soil, rhizosphere, roots, and watered and not watered conditions for both bacteria and fungi. The significance of the overall weighted mean of the within-group means of pairwise dissimilarities δ was tested using 9999 permutations.

We used differential abundance analysis with DESeq2 (Love et al., 2014) to identify features that were differentially abundant in watered or not watered conditions for rhizosphere and root microbiomes (defined here as taxonomic ranks or ASVs). This analysis, which is designed for sequencing data, is based on a gamma-Poisson distribution and uses generalized linear models with a logarithmic link for read normalization across samples. The dispersion among individual counts was estimated by the DESeq2 algorithm, and the resulting logarithmic fold changes (Log2FC) with the associated *p*-values were used to identify differentially abundant features. Analyses were performed separately for the bacterial and fungal rhizospheres and root microbiotas.

Phylogenetic Investigation of Communities by Reconstruction of Unobserved States (PICRUSt2) was used to infer microbial metabolic functions from the 16S rRNA sequencing dataset (Douglas et al., 2020). First, phylogenetic placements of reads were performed using the profile hidden Markov models (HMMER; Louca and Doebeli, 2018). Then, an evolutionary placement algorithm (EPA-ng) was used to detect the most optimal placement of each ASV in a reference phylogeny (Barbera et al., 2019). Hidden state prediction using the R package 'castor' was used to infer the genomic content of each sample (Louca and Doebeli, 2018), which was corrected based on the number of 16S rRNA gene copy number of each ASV. Annotation of genes was performed according to the Kyoto Encyclopedia of Genes and Genomes (KEGG) in the form of KEGG pathway maps (Kanehisa et al., 2012).

First, we assigned each KEGG Ortholog (KO) entry to its hierarchical classification systems according to the KEGG BRITE hierarchy files. Visualizations of the enrichment of each BRITE hierarchy genes according to the watered and non-watered conditions in the roots and rhizosphere was performed using STAMP software (https://beikolab.cs.dal.ca/software/STAMP).

Then, we extracted the KEGG modules M00175 (nitrogen fixation), M00531 (Assimilatory nitrate reduction), M00530 (Dissimilatory nitrate reduction), M00529 (Denitrification), M00528 (Nitrification), M00804 (Complete nitrification, comammox) and M00973 (Anammox) associated to the nitrogen metabolism pathway map00910. We then visualized the enrichment of each gene according to the compartment and conditions using an extended error bar, with the associated significativity of its effect size.

3. Results

3.1. Soil properties and global taxa identified

Bulk and rhizosphere soils are characterized by a high proportion of silica (76 and 69 % respectively). The rhizosphere harbored higher proportions of several atomic element compared to bulk soils such as aluminum (12.9 *versus* 9.4 %), iron (6.2 *versus* 4.9 %) potassium (1.6 *versus* 1.2 %), and calcium (4.9 *versus* 3.8 %). However, magnesium, phosphorus, titanium, chromium, manganese and pH values were similar across the two compartments (Table 1; Fig. S4).

Most of the root and rhizosphere bacteria identified were Actinobacteria, accounting for 11.6 to 71.5 % of the total relative abundance across the different conditions [watered and not watered] and compartments [bulk soil, rhizosphere and roots], followed by Chloroflexi (1.0 to 49.8 %), Proteobacteria (6.6 to 31.9 %), Firmicutes (1.3 to 33.7 %) and Planctomycetota (0.5 to 14.1 %). The main fungal lineages were Ascomycota (81.1 to 98.5 %), followed minor amounts Basidiomycota (1.4 to 9.0 %) and Chytridiomycota (0.02 to 6.3 %) (Fig. 1).

Most bacterial and fungal taxa were shared between the non-watered and watered conditions, where only few rare taxa were specific to each watering condition (Fig. S5). Most taxa were also shared between the roots and rhizosphere soils. However, a higher proportion of bacterial and fungal sequences were found exclusively in the rhizospheres and roots in the watered condition when compared to the non-watered one (Fig. S5).

