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# Rhizosphere bacterial communities of Namib Desert plant species: Evidence of specialised plant-microbe associations

Silindile Maphosa [a], Mégan Steyn [b], Pedro H. Lebre [a], Jarishma K. Gokul [a,b], Peter Convey [c,d,e], Eugene Marais [f], Gillian Maggs-Kölling [f], Don A. Cowan [a,*]

[a] *Centre for Microbial Ecology and Genomics, Department of Biochemistry, Genetics and Microbiology, University of Pretoria, Pretoria 0028, South Africa*
[b] *Department of Plant and Soil Sciences, University of Pretoria, Pretoria 0028, South Africa*
[c] *British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom*
[d] *Department of Zoology, University of Johannesburg, Auckland Park, 2006, South Africa*
[e] *School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, United Kingdom*
[f] *Gobabeb-Namib Research Institute, Walvis Bay, Namibia*

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## ABSTRACT

Rhizosphere microbial communities are intimately associated with plant root surfaces. The rhizosphere microbiome is recruited from the surrounding soil and is known to impact positively on the plant host via enhanced resistance to pathogens, increased nutrient availability, growth stimulation and increased resistance to desiccation. Desert ecosystems harbour a diversity of perennial and annual plant species, generally exhibiting considerable physiological adaptation to the low-water environment. In this study, we explored the rhizosphere bacterial microbiomes associated with selected desert plant species. The rhizosphere bacterial communities of 11 plant species from the central Namib Desert were assessed using 16S rRNA gene-dependent phylogenetic analyses. The rhizosphere microbial community of each host plant species was compared with control soils collected from their immediate vicinity, and with those of all other host plants. Rhizosphere and control soil bacterial communities differed significantly and were influenced by both location and plant species. Rhizosphere-associated genera included 67 known plant growth-promoting taxa, including *Rhizobium*, *Bacillus*, *Microvirga*, *Kocuria* and *Paenibacillus*. Other than *Kocuria*, these genera constituted the ‘core’ rhizosphere bacterial microbiome, defined as being present in > 90 % of the rhizosphere communities. Nine of the 11 desert plant species harboured varying numbers and proportions of species-specific microbial taxa. Predictive analyses of functional pathways linked to rhizosphere microbial taxa showed that these were significantly enriched in the biosynthesis or degradation of a variety of substances such as sugars, secondary metabolites, phenolic compounds and antimicrobials. Overall, our data suggest that plant species in the Namib Desert recruit unique taxa to their rhizosphere bacterial microbiomes that may contribute to their resilience in this extreme environment.

## 1. Introduction

The plant rhizosphere is a soil zone where root structures, soil particles and microbial communities form intimate associations, with the microbial populations significantly influencing the functional characteristics of the plant host (Siddharthan et al., 2022). The rhizosphere is a dynamic ecological environment where the specialised microbial diversity affects a range of local processes, including carbon turnover, phytohormone levels, nutrient availability (particularly phosphate solubilisation), plant disease susceptibility and water retention (Zia et al., 2021; Siddharthan et al., 2022). These interactions are critical for sustaining natural ecosystems. The functions of the rhizosphere microbiome and roles of plant growth-promoting bacteria (PGPB), a subset of taxa in the rhizosphere microbial community, are a focus of studies to explore the potential of desert plant microbes in enhancing plant growth, health and agricultural productivity through their functional attributes (Verma et al., 2017; Alsharif et al., 2020; Basu et al., 2021; Chauhan and Gohel, 2022; Roberts, 2022; Zarei, 2022; Sun et al., 2023).

The identification of PGPB, which are dominated by members of well-known aerobic genera including *Rhizobium*, *Bacillus*, *Burkholderia*, *Azotobacter*, *Azospirillum, Paenibacillus*, *Serratia*, *Pseudomonas* and *Klebsiella* (ALKahtani et al., 2020), has until recently relied primarily on

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* Corresponding author.
*E-mail address:* don.cowan@up.ac.za (D.A. Cowan).

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culture-dependent studies, limiting the extent of novel PGPB discovery (Armanhi et al., 2018; Romano et al., 2020). Given the well-known constraints of using culture-dependent methods (e.g., preferential selection of the microbial 'weeds'; (Armanhi et al., 2018; Wei et al., 2021), for accessing the complete microbiome, it is likely that many currently unrecognised rhizosphere (and endophytic) microbial taxa also contribute beneficially to host plant performance. This contention is strongly supported by recent comparative phylogenetic surveys of plants across aridity gradients (Marasco et al., 2021), and studies of the rhizosphere communities of drought-adapted plants (Genitsaris et al., 2020). Both approaches demonstrate that increasing environmental aridity results in changes in rhizosphere microbial communities (Karray et al., 2020), with one of the possible drivers being the selective recruitment of specific microbial taxa to form a core microbiome that contributes to a drought-tolerant phenotype (Fan et al., 2023).

Amongst the widely accepted positive effects of rhizosphere microbiomes on plant traits and performance (Olanrewaju et al., 2019; Qu et al., 2020; Fiodor et al., 2021), it is now well established that they contribute to plant drought-tolerance via a variety of different mechanisms (Mathur and Roy, 2021; Ahmad et al., 2022; Aslam et al., 2022). These include the production of extracellular polymeric substances (EPS) at and near the root surfaces, the hygroscopic and water-holding properties of which contribute to water acquisition and retention under drought stress (Naseem et al., 2018; Fetsiukh et al., 2021, Morcillo and Manzanera, 2021; Nadeem et al., 2021). In addition to such indirect effects, rhizosphere microbiota may directly drive the upregulation of drought-response genes in the host plant genome, a set of processes collectively termed Induced Systemic Tolerance (Vurukonda et al., 2016; Carlson et al., 2020; Liu et al., 2020; Rashid et al., 2021). While the mechanisms underlying this process are currently not fully understood, it has been shown that microbially-derived chemical signals interact with transcription factors and other gene expression regulators in the plant genome (Filgueiras et al., 2020; Hartmann et al., 2021). A number of plant phytohormones produced by bacteria (e.g., abscisic acid and jasmonate) are known to play a major role in the drought-resistance phenotype, while molecular interactions between phytohormones and plant transcription factors have also been identified (Hussain et al., 2021; Mathur and Roy, 2021; Iqbal et al., 2022), leading to a range of physiological and biochemical changes including the closing of guard cells (Yoshida et al., 2014; Liu et al., 2022), the accumulation of intracellular solutes (Medici et al., 2014; Murcia et al., 2017), a reduction or increase in ethylene production (Salvi et al., 2021; Naing et al., 2022) and other stress responses (Salvi et al., 2021).

The Namib Desert is one of the world's oldest hyper-arid deserts, and harbours unique geomorphological and biological features. Its inhabitants are adapted to polyextreme conditions including limited water availability, UV radiation, high temperatures, high salinity and low nutrient conditions (Seely, 1979; Eckardt et al., 2013). These environmentally extreme conditions drive the physiological adaptations and heterogeneous functions of desert microbial communities whose primary roles in ecosystem service processes are yet to be fully understood (Lebre et al., 2017; Scola et al., 2018; Cowan et al., 2020). This creates a unique opportunity to develop a deeper understanding of the roles of soil microbial communities, including rhizosphere communities, in some of Earth's harshest environments.

Soil microbiome research in the Namib Desert dates back a little more than a decade (Cowan et al., 2020) and the studies available have principally focused on the taxonomic diversity and functional properties of polyphyletic microbial communities in open soils across the ~200 km longitudinal water-availability gradient present in this desert (Van der Walt *et al.*, 2016; Vikram et al., 2016; Scola et al., 2018; Naidoo et al., 2022) and on the microbiomics of desert soil niche communities (Stomeo et al., 2013; Frossard et al., 2015; Cowan et al., 2020).

Plants in desert environments exhibit various genetic and morphological adaptation strategies, as well as complex interactions with intimately associated microbial communities through their root systems that provide resilience to desiccation (Bandurska, 2022; Chieb and Gachomo, 2023). Several recent studies have focussed on the nature and role of specialised root-associated structures (rhizosheath) that are characteristic of certain desert speargrasses in the genus *Stipagrostis* (Marasco et al., 2018; Marasco et al., 2022; Marasco et al., 2022). These studies have provided strong evidence of the selective recruitment of microbial taxa into the rhizosheath, and some evidence for the selection of beneficial functional characteristics (Marasco et al., 2018; Marasco et al., 2022). Extending this concept to other drought-adapted desert plant species, in this study we investigated the rhizosphere microbial communities of multiple plant species, also including some speargrasses, from this extreme desert ecosystem.

We focused on specific questions relating to the rhizosphere bacterial microbiomes of desert plant species: (i) are these root-associated microbiomes distinct from the local soil microbiome, indicating a selective recruitment process? (ii) do plant species assemble similar rhizosphere bacterial microbiomes, irrespective of location, indicating a generic recruitment mechanism? and (iii) are certain microbial taxa commonly identified in the rhizospheres of different plant species, suggesting that recruitment is driven by the potentially beneficial functional properties (phenotypes) of these microorganisms? This work seeks to advance our understanding of desert plant rhizosphere-associated microbial communities, which may be highly relevant to future land restoration efforts and sustainable agriculture in drylands.

