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Microbial diversity and functional potential of arid and semi-arid soils in Algeria: A metagenomic approach

Meriem Guellout [a], Hani Belhadj [b], Atef Jaouani [a], Byong-Hun Jeon [c,*], Hyun-Jo Ahn [c], Mohammad Raish [d], Yacine Benguerba [e,*]

[a] Faculty of Sciences of Tunis, Institut Supérieur des Sciences Biologiques Appliquées de Tunis, University of Tunis El Manar, 9, Rue Zouhair Essafi, 1007 Tunis, Tunisia
[b] Laboratory of applied microbiology, natural and life sciences faculty, University Ferhat Abbas Sétif1, 19000 Setif, Algeria
[c] Department of Earth Resources and Environmental Engineering, Hanyang University, 222 Wangsimni-ro, Seongdong-gu, Seoul 04763, Republic of Korea
[d] Department of Pharmaceutics, College of Pharmacy, King Saud University, P.O. Box 2457, Riyadh 11451, Saudi Arabia
[e] Laboratoire de Biopharmacie et Pharmacotechnie, Faculty of Medicine, Ferhat ABBAS University, Sétif 1, Sétif, 19000, Algeria

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ABSTRACT

Despite covering over 40% of Earth's land area, the microbial diversity and adaptive mechanisms of arid and semi-arid regions remain poorly understood. This gap is notable in Algeria, where prior studies focused on limited ecological aspects and used varying sequencing depths, leaving regions like Djanet largely unexplored. This research targets these environments, specifically Setif and Djanet, to investigate microbial community structures and functions in these tough conditions. Soil samples were analyzed for physicochemical properties, including pH, electrical conductivity, and elemental composition, using standard methods. Bacterial diversity and adaptation traits were examined through 16S rRNA gene amplicon sequencing (Illumina MiSeq V3–V4), revealing a detailed microbial profile. Significant differences ($p < 0.05$) appeared in calcium carbonate, organic matter, and calcium ions across sites. The sequencing yielded 255,206 quality reads, identifying 27 phyla, 71 classes, 151 orders, 205 families, 353 genera, and 7409 species. Actinobacteria and Chloroflexi were dominant, with Acidimicrobiota and Thermobilia also present. An unclassified Actinobacteria family (AKIW781, 15.2%) was most common in RM2 (Tassili Djanet) and RM3 (Forest Elouricia), while Nocardioides was prevalent in RM1 (Oasis Djanet, at 5.35%). Unique genera such as Skermanella and Agromyces appeared in RM1, whereas Bacillus was restricted to RM2. Alpha diversity was highest in RM1 and lower in RM2 and RM3. Overall, the study highlights significant variations in microbial diversity, gene potential, and soil properties among the sites. β-diversity analysis showed distinct microbial communities, with RM1 having a unique composition compared to RM2 and RM3. Functional prediction tools such as PICRUSt and KEGG pathways indicated that, in these arid zones, microbial metabolic pathways favored antioxidant production and osmotic regulation, both vital for survival in extreme conditions. Notably, functional shifts along the arid gradient revealed that RM1 possesses unique adaptive traits supporting the desert–oasis transition. This research provides essential data for bio-prospecting microbial resources in Algeria's arid zones and enhances understanding of microbial adaptation in extreme environments.

1. Introduction

A significant portion of the Earth's surface consists of arid, semi-arid, and hyper-arid regions, where life is shaped by extreme environmental pressures, including water scarcity, high solar radiation, temperature fluctuations, and nutrient-limited soils (Alsharif et al., 2020). These conditions create unique ecosystems where microbial communities play vital roles in maintaining ecological balance, supporting nutrient cycling, soil fertility, and climate regulation (Wardle, 2006; Delgado-Baquerizo et al., 2020). Despite their ecological importance, desert microbiomes remain among the least explored microbial ecosystems, leaving vast potential for scientific and biotechnological discoveries (Banerjee & van der Heijden, 2023).

Algeria, the largest country in Africa, encompasses diverse climatic zones ranging from the Mediterranean coast to the semi-arid highlands and the extreme aridity of the Sahara Desert. Based on the aridity index

* Corresponding authors.
E-mail addresses: bhjeon@hanyang.ac.kr (B.-H. Jeon), benguerbayacine@yahoo.fr (Y. Benguerba).

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(AI), >80% of Algeria's landmass is classified as arid or hyper-arid, with semi-arid regions covering about 20% (Bona et al., 2021). These extreme environments host highly specialized microbial communities adapted to harsh conditions, yet their diversity, ecological functions, and adaptive mechanisms remain poorly characterized. Investigating these microbial ecosystems is essential not only for understanding ecosystem resilience and biogeochemical cycling but also for potential applications in biotechnology, agriculture, and environmental sustainability (Dong et al., 2024). Recent advances in metagenomics and high-throughput 16S rRNA gene sequencing have revolutionized microbial ecology research, enabling comprehensive analyses of microbial community composition, diversity, and metabolic potential in extreme environments (Li et al., 2023). Studies conducted in major desert ecosystems—including the Atacama (Miralles et al., 2020), Namib (Vásquez-Dean et al., 2020), Negev (Frossard et al., 2022), and Gurbantunggut Deserts (Zhang et al., 2020)—have revealed unique bacterial taxa and biosynthetic gene clusters that reflect microbial adaptation to severe desiccation, salinity, and temperature stress. These studies have also highlighted functional pathways linked to oxidative stress, osmotic regulation, and nutrient uptake, which are crucial for microbial survival in nutrient-poor soils (Crits-Christoph et al., 2023).In North Africa, research on desert microbiomes has only recently gained attention. Studies from Tunisian oases (Ben Fekih et al., 2021), Egyptian desert soils (Abdelfattah et al., 2022), and Moroccan arid zones (Ezzahra et al., 2023) have provided new insights into microbial diversity and metabolic potential across aridity gradients. However, Algerian desert microbiomes remain largely underexplored, with only a few reports addressing microbial diversity in Saharan or steppe environments (Khemili et al., 2020; Bouanane et al., 2021). Most prior research in Algeria has focused on isolated soil types or used limited sequencing depth, overlooking microbial responses along desert–oasis transition zones, which represent ecologically dynamic interfaces between extreme aridity and localized vegetation.

This study aims to fill this gap by characterizing soil bacterial diversity and metabolic potential across three distinct sites in Algeria: Oasis Djanet (RM1), Tassili Djanet (RM2), and Forest Elouricia (RM3). These sites were selected for their contrasting environmental conditions, spanning the hyper-arid Sahara to semi-arid vegetated zones. Using Illumina MiSeq-based 16S rRNA gene sequencing, we analyzed bacterial taxonomic composition, diversity indices, and predictive functional profiles. We examined the influence of key soil physicochemical parameters (e.g., calcium carbonate, organic matter, and ion concentrations) on community structure. We hypothesize that microbial diversity and functional potential vary significantly across the three sites, driven primarily by differences in environmental conditions and soil physicochemical properties. By investigating these microbial ecosystems, this study enhances understanding of microbial diversity in Algeria's arid and semi-arid regions. It provides novel insights into microbial adaptation and functional specialization along desert–oasis gradients.