3.2. Alpha and beta diversity

The diversities of the rhizosphere and root microbial communities between the watered and not watered treatments did not significantly differ (Fig. 2). The bacterial diversity in the rhizosphere of the not watered treatment was greater than that of the watered treatment at $q = 0$. This was due to the low sample coverage, as rare taxa may have been responsible for most of the differences (Supplemental information, Fig. S3). Differences in beta diversity between root and rhizosphere microbiota (Fig. 3) were significant for both the bacterial communities ($R^2 = 0.32$; $p < 1e^{-5}$) and fungal communities ($R^2 = 0.12$; $p < 0.001$). The simulated precipitation had less of an effect on differences in bacterial ($R^2 = 0.05$; $p = 0.039$) and fungal community composition ($R^2 = 0.06$; $p = 0.013$) than on the differences between the roots and rhizosphere (Fig. 3). Overall differences in composition across the bulk soil, rhizosphere and roots were mainly due to species turnover rather than the nestedness, particularly for bacteria (Table 2: $\delta = 0.52$, $A = 0.26$, $p = 0.001$). Differences between the drought and watered conditions for both the roots and rhizosphere were driven by the nestedness (Table 2: rhizosphere: $\delta = 0.108$, $A = 0.38$, $p = 0.002$; root: $\delta = 0.13$, $A = 0.17$, $p = 0.04$). No significant differences were found for fungi, where the beta diversity was mainly driven by species turnover.

Table 1
Soil parameters for the bulk and rhizosphere soils. Mean values of pH and proportion of atomic elements measured with X-Ray fluorescence are presented with their standard deviation.

Soil parameter	Bulk	Rhizosphere
pH	8.6 ± 0.2	8.6 ± 0.1
Mg (%)	3.8 ± 0.2	3.9 ± 0.1
Al (%)	9.4 ± 0.2	12.9 ± 0.2
Si (%)	75.9 ± 0.9	69.3 ± 0.7
P (%)	0.2 ± 0	0.2 ± 0
K (%)	1.2 ± 0.1	1.6 ± 0
Ca (%)	3.8 ± 0.2	4.9 ± 0.1
Ti (%)	0.7 ± 0	0.8 ± 0
Cr (%)	0.1 ± 0	0.1 ± 0
Mn (%)	0.1 ± 0	0.1 ± 0
Fe (%)	4.9 ± 0.3	6.2 ± 0.2

3.3. Differential abundance reveals specific taxa following watering

Although it had little influence on the overall microbial community composition, simulated rain had a significant effect on the differential abundance of several taxa compared to samples from the unwatered controls (Fig. 4.A). For bacteria, taxa that were differentially more abundant in the rhizosphere after water addition compared to the dry rhizosphere samples mainly belonged to Planctomycetota (Fig. 4.B). Most of these Planctomycetota belonged to the Gemmataceae family (17 belonged to Gemmataceae out of 23 Planctomycetota). Some members of Proteobacteria and Chlorofexi were also differentially more abundant in the watered condition. For example, an ASV belonging to the *Lysobacter* genus was the most abundant in the watered rhizosphere (Log2FC = 6.84, $p < 0.036$). The responses differed in the roots, where the majority of Proteobacteria were differentially more abundant in the watered treatment. Steroidobacteraceae, Xanthobacteraceae, Oxalobacteraceae, Rhizobiaceae, and Devosiaceae were the main families identified (Fig. 4.B). The most differentially abundant ASVs identified in the watered root samples were from the *Mesorhizobium* (log2FC = 22.88, $p < 1e^{-15}$), *Hyalangium* (log2FC = 22.42, $p < 1e^{-12}$), *Niastella* (log2FC = 22.26, $p < 1e^{-11}$), and *Bacillus* (log2FC = 22.2, $p < 1e^{-11}$) genera. Bacterial families specific to the not watered samples belonged to the Streptomycetaceae and Glycomycetaceae families.

Fungal communities, however, were less responsive to simulated precipitation, where only a few taxa belonging to the Ascomycota phylum, were found to be differentially more abundant under the watered condition (Fig. 5.A). In the rhizosphere, only three taxa were found to be differentially abundant in the watered samples, whereas seven were specific to the drought controls. In the roots, one ASV of each of the Xylariaceae, Nectricaceae, Aspergilaceae and Microascaceae families were found to be more abundant in the watered samples (Fig. 5.B). For example, an ASV belonging to the Aphelidiomycota phylum was found exclusively in the watered rhizosphere (log2FC = 25.4, $p < 1e^{-15}$). Moreover, an ASV assigned to *Enterocarpus grenotii* in the Microascaceae family was found in the rhizosphere control samples (log2FC = −23.17, $p < 1e^{-18}$), and in the watered root samples (log2FC = 27.55, $p < 1e^{-18}$).

3.4. Functional inference using PICRUSt2

Between watered and unwatered rhizosphere samples, several genes involved in antibiotic compounds production were differentially more abundant in the watered samples (Fig. S6) such as monobactam biosynthesis ($p = 0.026$). This was also the case in the roots where penicillin and cephalosporin biosynthesis ($p = 0.01$) and staurosporine biosynthesis ($p = 0.018$) genes were differentially more abundant in the watered samples. Complete modules of genes involved in nitrogen metabolism (dissimilatory nitrate reduction, assimilatory nitrate reduction, denitrification, nitrogen fixation and nitrification) were also found in watered and unwatered samples (Fig. S7). The nitrite reductase gene NirK was differentially more abundant in the watered root samples ($p = 0.021$).

