# Differences in Precipitation Regime Shape Microbial Community Composition and Functional Potential in Namib Desert Soils

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## Abstract

Precipitation is one of the major constraints influencing the diversity, structure, and activity of soil microbial communities in desert ecosystems. However, the effect of changes in precipitation on soil microbial communities in arid soil microbiomes remains unresolved. In this study, using 16S rRNA gene high-throughput sequencing and shotgun metagenome sequencing, we explored changes in taxonomic composition and functional potential across two zones in the Namib Desert with contrasting precipitation regime. We found that precipitation regime had no effect on taxonomic and functional alpha-diversity, but that microbial community composition and functional potential (beta-diversity) changed with increased precipitation. For instance, Acidobacteriota and 'resistance to antibiotics and toxic compounds' related genes were relatively more abundant in the high-rainfall zone. These changes were largely due to a small set of microbial taxa, some of which were present in low abundance (i.e. members of the rare biosphere). Overall, these results indicate that key climatic factors (i.e. precipitation) shape the taxonomic and functional attributes of the arid soil microbiome. This research provides insight into how changes in precipitation patterns associated with global climate change may impact microbial community structure and function in desert soils.

**Keywords:** 16S rRNA; Shotgun metagenomics; Precipitation regime; Namib Desert; Functional potential

## Introduction

Deserts constitute one-fifth of the Earth's total surface area [1] and represent one of the harshest environments as they are characterised by scarce and irregular rainfall combined with very high temperatures [2]. Considering the current climate change scenarios, deserts and other dryland areas have been projected to increase by 11–23% by the end of this century [3, 4]. Notwithstanding these hard conditions, deserts harbour a surprisingly high biodiversity, including some of the most threatened species in the world [5].

Microbial communities are considered the dominant ecological drivers of these ecosystems [6] because they regulate, among others, organic matter decomposition, carbon cycling, nitrogen cycling and mediate nutrient acquisition [7]. Desert microbiomes display a lower species diversity and are phylogenetically and functionally distinct from those of other biomes [8, 9]. This suggests that their responses to fluctuating environmental changes might also be distinct [10]. Microbial diversity, composition, and activity in desert soils are highly dependent on factors such as temperature, moisture, and the availability of organic carbon [11]. Of these, water availability is the primary factor limiting microbial activity [12] and therefore the ability of the arid soil microbiome to sustain, among others, nutrient cycling functions [13].

The Namib Desert is a coastal desert on the western side of Southern Africa. It is the oldest hyper-arid desert on the planet (ca. 5 million years) with a highly variable surface temperature (0–60 °C) [14, 15]. The Namib Desert has scarce and unpredictable rainfall inputs, receiving an average of 5–18 mm in the central zone, increasing gradually from the coast inland (~ 10 mm at the coast to ~ 60 mm 100 km inland) [16, 17]. An important ecological feature of the Namib Desert is the frequently occurring coastal fog, reaching as far as 75-km inland. The fog is influenced by the cold Benguela current and the southwest trade winds on the coast [18]. The contribution of rainfall and fog has led to a well-defined gradient of xeric stress across the Namib desert [17].

Gradients of precipitation have been suggested as good systems to evaluate the impact of precipitation on microbial communities [13]. Initial studies analysing soils across low [19] and steep [20] precipitation gradients found that microbial diversity was not constrained by precipitation and that water availability had a significant effect on microbial community composition. More recent studies, however, found that both microbial diversity and community composition are shaped by steep precipitation gradients [13, 21]. These contrasting results call for further investigation on how precipitation regime shapes microbial community composition and function.

In an earlier study across the Namib Desert xeric gradient [17], it was shown that both microbial community structures and activities differed significantly between the three xeric zones (fog, mid- and high-rainfall). Microbial community structures were inferred using T-RFLP analysis, and their functional capacities were determined using extracellular enzyme activity assays. The combination of these methods does not, however, provide detailed information on the taxonomic compositions and functional attributes of those communities. This information is important because both taxonomy and function can influence the stability and resilience of microbial communities and their functions in the context of climate change. For instance, highly functional redundant microbial communities should be more functionally stable, as functional redundancy should act as a buffer against changes in diversity and composition [22].

Here, with the use of high-throughput amplicon sequencing (targeting 16S rRNA genes), we investigate the bacterial community diversity and composition in soils from two rainfall zones (medium rainfall and high rainfall) across the intrinsic xeric gradient in Namib Desert. In addition, the functional potential of those communities was assessed using shotgun metagenomics. The working hypotheses were (1) that the taxonomic and functional diversities would increase from the mid-rainfall zone to the high-rainfall zone due to an

increase in water availability, which also can influence nutrient availability and (2) that the taxonomic and functional composition between the two zones would be distinct. To investigate these hypotheses, three basic questions were addressed: Is precipitation regime and other environmental variables associated with specific microbial taxa? Is microbial diversity and composition altered across the two rainfall zones? Would possible changes in community composition have a direct effect on community function?

## Materials and Methods

### Study Site and Sampling

Eighteen surface soil (0–5 cm) samples were collected across a west–east transect (23°11’76.1"S 15°16’69.2"E), which spans three xeric zones (fog, mid- (MR) and high-rainfall (HR)) [16]. Samples were collected from the mid ($n$ = 9) and high rainfall ($n$ = 9) zones. The total annual precipitation in the year of collection (2018) was 3 mm for the MR zone and 111 mm for the HR zone (http://www.sasscalweathernet.org/). Data collected from 1998 to 2015 corroborates the delimitation of the three zones and revealed that the rainfall patterns of the mid- and high-rainfall zones have been stable over time [23]. Using sterile conditions, at each site (distant ca. 10 km apart), four aliquots of approx. 50 g of soil were taken with sterile 50-ml polypropylene Falcon tubes (Grenier, Bio-One) at 100-m spacing. The four aliquots at each site were combined in a whirl-pack sample bag (Nasco, WI, USA) to make a composite sample. Composite soil samples were kept at 4ºC, transported to the laboratory within 5 days of collection and stored at -80 °C for molecular analysis.