2. Materials and methods

2.1. Site selection and sampling

For this study, three distinct sampling sites were selected based on their underexplored microbial biodiversity and extreme climatic conditions. These sites represent different environmental settings within arid and semi-arid regions of Algeria (Fig. 1):

Oasis Djanet (RM1), Tassili Djanet (RM2), and Forest Elouricia (RM3) to represent a clear moisture–aridity gradient ranging from hyper-arid desert to semi-arid woodland environments. This gradient-based selection enables the assessment of how environmental factors such as aridity, vegetation cover, and soil composition influence microbial community diversity and functional potential. Oasis Djanet (RM1) Located in the eastern region of Djanet, this site represents an artificial oasis ecosystem influenced by palm vegetation and periodic

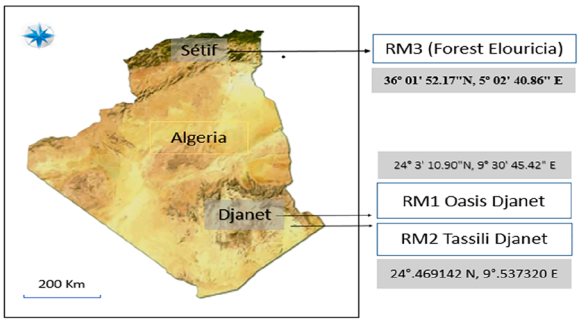

Fig. 1. Geographic chart of sampling three regions in Algeria (Setif and Djanet). Sampling site East of Djanet RM1 Oasis Djanet; sampling site West of Djanet RM2 Tassili Djanet; and sampling site at Setif Forest Elouricia RM3.

irrigation. The area experiences extreme temperature fluctuations, with daytime temperatures reaching 38 °C and relative humidity around 26%. Soil properties are affected by limited water availability and organic inputs from decomposing plant matter. Sampling was conducted on 1 May 2021, across an area of approximately 20 km^2. Tassili Djanet (RM2) is situated in the western region of Djanet. This site reflects natural hyper-arid desert conditions, characterized by intense solar radiation, minimal vegetation, and high surface temperatures (41 °C) with 20% relative humidity. Sampling occurred on 5 May 2021, covering an area of 20 km^2, representing the driest end of the aridity gradient studied.

Forest Elouricia (RM3) Located in the semi-arid region of Setif, this site provides a strong contrast to the Djanet locations. It features forested terrain with greater vegetation density and moderate climatic conditions (30 °C and 45% relative humidity). Sampling was conducted on 27 May 2021 within a 6 km^2 area, which served as the humid reference point along the gradient.

At each site, nine soil samples were collected using sterile glass Falcon tubes and a sterile spatula, with three samples per station. These were combined to form composite samples, ensuring a representative capture of local microbial diversity. All samples were collected following standardized aseptic and environmental sampling protocols. Together, these three sites form a progressive aridity–moisture gradient, enabling the evaluation of how environmental stress, vegetation cover, and soil physicochemical conditions shape microbial community composition and functional adaptation across Algeria's desert and semi-arid landscapes. Soil sampling was conducted following standardized protocols to ensure both representativeness and reproducibility. To prevent surface contamination, the top 5 cm of soil was carefully removed using a sterile spatula. Subsequently, samples were collected from depths of 5–20 cm at three distinct points arranged in a triangular configuration, with approximately 1 m between each point. At each of the three sampling points per site, approximately 500 g of soil was collected using sterile stainless-steel spatulas. The three subsamples were then thoroughly homogenized to form a composite sample (total ~1.5 kg per site), ensuring an integrated representation of the local microhabitat. In total, nine composite samples (three per site) were obtained across the study. Samples intended for physicochemical characterization were stored in sterile tubes and wrapped in sterile paper bags. At the same time, those designated for microbial diversity assessment were preserved in centrifuge tubes and stored in a liquid nitrogen tank to maintain DNA integrity. This rigorous sampling approach ensured a reliable representation of both microbial communities and soil physicochemical properties while minimizing the risk of external contamination.

2.2. Soil physicochemical analyses

Before analysis, soil samples were air-dried, fine-ground, and sieved

through a 2 mm mesh to achieve homogeneity. The assessment of physicochemical properties was conducted according to established procedures. The moisture content was determined gravimetrically by drying subsamples at 105 °C until a constant weight was achieved. Soil pH and electrical conductivity (EC) were measured in a 1:2.5 soil-to-water suspension using a glass-electrode pH meter and a conductivity meter, serving as indicators of acidity and salinity, respectively. Soil organic carbon (SOC) was measured using the modified Walkley and Black wet oxidation technique. The cation exchange capacity (CEC) was determined by summing the exchangeable Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+}, which were extracted using a mechanical vacuum system. Individual cation concentrations were measured using atomic absorption spectrophotometry. Grain-size analysis was performed following ASTM D422 (sieving) and ASTM D7928 (hydrometer method) to determine the sand, silt, and clay fractions. Soil texture was classified using the USDA system, resulting in texture classes for each sample (Smith & Jones, 2020). These analyses provide a thorough assessment of soil fertility, structural characteristics, and granular composition.

2.3. Microbial DNA extraction, sequencing

Following the manufacturer's instructions, 0.25 g of soil was used to extract genomic DNA with the DNeasy® PowerSoil® Kit (Qiagen, Milan, Italy). The DNA was then quantified using a fluorometric approach in line with the Qubit® 4.0 Fluorimeter methodology. The Microbiota Solution B kit (hypervariable regions V3-V6) from Arrow Diagnostics srl. (Genoa, Italy) was used to create the bacterial 16S DNA libraries. A 500-cycle MS-103–1003-MiSeq Reagent Nano Kit v2 (Illumina Inc.) was used to process the amplicon pool, with Phix as the internal standard. Barcoding and particular primers were used to amplify the 16S rRNA and 18S rRNA genes from different locations (16SV4, 16SV3, 16SV3-V4, 16SV4-V5, 18SV4, 18SV9). For example, 16SV4: 515F-806R, 18SV4: 528F-706R, and 18SV9: 1380F-1510R. Twenty-five microliters of Phusion® High-Fidelity PCR Master Mix from New England Biolabs, two micromilligrams of forward and reverse primers, and around ten nanograms of template DNA were used to carry out the PCR reactions. One minute of denaturation at 98 °C, followed by 30 cycles of denaturation at 98 °C, annealing at 50 °C, and elongation at 72 °C, ending with a final 5 min of elongation at 72 °C, was the thermal cycling procedure. The PCR products were purified using magnetic beads. The concentration of the PCR products dictated the equidensity ratios of the samples. After thorough mixing, the target bands were extracted, and the PCR products were identified.

To enable sample multiplexing, sequencing libraries were built using separate index adapters. Before using real-time PCR for precise quantification, the library's concentration and quality were assessed with Qubit fluorometric quantification. Using a Bioanalyzer, the distribution of fragment sizes was evaluated. Based on the necessary effective library concentration and sequencing depth, quantified libraries were combined in equimolar concentrations and sequenced on Illumina platforms. Before cutting the barcode and primer sequences, paired-end reads were demultiplexed using unique barcodes. To create high-quality consensus sequences, overlapping paired-end reads were merged using FLASH (Fast Length Adjustment of Short reads, v1.2.11; Magoc & Salzberg, 2011).