4. Discussion

4.1. Compartment is the main driver of the microbial composition

No changes of diversity between drought and 11 days after simulated precipitation in both the rhizosphere and roots were observed. This pattern was also identified in a study of microbial responses after precipitation in the Negev Desert (Šťovíček et al., 2017), where diversity returned to the same level as under drought conditions 10 days after precipitation, which is in line with the time frame of our experiment. For beta diversity, the rhizosphere and root compartments were the major drivers of the microbial community composition, rather than simulated precipitation, thereby suggesting a strong spatial niche partitioning.

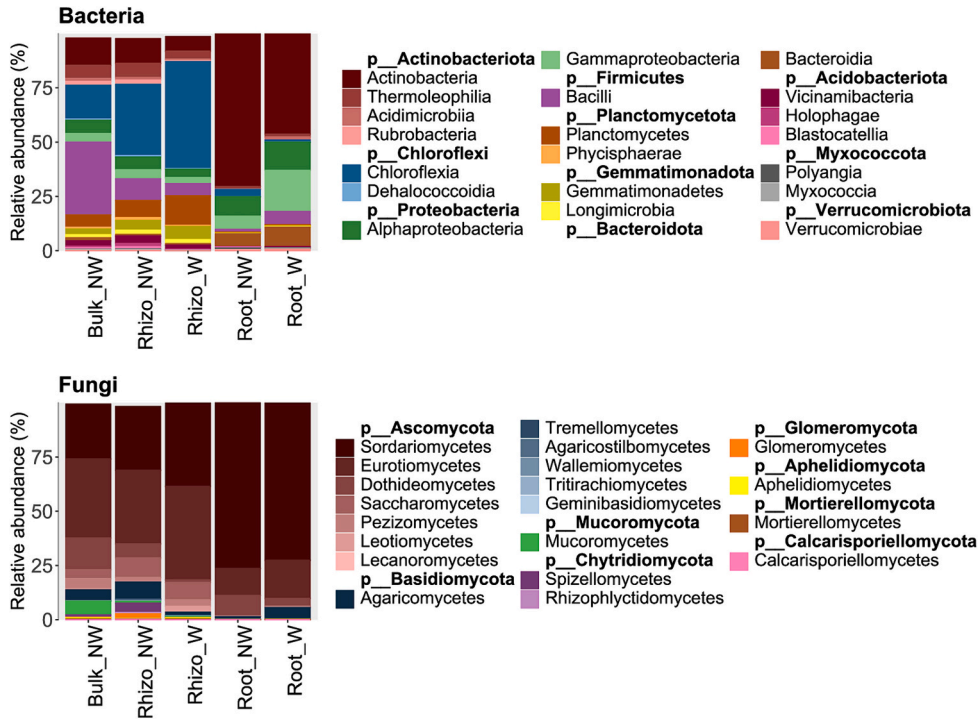

Fig. 1. Microbial compositions varied across compartments and conditions, and were responsive to watering. Mean relative abundance of bacteria and fungi across conditions (W = watered; NW = not watered) and compartments (bulk = bulk soil; rhizo = *H. salicornicum* rhizosphere; root = *H. salicornicum* roots). The mean relative abundances were calculated after rarefaction at 25,600 reads for bacteria and 40,000 reads for fungi. Colors represent different phyla (p_) shown in bold, while color gradients are associated with different classes within each phylum.

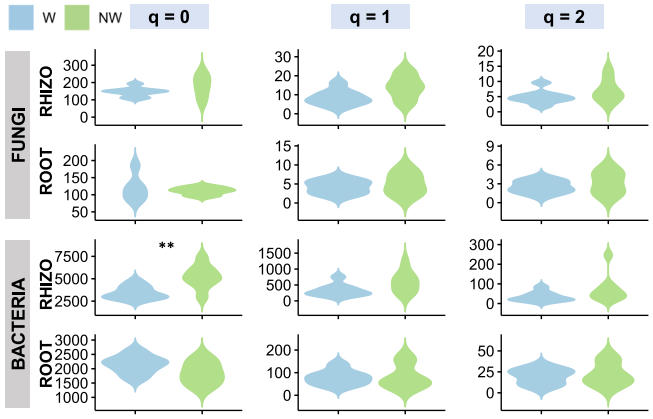

Fig. 2. Diversity is similar between watered and not watered conditions for both bacteria and fungi. Differences in Hill numbers between watered (W, in blue) and not watered (NW, in green) samples across the rhizosphere (RHIZO) and roots (ROOT) for both fungi and bacteria displayed in violin plots. Values are presented across three q values, which correspond to Hill number diversity orders 0 (q = 0), 1 (q = 1) and 2 (q = 2). The larger the q value, the less weight is given to rare ASVs. The y-axis represents the Hill number or the 'effective number of ASVs'. Stars (**) correspond to a significant difference, at $p < 0.01$ (Student's *t*-test).