### Sample Preparation and DNA Sequencing

Soils were analysed for soil pH, total carbon, nitrogen, phosphorous, and major cations (K, Na, Mg, Ca) at Bemlab, South Africa (Supplementary Table S1). Soil samples were sieved (2 mm) and dried overnight at 50 °C. Soil pH was measured using the slurry technique (1:3 soil/deionised water) with a Crison Bench pH meter (Crison Instruments, Barcelona, Spain). Total C and N were determined using a Truspec elemental determinator (LECO, USA). Total P was measured using the P Bray method [24]. Salt concentrations ($K^+$, $Ca^{2+}$, $Mg^{2+}$) were measured using ammonium acetate extraction with inductively coupled plasma atomic emission spectroscopy (ICP-OES; Spectro Genesis, Spectro Analytical Instruments GmbH, Germany). Rainfall data were accessed from two weather stations of the SASSCAL network (http://www.sasscalweathernet.org/) in the mid-rainfall area (Vogelfederberg station) and the high-rainfall area (Ganab station). Metagenomic DNA was extracted from the soil samples (n = 18), using the DNeasy Powersoil Kit (Qiagen, Valencia, CA, USA) as per the manufacturer’s instructions. Samples were submitted for sequencing at a commercial supplier (MR DNA Lab, Shallowater, TX, USA, http://www.mrdnalab.com). Shotgun metagenomic sequencing was performed on a HiSeq 2500 ultra-high-throughput sequencing system (IlluminaInc., San Diego, CA, USA) using paired-ends (2 × 250 bp) for 500 cycles as per the manufacturer’s instructions.

Targeted sequencing of the 16S rRNA gene amplicons were amplified using primers 515F (5'-GTGYCAGCMGCCGCGGTAA-3') and 806R (5'-GGACTACNVGGGTWTCTAAT-3'). Paired-end 2 × 250 bp sequencing was performed on an Illumina MiSeq instrument according to manufacturer’s instructions (Illumina Inc., San Diego, CA, USA) with the parameters as

described (https://support.illumina.com/16s-metagenomic-library-prep-guide-15044223-b.pdf).

The metagenome sequence data and 16S amplicon sequence data are available on NCBI (http://www.ncbi.nlm.nih.gov/PRJNA592367).

**Metagenome Assembly and Functional Annotation**

Raw reads were quality filtered using FastQC [25] and trimmed using PrinSeq [26]. Reads were assembled using SPAdes v3.12 [27], with default settings and the 'meta' parameter specified. The quality of each assembled metagenome (*n* = 18) was assessed using QUAST v5.0.2 [28]. Gene prediction was performed using Prodigal v2.6.3 [29] with the 'meta' parameter specified. The protein files from the gene prediction were then used for functional annotation. The functional annotation was carried out using two approaches. First, assembled contigs were uploaded and annotated with the Metagenomics Rapid Annotation using SEED Subsystems (MG-RAST) pipeline version 4 [30]. Broader functional pathways were generated using the SEED database (SEED levels 1 to 3), and frequency values of the hits of each individual subsystem for each metagenome were normalized before statistical analysis. Second, protein families were annotated using the pFam database [31]. For this, the prodigal protein files were scanned against Interpro's database (which houses member database signatures such as pFam) using the InterProScan software [32], which uses Hidden Markov Models (HMM) allowing for a high quality alignment. The latter approach was followed because it has been reported that MG-RAST does not apply very stringent thresholds (e.g. e-value < 1.0e-5 and identity > 60%), and therefore annotation lacks specificity at the individual functional level [33].

**Amplicon Sequencing Analysis**

Sequence reads were demultiplexed using Sabre (https://github.com/najoshi/sabre) and primers and barcodes were removed using Cutadapt [34]. Amplicon sequence variants (ASVs) were resolved using DADA2 version 1.14 [35] in R version 3.3 [36]. Quality filtering was done using the following parameters: MaxEE = (2,2), truncLen = (220, 200), with all other parameters were set to default. The error rates were estimated by learnErrors and sequences were dereplicated using derepFastq with default parameters. removeBimeraDenovo was used to remove chimeric sequences. Taxonomy was assigned against the Silva non-redundant database version 138 (https://www.arb-silva.de). The resulting taxonomy and read-count tables constructed in DADA2 were imported into phyloseq [37] for downstream analysis.

**Data Analyses**

The analyses were done in R [36] v3.3 using the packages phyloseq [37], microbiome [38], tidyverse [39], vegan [40] and metacoder [41]. Richness and Shannon diversities were calculated using the vegan package [40]. Faith's phylogenetic diversity (PD) was calculated using the picante package [42]. Taxonomic (ASVs) and functional (SEED level 3) community data were Hellinger-transformed, and both the Bray–Curtis and normalized UniFrac distance measures were used to generate dissimilarity matrices. The correlation between taxonomic and functional dissimilarities was assessed using a Mantel test. The differences in

community composition and function, and environmental conditions were visualised using Principal Coordinates Analysis (PCoA) and Principal component analysis (PCA), respectively. A permutational analysis of variance (PERMANOVA) was carried out to test for differences in composition between habitats (mid-rainfall and high-rainfall) using the 'adonis' function in vegan. In order to test for differences in composition within habitats, a test for homogeneity of multivariate dispersions (PERMDISP) was done using the 'betadisper' function in vegan. The effect of environmental conditions in explaining variation in microbial community structure was assessed by distance-based Redundancy Analysis (db-RDA). To assess the ASVs that differed in relative abundance between the two rainfall zones, generalized linear models implemented in DESeq2 [43] were used. For the analysis of ecotypes, the ASVs were clustered into 97% similarity OTUs using the Opticlust algorithm [44] with Mothur [45].

To determine the statistical differences between the functional profiles of the two climatic zones, the Statistical Analysis of Metagenome Profiles (STAMP) software was used [46]. The table of frequency of hits generated by the SEED database was used as the input file (at levels 1 and 2). The *P* values were calculated using the Welch's *t* test [47, 48] and corrected for multiple comparisons using Benjamini–Hochberg false discovery rate [49]. The alpha diversity metrics for the functional profiles were calculated using SEED level 3. In order to better understand the relationship between taxonomy (at the class level) and function (SEED level 2), network analysis was used. To this end, all possible Spearman's rank correlation coefficients were calculated. Only correlations with $\rho > 0.8$ and $P$ values $< 0.01$ were selected. We included only the positive correlations in the results because we were interested in those taxa that could potentially perform specific functions. The nodes in the reconstructed network represent taxonomical or functional groups and the edges represent significant correlations between the nodes [50]. The networks were visualized using Igraph [51]. Core functions were assessed using protein domain families generated by the pFam database and defined as those present in 95% of samples and at ≥ 0.01% of cumulative relative abundance. The core functional profile was represented by a heatmap that was created using the ComplexHeatmap [52] package in R.