2.4. Bioinformatics analysis

2.4.1. Paired-end reads assembly and quality control

High-throughput sequence data underwent rigorous quality control and bioinformatic processing to ensure accuracy and reliability. Raw sequencing tags were filtered with fastp (v0.23.1) to remove low-quality reads and adapters, yielding high-quality, clean tags (Bokulich et al., 2012). Chimera detection was performed by aligning tags against reference databases—SILVA (for 16S/18S rRNA; https://www.arb-silva.de) and UNITE (for ITS; https://unite.ut.ee)—using the vsearch tool (v2.16.0; Edgar et al., 2011). Chimeric sequences were removed to yield effective tags for downstream analysis. Denoising and Amplicon Sequence Variant (ASV) Inference were conducted using the DADA2 and deblur modules within QIIME2 (release 2022.2), enabling the generation of high-resolution ASVs. Taxonomic assignment was then performed in QIIME2 using the SILVA database for 16S/18S rRNA gene sequences, UNITE for fungal ITS regions, and Micro_NT (a curated subset of the NCBI NT database encompassing archaea, fungi, viruses, and bacteria) for unclassified or mixed areas. Phylogenetic analysis was conducted to assess evolutionary relationships among ASVs and identify dominant taxa across samples. Multiple sequence alignments were performed within QIIME2, and abundance data from the top 35 taxa at each taxonomic rank were visualized via heatmaps using the pheatmap package in R. Furthermore, ternary plots illustrating the distribution of the top 10 taxa across three samples were generated using the vcd package in R, providing a comparative overview of taxonomic composition and differential abundance.

2.4.2. Alpha diversity

Alpha diversity within microbial communities was assessed using seven well-established indices implemented in QIIME2 to evaluate species richness, diversity, evenness, and sequencing depth. Community richness was quantified using three indices: *Observed_OTUs*, which reflects the count of distinct taxa present (skbio.observed_otus); *Chao1*, a non-parametric estimator that accounts for rare species to predict total species richness (skbio.chao1); and *Dominance*, which measures the extent to which a community is dominated by a few abundant taxa (skbio.dominance). Community diversity was evaluated using the *Shannon* index, which incorporates both species abundance and evenness (skbio.shannon), and the *Simpson* index, which places greater weight on the most abundant taxa (skbio.simpson). To assess sequencing coverage, *Good's Coverage* was calculated to estimate the completeness of taxon sampling within each sample (skbio.goods_coverage). Finally, *Pielou's Evenness* index was used to determine the uniformity of species distribution within each community (skbio.pielou_e). In addition to QIIME2, the *vegan* package in R was used for complementary analyses of species richness and sample-size adequacy via rarefaction and ecological diversity measures.

2.4.3. Beta diversity

Differences in sample complexity and species composition were assessed using beta diversity analysis. QIIME2 was used to calculate weighted and unweighted UniFrac distances. To show variations in community structure and UniFrac distances across samples, a heatmap was created. We used Perl to create this graphic.

2.4.3.1. Unweighted pair-group method with arithmetic mean (UPGMA). A cluster tree was constructed utilizing UPGMA (Unweighted Pair Group Method with Arithmetic Mean) based on the weighted UniFrac distance matrix. The UPGMA dendrogram was produced using the upgma.tre function within QIIME2.

2.4.3.2. Cluster analysis. To reduce the dimensionality of the initial variables, we used the R packages ade4 and ggplot2 to perform Principal Component Analysis (PCA) before cluster analysis (V4.0.3). Deriving primary coordinates and facilitating the presentation of complicated, multidimensional data were the goals of Principal Coordinate Analysis (PCoA). The process began by computing a distance matrix using weighted or unweighted UniFrac distances between samples, which were then transformed into a new set of orthogonal axes. The first primary coordinate accounts for most of the variation. Each successive principal coordinate captures progressively less variation, with the second-highest variance represented by the second-most important coordinate. The ade4 and ggplot2 R tools were used to visualize the Principal Coordinates Analysis (PCoA) (Version 4.0.3). The data

dimension was further reduced using non-metric multidimensional scaling (NMDS). Unlike PCoA, NMDS uses a distance matrix and emphasizes the rank order of distances rather than their numerical values. Therefore, rather than providing exact distance measurements, the lengths shown in the diagram between the sample locations reflect their ranks. The NMDS analysis was carried out using the R packages ade4 and ggplot2.

2.4.4. Community difference analysis

Statistical analyses, including ANOSIM, Adonis, Multi-response Permutation Procedure (MRPP), SIMPER, T-test, MetagenomeSeq, and LEfSe, were conducted to elucidate the differentiation in community structure. ANOSIM, Adonis, and MRPP are non-parametric methods used to assess differences among groups in high-dimensional datasets. These tests assess whether the differences between groups are significantly larger than those within groups, thereby aiding in evaluating the meaningfulness of the grouping. The analyses were conducted utilizing the vegan and ggplot2 packages in R. SIMPER assesses the contribution of specific species to the differentiation among groups. The graph presents the top 10 species that contribute to differentiation. The analysis utilized the vegan and ggplot2 packages in R. MetagenomeSeq identifies species that display significant differences between groups. The analysis was conducted using the metagenomeSeq package in R. LEfSe (Linear discriminant analysis Effect Size) is frequently employed to identify biomarkers and investigate metagenomic features. The analysis utilized the Lefse package in R.

2.4.5. Function prediction

PICRUSt (V1.1.4) is an R package utilized for predicting metagenomic functions derived from marker genes. PICRUSt2 (V2.3.0) provides improved functionalities for enhanced functional prediction. Tax4Fun (V0.3.1) is an R package commonly used for analyzing intestinal and soil samples. It typically yields more precise results than PICRUSt, particularly when utilized for soil samples. BugBase is an effective tool for assessing the phenotypic traits of microbial communities. This classification categorizes microbial communities into seven distinct phenotypes: Gram-Positive, Gram-Negative, Biofilm-Forming, Pathogenic, Mobile Element-Containing, and Oxygen Utilization (including Aerobic).

2.4.5.1. Association analysis. Network diagrams in both 2D and 3D were developed to illustrate the symbiotic relationships among species and to analyze the impact of environmental factors on community structures. Subsequent analyses, including the Spearman rank correlation test, Canonical Correspondence Analysis (CCA), Redundancy Analysis (RDA), and distance-based redundancy analysis (dbRDA), were conducted to evaluate relationships between environmental factors and species abundance. All diagrams and studies were conducted utilizing R.

2.4.5.2. Statistical analysis. Linear discriminant analysis of effect size (LEfSe) was employed to identify significant differences among the sample communities. A p-value of <0.05 was deemed statistically significant. Spearman's rank correlation among soil bacterial communities was analyzed using the stats and ggplot2 packages in R, with a significance threshold of $p < 0.05$.

3. Results

3.1. Analysis of soil physical and chemical properties

These analyses provide critical insights into soil fertility, salinity, and chemical composition, helping to understand the relationship between microbial diversity and soil properties. The soil samples were weakly alkaline, with pH values of 8.04–8.6. The results revealed that total Na^+, K^+, Ca^{++}, Mg^{++}, Cl^-, and SO_4^- did not vary between the semi-arid and arid samples ($p > 0.05$). However, the maximum concentration of calcium carbonate was observed for the soil sample from RM3 Forest Elouricia (semi-arid). The other two arid samples from the deep south of Algeria, Djanet RM1 and RM2, contain less calcium carbonate. In addition, significant differences ($p < 0.05$) were observed for sand concentration, total organic matter, and relative humidity (Table 1).

These physicochemical gradients establish the environmental context to test whether differences in soil properties drive microbial diversity and functional variation across the sites.

3.2. Bacterial community composition

To gain a basic understanding of bacterial diversity in soil samples collected from different locations in Algeria, the taxonomic composition of RM1, RM2, and RM3 was initially investigated. To determine the bacterial composition in geotextile samples, Illumina HiSeq high-throughput sequencing was used to generate reads from the bacterial V3-V4 amplicon. Both the pre- and post-merging, quality-filtered raw read data for the samples are presented in Table 2.