## 2. Materials and methods

### 2.1. Experimental sites and sample collection

Plant rhizosphere and control soil samples were collected in triplicate from 30 sites in the central Namib Desert in April 2022 (locations, plant species and sample data are provided in Fig. 1A, B and Table S1, respectively). Plant roots were excavated using an ethanol-sterilised shovel and shaken to manually remove soil particles. For each plant, roots were then excised and placed in a sterile 50 mL Falcon tube. Control soil samples (0–5 cm depth, one per plant sampled) were aseptically collected from within 1 m of each sampled plant. All samples were stored at 4 °C and transported to the University of Pretoria, South Africa, where they were stored at -80°C until further processing.

### 2.2. DNA extraction and sequencing

After thawing, tubes containing root rhizosphere samples were agitated for 5 min in PBS buffer to detach and suspend the soil and rhizosphere microbiome from the root surface. The resulting resuspended biomass was spun down at 2 500 rpm for 3 min, and the pellets were resuspended in lysis buffer from the DNA extraction kit (QIAGEN DNeasy PowerSoil kit, QIAGEN, United States) for DNA extraction. For samples with rhizosheath structures, rhizosheath material was removed with a sterile scalpel, and used for DNA extraction. Genomic DNA was extracted following the manufacturer's protocol (QIAGEN, United States). For control soils and rhizosheath samples, 1 g samples were used for extraction. The resuspended rhizosphere pellets were transferred to the bead tubes in lysis buffer and subsequently processed following the manufacturer's instructions. Extracted DNA concentrations and quality were assessed using a NanoDrop 2000 spectrophotometer (ThermoFisher, United States) and UV visualization after 1 % agarose gel electrophoresis. DNA samples were subject to commercial 16S rRNA amplicon paired-end (2 × 300 bp) sequencing using standard Illumina 16S V3-V4 region bacterial primers 341 F (5'-CCTACGGGNGGCWG-CAG-3') and 805 R (5'-GACTACHVGGGTATCTAATCC-3') (Herlemann et al., 2011). Sequencing was performed commercially using the Illumina Miseq platform by Omega BioSciences (Norcross, USA), with a read coverage of 100 000 reads (50 000 in each direction).

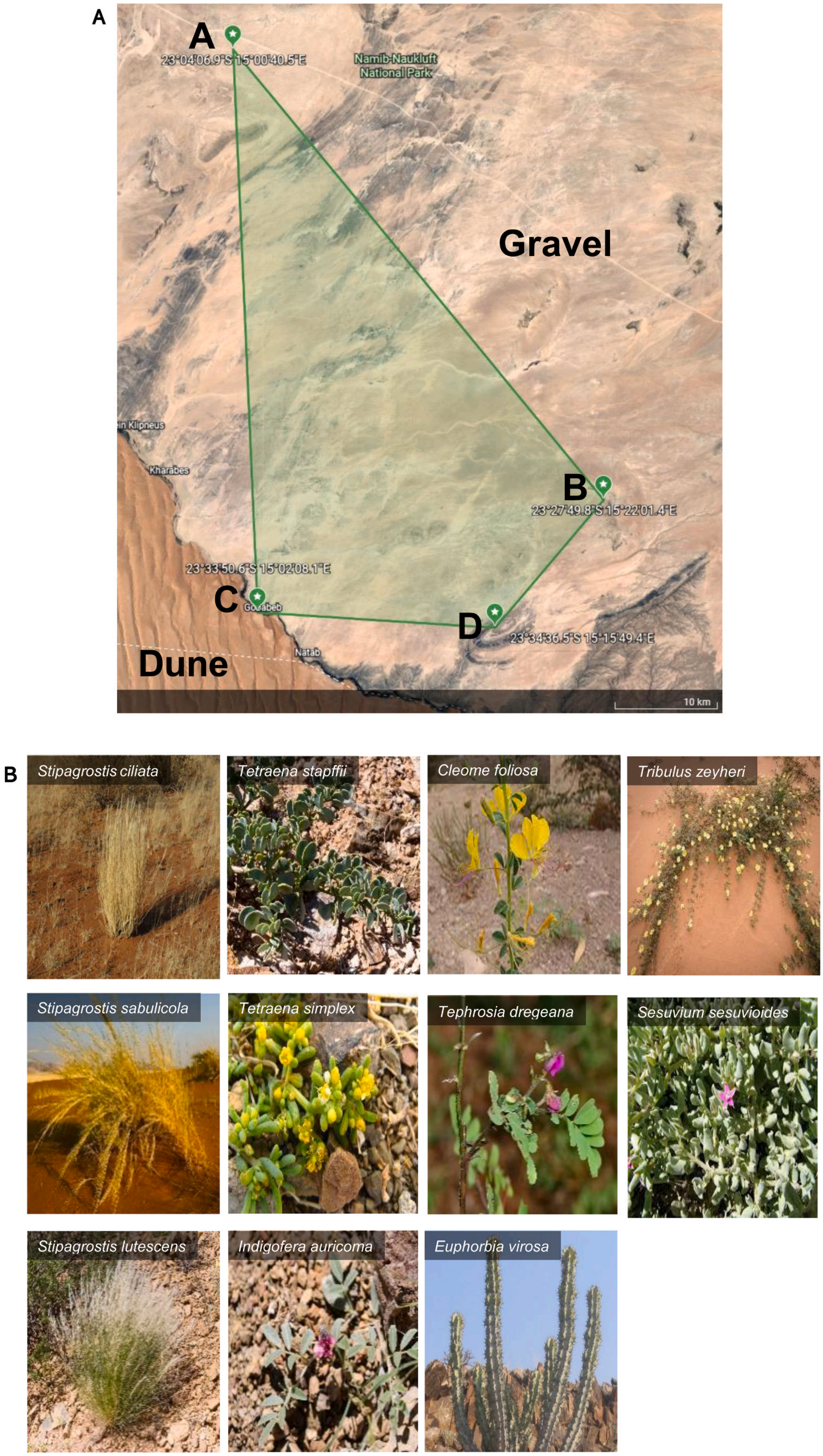

**Fig. 1.** Sampling locations in the Namib Desert gravel plains (A, B, D), and dunes (C) (A). Eleven desert plant species were sampled: *Stipagrostis ciliata, Tetraena stapffii, Cleome foliosa, Tribulus zeyheri* (top row), *Stipagrostis sabulicola, Tetraena simplex, Tephrosia dregeana, Sesuvium sesuvioides* (middle row), *Stipagrostis lutescens, Indigofera auricoma, Euphorbia virosa* (bottom row) (B).

### 2.3. Sequence processing

Raw sequence reads (BioProject PRJNA1160782) were processed using the Qualitative Insights Into Microbial Ecology 2 (QIIME2) pipeline (Bolyen et al., 2019). The DADA2 plug-in (Callahan et al., 2016) was used to trim and denoise raw reads, as well as assign unique amplicon sequence variants (ASVs). The denoise-pair function was used to trim 20 bp from the 5' end of reads in order to remove barcodes and primers. Additionally, trunc-length was set to 300 bp in order to discard nucleotides with quality scores of $< 20$ at the 3'-ends. The resulting trimmed/denoised ASVs were taxonomically assigned using the pre-trained classifier trained on the SILVA 138 SSURef NR99 database (Robeson et al., 2021).

### 2.4. Bacterial community composition and statistical analyses

Compositional and statistical analyses of ASV datasets were carried out in RStudio v4.3.1 (Team, 2020). Before statistical analyses, the dataset was filtered to remove unassigned reads and reads assigned to mitochondria, chloroplasts and eukaryotes using the Phyloseq v1.44.0 package (McMurdie and Holmes, 2013). Relative abundances of the dominant phyla and genera in the control and rhizosphere samples were determined using the 'phyloseq' package in R (McMurdie and Holmes, 2013). Plots were created using the 'ggplot2 v3.5.1' package in R (Wickham et al., 2018).

Differences in bacterial community diversity were assessed by evaluating alpha and beta diversity dissimilarities between samples (Oksanen et al., 2019). Normality of the sampled datasets was evaluated using the Shapiro normality test (Shapiro et al., 1968). The Shannon biodiversity index of samples was estimated using the *estimate_richness* function in the R package 'phyloseq' after rarefaction to the lowest common read count (8 302), which was performed using the 'vegan v2.6–4' package (Oksanen et al., 2019). To calculate significant differences in alpha diversity between the four sampling locations (A, B, C, D) and sample types (control soils or rhizosphere), analyses of variance (ANOVA) (Chambers et al., 2017) were followed, where significant, by Tukey's HSD tests (Tukey 1977) (for normally distributed data) or the Kruskal–Wallis test followed by the Wilcoxon Rank Sum test (Wilcoxon et al., 1970) (for non-normally distributed data) (McKight and Najab, 2010).

The Bray-Curtis dissimilarity between samples was calculated and subsequently visualised in a Principal Coordinates Analysis (PCoA) ordination plot (Jolliffe and Cadima, 2016) using the 'phyloseq' and 'ggplot2' packages. Beta dispersivity (1000 permutations) (Anderson et al., 2006) was used to test for statistically significant ($p < 0.05$) compositional variance between samples within each group, while analysis of similarities (ANOSIM) was used to test multivariate differences ($p < 0.05$) between sample groups using the 'vegan' package (Oksanen et al., 2019).