## Results

### Soil Chemistry and Climate

Physicochemical analysis showed low nutrient levels in all samples for most of the measured parameters (Supplementary Fig. S1). Statistically significant changes were observed for Ca and Na, which were both higher in the mid-rainfall zone (Kruskal–Wallis $\chi^2 = 7.7–10.1$; $p < 0.05$), while C, P, $NH_4$ and mean annual precipitation were higher in the high-rainfall zone (Kruskal–Wallis $\chi^2 = 5.7–13.1$; $p < 0.05$). PERMANOVA analysis showed a clear distinction in abiotic factors between the two rainfall zones (PERMANOVA: $F$ ratio = 7.97, $P < 0.001$).

### Soil Taxonomic Profiles

A total number of 667 353 reads were obtained (averaging 37 075 reads per sample), resulting in 4 366 ASVs. Of those, 1 047 (24% of the ASVs) were shared between the two zones, while 2 043 (47%) were unique to the high-rainfall zone and 1 276 (29%) were unique to the mid-rainfall zone (Supplementary Fig. S2).

The overall taxonomic analyses showed a total of seventeen phyla present across the two zones, with thirteen phyla showing relative abundances greater than 1% (Fig. 1a). *Proteobacteria* with a mean relative abundance of 28% (± 5% SD) dominated the soils in both rainfall zones, followed by *Actinobacteriota* (22% ± 8%), *Bacteroidota* (19 ± 8%) and *Acidobacteriota* (7 ± 3%). A relatively low abundance of *Firmicutes* (4 ± 5%), *Verrucomicrobiota* (3% ± 1%), and *Abditibacteriota* (3% ± 2%) was found; with *Crenarchaeota* (6% ± 3%) as the dominant archaeal group. A significant increase in the relative abundance of *Acidobacteriota* (Fig. 1b) from the mid-rainfall to the high-rainfall zone was noted (Kruskal–Wallis $\chi^2 = 10.4$; $P < 0.05$), while the other phyla were equally distributed between the two rainfall zones.

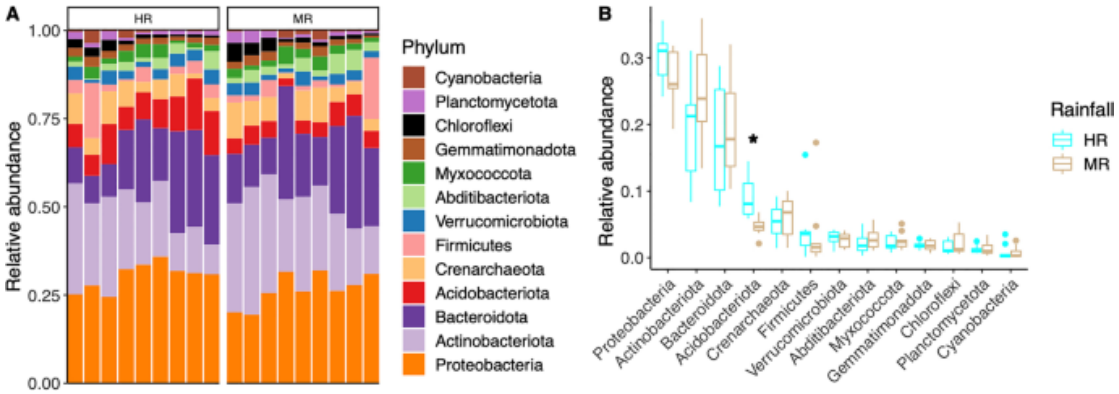



**Fig. 1.** Relative abundance of the major phyla based on 16S rRNA gene sequences in both rainfall zones (**a**), showing the significant increase of *Acidobacteriota* (KW, $P < 0.05$) in the high-rainfall zone (**b**). *HR* high-rainfall, *MR* mid-rainfall

Using DESeq we found that 86 ASVs differed in abundance between the two zones (Fig. 2). 53 ASVs increased significantly in the high-rainfall zone compared with the mid-rainfall zone. The largest increase (a 9.76 log-fold change) belonged to '*Candidatus* Nitrosphaera', phylum Crenarchaeota. Other ASVs that were more abundant in the high-rainfall zone were members of the genera *Bryobacter* (Acidobacteriota) and *Chlorogloeopsis* PCC − 7518 (Cyanobacteria). In contrast, 33 ASVs decreased significantly in the high-rainfall zone compared with the mid-rainfall zone. The largest decrease (a 10.02 log-fold change) was seen within the genus *Adhaeribacter* (Bacteroidota). By clustering of the 86 ASVs into OTUs (97% identity cut-off), it was found that several of these OTUs were composed of different ASVs with specific preferences for one of the two rainfall zones (Supplementary Table S2). For instance, OTU-02 (belonging to the genus *Adhaeribacter*, phylum Bacteriodota) was represented by 3 different ASVS: ASV-170 and ASV-57, more abundant in the mid-rainfall zone, and ASV-307, more abundant in the high-rainfall zone.