An average of 190,650 raw readings was recovered per sample. The overlapping sequence of the reads served as the basis for generating the paired-end reads (tags). Eligible pair-end reads (PE) were acquired after filtering out low-quality reads and removing barcodes, adaptors, primers, and chimera sequences. The total number of tags acquired from RM1, RM2, and RM3 was 62,377, 92,975, and 99,854, respectively. To determine the overall read1 and read2 counts in raw data files divided by barcode, four rows were used as the unit for raw PE. For combinations, we used the raw tags generated from the PE reads using the overlap method. To qualify for qualified tags, clean tags were extracted from raw tags using specific filtering parameters. After removing the Chimera sequences from Nochime, effective tags were taken. There are a total of 27,409 defined species spread throughout 71 classes, 151 orders, 205 families, 353 genera, and 205 sequences that are considered legitimate. The relative abundance plot of ASV at the orders, classes, families, genera, and species levels. See Fig. 2 for a breakdown of the three soil samples. The most prevalent bacterial classes, affiliated with the phyla *Actinobacteriota, Proteobacteria, Firmicutes, Bacteroidota, and Chloroflexota*, included *Bacilli, Acidimicrobiia, Chloroflexia, Thermoleophilia, Alphaproteobacteria*, TK10, *Gammaproteobacteria, Bacteroidia*, and *Rubrobacteria*.

At the class level, however, Actinobacteria were the dominant phylum (44.54%) in RM1 (Oasis soil). The most dominant sequenced phyla associated with the samples RM2 Tassili Djanet (35.11%) and RM3 Forest Elouricia (44.39%) were Chloroflexia, followed by Acidimicrobiota and Thermophilia (Fig. 2). At the bacterial family level, an

Table 1
Physico-chemical analyses of the three soil samples: RM1 (Oasis Djanet), RM2 (Tassili Djanet), and RM3 (Forest Elouricia).

Parameter	Oasis Djanet (RM1)	Tassili Djanet (RM2)	Forest Elouricia (RM3)
Sand	40.70 ± 17.89	55.35 ± 17.89	19.75 ± 17.89
Lim	28.62 ± 5.84	20.40 ± 5.84	31.70 ± 5.84
Clay	29.40 ± 5.69	19.80 ± 5.69	29.90 ± 5.69
pH	8.41 ± 0.28	8.60 ± 0.28	8.04 ± 0.28
Moisture (%)	5.40 ± 3.40	4.70 ± 3.40	10.90 ± 3.40
EC (ds/m)	10.30 ± 2.40	11.80 ± 2.40	7.10 ± 2.40
CEC (cmol/kg)	2.80 ± 0.30	3.10 ± 0.30	2.50 ± 0.30
$CaCO_3$ (%)	6.40 ± 8.73	4.20 ± 8.73	20.30 ± 8.73
OM (%)	5.30 ± 2.63	3.40 ± 2.63	8.60 ± 2.63
Na^+	55.40 ± 2.90	54.80 ± 2.90	60.10 ± 2.90
K^+	23.80 ± 1.39	24.00 ± 1.39	26.30 ± 1.39
Ca^{++}	39.40 ± 5.82	29.80 ± 5.82	40.30 ± 5.82
Mg^{++}	11.82 ± 2.25	9.22 ± 2.25	13.71 ± 2.25
Cl^-	50.21 ± 10.08	33.42 ± 10.08	51.47 ± 10.08
SO_4^-	35.80 ± 3.60	38.30 ± 3.60	31.20 ± 3.60
HCO_3^-	2.30 ± 0.15	2.10 ± 0.15	2.40 ± 0.15

Table 2
Raw read statistics and sequence quality assessment of the V3–V4 region of bacterial 16S ribosomal gene sequences from RM1 Oasis Djanet, RM2 Tassili Djanet, and RM3 Forest Elouricia.

Sample	RawPE	Combined	Qualified	Nochime	Base(nt)	Avglen(nt)	GC	Q20	Q30
RM1	160,585	159,654	157,351	62,377	23,323,906	373.92	57.89%	98.50%	94.96%
RM2	204,679	203,222	200,395	92,975	34,816,714	374.47	61.68%	98.44%	94.93%
RM3	206,696	204,611	202,106	99,854	37,347,347	374.02	62.73%	98.50%	95.12%

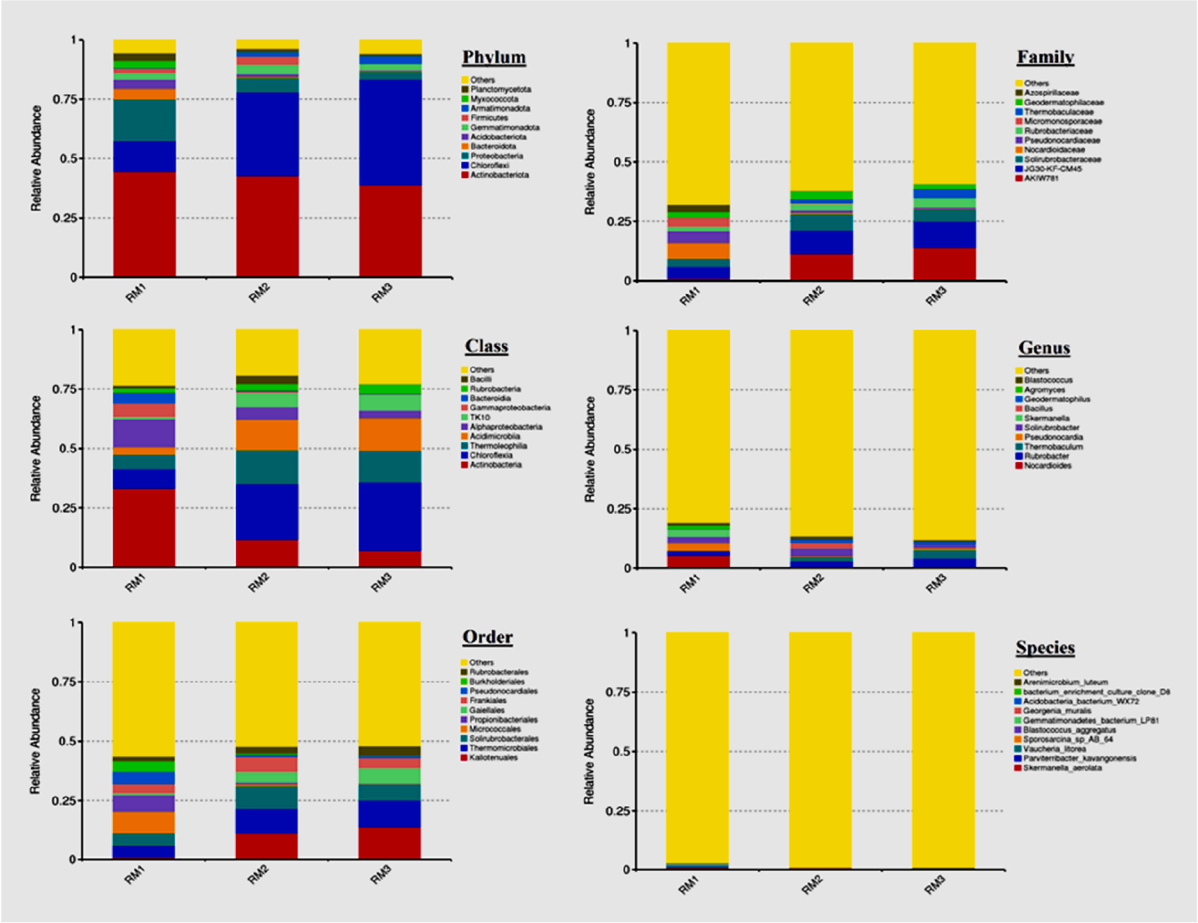

Fig. 2. Taxonomic composition and relative abundance of the most dominant bacterial phyla **(a)**, classes **(b)**, orders **(c)**, Families **(d)**, genera **(e)**, and species **(f)** of the three soil samples (RM1Oasis Djanet, RM2 Tassili Djanet, and RM3 Forest Elouricia).