This pattern was also observed in another *in situ* simulated precipitation experiment in Saudi Arabia (Aslam et al., 2016), where the soil compartment was a greater driver of the microbial composition than water pulses. However, in our study differences in composition were mainly shaped by species turnover and distinct communities were found in each compartment. This could be due to the high prevalence of resistance forms, particularly in this arid ecosystem (Fierer et al., 2012). Propagules and resistance forms, such as spores, are present before the rains, and it is in their expression and abundance that the addition of water would have an effect.

Root microbiota was the most responsive to water addition, with a higher proportion of differentially abundant taxa than that in the dry controls compared to rhizosphere microbiota. Rhizosphere microbiota is especially shaped by plant exudates (Sasse et al., 2018). As root exudation is dynamic, and dependent on numerous factors such as the plant genotype, root physiology and a multitude of transporters, it is challenging to characterize the latency in its production by the plant, and therefore its effect on rhizosphere microbiota assembly (Sasse et al., 2018). Moreover, new roots emitted by plants in response to water addition may be colonized rapidly by the surrounding soil and rhizosphere bacteria, a developmental pattern (*i.e.*, fresh roots are a different sub-niche that arise after watering) that could explain the higher proportion of taxa specific to watered roots noted in our study. In the same way as the circadian regulation of rhizospheric microbiota by root exudates (Staley et al., 2017), water supply could induce an indirect regulation of microbiota through the production of root exudates. Although the compartment was the major driver of the microbial community composition, there were differential responses between rhizosphere and root microbiota.

4.2. *Drought-tolerant Actinobacteria are specific to the unwatered condition*

Extended drought with little or no precipitation during the rainy season is expected to increase in desert regions, with critical implications regarding the microbial composition and ecosystem functionality (Moreno-Jiménez et al., 2019; Neilson et al., 2017). Furthermore, climate change may lead to an increase in the frequency of extreme precipitation. Microbial communities in desert environments evolved and adapted to the local climatic and edaphic conditions. For example, some taxa feature unique traits associated with drought tolerance, such as the ability to form endospores to withstand desiccation, or high tolerance to radiation and salt stress (Makhalanyane et al., 2015). In this

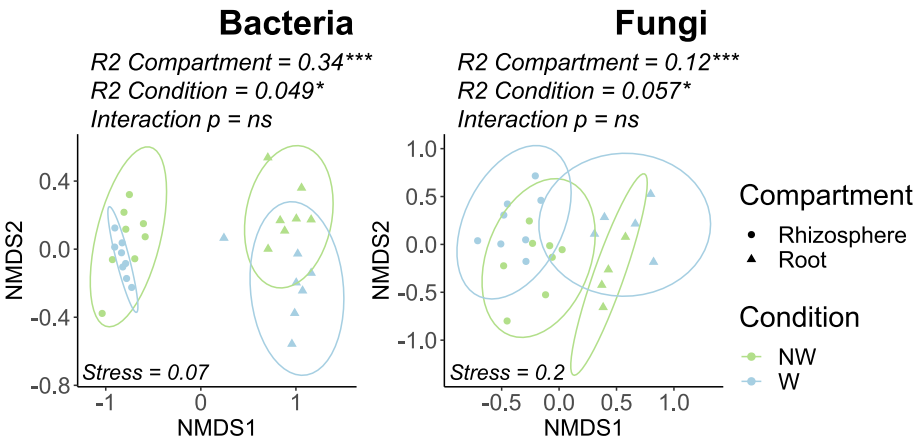

Fig. 3. Compartment rather than watering was the main driver of microbial community composition differences. Non-metric multidimensional scaling (nMDS) of bacterial and fungal ITS according to the compartment (rhizosphere or root) and condition (W = watered; NW = not watered). Analyses were performed on rarefied ASV tables (25,600 reads for bacteria and 40,000 for fungi), Hellinger transformation was then applied, and a distance matrix was drawn up with the Bray-Curtis index. Stress values and Permanova with associated R^2 and *p*-values are reported.

Table 2
Contrasted turnover and nestedness among compartment and condition for bacteria and fungi. Multiple response permutation procedure testing the significance of species turnover and nestedness among compartments and conditions for bacteria and fungi.