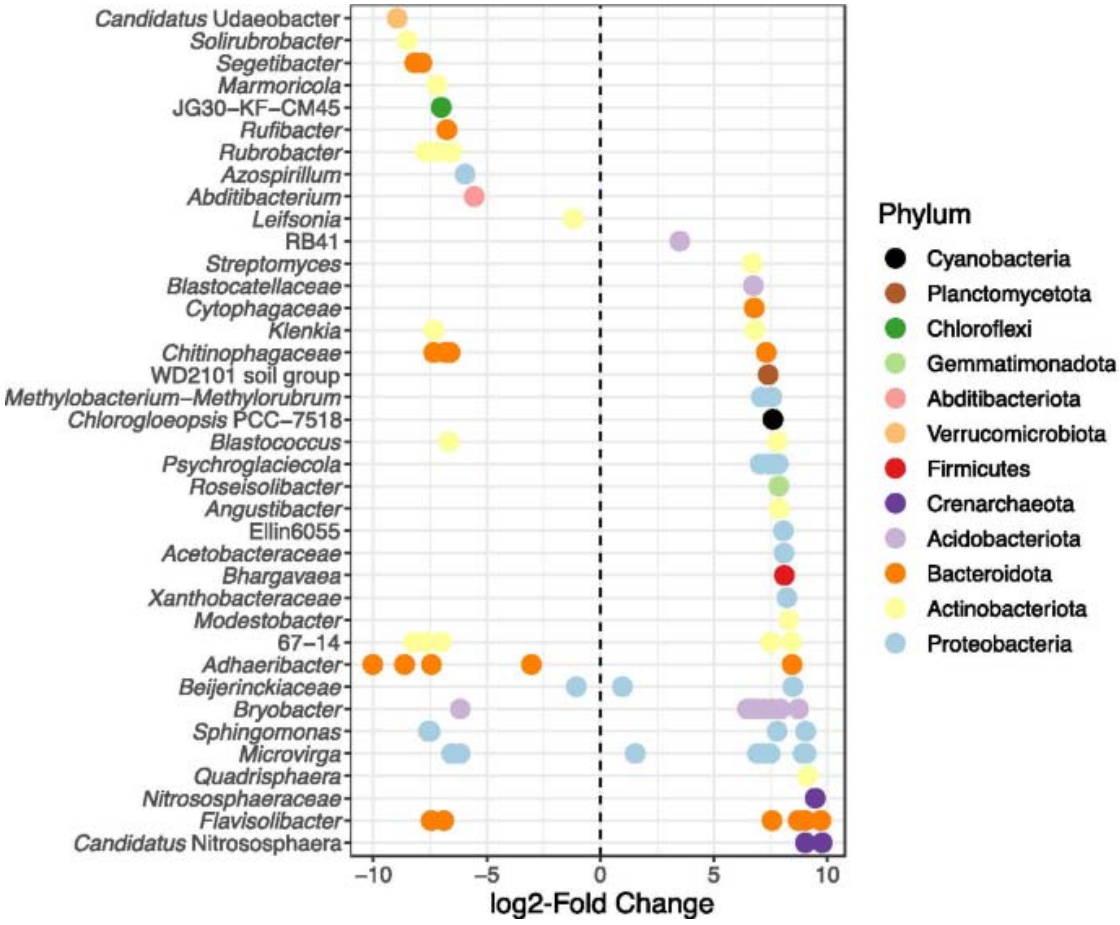



**Fig. 2.** Amplicon sequence variants (ASVs) in soil communities that significantly increased (positive log2-fold change values) or decreased (negative log2-fold change values) in relative abundance in the high-rainfall compared to the mid-rainfall zone

**Sources of Community Variation**

Based on the 16S rRNA gene sequence data, alpha-diversity (richness, Shannon and Faith's phylogenetic diversity (PD)) was not significantly different between the two zones (Kruskal–Wallis; $P > 0.05$). Principal coordinate analysis (PCoA) using Bray–Curtis dissimilarities after Hellinger transformation showed that the high-rainfall zone harbored different prokaryotic communities than the mid-rainfall zone (PERMANOVA: $F$ ratio = 3.6, $P < 0.001$) (Fig. 3). Comparable results were obtained using normalized weighted UniFrac distances (Supplementary Fig. S3). Thus, hereafter, we used Hellinger-transformed Bray–Curtis distances. Importantly, communities from the high-rainfall zone were considerably more variable in their ASVs composition than communities from the mid-rainfall zone (PERMDISP: $F$ ratio = 8.5, $P < 0.01$). Using distance-based redundancy analysis (db-RDA), it was observed that community composition was largely driven by the rainfall zone and the levels of phosphorous and nitrate, which together explained 38% (18% rainfall zone, 11% phosphorus and 9% nitrate) of community variation (Supplementary Fig. S4).

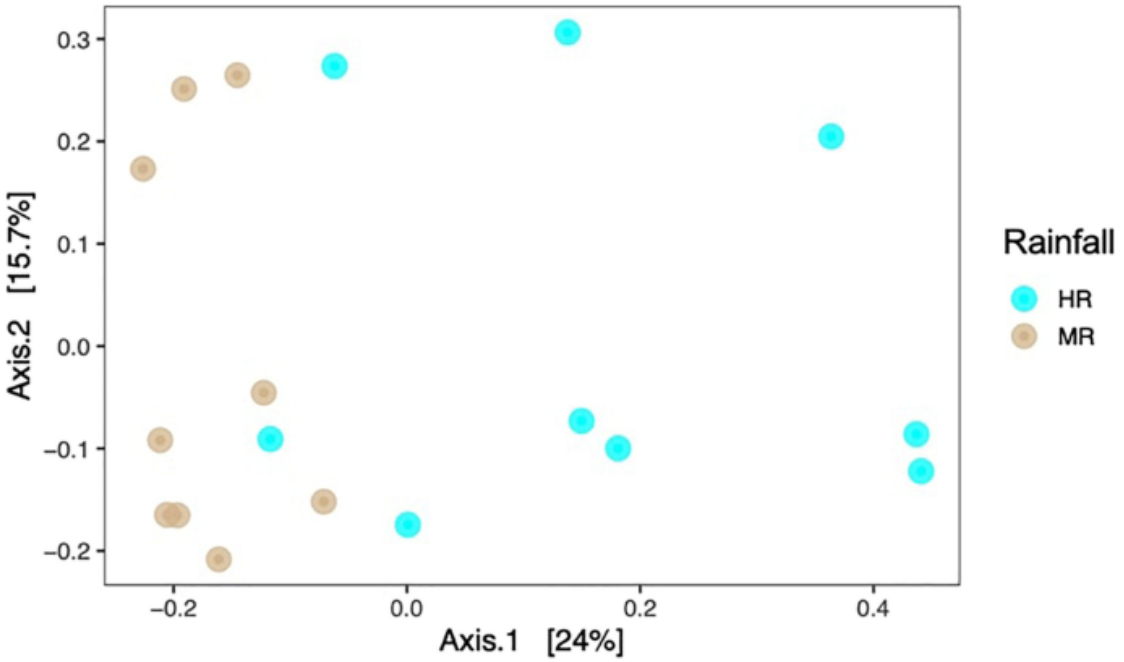



**Fig. 3.** PCoA ordination of Bray–Curtis distances (after Hellinger transformation) between microbial communities in the mid-rainfall (MR) and high-rainfall (HR) zones (PERMANOVA: *F* ratio = 3.6, $P < 0.001$)

**Soil Functional Profiles**

The number of sequence reads per metagenome ranged from 9 868 998 to 11 726 910 (10 632 908 on average). Using MG-RAST SEED level 3 data, richness was not significantly different between the two zones (Kruskal–Wallis; $P < 0.05$). However, Shannon diversity, which includes richness and evenness information, showed an increase in the high-rainfall zone (Kruskal–Wallis; $P > 0.001$). The Bray–Curtis distances (beta-diversity) after Hellinger transformation were determined for the functional profiles (SEED level 3), ordinated through Principal Coordinate Analysis (PCoA) and the differences between the two zones were tested using PERMANOVA analysis. The results showed that the high-rainfall zone harbored different functional profiles than the mid-rainfall zone (PERMANOVA: *F* ratio = 3.5, $P < 0.005$) (Fig. 4).