### 2.5. Identification of rhizosphere and plant growth-promoting bacteria

The bacterial genera present in the plant rhizosphere and control soil bacterial microbiomes were compared to identify specialist taxa recruited to the rhizosphere. To do this, the decontaminated ASV dataset was first clustered according to genus and split into control soil and rhizosphere sample groups, after which ASVs with zero counts were removed from the rhizosphere and control soil datasets. Thereafter, relative abundances of ASVs across the samples were calculated for each ASV dataset. The top 10 % most abundant ASVs present in at least 50 % of the soil control and rhizosphere samples were then compared to identify those that were commonly identified in both control soils and plant rhizospheres and those that were only present in the rhizosphere soils and/or were plant-species-specific. Commonly identified and plant-species-specific genera in the rhizospheres of the 11 plant species were visualised using Venn diagrams and the 'UpsetR v1.4.0' and 'ComplexUpset v1.3.3' packages (Conway et al., 2017). Plant growth-promoting bacteria identified in the entire rhizosphere dataset were visualised using averaged relative abundances as a heatmap using the 'pheatmap v1.0.12' package in R (Kolde, 2019). The PGPB taxa were clustered using Pearson correlation and the plant species using a binary scale (presence or absence of taxa).

### 2.6. Abundance comparisons of functional pathways in rhizosphere and control soil microbiomes

Linear discriminant analysis effect size (LefSe) (Segata et al., 2011) was used to identify biomarker pathways in the rhizosphere and control soil bacterial microbiomes based on normalised relative pathway abundances. The four sampling locations (A, B, C, D) and sample types (control and rhizosphere soil samples) were used as the subclasses and subjects, respectively, using default LefSe settings. Phylogenetic Investigation of Communities by Reconstruction of Unobserved States (PICRUSt2) (Douglas et al., 2020) was used to compare the putative functional capacities of taxa present in rhizosphere and control soil samples. Here, the putative pathway abundances were compared to identify those present in at least 50 % of the control and rhizosphere soils. A linear discriminant analysis (LDA) was used to evaluate and visualise the abundant functional pathways in the rhizosphere and control soil communities based on LDA scores. The Kruskal-Wallis rank sum test with an FDR adjusted $p < 0.05$ was used to identify PICRUSt2 predicted functions that were differentially represented between the rhizosphere communities of the different species, using the package MicrobiomeMarker (McKight and Najab, 2010; Cao et al., 2022). Correlations above 0.3 and 0.5 were considered indicative of strong and very strong influences from plant species, respectively.

### 2.7. ASV co-occurrence between plant rhizosphere communities

To assess the correlation between plant rhizosphere communities, pairwise comparisons based on ASV presence and absence in each plant dataset were performed using the Pearson method in the R package 'corrplot v0.92' (Friendly, 2002). Visualisations were generated using 'ggplot2' from the Pearson co-occurrence scores. Scores of $r > 0.5$ and $r < -0.5$ were defined as positive and negative correlations, respectively.

## 3. Results

### 3.1. The plant rhizosphere bacterial microbiome is distinct from the control soil microbiome

Bacterial richness metrics for all samples ranged from 16 to 1768 (Fig. 2A). Shannon index values fell between 0.9 and 6.9 (Fig. 2B) across all the samples in the study. The control soils had significantly higher bacterial richness ($W = 808.5$, $p = 0.0017$) and biodiversity ($W = 888$, $p = 0.001$) than the rhizosphere soils, based on Wilcoxon rank-sum exact test comparisons between groups. Despite this general trend, comparisons of diversity metrics between the rhizosphere of each plant species and their respective control soils (Fig. 2C) showed variable relationships between rhizosphere communities and surrounding soils. For instance, the rhizospheres of the speargrasses *Stipagrostis ciliata, S. sabulicola*, and *S. lutescens,* as well as those of *Sesuvium sesuvioides* and *Tetraena stapffii,* exhibited comparable Shannon diversity values to their control soils. The Kruskal-Wallis rank sum test indicated that rhizosphere community diversity was correlated with both sampling location ($H = 12.045$, $p = 0.0072$) and plant species identity ($H = 26.494$, $p = 0.0031$). The *Tetraena simplex* rhizosphere alpha diversity (Shannon metric score 1.32) was not only the lowest among the sampled rhizosphere soils but also very low compared to its control soil (Shannon metric score 5.06).

Analysis of beta-diversity dissimilarity (Fig. 2D) between samples showed that samples were significantly clustered according to soil type

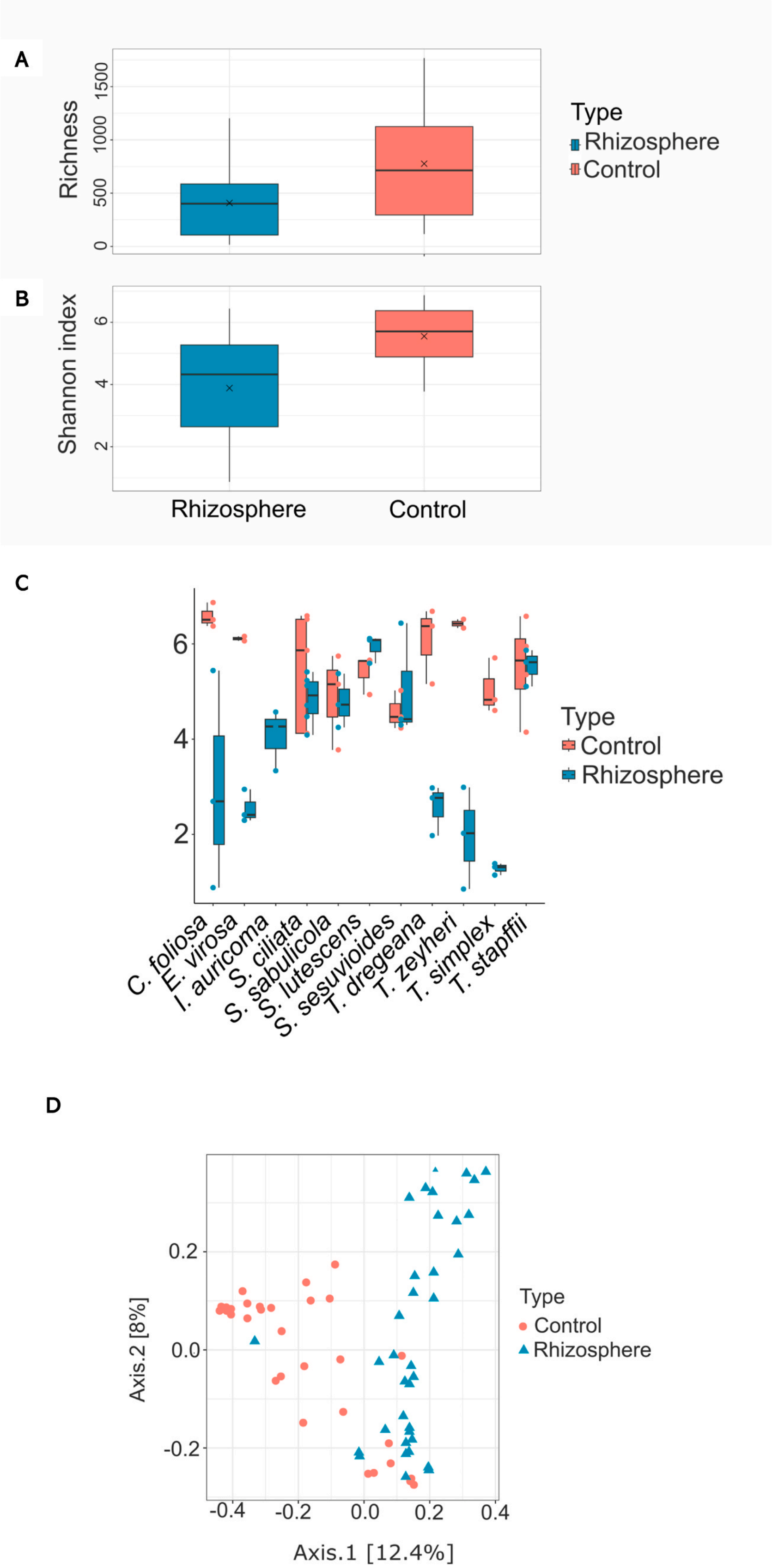

**Fig. 2.** Rhizosphere and control soil bacterial community diversity. Bacterial richness (A) and Shannon diversity indices (B) of the control and rhizosphere soils are shown as box plots. Median values are indicated by the horizontal lines and the mean values by crosses. The Shannon diversity indices (C) of bacterial communities associated with the plant rhizospheres and their respective control soils are illustrated as a box plot with median values of each indicated by a horizontal line. The principal coordinate analysis (PCoA) plot (D) shows the distances between the control soil (red) and rhizosphere samples (blue).

(rhizosphere vs control soils) ($R^2 = 0.0779$; $p = 0.001$). Samples were also clustered according to sampling location ($R^2 = 0.1333$; $p = 0.001$) (Figure S1).