Amplicon	Model tested		Turnover		Nestedness	
			Observed δ[a]	Chance corrected within-group agreement A[b]	Observed δ[a]	Chance corrected within-group agreement A[b]
16S	Global effect	Compartment (Bulk * Rhizo * Root)	0.52***	0.26	0.092	0.10
		Condition (W * NW)	0.73	−0.013	0.078***	0.24
	Effect by condition	Rhizosphere (W * NW)	0.46	−0.037	0.108**	0.38
		Root (W * NW)	0.63	0.006	0.13*	0.17
ITS	Global effect	Compartment (Bulk * Rhizo * Root)	0.91	−0.0028	0.034*	−0.0086
		Condition (W * NW)	0.91	0.0012	0.031	0.032
	Effect by condition	Rhizosphere (W * NW)	0.86	−0.0027	0.036	0.11
		Root (W * NW)	0.93	0.013	0.039	−0.19

*, **, and *** show statistical significance at the 0.05, 0.01, and 0.001 levels.

[a] Observed delta (δ) or significance of the overall weighted mean of the within-group means of pairwise dissimilarities was associated with the corresponding p-value (9999 permutations).

[b] Chance-corrected within-group agreement A is also reported and corresponds to $1 - \frac{\delta_{obs}}{\delta_{exp}}$, whose value is analogous to the coefficient of determination in a linear model.

study, we found that prolonged drought was characterized by an increased proportion of Actinobacteria in the *H. salicornicum* rhizosphere and roots. Actinobacteria are known to be tolerant to harsh abiotic desert environments (Bull and Asenjo, 2013) as some of their members are able to form endospores to withstand desiccation. Indeed, the main strategy to cope with harsh environmental conditions in desertic environments is the dormancy mechanism (Lennon and Jones, 2011; Leung et al., 2020), where spore-forming Actinobacteria and Firmicutes are the main representative in drylands. For example, *Bacillus* spp. and *Paenibacillus* spp. are known to form highly resistant spores, allowing them to withstand extreme environments (Nicholson, 2002; Nicholson et al., 2000).

Actinobacteria are widely reported to be characteristic of drought conditions in both the rhizosphere and roots (Naylor et al., 2017). Some Actinobacteria taxa, well adapted to abiotic stress, have already been found to improve plant fitness (Solans et al., 2022), such as *Streptomyces*, where some of their members are known to enhance wheat water stress tolerance (Yandigeri et al., 2012) and pathogen and plant disease avoidance (Schlatter et al., 2017; Seipke et al., 2012). Their presence was detected in not watered roots and characterization of their beneficial effects on plants could provide valuable restoration tools in the future. Dry-season microbiota of *H. salicornicum* was therefore partially characterized by the presence of taxa tolerant to edaphic and desert environmental constraints. In the climate change and land degradation context, these species could prove to be major assets for the revegetation and conservation of ecosystems.

4.3. Simulated precipitation stimulates key microbiome linked to plant fitness

The microbial compositions we observed were characteristic of desert ecosystems, with a high abundance of Actinobacteria, Proteobacteria, Firmicutes, and Gemmatimonadota for bacteria and the dominance of Ascomycota for fungi. A high proportion of Planctomycetota in both bulk and rhizosphere soils was also documented. The Planctomycetes family identified in this phylum represents a unique group of bacteria with atypical features compared to other bacteria (Wiegand et al., 2018) and their phylogeny is still debated (Van Teeseling et al., 2015). As most members of this family have been identified by 16S rRNA amplicon sequencing and are generally unculturable, little is known about their function in ecosystems. In deep-sea sediments, they have been reported to be involved in the nitrogen cycle as denitrifiers