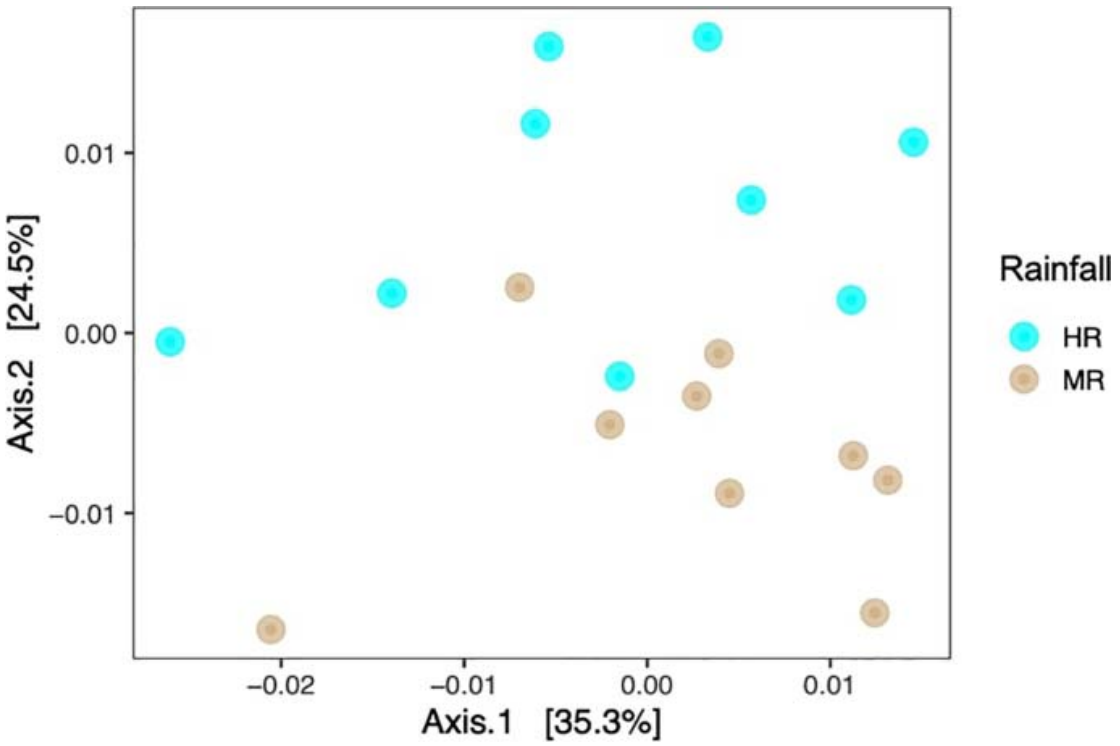
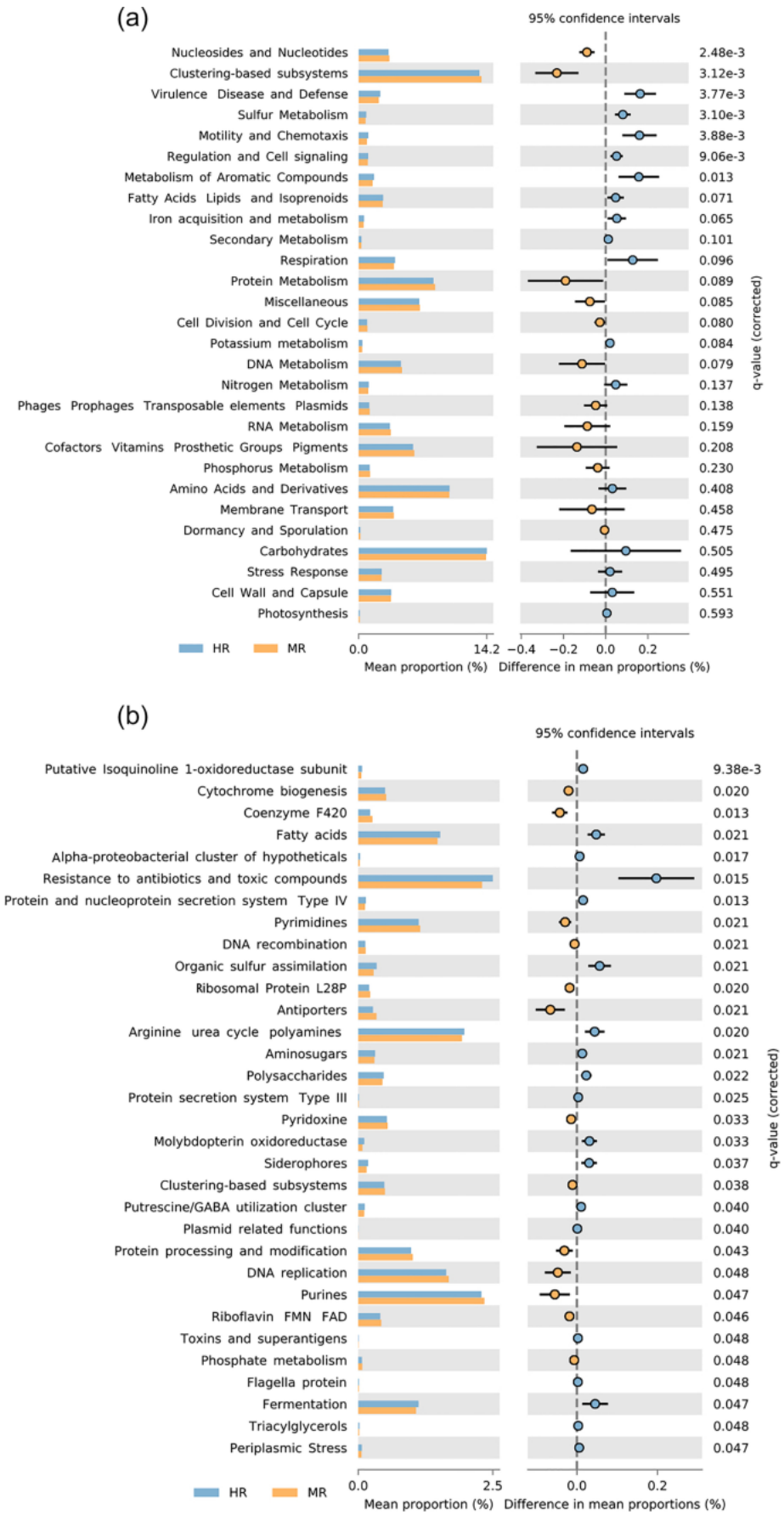



**Fig. 4.** PCoA ordination of Bray–Curtis distances (after Hellinger transformation) between functional profiles (SEED level 3) in the mid-rainfall (MR) and high-rainfall (HR) zones (PERMANOVA: *F* ratio = 3.5, $P < 0.005$)