### 3.2. *Plant species exhibit rhizosphere-specific bacterial species diversity*

To assess whether the 11 plant species studied were associated with specific rhizosphere bacterial microbiomes, the ASV data obtained from the rhizosphere soil samples were compared. The bacterial species richness of individual plants ranged from 16 to 1203 (Fig. 3A). The rhizosphere communities of speargrasses and *T. stapffii* exhibited higher species richness than other plant species. Lower species richness was observed for *Cleome foliosa*, *Euphorbia virosa*, *Tephrosia dregeana*, *Tribulus zeyheri*, *Indigofera auricoma* and *T. simplex*. Richness (Kruskal-Wallis H = 26.338, $p = 0.0033$) was significantly different across the 11 plant species (Fig. 3A). The analysis of microbial community structure using

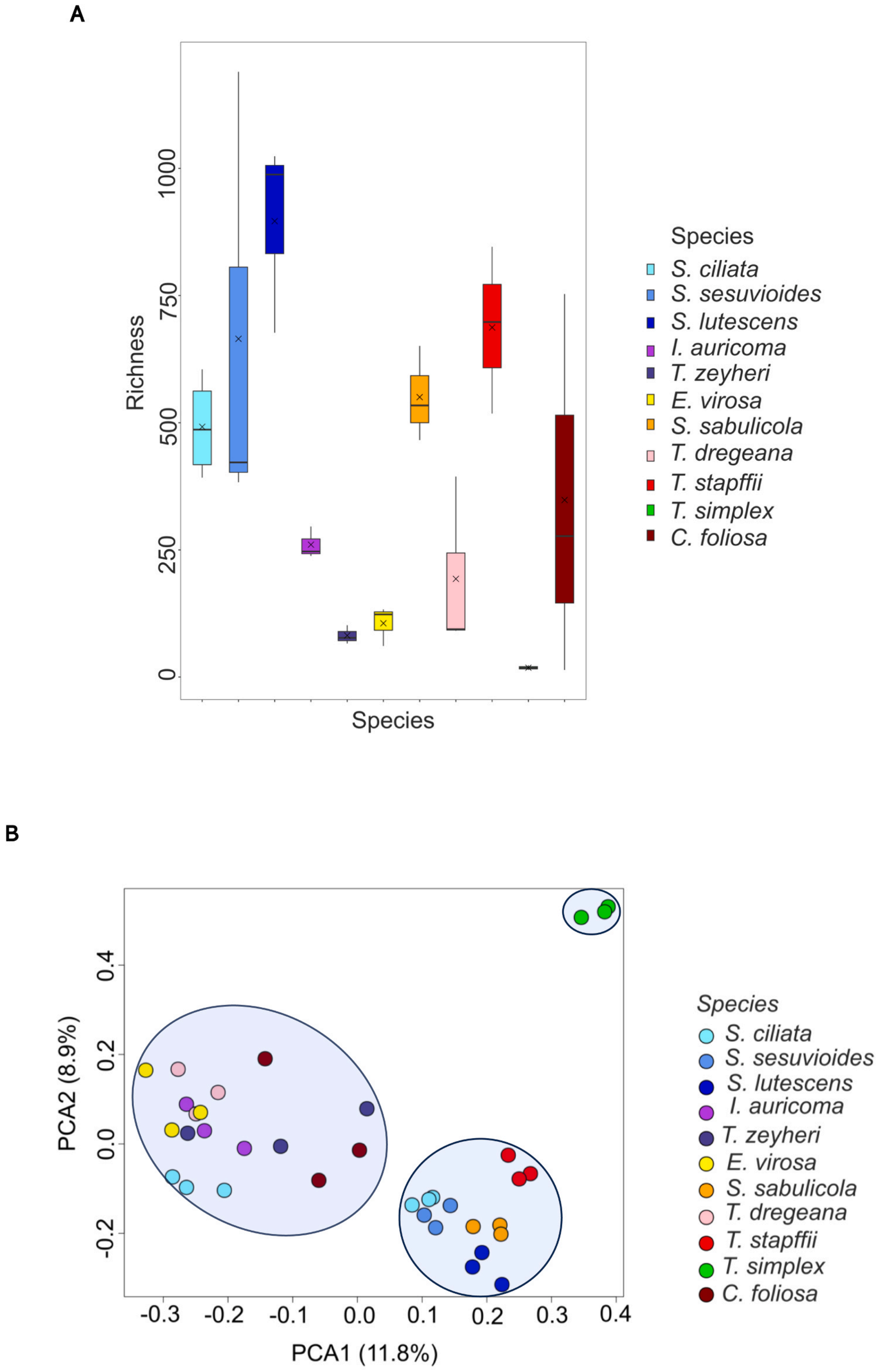

**Fig. 3.** Bacterial richness and beta diversity metrics of plant rhizosphere microbiota. The boxplot (A) shows the bacterial richness of the eleven plant species. The PCoA plot (B) illustrates the dissimilarities between the different plant rhizosphere communities.

the Bray-Curtis beta-diversity index also revealed significant compositional differences between the rhizosphere communities of the various plant species ($R^2 = 0.5222$; $p = 0.001$) (Fig. 3B). Three main clusters of samples were apparent in the PCoA: one containing the *T. simplex* samples, one containing the speargrasses, *T. stapffii* and *S. sesuvioides* samples and one containing the remaining species. However, the variation observed only accounted for 20.8 % of the total variation in the bacterial community.

### 3.3. Plant rhizosphere and control soil communities share similar dominant phyla and genera

To explore the composition of bacterial communities across the entire sample set, the ASV datasets from the rhizosphere samples and control soils were compared at both phylum and genus levels. Overall, 44 bacterial phyla and 1071 genera were assigned across the samples. The dominant phyla were Proteobacteria (Pseudomonadota) (33.1 %), Actinobacteriota (28 %), Firmicutes (19.7 %), Bacteriodota (6.4 %), Planctomycetota (2.5 %), Chloroflexi (2.6 %), Gemmatimonadota (1.7 %), Cyanobacteria (1.1 %) and Myxococcota (1.1 %) (Fig. 4).

Proteobacteria, Actinobacteriota and Firmicutes were, in rank order, the top three most abundant phyla in both the control and rhizosphere samples. Table S2 shows the relative abundances of the most dominant phyla for each plant species and the control soils. Relative abundances were higher in the rhizosphere compared to the control soil samples. Fig. 5A shows the relative abundances of the bacterial microbiome associated with the rhizosphere samples at the phylum level. At the genus level, comparisons between rhizosphere and control soils identified nine genera that were common across samples. These were *Geodermatophilus*, *Arthrobacter*, *Cellulomonas*, *Chthoniobacter*, *Blastococcus*, *Pseudomonas* and three unknown genera. By comparison, 60 and 51 genera (Table S3) were specific to the control and plant rhizosphere soils, respectively. Genera representing the phylum Proteobacteria (18) were dominant in the rhizosphere soils followed by representatives of the phylum Actinobacteriota (13) (Table S2). Rhizosphere-specific genera included *Rhizobium*, *Bacillus*, *Paenibacillus*, *Planococcus* and *Microvirga*. Thirteen genera were represented with over 1 % relative abundance in the rhizosphere soils (Fig. 5B, Table S4). *Bacillus* was the most abundant genus in *C. foliosa, S. sesuvioides, T. zeyheri* and *T. stapffii rhizospheres*. *Streptomyces* dominated the rhizospheres of two speargrasses, *S. sabulicola* and *S. lutescens*. *Massilia* and *Pseudomonas* were dominant in *I. auricoma* and *T. simplex* rhizospheres. The dominant genera for *T. dregeana*, *E. virosa* and *S. ciliata* rhizospheres did not have identified taxonomy at the genus level (Fig. 5B, Table S4).

### 3.4. Plant rhizosphere assemblages comprise variable numbers of shared and plant-species-specific ASVs

A total of 393 rhizosphere-associated ASVs were observed across the total rhizosphere sample dataset. A pairwise correlation matrix was generated to visualise the relationships between plant species based on bacteria co-occurrence in the rhizosphere communities (Figure S2). Weak to no co-occurrences were observed between *T. simplex* and the other 10 plant rhizosphere bacterial microbiomes. Amplicon sequence variant presence/absence was used to further explore the microbial composition similarities and differences between and across the 11 plant species. Upset plots were then used to visualise the intersections and divergences of the 11 sets of rhizosphere bacterial microbiomes. Fig. 6A shows the number of commonly identified ASVs from the rhizosphere sample dataset and Fig. 6B shows the number of ASVs commonly identified in over 50 % of the rhizosphere soils of the 11 plant species. The rhizosphere samples with the most shared ASVs were those of the speargrasses *S. sabulicola* and *S. lutescens*, which had a total of 101 co-occurring ASVs, followed by *S. lutescens* and *S. ciliata* with 100, *S. lutescens* and *S. sesuvioides* with 74, and *S. ciliata* and *S. sabulicola* with 71 co-occurring ASVs (Fig. 6A). *Stipagrostis ciliata* and *S. sesuvioides*, and *S. sabulicola* and *S. sesuvioides* samples each had 55 commonly identified ASVs. In contrast, *T. stapffii* and *T. simplex* only shared four of the 169 *T. stapffii*-associated ASVs. The ASVs assigned to three genera, *Microvirga*, *Streptomyces* and *Paenibacillus*, were found in 10 (91 %) of the plant rhizosphere soils—the exception being that of *T. simplex*. The rhizosphere soils of all 11 plant species shared a single ASV, classified within the genus *Bacillus* (Fig. 6B).