unclassified family (AKIW781) affiliated with Actinobacteria was most abundant (15.2%) in the samples RM2 and RM3, followed by GJ30KFCM45 (6.34%). At the genus level, the Nocardioides (5.35%) are abundant in the RM1 Oasis Djanet soil sample. Furthermore, Rubrobacter and Thermobaculum showed relatively higher abundances in the soil samples RM2 Tassili Djanet and RM3 Forest Elouricia, followed by an array of other genera within the population (Fig. 2). Specific bacterial genera, such as Skermanella and Agromyces, were unique to RM1 Oasis Djanet. Also, *Bacillus* is exceptional for the RM2 Tassili Djanet sample. The soil sample RM1Oasis Djanet was more diverse at the genera level, whereas the samples RM2 and RM3 were less diverse.

To better understand the relationships among rumen bacteria at different stages of soil sample preparation, a phylogenetic tree was constructed from representative genomes of bacterial species (Fig. 3). When it comes to colonizing different soil types, we discovered that bacteria with many genetic similarities work together. Sporosarcina and Bacillus, for instance, are pretty related. It just so happens that at RM2 Tassili Djanet, their abundance is higher. Close relatives of Anaerolinae, CTCFX1, Herpetosiphon, FFCH7168, and Chloronema were abundant at RM1 (Fig. 3). There may be a situation in which bacteria with close relatives are more likely to be colonized; however, this theory needs more substantial evidence.

In addition, some species are widely distributed across all samples, including Rubrobacter, Solirubrobacter, Pseudonocardia, Blastococcus, and Microvirga. However, the soil sample provided from Ouasis harbors the majority of species, and actinobacteria represent the dominant group in this soil type (RM1 Oasis Djanet). These community shifts suggest that soil moisture and nutrient availability may strongly influence bacterial assemblages along the aridity gradient. These results confirm that soil bacterial communities vary markedly across the aridity–moisture gradient, supporting our hypothesis that soil physicochemical differences shape microbial structure.

3.3. *Alpha diversity*

Theoretical estimation (Chao1) indicates that sample RM2 Tassili Djanet has the highest theoretical richness with a value of 3144, followed by RM3 Forest Elouricia (2948) and RM1 Oasis Djanet (2144) (see

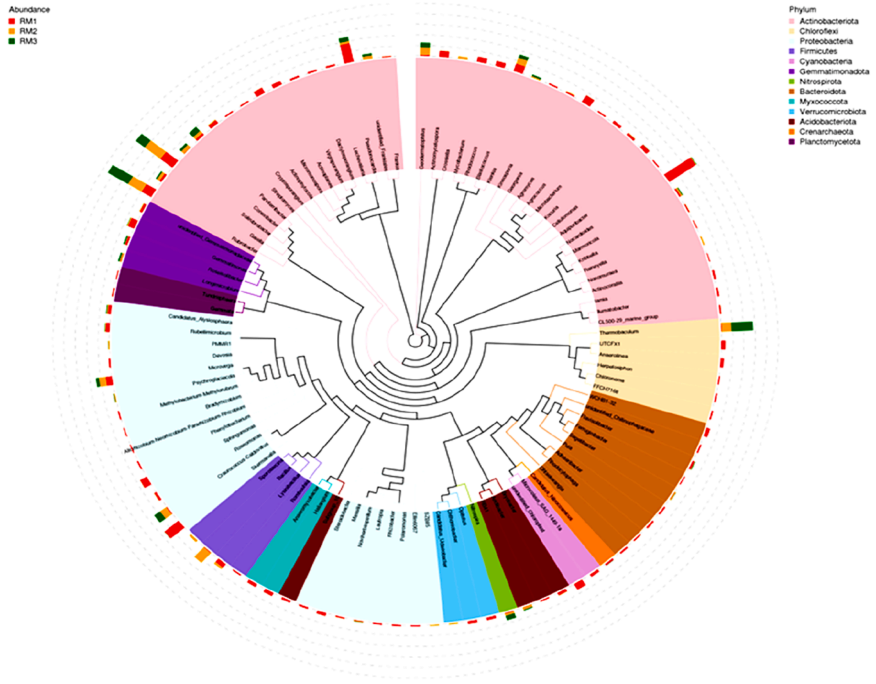

Fig. 3. Circular Phylogenetic Tree at the Genus Level with Relative Abundance Profiles. Each branch of the phylogenetic tree represents a distinct genus, with branch lengths corresponding to evolutionary distances. The outer histogram illustrates the relative abundance of genera across different sample groups. Circle colors denote taxonomic affiliation at the phylum level, allowing visual comparison of phylogenetic and compositional diversity.

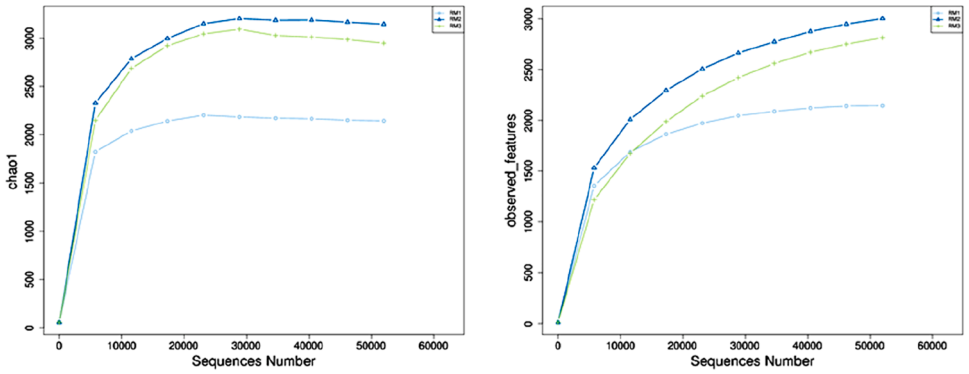

Fig. 4. Bacterial alpha diversity in soil samples based on rarefaction analysis: **(a)** Rarefaction curves depicting Chao1 diversity; **(b)** Rarefaction analysis based on observed OTUs.

Fig. 4). These estimates highlight a higher potential biodiversity for RM2 Tassili Djanet. Furthermore, the number of species detected follows a similar trend, with RM2 Tassili Djanet having the highest count (3002), followed by RM3 Foret Elouricia (2814) and RM1 Oasis Djanet (2144). These results suggest that RM2 Tassili Djanet is richer in species diversity, which could be linked to more favorable environmental conditions. In addition, Pielou's equitability index (Pielou_e) reveals that sample RM1Oasis Djanet displays the highest equitability (0.889), indicating a more uniform distribution of species. RM2 Tassili Djanet (0.867) and RM3 Frest Elouricia (0.812) show a slightly less homogeneous distribution. However, statistical analysis reveals a Low dominance value across all samples (< 0.01), indicating a lack of dominance by a single species or a small group of species. Thus, RM1Oasis Djanet presents a more balanced structure, with species better distributed than in the other samples. Also, the Shannon index indicates that sample RM2 Tassili Djanet presents the highest diversity (10.016), followed by RM1 Oasis Djanet (9.837) and RM3 Forest Elouricia (9.302).