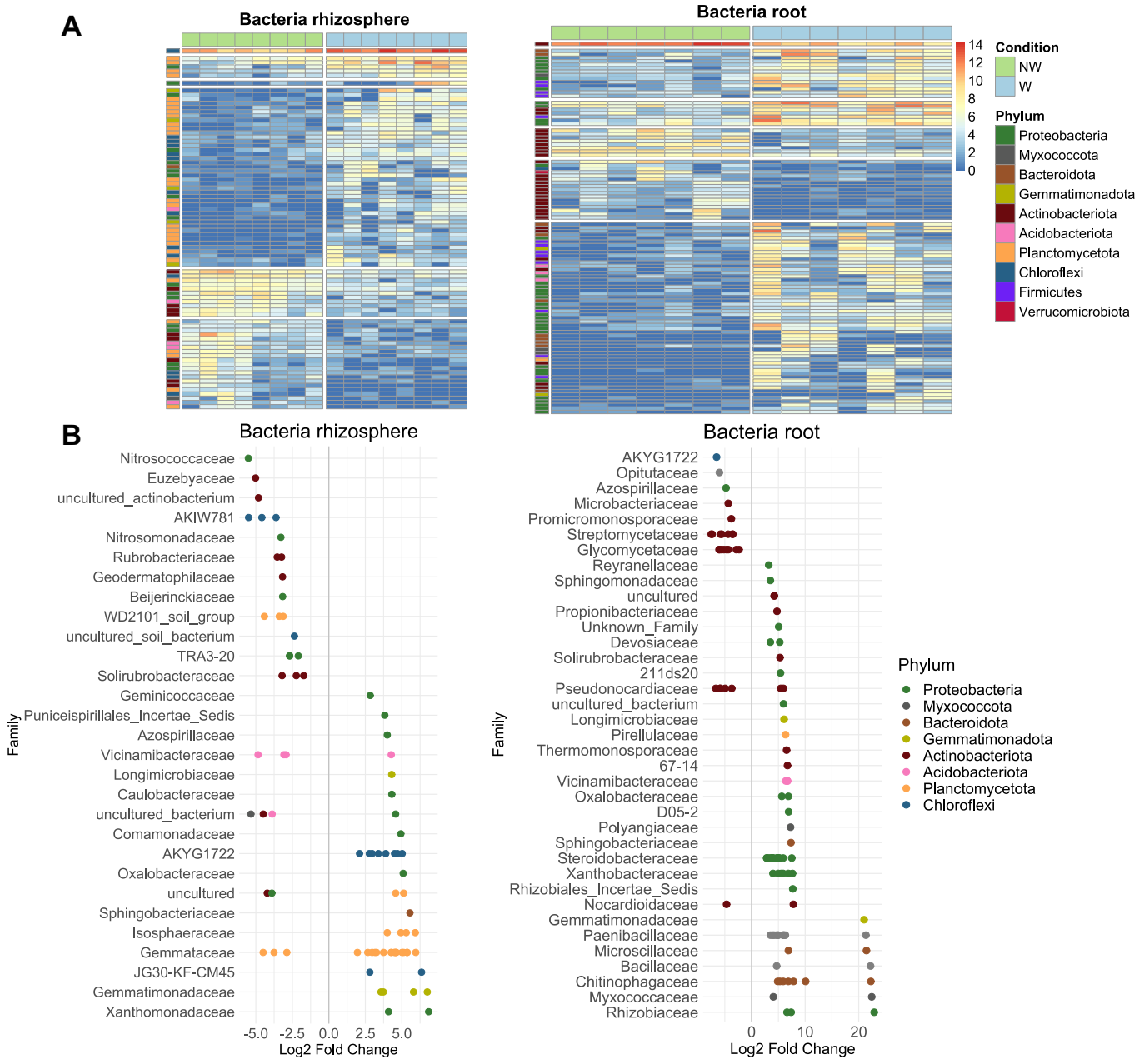

Fig. 4. Bacterial taxa are responsive to watering in both the roots and rhizosphere. (A) Heatmap of bacterial log fold changes (gradient color of cells) between the watered (W) and not watered (NW) conditions. Analysis was performed using DESeq2 for each compartment (rhizosphere and roots). (B) Log2FC of differentially expressed ASVs between W (watered; positive Log2FC) and NW (not watered; negative Log2FC) conditions for each compartment (rhizosphere and roots). ASV families are presented in rows and colored according to the phylum. Only ASVs with significant adjusted p-values ($p < 0.01$) are presented, and a Wald test using negative binomial GLM was used to assess the significance according to the p-values.

(Vigneron et al., 2017), their function in soil has yet to be explored but they are likely to affect N cycling through the Anammox process (Fuerst and Sagulenko, 2011; Van Teeseling et al., 2015). Generally, they are found in high abundance in aquatic environments and are sometimes associated with micro- and macro-algae (Lage and Bondoso, 2011) and diatoms (Bunse et al., 2016). In parallel to Planctomycetota, Aphelidiomycota species are obligate endoparasitoids of algae and diatoms (Karpov et al., 2014; Letcher and Powell, 2019). As a result, the co-occurrence of both taxa in rhizosphere after water addition is thus congruent according to their microbial niche. The sharp increase in their abundance in the watered rhizosphere may be evidence of reactivation of trophic chains involving algae and diatoms.