In addition to the shared ASVs, most plant species had species-specific members of their rhizosphere bacterial communities (Fig. 7). Fig. 7 shows the number of species-specific bacterial ASVs associated with each plant species. Eighty genera were associated with the rhizosphere of *T. stapffii* alone. Eight of the remaining 10 plant species, excluding *T. simplex* and *T. zeyheri*, also had exclusive ASVs. These were *S. lutescens* (43), *S. ciliata* (15), *S. sesuvioides* (12), *S. sabulicola* (10), *C. foliosa* (10), *T. dregeana* (2), *I. auricoma* (3) and *E. virosa* (1). These results suggest that *T. stapffii* had the most exclusive bacterial

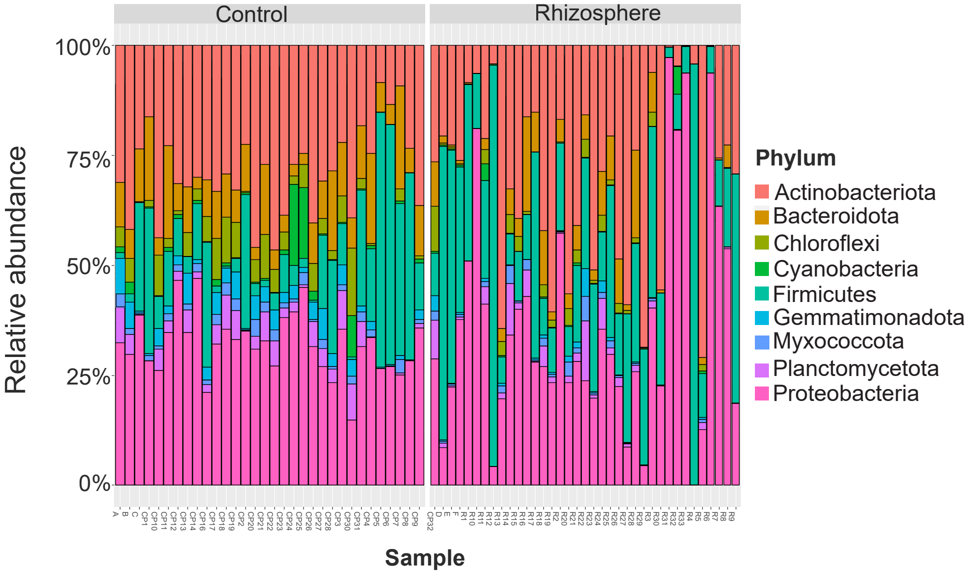

**Fig. 4.** Control and rhizosphere soil bacterial community relative abundances. The box plot depicts the abundance of phyla represented with over 1 % relative abundance in the control (left) and rhizosphere (right) samples.

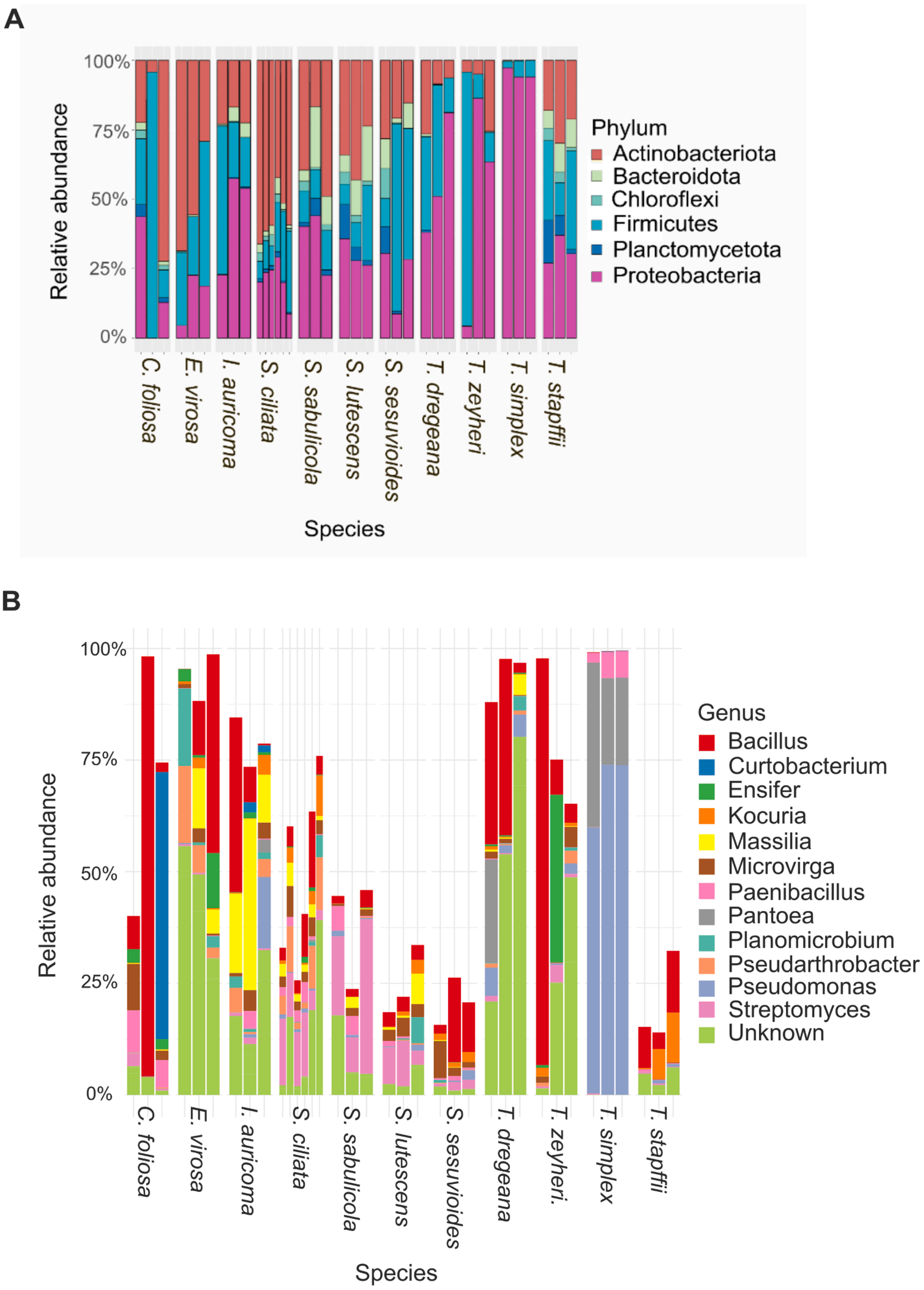

**Fig. 5.** Taxonomic analysis plot (A) showing the rhizosphere taxa obtained from each plant species at the phylum level. Taxonomic plot (B) shows the rhizosphere taxa obtained from each plant species at the genus level. The plots illustrate > 1 % relative abundance in the plant rhizosphere.

microbiome among the sampled plant species.

### *3.5. Shared and species-specific desert plant rhizosphere communities include plant growth promoting genera*

Sixty-seven genera of known plant growth-promoting bacteria were identified in the rhizosphere dataset (Table S5). The average relative abundances of the PGPB genera per plant species were determined (Fig. 8). The top three sources of *Bacillus,* the taxon identified in all rhizosphere samples, were *C. foliosa*, *T. zeyheri* and *T. dregeana*. Overall, *S. lutescens* had the highest proportion of known PGPB genera (64 %). Table S5 shows the overall relative abundance and the most abundant PGPB genera for each plant species. Of note, *T. stapffii* samples were predominantly composed of halotolerant PGPB. Species specific PGPB genera were identified in *S. ciliata* (2), *I. auricoma*, *S. lutescens* (5), *C. foliosa* (2), *S. sesuvioides* (1), *T. stapffii* (4) and *S. sabulicola* (3).

### *3.6. Plant rhizosphere bacterial communities are associated with specific functional pathways*

Differences in bacterial community structures between control and rhizosphere soils may be associated with functional differentiation and may be of ecological significance. We assigned biological functions to the soil communities using PICRUSt2. The rhizosphere and control soils shared 364 putative pathways. Eighteen and 22 putative pathways were uniquely identified for the control and the rhizosphere soil communities, respectively. The descriptions of the rhizosphere-associated pathways are shown in Table S6. These included the synthesis or degradation of