At the top SEED level (level 1), the subsystems 'sulphur metabolism', 'metabolism of aromatic compounds', 'regulation and cell signalling', 'motility and chemotaxis' and 'virulence, disease and defence' were more abundant in the high-rainfall zone compared with the mid-rainfall zone (Welch's *t* tests $P < 0.05$, Fig. 5(a)). In contrast, the subsystems 'Nucleosides and nucleotides' and 'clustering based subsystems' (i.e. protein biosynthesis, ribosomes and recombination related clusters) were more abundant in the mid-rainfall zone (Welch's *t* tests $P < 0.05$). Subsystems relating to dormancy and sporulation were present in very low abundance and did not differ between the two zones. In addition, several subsystems related to stress were identified in higher abundance but they did not differ significantly between the two zones. At SEED level 2 (Fig. 5(b)), the mid-rainfall microbiomes showed an increased abundance of functional groups responsible for carbohydrate fermentation and secondary functions such as resistance to antibiotics and toxic compounds (Welch's *t* tests, $P < 0.05$), while the high-rainfall microbiomes were more enriched in DNA replication and protein synthesis functions (Welch's t-tests, $P < 0.05$).


(a)
95% confidence intervals
Nucleosides and Nucleotides
Clustering-based subsystems
Virulence Disease and Defense
Sulfur Metabolism
Motility and Chemotaxis
Regulation and Cell signaling
Metabolism of Aromatic Compounds
Fatty Acids Lipids and Isoprenoids
Iron acquisition and metabolism
Secondary Metabolism
Respiration
Protein Metabolism
Miscellaneous
Cell Division and Cell Cycle
Potassium metabolism
DNA Metabolism
Nitrogen Metabolism
Phages Prophages Transposable elements Plasmids
RNA Metabolism
Cofactors Vitamins Prosthetic Groups Pigments
Phosphorus Metabolism
Amino Acids and Derivatives
Membrane Transport
Dormancy and Sporulation
Carbohydrates
Stress Response
Cell Wall and Capsule
Photosynthesis
2.48e-3
3.12e-3
3.77e-3
3.10e-3
3.88e-3
9.06e-3
0.013
0.071
0.065
0.101
0.096
0.089
0.085
0.080
0.084
0.079
0.137
0.138
0.159
0.208
0.230
0.408
0.458
0.475
0.505
0.495
0.551
0.593
q-value (corrected)
HR
MR
0.0
14.2
Mean proportion (%)
−0.4
−0.2
0.0
0.2
Difference in mean proportions (%)
(b)
95% confidence intervals
Putative Isoquinoline 1-oxidoreductase subunit
Cytochrome biogenesis
Coenzyme F420
Fatty acids
Alpha-proteobacterial cluster of hypotheticals
Resistance to antibiotics and toxic compounds
Protein and nucleoprotein secretion system Type IV
Pyrimidines
DNA recombination
Organic sulfur assimilation
Ribosomal Protein L28P
Antiporters
Arginine urea cycle polyamines
Aminosugars
Polysaccharides
Protein secretion system Type III
Pyridoxine
Molybdopterin oxidoreductase
Siderophores
Clustering-based subsystems
Putrescine/GABA utilization cluster
Plasmid related functions
Protein processing and modification
DNA replication
Purines
Riboflavin FMN FAD
Toxins and superantigens
Phosphate metabolism
Flagella protein
Fermentation
Triacylglycerols
Periplasmic Stress
9.38e-3
0.020
0.013
0.021
0.017
0.015
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0.043
0.048
0.047
0.046
0.048
0.048
0.048
0.047
0.048
0.047
q-value (corrected)
HR
MR
0.0
2.5
Mean proportion (%)
0.0
0.2
Difference in mean proportions (%)

**Fig. 5.** Relative abundance of functional categories for the high-rainfall (MR) and mid-rainfall (HR) zones. (**a**) SEED subsystem level 1 and (**b**) SEED subsystem level 2. Statistical differences of the functional profiles were determined using Welch's *t* tests in STAMP. Corrected *q* values were calculated using the Benjamini–Hochberg false discovery rate

## Core Functional Profile

Core functions were defined as those present in 95% of the samples and at ≥ 0.01% of cumulative relative abundance (Supplementary Fig. S5). As expected, the predicted core functional profile revealed a relatively high abundance of protein families linked to general housekeeping functions (i.e. DNA repair, cellular regulation, protein biosynthesis) (3, 2 and 2% relative abundance). Proteins involved in general homeostasis functions of the soil system (nutrient and energy metabolism) were also detected (13%), as well as the presence of general stress response (7%) and oxidative stress (5%) protein families.

## Relating Microbial Taxonomy and Function

For alpha-diversity, taxonomic richness and phylogenetic diversity were positively correlated with functional diversity (Spearman $\rho = 0.7$, $P < 0.001$ in both cases); however there were no positive correlations with Shannon diversity. Likewise, changes in microbial community composition were positively correlated with changes in microbial community function (Mantel $\rho = 0.6$, $P < 0.001$).

Network analysis showed that the networks for the two rainfall zones were substantially different (Fig. 6). Overall, the number of positive correlations was higher in the mid-rainfall compared with high-rainfall zone. In the mid-rainfall zone, the network presented 97 nodes and 153 edges; while for the high-rainfall zone, the network had 104 nodes and 118 edges. For the mid-rainfall zone, *Planctomycetes* (0.9% relative abundance), *Rubrobacteria* (9.7%), *Chloroflexia* (1.9%) and *Vicinamibacteria* (0.1%) were the classes that were positively correlated with more functions, whereas *Alphaproteobacteria* (24.7%), *Entotheonellia* (0.04%), *Actinobacteria* (8.2%) and *Rubrobacteria* (6.3%) were the microbial classes that were positively correlated with more functions in the high-rainfall zone.