This index reflects a slightly higher overall biodiversity in RM2 Tassili Djanet. The Simpson index strengthened these results. High values near 1 (0.996–0.998) indicate high diversity across all samples, reinforcing the Shannon index's observations. These results confirm that RM2 Tassili Djanet combines both richness and high diversity, while RM3 Oasis Djanet appears slightly less diverse. Regarding Good's Coverage, high proportions (>99%) in the three samples indicate exhaustive sampling of the diversity present. RM1 Oasis Djanet stands out for its perfect coverage (1000), which may reflect the optimal representativeness of its specific richness. In addition, there was sufficient sequencing data, as all samples had flat rarefaction curves. Differences in sample complexity and species composition were assessed using β-diversity analysis. QIIME2 was used to calculate both weighted and unweighted UniFrac distances to capture phylogenetic dissimilarities between microbial communities. To visualize variation in community structure across samples, we generated a heatmap of UniFrac distances using a custom Perl script. To statistically validate the separation of microbial communities, we performed three complementary analyses: ANOSIM (Analysis of Similarities) revealed a significant separation among groups ($R = 0.65$, $p = 0.001$), suggesting strong dissimilarity in community structure. PERMANOVA (Adonis test)

further confirmed this with an F-model value of 3.72 and a p-value of 0.001, indicating that group differences are statistically meaningful. PERMDISP (Permutational Analysis of Multivariate Dispersions) showed no significant differences in dispersion among groups (F = 0.84, p = 0.41), confirming that the β-diversity separation was not driven by within-group heterogeneity. Together, these results confirm that observed differences in microbial community composition reflect true biological variation rather than differences in dispersion or variance.

3.4. Differences in taxonomic composition between the three sampling sites

β-diversity was used to compare the similarity of microbial composition between sampling sites, and a Principal Coordinate Analysis (PCoA) was conducted. The three samples from different geographic locations were grouped based on Axis 1 and Axis 2 (Fig. 5).

According to Axis 1, the distance between the three groups was significant, indicating distinct differences in the microbial communities. As a result, the compositional variation was further analyzed at different taxonomic levels. The PCoA analyses were performed using both Bray-Curtis and weighted UniFrac distances (Fig. 5). The similarity distances revealed that RM1 Oasis Djanet was notably separated from the other soil samples (Bray-Curtis PC1 = 93.59%, PC2 = 6.41%; weighted-Unifrac PC1 = 71.39%, PC2 = 28.61%). These results suggest that the microbiota of RM1 Oasis Djanet differed significantly from those of the other samples (RM2 Tassili Djanet and RM3 Forest Elouricia), which clustered together into a single group. These indicator taxa reflect ecological specialization driven by site-specific soil conditions and confirm that aridity and nutrient gradients select for distinct microbial lineages.

3.5. Functional profiles of bacteria in the arid and semi-arid soil samples

The three soil samples were analyzed and grouped into 35 functional categories at Subsystem Level 1 (Fig. 6). Furthermore, 390 functional groupings were identified at Level 3 KEGG Orthology by PICRUSt analysis. The bacterial consortia from the three soil samples taken from dry and semi-arid regions showed the highest expression and greatest homogeneity in genes related to metabolism, genetic information processing, environmental processing, cellular processing, and human diseases (Fig. 6). Transporters, ABC transporters, two-component systems, purine metabolism, bacterial motility proteins, secretion systems, ribosomes, oxidative phosphorylation, and DNA repair and recombination proteins were among the most abundant functional groups. The majority of the 6443 KEGG Orthologies (KOs) identified across all samples by Piphillin analysis were involved in metabolism, environmental information processing, and genetic information processing. In addition, there were notable variations in the abundances of functional genes (p < 0.05). Oasis soil (RM1 Oasis Djanet) showed greater gene abundances across most functional categories, suggesting that soil type greatly impacted the abundance of functional genes (p < 0.001). (Fig. 6). The distribution of functional genes among samples was also significantly affected by dryness.

Soil samples from the Oasis region contained higher concentrations of genes associated with cellular processing and signaling, enzymatic activity, transport, cellular growth and death, infectious and neurodegenerative disease genes, glycan biosynthesis and metabolism, cellular processing and repair, and secondary metabolite biosynthesis. The semi-arid soil, on the other hand, had a higher concentration of genes related to the immune system, aging, cancer, the neurological system, carbohydrate metabolism, the endocrine system, amino acid metabolism, lipid metabolism, terpenoids and polyketide metabolism, genetic information processing, energy metabolism, and the immune system (RM3 Forest Elouricia, soil sample from Setif province). RM1 Oasis Djanet, RM2 Tassili Djanet, and RM3 Forest Elouricia have significantly different functional potentials of their microbial communities, as indicated by principal component analysis based on KO relative abundances. PC2 accounted for 15.58% of the total variance, while PC1 explained 84.42%. These functional patterns suggest that microbial communities adapt to environmental constraints by modulating energy production, transport systems, and stress response pathways, supporting the hypothesis that soil physicochemical gradients shape both taxonomic and functional diversity.

4. Discussion

4.1. Discussion for soil analysis

Soil sample analysis showed a trace amount of alkalinity, indicative of dry and semi-arid climates where alkaline salts accumulate and precipitation is limited (Doe et al., 2020). Chemically, the samples showed little change, suggesting shared pedogenic processes. Higher quantities of calcium carbonate were found in semi-arid soils, suggesting that regional climatic and hydrologic circumstances were responsible for this variation. Wind erosion, sediment transport, and low biological activity in dry areas are reflected in the significantly different sand content, organic matter, and humidity levels (Brown et al., 2018). These findings demonstrate how weather conditions affect the composition and characteristics of soil in ecosystems characterized by aridity.

4.2. Discussion for bacterial community composition

A diverse microbial community spanning many taxonomic levels was uncovered by 16S rRNA sequencing of the V3-V4 area in the soils of

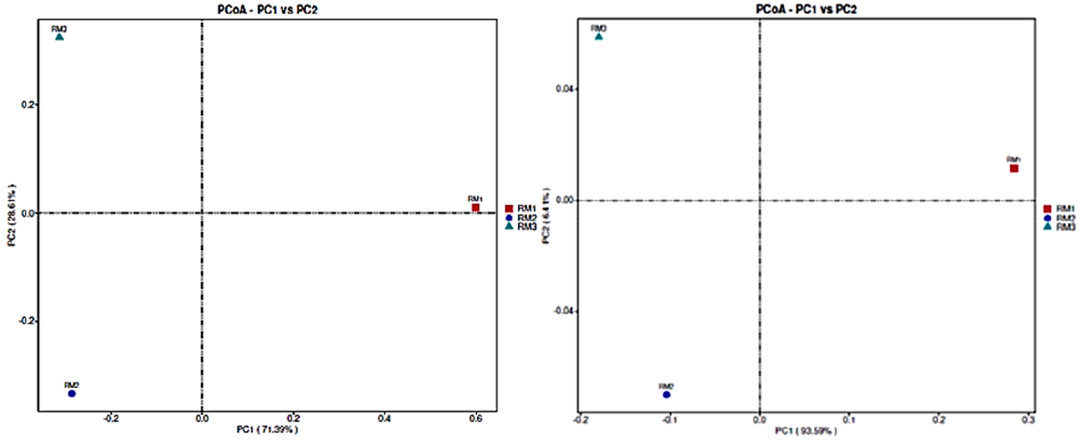

Fig. 5. Beta diversity analyses of the three soil samples. PCoA analysis based on Bray-Curtis, and (Right) PCoA analysis based on weighted-unifrac.