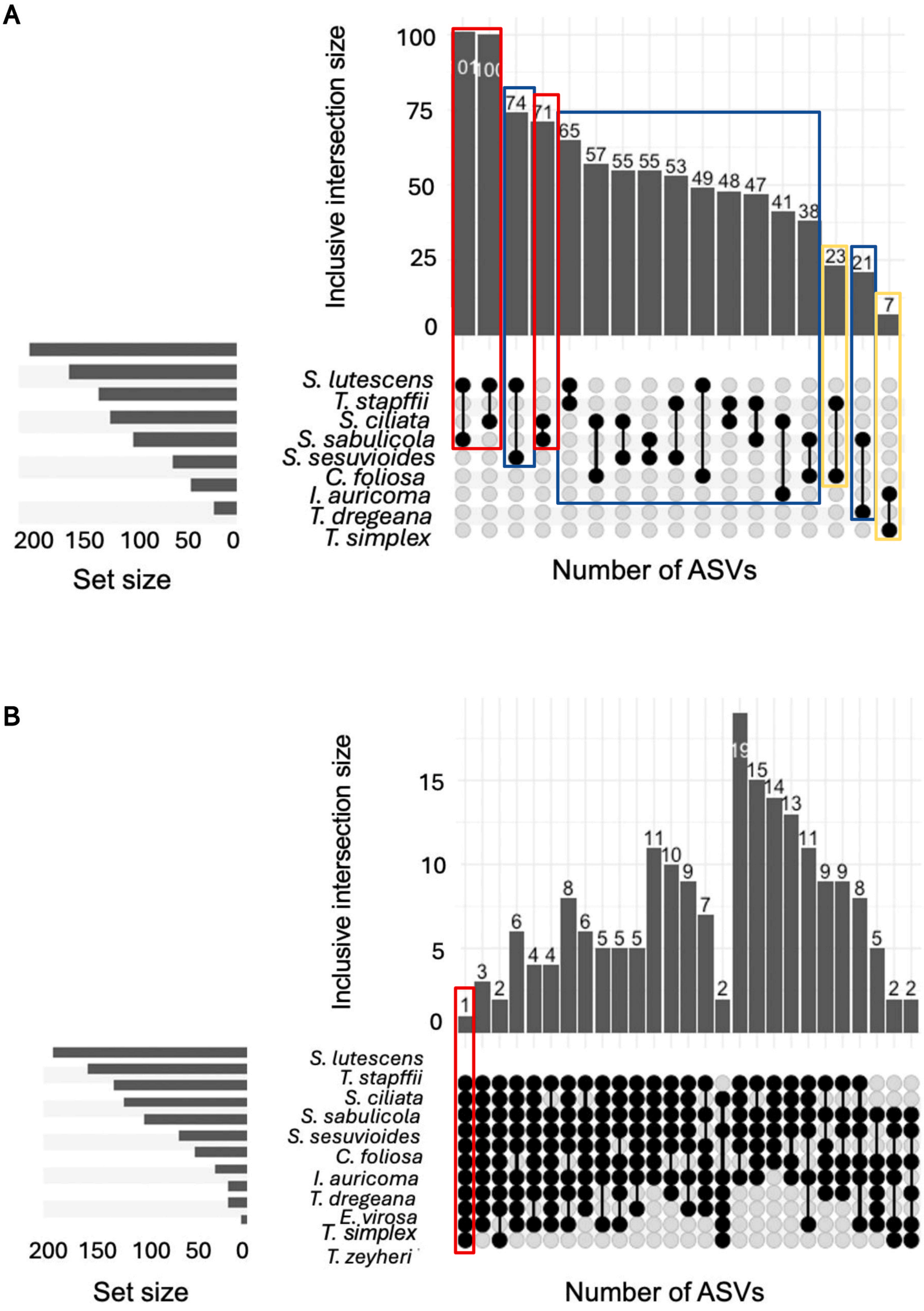

**Fig. 6.** Intersection matrix of individual plant species rhizosphere ASVs. The Upset plot (A) shows the number of shared genera between pairs of plant species. Red boxes highlight the genera shared between speargrasses, blue boxes highlight genera shared between speargrasses and other plant species and yellow boxes highlight genera shared between other non-speargrasses. In all the plots, the numbers represent the number of genera. The Upset plot (B) shows the number of ASVs shared between 6 and 11 plant species. The linked black nodes indicate the plant species that are part of the intersecting sets and the grey dots show the species that are not part of a set. The red box highlights the representative of *Bacillus* found in all 11 plant species rhizosphere soils.

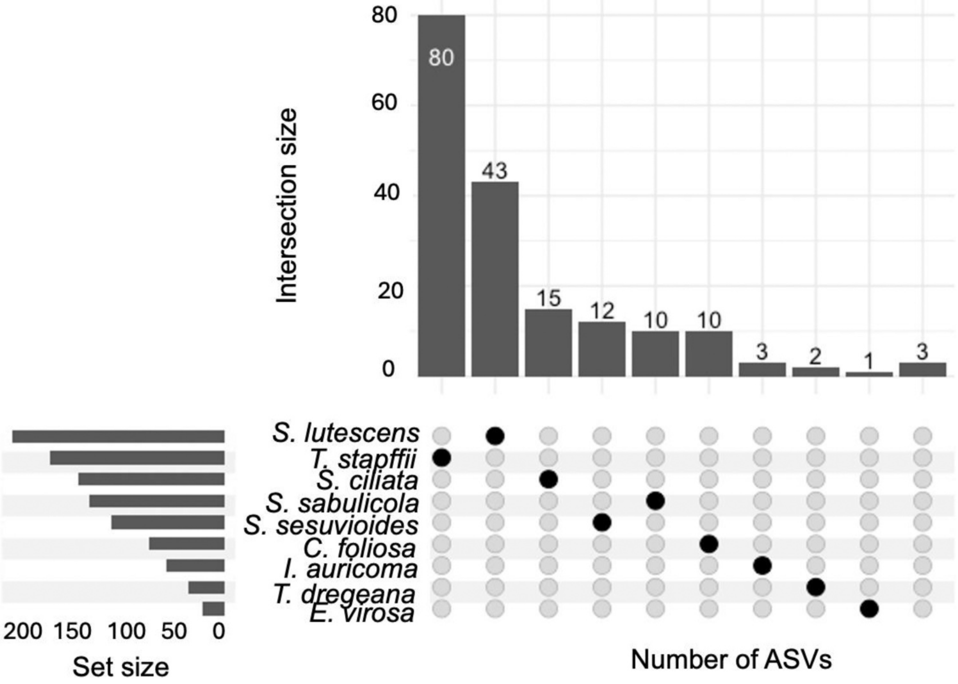

**Fig. 7.** Rhizosphere-associated ASVs for each plant species. The Upset plot shows the number of ASVs that were associated with a single plant species. The black dots show the identity of the species associated with each set of unique ASVs. The numbers indicate the number of ASVs per plant species.

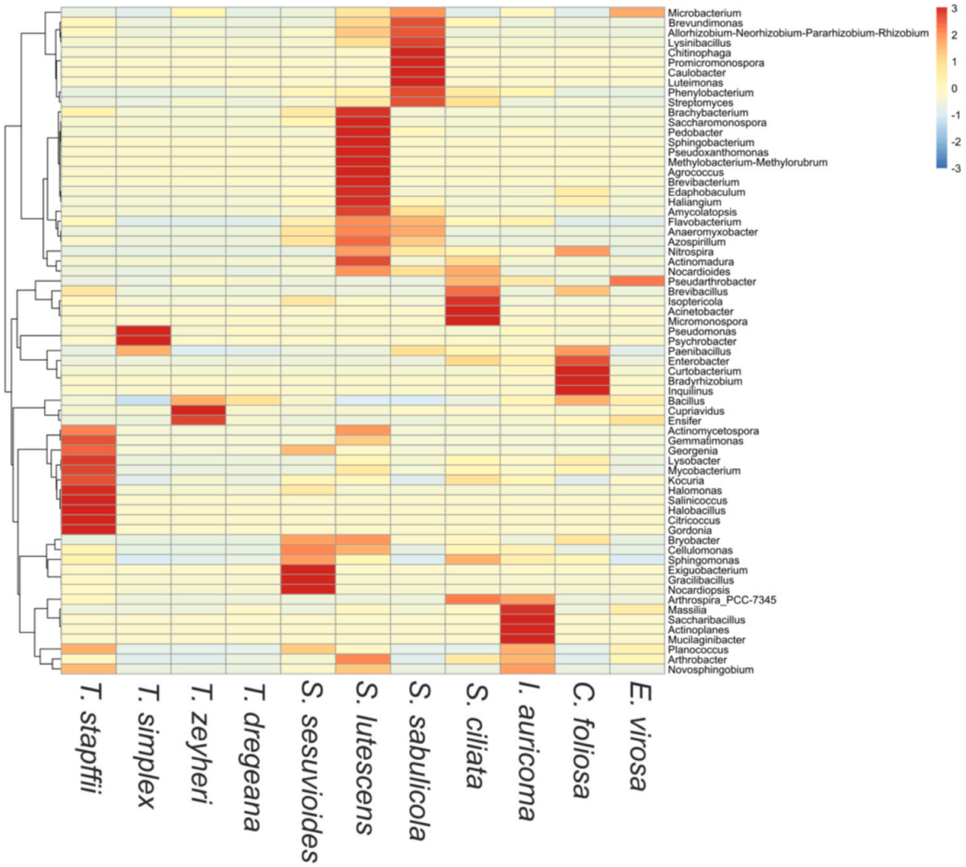

**Fig. 8.** Relative abundance of differentially abundant PGPB genera in the rhizosphere samples of each of the studied plant species. Samples clustered by plant species groups. The heat maps represent known shared and plant-specific PGPB genera present in at least half of the samples analysed of each plant. Each row scale shows the differential abundance of each identified PGPB taxon across the plant species. The scale indicates low (blue), medium (yellow), and high relative abundance (red).

carbon sources and other compounds such as vitamin B6, D-galacturonate, coumarins, polyamines and a range of antimicrobials (Table S6). Linear discriminant analysis (LDA) was used to compare the abundant functional pathways between these two communities. Based on the PICRUSt2 pathway abundance data, 18 pathways were abundant in the rhizosphere soils at the set cut-off value (Fig. 9A). The biosynthesis of the antibiotics carbapenem carboxylate erythromycin, megalomicin A and tylosin were the most abundant pathways associated with the rhizosphere samples (Table S6).