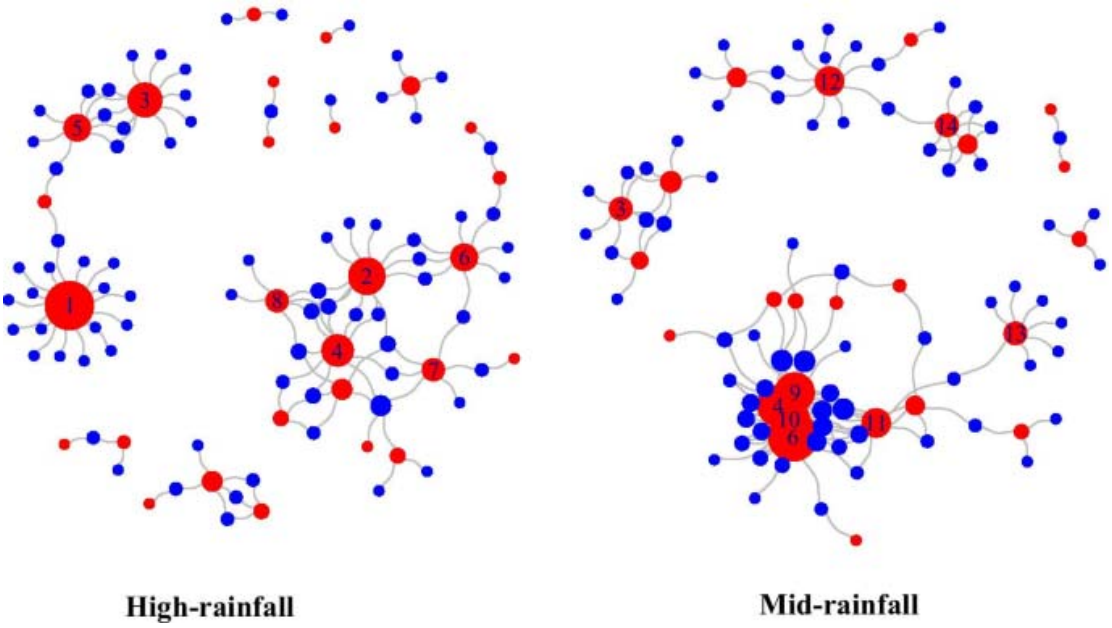


**Fig. 6.** Networks based on correlation analysis (Spearman's ρ > 0.8, *P* < 0.01) with the taxonomic and functional profiles in the mid-rainfall (MR) and high-rainfall (HR) zones. Red nodes indicate taxonomic affiliation (at the class level) and blue nodes indicate functional categories based on subsystems at level 2 (SEED database). The size of the nodes is proportional to the number of connections (degree). (1) *Alphaproteobacteria*, (2) *Entotheonella*, (3) *Actinobacteria*, (4) *Rubrobacteria*, (5) *Myxococcia*, (6) *Planctomycetes*, (7) *Longimicrobia*, (8) *Thermoleophilia*, (9) *Chloroflexia*, (10) *Vicinamibacteria*, (11) *Nitrospira*, (12) *Gammaproteobacteria*, (13) *Acidimicrobiia* and (14) *Bacteroidia*

## Discussion

### The Effect of the Environment on the Diversity of the Soil Microbiome

The physicochemical soil analysis revealed low nutrient levels comparable with other studies performed in the region [14, 17, 53]. The levels of $Ca^{2+}$ and $Na^{2+}$ decreased significantly from the mid-rainfall to the high rainfall zone. Since the Namib is a coastal desert, salt aerosol deposition is expected to decrease from the coast inland [54]. Conversely, the content of C, P and $NH_4^+$ were higher in the high-rainfall zone. These observations in combination with the PERMANOVA results support the conclusion that the two zones have contrasting environmental conditions and that the high-rainfall zone appears to support more benign conditions.

The ubiquitous presence of phyla such as *Proteobacteria*, *Actinobacteriota*, *Bacteroidota* and *Acidobacteriota* across the two zones was expected, as these phyla have been consistently reported in studies across the Namib Desert [55,56,57,58] and seem to be among the most dominant in soil bacterial communities worldwide [59]. Interestingly, *Acidobacteriota* were over-represented in the high-rainfall zone compared to the mid-rainfall zone. This pattern has been observed in other studies [60,61,62] and appears to be related to the alteration of nutrient pools in the soil, for example, after precipitation events

[61]. However, in addition to nutrient availability, other factors such as microbial interactions (e.g. competition) may contribute to the abundance of *Acidobacteriota*.

There were no significant differences (at the ASV level) in alpha-diversity (richness, Shannon and Faith's phylogenetic diversity) between the two zones. Thus, rejecting the initial hypothesis that microbial diversities would increase from the mid-rainfall zone to the high-rainfall zone. These findings are in agreement with those from a recent experimental study [63], suggesting that an increase in precipitation does not always result in higher microbial diversity. However, these results were in contrast with results from Scola et al. (17), who found that alpha diversity increased from the coast inland. This study employed T-RFLP analysis which, although a reliable technique, may have not detected fine scale changes in bacterial community diversity [64]. The results presented here also indicate that the microbial diversity of these soils is not affected by salt levels. More likely, the narrow range in precipitation differences in these study sites contributed to the pattern observed. However, the structure and composition (beta-diversity) of the microbial communities were significantly different between the two zones.

The distance-based redundancy analysis revealed that in addition to precipitation regime, P and $NO_3^+$ were other important factors shaping microbial community composition. This is not unexpected, as it is well known that the levels of nitrogen and phosphorous commonly shape the composition and structure of microbial communities in soils [65, 66] and other ecosystems [67]. Furthermore, the decrease in beta-diversity among the microbial communities from the mid-rainfall zone might be an indication of biotic homogenization [68], the process by which the similarity of communities increases over time and/or space. Biotic homogenization can occur, for instance, in harsher environmental conditions because a substantial proportion of the regional species pool can be filtered out due to niche-selection [69]. Indeed, the mid-rainfall zone seems to contain fewer microbial ASVs compared with the high-rainfall zone (2 323 $ASVs_{MR}$ vs 3 090 $ASVs_{HR}$). In addition, higher productivity due to higher nutrient levels and/or heterogeneities in one or more environmental factors might have led to more divergent communities in the high-rainfall zone [68, 70].

We detected differences in the abundances of several ASVs between the two rainfall zones. For instance, seven ASVs belonging to the genus *Bryobacter* (phylum Acidobacteriota) were more abundant in the high-rainfall zone compared to the mid-rainfall zone. This could be due to the relatively higher levels of carbon in these soils compared to mid-rainfall soils, as members of this genus are known to degrade plant-derived polymers such as cellulose [71]. The increased abundance of *Chlorogloeopsis* PCC − 7518 (Cyanobacteria) in the high-rainfall zone could be attributed to the increased levels of phosphorus in this zone. Many cyanobacteria fix nitrogen, which requires high levels of energy and therefore P (e.g. ATP). Conversely, the mid-rainfall zone was enriched with ASVs within the genus *Rubrobacter* and *Solirubrobacter* (both from the phylum Actinobacteriota). Members from these genera were also abundant in the driest locations in other desert studies [21, 63]. Several strains of extremophilic *Rubrobacter* have been shown to express classic phenotypes of UV- and γ-radiation and desiccation resistant bacteria [72]. In addition, some *Rubrobacter* have mechanisms which aid in the resistance of water deficits in soils, such as the increased production of enzymatic systems that counteract the production of reactive oxygen species (ROS) under drought [73].