Together with fungi and other non-vascular cryptogams, algae and cyanobacteria can form biocrusts on soil surface. Highly present in arid ecosystems, they are responsible for many biogeochemical processes (*e.g.*, aggregation of soil particles, N_2 and carbon dioxide fixation) and are especially tolerant to extreme conditions such as desiccation (Weber et al., 2022). The indirect detection of algae could therefore reveal the resuscitation of surface biocrusts, known to respond to water availability (Angel and Conrad, 2013). Overall, the presence of these taxa highlighted that the rhizosphere microbiota was highly responsive to water availability and that the trophic chains quickly reactivated upon water addition. We also identified a high proportion of Planctomycetota in both the unwatered bulk and rhizosphere soils, as also widely reported in soils (Buckley et al., 2006), thereby suggesting that the differences in composition noted may not have been caused by water contamination.

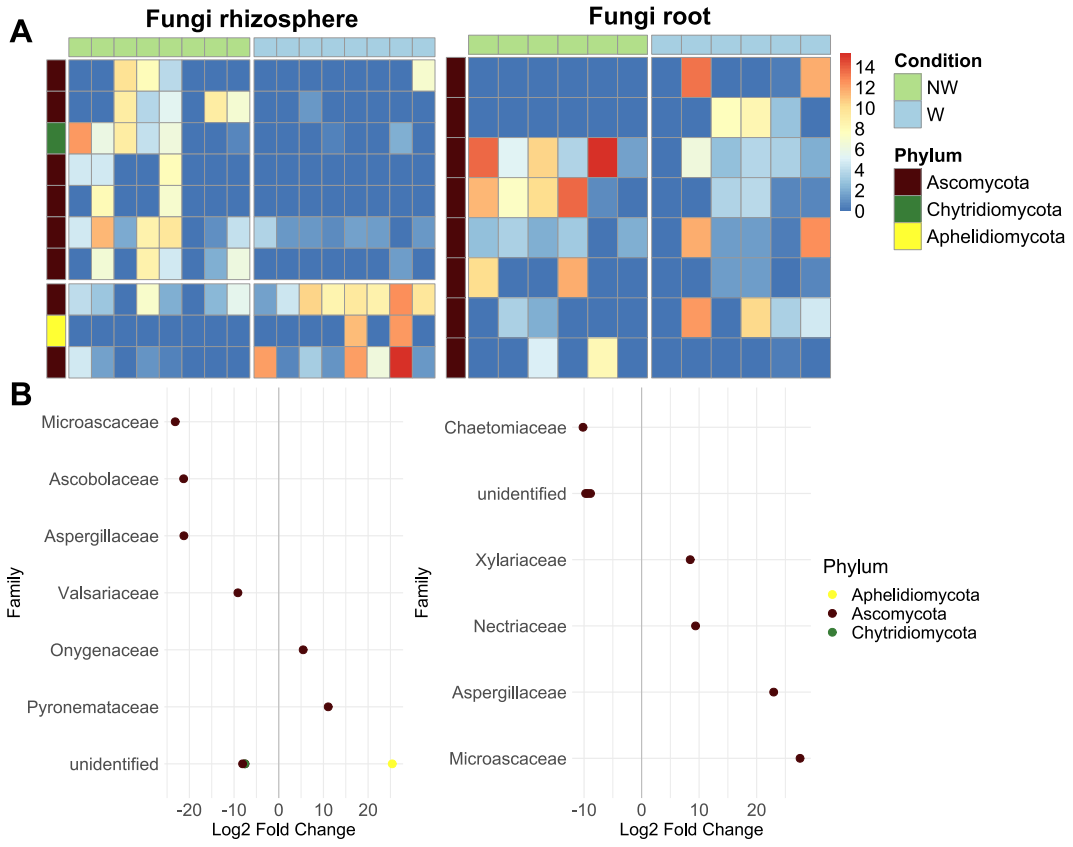

Fig. 5. Fungal taxa are less responsive to watering in both the roots and rhizosphere compared to bacteria. (A) Heatmap of fungal log fold changes (gradient color of cells) between W (watered) and NW (not watered) conditions. The analysis was performed using DESeq2 for each compartment (rhizosphere and roots). (B) Log2FC of differentially expressed ASVs between W (watered; positive Log2FC) and NW (not watered; negative Log2FC) conditions for each compartment (rhizosphere and roots). ASV families are presented in rows and colored according to the phylum. Only ASVs with significant adjusted p-values ($p < 0.01$) are presented, and a Wald test using negative binomial GLM was used to assess the significance according to the p-values.