The Kruskal-Wallis rank sum test was used to investigate the influence of plant species on the PICRUSt2-predicted pathways (Fig. 9B). A total of 113 pathways were identified as being differentially represented across the rhizosphere communities of different plant species (Table S7). The plant species with the highest number of differentially abundant pathways were *T. stapffii* (30 pathways), *T. simplex* (15 pathways) and *S. sabulicola* (15 pathways). In contrast, the species with the fewest differentially abundant pathways were *T. zeyheri* (5 pathways), *I. auricoma* (4 pathways) and *T. dregeana* (2 pathways).

Of the 113 pathways, 87 (76 %) exhibited a very strong influence by plant species (eta squared value $>0.5$), excluding pathways correlated with the rhizosphere of *T. dregeana*. Specifically, tetrahydromethanopterin biosynthesis was strongly correlated with the rhizosphere microbiome of *T. stapffii*, while the rhizosphere of *T. simplex* was strongly enriched in nitrate reduction I (denitrification). Other functional pathways strongly correlated with the rhizosphere microbiomes of the remaining eight plant species included ectoine biosynthesis, mannosylglycerate biosynthesis I mycolyl-arabinogalactan-peptidoglycan complex biosynthesis, peptidoglycan biosynthesis V, mycothiol biosynthesis, the superpathway of lipopolysaccharide biosynthesis and the superpathway of polyamine biosynthesis II.

## 4. Discussion

Microbial communities are considered to be important drivers of desert ecosystem functions. For desert plants, these microbial communities form an essential component of their survival mechanisms (Eida et al., 2018; Liu et al., 2013; Marasco et al., 2018). Rhizosphere microorganisms can augment the plant genome via a plethora of functions that support plant growth and health (Huang et al., 2015; Contreras et al., 2023). It is widely assumed that the rhizosphere bacterial microbiome is an enriched subset of taxa derived from the local soil microbial community, formed through processes stimulated by the chemotactic influence of plant root exudates (Korenblum et al., 2022; Chen et al., 2023; Chen and Liu, 2024).

Here, we investigated the bacterial root microbiomes of 11 plant species native to the Namib Desert. The data obtained clearly demonstrate that bacterial richness and diversity in the plant rhizospheres investigated differed from those of the respective local control soils, while also being influenced by sampling location and plant species. This was particularly the case for the plant species sampled in the gravel plains, *C. foliosa*, *E. virosa*, *I. auricoma*, *T. dregeana*, *T. zeyheri* and *T. simplex* (Fig. 2). The bacterial communities present in the control soils were more heterogeneous than those of the rhizospheres, supporting the suggestion that selective recruitment is likely to occur in the vicinity of the plant roots (Liu et al., 2021; Zhao et al., 2021). Given that the bacterial communities in control soils from different locations differed significantly (Supplementary Figure S1B), our data support the hypothesis that the rhizosphere communities of different plant species are, at least in part, a function of the microbial diversity in the immediately surrounding soils. Consistent with this observation, Marasco et al. (2018), in a study of Namib Desert dune soils, reported that 64 % of Namib Desert dune speargrass rhizosheath-associated bacterial taxa originated from the adjacent non-rhizosphere mineral soils.

The 11 rhizosphere soils examined exhibited a range of bacterial species richness and diversity values. We suggest that this is consistent with a mechanism by which exudate compositions from different plant species drive distinct recruitment processes. Exudates such as organic acids, amino acids, sugars, fatty acids, phytochemicals and phytoalexins are known to recruit members of the dominant phyla found in rhizosphere soils, resulting in a positive impact on plant stress response and growth (Korenblum et al., 2022; Afridi et al., 2024). Several previous studies (Johnston-Monje et al., 2016; Mapelli et al., 2018; Marasco et al., 2018; Mosqueira et al., 2019; Siddharthan et al., 2022; Maurice et al., 2024) have provided evidence in support of this hypothesis. Furthermore, the variation in alpha-diversity observed between the rhizospheres of different plant species and the surrounding soils (Fig. 2C) suggests that this recruitment process is not consistent across plant species, with the *Stipagrostis* grasses and *T. stapffii* displaying less stringent recruitment than the other plant species (Fitzpatrick et al., 2018). The PCoA clusters of the rhizosphere bacterial communities (Fig. 3B) showed these less stringent recruiters grouped together. One cluster comprised of the more flexible recruiters T. *stapffii, S. sesuvioides* and the *Stipagrostis* grasses, whose bacterial microbiomes were more comparable with those of their control soils, while the other plant species cluster included the more stringent recruiters, with fewer associated bacterial taxa, both in numbers and diversity. Notably, the rhizosphere of the herb *T. simplex* had very low bacterial species richness and diversity. This species may have a highly selective recruitment system in the Namib Desert gravel plains environment, contrasting with an observation made in the same species in Cholistan (Pakistan) and Saudi Arabian desert soils (Eida et al., 2018; Mukhtar et al., 2021).

Proteobacteria was the most dominant phylum in the rhizosphere soils followed by Actinobacteriota and Firmicutes (Table S2, Fig. 5A). Proteobacteria and Actinobacteriota are generally the dominant rhizosphere colonizers and part of the persistently active microbial fraction in Namib Desert soils (León-Sobrino et al., 2019). This distribution was also observed in rhizosphere samples from the Atacama Desert, the Gurbantünggüt Desert, an arid reserve at its western boundary, and the Cholistan and Gobi Deserts (Fuentes et al., 2020; Mukhtar et al., 2021; Li et al., 2022; Contreras et al., 2023; Wu et al., 2023; Yang et al., 2023; Castro-Severyn et al., 2024). Their abundance has been suggested to be due to a combination of edaphic parameters, plant host–derived factors and adaptation to saline, UV radiation, nutrient cycling and plant growth in arid environments (Mukhtar et al., 2021; Yang et al., 2023). *Streptomyces*, dominant in the rhizospheres of *S. sabulicola* and *S. lutescens*, is a major genus of Actinobacteriota, with well-documented drought-tolerance and antifungal capabilities (Abdelmoteleb et al., 2020; Warrad et al., 2020). Bacteria with a capacity for biocontrol activity have been reported to be more abundant in the rhizosphere than in soils (Mukhtar et al., 2021). In our study, putative pathway analyses suggested a particularly high level of inter-species competition in the rhizosphere (Tables S6 and S7), consistent with recent suggestions that the plant rhizosheath–root niche is a "mini-oasis" of intense microbial competition (Marasco et al., 2022). Representatives of *Bacillus*, which are well-known PGPB taxa (Wang et al., 2012; Timmusk et al., 2014; Hashem et al., 2019) were common in the rhizospheres of all 11 plant species examined in this study. Highly abundant PGPB, *Haliangium, Bryobacter* and *Bacillus,* which form part of the core microbiome in the rhizosphere of Atacama Desert plants, were among the 67 PGPs identified in this study (Contreras et al., 2023). Genera identified in the rhizosphere soils (Table S3) included other known PGPB taxa (Table S5), such as *Rhizobium* and *Paenibacillus* (Alkahtani et al., 2020) and *Planococcus* (Kaplan et al., 2013), as well as the desert-adapted *Microvirga* (Veyisoglu et al., 2016; Sathiyaraj et al., 2018). *Bacillus*, *Paenibacillus* and *Rhizobium* are known to confer drought tolerance properties to their host plants (Vardharajula et al., 2011; Gontia-Mishra et al., 2016; Vurukonda et al., 2016; Liu et al., 2020; Chieb and Gachomo, 2023).

Plant species from location D (Table S1) had a high abundance of salt tolerant PGPB representatives (Fig. 8). Salt stress induces significant osmotic stress and previous research has demonstrated that fluctuating salt levels are a significant determinant factor for bacterial communities in the gravel plains of the Namib (Stomeo et al., 2013). Rhizosphere