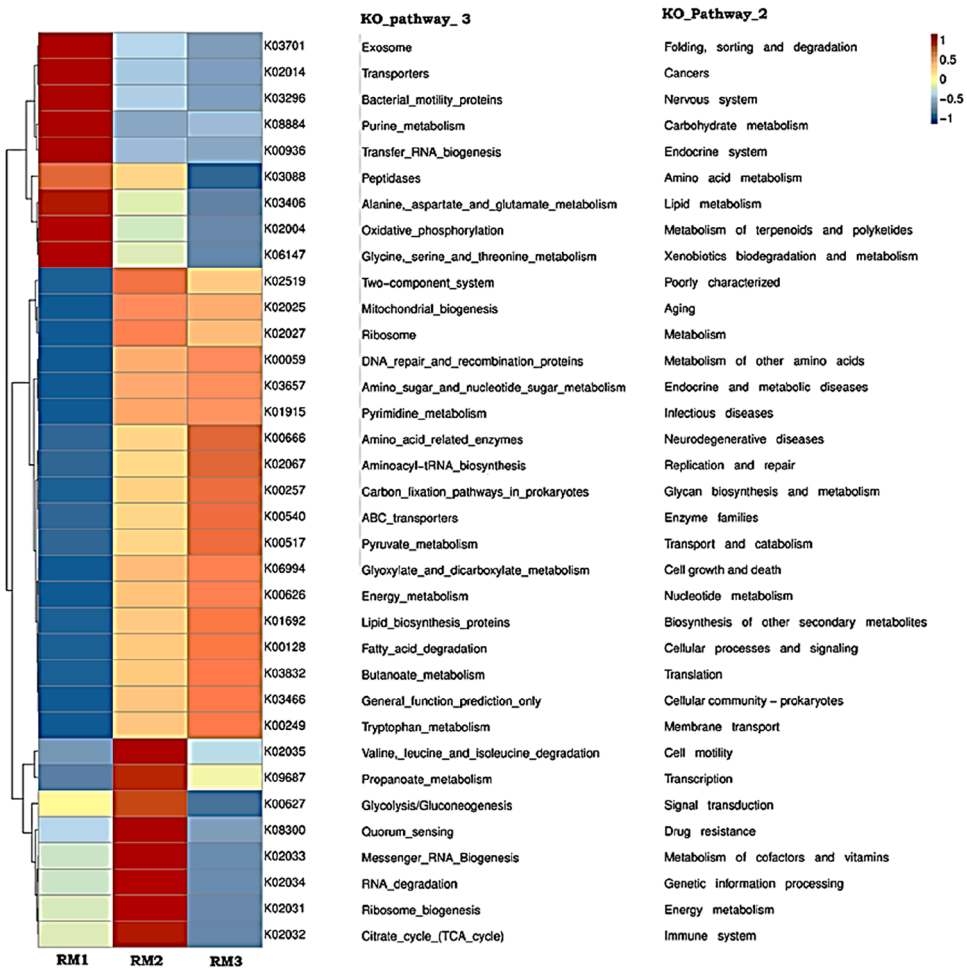

Fig. 6. Heatmap Analysis of the Top 35 Most Abundant KEGG Pathways. Heatmap analysis of the top 35 most abundant KEGG pathways in soil samples RM1, RM2, and RM3, with normalized abundance at levels 2 and 3. The heatmap is color-coded by row z-scores, which standardize the data to facilitate comparison of relative pathway abundance across samples. A continuous color bar ranging from -1 (blue) to 1 (red) indicates the z-scores for each pathway. This visualization highlights differences in the distribution of functional pathways among the soil samples.

Oasis Djanet, Tassili Djanet, and Forest Elouricia. This variety aligns with recent research on dry and semi-dry soils, which found that soil physicochemical properties and weather conditions influence microbial composition (Miralles et al., 2020). Significant variation in bacterial diversity was observed in the Illumina HiSeq sequencing data between samples. This variation is most likely attributable to differences in organic matter content, moisture levels, and pH, all of which play essential roles in determining microbial communities (Mhete et al., 2020). The most common phyla were Firmicutes, Actinobacteria, and Proteobacteria; the latter was notably associated with better degradation of organic materials and resistance to water stress in dry regions (Lyra et al., 2021).

Additionally, the research demonstrated high sequence quality, a sign of trustworthy data, along with GC content typical of bacteria adapted to harsh environments. This suggests that the bacteria have mechanisms that protect them from heat and desiccation (Wang et al., 2022). These results highlight the vast bacterial diversity in dry and semi-dry soils, underscoring its importance in maintaining stable, resilient ecosystems. To better manage soil and increase fertility, it may be helpful to understand microbial interactions and ecological activities. Soil samples from Oasis Djanet, Tassili Djanet, and Forest Elouricia showed notable variations in the distribution of major bacterial groups, according to the taxonomic composition study. The most prevalent bacterial classes across all samples were Bacilli, Acidimicrobiia, Chloroflexia, Thermoleophilia, Alphaproteobacteria, TK10, Gammaproteobacteria, Bacteroidia, and Rubrobacteria, consistent with previous reports on dry and semi-arid soils (Diatta et al., 2020). Actinobacteria predominated in the typical oasis soil of Oasis Djanet, Tassili Djanet, and Forest Elouricia, whereas Chloroflexia was the most prevalent in the other two classes. Important site-specific environmental variables that determine bacterial community dispersion are likely to affect these variations. These parameters include pH, nutrition availability, and organic matter concentration (Miralles et al., 2020).

At the family level, GJ30KFCM45 was the most common, followed by an unclassified Actinobacteria-affiliated family (AKIW781) in Tassili Djanet and Forest Elouricia. Findings from other dry habitats corroborate the preponderance of actinobacteria, which are essential for decomposing organic matter and maintaining soil resilience under harsh conditions (Lyra et al., 2021). In terms of genus, Rubrobacter and Thermobaculum were more common in Tassili Djanet and Forest Elouricia, but Nocardioides was most prevalent in Oasis Djanet. Soils in dry and semi-arid regions are often dominated by the bacterium Rubrobacter, which can withstand conditions including desiccation and ultraviolet light (Belov & Cheptsov, 2023). Skermanella and Agromyces were found only in Oasis Djanet, whereas Bacillus was found only in Tassili Djanet; these bacteria were determined to be sample-specific.

Oasis Djanet's more diverse ecosystem is likely a result of its more stable and prosperous microclimate and the abundance of organic matter (Li et al., 2022). The findings support the idea that regional abiotic factors influence the distribution of dominant phyla and specific

species in bacterial communities in dry and semi-dry soils. Soil management in harsh situations should benefit from a better understanding of these microbes' ecological roles and functional interactions (Vásquez-Dean et al., 2020). Soil, Oasis Djanet, Tassili Djanet, and Forest Elouricia microbiome evolutionary links were uncovered by phylogenetic analysis of representative bacterial families. The results show that soil colonization is enhanced by genetically related bacteria, indicating that related species tend to co-occur more frequently. Whereas microbial phylogeny is affected by moisture and nutrient availability, the same trend has also been noticed in other dry settings (Miralles et al., 2020). One possible indicator of adaptation to local environmental conditions is the abundance of closely related genera in Tassili Djanet, such as Bacillus and Sporosarcina. Oasis Djanet was also rich in taxa with close phylogenetic ties, including Anaerolinae, Chloronema, Herpetosiphon, FFCH7168, and CTCFX1. Such genetically based community structuring is prevalent in semi-arid soils, where particular bacterial species live in proximity to one another (Ma et al., 2021). Also, some taxa were present in every sample; these include Rubrobacter, Solirubrobacter, Pseudonocardia, Blastococcus, and Microvirga, which are known for their ability to adapt to dry conditions by developing resistance to abiotic stress and desiccation (Vásquez-Dean et al., 2020). Among the oasis soil samples, Oasis Djanet had the most diverse community composition, with Actinobacteria predominating. Studies have shown that Actinobacteria can withstand high levels of water stress and create spores that are robust to dry environments; thus, this dominance makes sense (Su et al., 2020). Additional research using state-of-the-art metagenomic and functional analyses is necessary to test the hypothesis that closely related bacteria preferentially inhabit the same environments. To evaluate their effect on the stability of microbial ecosystems and nutrient cycling in dry soils, it is necessary to comprehend these interactions (Ayuba et al., 2021).