We also found a relative increase in the potential production of several antibiotics compounds in the watered condition inferred using PICRUSt2 for both the roots such as the biosynthesis of monobactam, and rhizosphere such as penicillin, cephalosporin and Staurosporine biosynthesis (Fig. S6). These changes suggest that water triggers competition, as new niche and resources are available for microbial members. Furthermore, several genes involved in nitrogen metabolism were identified, where nitrate reduction, denitrification, N_2 fixation and nitrification modules were complete. Changes in water availability have increased the abundance of nitrite reductase genes in roots, which may lead to a loss of soil nitrogen. In these ecosystems, where nutrient levels are already very low, it is crucial to determine to what extent nitrogen is actually recycled in the soil, and how much is fixed by microorganisms. For example, NH_3 emissions were found to be a major N loss in the Atacama Desert, caused by an alkaline pH and slow rates of nitrification (Jones et al., 2023). Here, we have identified that within the rhizosphere and roots of a plant species considered as non-symbiotic, genes linked to nitrogen cycles are present. Addressing these little-considered species in the nitrogen cycle and ecosystem restoration could therefore yield crucial information in desert environments. However, caution is advised when interpreting functional predictions based on amplicon sequencing. This method does not provide strain-specific resolution, and cannot distinguish metabolically active from dead or dormant taxa (Douglas et al., 2020). These results therefore represent a functional potential of microbial taxa, but the expression of functions needs to be confirmed.

Another interesting feature we found was the high abundance of *Enterocarpus* species in the rhizosphere under drought conditions. These dark septate endophytes switched to roots after precipitation simulation, suggesting a dispersion towards roots in response to water availability. Thus, after precipitation, these species may activate and colonize the roots quickly to forage for soil water and nutrients and thereby increase the fitness of their host plant. Although arbuscular fungi are known to improve plant water availability and nutrition (Allen, 2007; Apple, 2010), dark septate endophytes have received less attention. Taxa such as Enterocarpus may however also be important symbiotic partners for plants fitness, as they have been reported to improve plant water stress resistance (Santos et al., 2017) and biomass (Newsham, 2011). They may also have a significant role in the microbiota functions through their interaction with microbial symbionts, where they have been reported to increase the abundance of fungal symbiotrophs and growth-promoting bacteria (He et al., 2021). These taxa would thus warrant further in-depth study, particularly in arid environments, where water resources are limited for primary production. However, their functional characterization and isolation currently remain difficult, but could constitute an interesting field of research in the adaptation of agriculture to climate change.

A high proportion of Rhizobiales bacteria were found to be specific to roots upon water addition. Bacteria belonging to this order are well known for their plant nutrition benefits, as some of them fix atmospheric N_2 (Zahran, 1999). Although *H. salicornicum* is considered a non-symbiotic species, its endophytic and/or epiphytic root colonization by N_2 fixers may be highly beneficial for restoration programs in these nutrient-depleted environments. The establishment of this plant species could trigger a fertility island effect, thereby subsequently improving the soil conditions so as to be suitable for the growth and development of other plant species or microorganisms less tolerant to abiotic stress (Rathore et al., 2015). The microbiome may be under reduced activity during drought. With increased water availability, it quickly responds to

resource availability and rapidly colonize roots. Thus, both trophic chains and nutrient acquisition may be reactivated, even during an intense precipitation.

These trailblazing results will benefit restauration and preservation programs in desert ecosystems facing the ongoing climate change and desertification. Notably, the plant species we studied are rapidly colonized by microbial taxa potentially crucial to ecosystem functioning in response to increased water availability. In addition, we have identified little-known taxa whose functions would be interesting to describe more precisely in future studies.

5. Conclusion

Compartmentalization of rhizosphere and root environments emerged as the most important factor influencing microbial composition, with distinct communities identified in each compartment, highlighting the role of spatial niche distribution in shaping microbial diversity. Prolonged drought conditions were associated with increased abundance of actinobacteria, known for their tolerance of harsh desert environments, and of specific taxa, such as Streptomyces, known to enhance water stress tolerance in plants. Finally, the detection of *Enterocarpus* species in the rhizosphere under drought conditions, and then in roots after watering, highlights the dynamic responses of this taxa to water availability and its potential importance for plant health should be further characterized. Increased microbial competition may also be triggered following increased water availability as revealed by the increase of antibiotic compounds production. Overall, these results provide valuable insight on the rapid root colonization by microbial symbionts of a plant species of major interest following an increase in water availability. Our study is one of the few conducted in a natural desert environment, and paves the way for a finer characterization of the link between microorganisms, plants and nutrient cycles.

Data availability statement

Demultiplexed sequences data are available at NCBI, SRA GenBank (BioProject: PRJNA1099423).

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CRediT authorship contribution statement

Kenji Maurice: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Amélia Bourceret:** Writing – review & editing, Software, Data curation. **Alexandre Robin-Soriano:** Writing – review & editing, Resources. **Bryan Vincent:** Writing – review & editing. **Hassan Boukcim:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Marc-André Selosse:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Marc Ducousso:** Writing – review & editing, Supervision, Project administration, Funding acquisition.

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.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2024.105412.

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