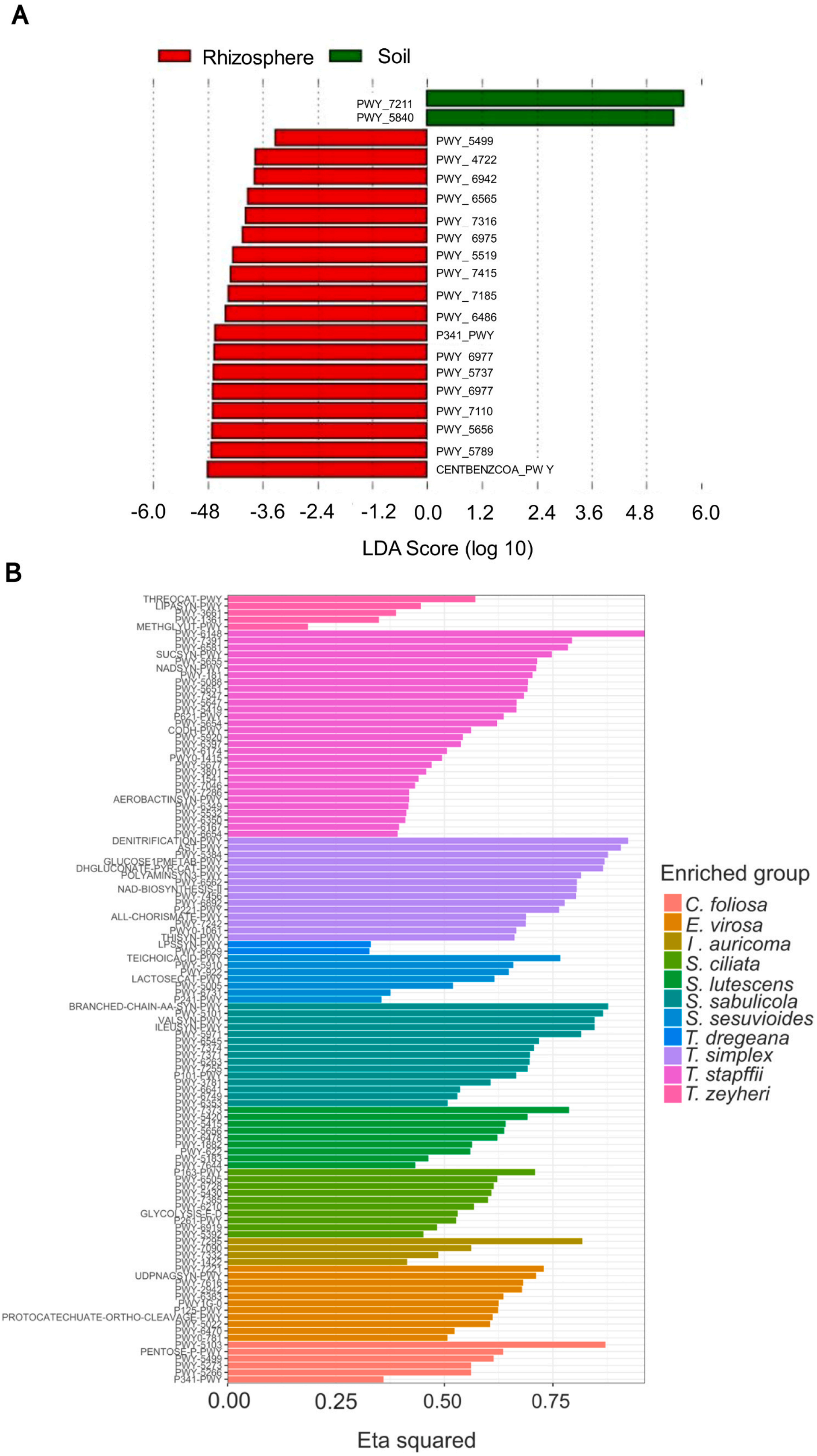

**Fig. 9.** Functional pathways predicted in the rhizosphere and control soil bacterial communities. The linear discriminant analysis plot (A) shows the PICRUSt2 predicted functional pathways in 50 % of the rhizosphere or control soils, with ($\log_{10}$) transformed LDA scores for rhizosphere (red) and control (green) soil communities. The effect size plot (B) shows the most abundant PICRUSt2 predicted functional pathways for each plant species.

samples from the other locations, including the gravel plain sites A and B (Table S1), showed a range of PGPB genera known for their abilities to form symbiotic relationships with plants, fix nitrogen, degrade organic compounds and produce bioactive compounds (Table S5).

The presence of certain genera in desert plant rhizosphere communities is consistent with their potential involvement in plant resilience to the challenging environmental conditions of the Namib Desert. We identified a range of bacterial genera unique to each plant species that may offer specific functions and resilience to their hosts (Fig. 7). For instance, the genus *Bradyrhizobium*, which was associated with *C. foliosa* samples in this study, has been associated with nodule mass and salt stress tolerance (Jenkins, 2003; Lester et al., 2007; Msaddak et al., 2017). *Halobacillus* and *Nitrococcus*, associated with T. *stapffii* samples, are genera with recognised salt-tolerance adaptations (Guesmi et al., 2013). The latter are also key ammonia oxidisers (Guesmi et al., 2013; Sun et al., 2022, Sun et al., 2023). *Fictibacillus* has been linked with nitrogen turnover and phosphate solubilization processes (Guo et al., 2020). *Methylobacterium* may be beneficial to *S. lutescens* as a phytobiosymbiont that produces the phytohormone cytokinin, which is important in seed germination and growth (Kumar et al., 2016). The transfer of key traits through desert plant rhizospheric microbiomes thriving under such polyextreme conditions shows great potential (Castro-Severyn et al., 2024).

A visual representation of the pairwise correlation heatmap obtained using ASV abundance data of the rhizosphere samples from the 11 plant species (Figure S2) showed 18 strongly positive correlation scores. Exploration of co-occurrence relationships is considered to be a useful indicator of functional potential, since co-occurring species pairs may share ecological characteristics (Williams et al., 2014). However, we acknowledge the limitations in exploring microbial co-occurrence relationships in a preliminary and relatively small-scale study such as this. Nonetheless, the use of Upset visualisation to show intersections among the 11 datasets of the plant species (Figs. 6, 7) highlighted the potential functional importance of certain microbial taxa. Amongst taxa identified here, polyamine biosynthesis has been linked to enhanced plant tolerance to drought, heavy metal contamination, salinity, and low and high temperature stresses in cold and hot desert ecosystems (Zhou et al., 2016; Li et al., 2022). The osmotic stress and water retention response pathways such as ectoine biosynthesis and mannosylglycerate biosynthesis I which were strongly correlated with speargrasses *S. sabulicola* and *S. lutescens* rhizosphere soils (Table S7) could potentially benefit the species by increasing their resilience to drought in the arid environment (Richter et al., 2019; Becker and Wittmann, 2020). Pathways related to antimicrobial activity and plant-microbe interactions such as peptidoglycan biosynthesis V and superpathway of polyamine biosynthesis II, were over-represented in the microbiomes associated with *T. stapffii*, *E. virosa*, *T. dregeana*, and *T. simplex*, which could be due to the over-representation of Actinobacteriota in the rhizospheres of these species. Jalal et al. (2022) have previously highlighted an association between the prevalence of Actinobacteriota and the above-mentioned functions, highlighting the significance of this phylum in desert soil microbial communities. The same study also established a correlation between Proteobacteria and stress resilience through the production of polyamines (Jalal et al., 2022), which correlates with the data from this study showing an over-representation of the polyamine biosynthesis pathways in the rhizosphere of species that had a high abundance of Proteobacteria.

The rhizosphere microbiome of *T. simplex*, despite having a low species diversity, was one of the top three microbiomes with the highest number of over-represented pathways. This further supports the hypothesis that *T. simplex* exhibits a stringent selective capacity that may be specifically tailored to suit the needs of the plant. Of note is the nitrate reduction pathway, which exhibited the highest significant correlation which the rhizosphere of *T. simplex, but* remains understudied in desert environments (Ramond et al., 2022). Several of the pathways over-represented to specific plant species are predicted to enhance nutrient metabolism, defence, stress tolerance and plant-microbe interactions, all of which contribute to plant health and growth in the Namib Desert (Vejan et al., 2016; Alsharif et al., 2020). For example, tetrahydromethanopterin, an important coenzyme in methanogenesis, plays a key role in carbon cycling, while nitrate reduction aids nitrogen cycling, both improving soil conditions for plant growth. These processes, in turn, enhance the plant's ability to respond to drought and high temperatures (Mashhadi, 2010; Ramond et al., 2022). Overall, the varied functional pathways associated with the rhizosphere microbes of the 11 plant species emphasize their potential benefits to the plants, particularly in relation to drought, pathogen stress, and plant-microbe interactions. However, we acknowledge that the use of PICRUST2, which is based on functional interpretations from known genomes, may overestimate or underestimate the functional diversity of specialised environments, such as hyper-arid desert soils, and therefore should be interpreted with caution.

The findings of this study emphasise the potential importance of research into desert microflora as sources of PGPBs to ameliorate soils for diverse plant benefits. The functional pathways identified here align with the assumed physiological needs of desert-adapted plants, suggesting that Namib Desert plant rhizospheric microbiomes play important roles in adaptation to the challenges presented by water scarcity, other environmental stressors and pathogens. Moreover, while this study revealed 67 known PGPB genera and highlighted certain plant species as viable sources of these, of the 393 rhizosphere-associated ASVs identified at generic level, 254 are either currently unknown or uncultured. These findings further emphasise the currently limited knowledge of the functional potential of desert plant rhizosphere bacteria.

## CRediT authorship contribution statement

**Maggs-Kölling Gillian:** Writing – review & editing, Resources, Investigation. **Cowan Don A:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Lebre Pedro H:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Gokul Jarishma K:** Writing – review & editing, Validation, Supervision, Investigation, Formal analysis, Conceptualization. **Convey Peter:** Writing – review & editing, Supervision. **Marais Eugene:** Resources, Investigation. **Maphosa Silindile:** Writing – original draft, Visualization, Validation, Methodology, Formal analysis. **Steyn Mégan:** Methodology, Investigation, Formal analysis.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.micres.2025.128076.

## Data availability

We have submitted the raw sequences to a public repository and attached the link at the attach file step.

The rhizosphere bacterial communities of Namib desert plant species (BioProject-NCBI)

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