Interestingly, several OTUs (e.g. OTU-02 belonging to the genus *Adhaeribacter*, phylum Bacteriodota) were composed of many ecotypes (ASVs). Different ecotypes of a species (OTUs) seem to be adapted to different values of environmental factors such as available water, carbon and phosphorus concentrations, and the presence of ecotypes within a species (microdiversity) has been proposed as a mechanism to promote functional stability under changing environmental conditions [73]. This is important for desert ecosystems, as they are extremely sensitive to global climate change.

**Soil Functional Profile**

Overall, the functional profile of these soils is consistent with reports from other studies carried out in hot deserts [74, 75]. Expectedly, the core functional profile included a relatively high abundance of protein families linked to general housekeeping functions (i.e. DNA repair, cellular regulation), which play important roles in maintaining the basic metabolism of bacterial cells for survival. Core protein families responsible for nutrient and energy metabolism were also reported, suggesting that these communities have a higher degree of metabolic flexibility, which could result in communities that are more resilient [76]. Unexpectedly, genes relating to dormancy and sporulation in these soils were in very low abundance. This is in contrast to other studies that detected a high abundance of gene categories relating to dormancy and sporulation due to the ecological selection of moisture stress and frequent drying and rewetting cycles typical to desert environments [8, 77]. A possible explanation for this observation is that those taxa associated with functions relating to dormancy and sporulation may be present in low abundance.

In hot desert soils, microbial community members are exposed to high levels of irradiation, low levels of water, wide temperature fluctuations and desiccation [1, 3], which results in high levels of biotic stress. Stress forces microbes to shift resource allocation, which can alter the C and N flows imposing considerable influences on ecosystem functioning [78]. Indeed, several core protein families relating to stress response and subsystems (SEED level 2) involved in coping with stress (i.e. oxidative, osmotic, heat and cold shock stress) were found in the soil metagenomes of the two zones and in the same proportion. This suggests that the microbes from the two zones have probably developed similar adaptation mechanisms to thrive in these stressful environments [79], for instance, cold shock proteins which are usually produced in response to a rapid decrease in temperature can also contribute to osmotic and oxidative stress tolerance [80].

One of the most noticeable differences between the microbial communities of the high-rainfall and mid-rainfall zones was the differential abundance of genes involved in ‘resistance to antibiotics and toxic compounds’ (SEED level 2). These genes were more abundant in the high-rainfall zone compared with the mid-rainfall zone. This pattern might reflect increased competition in the high-rainfall zone as this zone presents higher moisture and nutrient levels, which might result in a more benign environment. Competition is hypothesized to be more intense in more benign environments, compared with more stressful environments in which cooperation should be more common [81, 82].

Several microbial classes that showed more positive correlations with functional categories (e.g. *Entotheonella* and *Nitrospira*) were found in very low abundance. Microorganisms that occur in very low abundance are referred to as the ‘rare biosphere’ [83]. Members of the

rare biosphere can become abundant under the appropriate conditions and some have been shown to drive key processes in biogeochemical cycles [84]. In this study several rare taxa seem to have the potential to perform many functions. This suggests that the functional redundancy provided by rare taxa might contribute to ecosystem resilience in a scenario of global change.

**Coupling Between Taxonomy and Functional Potential**

The relationship between microbial community composition and functional potential is largely unknown [85]. One of the first comparative metagenomics studies of soil microbial communities [8] showed that functional profiles were highly correlated with taxonomic profiles; that is, that taxonomy and function were coupled. In contrast, other studies [86, 87] point out to a decoupling between these two components of microbial diversity, due to high functional redundancy (the coexistence of multiple distinct taxa capable of performing the same biochemical function) in soil microbial communities. Adaptive gene loss, convergent evolution and lateral gene transfer can result in the wide distribution, phylogenetically speaking, of many traits [88].

In this study, a significant correlation (coupling) between microbial and functional potential diversity was observed, at both alpha and beta diversity levels. Therefore, in this system the microbial functional potential appears to be largely determined by microbial community composition. Although individual functions may not necessarily be correlated with community structure (e.g. due to horizontal gene transfer), these results indicate that the overall functional profiles of these microbial communities seem to be predictable, at least to a certain extent, from the taxonomic community profiles.

## Conclusion

The main objective of this study was to investigate whether precipitation regime affected microbial communities in terms of diversity, composition and function. Precipitation regime had no effect on microbial taxonomic alpha-diversity which rejects the initial hypothesis that microbial diversities would increase from the mid-rainfall zone to the high-rainfall zone. However, the composition (e.g. significant increase of *Acidobacteriota* in the high-rainfall zone) and function (e.g. increase in ‘resistance to antibiotics and toxic compounds) of microbial communities differed between the two zones in response to precipitation regime (and likely other environmental factors), confirming the second hypothesis. Additionally, the decrease in beta diversity in the mid-rainfall zone could be due to biotic homogenization in response to the harsher environmental conditions (i.e. lower rainfall and nutrients).

Furthermore, the changes in microbial community and function were governed by a narrow range of taxa including several that were rare, pointing out to an important role of the rare biosphere in ecosystem resilience. Overall, this study demonstrates that microbial functional potential appears to be largely determined by microbial community composition, and that the taxonomic and functional profiles of desert soil microbial communities are strongly influenced by precipitation. This is important in the context of climate change, which is expected to alter precipitation patterns (precipitation events are predicted to become more extreme but less frequent). This, in turn, will likely affect the biogeochemical processes linked to desert soil microbial communities.

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**Contributions**

Yashini Naidoo, conceptualization, investigation, writing (original draft); Angel Valverde Portal, writing (review and editing), supervision, funding acquisition; Rian Pierneef, software, validation, writing (review and editing); Don Cowan, supervision, funding acquisition, writing (review and editing).

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**Availability of Data and Material**

The metagenome sequence data and 16S amplicon sequence data are available on NCBI (http://www.ncbi.nlm.nih.gov/PRJNA592367).

**Code Availability**

There are no unreported custom computer code or algorithms used to generate results in this paper.

## Declarations

**Ethics Approval**

Not applicable.

**Consent to Participate**

Not applicable.

**Consent for Publication**

All authors are accountable for all aspects of the work relating to accuracy and the integrity of the investigation carried out to generate the results presented here.

**Conflict of Interest**

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

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