4.3. Discussion alpha diversity

Homologous sequences within species are often defined *As otus* or ASVs retrieved by clustering or ASVs produced by noise filtering. To examine microbial diversity in samples, these techniques use alpha-diversity metrics (Li et al., 2013). The following is a summary of the diversity statistics: The results showcase the evaluation of species richness and evenness in the samples, using seven distinct alpha diversity indices: ACE, Chao1, Good's coverage, Observed species, Shannon, Simpson, and PD whole tree. The index values show how complex the sampled communities were. Using alpha diversity indices, we observe notable differences in species richness and evenness across the bacterial communities of soils in Oasis Djanet, Tassili Djanet, and Forest Elouricia. Because of its more favorable environmental conditions, including higher organic matter concentrations and greater moisture availability, Tassili Djanet likely has the highest bacterial diversity (Mhete et al., 2020). Conversely, Oasis Djanet shows a more even distribution of species, suggesting a more stable community structure (Miralles et al., 2020). Even if RM3 is slightly lower in a few criteria, it still shows significant variety and completeness. Using rarefaction analysis and Good's coverage index, it has been confirmed that sequencing accurately reflected microbial diversity (Diatta et al., 2020). Environmental factors, community dynamics, or sampling techniques may all contribute to these discrepancies. The processes underpinning these findings could be better understood with a comprehensive examination of relevant ecological parameters.

4.4. Discussion: difference in taxonomic composition between the three sampling sites

The β-diversity analysis, using Principal Coordinates Analysis (PCoA), revealed significant differences in microbial communities among the three soil samples (Oasis Djanet, Tassili Djanet, and Forest Elouricia). The distinct grouping of samples along axes 1 and 2 suggests that bacterial composition is influenced by local environmental conditions, with RM1 showing greater dissimilarity than Tassili Djanet and Forest Elouricia, which are clustered together (Xu et al., 2024). Similarity distances based on Bray-Curtis and weighted UniFrac confirmed that Oasis Djanet possesses a significantly different microbial community. This differentiation may be attributed to soil composition, pH, organic matter content, and moisture, which are critical in shaping bacterial communities in arid environments. Previous studies indicate that microbial β-diversity in semi-arid ecosystems is primarily driven by the combined effect of geographic distance and abiotic factors, leading to distinct community assembly patterns (Zheng et al., 2020). In desert and semi-desert environments, shifts in bacterial diversity are often explained by environmental selection processes and limited dispersal, which likely contribute to the distinct microbial profile of Oasis Djanet (Diatta et al., 2020). Overall, these results suggest that differences in bacterial communities among the studied soils are influenced by geographic location and specific environmental conditions, aligning with previous research indicating that microbial diversity in arid soils is mainly shaped by climatic and pedological factors (Miralles et al., 2020).

4.5. Discussion functional profile

The distribution of functional genes varies significantly across soil types. Oasis soils harbor a higher abundance of genes involved in critical functions, such as DNA repair, glycan biosynthesis, and enzymatic processes. In contrast, semi-arid soils (such as Forest Elouricia from Setif province) show a preponderance of genes involved in energy metabolism, immunity, and aging. These differences are likely explained by microbial adaptations to the unique environmental conditions of each soil type, including nutrient levels and humidity. Aridity influences the distribution of functional genes in the samples. Genes related to neurodegenerative diseases, infectious diseases, and DNA repair are more abundant in Oasis soils. This may indicate selection pressure for microbial survival in water-poor, organic-rich environments (Guellout et al., 2025).

In contrast, semi-arid soils promote energy metabolism and mechanisms related to adaptation to environmental stress, such as cofactor and vitamin metabolism, as well as immunity (Smith et al., 2020). PCA analysis revealed a clear separation between the functional capacities of microbial communities across samples. The principal components showed that differences between metabolic and genetic processes accounted for >84% of the total variance. This reflects distinct metabolic strategies, as microbial communities in arid and semi-arid soils likely coevolved to optimize their survival in resource-limited environments (Wang et al., 2021). The results suggest that microbial communities in arid and semi-arid soils play a key role in soil ecological stability and resilience to climate change. For example, genes related to energy metabolism and environmental processes could provide clues to the adaptive capacities of soils for carbon storage and pollutant biodegradation. These functions could be exploited to improve land management in arid regions.

5. Conclusion

This study provides foundational insights into microbial community structure and functional potential across contrasting arid and semi-arid ecosystems in Algeria, namely Oasis Djanet, Tassili Djanet, and Forest Elouricia. Through comparative analysis of soil physicochemical parameters, taxonomic diversity, and predicted functional genes, we demonstrate that local environmental conditions — including organic matter, moisture availability, and pH — shape microbial assemblages and metabolic pathways in site-specific ways. Dominant phyla such as Actinobacteria, Proteobacteria, and Firmicutes showed distinct genus-level patterns, reflecting adaptive responses to abiotic stressors in desert and forested dryland habitats. The identification of aridity-related

functional genes involved in oxidative stress response, nutrient cycling, and cellular repair highlights the role of microbial communities in promoting ecosystem resilience and soil health under extreme environmental pressures. Importantly, this work advances our understanding of extremophile adaptations in North African drylands and positions these ecosystems as promising reservoirs for microbial bioprospecting. The functional potential uncovered here may have practical applications in bioremediation, sustainable agriculture, and the discovery of novel bioactive compounds with industrial or pharmaceutical relevance (Smith et al., 2020; Wang et al., 2021). By characterizing both taxonomic and functional microbial profiles across underexplored Algerian ecosystems, this study contributes to the global effort to map microbial diversity in arid zones. It lays the groundwork for future biotechnological exploitation of extremophilic microorganisms.

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Ethical statement – studies in humans and animals

This study did not involve any experiments on humans or live animals. Soil samples were collected from natural environments (Oasis Djanet, Tassili Djanet, and Forest Elouricia, Algeria) with no impact on protected areas, endangered species, or ecological integrity. All sampling procedures complied with national and institutional ethical guidelines for environmental research. No human or animal subjects were used in this work.

CRediT authorship contribution statement

Meriem Guellout: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Hani Belhadj:** Methodology, Investigation, Validation, Writing – review & editing. **Atef Jaouani:** Supervision, Validation, Writing – review & editing. **Byong-Hun Jeon:** Writing – review & editing, Visualization, Validation, Investigation. **Hyun-Jo Ahn:** Data curation, Formal analysis, Visualization, Writing – review & editing. **Mohammad Raish:** Writing – review & editing, Visualization, Validation, Investigation. **Yacine Benguerba:** Writing – review & editing, Visualization, Validation, Investigation.

Declaration of competing interest

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

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Data availability

No data was used for the research described in the article.

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